WWT Wetlands for life

Wildfowl 64

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Editor

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Published by
Wildfowl & Wetlands Trust
Slimbridge, Gloucestershire
GL2 7BT, UK
Registered Charity No. 1030884

Wildfowl

Cover photograph: Adult female Goosander with duckling on the fast-flowing River Wye, Derbyshire, UK by Gary K. Smith/FLPA.

Cover design by Paul Marshall

Published by the Wildfowl & Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, UK

Wildfowl is available by subscription from the above address. For further information call +44 (0)1453 891900 (extension 257), or e-mail wildfowl@wwt.org.uk

ISBN 0 900806 64 8
Print ISSN 0954-6324
On-line ISSN 2052-6458

Printed on FSC compliant paper by Berforts Information Press Ltd.

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Wildfowl 64: Editorial

Wildfowl and other waterbirds have long been known and appreciated by man, so it is not every year that a new species or subspecies is described for science. Only one live species has been discovered in the last 50 years (the White-headed Steamer Duck *Tachyeres leucocephalus*, reported by Philip Humphrey and Max Thompson in 1981), and with the recent tendency towards grouping rather than separating taxa, the classification of the Greenland White-fronted Goose *Anser albifrons flavirostris* by Christopher Dalgety and Peter Scott as a separate race back in 1948 remains a comparatively unusual event. Discovery of new extinct or fossil forms is also unusual, so in *Wildfowl* 64 we are particularly privileged to include a paper by Murray Williams, Alan Tennyson and Dalice Sim, who present the evidence for confirming one of New Zealand's extinct island merganser populations, the Chatham Island Merganser *Mergus milleneri*, as a separate species. The bird is named in honour of Dr Philip Millener, palaeontologist and former Curator of the National Museum in Wellington, New Zealand, who with his colleague Noel Hyde retrieved bones from 30 avian species, including the fossil bones of *Mergus milleneri*, during their excavation of the Te Ana a Moe cave deposit on Chatham Island.

In addition to the Chatham Island Merganser paper, results from several other fascinating research programmes are presented in this issue of the journal. The papers, which are wide-ranging both geographically (*i.e.* in terms of the location of the study area) and in their remit, include a review of the priority sites for waterbird conservation in Madagascar, an update on the status of Ferruginous Duck *Aythya nyroca* in China, a description of the extension of Goosander *Mergus merganser* distribution into the Carpathian Mountain range, analysis of Musk Duck *Biziura lobata* diving behaviour, and insights into the breeding phenology of Spotted Crakes *Porzana porzana* in Denmark. Moreover, following the 5th International Swan Symposium of the Wetlands International/IUCN-SSC Swan Specialist Group, which was hosted by the Trumpeter Swan Society and held at Easton, Maryland, USA from 3–6 February 2014, seven key papers presented at the meeting are now published here as a "mini proceedings" in *Wildfowl* 64. That they should appear in *Wildfowl* seems highly appropriate as the proceedings of the 1st International Swan Symposium were published in *Wildfowl* 24 in 1973 (following the meeting held at Slimbridge in December 1971) and the proceedings of the 3rd International Swan Symposium (held in Oxford in 1989) became the first special issue of the journal in 1991.

Following on from the publication of two volumes of *Wildfowl* in 2013 – *Wildfowl* 63 and also *Wildfowl* Special Issue No. 3 (which focussed on recent Brent Goose studies) – we are delighted that there are again to be two issues of the journal in 2014. In addition to the standard issue presented here, an impressive special issue publishes the proceedings of the 6th North American Duck Symposium (NADS 6) held at Memphis, Tennessee from 27–31 January 2013. This volume – entitled *Ecology and Conservation of North American Waterfowl* (ECNAW) – was extended to include publications by eminent scientists across the Northern

Hemisphere, and gives current understanding of the ecology, ongoing conservation efforts and future conservation actions required to sustain waterfowl and their habitats throughout the region. That the special issue is coming to fruition is not only a reflection of the wealth of expertise and commitment from the authors of the various papers and the support of financial donors, but particularly thanks to the indomitable efforts of Prof Rick Kaminski of the Mississippi State University, who led from the front not only in convening the symposium in the first instance but in coordinating, editing and fund-raising for publication of the proceedings.

At the start of the year Dr David Roshier considered that he should stand down from the Editorial Board following a career move from Deakin University to the Australian Wildlife Conservancy. I'm immensely grateful to David for his help and expertise over the four years that he has served on the Editorial Board and am delighted that he is willing to maintain his involvement in *Wildfowl* by reviewing papers for the journal. As always, I remain greatly indebted to Tony Fox (Associate Editor of *Wildfowl*) for his invaluable advice and word-smithing skills, and to Editorial Board members Jeff Black, Bruce Dugger, Andy Green and Matt Guillemain for providing their expert comments, suggestions and feedback on papers so promptly and effectively. I also thank the referees for their careful and constructive reviews of submitted manuscripts, Ellen Matthews (EM Typesetting) and the staff at Berforts Ltd. for taking the papers forward to publication, and my colleagues Maggie Sage, Jessica Tagney, Linda Dickerson and Jane Gawthorne-Dover for their administrative support. Finally I thank readers for their interest in the work published in the journal, and I hope that you enjoy reading it in the coming weeks and years.

Eileen Rees

Editor: *Wildfowl*
WWT Martin Mere

Island differentiation of New Zealand's extinct mergansers (Anatidae: Mergini), with description of a new species from Chatham Island

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Abstract

Measurements of major bones from three island populations (New Zealand mainland, Auckland Islands, Chatham Island) of extinct mergansers presently known as *Mergus australis* indicate that birds from Chatham Island differed in size and proportion from those at Auckland Islands. The Chatham Island specimens were smaller overall, with a shorter skull, relatively shorter premaxilla, smaller sternum and keel, relatively shorter wing bones and a narrower pelvis. These differences support its taxonomic recognition as the new species, *Mergus milleneri*, described in this paper. Determining reliably the magnitude of the size differences of major bones between mergansers from mainland New Zealand and Auckland Islands or Chatham Island was not possible due to inadequate samples of these sexually dimorphic taxa. However, mainland mergansers may also have been smaller than Auckland Islands birds. Based on these measurements, Holocene fossils of mergansers on New Zealand's mainland therefore are considered to be *Mergus* sp. indeterminate and we recommend that *Mergus australis* henceforth be called the Auckland Islands Merganser.

Key words: Auckland Islands, Chatham Island, Merganser, *Mergus australis, Mergus milleneri*, new species, New Zealand.

When humans first settled in New Zealand, late in the 13th Century, a merganser (Anseriformes: Anatidae: Mergini) was present on mainland New Zealand (North, South and Stewart Islands) and on two nearby archipelagos: Chatham Islands, 800 km east of New Zealand, and Auckland Islands, 450 km to its south (Holdaway *et al.* 2001). Mergansers from New Zealand and Chatham Island did not survive initial human impacts, but those at Auckland Islands (islands visited briefly but not settled by Polynesians; Anderson 2005) persisted into the 19th Century before ultimately being exterminated (in 1902) by a flurry of specimen collecting (Williams 2012). Whereas Auckland Islands' mergansers are now represented by 27 skins and some bone specimens therefrom (Kear & Scarlett 1970; Williams 2012), those from New Zealand and Chatham Island are known only from bones retrieved from archaeological and/or natural deposits (Worthy 1998a,b, 2004; Millener 1999).

Mergansers from mainland New Zealand, Auckland Islands and Chatham Island are currently considered to be a single species *Mergus australis* (after Hombron & Jacquinot 1841), with Auckland Islands being the type locality (see Gill *et al.* 2010). However, two observations provide potential challenges to this classification. Livezey (1989) suggested that Auckland Islands' mergansers had reduced keels (carina sterni) and disproportionately short wing bones relative to other, and more vagile, merganser species and were on the verge of flightlessness. These interpretations of keel and wing bones, but not of flightlessness, were confirmed by Williams (2012). Millener (1999) commented that merganser bones he extracted from a natural deposit on Chatham Island seemed smaller than Auckland Islands specimens and may represent a different species. These two observations raise the hypothesis that mergansers of the wider New Zealand region may have responded to their isolation on separate archipelagos with morphometric changes, similar to those of New Zealand's brown-plumaged teals (*Anas chlorotis*, *A. aucklandica*, *A.nesiotis*; Williams *et al.* 1991) and each may warrant separate taxonomic recognition.

In this study we test the hypothesis that mergansers from all three populations in the wider New Zealand region were of similar size and body proportion, characteristics necessary to justify their aggregation as a single taxon. We would consider this hypothesis falsified if, statistically, the sizes or proportions of major skeletal elements from any one population were significantly different from one or both of the others.

Methods

Sources of samples

We measured all major merganser skeletal elements from New Zealand mainland (NZ), Auckland Islands (AI) and Chatham Island (CI) held in the collections of four museums: Otago Museum, Dunedin, New Zealand (OMNZ); Canterbury Museum, Christchurch, New Zealand (CMNZ); Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ); and Natural History Museum, Tring, England (NHMT) (see Appendix 1). The material included a coracoid bone (OR 23515) from Auckland Islands held at NMNZ not listed by Williams (2012). One NZ merganser femur held in the Auckland Museum, Auckland, New Zealand (LB10058) and a second at the Anthropology Department, Otago University, Dunedin (SRM BB324-01) were not sufficiently intact to allow accurate measurements. Four bones from NZ originally lodged in the collection of the Geology Department, Auckland University, Auckland, New Zealand and described by Millener (1981) as "an almost complete mandible (AU4834), and a coracoid, humerus and femur 'possibly of *Mergus*' (AU7868)" can no longer be located (N. Hudson, pers. comm. 2013).

All bones examined had sufficient location data to discriminate among the three geographic areas mentioned above. The NZ specimens, retrieved from both natural and archaeological sites, came from North Island (Ponui Island, Lake Poukawa, Mataikona, Paremata), South Island (Lake Grassmere/Marfells Beach, Oamaru, Cannibal Bay), and Stewart Island (Native Island, Old Neck) but their small number ultimately required us to combine all bones from NZ for our analyses. For CI bones a distinction was made between those recovered from a cave deposit (Te Ana a Moe (the cave of Moe): Simmons 1964; Millener 1999) and those recovered in dunes elsewhere on the island. No merganser bones have been retrieved from archaeological sites on Chatham Island. All AI bones were from birds shot between 1890 and 1902 (Williams 2012).

We also measured bones of Red-breasted Merganser *Mergus serrator* for comparative analyses. These specimens were from museums in Frankfurt, Basel, Vienna, Paris, Dublin, NHMT and NMNZ (see Appendix 1).

Sample sizes

No bones from either CI or NZ mergansers could be associated with any others as belonging to the same individual bird. Because the similar number of wing and leg bones and half that number of cranial elements from the CI cave site indicated that we were examining the remains of at least 51 individuals (based on tarsometatarsi) we separated their left and right wing and leg elements and measured whichever provided the larger dataset.

The AI sample comprised three almost complete skeletons of known sex (2♀, 1♂) and partial skeletons from two skins to which sex data were attached (1♀, 1♂); however, one (CMNZ 5176) is incorrectly sexed as a male (see Williams 2012: Appendix 1). Thus, we studied material from 4♀ and 1♂. Additionally, we examined coracoid bones and a single sternum of three mounted specimens registered as being AI females.

Overall, 92 measurements were obtained from unsexed NZ bones, 81 measurements from AI bones of known sex, 762 measurements of CI bones from the cave deposit, and 11 measurements of unsexed CI bones from dune deposits. Comparative data for *Mergus serrator* comprised 258 measurements from birds of known sex. Numbers of each bone measured and used in this study are provided in the summary statistics (Appendix 2).

Measurements

We used vernier callipers to measure wing and leg bones, sternum, pelvis and skull. Measurements, made (to 0.1 mm), were: skull length (maximum length from prominentia cerebellaris to tip of premaxilla), nares to tip (anterior edge of nares opening to tip of premaxilla), cranium post-orbital width (maximum width between left and right processus postorbitalis), cranium inter-orbital width (minimum dorsal width between the orbits), sternum length (maximum length taken along the midline, measured on the dorsal (visceral) surface), sternum anterior width (maximum width between the processus craniolaterali), sternum posterior width (maximum caudolateral width), carina sterni (keel) length (maximum chord length from apex carinae to margo caudalis), carina sterni (keel) area (determined from two–three thin plasticine impressions of the carina sterni, each subsequently scanned against 1 mm grid graph paper and measured to 1 mm^2, and the results averaged), coracoid(eum) length (maximum length from processus acrocoracoideus to angulus medialis), coracoid(eum) width (maximum width between processus lateralis and angulus medialis), humerus length (maximum length), ulna length (maximum length), carpometacarpus length (maximum length), pelvis length (length from anterior of ala preacetabularis ilii to rear of apex pubis), pelvis anterior width (maximum width between left and right ala preacetabularis ilii), pelvis posterior width (maximum width between left and right apex pubis), antitrochanter width (maximum width between left and right processus antitrochanter), femur length (maximum length parallel to shaft), tibiotarsus length (maximum length from proximal articular surface, i.e., excluding the crista cnemialis cranialis), and tarsometatarsus length (maximum length). Anatomical names are as described by Baumel *et al.* (1993). Mean values are given ± s.d. throughout.

The presence or absence of any conspicuous salt gland impression on the cranium above the orbit was also recorded, as depicted in Fig. 3.

Data recording, analyses and presentation

All measurements were recorded in MS Excel spreadsheets and an electronic record of these data has been deposited in NMNZ archives. Compilation of size-frequency distribution tables (in which most measurements are summarised in 1 mm (0.0–0.9) groupings) used the statistical analysis functions of MS Excel 2007. Measurements of AI specimens in all tables discriminate the single male (M) from all others, which are females. Non-parametric tests (Mann-Whitney U, Kruskall-Wallis) were performed using IBM SPSS Statistics v. 19.0.

The small sample sizes from AI (2–4 in most instances) largely precluded a statistical comparison of mean dimensions of bones from it and the other two populations. Our primary analytical approach, therefore, was to use the Mann-Whitney U test to determine the probability of the AI bones being drawn from the size-frequency distribution of bones from CI. A probability of ≤ 0.05 was taken to indicate a difference in size of the selected bone between the compared populations.

To appraise overall skeletal differences between populations and taxa we calculated the mean dimensions of selected bones from one population as a percentage of the mean of those from the population or taxon with which it was being compared. The associated 95% confidence interval was adjusted by that percentage. A significant difference in relative bone length is indicated when 95% confidence intervals do not overlap. We also compiled a logarithm-based ratio diagram, commonly referred to as a "Simpson diagram" (Simpson 1941; Göhlich & Mourer-Chauviré 2005) to depict differences in mean bone measurements from CI and NZ, converted to logarithms, as a ratio of those from AI. For example, we calculated $\log_{10}$ (mean CI) – $\log_{10}$ (mean AI) (= $\log_{10}$ (mean CI/mean AI)) to compare bones from CI and AI populations. Statistical variance associated with the mean measurement of each bone is not expressed.

To assess size-related proportional differences between populations and taxa we divided the mean dimensions of selected bones from each by its mean femur length (femur is the single bone best reflecting body mass; Campbell & Marcus 1992; Field *et al.* 2013). To recognise statistical variance associated with the mean values we required a ≥ 5% difference in the resulting statistic between populations and taxa to indicate a proportional difference.

Evaluation of Chatham Island cave sample

Chatham Island, the only island in the Chatham Islands archipelago on which merganser bones have been found, is dominated by an extensive barrier-bar lake (Te Whanga lagoon). A small single-chambered cave (Te Ana a Moe) lies near the base of a limestone cliff on the western shore of the lagoon (Simmons 1964). Millener (1999) described its entrance as being about 3 m above present lagoon level with its main fossil bird bearing sediment lying 0.6–1.5 m below the level of the cave's entrance. He recorded bird remains being most abundant in short (1–3 m) blind tunnels leading from the cave's 2 m-wide main chamber and obtained radiocarbon dates from those remains of 1150–3900 CAL BP. Considering the range of faunal specimens found (*e.g.* 17 land snail and 30 bird species), Millener (1999) suggested that the cave had acted as a pitfall trap.

The fortuitous aggregation of merganser bones appears to be a consequence of the cave having been used by mergansers as a nesting site, an interpretation supported by the copious amount of (unidentified) eggshell removed from the cave (now held at NMNZ) as well as a premaxilla (NMNZ S.30635) and a mandible (NMNZ S.27377) of merganser hatchlings. Other merganser species are hole-nesters (Cramp & Simmons 1977; Kear 2005) and females, not males, investigate and enter nest holes and undertake all incubation.

Extant merganser species are all sexually dimorphic in size; in general, linear dimensions of females are 6–10% smaller and weights 15–20% less than males, with little overlap of their dimensions or weights (Cramp & Simmons 1977; Kear 2005). Measurements of culmen and wing of male and female skins of AI mergansers recorded a 7–9% difference in size (Williams 2012: Appendix 2).

We examined the size-frequency distributions of lengths of premaxillae, humeri, ulnae, carpometacarpi, coracoids, sterna, femora, tibiotarsi and tarsometatarsi of the CI cave specimens (see Tables 1–4 and Table 7). The strictly unimodal distributions of all nine measurements examined indicate either there was no sexual size dimorphism in CI mergansers or, more likely, that all bones were from a single sex. Within the small sample of bones from non-cave sites on CI, measurements of some bones overlapped and others exceeded the ranges of those from the cave (Appendix 2).

The archive of these merganser bones at NMNZ included a large assortment of tracheal rings and syrinxes (the element where the trachea bifurcates) but not one ossified enlarged syrinx (bulla) characteristic of a merganser male (Johnsgard 1961). Syringeal bullae are common in caves throughout NZ where depositions of waterfowl (*e.g.* Finsch's Duck *Chenonetta finschi* (now extinct) and Brown Teal *Anas chlorotis*) have accumulated by pitfall (T.H. Worthy, pers. comm.).

We regard the CI cave adult *Mergus* bones as being all from females. These are referred to in the text as "CI cave" or "CI females", as distinct from "CI mergansers" or "CI bones" which cover all CI specimens irrespective of site.

Treatment of the New Zealand sample

The size-frequency distributions of merganser bones most commonly found in NZ (humerus, ulna, tibiotarsus, femur, coracoid) were all weakly bimodal (see Tables 2, 3 and 7) and extend above the ranges of the same bones retrieved from the CI cave site. We regard this sample as including birds of both sexes. We attempted an approximate differentiation of sex by separating each distribution into non-overlapping upper (male?) and lower (female?) samples such that their means differed by 7–9%, their standard deviations were similar, and their ranges were separated by ≥ 1 mm (Appendix 2). We used the resulting distributions for putative females to compare with those of females from AI and the CI cave sample.

We paid particular attention to the smallest bones in each set, mindful of Worthy's (2004) observation of potential confusion of *Mergus* bones with those of *Anas chlorotis*, *Aythya novaeseelandiae* and New Zealand fossil *Oxyura vantetsi*. In a few cases (identified in Appendix 1) we deliberately excluded outstandingly small "*Mergus*" bones from our analyses.

Results

Comparative sizes of bones

Skull

No intact skulls of NZ mergansers have been found, just two premaxillae and one cranium. Of the premaxillae (Table 1), one was smaller than any of three AI females and within the lower quartile of the measurements for CI cave premaxillae, while the other was the same size as the single AI male. All three AI female measurements were larger (1.7–6.0%) than the largest from the CI cave sample and the size-frequency distributions of these two samples were significantly different (Mann-Whitney $U = 0.0$, $P < 0.0005$). Similarly, the total lengths of two AI female skulls both exceed the largest of six intact CI cave skulls (Appendix 2). Thus, AI females had longer skulls and longer premaxillae than CI females (see Fig. 3).

Table 1: Size-frequency distribution of nares-tip lengths (mm) of premaxillae from New Zealand, Auckland Islands and Chatham Island mergansers. NZ = New Zealand; AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Nares–bill tip length (mm)**										***n***
	31	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	
NZ		1								1	2
AI					1	1	1			1M	4
CI cave	2	6	15	20	3						46

The widths of 44 CI cave crania at the post-orbital process grouped tightly around the mean (27.7 ± 0.3 mm) and included only one specimen smaller than the two AI female crania, both of which were 27.2 mm (Appendix 2). The one AI male measurement (29.0 mm) exceeded all others. The NZ cranium (specimen CM 11532) had a width at the post-orbital process of 25.3 mm, conspicuously smaller than any skull of CI and AI mergansers.

The inter-orbital widths from 43 CI cave crania (mean = 6.1 ± 0.3 mm) included just four measurements smaller than the maximum (5.8mm) from three female AI crania (Appendix 2). The post-orbital/inter-orbital width ratio for CI cave crania (mean = 4.5 ± 0.2) differed sufficiently from that of two AI female measurements (mean = 4.9) as to suggest proportional differences in the crania of the two populations.

Salt gland impressions, conspicuous on all CI cave crania (see Fig. 3; also depicted in Fig. 13 of Millener 1999 and Fig. 7.2 of Worthy & Holdaway 2002), were discernible but inconspicuous on the AI crania.

Wing bones

Humerus. Whereas the lengths of 47 CI cave humeri differed by 3.9 mm between shortest and longest, the 16 humeri from NZ extended over twice that range and their size-frequency distribution (Table 2) strongly indicated the inclusion of both sexes. The size-frequency distribution of putative NZ females (range 65–68 mm) was not significantly different from the CI cave sample (Mann-Whitney U = 232.5, P = 0.64). The lengths of the two AI female humeri overlapped only the longer of the CI cave humeri and the distributions of these two samples were significantly different (Mann-Whitney U = 3.5, P = 0.01). The AI male humerus was approximately 5% longer than the longest of the CI and AI female humeri and of similar length to the longest NZ humerus.

Ulna. The lengths of two AI female ulnae exceeded the longest from the CI cave and the two size-frequency distributions (Table 2) were significantly different (Mann-Whitney U = 2.5, P = 0.03). The AI male bone was longer than any from New

Zealand. The size-frequency distribution of 14 NZ bones, however, was unlike that of humeri (Table 2) by including four bones shorter than any found on CI. As a consequence the size-frequency distribution of putative NZ female ulnae (range 48–53 mm) was significantly different from that of CI cave specimens (Mann-Whitney $U = 309.0$, $P < 0.0005$).

Carpometacarpus. Both AI female carpometacarpi were the length of the longest found on CI, and that of the single AI male was the same length as the longest of three bones found in NZ (Table 2). The size-frequency distributions of AI female carpometacarpi and those of CI cave were significantly different (Mann-Whitney $U = 2.0$, $P = 0.02$).

Coracoid. AI female coracoids were generally larger than those from CI cave and the size-frequency distributions of both lengths and widths (Table 3) were significantly different (length: Mann-Whitney $U = 0.0$, $P < 0.0005$; width: Mann-Whitney $U = 26.0$, $P = 0.005$). However, they were similarly proportioned (mean length/width ratios: AI = 2.61 ± 0.06; CI cave = 2.58 ± 0.06; Mann-Whitney $U = 74.0$, $P = 0.19$; Fig. 1). NZ coracoid bones were narrower than all others and their mean length/width ratio (2.89 ± 0.08) conspicuously different from the other two populations (overall Kruskall-Wallis test $\chi^2_2 = 19.46$, $P < 0.0005$, AI *vs.* NZ, Mann-Whitney $U = 0.0$, $P = 0.004$; NZ *vs.* CI cave, Mann-Whitney $U = 0.0$, $P < 0.0005$). The size-frequency distribution of lengths of putative NZ female coracoids (range 39–42 mm) was different from that of CI cave (Mann-Whitney $U = 52.5$, $P = 0.001$) and the bones conspicuously narrower (Mann-Whitney $U = 0.0$, $P < 0.0005$; Fig. 1). Figure 1 also depicts the larger size of the AI male coracoid bone and suggests that the NZ sample similarly included one larger male.

Sternum and keel

No sternum of a NZ merganser has been found and, on CI, none other than those in the cave deposit.

Sternum length and width. The size-frequency distributions of AI female and CI cave sternum lengths were significantly different (Mann-Whitney $U = 0.00$, $P = 0.001$). So too were their distributions of sternum posterior widths (Mann-Whitney $U = 1.5$, $P = 0.02$) but sternum anterior widths were not (Mann-Whitney $U = 52.5$, $P = 0.46$, n.s.; Table 4). Thus, AI females had longer and posteriorly wider sterna than CI females. The single AI male's sternum was 10 mm (15%) longer than the longest CI female and 7% longer than the longest AI female. Its anterior sternum width was 5% wider than the widest CI female and 11% wider than the widest AI female (Appendix 2).

Keel length and area. Lengths of keels on four AI female merganser sterna averaged 14% longer than those from CI cave (Mann-Whitney $U = 0.0$, $P = 0.001$; Appendix 2) and respective size-frequency distributions of their lengths did not overlap (Table 5). The longest keel, of an AI male, exceeded the longest from CI cave by 20% and the longest AI female by 7%.

Although the keel areas of two (of four) AI females were smaller than the two largest from CI cave, the mean keel area of AI

Table 2: Size-frequency distribution of wing bones lengths (mm) from New Zealand, Auckland Islands and Chatham Island mergansers. NZ= New Zealand; AI = Auckland Islands; CI cave (largest sample from one side used = right humeri, left ulnae, right carpometacarpi); CI dune = from other Chatham Island sites; M = male.

Population	**Humerus length (mm)**									***n***
	64	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	
NZ		5	1	1	2	2	1	1	3	16
AI				1	1				1M	3
CI cave	3	9	16	17	2					47
CI dune							2			2

Population	**Ulna length (mm)**										***n***
	48	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	
NZ	1	1	1	1	3	1	1	1	4		14
AI							1	1		1M	3
CI cave				2	9	20	12				43
CI dune				1							1

Population	**Carpometacarpus (mm)**								***n***
	35.5–35.9	**36.0–36.4**	**36.5–36.9**	**37.0–37.4**	**37.5–37.9**	**38.0–38.4**	**38.5–38.9**	**41.0–41.4**	
NZ				2				1	3
AI							2	1M	3
CI cave	1	1	7	16	11	3	1		41
CI dune	1								1

females was 11% larger than CI females (Appendix 2, Table 9) and the size-frequency distributions of the two groups differed significantly (Mann-Whitney U = 6.0, P = 0.01; Table 5). However, the mean (± s.d.) keel area/keel length ratios were

Table 3. Size-frequency distribution of coracoid lengths and widths (mm) from New Zealand, Auckland Islands and Chatham Island mergansers. NZ = New Zealand; AI = Auckland Islands; CI cave = left coracoids from Chatham Island cave site; CI dune = from other Chatham Island sites; M = male.

Population	**Coracoid length (mm)**												***n***
	37	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	
NZ			1	4		3	1	2	1				12
AI								5				1M	6
CI cave					2	11	28	6					47
CI dune	1		1						1				3

Population	**Coracoid width (mm)**												***n***
	13.5–13.9	**14.0–14.4**	**14.5–14.9**	**15.0–15.4**	**15.5–15.9**	**16.0–16.4**	**16.5–16.9**	**17.0–17.4**	**17.5–17.9**	**18.0–18.4**	**18.5–18.9**	**19.0–19.4**	
NZ	2	3	2			1							8
AI							2	2	1			1M	6
CI cave					3	21	20	3					47

similar (AI = 6.60 ± 0.38, CI cave = 6.80 ± 0.44; t_{22}= 0.42, P = 0.43, n.s.), indicating they were similarly proportioned.

Keel length and area relative to sternum length. Lengths of keels of AI females, relative to their sternum lengths, were slightly longer (mean 3%) than CI females and their apex carinae projected slightly further forward of the sternum. The size-frequency distributions of keel length/sternum length ratios (Table 6) were significantly different (Mann-Whitney U = 8.0, P = 0.005) and the means also (AI = 1.21 ± 0.01, CI cave = 1.18 ± 0.02; t_{32} = 2.93, P = 0.006).

Despite this difference however, keel area/sternum length ratios were very similar (AI female mean = 8.01 ± 0.33, CI cave mean = 8.05 ± 0.52; t_{22} = 0.23, P = 0.83, n.s.).

Overall, the sterna of CI female mergansers were shorter and posteriorly narrower than those of AI female mergansers and had keels that were shorter and less forward projecting.

Leg bones

Femur. There was complete overlap in the size ranges of femora from all three

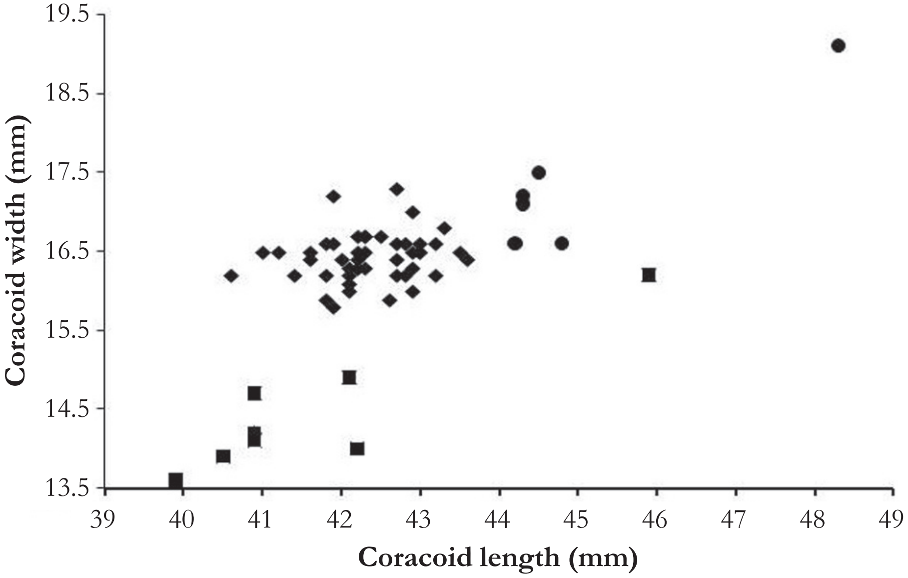

Figure 1. Scatterplot of lengths and widths of merganser coracoid bones. ● = Auckland Islands, ■ = New Zealand, ♦ = Chatham Island. The largest Auckland Islands specimen is from a male. The largest New Zealand specimen is similarly proportioned to all other New Zealand coracoid bones and may also be from a male.

populations (Kruskall-Wallis test $\chi^2_2 = 3.47$, $P = 0.18$, n.s.) (Table 7) and despite the NZ sample presumably including both sexes, its size-frequency distribution was not different from the CI cave sample (Mann-Whitney U = 288.0, $P = 0.09$, n.s.). However, the size-frequency distribution for the putative New Zealand females (40–41 mm) was significantly different from that of the CI females (Mann-Whitney $U = 0.0$, $P < 0.0005$).

Tibiotarsus. Most NZ tibiotarsi were similar in length to those from CI, but some were longer (Table 7). The lengths of the two female AI tibiotarsi were within the range of CI females.

Tarsometatarsus. There was complete overlap in tarsometatarsus measurements from all three populations (Kruskall-Wallis test $\chi^2_2 = 2.96$, $P = 0.23$, n.s.; Table 7) and the distributions of the CI and AI samples did not differ (Mann-Whitney $U = 12.0$, $P = 0.07$, n.s.).

Pelvis

The pelves of CI females appeared conspicuously small. The two AI pelves were both longer than those of CI females (Table 8) and the size-frequency distributions of the two populations were significantly different (Mann-Whitney $U = 0.0$, $P = 0.004$). Similarly, the three AI female antitrochanter widths all exceeded those from CI cave and the means of the two samples (Appendix 2) were significantly different ($t_{36} = 9.57$,

Table 4. Size-frequency distribution of sternum lengths and their anterior and posterior widths (mm) from Auckland Islands and Chatham Island mergansers. AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Sternum length (mm)**									***n***
	60–61	**62–63**	**64–65**	**66–67**	**68–69**	**70–71**	**72–73**	**74–75**	**76–77**	
AI						2	2		1M	5
CI cave	1	10	13	7						31

Population	**Sternum anterior width (mm)**								***n***
	40	**41**	**42**	**43**	**44**	**45**	**46**	**47**	
AI		1	2	1				1M	5
CI cave	1	4	5	10	9	3	2		34

Population	**Sternum posterior width (mm)**								***n***
	42	**43**	**44**	**45**	**46**	**47**	**48**	**49**	
AI				1		3		1M	5
CI cave	2	3	10	12	1				28

$P < 0.0001$). However, anterior pelvis widths from the two populations entirely overlapped (Table 8).

Posterior pelvis widths were widest in CI females (AI mean 47.4 ± 0.5 mm; CI mean 49.1 ± 1.6 mm) but three of the CI measurements were conspicuously larger than all others, suggesting the ischia were splayed during preservation in the cave deposit. Excluding these three measurements the mean CI cave posterior pelvis width was 48.9 ± 1.5 mm, which was not significantly different from the AI female mean width ($t_{26} = 1.80$, $P = 0.084$, n.s.). However, with or without these three measurements, the posterior pelvis width/antitrochanter width ratios differed significantly between the two populations (Table 8). Their size-frequency distributions did not overlap, and the means of the two samples (three widest CI measurements excluded) were significantly different ($t_{27} = 6.93$, $P < 0.0001$). The width ratios from the three CI females with the

Table 5. Size-frequency distribution of keel (carina sterni) length (mm) and area (mm^2) from Auckland Islands and Chatham Island mergansers. AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Keel length (mm)**													***n***
	69–70	**71–72**	**73–74**	**75–76**	**77–78**	**79–80**	**81–82**	**83–84**	**85–86**	**87–88**	**89–90**	**91–92**	**93–94**	
AI							1		1	2			1M	5
CI cave	2		7	17	5									31

Population	**Keel area (mm^2)**									***n***
	426–450	**451–475**	**476–500**	**501–525**	**526–550**	**551–575**	**576–600**	**601–625**	**626–650**	
AI					1	1	1	1	1M	5
CI cave	1	2	5	2	5	3	1			19

conspicuously larger posterior pelvis widths were three of the four highest, also suggestive of possible distortion.

Comparative size and proportional relationships

Relative skeletal size

Comparison of Auckland Islands and Chatham Island females. Based on mean dimensions (Appendix 2), major skeletal elements of CI mergansers were generally smaller than those of AI female mergansers, most by 3–6%, although sternum lengths differed by 10%, as did keel lengths and areas (Table 9, Fig. 2). Mean wing bone lengths also differed by about 3%. Differences in pelvis length, and width at the antitrochanter, indicate the CI merganser had a significantly shorter and narrower pelvis, but which may have been wider posteriorly. As a consequence, posterior width/antitrochanter width ratios differed. However, leg bones were of similar size.

Comparison of Chatham Island and New Zealand putative females. The lengths of ulnae from NZ putative females were shorter than those of CI females, but not so the humeri (Table 9). Additionally, NZ coracoid bones were conspicuously narrower distally. The legs of NZ putative females may have been shorter than CI mergansers.

Comparison of Auckland Islands and New Zealand putative females. Although mean

Table 6. Size-frequency distributions of keel length / sternum length ratios and keel area / sternum length ratios for Auckland Islands and Chatham Island mergansers. AI = Auckland Islands; CI cave = Chatham Island cave site. M = male.

Population	**Keel length/sternum length ratio**											***n***
	1.13	**1.14**	**1.15**	**1.16**	**1.17**	**1.18**	**1.19**	**1.20**	**1.21**	**1.22**	**1.23**	
AI							1		2	1	1M	5
CI cave	2		2	1	5	10	7	1	3			31

Population	**Keel area/sternum length ratio**									***n***
	7.0–7.24	**7.25–7.49**	**7.50–7.74**	**7.75–7.99**	**8.0–8.24**	**8.25–8.49**	**8.50–8.74**	**8.75–8.99**	**9.0–9.24**	
AI			2		1M	2				5
CI cave	1	3	3	1	4	3	2	1	1	19

lengths of main wing and leg bones of NZ putative female mergansers were all shorter that AI females (Table 9), sample sizes from both populations were too small to confirm any difference statistically. Despite uncertainty which accompanies our discrimination of sex for the NZ sample (see Methods), coracoid dimensions alone suggest AI birds were conspicuously larger.

Comparison with Mergus serrator *females.* Female mergansers from all three New Zealand region populations were smaller than *M. serrator* females (Table 9, Fig. 2). While skulls (of AI birds) and pelvic bones (of both AI and CI) were comparable in size to those of *M. serrator*, wing bones and sternal elements were considerably smaller (10–20%), indicating a much smaller overall body size.

The conspicuously diminished sternum and keel characteristics of female AI and CI mergansers also provide other relative differences. Mean keel length/mean sternum length ratios (*M. serrator* = 1.32 ± 0.04, *n* = 8; AI = 1.21 ± 0.02, 4; CI cave = 1.18 ± 0.02, 31) emphasise a difference in the extent of the apex carinae projecting forward of the sternum. Similarly, mean keel area/mean sternum length ratios (*M. serrator* = 9.32 ± 0.4, *n* = 5; AI = 8.01 ± 0.4, 4; CI = 8.05 ± 0.5, 19) emphasise a relative diminution in pectoral muscle mass of the Antipodean forms and, thus, their diminished flight capabilities.

Leg bones, especially femora, were only

Table 7. Size-frequency distribution of leg bone lengths (mm) from New Zealand, Auckland Islands and Chatham Island mergansers. NZ= New Zealand; AI = Auckland Islands; CI cave = Chatham Island cave site (left femur, right tibiotarsus, left tarsometatarsus); CI dune = other Chatham Island sites; M = male.

Population	**Femur length (mm)**						***n***
	40	**41**	**42**	**43**	**44**	**45**	
NZ	1	6	3	3	2	1	16
AI			2	1		1M	4
CI cave		1	20	21	2		44
CI dune	1	1		1	1		4

Population	**Tibiotarsus length (mm)**							***n***
	69	**70**	**71**	**72**	**73**	**74**	**75**	
NZ	3	1		4		3	1	15
AI		1		1				2
CI cave		9	9	13	14	2		47
CI dune	1							1

Population	**Tarsometatarsus length (mm)**							***n***
	38	**39**	**40**	**41**	**42**	**43**	**44**	
NZ	2	1	1	1			1	6
AI			1	1				2
CI cave	5	18	25	3				51

slightly smaller than those of *M. serrator*, perhaps indicating a more "terrestrial" habit (*e.g.* exploiting smaller and shallower stream habitats) for the Antipodean populations. The pelves of *M. serrator* and CI mergansers were of similar width and their posterior/antitrochanter width ratios did not differ (*M. serrator* = 1.86 ± 0.11, n = 6; CI = 1.92 ± 0.013, 26; t_{30} = 1.8, P = 0.08, n.s.).

Table 8. Size-frequency distribution of pelvis measurements (mm) and ratio of widths from Auckland Islands and Chatham Island mergansers. * Posterior measurements (52.6, 54.2, 54.6 mm) and the derived width ratio may indicate distortion. AI = Auckland Islands; CI cave = Chatham Island cave site; M = male.

Population	**Length (mm)**						***n***
	80–81	**82–83**	**84–85**	**86–87**	**88–89**	**≥ 90**	
AI				1	1	1M	3
CI cave	12	10	3				25

Population	**Anterior width (mm)**					***n***
	16	**17**	**18**	**19**	**≥ 20**	
AI			2	1M		3
CI cave	3	11	11	1		26

Population	**Antitrochanter width (mm)**									***n***
	23	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	
AI						2	1		1M	4
CI cave	1	7	18	9						35

Population	**Posterior width (mm)**							***n***
	45	**46**	**47**	**48**	**49**	**50**	**>51***	
AI			2	1	1M			4
CI cave	1	1	5	7	5	7	3	29

Population	**Posterior/antitrochanter width ratio**						***n***
	1.6	**1.7**	**1.8**	**1.9**	**2.0**	**2.1**	
AI	3 + 1M						4
CI cave		1	9	10	7*	1*	28

Table 9. Mean (± 95% confidence intervals, *n*) percentage size relationships of selected skeletal elements of Chatham Island cave and putative female New Zealand mergansers, and *Mergus serrator* females, relative to those of Auckland Islands female mergansers. All data from Appendix 2 ([a] = significant size difference between AI and CI; [b] = significant size difference between CI and NZ; * = excluding three longest measurements, see Table 8).

Population/ Bone	**Auckland Islands**	**Chatham Island**	**New Zealand**	***Mergus serrator***
Skull length	100 ± 0, 2	94.6 ± 1.5, 6		99.3 ± 3.1, 4
Nares-tip	100 ± 4.0, 3	92.3 ± 0.7, 46[a]		100.0 ± 1.1, 4
Post-orbital width	100 ± 0, 2	104.1 ± 0.3, 44		103.0 ± 0.2, 8
Inter-orbital width	100 ± 0.6, 3	115.1 ± 0.1, 43		115.0 ± 0.2, 7
Humerus length	100 ± 0, 2	97.4 ± 0.4, 47[a]	97.2 ± 1.4, 9	121.8 ± 2.4, 9
Ulna length	100 ± 0, 2	97.4 ± 0.4, 43[a]	93.4 ± 2.6, 8[b]	125.5 ± 2.0, 10
Carpometacarpus length	100 ± 0, 2	96.9 ± 0.5, 41[a]		128.3 ± 1.9, 6
Coracoid length	100 ± 0.5, 5	95.5 ± 0.5, 46[a]	92.8 ± 1.7, 8[b]	119.8 ± 2.1, 9
Coracoid width	100 ± 2.7, 5	96.5 ± 0.5, 46[a]	83.5 ± 1.4, 7[b]	113.5 ± 0.5, 8
Sternum length	100 ± 1.0, 4	89.0 ± 0.8, 31[a]		114.1 ± 1.1, 11
Sternum anterior width	100 ± 1.6, 4	100.5 ± 1.1, 34		112.0 ± 1.5, 12
Sternum posterior width	100 ± 2.4, 4	94.9 ± 0.7, 28[a]		110.8 ± 1.7, 10
Keel length	100 ± 5.0, 4	87.5 ± 0.7, 31[a]		124.9 ± 2.1, 9
Keel area	100 ± 6.5, 4	89.8 ± 3.1, 19[a]		132.5 ± 17.4, 5
Femur length	100 ± 0, 2	100.2 ± 0.4, 44	96.3 ± 1.3, 7[b]	103.7 ± 0.8, 10
Tibiotarsus length	100 ± 0, 2	101.0 ± 0.5, 47	95.8 ± 1.9, 7	108.4 ± 1.5, 7
Tarsometatarsus length	100 ± 0, 2	97.8 ± 0.5, 51		105.4 ± 1.0, 9
Pelvis length	100 ± 0, 2	93.6 ± 0.5, 25[a]		
Pelvis anterior width	100 ± 0, 2	97.8 ± 1.6, 26		
Antitrochanter width	100 ± 1.3, 3	88.5 ± 0.7, 36[a]		88.2 ± 0.5, 9
Pelvis posterior width	100 ± 1.6, 3	103.3 ± 0.6,26*		97.0 ± 1.5, 9

Size-related skeletal proportions

Size-standardised measurements (i.e. mean bone lengths divided by mean femur length) were used to appraise proportional differences in skeletal elements of the three Antipodean populations and *M. serrator* (Table 10). These data indicate that AI mergansers had longer skulls than CI

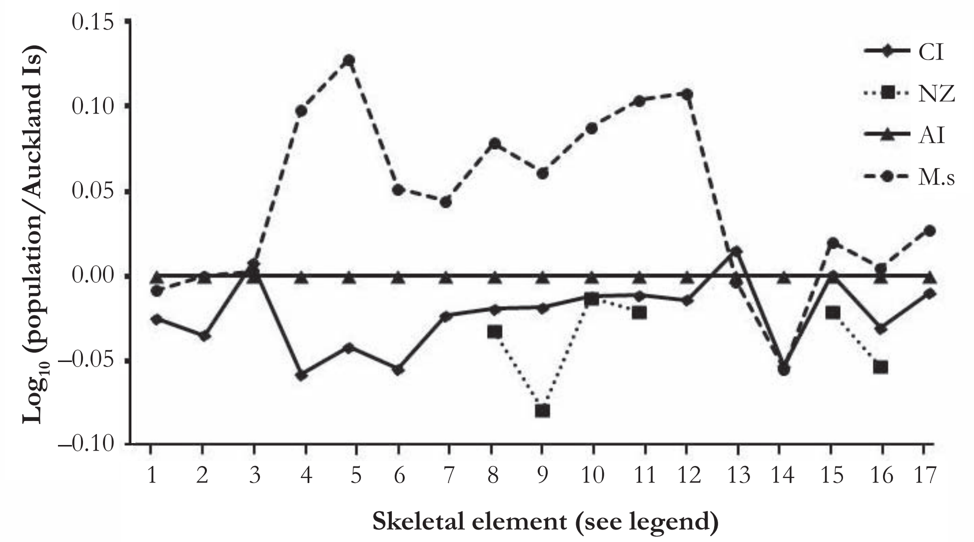

Figure 2. Ratio diagram depicting log differences in mean dimensions of selected *Mergus serrator* (M.s.), Chatham Island female (CI) and New Zealand putative female (NZ) merganser skeletal elements relative to those of Auckland Islands female (AI) mergansers. The vertical distance between points of the same element is proportional to the ratio of their actual dimensions. Skeletal elements compared are, in order: Skull = total skull length (1), nares to tip (2), post-orbital width (3); Sternum = keel length (4), keel area (5), sternum length (6), sternum posterior width (7); Wing = coracoid length (8), coracoid width (9), humerus (10), ulna (11), carpometacarpus (12); Pelvis = posterior width (13), antitrochanter width (14); and Leg = femur length (15), tibiotarsus length (16), and tarsometatarsus length (17). For further explanation of diagram see Methods. Data derived from Table 9; variance estimates not depicted.

because of their more elongate premaxillae, and that relative to *M. serrator* females, mergansers from all three Antipodean populations had reduced pectoral and sternal elements. CI female mergansers had a proportionately shorter coracoid and sternum than AI female mergansers, perhaps indicating a reduced flying ability, and differing pelvic proportions also. The limited data for NZ putative female mergansers indicate a clear reduction in the pectoral girdle relative to *M. serrator* females and hint at a possible difference from the CI and AI populations.

Discussion

Comparison of female mergansers from Auckland Islands and New Zealand

Our analyses have not established statistically significant differences between bone lengths of female mergansers from AI and NZ, with the exception of coracoids (Fig. 1, Fig. 2). Testing for possible differences between these two populations has been hampered by the paucity of bones from both, and especially by the absence of sterna from NZ. That differences in skeletal

Table 10. Size-related proportional relationships of selected skeletal elements of female mergansers from Auckland Islands, Chatham Island and New Zealand (putative females), and *Mergus serrator*. All data from Appendix 2. Mean length of selected skeletal element is divided by mean femur length from the same population/taxon. * = differ from AI by >5% († = mean length excludes three longest measurements, see Table 8).

Population/ Skeletal element	**Auckland Islands**	**Chatham Island**	**New Zealand**	***Mergus serrator***
Skull length	2.40	2.27*		2.30
Nares-tip	0.85	0.79*		0.82
Post-orbital width	0.62	0.64		0.61
Inter-orbital width	0.12	0.14*		0.14
Humerus length	1.59	1.55	1.61	1.87*
Ulna length	1.28	1.28	1.24	1.55*
Carpometacarpus length	0.90	0.87		1.11*
Coracoid length	1.03	0.99	1.00	1.20*
Coracoid width	0.40	0.37*	0.34*	0.43*
Sternum length	1.67	1.49*		1.84*
Sternum anterior width	0.99	0.98		1.07*
Sternum rear width	1.10	1.04*		1.17*
Keel length	2.00	1.75*		2.41*
Keel area	13.40	12.00*		17.10*
Tibiotarsus length	1.67	1.68	1.66	1.74
Tarsometatarsus length	0.95	0.93		0.97
Pelvis length	2.05	1.91*		
Pelvis anterior width	0.42	0.41		
Antitrochanter width	0.67	0.59*		0.57*
Pelvis posterior	1.10	1.14†		1.03

characteristics may exist, however, are hinted at by the minimum lengths of all NZ bones, except femur, being shorter than those from AI. The smaller NZ coracoid bones hint at a relatively weaker pectoral apparatus. The putative NZ females were more similar in size and proportion to females on CI than AI, but we cannot rule out the possibility that larger NZ females were mis-diagnosed by our methodology. Maximum lengths (likely to be of adult males) of humeri and ulnae from NZ were similar to the single AI male (Appendix 2).

The NZ sample, by amalgamating bones from North, South and Stewart Islands, is drawn from a 13° latitudinal range and may mask any possible north-south size gradient expected under both Bergmann's (Mieri & Dayan 2003) and Allen's rules (Nudds & Oswald 2007) and demonstrated by other New Zealand waterfowl, for instance *Hymenolaimus malacorhynchos* (see Marchant & Higgins 1990; Godfrey *et al.* 2003) and *Anas chlorotis* (see Matthews 1936; Marchant & Higgins 1990).

Comparison of female mergansers from Auckland Islands and Chatham Island

Our comparative measurements of female merganser bones from AI and CI recorded significant size differences (Tables 1–9) and proportional differences (Table 10) between these two populations. Mergansers from CI were smaller birds (Table 9) with differing skull, sternal and pelvic proportions (Table 10, Fig. 2), and we consider these differences, in combination, sufficient to establish the CI merganser as a taxon distinct from *M. australis* at Auckland Islands. We propose that it be recognised as a new species.

Systematics

Order Anseriformes

Family Anatidae Leach, 1819

Mergus Linnaeus, 1758

Mergus milleneri **Williams & Tennyson, sp. nov.**

VERNACULAR NAME: Chatham Island Merganser.

TYPE LOCALITY: The cave Te Ana a Moe, Chatham Island, Pacific Ocean (Holocene age).

DISTRIBUTION: Chatham Island.

ETYMOLOGY: The species epithet is a noun in the genitive case honouring Dr Philip Ross Millener (former Curator of Fossil Birds at NMNZ) who collected most of the fossil Chatham Island *Mergus* material referred to in this paper, including all specimens from Te Ana a Moe.

HOLOTYPE: NMNZ S.29496.3 – Skull (Fig 3A), collected by P.R. Millener, 20 February 1991, sample 93/91. Sex female.

MEASUREMENTS OF HOLOTYPE: Complete skull: cranium + premaxilla length 99.2 mm, nares to tip 34.8 mm, width at post-orbital process 27.7 mm, inter-orbital width 6.2 mm.

PARATYPES: NMNZ S.32198.4 – sternum (Fig. 4A), collected by P.R. Millener & N.H. Hyde, 15 February 1992, sample 152/92, sex female. NMNZ S.32198.6 – pelvis (Fig. 4B), collected by P.R. Millener & N.H. Hyde, 15 February 1992, sample 152/92, sex female. Both collected in Te Ana a Moe, Chatham Island.

MEASUREMENTS OF PARATYPES: NMNZ S.32198.4, sternum: length carina sterni 76.5 mm; sternum length (basin length, pila coracoidea to caudal margin) 63.0 mm; anterior width 43.8 mm; posterior width 45.7 mm; carina sterni area 543 mm^2. NMNZ S.32198.6, pelvis: length 84.9 mm, anterior width 17.7 mm, posterior width 47.7 mm, width at antitrochanter 25.8 mm, posterior width/antitrochanter width = 1.85.

NON-TYPE SPECIMENS EXAMINED: See Appendix 1.

Figure 3. A = Lateral and dorsal views of Holotype (NMNZ S.29496.3, female) of Chatham Island Merganser *Mergus milleneri*; B = dorsal view of female Auckland Islands Merganser *Mergus australis* skull (NHMT 1904.8.4.4).

DIAGNOSIS: Compared with *M. australis* (AI) the skull has a shorter premaxilla, a broader inter-orbital width, and larger, more conspicuous, salt gland impressions. Proportionately, the skull and premaxilla are shorter but the inter-orbital width is greater. The humerus, ulna, carpometacarpus and coracoid are shorter and the coracoid absolutely and proportionately narrower. The sternum differs by being absolutely and proportionately narrower posteriorly, shorter, with the carina sterni less forward projecting, shorter, and of smaller area. The pelvis is absolutely and proportionately shorter, and narrower between the processus antitrochanter. The pelvis has a posterior width/antitrochanter width ratio > 1.7, whereas for *M. australis* this ratio is 1.6. The new species differs from all other *Mergus* species by smaller

Figure 4. Dorsal and lateral views of paratypes of Chatham Island Merganser *Mergus milleneri*. A = sternum (NMNZ S.32198.4, female) ; B = pelvis (NMNZ S.32198.6, female).

size and reduced pectoral and sternal elements.

REMARKS: We recognise the size and proportional differences between the Chatham Island Merganser and mergansers from the Auckland Islands as being small but many, indicative of prolonged geographic separation, and indicative of a response to local environmental conditions. The taxonomic distinction we propose is an example of allopatric speciation (Price 2008) and the species-level status is conferred under the phylogenetic species concept (*sensu* Cracraft 1983; McKitrick & Zink 1988). Although our discrimination of putative females in the New Zealand sample suggests there may be a size distinction between mergansers from AI and NZ, we have been unable to validate the difference statistically, other than for coracoids, because of small comparative sample sizes, the possibility of a geographic size cline in NZ birds, and the uncertainty of our sexing of the NZ bones. We suggest that the New Zealand population should be considered *Mergus* sp. until subsequent mensural and/ or genetic distinctions provide clarity. Therefore, we suggest that the vernacular name of mergansers from Auckland Islands revert to 'Auckland Islands Merganser', as the name 'New Zealand Merganser' *sensu* Gill *et al.* (2010) is no longer appropriate.

Island differentiation

It is not a novel prospect that populations of a merganser established in the New Zealand region should have differentiated mensurably from each other upon colonising the isolated Auckland Islands and Chatham Island. Many New Zealand avian taxa have done so following dispersal to these, and to other neighbouring archipelagos or islands (*e.g.* kaka *Nestor* sp., pigeon *Hemiphaga* sp., pipit *Anthus novaeseelandiae* subsp., banded dotterel *Charadrius bicinctus* subsp.). Most of the land and freshwater birds present on the Chatham Islands prior to human arrival have been identified as taxa mensurably differentiated from congeners on mainland New Zealand (Gill *et al.* 2010) with consequent endemism being recognised at both species and subspecies level (Miskelly 2008). The Chatham Islands archipelago is sufficiently distant (800 km) and sufficiently large (966 km^2) to have intercepted and retained not just species dispersing downwind from New Zealand but also direct from Australia (*e.g.* Tennyson 1998). Descendents of some successful colonists (for instance *Prosthemadera novaeseelandiae chathamensis*, *Hemiphaga chathamensis*, *Bowdleria rufescens*, *Fulica chathamensis*, *Gallirallus dieffenbachii*), conform to the "island rule" by being larger than their mainland forebears (see Marchant & Higgins for data; Clegg & Owens 2002; Lomolino 2005).

None of Chatham Island's recent or contemporary duck species (notably *Anas chlorotis*, *A. gracilis*, *A. rhynchotis*, *A. superciliosa, Aythya novaeseelandiae*) have been examined to determine mensural differences from populations in New Zealand. However, Tennyson & Millener (1994) and Worthy & Holdaway (2002) have suggested that two undescribed Holocene fossil waterfowl (a shelduck *Tadorna* sp. and a swan *Cygnus* sp.) may be of distinctly different size from congeners in New Zealand and warrant taxonomic distinction. Molecular analyses have detected mtDNA haplotypes unique to the Chatham Island population of *A. superciliosa* (see Rhymer *et al.* 2004) and determined that the large, extinct Chatham Island duck (*Pachyanas chathamica*) is a sister taxon to *A. chlorotis* (see Mitchell *et al.* 2014).

Many waterfowl (especially *Anas* sp. in the 400–800 g weight range), once established on remote southern islands, have become smaller than their source congeners (*e.g. Anas marecula, A. eytoni, A. aucklandica, A. nesiotis*) and some flightless (Lack 1970; Weller 1980; Mourer-Chauviré *et al.* 1999). McNab (1994a,b) considered this to be an energy conservation response in the face of increased intra-specific competition. The diminished wing bone lengths and sterna of mergansers from Auckland Islands and Chatham Island relative to *M. serrator* may be evidence of this "island" response. Their lesser flight capability (Livezey 1989) could also imply an ecology that featured year-round site fidelity and small foraging ranges for all New Zealand region mergansers.

For mergansers, Chatham Island may have provided a very different environment from New Zealand and, particularly, from Auckland Islands. It is, presently, a low flat island of recent (~2.5 mya) emergence with 350,000 years of peat accumulation and a shoreline of contrasting exposed cliff and rock-strewn sections (south and southwest), extensive sand-floored protective bays (west and east) and a broad northern shoreline with both sand and rock seafloors (Campbell 2008; Schiel 2008). Most of the island's northern, eastern and western shorelines are flanked by low barrier dunes. Modern (from 6500 years ago) Chatham Island has many small lakes, small slow peat-stained rivers draining the southern "uplands", and the dominating barrier-bar lake (Te Whanga lagoon), which comprises 20% of the island's area. A freshwater fish fauna of nine species (Bott 2008) could have offered mergansers lacustrine and riverine fare. If mergansers occupied coastal margins (as the presence of fossil merganser bones in coastal dunes implies) they were likely to have been widely dispersed and foraging over a largely featureless sand seafloor, a distinct contrast to habitats occupied on Auckland Islands (Williams 2012). Mergansers exploiting Te Whanga Lagoon (as their retrieval from Te Ana a Moe implies) similarly would have foraged over a shallow, macrophyte-laden sandfloor below windswept waters. Stable isotope analyses indicate a predominantly marine-sourced (lagoon or sea) diet for mergansers recovered from Te Ana a Moe whereas mergansers at Auckland Islands had a mixed freshwater and marine-sourced diet (Williams *et al.* 2012). Thus, the influences that may have induced change in skeletal size and proportion in Chatham Island mergansers are most likely to reflect a feeding environment which contrasted with that at Auckland Islands and, possibly, mainland New Zealand.

Phylogeographic considerations

Phylogeographic questions highlighted by our appraisal of size differences of mergansers in the New Zealand region include:

1) Did the Auckland Islands and Chatham Island populations arise from the same geographic source? Because mergansers on mainland New Zealand extended over 13° of latitude, clinal changes in body dimensions might be expected. The two island populations, if derived from widely-separated areas of New Zealand, may have been established by birds already of differing size.

2) Was dispersal and settlement a one-off event? The ability of waterfowl to cross significant ocean gaps to reach and establish in New Zealand and on its nearby islands (*e.g.* Rhymer *et al.* 2004; Williams *et al.* 2006; Gill *et al.* 2010) suggests merganser dispersal to the island archipelagos was unlikely to have been a one-off event. Repeat dispersal and settlement events are likely to have left a genetic rather than a mensural footprint.

A wider perspective recognises the presence of a merganser in the geographically isolated New Zealand region as a biogeographic conundrum. From where did it come? For example:

3) Were New Zealand's mergansers the consequence of trans-hemispheric dispersal and, thus, an isolated relative of an extant northern-hemisphere

congener such as *M. squamatus* or *M. merganser*, as suggested by Humphrey (1955) and reiterated by Johnsgard (1965) and Kear & Scarlett (1970)? Contemporary trans-hemispheric movements of waterfowl in the Asia-Pacific-Australasia region (Williams *et al.* 2006; Gill *et al.* 2010) are scant.

4) Alternatively, is there a closer phylogenetic relationship with the only other extant southern hemisphere merganser, *M. octosetaceus*? Downy ducklings of these two species are more similar in colour and patterning to each other than to any northern merganser (see Kear 2005). Livezey (1989) suggested "*M. australis* is a member of a basal grade of comparatively small, southern hemisphere mergansers; the Brazilian Merganser (*M. octosetaceus*) branched next and is the sister-group to the larger, more derived, northern hemisphere species of *Mergus*."

Solovyeva & Pearce (2011) used molecular analysis to further resolve phylogenetic relationships of northern hemisphere mergansers. The questions posed above are potentially resolvable by similar means should mtDNA be extracted from the remains of all three New Zealand *Mergus* populations.

Establishing the nearest living relative of New Zealand's mergansers may elucidate a rarely-evidenced route for avifaunal colonisation of New Zealand. Identifying relationships and divergence times between all three New Zealand *Mergus* populations will help inform waterfowl dispersal and establishment on New Zealand's surrounding archipelagos, especially when viewed alongside the pattern of divergence and dispersal Mitchell *et al.* (2013) reported for New Zealand's brown-plumaged teals and Chatham Island's extinct duck *Pachyanas chathamica*.

Acknowledgements

We gratefully acknowledge the assistance of Paul Scofield (CMNZ), Cody Fraser (OMNZ), Neville Hudson (Auckland University Geology Dept.), Ian Smith (Otago University Anthropology Dept.), Mark Adams, Joanne Cooper and Judith White (NHMT), Gerald Mayr (Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt), Loic Costeur & Vanesa De Pietri (Naturhistorisches Museum Basel), Anita Gamauf and Hans-Martin Berg (Naturhistoriches Museum, Vienna), Marie Portas (Museum Nationale d'Histoire Naturelle, Paris), and Nigel Monoghan (National Museum of Ireland Natural History, Dublin) for access to merganser bones under their curatorial care. We thank Jean-Claude Stahl for photographs of the holotype and paratypes and Tane Williams for preparation of the composite images. We appreciated the insightful comments of Ricardo Palma and Trevor Worthy as our study progressed, thank Trevor, Marco Pavia and Storrs Olson for their reviews of our submitted script, and thank Eileen Rees for her willing help and editorial craft.

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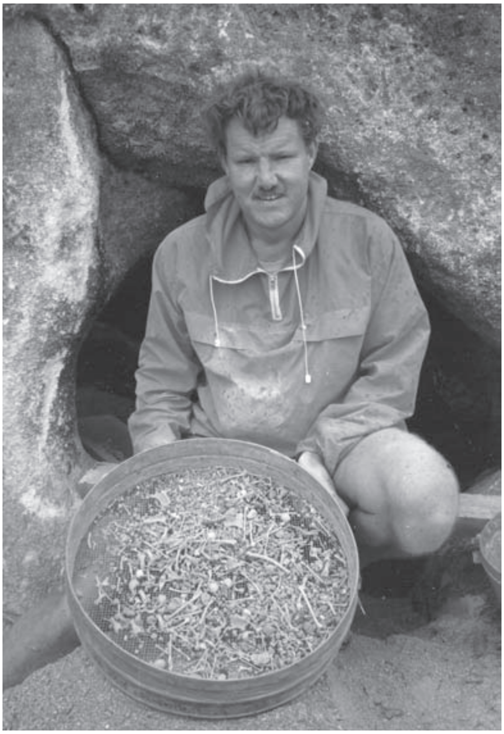

Photograph: Former Museum of New Zealand Curator Dr Philip Millener, after whom *Mergus milleneri* is named. Along with his colleague Noel Hyde, he excavated Chatham Island's spectacular Te Ana a Moe cave deposit of fossil bird bones (shown), retrieving bones from 9 marine and 21 terrestrial and freshwater species, including the collection of *Mergus* bones analysed in this study. (Photograph by N.H. Hyde).

Appendix 1: Institutional source and specimen number of all *Mergus* bones examined.

I. Bones of Chatham Island Merganser. Most Museum of New Zealand specimen numbers refer to multiple bones, each of which has a unique subsidiary number.

Canterbury Museum, Christchurch, New Zealand: Non-cave specimens. AV27501, AV29860.
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: Non-cave specimens. S.26362, S.27743, S.28456, S.29534, S.30828, S.31176, S.31259, S.31298, S.35277. Cave specimens. S.27140–27142, S.27144, S.27145, S.27147–27158, S.27520, S.29183, S.29231, S.29702, S.29713, S.29477, S.29478, S.29496, S.29677, S.29689, S.29749, S.30046, S.30052, S.30080, S.30110, S.30126, S.30136, S.30234, S.30243, S.30276, S.30284, S.30618, S.30627, S.30634, S.31634, S.31700, S.31756–31758, S.31777, S.32093, S.32094, S.32109, S.32198, S.44360, S.44361, S.45516, S.45517–45519, S.45521, S.45523–45528.

II. Bones of New Zealand mainland (North Island, South Island, Stewart Island) mergansers. Some Museum of New Zealand specimen numbers refer to multiple bones, each of which has a unique subsidiary number.

Canterbury Museum, Christchurch, New Zealand: AV11532, AV11600, AV13496, AV13512, AV13648, AV13649, AV21264, AV24919, AV26397, AV26398, AV33852, AV33853, AV36201, AV37112, AV37117, AV37125, AV37328.
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: S.2363, S.22131, S.22168, S.22169, S.33294–33297, S.35437, S.35947, S.36845, S.37217, S.38954, S.43865, S.43873, S.44466.
Note: Two femora (S.33294.2, S.35947.8) and three tibiotarsi (S.33294.1, S.33295, S.37217.2) were conspicuously smaller than all others and were excluded from analyses.

III. Bones of Auckland Islands Merganser.

Canterbury Museum, Christchurch, NZ: AV1582, AV5176, AV7157.
Museum of New Zealand Te Papa Tongarewa, Wellington, NZ: OR23515.
Otago Museum, Dunedin, NZ: AV1110.
Natural History Museum, Tring, United Kingdom: 1904.8.4.2, 1904.8.4.3, 1904.8.4.4.

IV. Bones of *Mergus serrator*.

Naturmuseum Senckenberg, Frankfurt, Germany: 1943, 7821, 7825, 7845.
Naturhistorisches Museum, Basel, Switzerland: 1200, 1543, 7730.
Museum Nationale d'Histoire Naturelle, Paris, France: 1996/39.
National Museum of Ireland, Natural History, Dublin, Ireland: 1927.6.1, 1932.13.1, 2004.79.26.
Naturhistorisches Museum, Vienna, Austria: 4456, 4457, 4827, 8639, 8704.
Natural History Museum, Tring, United Kingdom: 1898.2.12.5, 1930.3.24.240, 1930.3.24.242, 1930.3.24.633, 1997.78.1.
Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: OR12707.

Appendix 2: Summary statistics of measurements of merganser bones from New Zealand, Auckland Islands and Chatham Island (cave, dune), and of Red-breasted Merganser *Mergus serrator*.

New Zealand measurements are of all bones (both sexes combined) followed by putative (?) females and putative (?) males determined as described in Methods. Chatham Island dune measurements are of all bones (both sexes combined). Chatham Island cave measurements are of females. All measurements in mm. Abbreviations: Tsk = total skull length; N-t = nares to rostrum tip; Pop = cranium post-orbital process width; Iow = cranium inter-orbital width; Hum = humerus length; Uln = ulna length; Cmc = carpometacarpus length; Col = coracoid length; Cow = coracoid width; Stv = sternum visceral(dorsal) length; Sta = sternum anterior width; Stp = sternum posterior width; Kel = Keel (carina sterni) length; Kea = Keel (carina sterni) area (mm^2); Fem = femur length; Tbt = tibiotarsus length; Tmt = tarsometatarsus length; Pel = pelvis length; Pea = pelvis anterior width; Pep = pelvis posterior width; Ant = process antitrochanter width; s.d. = standard deviation; *n* = sample size.

New Zealand

All bones	**N-t**	**Hum**	**Uln**	**Cmc**	**Col**	**Cow**	**Fem**	**Tbt**	**Tmt**
Mean	36.5	68.5	53.2	38.6	42.3	14.5	42.6	71.2	40.2
s.d.		2.7	2.7	2.3	1.9	0.8	1.5	2.9	1.8
Maximum	40.4	72.4	56.8	41.3	45.9	16.2	45.0	75.4	43.2
Minimum	32.5	65.3	48.8	37.2	39.9	13.6	40.0	66.6	38.6
Median		68.1	53.0	37.4	42.1	14.1	43.8	72.0	39.6
n	2	16	14	3	12	8	16	15	6
?Females									
Mean		66.5	51.3		41.2	14.2	41.3	68.5	
s.d.		1.2	1.7		0.9	0.4	0.57	1.5	
Maximum		68.1	53.3		42.2	14.9	41.7	70.3	
Minimum		65.3	48.8		39.9	13.6	40.0	66.6	
Median		65.7	51.8		40.9	14.1	41.3	69.2	
n		9	8		8	7	7	7	
?Males									
Mean		71.0	55.8		44.6	16.2	43.7	73.6	
s.d.		1.5	0.8		0.9	–	0.9	1.3	
Maximum		72.4	56.8		45.9	–	45.0	75.4	
Minimum		69.0	54.6		43.8	–	42.9	72.0	
Median		71.7	56.1		44.3	–	43.8	74.2	
n		7	6		4	1	9	8	

Auckland Island

Females	**Tsk**	**N-t**	**Pop**	**Iow**	**Hum**	**Uln**	**Cmc**	**Col**	**Cow**	**Stv**	**Sta**
Mean	103.1	36.6	27.2	5.3	68.4	54.9	38.5	44.4	17.0	71.8	42.5
s.d.		0.8		0.5				0.2	0.4	0.5	0.5
Maximum	103.6	37.3	27.2	5.8	68.9	55.0	38.5	44.8	17.5	72.3	43.1
Minimum	102.6	35.8	27.2	4.8	67.8	54.7	38.5	44.2	16.6	71.2	41.9
Median		36.6		5.2				44.3	17.1	71.8	42.4
n	2	3	2	3	2	2	2	5	5	4	4
Male (1)	109.9	40.2	29.0	5.4	72.1	57.7	41.0	48.3	19.1	77.1	47.7

Females	**Stp**	**Kel**	**Kea**	**Fem**	**Tbt**	**Tmt**	**Pel**	**Pea**	**Pep**	**Ant**
Mean	47.1	85.9	575	42.9	71.5	40.8	87.9	18.2	47.4	28.8
s.d.	0.8	3.1	27						0.4	0.2
Maximum	47.9	88.5	601	43.1	72.1	41.2	89.7	18.4	48.0	29.0
Minimum	45.9	81.5	545	42.6	70.9	40.4	86.0	18.0	47.0	28.7
Median	47.3	86.7	576						47.1	28.7
n	4	4	4	2	2	2	2	2	3	3
Male (1)	49.6	94.8	628	45.4			94.9	19.3	49.9	31.2

Chatham Island cave

Females	**Tsk**	**N-t**	**Pop**	**Iow**	**Hum**	**Uln**	**Cmc**	**Col**	**Cow**	**Stv**	**Sta**
Mean	97.5	33.8	27.7	6.1	66.6	53.5	37.3	42.4	16.4	63.9	42.7
s.d.	1.4	0.5	0.3	0.3	0.9	0.8	0.6	0.7	0.3	1.5	1.3
Maximum	99.2	35.2	28.3	6.5	68.3	54.9	38.8	43.6	17.3	67.0	45.5
Minimum	95.7	31.3	26.7	5.2	64.4	51.6	35.8	40.6	15.8	60.7	40.0
Median	97.8	34.1	27.7	6.2	66.6	53.6	37.3	42.3	16.4	63.9	42.8
n	6	46	44	43	47	43	41	46	46	31	34

Females	**Stp**	**Kel**	**Kea**	**Fem**	**Tbt**	**Tmt**	**Pel**	**Pea**	**Pep**	**Ant**
Mean	44.7	75.2	516	43.0	72.2	39.9	82.3	17.8	49.4	25.5
s.d.	0.8	1.6	37	0.6	1.1	0.7	1.1	0.7	2.0	0.6
Maximum	46.0	78.3	577	44.1	74.0	41.8	85.0	19.3	54.6	26.5
Minimum	42.4	69.4	447	41.8	70.0	38.4	80.7	16.4	45.3	23.9
Median	44.8	76.0	516	43.1	72.3	40.0	82.1	17.9	49.2	25.6
n	28	31	19	44	47	51	25	26	29	35

Chatham Island dunes

All bones	Hum	Uln	Cmc	Col	Fem	Tbt
Mean	70.7	51.7	35.5	41.0	43.2	69.9
s.d.				4.3	1.1	
Maximum	70.8			45.7	44.2	
Minimum	70.6			37.4	41.7	
Median				39.9	43.8	
n	2	1	1	3	3	1

Mergus serrator

Females	Tsk	N-t	Pop	Iow	Hum	Uln	Cmc	Col	Cow	Stv	Sta
Mean	102.4	36.6	27.4	6.1	83.3	68.9	49.4	53.2	19.3	81.9	47.6
s.d.	3.2	1.1	0.3	0.2	3.0	2.6	1.9	2.7	0.6	1.6	2.4
Maximum	105.5	37.7	27.7	6.4	89.9	73.9	52.6	56.9	20.1	84.7	50.1
Minimum	98.2	35.5	27.1	5.9	81.4	64.7	46.7	49.2	18.1	79.2	45.3
Median	102.8	36.3	27.3	6.0	82.7	68.7	49.1	52.4	19.2	81.6	47.2
n	4	4	8	7	9	10	6	9	8	11	12
Males											
Mean	108.4	40.4	30.0	6.6	89.7	73.8	52.2	58.7	20.5	91.0	54.9
s.d.	3.7	2.1	0.8	0.3	1.5	1.4	0.8	2.0	0.8	3.0	2.5
Maximum	110.7	42.8	31.1	7.1	91.2	76.2	52.8	60.7	21.6	94.8	58.6
Minimum	104.2	38.5	29.2	6.2	87.6	72.2	51.2	56.0	19.8	86.3	52.3
Median	110.3	40.1	29.7	6.6	90.3	73.7	52.4	58.8	20.3	91.7	54.0
n	3	4	5	5	7	7	4	5	5	8	7

Females	Stp	Kel	Kea	Fem	Tbt	Tmt	Pep	Ant
Mean	52.2	107.3	762	44.5	77.5	43.0	46.0	25.4
s.d.	2.5	2.6	15	1.3	1.9	1.4	2.4	0.8
Maximum	57.7	110.9	771	48.0	81.9	45.4	49.6	27.1
Minimum	48.4	103.1	740	43.7	76.4	41.4	43.6	24.6
Median	52.3	108.5	769	44.7	76.8	42.7	45.6	25.2
n	10	9	5	10	7	7	9	9
Males								
Mean	58.0	121.7	982	47.7	82.7	46.9	47.9	27.4
s.d.	2.4	1.8	80	1.4	1.2	1.0	2.2	1.6
Maximum	60.5	123.4	1090	49.2	84.2	48.4	49.8	29.3
Minimum	54.8	118.7	876	45.9	81.5	45.6	44.7	25.7
Median	57.8	122.1	981	47.5	82.1	46.7	48.8	26.8
n	7	5	5	5	6	6	5	5

Patterns of waterbird diversity in central western Madagascar: where are the priority sites for conservation?

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Abstract

Madagascar still retains extensive wetlands important for fishing, hunting and agriculture. They also support a high proportion of the island's globally threatened endemic birds. However, as a result of widespread modification through human activity, wetlands are under severe pressure across the island, resulting in the decline of many waterbird species. For the effective conservation of waterbirds in Madagascar, it is vital that wetlands supporting important assemblages of species are identified and protected. In this study, we surveyed the wetlands of central western Madagascar (southern Melaky and Menabe Regions) to investigate patterns of waterbird diversity and map priority sites. Thirty-four wetland sites were surveyed in 2004, during which a total of 56 waterbird species were recorded. Waterbird species richness was associated with the size of the water body and presence of rice cultivation. All sites were ranked according to an index of vulnerability, based on the cumulative score of the degree of threat for every wetland bird species found in a site. We show that wetlands in western Madagascar hold important numbers of several globally threatened species; five of the rarest bird species in Madagascar are found here. The 10 highest-ranking wetland sites fall within BirdLife International IBAs, but four wetlands fall outside current or planned protected areas. We recommend that monitoring of wetland sites in western Madagascar is undertaken at regular intervals and that all sites are included in a network of protection that can ensure the survival of wetland bird diversity in the country.

Key words: conservation status, diversity, Madagascar, prioritisation, vulnerability, waterbirds.

Species richness in wetland ecosystems in Madagascar is low for many animal groups such as fish (Reinthal & Stiassny 1991) and birds (Wilmé 1996), but may be relatively high for others (*e.g.* mayflies: Ephemeroptera order; Sartori *et al.* 2000). Freshwater ecosystems on the island, however, host some of the most endangered taxa in the country. Of around 56 endemic freshwater and euryhaline fish occurring in Madagascar (De Rham 1996), 22 (39%) are threatened with extinction (Hilton-Taylor 2000) and 64% of those endemic birds that are considered Critical (CR) or Endangered (EN) by the International Union for Conservation of Nature (IUCN) (BirdLife 2014) are wetland specialists.

Madagascar has extensive wetlands. These areas have long been important to the Malagasy people for fishing, hunting and agriculture. However, in recent decades, resource use has changed, becoming more intensive and less discerning, to a degree that seriously threatens native biodiversity. To date, wetlands including mangrove forest in Madagascar have received little or no protection, and are often in poor condition (Langrand & Wilmé 1993; Langrand & Goodman 1995; Young 1996). The most grave and widespread threats are the conversion of wetland habitat to intensive production of rice *Oryza* sp. or drainage for upland crops (Pidgeon 1996), hunting of birds at nesting and moulting sites (Young 1996) and overfishing. Fishing using fine-mesh nets affects birds and turtles as well as endemic fish. Invasive alien species, especially plants and fish, have also become abundant locally, altering the character and species composition of many wetlands, as well as contributing to extinctions of some endemic fish.

For bird conservation purposes, Malagasy wetlands have been divided into two Endemic Bird Areas (EBAs) (BirdLife International 2014): western and eastern, corresponding to the dry, low-lying western region; and the humid, mountainous east. The West Malagasy Wetlands EBA is a 26,000 km^2 complex of lakes, rivers, marshes, deltas, rocky shorelines and mangroves. It is the unique habitat of six threatened species: one Critically Endangered (Madagascar Fish-eagle *Haliaeetus vociferoides*), four Endangered (Madagascar Heron *Ardea humbloti*, Madagascar Sacred Ibis *Threskiornis bernieri*, Madagascar Teal *Anas bernieri*, Sakalava Rail *Amaurornis olivieri*) and one Vulnerable (VU; Madagascar Plover *Charadrius thoracicus*); these occur alongside four other threatened species that are also found in eastern Madagascar. These wetlands additionally serve as important habitats for migratory waterbird species.

BirdLife International has recognised the importance of the wetlands of central-west Madagascar for birds. Three wetland sites are included in the Important Bird Areas (IBA) network: the Bemamba Wetland Complex, the Manambolomaty Wetland Complex and the Tsiribihina Delta and Upper River (Fishpool & Evans 2001). However, distribution data for birds in western Madagascar are generally not of sufficient quality for effective conservation planning at localised scales. Published information on waterbird distributions for central-west Madagascar (*e.g.* Rand 1926; Langrand 1990; Morris & Hawkins 1998) are highly generalised and often based on patchy observations made by infrequently visiting scientists, tourists and hunters. Reliable data on the distribution of waterbirds in central western Madagascar are crucial to prioritise sites for conservation of these taxa within the region.

Here we present population estimates of birds within the wetland complex along the coastal region in west-central Madagascar based on intensive surveys conducted during 2004. Although these data are from a ten-year old survey the authors believe that they are still relevant. Wetlands were also classified according to a number of environmental variables taken within each site. For all species assemblages we used the measured environmental variables to correlate with species diversity and vulnerability, the latter determined by the conservation status of each species. Finally, we identified those wetland sites supporting the highest waterbird diversity and/or species of conservation concern. Those sites holding > 1% of the total population of a globally threatened species qualify for designation as a wetland of international importance under the Ramsar Convention, to which Madagascar is a signatory (Delany & Scott 2006; Ramsar 2013).

Study area

Large river estuaries and deltas, extensive mangrove forests, and shallow lakes behind coastal dune systems, typify the wetlands found in western Madagascar. These wetlands are largely associated with the Tsiribihina and Manambolo river systems. The study area (Fig. 1), hereafter referred to as the Greater Menabe, extends from the Kirindy Mitea National Park in southern Menabe (*c.* 20°48"37'S, 44°8"32'E) to the Soahany River (except for the Manambolomaty Lakes Complex) in Melaky (*c.* 18°36"07'S, 44°26"31'E). There were three major towns, Morondava, Belo-sur-Tsiribihina and Miandravazao.

The study region covers an area of *c.* 30,000 km^2, encompassing three main lake systems (Bemamba: A3 in Table 1, Fig. 1, Masama: A2 and Antsamaky: C1) to the north of the Soahany River, and numerous small lakes and pools along the large river systems. Seasonal flooding of these large rivers develops a series of shallow flood plain lakes that become cut off from their source as water levels drop during the dry-season. There are also extensive areas of shallow water (tannes) created by the mixing of seawater on occasional high tides with seasonal floodwater on the landside of coastal mangroves. Within these highly seasonal and often hyper-saline tannes, several shallow, marginally more permanent and less saline, lakes have developed (*e.g.* Lac Bedo: C3). Some areas of tanne have been modified for aquacultural purposes (*e.g.* prawn farming at the Aquamen site at Tsangajoly: C2) and for the continual (rather than seasonal) extraction of salt (*e.g.* at the Antsira salt pans north of Morondava: C4). In southern Melaky, near the coast, there are a series of slightly deeper and more permanent lakes. Throughout central western Madagascar numerous, often very small and seasonal pools occur within the baobab and dry forest areas.

Western Madagascar is characterised by marked dry and wet seasons. Rains typically arrive in late December or early January; water levels in rivers and lakes increase

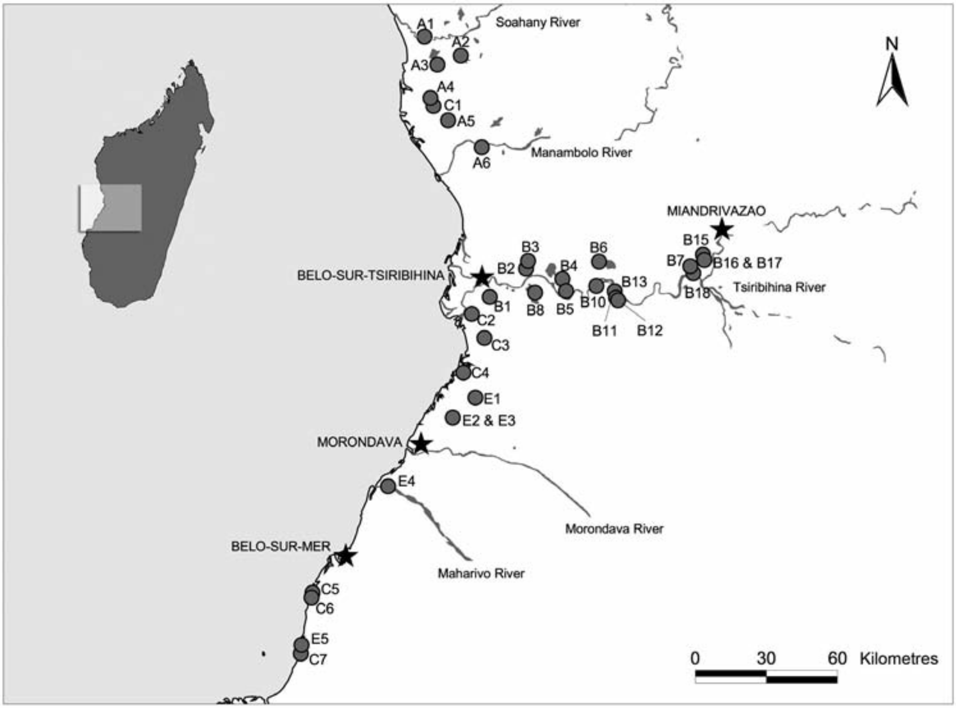

Fig. 1. Wetland sites in central western Madagascar surveyed in 2004. Site codes refer to the sites listed in Table 1.

accordingly. Following cessation of the rains in late March, river and lake levels drop steadily throughout the dry season (April–December) and some wetlands may dry out completely in some years.

Before commencing the ground surveys we first identified all wetlands in central western Madagascar using a 1:100,000 Foiben-Taosarintanin'I Madagasikara (FTM, Antananarivo) map and recent (2000) satellite images (Landsat from FTM). We also relied on the survey team's knowledge of the area as well as discussions with local people (*e.g.* Association Nationale pour la Gestion des Aires Protégées (ANGAP: now Madagascar National Parks), hunters and villagers) to identify sites for surveying. Wetlands entirely converted to rice production were not explored. A total of 34 wetland sites were considered suitable and surveyed in this study (Fig. 1). All surveys were carried out between 23 September and 6 November 2004. This time of year, towards the end of the annual west coast dry season, was chosen as waterbirds are forced to concentrate in the shrinking wetlands and to avoid the difficulty of surveyors moving around the region in the wet season. Overall bird numbers are augmented at this time by the arrival of Palearctic migrants following the Northern Hemisphere breeding season, while locally breeding species will, typically, not breed until after the start of the wet season normally in January.

Methods

Survey methodology

Wetlands were surveyed between 06:00–12:00 h. Waterbirds of 17 families (see definition of waterbirds in Delany & Scott 2006) with one species of Accipitridae (the Madagascar Fish-eagle) were counted from the shoreline or from pirogues on the water using binoculars and telescopes to aid identification. In larger wetlands, the field team split into smaller groups to survey different areas. In Lac Bedo we counted birds over two days: 23 September 2004 (birds in the water *e.g.* wildfowl, flamingos, herons and coots) and 13 October 2004 (shorebirds) due to the large numbers present. Rarer bird species were also counted during both visits.

Birds were identified using two regional field-guides: Sinclair & Langrand (1998) and Morris & Hawkins (1998). All those species considered dependent on the wetland were counted, except Cattle Egret *Bubulcus ibis*. Cattle Egrets regularly roost in wetlands but rarely feed in them, preferring to migrate daily to agricultural land, and so were not counted and were not included in the totals. Similarly the highly vocal Purple Swamphen *Porphyrio porphyrio* is often easy to observe but may become nocturnal in many wetlands, especially if persecuted, and was not counted but is included in species totals and vulnerability index. Presence of rail species (*e.g. Porzana* and *Dryolimnas*) and Painted Snipe *Rostratula benghalensis* was noted but it was impractical to count these species associated with marshland adjacent to the wetlands and they were not included in species totals.

A number of environmental variables were also recorded for each wetland. Salinity (as percentage dissolved sodium chloride (NaCl) in water) was determined with an Eclipse 45–65 Optical Hand Refractometer (range 0–28% dissolved NaCl) (Bellingham & Stanley, Lawrenceville, USA) at each wetland. The pH level of each wetland was measured at up to five points in each wetland using a Hanna Instruments pHep®4 (pH 0.0–4.0) waterproof pH meter (Hanna Instruments, Woonsocket, USA). The overall size of each wetland was estimated during the visit to each site and placed in one of seven size categories (< 5 ha; 5–20 ha; 20–50 ha; 50–100 ha; 100–500 ha; 500–1,000 ha; and >1,000 ha). The mean and maximum depth of water was also estimated by interviewing local fishermen. Seasonality, and whether the wetland dries up in most years, was determined through interview and the percentage of the wetland available to birds at the time of the survey calculated. The location of each wetland was recorded by taking a GPS reading at the water's edge closest to the access point to each site using a Garmin eTrex 12 Channel GPS (Garmin, Olathe, USA). Land ownership of each site was identified through interviews with local inhabitants. Data check-sheets were used by all survey members to standardise recording of data.

Data analysis

For each wetland body, the total number of birds counted and the number of species recorded (*i.e.* species richness) was summed and a Simpson's index of diversity (D) calculated:

$$D = \frac{1}{\sum_{i=1}^{S} P_i^2} \qquad (1)$$

The proportion of individuals (P_i) of species i was determined, relative to the total number of individuals across all species, and the resulting product was squared and summed across all species (S).

We also generated an index of vulnerability, for each wetland body, given by $\sum_{i=1}^{s} V_{ti}/S_t$, where V_{ti} is the vulnerability score of a species occurring in a wetland body. The vulnerability score for each wetland bird species was based on its world range and degree of threat, determined by BirdLife International (2014) for taxa fully endemic to Madagascar and by H.G. Young, R.J. Safford (BirdLife International) and A.F. Hawkins (Conservation International) for sub-species and national populations of widespread species. Each taxon recorded during the survey was given a score of 1–5 (Appendix 1), based on a combined total of scores allocated for the range and the degree of threat. For range, every taxon except endemics scored 1, and endemic taxa (species and sub-species) scored 2. For degree of threat: widespread species under little threat globally scored 0; endemic taxa considered data deficient but not threatened scored 1; widespread species (*e.g.* Yellow-billed Stork *Mycteria ibis* and Crested Coot *Fulica cristata*) not considered threatened globally but where localised population is under obvious threat in Madagascar (Young, Safford & Hawkins, pers. comm.) and is probably only rarely boosted by immigration from outside the island scored 2; vulnerable endemics (IUCN and Madagascar status VU) scored 2; and endangered endemics (IUCN and Madagascar status EN and CR) scored 3. To identify wetland bodies with high diversity that also support vulnerable species, we produced a combined index of diversity and vulnerability. Firstly, the Simpson's index of diversity and index of vulnerability were both standardised by dividing the individual index value for each wetland body by the overall mean for that index. The standardised values for these two indices were then summed to produce a combined index of diversity and vulnerability for each wetland body. To prioritise sites for conservation we ranked all the wetlands according to the index of diversity and vulnerability. We also used figures for minimum overall population size for waterbird species published in Delany & Scott (2006) to evaluate whether any of the wetland bodies contained > 1% of the global population of a particular species and therefore qualified automatically as a wetland of international importance under the terms of the Ramsar Convention.

Species richness, diversity and the combined index of diversity and vulnerability of each wetland body were mapped in a GIS (ArcView 3.3, Esri, California, UK) to investigate any spatial patterns in these variables. We then overlaid maps of the locations of the highest priority sites with boundaries of (current and planned) protected areas to identify any wetlands that fell outside of this network. We also overlaid boundaries of Important Bird Areas (IBAs) to identify any important wetlands excluded from areas already prioritised for the conservation of birds.

Generalized linear models (GLMs) were used to test the principal effects of environmental characteristics of wetlands on waterbird species richness and abundance, measured as the Simpson's index of diversity and the combined index of diversity and vulnerability (the dependent variables). For the count variables (*i.e.* the number of species, indicative of species richness, and the total number of birds recorded) we used a GLM with a Poisson error distribution and a log-link function model. For the Simpson's index and combined index of diversity and vulnerability, when included as dependent variables, we used a GLM with a normal error distribution and an identity log-link function model (Crawley 1993). We considered *a priori* as potential explanatory environmental characteristics the following covariables: salinity, pH level, estimated mean depth (m), easting and northing; and factors: presence of mangroves (1 = present; 0 = absent), presence or absence of rice cultivation (but not covering the whole of the wetland), and categories for the size of the waterbody (1 = < 5 ha; 2 = 5–20 ha; 3 = 20–100 ha; 4 = 100–50 ha; 5 = 500–1,000 ha; and 6 = > 1,000 ha). Salinity and the presence of mangrove were omitted from a second set of analyses because we have relatively few data for these two variables which reduced the dataset substantially. Normality of the residuals of the models and of the covariables was tested using a Kolmogorov-Smirnov test (Fowler & Cohen 1992). Non-normal variables were log transformed prior to analysis (Fowler & Cohen 1992). The SPSS 15.0 software package (IBM, USA) was used for all statistical analyses. Means are given with their standard errors.

Results

Waterbird assemblage of central western Madagascar

Of 69 resident and regular migrating waterbird species in Madagascar 61 are found exclusively or partly in the west of the island (Young 2003) and 58 were recorded during this survey (Appendix 1). Three species known from the region were not recorded during the survey: the elusive Sakalava Rail, the Crested Ibis *Lophotibis cristata*, predominantly a forest bird (Young 2003), and Hammerkop *Scopus umbretta bannermanni*, a waterbird not closely tied with wetlands (Young *et al.* 1993). The Madagascar Harrier *Circus macrosceles,* although not restricted to wetlands, often hunts over reedbeds but was also not recorded during this survey.

Five of the rarest bird species in Madagascar were recorded during the survey. The Madagascar Fish-eagle (IUCN CR) was recorded at eight sites in the north of the region with clusters around the northern lakes and water bodies along the Tsiribihina River. Madagascar Teal (IUCN EN) was found at eight sites distributed throughout the survey region, but in close proximity to the coast. Teal were recorded for the first time at Antsira (Grands Salins du Menabe: C4 in Table 1, Fig. 1) and nesting was confirmed for the first time in Kirindy Mitea National Park (at Lac Andio: C7). Madagascar Heron (IUCN EN) was widely distributed in all wetland types with 100 birds found at 22 sites while only 14 Madagascar Pond Heron *Ardeola idae* (IUCN EN) were seen at 13 sites. However, the latter species was probably returning from Africa during the survey. Madagascar Sacred Ibis (IUCN EN) are predominantly found in northwest Madagascar and only a single site (Lac Ambondrombe: A6) in the north of the survey region held any birds. Small numbers of ibis, however, were observed in coastal mangrove near Belo sur Mer and in the Tsiribihina River delta in central west Madagascar but were not included in this report. Madagascar White-backed Duck *Thalassornis leuconotus insularis* (TWSG EN) was located at three sites with 79 birds (7.9% of the minimum world population; Delany & Scott 2006) at one site: the northern Lac Antsamaky (C01). Madagascar Plover (IUCN VU) was found at eight sites, several new for the species, and breeding confirmed at two.

Our survey data revealed that, overall, the wetlands of central western Madagascar hold important numbers of several globally threatened species, including (based on minimum overall population figures in Delany & Scott 2006) an estimated 10.3% of the world's Madagascar White-backed Ducks, 7.4% of Madagascar Teal, 10% of Madagascar Herons, 12.4% of Madagascar Plover and (based on BirdLife International 2013) 5.6% of Madagascar Fish-eagles. Seven wetlands in the survey region appeared to support > 1% of the global population of one or more globally threatened species and thus fulfil Ramsar Criterion 6 that a wetland should be considered internationally important if it regularly supports 1% of the individuals in a population of one species or subspecies of waterbird. (Ramsar 2013): Lac Bemamba (A3) (Madagascar Heron); Lac Andranolava (Avaratsy; A4) (Madagascar White-backed Duck); Lac Andranolava (Andrakapony; A5) (Madagascar Heron); Lac Antsamaky (C1) (Madagascar Heron, Madagascar White-backed Duck); Lac Bedo (C3) (Madagascar Teal, Madagascar Heron, Madagascar Plover); Lac Ambondro (C5) (Madagascar Plover); Lac Andio (C7) (Madagascar Teal, Madagascar Plover).

Patterns in species richness, diversity and vulnerability

The number of individual waterbirds counted, species richness, Simpson's index of diversity and the combined index of diversity and vulnerability for each wetland is given in Table 1. Three wetlands had distinctively high species richness: the saline lake Lac Bedo (41 species), the forest lake Lac Antsamaky (31) and the floodplain lake of Lac Komanaomby (30), although the latter scored comparatively low on the Simpson's index of diversity. Lac Bedo and Lac Antsamaky also had distinctively high species diversity, with the former being clearly the most species rich and diverse wetland body in the region. Lac Bedo is a highly seasonal lake at the southern end of extensive highly saline tannes, and holds the highest numbers of waterbirds recorded during this survey (3,105 individuals), including six species on the IUCN red list. We estimate (based on counts made during this survey and minimum population figures from Delany & Scott 2006) that Lac Bedo holds 22.1% of Madagascar's African

Spoonbills *Platalea alba* and 10% of the island's Crested Coot, high numbers of both flamingo species (Lesser *Phoeniconaias minor* and Greater *Phoenicopterus roseus* Flamingos), ducks and resident and migrant shorebirds. Lac Antsamaky is estimated to hold 4.3% of African Pygmy Goose *Nettapus auritus*, 2.5% of African Openbills *Anastomus lamelligerus* and 12.6% of African Darters *Anhinga rufa*. Lac Andio, a saline lake, had the second highest index of diversity despite a relatively low number of species (21). It is noteworthy for holding 1.3% of the global population of Madagascar Teal.

Lac Bedo also scored highest on the combined index of diversity and vulnerability, because as well as supporting high diversity the following vulnerable species occur there: Madagascar Teal, Madagascar Pond Heron, Black Egret *Egretta ardesiaca*, Madagascar Heron, Lesser and Greater Flamingos, African Spoonbill, Crested Coot, Madagascar Pratincole *Glareola ocularis* and Madagascar Plover. Of the ten highest ranking wetlands, according to the combined index of diversity and vulnerability, six occurred in a cluster within the Antsalova region in Melaky in the north of the survey area. The three remaining high-ranking wetlands included Lac Andio (C7) in Kirindy Mitea National Park in the south of the survey area and Lacs Sariaka (B2) and Berevo (B10) within the Tsiribihina flood plain. Six of the wetland bodies that potentially support > 1% of the total population of a globally threatened species were also in the ten highest ranking wetlands with only Lac Ambondro being ranked relatively low according to the index of diversity and vulnerability.

All of the ten highest-ranking wetland bodies plus Lac Ambondro fall within areas delineated as IBAs by BirdLife International (BirdLife International 2014), but four wetlands fall outside of current or planned protected areas: Lac Bemamba, Lac Andranolava, Lac Berevo and Lac Andio.

Correlates of species richness, abundance, diversity and vulnerability

Species richness was positively affected by the size of the wetland, northing and water pH; and negatively by the presence of rice cultivation patches (Table 2a). Species abundance was negatively affected by the wetland depth and positively by the size of the wetland (Table 2b). The model for bird diversity showed positive effects of northing and the size of the wetland, as well as negative effects of the presence of rice cultivation patches and water depth (Table 2c). Finally, the combined vulnerability and diversity index was only positively related to northing (Table 2d).

Discussion

Our study is a rapid assessment of the waterbird diversity of central western Madagascar. In order to assess all wetland bodies in the area during a similar time frame, visits had to be undertaken in a single day during the dry season when birds were not dispersed and nesting. While there are biases towards those birds that collect in open water areas and may be more obvious it must also be assumed that drying of well vegetated margins and highly dispersed seasonal wetlands forces waterbirds into those sites with water still present. Migration patterns within Madagascar and between the

Table 1. Waterbird species richness, diversity and vulnerability of wetlands in central western Madagascar. Wetlands are ranked in descending order of the combined index of diversity and vulnerability. Site codes: A = "northern" lakes in southern Melaky; B = Tsiribihina flood plain lakes (river sections were also surveyed, not listed here); C = saline wetlands in both regions; D = mangroves (habitat availability snapshots not included in this study); and E = ponds in both regions.

Code	Wetland name	Description	Species richness	Total number of birds counted	Simpson's index of diversity	Index of vulnerability	Index of diversity and vulnerability
C3	Lac Bedo	Saline lake	41	3,105	10.62	1.88	3.25
C1	Lac Antsamaky	Forested lake	31	1,199	9.08	2.26	3.10
C7	Lac Andio	Saline lake	21	292	9.25	1.81	2.92
B2	Lac Sariaka	Flood plain lake	17	138	7.94	1.88	2.67
A5	Lac Andranolava (Andrakapony)	Lake	23	396	7.84	1.87	2.64
A1	Nosibe (Bemia)	Lake	18	267	7.77	1.83	2.61
A2	Lac Masama	Forested lake	21	382	6.43	2.19	2.49
A3	Lac Bemamba	Lake	25	3,023	5.77	2.28	2.39
B10	Lac Berevo	Flood plain lake	14	77	6.79	1.71	2.33
A4	Lac Andranolava (Avaratsy)	Lake	22	283	5.47	2.18	2.28
B4	Lac Mikoboka	Flood plain lake	18	149	6.75	1.61	2.27
B18	Tsiribihina – Mahajilo	Flood plain lake	10	40	6.30	1.70	2.22
A6	Lac Ambondrombe	Lake	13	245	3.88	2.69	2.18
B16	Lac Begogo	Flood plain lake	8	14	5.76	1.75	2.13

E5	Ambolovoroky Lagoon	Lagoon connected to sea	11	81	6.33	1.45	2.10
B6	Lac Andranomena/Ankalobe	Flood plain lake	9	77	5.51	1.44	1.92
E1	Étang Andranovorinampela (Andranomena Special Reserve)	Forest pond	12	216	3.73	2.08	1.85
B1	Lac Ampamandrika	Flood plain lake	6	72	2.57	2.50	1.80
C5	Lac Ambondro	Saline lake	24	618	3.30	2.08	1.75
B5	Lac Mamotsaky	Flood plain lake	13	77	3.10	2.08	1.71
C6	Lac Sirave	Saline lake	6	525	1.10	2.83	1.64
B13	Lac Soalemy	Flood plain lake	4	8	2.91	2.00	1.63
C2	Aquamen (Tsangajoly)	Commercial prawn farm	8	248	3.37	1.63	1.54
E4	Étang Andranojongy	Small roadside pond	6	30	2.08	2.17	1.53
B15	Lac Maombe	Flood plain lake	9	51	2.63	1.89	1.51
B8	Lac Komanaomby	Flood plain lake	30	1,735	2.84	1.73	1.48
B3	Lac Iboboka	Flood plain lake	15	162	2.39	1.93	1.48
B7	Lac Ankazomanga	Flood plain lake	14	160	2.06	2.00	1.44
E3	Étang Andranovorindremalaza	Small roadside pond	10	111	2.03	1.90	1.38
B17	Lac Ampanihy	Flood plain lake	3	3	3.00	1.33	1.32
C4	Antsira (Grands Salins du Menabe)	Commercial salt pans	17	2,095	1.10	1.53	1.00
B11	Lac Riamena	Flood plain lake	2	15	1.14	1.50	0.99
E2	Étang N of Allee de Baobab	Small roadside pond	1	1	0.00	5.00	0.00
B12	Lac Ampanihy	Flood plain lake	0	0	0.00	0.00	0.00

Table 2. Environmental and geographical variables associated with (a) species richness, (b) species abundance, (c) bird diversity of wetlands, and (d) the combined vulnerability and diversity index. Rice cultivation is the presence of patches of cultivation of this cereal not entirely covering the waterbody. Northing is the latitudinal position of the wetland. The ß parameter (± s.e.) is the coefficient of each independent variable in the model and is related to the direction and magnitude of each effect.

(a) Model for species richness (poisson error distribution with log-link function)

Source of variation	**ß ± s.e.**	**Wald statistic**	**d.f.**	***P***
Size of wetland	0.34 ± 0.07	24.11	1	<0.001
Rice cultivation patches	–0.57 ± 0.12	21.91	1	<0.001
Northing	0.32 ± 0.10	9.84	1	0.002
Water pH	0.19 ± 0.09	5.13	1	0.024

(b) Model for species abundance (poisson error distribution with log-link function)

Source of variation	**ß ± s.e.**	**Wald statistic**	**d.f.**	***P***
Wetland depth	–0.64 ± 0.03	5.56	1	0.018
Size of wetland	0.37 ± 0.05	5.12	1	0.024

(c) Model for bird diversity (normal error distribution and an identity log-link function)

Source of variation	**ß ± s.e.**	**Wald statistic**	**d.f.**	***P***
Northing	1.82 ± 0.43	17.57	1	<0.001
Rice cultivation patches	–1.54 ± 0.53	8.57	1	0.003
Size of wetland	0.55 ± 0.23	5.55	1	0.018
Water deep	–1.27 ± 0.55	5.36	1	0.021

(d) Model for combined vulnerability and diversity index (Normal)

Source of variation	**ß ± s.e.**	**Wald statistic**	**d.f.**	***P***
Northing	0.45 ± 0.05	4.65	1	0.031

island and mainland regions are unclear with only a small number of breeding species known to leave the area after breeding. Many waterbirds in Madagascar are the subject of often indiscriminate subsistence hunting, particularly when nesting. During the survey the majority of the sites visited received no official protection. In 2004 only those wetlands within the Kirindy Mitea National Park had any protected status. The combination of avoiding persecution and access to a larger area for dispersal during the wet season allied to impracticalities of travelling and surveying during the wet season makes the dry season the ideal time to undertake a waterbird survey. However, this is the first time a systematic field survey of waterbirds of the central western Madagascar's wetlands has been conducted and therefore is valuable even though it represents a snapshot.

The greatest numbers of wetland bird species were found in three wetlands (Lac Bedo, Lac Antsamaky, Lac Komanaomby). The results of our wetland bird surveys in the Greater Menabe confirm that the area is of significance in terms of species richness as well as high conservation value taxa. Priority species, especially Madagascar Teal, are well represented and the protection of several key sites in this region would increase the survival chances of several endangered birds. The distribution of waterbirds recorded during this survey shows that the 1) 'Northern Lakes' (A1–A6 and C1) are priority sites, 2) the Tsiribihina flood plain lakes (B1–B8, B10–B13, B15–B18) are heavily exploited and on the whole, at least in the dry-season, do not represent important wetlands for priority species. Moreover, effective legislation to protect birds and their habitats should be sought for nine priority sites: Lac Masama (A2); Lac Bemamba (A3); Lac Andranolava (A4, A5); Lac Antsamaky (C1); Tsiribihina Delta (D1); Lac Komanaomby (B8); Lac Bedo (C3); Antsira (Grands Salins du Menabe) (C4); Lacs of Kirindy Mitea National Park (C5, C6 and C7). Furthermore, the étangs at Andranovorinampela (E1) and Andranovorindremalaza (E3) require special and urgent protection.

Waterbird species richness was associated with lake size, the wetland latitudinal position, the water pH as well as an absence of rice cultivation. The model suggested that higher numbers of species were found in larger water bodies, closer to higher latitudes or with hard water rather than acid. However, richness declined in the presence of rice cultivation. These results are within what we can expect for the species richness trends: a positive latitudinal effect, i.e. more richness near the tropics; in bigger wetlands (Sebastián-González & Green 2014) or a negative impact of water acidification or human rice exploitation. In the case of bird diversity the only new covariable in the model is water depth, again a well-known environmental factor affecting diversity trends (Sebastián-González & Green 2014).

The majority of the lakes surveyed are quite shallow, at least around the margins, and are ideal for rice cultivation. The presence of rice at a wetland is often a clear indication of high levels of human habitation and exploitation. Human disturbance is also associated with the introduction of invasive exotic fish such as cichlids (*Oreochromis* sp. and *Tilapia rendalli*) and Asian Snakehead *Channa maculata;* species which have had immense negative impacts on wetland biodiversity and waterbirds throughout Madagascar (Young 1996; Young & Kear 2006). Furthermore, all diving waterbirds are vulnerable to bycatch during fishing practices, particularly because of the extensive use of nylon monofilament nets. Madagascar White-backed Duck, grebes, coots, cormorants and darters are vulnerable to incidental capture in nets. These birds were rare in our study and missing from wetlands with people. Rice cultivation also reduces suitable foraging area for many bird species and may bring some species, notably ducks, into direct conflict with farmers.

Without persecution some waterbirds will continue to thrive in even highly exploited wetlands. The larger herons and Madagascar Fish-eagle appear to be very tolerant of humans if they are not hunted or otherwise persecuted. Full and adequately implemented protective measures including protection of all nest sites would potentially allow these birds to thrive outside protected areas.

We recommend that the Greater Menabe sites are surveyed on a regular basis with counts of birds made during the wet-season and that a programme of at least half yearly repeatable visits is prepared. Methodology of all wetland visits should remain the same as that employed in the first survey. However, other sites, including those apparently of little value to waterbirds, should also be visited periodically if possible. Directors and personnel at Aquamen and Grands Salins du Menabe should be involved in conservation planning and encouraged to maintain "bird friendly" conditions (and eco-tourism) within their establishments. Lac Bedo was recommended for Ramsar on the basis of this survey and was designated in 2007.

All priority birds should be monitored closely and research conducted to establish movements through further ringing and satellite tracking. Habitat limitations for each species should also be established. A village-based education programme should be further established to encourage local support and protection for habitat and waterbirds. Lobbying for site and bird protection must be increased until a network of reserves is established and species are given adequate protection. In addition to measures established to protect priority species, a better understanding of other species (notably cormorants, darters, herons, pygmy-geese, coot, jacanas, spoonbills and storks) be developed and protection for these birds established. It is further recommended that a local red-list style publication be produced for all waterbirds in Madagascar, including non-endemic species.

Acknowledgements

We would firstly like to thank the other members of the field team: Juliette Velosoa, Aimée Céleste Rahelivololona, Randriamahita ("Mahita"), Bruno Razanadraibe (our driver), Jonah Ratsimbazafy and William Francisco Rakotombololona ("Coco"). Hanasy Fanhler of ANGAP joined us during our time in the Kirindy Mitea National Park. This work would not have been possible without the support of Durrell Wildlife Conservation Trust and in particular Joanna

Durbin. We are grateful to Venty Odile of ANGAP for permission to visit Étang Andranovorinampela, to Didier Chauty and Barnabe Botokeky for our visit to Aquamen at Tsangajoly and to Daniel Droussin for access to the Grands Salins du Menabe site at Antsira. Herizo Andrianandrasana and Tim Wright (Durrell) and Mark Balman (BirdLife International) helped with the production of the maps. Thanks are also due to Andy Green, Frank Hawkins, David Jeggo, Roger Safford and Sarah Seymour. Jesus Duarte gave useful advice on statistical procedures.

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Photograph: Lake Ambondro with flamingos and Madagascar Teal, by Glyn Young.

Appendix 1. Biogeographical range, global and national conservation status and estimated population size in Madagascar of waterbird species recorded during the survey of central western Madagascar. For each species, the vulnerability score, total number of individuals and maximum count is also given along with the number of sites at which the species was recorded. Note Madagascar populations of some widespread and/or migratory species have not been estimated.

Species	Range[1]	IUCN status[2]	Madagascar status if different to IUCN[3]	Estimated population in Madagascar[4]	Vulnerability score	Sum of counts	Max count	No. of sites
Haliaeetus vociferoides	1	CR		240–360†	5	13	2	8
Anas bernieri	1	EN		1,500–2,500	5	74	17	8
Ardeola idae	1**	EN		2,000–6,000	5	14	2	13
Ardea humbloti	1	EN		1,000–3,000	5	100	17	22
Threskiornis bernieri	1	EN		1,200–2,500	5	7	7	1
Charadrius thoracicus	1	VU		750–3,100	5	93	23	8
Thalassornis leuconotus	2,8	LC	EN***	1,000–2,000	5	103	79	3
Phalacrocorax africanus	2,8	LC	EN	500–2,500	5	66	63	3
Anhinga rufa	2,8	LC	EN	500–1,500	5	32	7	6
Tachybaptus pelzelnii	1	VU		5,000	4	30	29	2
Glareola occularis	1**	VU		5,000–10,000	4	14	5	4
Anastomus lamelligerus	2,8	LC	EN	<1,000	4	52	25	5
Phoenicopterus minor	3	NT	EN		3	603	350	3
Egretta ardesiaca	2	LC	VU	–	3	809	400	12
Mycteria ibis	2	LC	EN	<1,000	3	3	3	1
Ardea alba	2	LC	EN	1,000–5,000	3	261	221	3
Phoenicopterus roseus	3	LC	EN		3	311	229	3
Fulica cristata	4	LC	VU	2,000–6,000	3	207	200	2
Actophilornis albinucha	1	NT		<10,000	3	74	21	5

Appendix 1 (*continued*).

Species	Range[1]	IUCN status[2]	Madagascar status if different to IUCN[3]	Estimated population in Madagascar[4]	Vulnerability score	Sum of counts	Max count	No. of sites
Sarkidiornis melanotos	3	LC		10,000–25,000	2	330	66	18
Nettapus auritus	2	LC		5,000–10,000	2	565	215	7
Ixobrychus minutus	4,8 + 7	LC	DD	3,000–15,000	2	3	2	2
Egretta dimorpha (white)	1	LC		6,000–20,000	2	320	100	22
Egretta dimorpha (blue)	1	LC	DD	Included in above	2	25	10	6
Ardea purpurea	4,8	LC	VU	5,000–10,000	2	70	24	17
Ardea cinerea	4,8	LC	VU	5,000	2	120	21	20
Dendrocygna bicolor	5	LC		10,000–20,000	1	2,163	1,000	6
Dendrocygna viduata	5	LC		20,000–50,000	1	1,687	470	24
Anas erythrorhyncha	2	LC		15,000–25,000	1	470	223	10
Anas hottentota	2	LC		5,000–10,000	1	503	173	15
Tachybaptus ruficollis	4	LC		–	1	105	76	6
Nycticorax nycticorax	6	LC		–	1	51	39	7
Ardeola ralloides	4	LC		–	1	430	160	20
Butorides striatus	5,8	LC		<10,000–25,000	1	105	27	22
Area alba	6	LC		–	1	460	83	26
Plegadis falcinellus	6	LC		<5,000	1	943	801	6
*Dryolimnas cuvieri**	1	LC			1	–	–	–
Porzana pusilla	4,8	LC			1	1	1	1
*Porphyrio porphyrio**	4	LC	VU		1	25	18	5

Porphyrio alleni	2	LC	VU		1	30	26	2
Gallinula chloropus	6,8	LC			1	375	245	14
*Rostratula benghalensis**	3	LC			1			
Himantopus himantopus	6	LC		5,000–10,000	1	280	56	18
Charadrius hiaticula	7	LC			1	6	5	2
Charadrius pecuarius	2	LC			1	38	13	7
Charadrius tricollaris	2,8	LC		10,000–30,000	1	52	12	9
Charadrius marginatus	2,8	LC		5,000–15,000	1	76	24	9
Charadrius leschenaultii	7	LC			1	1	1	1
Pluvialis squatarola	7	LC			1	9	5	2
Numenius phaeopus	7	LC			1	8	5	2
Tringa nebularia	7	LC			1	146	25	18
Actitis hypoleucos	7	LC			1	60	6	14
Arenaria interpres	7	LC			1	27	25	2
Calidris minuta	7	LC			1	2	2	1
Calidris ferruginea	7	LC			1	3,170	2,000	8
Larus cirrocephalus	3	LC	VU		1	2	2	1

Notes: [1]Ranges: 1 = Endemic; 2 = Afrotropical; 3 = Predominantly Afrotropical but also occurs elsewhere; 4 = Old World; 5 = Predominantly Afrotropical, Oriental and Neotropical; 6 = Worldwide; 7 = Palearctic migrant; 8 = Endemic sub-species. [2]IUCN status: from BirdLife 2014. [3]Madagascar status: H.G. Young, R. Safford & F. Hawkins *in litt.* 2006. [4]Madagascar population estimate: from Delany & Scott 2006; those species left blank have no regional estimate; † *Haliaeetus vociferoides* population estimate comes from BirdLife International 2014.

* = species were recorded during the survey, but their secretive and/or nocturnal behaviour prevented adequate counts; ** = endemic species that migrate to the Afrotropics; *** = *T. leuconotus insularis* is considered EN by the IUCN Threatened Waterfowl Specialist Group (TWSG 2006).

Editor's note: The Madagascan population of *Charadrius tricollaris* was recently listed as a separate endemic species *C. bifrontatus* (IUCN status LC; del Hoyo *et al.* 2014)

Movements and survival of Lesser Snow Geese *Chen caerulescens caerulescens* wintering in two habitats along the Gulf Coast, Louisiana

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Abstract

Lesser Snow Geese *Chen caerulescens caerulescens* (hereafter Snow Geese) use two wintering habitats in southwest Louisiana. Snow Geese in coastal marshes generally have larger bodies and proportionally thicker bills, longer skulls and longer culmen lengths than do those in adjacent rice-prairies. An important question is whether or not these morphs are sub-populations that segregate during winter. Using a mark-resightings analysis of observations of neck-collared birds, annual apparent survival (Φ) and movement probabilities (Ψ) of Snow Geese were compared between habitats during winters 2001/02–2003/04. The analysis tested the hypothesis of Alisauskas (1998), based on his data collected in winter 1983/84, that larger bill size would increase Φ and decrease Ψ in coastal marshes. Specific predictions were that: 1) larger-billed Snow Geese would be relatively more likely to move from rice-prairies to coastal marshes, or have higher Φ within coastal marshes; and 2) smaller-billed Snow Geese would be relatively more likely to move from coastal marshes to rice-prairies, or have lower Φ within coastal marshes. Estimated annual Φ (± s.e.) was 0.601 ± 0.082, independent of both habitat and time interval. A body size covariate, used to index the morphs, did not improve model fit, indicating that Φ was unrelated to body size after accounting for habitat effects. Estimates of Ψ differed widely between intervals (November–December inclusive, *versus* the rest of the year) and habitats; they averaged 0.18 (range: 0.00–0.56) for birds moving from rice-prairies to coastal marshes and 0.57 (0.00–0.98) on moving from coastal marshes to rice-prairies. Movements of marked individuals were frequent from marshes to rice-prairies, and Ψ was independent of body size. However, movement probabilities were dependent on time intervals and we interpret such interval-specific movement probabilities as responses to shifts in environmental conditions. Thus, the two groups differ in morphology and generally remain segregated except that they mix during intervals of high movements, which occur every 1–3 years.

Key words: ecological segregation, geese, habitat selection, Louisiana, morphology, phenotype.

The total estimated population of Lesser Snow Goose *Chen caerulescens caerulescens* (hereafter Snow Goose) increased from approximately 1 million adult birds in 1970 to 13–15 million in 2000–2005 (Alisauskas *et al.* 2011). The population increase caused high grazing pressure that had negative ecological consequences for plants and other herbivores on Arctic breeding areas of Snow Geese (Samelius & Alisauskas 2009). Thus, a special hunting season (officially termed the special conservation order) was implemented in 1998 in an attempt to counteract this population increase (Alisauskas *et al.* 2011). Once the conservation order was in place, local concerns were raised for the declining numbers of Snow Geese using coastal marshes in southwest Louisiana and whether those birds would be negatively affected by the conservation order (Wilson 2002).

Historically, Snow Geese wintered in coastal marshes along the Gulf of Mexico coast; however, they began using rice-prairies within the last 80 years (Bateman *et al.* 1988). An important question is whether or not Snow Geese in coastal marsh habitats comprised a segregated sub-population, perhaps requiring population-specific habitat management actions (Wilson 2002). Specific threats for Snow Geese in coastal marshes include continued coastal erosion, increased disturbance and habitat alteration from oil exploration and extraction activities, droughts, salt water intrusion following hurricanes (such as Rita in 2005 and Ike in 2008), or other natural or human-related disasters which potentially will affect habitat use and availability for Snow Geese in the future (Jónsson & Afton 2006).

Variation in bill size and shape can result in adaptations to changes in food availability that eventually lead to divergent selection towards morphs that are specialised for different food types (Smith 1990; Grant & Grant 2002; Scott *et al.* 2003). Intraspecific bill size variation commonly is associated with differences in habitat use in geese (Larsson & Forslund 1991, Alisauskas 1998, Williams *et al.* 2008). Snow Geese collected from marsh habitats have larger bodies and proportionally thicker bills, longer skulls and longer culmen lengths than do those collected from adjacent rice-prairie habitats (Alisauskas 1998; Jónsson 2005).

Individual geese with larger bills attain larger bite sizes (Durant *et al.* 2003; Cope *et al.* 2005; van der Graaf *et al.* 2006). Morphometric differences correspond to differing foraging behaviours: Snow Geese in coastal marshes forage primarily by grubbing for below-ground vegetation, whereas those in rice-prairies mostly graze on agricultural plants and consume above-ground vegetation (Alisauskas *et al.* 1988; Alisauskas 1998). Snow Geese from these habitats differ markedly in time budgets and food intake rates (Jónsson & Afton 2006), indicating that different feeding adaptations may be beneficial within each habitat as suggested by Alisauskas (1998). These combined differences in morphology and foraging behaviour may be explained by ecological segregation by two separate morphs (Phenotypic Selection Hypothesis; Alisauskas 1998) or individual differences in habitat selection based on bill size and associated foraging efficiency (Habitat Selection Hypothesis; Alisauskas 1998).

Alisauskas' (1998) hypothesis of two separate morphs is consistent with the idea that Snow Geese in coastal marshes are a segregated sub-population (see Wilson 2002). Mark-resighting methodology was used to estimate annual apparent survival of Snow Geese and probabilities of movement between habitats, to inform waterfowl managers regarding the possible need for sub-population specific habitat management. Sub-populations were defined in the classical sense; *i.e.* as a group of conspecific individuals that is demographically, genetically or spatially separated from other groups of individuals. It was assumed that if the two groups were demonstrated to be spatially separated, such results would support a conclusion that the two groups of Snow Geese constituted sub-populations that segregate during winter. Pair bonds are formed on the wintering grounds in Snow Geese (Ganter *et al.* 2005); thus, winter pairing provides opportunities for genetic differentiation between winter habitats.

The main objective was to refute a working hypothesis of limited exchange of individual Snow Geese between habitats during winter. Movement probability (Ψ), estimated after model selection based on banding data, was used to determine whether or not Snow Geese moved between habitats and, if so, with what movement probabilities. The analysis also tested the hypothesis of Alisauskas (1998) that larger bill size would increase annual apparent survival (Φ) in coastal marshes because of a larger bite size, essential to successfully excavate marsh plants. Specific predictions were as follows: 1) larger-billed Snow Geese would be more likely to move from rice-prairies to coastal marshes, or have higher Φ within coastal marshes, than smaller-billed Snow Geese; and 2) smaller-billed Snow Geese would be more likely to move from coastal marshes to rice-prairies, or have lower Φ within coastal marshes, than larger-billed Snow Geese.

Methods

Study area

The study area comprised a 10,764 km^2 area in southwest Louisiana, where the Intracoastal Canal separates coastal marshes and rice-prairies (Fig. 1). Coastal marshes are comprised of fresh, intermediate, brackish and saline wetlands; however, fresh and intermediate marshes are not used regularly by Snow Geese (Bateman *et al.* 1988). Brackish marshes are separated from rice-prairies by a 30 km wide area of fresh and intermediate marshes (Bateman *et al.* 1988). The study area was described in detail by Alisauskas *et al.* (1988) and Bateman *et al.* (1988).

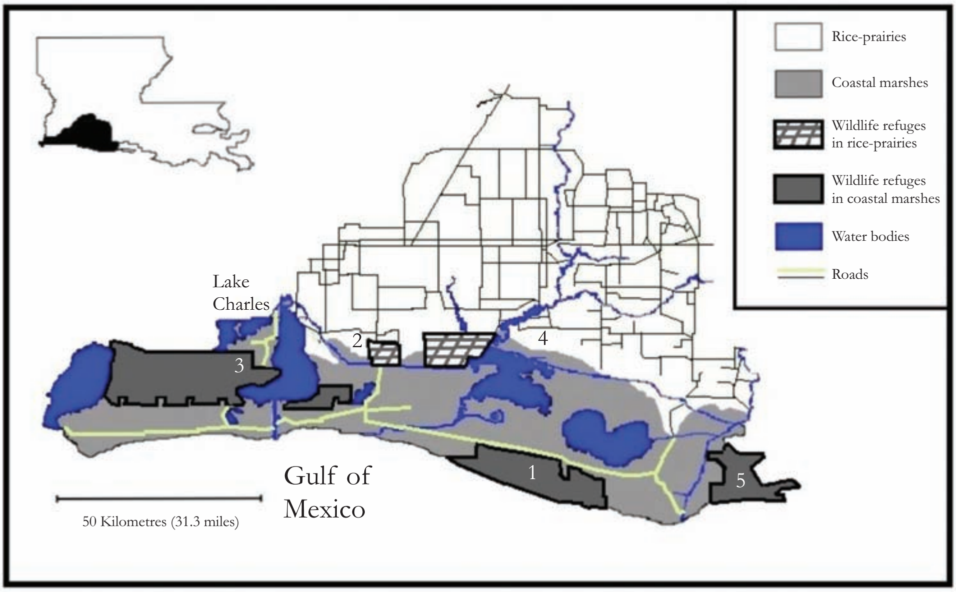

Figure 1. Map of the study area in southwest Louisiana during winters 2001/02, 2002/03, and 2003/04. Snow Geese were captured and marked at 1: Rockefeller State Wildlife Refuge; 2: Cameron Prairie National Wildlife Refuge (NWR); 3: Sabine NWR; and 4: Oak Island (private ownership). Also shown is 5: State Wildlife Refuge.

Estimated numbers of Snow Geese using the study area during the mid-winter waterfowl survey (conducted during the first week of January) were 278,833, 263,737 and 363,420 during winters 2001/02, 2002/03 and 2003/04, respectively (Fronczak 2004). Annual waterfowl surveys, conducted concurrently with our study (in winters 2001/02–2003/04), indicated that 65–70% of all Snow Geese were found in the rice-prairies and 60–77% of all Snow Geese in coastal marshes were sighted at State Wildlife Refuge and/or Marsh Island State Wildlife Refuge (SWR) (Fronczak 2004). Snow Geese arrived in mid-November and began to migrate north in late January – early February (Jónsson 2005). Snow Geese in rice-prairies formed mixed flocks with Ross's Geese *Chen rossii*, but Ross's Geese rarely are observed in coastal marshes (Alisauskas 1998; Jónsson & Afton 2006, 2008, 2009).

Capture and sighting effort

Snow Geese were captured using rocket nets on grit sites (patches of sand and gravel, created for gizzard-grit consumption by waterfowl), which they visit daily to ingest grit to grind their food (Harris 1990; Amat & Varo 2008). Grit sites were located at Cameron Prairie National Wildlife Refuge (NWR) and Oak Island within rice-prairies, and at Sabine NWR and Rockefeller SWR in coastal marshes (Fig. 1). Snow Geese were captured and marked under the following permits: banding permit 08810 from the U.S. Geological Survey-Bird Banding Lab; U.S. Fish and Wildlife Service special use permits 43612-03004 (Cameron Prairie NWR) and 43640-02028 (Sabine NWR); and the Louisiana State University Agricultural Center Institutional Animal Care and Use Committee (LSU AgCenter IACUC) permit number A01-09.

Snow Geese were caught and marked at all locations in all three winters but capture efforts in coastal marshes were more restricted in time than those in rice-prairies, especially in the first winter 2001/02. Snow Geese were catchable in rice-prairies from 20 November to 10 February, whereas this period was 17 December to 20 January in coastal marshes. Marking events were subsequently treated as the first sighting in each sighting history. Marking efforts began in November 2001 and ended in January 2004. In the rice-prairies, Snow Geese were generally marked at Cameron Prairie NWR in November or December 2001–2003. Oak Ridge was added as a rice-prairie marking site in the second winter, and was used on three occasions (2 February 2003, 6 December 2003 and 15 December 2003). In the coastal marshes, Snow Geese were marked in December or January. Observation efforts began 10 November and lasted until 10 February (give or take 2–5 days) each winter.

Captured Snow Geese were individually marked with black neck-collars that had white, three-digit alpha numeric codes and aged by plumage colour (Mowbray *et al.* 2000). We assumed that the sample of Snow Geese was unbiased with respect to body condition (*cf.* Weatherhead & Ankney 1984) because Snow Geese were caught at sites they used regularly and bait or foods were not added to grit sites. Moreover, an experimental study on Greater Snow Geese *C. caerulescens atlanticus* found no evidence of condition-bias for those captured using bait (Morez *et al.* 2000). A subsample of captured adults was measured with callipers (± 0.1 mm): total tarsus, head length, bill nares, bill thickness, culmen length, gape length, skull width, skull height and wing length (see Dzubin & Cooch 1992; Alisauskas 1998). Hereafter, marked Snow Geese in the study are referred to as "marsh Snow Geese" and "rice Snow Geese", according to their capture sites; however, the use of these terms is not meant to imply two separate morphs or sub-populations.

Observers used spotting scopes (20–60×) and recorded locations of sightings with aide of GPS units. In winter 2001/02, one observer scanned goose flocks for neck-bands four days each week with an additional observer for two of those days. In winters 2002/03 and 2003/04, two observers scanned goose flocks for neck-bands for four days each week with an additional observer for two of those days. Goose flocks generally were too dense to quickly infer social or family status of individuals during scans for neck-collars, although pair status was obvious if both members were neck-collared. Occasional collar-readings were recorded during separate time-budget observations for another study (Jónsson & Afton 2006, 2008, 2009).

Observers scanned goose flocks less frequently in coastal marshes than in rice-prairies because of logistical constraints and lower numbers of geese in the former habitat during 2001–2004 (Jónsson 2005; see also Prevett & MacInnes 1980). Road access was good in the rice-prairies (Fig. 1), whereas vast areas of coastal marshes are accessible only by airboat or aircraft, which flush geese on approach. These logistical constraints meant that marked geese were observed more frequently in the rice-prairies. Thus, we included a habitat effect on resighting probability (p) in all models in subsequent mark-resighting analyses. Hereafter, rice-prairies and coastal marshes are collectively termed *habitats* (equivalently termed landscapes; Alisauskas 1998) and their "site" effect in the models (Lebreton *et al.* 2002) is termed *habitat effect*.

Mark-resighting analysis

Multi-state models for live recaptures (hereafter sightings) were implemented in Program MARK (White & Burnham 1999; White *et al.* 2006; Cooch & White 2010) to estimate probabilities of Snow Geese surviving and moving between two habitats, *i.e.* rice-prairies and marshes. Observation histories were collated for Snow Geese caught and released in either rice-prairies or coastal marshes (Jónsson 2005). Model parameters were defined as follows (Lebreton *et al.* 2002):

Annual apparent survival ($\Phi_{t,j}$) = the probability that a bird survives from i to i + 1 and remains within the overall study area, given that it was in habitat j at occasion i;

Movement probability ($\Psi^{j \rightarrow k}_{t,j}$) = the probability of being in habitat k at occasion $i + 1$, given that the bird was alive and in the overall study area at occasion $i + 1$ and in habitat j at occasion i;

and

Sighting probability ($\mathbf{p}_{i,j}$) = the probability that a bird alive in habitat j during occasion i is sighted during that occasion.

As is general for restricted-area capture-mark-resighting studies based on live encounters only, the estimates of survival ignore potential permanent emigration from the study area and therefore were likely biased low. Although we tested for movements between two habitats, our birds could still be alive but move out of our study area that covered both habitats.

This modelling approach is well suited for our dataset, which is limited to six occasions (the periods when birds are sighted) and five intervals with the main objective to evaluate movements between two habitats. The study spanned three winters (2001/02, 2002/03, and 2003/04) and each winter was divided into two occasions: 1) early winter, from 1 November–31 December; and 2) late winter, from 1 January–28 February. We split each winter into two occasions because: 1) Snow Geese arrived from mid-November through December and began to leave in mid-January through February (Jónsson 2005); and 2) the analysis needed to allow for movements within winter because if Snow Geese in the two habitats were one population, we assumed they would use both habitats within each winter. During field observations, occasions within each of the three winters were defined as: 1) early winter, from 1 November–31 December; and 2) late winter, from

1 January–28 February. The survival intervals thus lasted respectively 2 months (1 November–31 December) and 10 months (1 January to 1 November). The estimates of **Φ** were scaled to the estimated annual apparent survival (by adjusting interval length values so they added up to 1.0, *i.e.* 0.167 (2 months) and 0.833 (10 months)), whereas **Ψ** measured the probability of moving from one habitat to the other between successive occasions and **p** measured the probability of encounter on each occasion.

Minimising possible violations of independence

When individuals were sighted more than once (range = 2–4 times) for a given occasion (within early or late winter), we coded it as one sighting event. With three exceptions, all such multiple sightings occurred within the same habitat; habitats were assigned to the three exceptions using random numbers, with even numbers being assigned to rice-prairies and odd numbers to coastal marshes.

The analyses were restricted to adults because: 1) only 28 sightings were obtained of juveniles (141 were banded, Jónsson 2005); and 2) juveniles do not behave independently of their parents (Lebreton *et al.* 2002). Including both members of a marked pair would cause their respective observation history to be over-represented by the frequency of one (Schmutz *et al.* 1995), and paired birds where both individuals were marked comprised 8.5% (25 pairs in total) of resighted neck-collared Snow Geese (see Jónsson & Afton 2008 for frequencies of pairs and families in this population). Thus, one observation history representing one member of each pair from the distribution of observation histories was removed by: 1) assigning random numbers from a set of 100 numbers to each pair; 2) then deleting male data from pairs with odd random numbers; and 3) deleting female data from pairs with even random numbers.

Sex effects frequently are analysed in mark-recapture studies of birds; however, our preliminary analyses indicated that models with sex effects performed poorly (see Jónsson 2005). Thus, we pooled the sexes in the analysis.

Two rounds of model selection

Currently, we are not aware of methods for directly testing for population segregation using mark-resightings data. We therefore followed conventional model selection (Cooch & White 2010), where effects of site (habitat) and time, and their interaction were included and evaluated. Our research question focused on whether Snow Geese moved between rice-prairies and coastal marshes, *i.e.* the value of **Ψ** that would eventually be estimated by the final model determined by AIC model selection. Assuming no interval variation in **Ψ**, no movements detected between habitats (**Ψ** = 0) could be inferred, as there were two, segregated sub-populations, despite there being insufficient time for the evolution of genetic differentiation. Conversely, under the same assumption of no interval variation, if movements (**Ψ** notably higher than 0) were detected, we could conclude that marked Snow Geese comprised one population. However, the situation may not represent such polar opposites if there is substantial variation in movement probabilities between intervals. In fact, a finding of substantial interval variation would indicate a more dynamic situation than that predicted by either liberal habitat selection or strict population segregation.

To obtain estimates of **Ψ**, we selected the best model using conventional multi-state model selection in MARK (Cooch & White 2010). The model selection process determined only the most parsimonious models on the basis of the data available, however, and estimated whether parameters differed or were similar between intervals. We tested for habitat effects on **Φ**, but for **Ψ** and **p** we kept habitat effects in all models due to design considerations. For example: 1) removing habitat from **p** would have ignored obvious differences in sighting probabilities between habitats; and 2) there is no real biological reason to expect **Ψ** to be the same for each habitat, especially since Snow Geese arrive later at the coastal marshes (December) than at the rice-prairies (November; Jónsson 2005). A previous study reported that marsh Snow Geese were larger but also displayed less variation in body size measurements than rice-prairie Snow Geese, indicating more restrictive selection on bill size in marshes than in rice-prairies (Alisauskas 1998). This knowledge, which is confirmed by the data (Jónsson 2005), further contributed to the view that models without a habitat effect on **Ψ** made no biological sense.

We had *a priori* reasons to expect stronger habitat effects on **Ψ** in marshes, which was accounted for by comparing interactive (h*t) models to additive (h + t) models, with t being the time interval in each case. For **Ψ**, interactions might be expected where the parameters could be positively related to conditions in the marsh, but not the rice-prairies. This led to the inclusion of additive models, *i.e.* comparing h + t *versus* h*t for **Ψ**. The additive models (habitat + interval) tested if habitat differences in **Ψ** were constant over all the 5 intervals, whereas the interactive models (habitat*interval) allowed habitat differences in **Ψ** to differ among the 5 intervals.

Two multi-state analyses were conducted. Firstly, **Φ** and **Ψ** were estimated for all observation histories (hereafter full dataset analysis). A second analysis was restricted to the subsample of 388 adults for which morphometrics data were available, to examine whether body size, an index of the morphs based on principal components analysis (following Alisauskas 1998), was related to **Φ** or **Ψ** (hereafter covariate analysis).

Model selection one: full dataset

Given that we pooled the sexes, the most general model (hereafter global model) was **Φ**(habitat*interval) **p**(habitat*interval) **Ψ**(habitat*interval), with 30 structural parameters. In this global model, effects of habitat and the time interval were interactive, *i.e.* effects of one variable were dependent on the level of the other for all three parameters. This model had 28 estimable parameters of 30 possible parameters, which was expected given that one combination of the final **Φ**, **p** and **Ψ** was unidentifiable for each site. Model selection began with the global model and created the subsequent models considered by removing the time effect from one, two or all parameters: **Φ**, **p** or **Ψ**. The relevant models were then added without habitat effect (**Φ**. models) on annual apparent survival. Finally, additive models (main effects models) were considered, *i.e.* the habitat + interval (main effects) models that corresponded to the habitat*time models (interactive models) for **Ψ** because of the biological interest in movements between habitats. Thus, 17 models in total were considered in the analysis of the full dataset.

U-Care (Pradel *et al.* 2003) was used to examine models for structural integrity (goodness-of-fit, hereafter GOF). U-Care was also used to calculate $\hat{c}$ to adjust model selection for overdispersion. When needed, Quasi-likelihood adjusted Akaike's Information Criterion (QAIC$_c$) was used to rank models according to QAIC$_c$ differences between models (ΔQAIC$_c$; Burnham & Anderson 2002); otherwise, we present AIC$_c$.

Model selection two: covariate analysis

As observed in 1983 and 1984 by Alisauskas (1998), marsh Snow Geese in our study (from winters 2001/02–2003/04), had proportionally thicker bills and wider skulls than did rice Snow Geese (see Jónsson 2005), which may affect their habitat selection, movement probability and survival rates. The effects of body size therefore were evaluated by their inclusion as a covariate in the mark-resighting analyses. Prior to the covariate analysis, morphometrics were chosen by comparing the morphology of rice and marsh Snow Geese using principal components analysis (PCA; body size measures assessed are listed in Appendix 1). The highest ranked model from the full dataset analysis was used as starting models in the covariate analysis (see results). Based on the findings of Alisauskas (1998), we expected *a priori* that the first principal score (PC1), which has similar loadings for all variables and thus represents overall body size, would represent the bulk of the variation in morphometrics (≥ 50%) and this proved to be the case (Appendix 1). PC1 therefore was added to the highest-ranked model from the first analysis to examine if overall body size affected **Φ**, **Ψ**, or both. Other PC scores each represented < 10% of the overall variation, and thus, are not included here. The covariate analysis had an effective sample size of 525, whereas the analysis of the full dataset had an effective sample size of 1,190. Basically, if parameters **Φ** or **Ψ** were influenced by body size, the respective covariate model(s) would: 1) have lower AIC values than the model used as a starting point in the covariate analysis; 2) contain a significant relationship between PC1 and individual **Ψ** or **Φ**, with a slope (β) significantly different from zero.

If larger bill size or body size improved survival within coastal marshes or rice-prairies, models which included them as covariates on annual apparent survival would represent improvements over models without covariates. If bill size or body size were related to habitat choice, models which included them as covariates on movement probability would represent improvements over models without covariates.

Results

A total of 993 adult Snow Geese were captured and marked with neck-collars. In the field, 906 sightings were recorded (not counting initial marking) of 295 adults during the study and used for the full analysis. We recorded morphometrics for a subsample of 388 adult Snow Geese and obtained 180 sightings (not counting initial marking) of 120 individuals for the covariate analysis.

Full dataset analysis

For the full data set, results from GOF analysis were as follows: 1) Test WBWA: $\chi^2_5 = 6.8$, $P = 0.236$, n.s., indicated no memory effect. 2) Test 3G.SR: $\chi^2_6 = 22.5$, $P = 0.001$ indicated a transience, *i.e.* higher probability of mortality or higher permanent emigration after first capture. 3) Test 3G.Sm: $\chi^2_{15} = 29.6$, $P = 0.013$, indicated further heterogeneity related to time since marking. 4) Test M.ITEC: $\chi^2_4 = 8.7$, $P = 0.069$, n.s., indicated no immediate trap-dependence. 5) Test M.LTEC: $\chi^2_2 = 0.8$, $P = 0.683$, n.s., indicated no long-term trap-dependence. 6) Total: $\chi^2_{32} = 68.4$, $P < 0.0001$, indicated an overall lack of fit. Thus, there was some heterogeneity in survival in the full dataset, related to time since marking, and a variance inflation factor ($\hat{c}$) therefore was calculated and used to adjust the fit of the data (68.4/32 = 2.14).

Based on QAIC_c values < 2, the model $\Phi(.)\ \mathbf{p}(h{*}t)\ \Psi(h{*}t)$ was the preferred model (Table 1). This model estimated annual apparent Φ ($\Phi \pm$ s.e.) as 0.601 ± 0.082, independent of both habitat and interval (Table 2). Estimated sighting probabilities were much higher for rice-prairies (range: 0.287–0.534 for 5 time intervals) than coastal marshes (0.020–0.072, for 3 of 5 intervals; Table 2). Two **p** estimates were reported as 1.000 for intervals 1 and 2 in coastal marshes, which corresponds to the model inferring that all marked geese were seen alive and present in the marsh habitat on these first two occasions. We believe that these two estimates of **p** are overestimates, caused by sparse data for these two intervals within the coastal marshes within the first winter 2001/02. Estimates of **p** improved as the study progressed with improved observation efforts and more bandings. Estimated probabilities of moving from coastal marshes to rice prairies were higher (range: 0.000–0.981) than the probabilities of moving from rice prairies to marshes (range: 0.000–0.564) (Table 2). The Ψ for intervals 1 and 5 in rice-prairies and interval 5 in coastal marshes were estimated as 0 (with s.e. > 0), indicating that any movements between these habitats during these within-winter time periods were rarely observed.

Covariate analysis

For the covariate data set, the GOF results were as follows: 1) Test WBWA: $\chi^2_2 = 0.6$, $P = 0.746$, n.s., indicated no memory effect; 2) Test 3G.SR: $\chi^2_7 = 6.3$, $P = 0.505$, n.s., indicated that there was no transience effect; 3) Test 3G.Sm: $\chi^2_{14} = 14.5$, $P = 0.416$, n.s., indicated no further heterogeneity related to time since marking; 4) Test M.ITEC: $\chi^2_3 = 1.5$, $P = 0.685$, n.s., indicated no immediate trap-dependence; 5) Test M.LTEC: $\chi^2_2 = 0.5$, $P = 0.792$, n.s., indicated no long-term trap-dependence; and 6) Total: $\chi^2_{28} = 23.3$, $P = 0.718$, n.s., indicated no lack of fit. Thus, we did not calculate a $\hat{c}$ to adjust the covariate analysis (see Cooch & White 2010) and present AIC_c instead of QAIC_c. We suspect the

Table 1. Model selection for obtaining parameter estimates of annual apparent survival ($\boldsymbol{\Phi}$), sighting probability ($\mathbf{p}$), and movement probability ($\boldsymbol{\Psi}$) for Lesser Snow Geese neck-collared in southwest Louisiana in winters 2001/02, 2002/03, and 2003/04. Models with $\Delta QAIC_c$ > 2 essentially have little or no support. K = the number of parameters in each model; Qdev = deviance. Model used for inference is indicated in bold.

Rank	**Model**	**$\Delta QAIC_c$**	**$\Delta QAIC_c$ weight**	**Model likelihood**	**K**	**Qdev**
1	$\boldsymbol{\Phi}$(.) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h*t)	0.0	0.428	1.0000	21	123.1
2	$\boldsymbol{\Phi}$(h) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h*t)	1.7	0.182	0.4244	22	122.7
3	$\boldsymbol{\Phi}$(.) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h+t)	2.3	0.134	0.3129	17	133.7
4	$\boldsymbol{\Phi}$(h) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h+t)	3.8	0.065	0.1517	18	133.0
5	$\boldsymbol{\Phi}$(h*t) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h+t)	3.8	0.065	0.1515	23	122.7
6	$\boldsymbol{\Phi}$(h) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h*t)	4.0	0.059	0.1376	14	141.5
7	$\boldsymbol{\Phi}$(.) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h*t)	4.3	0.051	0.1194	13	143.8
8	$\boldsymbol{\Phi}$(h*t) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h)	9.5	0.004	0.0087	22	130.5
9	$\boldsymbol{\Phi}$(h*t) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h*t)	9.6	0.004	0.0084	22	130.6
10	$\boldsymbol{\Phi}$(h*t) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h*t)	9.6	0.004	0.0084	28	118.0
11	$\boldsymbol{\Phi}$(.) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h)	10.1	0.003	0.0063	13	149.7
12	$\boldsymbol{\Phi}$(.) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h+t)	11.4	0.001	0.0033	9	159.2
13	$\boldsymbol{\Phi}$(h) $\mathbf{p}$(h*t) $\boldsymbol{\Psi}$(h)	12.0	0.001	0.0025	14	149.5
14	$\boldsymbol{\Phi}$(h) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h+t)	12.1	0.001	0.0023	10	157.8
15	$\boldsymbol{\Phi}$(h*t) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h)	15.8	0.000	0.0004	14	153.3
16	$\boldsymbol{\Phi}$(h) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h)	26.0	0.000	0.0000	6	179.8
17	$\boldsymbol{\Phi}$(.) $\mathbf{p}$(h) $\boldsymbol{\Psi}$(h)	26.3	0.000	0.0000	5	182.2

habitat (h): rice-prairies or coastal marshes.
time (t): temporal variation, *i.e.* early or late winter, specific for each winter (2001/02, 2002/03, and 2003/04).
(.) with a variable means it was independent of habitat and time, *i.e.* held constant.
* indicates an interaction between variables.
\+ indicates that effects of variables were additive.

morphometric sub-sample may have become more balanced with respect to movements than the full dataset (possibly by chance or an inherent randomness of the sub-sample), and thus, not requiring an $\hat{c}$ adjustment.

Table 2. Parameter estimates for annual apparent survival (Φ), sighting probability (**p**) and movement probability (Ψ) for Lesser Snow Geese neck-collared in southwest Louisiana during winters 2001/02–2003/04, based on the highest ranked model in Table 1. The model indicated that Φ was constant (no interval effect) and the same for both habitats, whereas **p** and Ψ differed between habitats and were time-dependent (had an interval effect).

		Rice-prairies		**Coastal marshes**	
Parameter	**Interval**	**Estimate**	**s.e.**	**Estimate**	**s.e.**
Annual apparent survival (Φ)	Constant	0.601	0.082	0.601	0.082
Sighting probability (**p**)	1	0.299	0.071	1.000	0.000
	2	0.287	0.063	1.000	0.000
	3	0.489	0.118	0.033	0.021
	4	0.534	0.082	0.020	0.014
	5	0.343	0.087	0.072	0.028
Movement probability (Ψ)	1	0.000	0.000	0.797	0.085
	2	0.017	0.024	0.981	0.019
	3	0.564	0.129	0.845	0.119
	4	0.000	0.000	0.220	0.068
	5	0.148	0.165	0.000	0.000

Intervals: 1 = observations made in 1 Nov–31 Dec 2001 compared with those in 1 Jan–28 Feb 2002; 2 = from 1 Jan–28 Feb 2002 to 1 Nov–31 Dec 2002; 3 = from 1 Nov–31 Dec 2002 to 1 Jan–28 Feb 2003; 4 = from 1 Jan–28 Feb 2003 to 1 Nov–31 Dec 2003; 5 = from 1 Nov–31 Dec 2003 to 1 Jan–28 Feb 2004. s.e. = standard error.

We began the covariate model selection with the most parsimonious and best supported model from Table 1. We then proceeded to add our index of overall body size, PC1, as a covariate to this starting model, as follows: 1) PC1 was added to Ψ for all intervals; 2) PC1 was added to Ψ for all intervals but only for coastal marshes and not rice-prairies; 3) PC1 was added to the Φ parameter; 4) PC1 was added to the Φ parameter but only for coastal marshes and not for rice-prairies; 5) PC1 was added to Φ and Ψ parameters simultaneously; 6) PC1 was added to Φ but only for the interval November–February (within winter) and not the March–October interval; and 7) PC1 was added to a habitat effect on Ψ, testing an interaction between habitat and body size. All these covariate models failed to outperform the starting model (see Appendix 2), and thus, we concluded that there was no effect of body size on annual apparent survival or movement probabilities.

Adding PC1 (Appendix 1 for PCA results) as a continuous covariate did not improve the best model, nor did it improve any of the 17 models in Table 1; it generally increased AIC values by 1–3.2, despite adding only 1 or 2 parameters to each model (Appendix 2). Since all of the covariate models failed to out-perform the starting model, they cannot be considered equally plausible despite some of them having a ΔAIC < 2.0. The starting model was the best supported model in this analysis. The second-best model, *i.e.* relatively the best of the covariate models, which included an effect of PC1 on movement probability for all intervals and both habitats, was poorly supported (ΔAIC_c = 1.0 (Appendix 2), and the estimated slope was negative (β = –0.127, 95% C.I. = –0.327–0.073). The third-best model, (*i.e.* second best of the covariate models), which included an effect of PC1 on movement probability for all intervals but only in the coastal marshes, was likewise poorly supported (ΔAICc = 1.2 (Appendix 2), and the estimated slope was negative again, opposite to expectations that the larger marsh birds would be less likely to move to the rice fields (β = –0.121, 95% C.I. = –0.324–0.083). All the covariate models had β that did not differ from 0; *i.e.* had 95% C.I. that surrounded 0. Thus, we concluded on the basis of the current dataset that PC1 did not affect Φ or Ψ for candidate models that included body size as a covariate.

Discussion

We frequently observed Snow Geese moving between coastal marshes and rice-prairies. Admittedly, the sample power is low, study duration was short and **p** for two intervals were non-estimable; nevertheless, we believe the analysis is valid for addressing the main question regarding the presence of movements between habitats in Louisiana. The dataset shows that such movements can be common, at least from coastal marshes to the rice-prairies, and that there is temporal variation in movement probabilities. We suspect that certain groups of Snow Geese are more likely to use the marshes and that Snow Geese are somewhat site-faithful, but as indicated by the interval effect on movement probability, this may depend on temporal variation in weather conditions or perhaps local depletion of food. The addition of a body size covariate did not improve any of the models considered. There was no reason to doubt a habitat effect (h*t or h) on movement probability (Ψ) but there was little support for a habitat effect on annual apparent survival (Φ). Thus, although Snow Geese that frequent marsh habitats in winter are generally larger in size than those from adjacent rice-prairies (Alisauskas 1998; Jónsson 2005), there was little evidence from our study to suggest that bill size influences annual apparent survival or movement probabilities across these two habitats.

Our findings also indicate that movement probabilities were highly variable between intervals, as indicated by models with only habitat effects on Ψ performing poorly in the model selection. For birds marked in the rice-prairies, movements to the coastal marshes were extremely rare in three intervals, but during two of them, movements were at least notable (interval 5, within the 2003/04 winter) and common (interval 3, within the 2002/03 winter). For birds marked in the coastal marshes, movements to the rice-prairies were very common during the first three intervals, notable in interval 4 but extremely rare in the fifth interval. We interpret these interval-specific movement probabilities as responses to shifts in environmental conditions. Although Snow Geese banded in coastal marshes moved into rice-prairies and *vice versa*, the banded birds still differed in morphological size between the habitats (Jónsson 2005). The morphometric differentiation varied annually between habitats in the study area (Jónsson 2005), as reported by Alisauskas (1998). Morphology and associated niche selection may vary annually in relation to alternation of wet and dry years, or frequencies of storm fronts, which potentially affect food resources (Alisauskas *et al.* 1988, 1998). For example, wet years may favour one bill morph type whereas drier years favour the other (Grant & Grant 2002). The predicted relationships, based on the hypotheses, presumed constant environmental conditions, but once environmental variation (weather, food depletion) alters the habitat conditions for Snow Geese, then further interactions between rice-prairies and coastal marshes are expected.

Mid-winter survey numbers of Snow Geese, averaged for the three winters of the study, were 213,954 and 88,042 for rice-prairies and coastal marshes, respectively (Fronczak 2004). If these numbers are multiplied with movement probabilities in Table 2, up to 120,000 Snow Geese moved between the two habitats, during the intervals with the highest movement probabilities, which in turn represents 40–50% of the Snow Geese observed within winter surveys 2001/02–2003/04 (Fronczak 2004). Conversely, there were 3–4 intervals where hardly any movements were observed from either habitat. Thus, the two groups of banded birds can interact, at least once every 1–3 years, suggesting that they do not represent segregated sub-populations, and that population-specific habitat management may not be necessary. Humphries *et al.* 2009 found no differentiation in mitochondrial DNA between Snow Geese from these two habitats, although they urged further work with nuclear DNA to better understand population connectivity and structuring. However, a genetic component to the population structure may be unlikely, given that our findings suggest that movements can be substantial between habitats in 1–2 out of every five intervals. Despite the winter pair formation in Snow Geese (Ganter *et al.* 2005), we suspect that some mixing of the two groups may also occur on the breeding grounds.

Annual apparent survival estimates were similar between habitats. Our estimate of apparent annual survival (0.601) was within the lower range of those reported for other Snow Goose populations (0.6 and 0.9, depending on location and year; Mowbray *et al.* 2000; Calvert & Gauthier 2005; Table 4 in McWilliams *et al.* 2008; Fig. 9 in Alisauskas *et al.* 2011). These estimates are also slightly lower than those reported for Ross's Geese (Drake & Alisauskas 2004; Alisauskas *et al.* 2006) and for Black Brant *Branta bernicla nigricans* within certain years (Lindberg *et al.* 1998). As mentioned above, our survival estimates are likely to be biased low due to permanent emigration from the overall study area. Contrary to that for movement probabilities, there was no evidence to suggest that survival rates differed between the time intervals, similar to results reported for other large waterfowl (Varner & Eichholz 2012).

Neck-collars have been reported to reduce body condition and survival of Snow Geese (Legagneux *et al.* 2013) and the closely related Ross's Geese (Caswell *et al.* 2012). A suspected effect on body condition is that neck-collars increase energy expenditure (due to elevated drag during flight or to stress) or reduce their foraging efficiency (Legagneux *et al.* 2013). While we acknowledge that such effects probably were present in our study, predicting any directional or behavioural effects on movement probabilities, or habitat choices, is difficult without further empirical data. Apparently, breeding propensity is reduced in neck-collared Snow Geese (Legagneux *et al.* 2013) and we noted that although we frequently caught pairs and observed them together, these birds were only twice reliably seen accompanied by juvenile geese. Thus, our collared birds could have been of mid- or lower social status (Jónsson & Afton 2008) and such birds may be more exploratory or more easily displaced from favourable feeding locations.

Annual apparent survival estimates from our dataset possibly were confounded by differing emigration rates (Williams *et al.* 2008). Coastal marshes are the southernmost part of the mid-continental population's winter range. The geographical distribution of marshes is restricted to the Gulf Coast, whereas that of rice-prairies includes all inland agricultural habitats in general, from southwest Louisiana northwards and even into Arkansas or Missouri.

Snow Geese are hunted on most days within the sighting periods, both during regular season and during the special hunting season. Hunting pressure may be variable within rice-prairies or coastal marshes from year to year, and potentially differs between habitats, at least in some years. We suspect that hunting opportunities in coastal marshes have a more clumped distribution than those in the rice-prairies. Most Snow Geese in the coastal marshes are found at State Wildlife Refuge or the Marsh-Island NWR, where hunting is not allowed. Thus, we suspect that some Snow Geese may use the marshes as refuge from the hunter pressure in the rice-prairies, and return to the rice-prairies on days when hunting pressure declines.

In recent decades, environmental conditions generally have been favourable on the wintering grounds of Snow Geese (Abraham *et al.* 2005). The acreage of wildlife refuges or semi-natural wetlands in the vicinity of feeding habitats positively influences the survival of wintering geese (Gauthier *et al.* 2005; Elphick 2008). The combination of refuges and rice-farming may explain why Snow Geese continue to use both habitats, despite the population increase in agricultural habitats and the higher intake rates in rice-prairies (Jónsson

& Afton 2006). Movements between these habitats may be diurnal movements or restricted to certain time-periods within winter. Subsequent research using telemetry could determine the exact nature of these movements. Our study spanned winters 2001/02–2003/04. Hunter recoveries of these banded birds from 2001/02–2012/13 (Jónsson & Afton, unpubl. data) have shown that the timing of sampling and the earliest migratory movements by Snow Geese coincide with one another. In fact, data from 2001/02–2012/13 have shown that our marked Snow Geese can be recovered in Louisiana, Arkansas or Missouri in late January or early February. We suspect that such early, northwards migratory movements may partly explain the asymmetry in movements from coastal marshes to rice-prairies. This stems partly from logistical restraints on the sampling design, as well as the ability of Snow Geese to alter migratory patterns in response to early or late onsets of spring at locations throughout their midcontinent flyways.

We conclude, based on our data, that Snow Geese in coastal marshes do not comprise a segregated sub-population. Annual apparent survival does not differ appreciably from that of Snow Geese in the rice-prairies or other parts of their wintering range. Snow Geese select and use both habitats, but the general importance of each habitat may differ between years. Although Snow Geese can display strong fidelity to winter locations (Johnson 1996; Williams *et al.* 2008), they also change diets or habitats within a given winter, and during migration through adjacent habitats. These changes may be influenced by weather or hunting pressure as well as resource availability (Hill & Frederick 1997; Hénaux *et al.* 2012). In Louisiana, combinations of frost and drought can kill emerging green vegetation in some years and such events can impact food availabilities differently in rice-prairies and coastal marshes (Alisauskas 1998). In certain years, Gulf Coast marshes may be important habitats, even to Snow Geese that normally would not winter there (Alisauskas *et al.* 1998). Furthermore, if rice acreage decreases in the future, or vast areas of rice-fields are destroyed by salt-water intrusion, increased use of the coastal marshes by Snow Geese may occur. Notably, rice acreage in the state of Louisiana averaged 520,600 acres/year during 2001–2005, but declined to an average of 428,150 acres/year in 2006–2013 (U.S. Department of Agriculture 2014). Annual variation in food availability and concomitant variation in movement patterns may also be affected by variation in rice production or the timing of rice harvesting.

Rainfall affects water levels in rice-fields and coastal impoundments and can interfere with beneficial marsh burns in coastal marshes; lack of successful marsh burns reduce the attractiveness of coastal marshes to Snow Geese (Gabrey & Afton 2004). Climate events such as hurricanes can alter water levels or other factors that affect access to feeding grounds or interfere with marsh burns or rice plantings. All these variations probably favour some movements between habitats, which are adaptive for the long-term future of Snow Geese.

The movements documented here and the observed differences between habitats by bill size may be more congruent with habitat selection than with phenotypic selection (both scenarios were hypotheses of Alisauskas 1998) because the phenotypic selection hypothesis posits natural selection within habitats, which leads to different bill morphologies, which ultimately must assume limited exchange of Snow Geese between habitats. Resource availability probably affects use of these two habitats by wintering Snow Geese. New research to assess relative values of rice-prairies and coastal marshes under different conditions across the size spectrum of Snow Geese would be useful to inform wildlife managers. However, such a study would take many years, and need to account for annual variation due to weather (particularly precipitation) and the resulting availability of standing water, frequency of marsh burns and Snow Goose numbers present. Such a study should also quantify hunter activity or hunting pressure, collect data on movements of Snow Geese using radio telemetry, and lastly, consider annual variation in morphological measurements (Alisauskas 1998; Jónsson 2005).

Acknowledgements

Our study was funded by the Canadian Wildlife Service, Louisiana Department of Wildlife and Fisheries (LDWF), Delta Waterfowl Foundation, Rockefeller Scholarship program, and the USGS-Louisiana Cooperative Fish and Wildlife Research Unit, Graduate School, Agricultural Center, and School of Renewable Natural Resources at Louisiana State University. We thank D. Blouin, B. Barbe, M. Chamberlain, W. Henk, D. Homberger, R.N. Helm (deceased), D. Caswell, R. Elsey, G. Perrie, C. Jeske (deceased), J. Linscombe, T. Hess (deceased), M. Hoff, W. Norling and S. Lariviere for their valuable input and support. R. Choquet and C. Nicolai advised on the use of MARK and U-Care. We especially thank the staff of Rockefeller SWR, Cameron Prairie NWR, Sabine NWR, Sweet Lake Land and Oil Co. and LDWF, who kindly provided housing and logistical support. C.J. Michie, B. Meixell, M. Pollock, T. Blair, J. Yurek, and P. Becnel read neck-collars. We thank all those who volunteered to assist with capture and neck-collaring of Snow Geese (see list in Jónsson 2005). R. Alisauskas, B. Clark, J.-F. Giroux, T.G. Gunnarsson and an anonymous reviewer provided helpful comments on earlier drafts of the manuscript.

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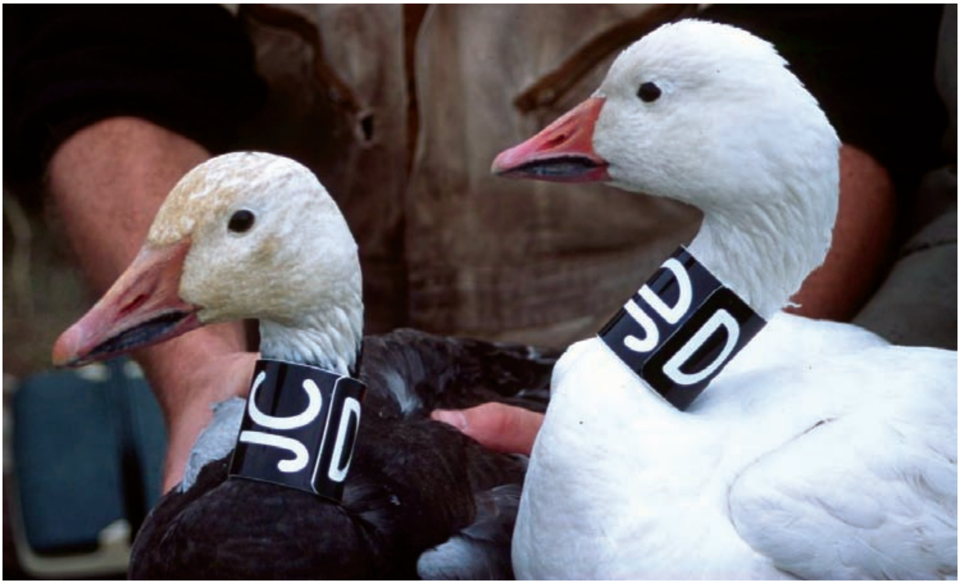
Appendix 1. Principal components analysis of morphological measurements of 388 adult Lesser Snow Geese caught in southwest Louisiana in winters 2001/02, 2002/03 and 2003/04. Numbers in bold correspond to variables that covaried the strongest with each PC score (*i.e.* had the highest loadings).

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**
Wing length	**0.30**	0.28	**–0.42**	**–0.58**	0.28	**0.41**	0.27	–0.05	0.04
Culmen length	**0.37**	–0.33	0.01	–0.05	–0.17	0.13	–0.35	**–0.63**	**0.42**
Bill nares	**0.30**	**–0.52**	**0.45**	–0.37	–0.04	0.08	0.10	**0.53**	0.09
Bill thickness	**0.32**	0.10	–0.34	0.14	**–0.82**	0.01	0.16	0.21	–0.04
Gape length	**0.30**	–0.36	**–0.27**	**0.64**	0.37	0.16	0.36	0.06	0.04
Head length	**0.40**	–0.08	0.02	–0.02	0.08	–0.01	–0.35	–0.10	**–0.83**
Total tarsus	**0.35**	0.08	–0.04	–0.15	0.15	**–0.86**	0.25	–0.11	0.10
Skull width	**0.28**	**0.45**	**0.66**	0.20	–0.06	0.21	0.37	–0.25	–0.03
Skull height	**0.35**	**0.43**	0.01	0.21	0.21	0.00	**–0.56**	**0.43**	0.33
% variance explained	55.5	9.5	8.5	6.7	5.8	4.8	4.1	3.1	2.2

Appendix 2. Model selection ranks, ΔAICc, ΔAICc weights, model likelihoods, and number of parameters (K) for the covariate size analysis of movements of Lesser Snow Geese collared in southwest Louisiana in winters 2001/02, 2002/03 and 2003/04. Model $\mathbf{\Phi}_{.}$; $\mathbf{p}_{h*t}$; $\mathbf{\Psi}_{h*t}$ was the starting model in this analysis, and covariates were only added to **Φ** and **Ψ**.

Rank	Model	ΔAIC_c	AIC_c weight	Model likelihood	*K*	Deviance
1	**Φ**(.) **p**(h*t) **Ψ**(h*t)	0.0	0.259	1.000	21	1036.0
2	**Φ**(.) **p**(h*t) **Ψ**(h*t-PC1)	1.0	0.156	0.602	22	1034.9
3	**Φ**(.) **p**(h*t) **Ψ**(h*t-PC1-marsh only)	1.2	0.140	0.540	22	1035.1
4	**Φ**(.PC1) **p**(h*t) **Ψ**(h*t)	1.5	0.122	0.470	22	1035.3
5	**Φ**(.PC1-marsh only) **p**(h*t) **Ψ**(h*t)	2.1	0.093	0.358	22	1035.9
6	**Φ**(.PC1) **p**(h*t) **Ψ**(h*t-PC1)	2.1	0.090	0.345	23	1033.8
7	**Φ**(.PC1 within winter only) **p**(h*t) **Ψ**(h*t)	2.2	0.087	0.337	22	1036.0
8	**Φ**(.) **p**(h*t) **Ψ**(h*t-habitat*PC1 interaction)	3.2	0.052	0.202	23	1034.8



Photograph: Lesser Snow Geese caught at Cameron Prairie National Wildlife Refuge, Calcasieu Parish, Louisiana, USA in November 2001, by Jón Einar Jónsson. The Snow Goose on the left (blue colour phase) is representative of geese from coastal-marsh habitat whereas the Snow Goose on the right (white colour phase) is representative of those from rice-prairie habitat.

Assessment of spatial changes in the duck harvest within the Central Flyway, 1997–2011

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Abstract

Knowledge of the factors which influence the spatial distribution of duck harvest would be useful to managers when setting dates for the duck hunting seasons. Here we used changes in mean latitude of harvest to represent changes in distribution of duck harvest during the hunting season within the Central Flyway from 1997–2011, derived from harvest data from the U.S. Fish and Wildlife Service Parts Collection Survey. A candidate set of models was developed to represent competing hypotheses of corn availability, weather, water on the landscape, competition via population density, hunting pressure, and regulatory change to explain the variation in harvest distribution of Mallard *Anas platyrhynchos*, dabbling ducks *Anas* sp., and diving ducks *Aythya* sp. The model selection process revealed that hunting pressure, the amount of water on the landscape, and Mallard density best explained the distribution of Mallard harvest. Mallard harvest distributions tended to be further north during wet years of high Mallard densities and low hunting pressure, relative to dry years with high Mallard densities and low hunting pressure. High hunting pressure shifted the spatial distribution of Mallard harvest further south. Regulations had the largest influence on both dabbling (non-Mallard) and diving duck harvest distribution. Dabbling duck harvest distribution was further north under the 2002–2011 frameworks, relative to the 1997–2001 frameworks. During the 2002–2011 frameworks, diving ducks were more likely to be harvested further south early in the season and further north later in the season, relative to 1997–2001 frameworks. Trends in the distribution of harvest should be informative for future harvest management decisions.

Key words harvest distribution, hunting pressure, Parts Collection Survey, regulations, waterfowl.

Waterfowl managers try to coincide hunting seasons with duck availability to maximise hunting opportunities (Bellrose 1980; Vrtiska 2012). However, annual variation makes it difficult for waterfowl managers to predict duck availability, both spatially and temporally. Although precise knowledge of duck migration chronology prior to setting season dates is improbable, managers still need to set reasonable hunting seasons. Setting hunting seasons too early or too late may result in hunter dissatisfaction, which in turn may influence hunter recruitment and retention rates (Stankey *et al.* 1973; Case 2004). Subsequently, funding for habitat conservation or management activities may be affected (Vrtiska *et al.* 2013). As such, setting appropriate hunting seasons could extend to waterfowl conservation.

Many factors may influence the annual variation in duck distribution, movement, and migration. For example, weather has been found to influence duck migration and movement (Richardson 1978; Nichols *et al.* 1983; Pearse 2007; Schummer *et al.* 2010). The distribution of water in the landscape (*i.e.* wetlands) in terms of availability and diversity may also affect duck distribution (Kaminski & Prince 1981; Kaminski & Prince 1984; Webb *et al.* 2010; Pearse *et al.* 2012). Studies also suggest changes in hunter regulation and activity can affect wildlife movement and habitat selection (Root *et al.* 1988; Conner *et al.* 2001; Cox & Afton 1997; Casazza *et al.* 2012). Finally, food availability and competition may affect duck behaviour (Jorde *et al.* 1983; Baldassarre & Bolen 1984), which in turn may affect duck distribution. All these factors which determine duck distribution, movement and migration may consequently influence the distribution of the duck harvest. However, few studies have attempted to offer explanations as to whether or why harvest distribution patterns change over time (Delta Waterfowl 2012).

Understanding changes in harvest distribution may allow managers to predict duck availability during hunting seasons more accurately. Thus, we used the U.S. Fish and Wildlife Service's (USFWS) Parts Collection Survey (PCS) database to examine what factors influence recent patterns of duck harvest distribution (Fig. 1). Our objective was to use a candidate set of competitive models to explain the variation in duck harvest distribution.

Methods

Parts Collection Survey data were obtained from the USFWS Branch of Harvest Surveys and only Central Flyway records from the 1997–2011 regular duck seasons were selected. Ducks were classified as one of three groups: Mallard *Anas platyrhynchos*, dabbling ducks *Anas* sp. (excluding Mallard), and diving ducks *Aythya* sp., to account for differences in management concern and life history strategies. The dabbling duck group included American Green-winged Teal *A. crecca*, Blue-winged Teal *A. discors*, Gadwall *A. strepera*, Northern Pintail *A. acuta*, American Wigeon *A. americana* and Northern Shoveler *A. clypeata*. The diving duck group included Redhead *Aythya americana*, Canvasback *A. valisineria*, Greater Scaup *A. marila* and Lesser Scaup *A. affinis*.

Principle hypotheses

Six principle hypotheses were tested to assess variation in harvest distribution for

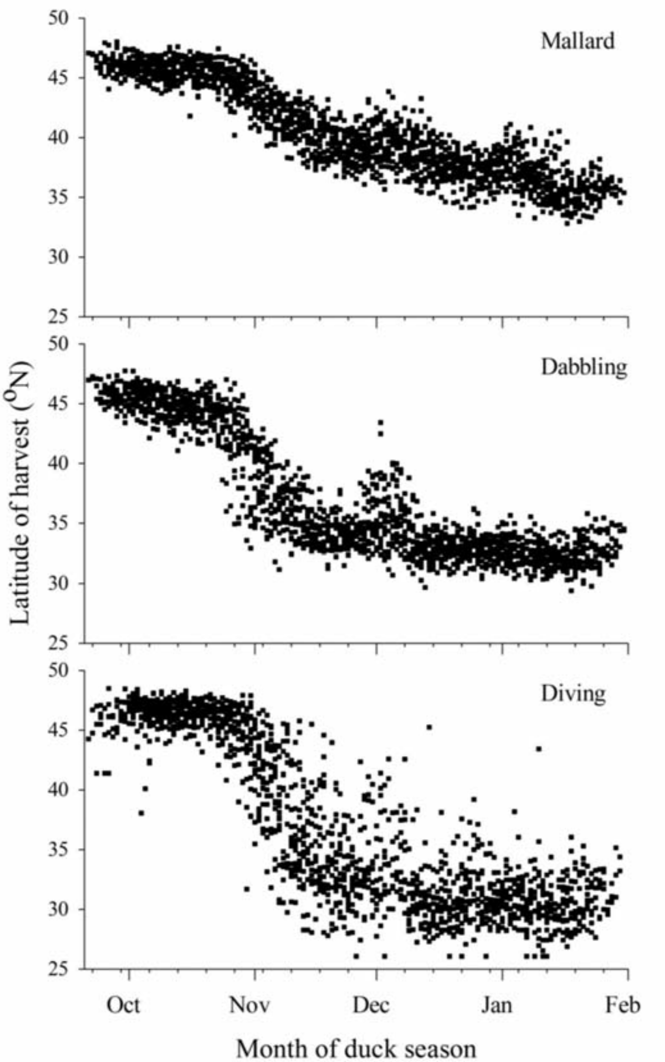

Figure 1. Variation in harvest distribution for Mallard, dabbling ducks *Anas* sp., and diving ducks *Aythya* sp. Figures represent mean annual (1997–2011) latitudes of duck harvest (weighted county centroids) on a given day during the autumn hunting season. Derived from U.S. Fish and Wildlife Service Parts Collection Survey data from the Central Flyway, 1997–2011.

Mallard, dabbling, and diving ducks (Fig. 1): corn availability, weather, relative wetness of the landscape at varying latitudes, competition via population density, hunting pressure and regulatory influences. These factors were assessed by calculating an average estimate across years for each factor. We then categorised each annual estimate either as above or below average, unless otherwise noted. Treating principle hypotheses as factors created a threshold effect around the average. However, thresholds should allow managers to anticipate changes in the distribution of harvest, depending on whether a variable is above or below a certain threshold on a given year. All factors were constant for a given year, so we used the variation inherent in the causal variables to precisely account for annual variation in distribution; we did not include "year" as a random effect.

Corn acres planted annually in North and South Dakota ($\text{CORN}_{\text{DAKOTAS}}$), as well as total corn acres planted annually in Nebraska (CORN_{NE}) from 1997–2011 were used to examine if corn availability influenced duck harvest distribution at different latitudes (U.S. Dept. of Agriculture 2013). Total corn acres planted were used because it is a food source readily used by most dabbling ducks (Moore 1980) and, if residual corn is sufficiently abundant, ducks may delay migration, which could influence harvest distribution. Estimates of total corn acres planted were categorised into high and low corn years (Fig. 2).

A daily cumulative weather severity index (hereafter WSI; Schummer *et al.* 2010) was used to examine weather's influence on the distribution of duck harvest. The WSI index includes factors of daily snowfall, consecutive days with snow depths ≥ 2.54 cm, temperature, and consecutive days with temperatures at or below 0°C (Schummer *et al.* 2010). Only weather data from North and South Dakota in October and November (WEATHER) were used in the analyses. Weather in these two months would better indicate when ducks migrate to southern latitudes as the breeding grounds are located in these states. Thus, a majority of ducks may be influenced by the same weather patterns. U.S. Historical Climatology Network data were used from eight weather stations (Menne *et al.* 2013), four each in North and South Dakota, to calculate a daily WSI. These were the Crosby, Grand Forks (Univ Nws), Jamestown (State Hosp), and New England weather stations in North Dakota and Alexandria, Clark, Cottonwood, and Dupree in South Dakota (Menne *et al.* 2013). To obtain an annual WSI across all stations, the average of the maximum daily WSI estimates was calculated for each station sampled. Annual estimates above average were classified as severe and below average estimates were classified as mild (Fig. 2). A model that incorporated both weather and corn factors was also created, because abundant corn on the landscape may delay migration even in the face of inclement weather.

High densities of ducks were expected to cause competition for limited resources, which may influence duck movements. To test for competition via population density (DENSITY) effects on harvest distribution, we first created an autumn population size index for a given species. Corrected age ratios of harvested birds were calculated in relation to the proportion of a species harvested in the Central and Mississippi Flyways, because breeding population estimates are for ducks from both the Mississippi and Central Flyways. Breeding population estimates were obtained from the U.S. Fish and Wildlife Service (USFWS 2013), and females were assumed to

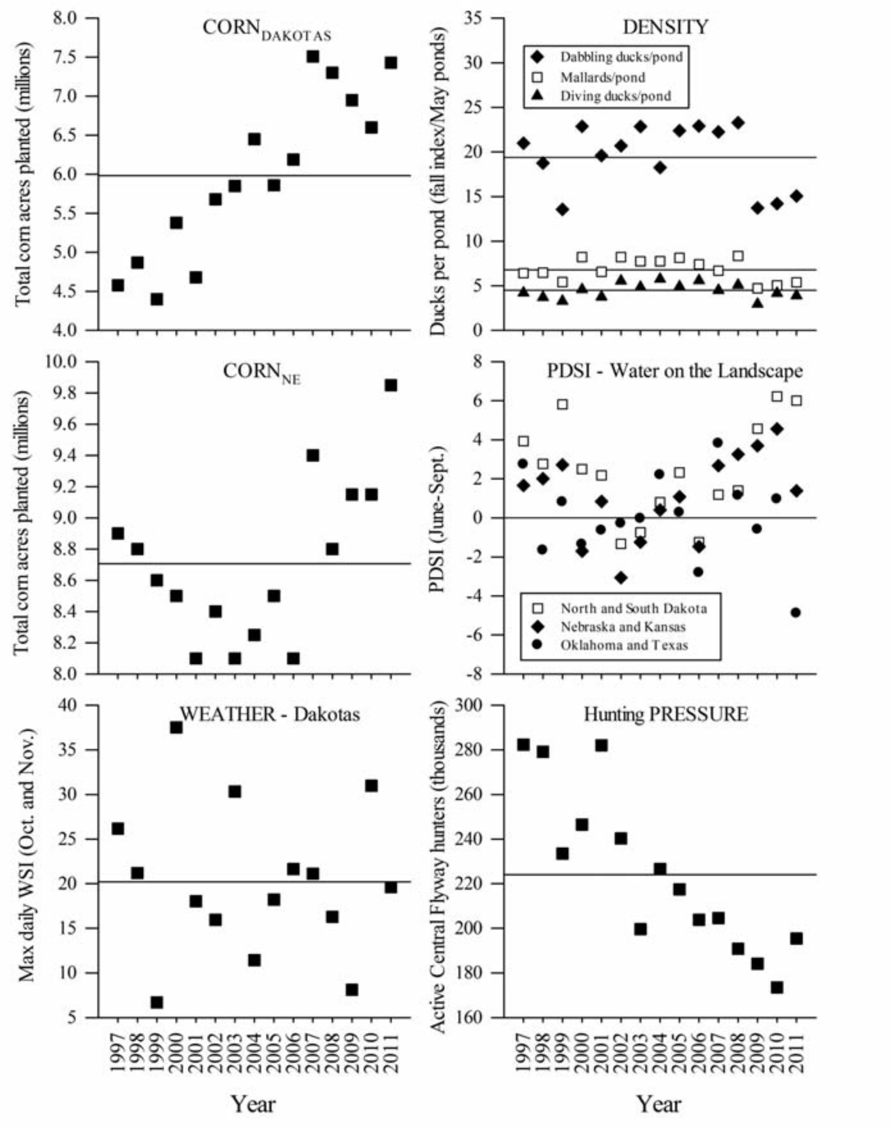

Figure 2. Annual estimates (1997–2011) for potential corn availability in North and South Dakota and Nebraska (U.S. Dept. of Agriculture 2013), weather severity indices (WSI) in North and South Dakota from October and November (U.S. Historical Climatology Network, Menne *et al.* 2013), density (autumn population index/U.S. May ponds), water on the landscape (mean Palmer Drought Severity Index; National Climate Data Center 1994), and hunting pressure (Central Flyway Harvest and Population Survey Data; Kruse *et al.* 2002; Kruse 2013). Annual estimates were treated as factors. Values above the line were categorised as high, whereas values below the line were categorised as low. Values for weather were categorised as severe or mild. Water on the landscape was categorised as wet or dry.

represent half the breeding population. The estimated female population size was then multiplied by the corrected age ratio to obtain an estimate of young produced. Finally, we added the estimated number of young to the breeding population, which resulted in our autumn population size index for a given species. Species estimates of production were summed within their respective duck groups (*e.g.* Redhead, Canvasback and Scaup estimates were summed to provide the total autumn diving duck population index). Population estimates were then divided by the abundance of ponds in the north-central U.S. (approximating to the U.S. prairie pothole region) during the annual waterfowl breeding population and habitat survey (U.S. "May ponds"; USFWS 2013), which resulted in our estimate of density (*i.e.* ducks per pond). DENSITY was categorised into high or low categories for each group of ducks (Fig. 2). A model that incorporated DENSITY and $\text{CORN}_{\text{DAKOTAS}}$ was constructed, because high competition for food with other ducks may cause some ducks to move to areas with less competition, and thereby influence the distribution of harvest.

The mean Palmer drought severity index (PDSI) from June–September for 1997–2011 was used to examine the effect of water on the landscape on the distribution of the duck harvest (National Climate Data Center 1994). An average PDSI was calculated for northern (North Dakota and South Dakota; $\text{PDSI}_{\text{NORTH}}$), mid (Nebraska and Kansas; PDSI_{MID}), and southern (Oklahoma and Texas; $\text{PDSI}_{\text{SOUTH}}$) latitudes for each year in the sampling frame. Interactions between the annual PDSI estimates at north, mid and south latitudes were used to examine where water on the landscape was most influential to harvest distribution. Annual PDSI estimates were categorised into wet or dry years, depending on whether they were > 0.0, or ≤ 0.0 for a given year, respectively (Fig. 2). Additional models were tested that included water on the landscape and either WEATHER, $\text{CORN}_{\text{DAKOTAS}}$, or DENSITY factors. Inclement weather may generally cause ducks to migrate, but ducks that encounter suitable water or food resources may delay migratory movements.

Estimates of the number of active hunters were used as an indicator of hunting pressure (PRESSURE). Active hunter estimates were summed annually for all Central Flyway states from both the Mail Questionnaire Survey (1997–1998; Kruse *et al.* 2002) and the Harvest Information Program (1999–2011; Kruse 2013). The distribution of active hunter estimates across states in the Central Flyway did not change during the sampling period (M. Haugen, unpubl. data). Thus, active hunters were assumed to have changed uniformly across the Central Flyway. Annual estimates were categorised into high or low hunting pressure years (Fig. 2). A model that incorporated hunting pressure and water on the landscape was also included, because hunting pressure may affect duck distribution differentially depending on water availability (Webb *et al.* 2010).

Finally, the sampling frame was divided into two periods, 1997–2001 and 2002–2011, to test the influence of hunting regulation on duck harvest distribution (FRAMEWORKS). From 2002–2011, hunting seasons were allowed to start earlier and end later compared to 1997–2001, but still retained the same season lengths and daily limits each year (Kruse *et al.* 2002; Kruse 2013). Thus, more ducks may be harvested or exposed to hunting pressure prior to or after the initiation of migration in 2002–2011. As such, more harvest may occur in the north and vulnerability may decrease in the south (Eadie *et al.* 2002; Szymanski & Afton 2005), which may influence harvest distribution.

Multi-model inference

Mean latitude of harvest was used to represent duck distribution across time during the autumn migration. We used SAS® software (SAS Institute 2009) to calculate mean latitudes of harvest for each group of ducks for each day (*i.e.* an ordinal day that starts on 21 September and ends on 31 January) during each hunting season from 1997–2011. Because the county is the smallest geographical unit in the PCS, mean latitudes of harvest were weighted averages of county centroids where ducks were reported to be harvested. Data that did not contain county information were removed, as it was not possible to determine reliably where the duck had been harvested.

Initial sets of generalised linear models were constructed and evaluated to determine whether the principle hypotheses were best represented as an additive or interactive model for each duck group. Mean latitude of harvest was used as the response variable, and a corrected Akaike Information Criterion (AIC_c) was used to select among the alternatives. Ordinal day (DAY) was included in all models, and AIC_c was used to determine if a quadratic or linear ordinal day best explained the variation in harvest distribution. From the initial model fitting, a candidate model set (Table 1) was developed for each group of ducks separately. A null model (*i.e.* the DAY-only model) was included in all candidate models sets, and AIC_c was again used to select among the alternative hypotheses. The distance between the AIC_c scores of our top model and the null model, relative to penalties inherent to an increase in model complexity, were used to assess the fit of our model (Maydeu-Olivares & García-Forero 2010). A Pearson's correlation test ($\alpha = 0.05$) tested for associations between explanatory variables, with a view to modifying or eliminating correlating variables prior to analysis.

Results

A quadratic description of harvest distribution by ordinal day provided a better fit than a linear model (linear model: Mallard $\Delta AIC_c = 149.1$; dabbling duck $\Delta AIC_c = 981.8$; and diving duck $\Delta AIC_c = 355.9$), so a quadratic function of day (*i.e.* $DAY + DAY^2$) was used in all models (Fig. 3).

Several variables were correlated, and so were omitted from the candidate models. For instance, as the landscapes in North and South Dakota ($PDSI_{NORTH}$) and Nebraska and Kansas ($PDSI_{MID}$) became wetter, DENSITY of Mallard and dabbling and diving ducks declined ($P < 0.05$). Thus, $PDSI_{NORTH}$ and $PDSI_{MID}$ were removed from the analyses; Mallard, dabbling, and diving duck DENSITY represents $PDSI_{NORTH}$ and $PDSI_{MID}$ in our models. Total corn acres planted in North and South

Table 1. Candidate models set (with number of parameters; k) used (x) for three groups of duck species to assess variation in harvest distribution in the Central Flyway, 1997–2011.

Candidate models	**Mallard**	**Dabbling duck**[a]	**Diving duck**[b]	**k**
DAY[c]	×	×	×	3
DAY + $\text{CORN}_{\text{DAKOTAS}}$[d]	×	×	×	5
DAY + WEATHER[e]	×	×	×	5
DAY + DENSITY[f]	×	×	×	5
DAY + PRESSURE[g]	×	×	×	5
DAY + FRAMEWORKS[h]	×	×		5
DAY × FRAMEWORKS			×	9
DAY + WEATHER + $\text{CORN}_{\text{DAKOTAS}}$	×	×	×	7
DAY + DENSITY + $\text{CORN}_{\text{DAKOTAS}}$	×	×	×	7
DAY + WEATHER + DENSITY		×		7
DAY + PRESSURE + DENSITY		×		7
DAY + DENSITY × $\text{PDSI}_{\text{SOUTH}}$[i]	×		×	11
DAY + $\text{CORN}_{\text{DAKOTAS}}$ + DENSITY × $\text{PDSI}_{\text{SOUTH}}$	×		×	13
DAY + WEATHER + DENSITY × $\text{PDSI}_{\text{SOUTH}}$	×		×	13
DAY + PRESSURE + DENSITY × $\text{PDSI}_{\text{SOUTH}}$	×		×	13

[a]Dabbling duck: American Green-winged Teal, Blue-winged Teal, Gadwall, Northern Pintail, American Wigeon and Northern Shoveler; [b]Diving duck: Canvasback, Redhead and Scaup; [c]Quadratic function for ordinal day from 21 Sept to 31 Jan in all models; [d]Factor of total corn acres planted in North and South Dakota; [e]Factor of a weather severity index for North and South Dakota in Oct and Nov; [f]Factor of an autumn population index/May ponds in the U.S.; [g]Factor of Central Flyway active hunter estimates; [h]Year factor, for 1997–2001 and 2002–2011, representing changes in the federal framework for allowable season dates; [i]Factor of Palmer Drought Severity Indices for Oklahoma and Texas (south).

Dakota ($\text{CORN}_{\text{DAKOTAS}}$) and Nebraska ($\text{CORN}_{\text{NE}}$) were positively correlated ($P < 0.05$), so CORN_{NE} was removed from the analyses because $\text{CORN}_{\text{DAKOTAS}}$ may have a stronger influence on the distribution of duck harvest as it is on the breeding grounds (*i.e.* corn in North and South Dakota may affect more ducks and ducks prior to migration). PRESSURE and $\text{CORN}_{\text{DAKOTAS}}$ were negatively correlated, but we retained both parameters in the candidate model sets as corn and hunting

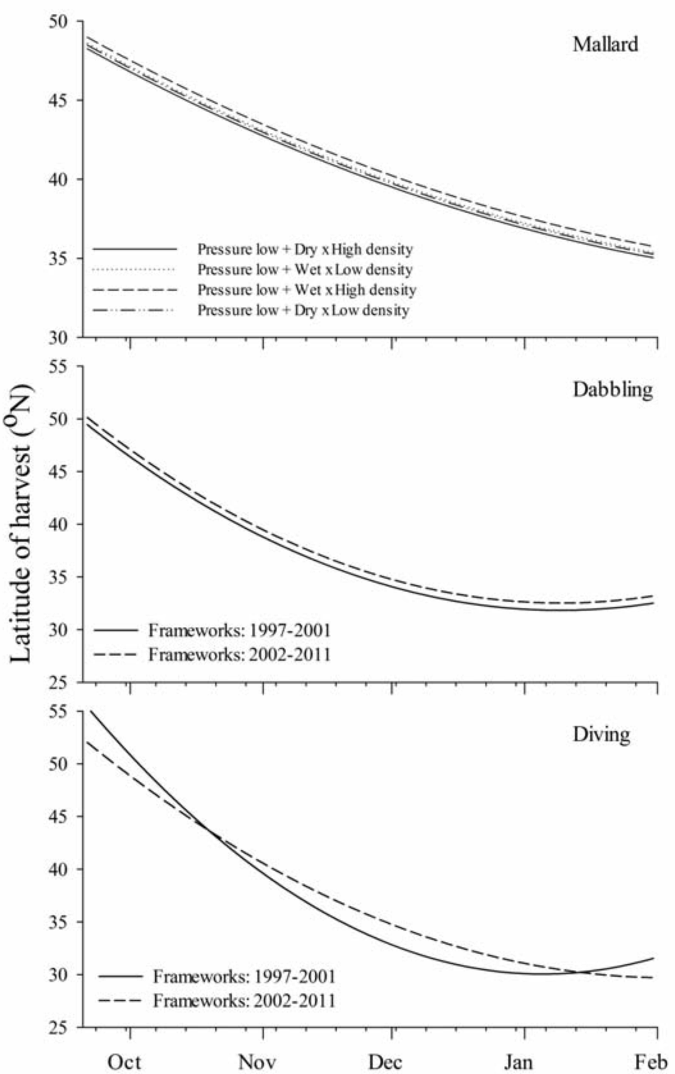

Figure 3. Plots of best models to explain variation in duck harvest distribution in the Central Flyway from 1997–2011 for Mallard, dabbling ducks *Anas* sp., and diving ducks *Aythya* sp. The variation in distribution of Mallard harvest was best explained by hunting pressure (factor of active Central Flyway duck hunters: low < 224,000 < high), water on the landscape (mean annual Palmer Drought Severity Indices from June–September for Oklahoma and Texas: dry ≤ 0.0 < wet), and density (Mallard autumn flight index/U.S. May ponds: low < 6,800 < high). The variation in the distribution of dabbling and diving duck harvest were best explained by framework changes in 2002 which allowed duck seasons to be set earlier and end later. Derived from U.S. Fish and Wildlife Service Parts Collection Survey data.

pressure may not be mechanistically correlated. For example, acres of corn may have increased due to increases in corn prices (U.S. Dept. of Agriculture 2013) and hunting pressure may have decreased because of increased urbanisation and other societal factors (Heberlein 1987). Thus, both parameters were included, and we were prepared to make *a posteriori* decisions to eliminate a model if it appeared the correlation was affecting model results.

Mallard

The variation in Mallard harvest distribution was best explained with a model that incorporated DAY, PRESSURE, and an interaction between $\text{PDSI}_{\text{SOUTH}}$ and Mallard DENSITY (Table 2; $\text{AIC}_c = 6472.3$, weight (w_i) = 0.996, parameters (k) = 13). The runner-up model contained DAY, $\text{CORN}_{\text{DAKOTAS}}$, and an interaction between $\text{PDSI}_{\text{SOUTH}}$ and Mallard DENSITY ($\Delta\text{AIC}_c = 11.1$, $w_i = 0.004$, $k = 13$). Only the top model was considered as it contained > 99% of the weight. The relative improvement of the value of the AIC_c for our top model, relative to the null model containing only the effect of DAY ($\Delta\text{AIC}_c = 124.7$, $w_i = 0.000$, $k = 3$) suggested that model fit improved considerably beyond the penalties inherent (+ 20 AIC_c) on adding 10 additional model parameters to the null model.

If hunting pressure was held constant at low pressure, wet landscapes (*i.e.* water at southern latitudes) and high Mallard density resulted in the most northerly harvest relative to other landscape and Mallard density scenarios (Fig. 3). Day-specific mean latitude during wet years and high densities was 0.39 (95% CI: 0.19–0.58 degrees) degrees latitude (43 km) farther north than mean latitude during wet years with low densities of Mallard. Also relative to wet, low density years, the distribution of Mallard harvest during dry years with low Mallard densities was 0.12 degrees further south (56 km; 95% CI: 0.30 degrees south to 0.07 degrees north). Finally, dry landscapes and high Mallard densities shifted the distribution of Mallard to their most southerly distribution: 0.34 degrees latitude to the south (81 km; 95% CI: 0.97 degrees south to 0.29 degrees north) of distributions during wet years with high Mallard densities (Fig. 3). High hunting PRESSURE shifted any of these distributions of Mallard harvest 0.57 (95% CI: 0.43–0.70) degrees latitude (63 km) southward on any given day relative to distribution estimates from low hunting PRESSURE (Table 2, Fig. 3).

Dabbling duck

Annual variation in dabbling duck harvest distribution was best explained by DAY and FRAMEWORKS (Table 2; $w_i = 1.00$, $k = 5$). The relative improvement of the value of the AIC_c for our top model, relative to the null model containing only the effect of DAY ($\Delta\text{AIC}_c = 43.8$, $w_i = 0.000$, $k = 3$) suggested that model fit improved considerably beyond the penalties inherent (+ 4 AIC_c) when adding two additional model parameters to the null model.

Dabbling ducks were harvested at a latitude 0.69 degrees higher (95% CI: 0.49–0.88), equating to a distance of 77 km, under the 2002–2011 frameworks which allowed seasons to be set one week earlier and end one week later relative to 1997–2001 frameworks (Fig. 3). Actual PCS

Table 2. Parameter estimates from the best model explaining the variation in harvest distribution across the hunting season in the Central Flyway for each duck group (Mallard, dabbling duck *Anas* sp. (excluding Mallard), and diving duck *Aythya* sp.), as determined by Akaike's Information Criterion correct for small sample sizes (s.e. = standard error) from U.S. Fish and Wildlife Service Parts Collection Survey data, 1997–2011.

Duck group	**Effect**	**Estimate**	**s.e.**	$P > \vert t \vert$
Mallard[a]	Intercept	48.7513	0.1351	<0.001
	DAY	–0.1508	0.0041	<0.001
	DAY^2	0.0004	0.0000	<0.001
	DENSITY			
	High	0.3859	0.0980	<0.001
	$PDSI_{SOUTH}$[f]			
	Dry	–0.1150	0.0919	0.211
	DENSITY × $PDSI_{SOUTH}$			
	High × Dry	–0.6110	0.1340	<0.001
	PRESSURE[g]			
	High	–0.5667	0.0675	<0.001
Dabbling duck[b,d]	Intercept	49.7686	0.1821	<0.001
	DAY	–0.3221	0.0055	<0.001
	DAY^2	0.0014	0.0000	<0.001
	FRAMEWORKS[h]			
	2002–2011	0.6850	0.0984	<0.001
Diving duck[c,e]	Intercept	55.8622	0.5290	<0.001
	DAY	–0.4816	0.0179	<0.001
	DAY^2	0.0022	0.0001	<0.001
	FRAMEWORKS[h]			
	2002–2011	–3.5110	0.5997	<0.001
	DAY × FRAMEWORKS			
	2002–2011	0.1496	0.0203	<0.001
	DAY^2 × FRAMEWORKS			
	2002–2011	–0.0010	0.0001	<0.001

[a]Model: Mean latitude of harvest = Intercept + DAY + Hunting PRESSURE + DENSITY × $PDSI_{SOUTH}$; [b]Model: Mean latitude of harvest = Intercept + DAY + FRAMEWORKS; [c]Model: Mean latitude of harvest = Intercept + DAY × FRAMEWORKS; [d]Dabbling duck: American Green-winged Teal, Blue-winged Teal, Gadwall, Northern Pintail, American Wigeon and Northern Shoveler; [e]Diving duck: Canvasback, Redhead and Scaup; [f]Factor of Palmer Drought Severity Indices for Oklahoma and Texas (south); [g]Factor of Central Flyway active hunter estimates; [h]Year factor, for 1997–2001 and 2002–2011, representing changes in the federal framework for allowable season dates.

harvest indicated similar temporal trends in the average daily harvest recorded for dabbling ducks between frameworks (Fig. 4).

Diving duck

Variation in the harvest distribution of diving ducks was also best explained by an interaction between DAY and FRAMEWORKS (Table 2; $w_i = 1.00$, $k = 9$). The relative improvement of the value of the AIC_c for our top model, relative to the null model containing only the effect of DAY ($\Delta AIC_c = 34.4$, $w_i = 0.000$, $k = 3$) suggested that model fit improved considerably beyond the penalties inherent (+ 12 AIC_c) when adding six additional model parameters to the null model.

Under the 2002–2011 frameworks, diving ducks were harvested further south at the beginning of the hunting season, but harvest distributions in mid- to late October shifted northward relative to 1997–2001 (Fig. 3). Harvest distribution between frameworks converged upon similar latitudes towards the end of the hunting seasons (*e.g.* 31 January, Fig. 3). The maximum degrees to which harvest distribution shifted southward on any day between frameworks was 3.36 degrees (373 km, on 21 September) and the maximum northward shift on any day between frameworks was 1.92 degrees (213 km, on 2 December). Actual PCS harvest indicates that differences existed in the temporal trends of average daily harvest between regulation sets (Fig. 4). Frameworks for 2002–2011 resulted in more diving duck being harvested during the first half of the hunting season relative to the 1997–2001 frameworks; however, harvest was similar between frameworks later in the hunting season (Fig. 4).

Discussion

Hunting pressure, wetland conditions in Oklahoma and Texas, and Mallard density best explained the variation in the distribution of Mallard harvest. Duck movements may be influenced by hunting pressure (Cox & Afton 1997; Casazza *et al.* 2012), as well as water availability (Kaminski & Prince 1984; Webb *et al.* 2010; Pearse *et al.* 2012), and competition (Jorde *et al.* 1983; Baldassarre & Bolen 1984). Thus it seems plausible that all three factors may affect the distribution of Mallard harvest, singly or in combination.

High Mallard DENSITY resulted in a northward shift in harvest distribution relative to low Mallard DENSITY. By definition, high Mallard densities can indicate either higher production or lower water availability. In either scenario, more ducks may be harvested on the breeding grounds prior to southward movements resulting in northward shifts in the distribution of Mallard harvest. For example, dry wetland conditions may concentrate ducks onto more finite resources, but it may also concentrate hunting pressure, which could hypothetically increase harvest. Increases in hunting PRESSURE resulted in a southward shift in harvest distribution. Because ducks react to hunter activity (Cox & Afton 1997; Casazza *et al.* 2012), increased hunting pressure, specifically on the breeding grounds, may cause ducks to initiate migration sooner, thereby causing a southward shift in harvest distribution. Dry conditions in the south resulted in a

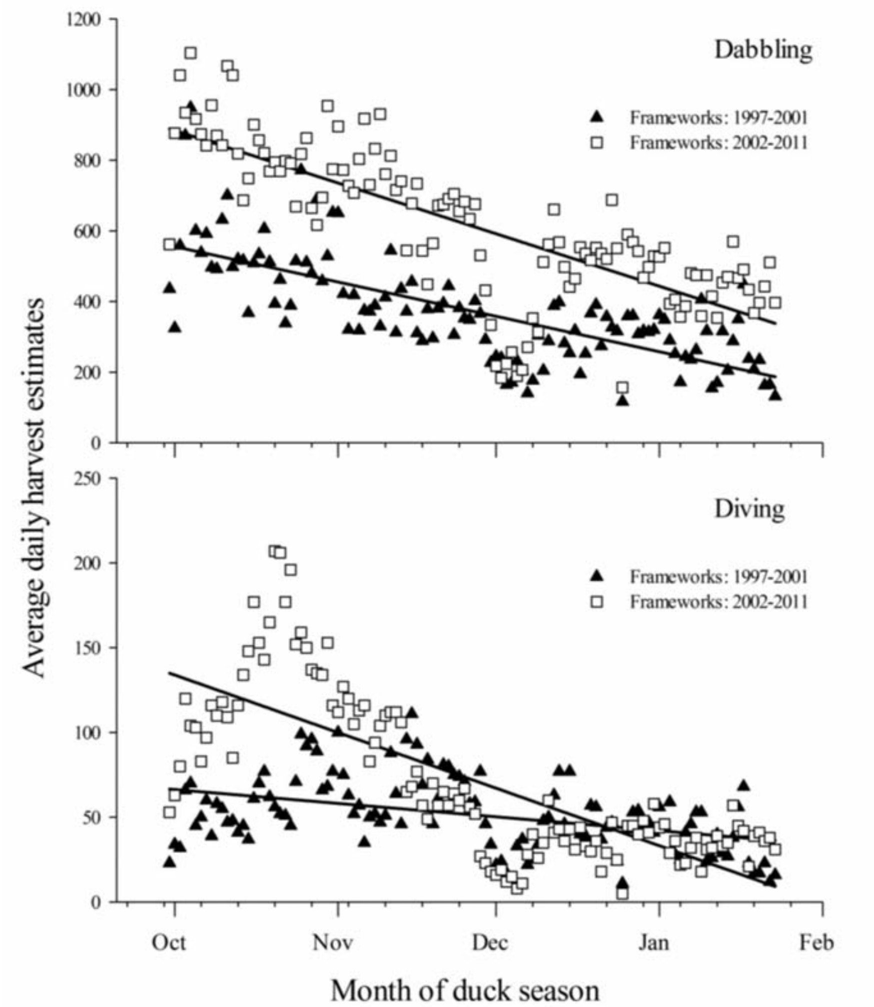

Figure 4. Average daily harvest estimates both for dabbling ducks *Anas* sp. (excluding Mallard) and for diving ducks *Aythya* sp. over each regulatory period, 1997–2001 and 2002–2011 (*i.e.* when changes in frameworks allowed states to set seasons earlier and end seasons later relative to 1997–2001; season length and daily bag limits were comparable). Derived from U.S. Fish and Wildlife Service Parts Collection Survey data.

southward shift in the distribution of harvest, and the interaction between dry conditions in the south and high densities of Mallards resulted in an even larger southward shift in harvest distribution. Similar to the previous example, Mallards may become concentrated in southern states, resulting in a southward shift in harvest distribution under dry conditions and high densities of Mallards. Managers should focus on Mallard densities, water conditions, and local hunting regimes when they consider the distribution of Mallard harvest and regulation setting.

Framework changes provided the greatest explanation for the variation in harvest distribution for both dabbling and diving ducks. Northward shifts in the distribution of dabbling duck harvest may have occurred because earlier seasons allowed more dabbling ducks to be exposed to hunting pressure closer to the breeding grounds prior to migration. Specifically, there may be fewer ducks available at southern latitudes in addition to a higher proportion of ducks at southern latitudes that have been exposed to hunting pressures, which may reduce their vulnerability (Eadie *et al.* 2002; Szymanski & Afton 2005; Ackerman *et al.* 2006). Diving ducks were also influenced by framework changes; however, contrary to the situation with dabbling ducks, an interaction between FRAMEWORKS and DAY provided the best fit. Similar to dabbling ducks, decreased vulnerability at southern latitudes may account for at least the northward shifts in harvest of diving duck, but that alone may not completely explain the interaction between FRAMEWORKS and DAY. Scaup daily bag limits were reduced in 1999 from six to three (Kruse *et al.* 2002), which may account for the interaction between FRAMEWORKS and DAY. Although daily limits on other diving duck species remained comparable among framework sets (Kruse 2013), it appears that actual diving duck harvest increased earlier in the hunting season during 2002–2011 (Fig. 4), which may have also triggered the interaction between FRAMEWORKS and DAY. Dabbling ducks did not exhibit the same noticeable changes in actual harvest between the framework sets.

Although our model predicted small spatial shifts in harvest, it is important to consider the scale at which these shifts occurred. Specifically, a change of 1° latitude may be very small when focusing on a county inference. However, when considering our explanatory variable affected the spatial distribution of harvest at the flyway level our results become much more significant. Future management actions should consider the temporal and spatial changes in duck harvest. That is, changes in allowable start and end dates for hunting seasons can affect the harvest distribution of dabbling and diving duck species. Additionally, anthropogenic and environmental stimuli appeared to influence harvest distribution for Mallard. Hunters appreciate opportunities to harvest waterfowl (Stankey *et al.* 1973; Brunke & Hunt 2007), and an appropriate hunting season is critical for hunter satisfaction. Increased hunter satisfaction may lead to increased hunter retention (Case 2004), which is important as hunters provide support to wildlife and habitat conservation efforts (Vrtiska *et al.* 2013). Our results should help mangers in setting appropriate hunting seasons. The distributions we provide also may help managers inform their hunters as to the reasons for temporal and spatial changes in harvest.

Acknowledgments

We thank the USFWS for providing us with the Parts Collection Survey (PCS) data, particularly K. Wilkins and R. Raftovich. We also thank all the hunters participating in the PCS. We are grateful to K. Pope, E. Rees, T. Fox, and three anonymous referees who provided comments on earlier drafts of this manuscript. Funding was provided by the Nebraska Game & Parks Commission, and this research was supported by Hatch Act funds through the University of Nebraska Agricultural Research Division, Lincoln, Nebraska.

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Extension of Goosander *Mergus merganser* distribution into the Carpathian Mountain range

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Abstract

The Goosander *Mergus merganser* occurs mainly in the Holoarctic boreal zone but isolated populations also exist in the Alps, the Balkans and in central Asia. In the late 20th century, the breeding distribution extended to the Carpathian Basin in central Europe, and the species is now widespread in the west of the Carpathian Mountain range, whilst remaining scarce in the east Carpathians and breeding only occasionally in the southern Carpathians. It was estimated that at least 240–360 pairs bred in the Carpathian Mountains in 2010–2013 (of which *c.* 80% were in Poland), where they are restricted to river valley systems which are generally in a natural or semi-natural state. This remains a rare species in central Europe, meriting conservation measures in the Carpathians and monitoring of its continued expansion in the region.

Key words: conservation status, distribution, expansion, mountains, *Mergus merganser*.

The three Common Goosander *Mergus merganser* sub-species occur mainly in the boreal zones of Eurasia (*M. m. merganser*), central Asia (*M. m. orientalis*) and North America (*M. m. americanus*) (del Hoyo *et al.* 1992). In Europe, their range stretches from the British Isles, across Scandinavia and the southern coast of the Baltic Sea to Belarus and northern Russia. Isolated populations also exist in Iceland, the Alps and the Balkans (Scott & Rose 1996; Marti & Lammi 1997; Marinkovi *et al.* 2008; Keller 2009). The European population was estimated at < 74,000 pairs at the end of the 20th century, with the majority of the birds breeding in Fennoscandia and Russia (BirdLife International 2004). In the Alps, numbers are estimated at 1,000–1,400 pairs (Keller 2009), whereas in the Balkans it is a rare species (40–80 pairs) (BirdLife International 2004; Marinkovi *et al.* 2008). At the end of the 20th century, Goosanders also started to breed in the Carpathian Basin (Poluda 1991; Kondêlka 2000; István & Tamás 2003; Kajtoch & Piestrzyńska-Kajtoch 2005; Lešo & Kropil 2005). This study reviews the history of Goosander expansion in the Carpathians and assesses its present distribution and abundance in the region.

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Methods

Data on breeding Goosanders in the Carpathians were collected from several sources. Firstly, their distribution in the Polish Carpathian Mountains was recorded and verified via field surveys. Data from a survey of the key bird species of the Polish Carpathians carried out by the Polish Society for the Protection of Birds (OTOP) were included in this review. In 2012–2013, the OTOP surveyed a total of 485 km (97 5-km sections) of river valley systems which were randomly selected and surveyed three times (once per month) during the breeding season (April–June). During these surveys experienced observers counted all riparian breeding birds including Goosanders. Records entered by volunteer observers onto an online database of bird observations developed for the OTOP's project were also used. From 2000 onwards, the most abundant Goosander populations in the Polish Carpathians, those of the Raba River (50 km of river surveyed) and Dunajec River catchments (30 km) were monitored for Goosander abundance 1–3 times per year. Secondly, data on Goosander numbers and distribution in the literature were collected and analysed (specifically: Tomiałojć & Stawarczyk 2003; Mohr *et al.* 2007; Kajtoch & Piestrzyńska-Kajtoch 2005 and Kajtoch *et al.* 2010 from Poland; Kondêlka 2000; Šuhaj *et al.* 2003 and Šťastný *et al.* 2006 from Czech Republic; Lešo & Kropil 2005, 2007 and Šrank 2011 from Slovakia; Poluda 1991; Potish 2009 and Grishchenko & Yablonovska-Grishchenko 2010 from Ukraine; and István & Tamás 2003 from Romania). Finally, unpublished data were gathered via personal communication with individual researchers and amateur ornithologists (see Acknowledgements). Birding mailing lists, forums and web pages (mainly the Polish "PTAKI yahoo group", the Slovakian "Aves vtaky" and the "Hungarian birdwatchers' site") were also consulted.

Breeding localities were defined as those sites where females were seen with broods (pulli or juveniles) by 20th July. All females with broods, regardless of the age of the young, were counted on the 5 km sections, and used to estimate of total number of breeding females, on the assumption that movement of birds to another part of the river valley (and thus the likelihood of double-counting) was limited during an single count. During counts of long river sections, only females with the youngest broods (approximately up to one week old) were recorded. Counts were confined to young broods to avoid overestimating the total numbers of breeding females, as females with older broods are not sedentary, often moving (swimming) along river channels to be potentially counted again, especially as human (observer) presence might encourage the birds to move (see Kajtoch *et al.* 2014). The movement of families was especially considered a problem when counting long river sections; on shorter stretches the birds can usually be tracked to avoid counting them twice. Breeding was considered to have taken place in valleys where the birds were frequently seen between the 20th April and 20th July and showed territorial, mating and/or breeding behaviour. Single sightings of birds, mainly males, during the breeding season were not included as potential breeding localities because males do not stay with breeding females and non-breeders are known to move between river valley systems. Moreover, Carpathian Goosanders remain within the river valleys and do not appear to undertake the moult migration described for those in the British and Alpine populations (see Marquiss & Duncan 1994; Keller & Gremaud 2003; Hatton & Marquiss 2004). Sightings of family groups with young birds capable of flight after 20th July were also omitted, as the precise breeding locality of such birds could not be determined.

Results

First breeding records for the Carpathian Mountains

Prior to Goosanders breeding in the Carpathian Mountains, the closest breeding sites were thought to be in the catchment of the San and Upper Vistula Rivers, in the Sandomierz Valley of southern Poland, where birds have bred since the 1980s (Czyż 1992; Fig. 1). The expansion of Goosanders into the Carpathians started almost simultaneously in several areas and in different countries. The first broods in the Polish and Czech Carpathians had been preceded by irregular breeding attempts, which started approximately 10 years earlier (in 1986 and 1987) in the Ukrainian Transcarpathia and near Ivano-Frankivsk, also in the Ukraine. Birds first bred regularly in the upper Oder River and the Olza River in the Czech Republic in 1999. In the Raba and Dunajec Rivers in Poland, the first broods were also found in 1999, but the birds must have settled there much earlier, as about 16 pairs were found in the Raba River valley in 2000 (Fig. 2). Thus, Goosanders are likely to have started breeding there several years earlier, most likely after the severe flood of 1997, which had restored riparian habitats (*i.e.* restored the braided riverbed with gravel alluvia and isles, scarps on riverbanks and an accumulation of large amounts of wood), as was also observed following the flood in 2010 (Kajtoch & Figarski 2013; Fig. 2). The first case of breeding in Slovakia was tentatively reported from the Hron River in 2004 and confirmed in 2007. The first nesting Goosanders in Romania were sighted in 2003 in the gorge of the Mures River. In Hungary, a possible case of breeding was observed on the Danube River in 2004. These records suggest that the expansion of the Goosander's breeding ranges was quite rapid. It commenced in the northern part of the west Carpathian range in 1999, and over the next five years breeding birds were detected across most parts of this mountain range (Fig. 1); however, the most numerous populations are still restricted to the western Carpathians.

Current estimates for Goosander breeding in the Polish Carpathians

Goosanders are now present in almost all river systems in the Polish part of the Carpathian range, with the two central catchments of the Raba and Dunajec Rivers being the most densely populated. By 2010, 30–35 pairs bred within the surveyed sections of the Raba River catchment and 15–20 pairs in the Dunajec River catchment. Extrapolation of these numbers in relation to the total length of suitable river valleys within these catchments gave an estimated total of

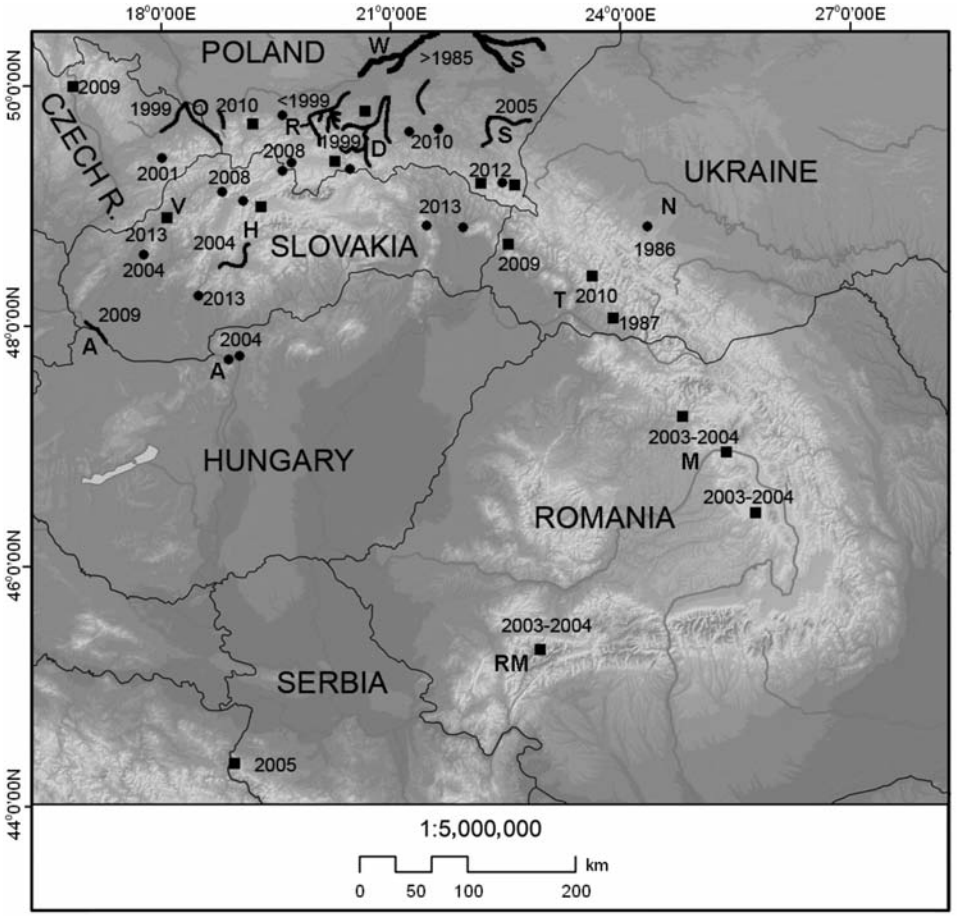

Figure 1. Distribution of breeding sites recorded for Goosanders in the Carpathian Mountains and surrounding areas (thick black lines = rivers where breeding is established, black squares = additional known breeding localities, black dots = possible breeding localities). The Carpathian range (white elevation) extends in an arc from the Czech Republic in the northwest through southern Poland, Slovakia, northern Hungary and southwest Ukraine to Romania in the east and Serbia in the south. Dates indicate the first year in which Goosanders were detected in particular areas. Major river catchments mentioned in the text: O = Oder and Olza, W = Vistula, R = Raba, D = Dunajec, S = San, V = Vah, H = Hron, A = Danube, T = Tisza, N = Dniester, M = Mures and RM = Retezat Mountains. Map of the Carpathian after Jarvis *et al.* 2008 and OpenStreetMap, www.openstreetmap.org.

50–70 and 40–60 pairs of Goosanders breeding there, respectively. Since 2010, Goosanders have also been found in the western part of the Polish Carpathians, in the upper Vistula River (several pairs), the Soła River, the Skawa River and the Czarna Orawa River (single pairs in each). In the central part of the Polish western Carpathians, except for

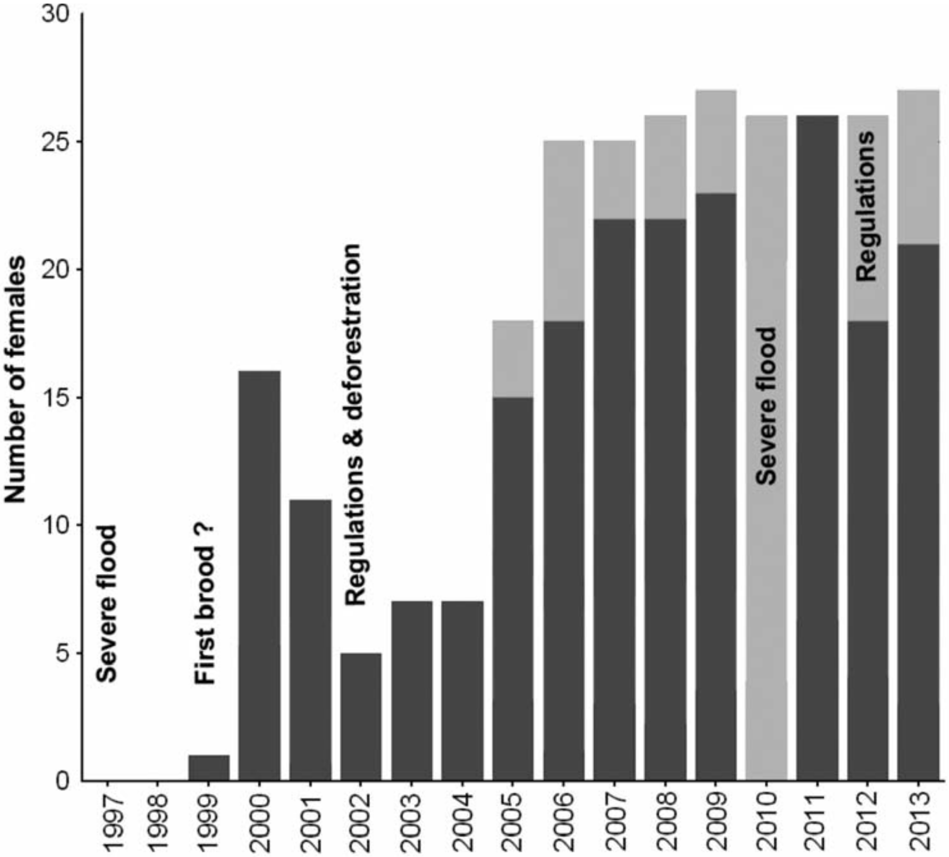

Figure 2. Number of Goosander pairs breeding in the middle part of the Raba River valley (from Dobczyce to Bochnia, *c.* 30 km), with the first brood recorded in 1999. Dark grey = maximum number of breeding females (recorded as females with broods); light grey = approximate additional number of non-breeding females and females which lost their broods (in 2010 these mainly comprised females which lost their broods during a severe flood).

the valleys of the Raba and Dunajec Rivers, Goosanders have been detected only since 2010 on the Wisłoka (several pairs), Ropa, Jasiołka and Wisłok Rivers (single pairs in each). In 2005, the birds started to breed in the eastern part of the Polish Carpathians, on the San River and its tributaries in the Bieszczady and the Beskid Niski Mountains as well as in the Przemyśl foothills, where probably > 30 pairs are now breeding. Most of the river systems in the Polish Carpathians in which Goosanders breed are tributaries of the Vistula River.

The number of Goosanders breeding in the middle part of the Raba River valley increased significantly between 1999 and 2013 (Linear regression: $F_{1,14} = 11.9$, $P = 0.005$), but that period also saw some fluctuations caused by natural factors (*e.g.* floods) and anthropogenic factors (*e.g.* regulation of the river channels and deforestation of river banks) (Fig. 2). The total number of breeding Goosanders in the Polish Carpathians is currently estimated at 200–270 pairs (Table 1).

Goosanders breeding elsewhere in the Carpathians

In 2001, Goosanders breeding in the Czech Republic Carpathians and their foothills were found to occur mainly on the Olza River (probably several pairs) (Oder catchment) and in ponds in the upper Bečva River valley (Morava catchment) (Kondêlka 2000; Šuhaj *et al.* 2003; and Šťastný *et al.* 2006). Some 10–20 pairs are now thought now to breed in the Czech Carpathians (Table 1).

In Slovakia, Goosanders have been regular breeders in the Hron river valley (since 2007–2008, several pairs), the catchment of the Vah River (since 2004, several pairs) and on the Danube near Bratislava (since 2009, several pairs) (Lešo & Kropil 2005, 2007; Šrank 2011). Individual possibly breeding pairs were also observed on the Orava River in 2010 (Ł. Kajtoch unpubl. data). In the eastern part of the Slovakian Carpathians, Goosanders were observed on small rivers in the Torysa and Laborec catchments in 2013 ("Aves vtaky" site). Goosander sightings

Table 1. Estimated number of breeding pairs for Goosanders in Carpathian countries. * = estimates highly uncertain due to insufficient data.

Country	River catchment	Estimated numbers of breeding pairs
Poland	Raba	50–70
	Dunajec	40–60
	Elsewhere in west Carpathians	80–100
	San	30–40
Czech Republic	Oder	10–20
	Morava	1–2
Slovakia	Danube	15–25
	Tisza	2–5
Hungary	Danube	2–3
Ukraine	Dniester*	0–5
	Tisza*	5–20
Romania	Tisza*	5–10
Total		240–360

during the breeding season peaked in 2013 and, although the total number of pairs has not been determined, there are estimated to be 15–25 pairs breeding in the country (Table 1).

In the Hungarian Carpathians, single pairs of Goosanders were present only on the Danube River near Veröce in 2004 and 2009 ("Hungarian birdwatchers' site").

In the Ukraine these birds breed near Ivano-Frankivsk on the Lukva River (Dniester catchment) (1986) and in Transcarpathia on the Tereblya River (1987), the Rika River (2010), and the Uzh River (2009 or earlier) (on the last three rivers in the Tisza catchment) (Poluda 1991; Potish 2009; Grishchenko & Yablonovska-Grishchenko 2010). There are insufficient data to determine the total number of Goosanders breeding in the Ukrainian Carpathians, but taking into account numbers in the Polish east Carpathians (in the San River catchment) on the border with Ukraine, and the expansion of Goosanders into Slovakia, the species bird is possibly also more widespread in Ukraine (Table 1).

In Romania, Goosanders were found in the eastern Carpathians in 2003–2004 on the Bistrita River, on the Mures River and on the Tarnava Mare River, all within the Tisza catchment. A single breeding site was also detected in the southern Carpathians on a lake near the Retezat Mountains in 2003 or 2004 (István & Tamás 2003). The total number of Goosanders breeding in the Romanian Carpathians is not known but they amount to at least 5–10 pairs (Table 1).

Goosanders in the Carpathians are found mostly in the foothill zones and in the lower and middle parts of larger mountain rivers at altitudes of 250–500 m a.s.l. They mainly occur on rivers, and rarely on artificial dam lakes and ponds. Only a few breeding sites have been found higher in the mountains, on typical mountain rivers or, occasionally, on natural mountain lakes.

Discussion

From their initial colonisation in the 1990s, the Goosander is now widespread as a breeding species in the western Carpathians, especially in the northern part of these mountains in Poland and the Czech Republic, as well as locally on their southern slopes in central-western Slovakia (Fig. 1). There are also breeding birds along the Danube valley in Slovakia and Hungary (Fig. 1). On the other hand, Goosanders are still scarce breeders in the eastern Carpathian Mountain range, except in the San River valley in Poland, as only several isolated breeding sites have been detected in eastern Slovakia, Ukraine and Romania. This species is thought to breed only occasionally in the southern Carpathians, where it was reported breeding just once, in Romania. It is probable that some breeding localities in the eastern and southern Carpathians either still remain unknown or that Goosanders will also breed in these areas in the near future. It is worth noting that maximum numbers of Goosanders breeding in the western Carpathians in Poland were recorded in *c.* 2007–2009 and in 2011 (after a major flood, Kajtoch & Figarski 2013). In some river systems numbers declined thereafter, mainly because of habitat changes due to river channel regulation (which includes strengthening of river banks and riverbeds, often in conjunction with the construction of small dams), such as when the Raba River system was subject to severe regulation and the catchment deforested in 2001–2002 (Fig. 2). In some river valleys the number of breeding pairs may have peaked in recent years, especially the Raba and Dunajec in Poland, where the increase in the number of breeding birds stabilised in 2007 at a density of *c.* 0.8 breeding female/1 km of river length. During the 2013 breeding season, the highest numbers of Goosanders were observed in Slovakia and the east Polish Carpathians. This suggests that there may in future be an increase in the intensity of expansion to the south and east.

The relatively short and rapid expansion of the Goosanders into the Carpathians is analogous to the range change recorded for this species in the Dynaric Alps, where birds also started breeding in 1986 and increased in number and distribution over the next 20 years (Marinković *et al.* 2008). These rapid expansions are in contrast to the long-term expansion of Goosander populations in the Alps (Keller & Gremaud 2003; Keller 2009) and in Britain (Holloway 1996; Rehfisch *et al.* 1999), where Goosanders started breeding in the 19th century and increased slowly. The different patterns of Goosander expansion could perhaps reflect different levels of persecution (the species has come into conflict with fishing interests in some regions, but not in the Carpathians), or be a result of the breeding birds having different origins. For instance, it's possible that only relatively small numbers of birds settled in Britain and the Alps in the 19th century, resulting in local populations which increased in number independently of the north European population, whereas newly-established populations in the Carpathians and possibly in the Dynaric Alps may be more regularly reinforced by immigration of birds from the north.

It is difficult to determine the total number of breeding pairs in the Carpathians, due to a lack of precise counts in most countries and most of the river catchments. Simple summary of breeding Goosanders estimates from the Carpathian countries suggests a total of at least 240–360 pairs (2010–2013), of which at least 80% are located in Poland (Table 1). It is possible that actual number of breeding Goosanders in the Carpathians is even larger and that total population fluctuates due to dynamic changes in river and riparian habitat quality and suitability (which may result from anthropogenic and natural causes) and demographic reasons (it is uncertain to what extent Carpathian Goosanders depend on inflow of birds from northern areas to sustain numbers). The estimated number of breeding Goosanders makes those in the Carpathians the third most numerous concentration of Goosanders in Europe, exceeding those in the Balkans (40–60 pairs) and Iceland (100–300 pairs) (Bird Life International 2004).

In the Carpathians, Goosanders breed almost exclusively on rivers which are generally in natural or semi-natural state (unregulated channels and banks covered by riparian forests) (Kajtoch *et al.* 2014). Breeding birds have only rarely been found on ponds and artificial reservoirs, mostly in Poland, Slovakia and Romania. There has probably been only a single breeding attempt on a natural lake in the southern Carpathians (near the Retezat Mountains) in Romania. This preference for river valleys with fastrunning water as breeding sites probably results from the availability of suitable habitats as artificial reservoirs often have treeless banks, while mountain lakes in the Carpathians are extremely rare and located in highest parts of the mountains, above the tree line. Breeding in river valleys makes the Carpathian population similar to populations from the Balkans and also the British Isles and Iceland, but distinct from populations in the Alps (where Goosanders breed mostly on sub-montane lakes, Keller & Gremaud 2003) and northern Europe (where they mostly breed on lakes and large lowland rivers). In several localities, semi-colonial Goosanders have been found (up to 8 pairs on the Raba River, Kajtoch *et al.* 2009). This phenomenon was earlier known for this species amongst its island (Madge & Burn 1988) and mountain populations (Keller & Gremaud 2003).

It is not certain if birds breeding in the Carpathians are sedentary or migrate to the south, as during the winter large numbers of birds (probably mainly of northern origin, but possibly also local individuals) flock on some river stretches and reservoirs. The source of Goosanders movement into the Carpathians is most likely from northern European (particularly from northern Poland, Latvia and/or Scandinavia), but other expansion routes (*e.g.* from the mountain areas of the Alps or the Balkans) cannot be excluded. Ringing and/or genetic studies are needed to confirm the source of colonising birds. It has recently been shown that Goosander populations are structured genetically (Hefti-Gautschi *et al.* 2009) and each geographically isolated population of these birds should be considered as an evolutionarily significant unit in conservation biology. It would be interesting to verify how Carpathian Goosanders are related genetically to other European populations.

At the same time as Goosanders were expanding their range into the Carpathians, the species also settled on the Morava River in the Sudetes (in 2009), on the Otava River in southwest Bohemia, Czech Republic (in 2006; Šuhaj *et al.*2003; Šťastný *et al.* 2006; Adamík & Beran 2010; Hudec *et al.* 2011), and in Dunaj River in Lower Austria (2007; P. Lešo, pers. comm.). These two range extension routes will probably connect the northern populations with the populations inhabiting the Alps in the near future. However, it seems unlikely that Goosander expansion to the south connected the Carpathian and Balkan populations as no population of these birds in the Southern Carpathians has been established yet.

In addition to the zoogeographic implications of this work, some conservation recommendations can be offered to provide better protection for Goosanders in the Carpathians in the future. To maintain populations of these birds, and to enable their further expansion, it is necessary to maintain river valleys in natural or semi-natural state, for instance by leaving river channels unregulated (retaining numerous alluvia, scarps and woody debris) and their banks afforested. It is also important to work on improving the water quality and fish populations in the rivers. Goosanders are not threatened in Europe as their northern populations are very numerous; however, in central Europe it remains a rare species, and in several countries it is a newly colonised breeder. Moreover, due to their habitat and food preferences, Goosanders could be good indicators of naturalness and biodiversity of sub-montane river valleys (Kajtoch *et al.* 2014). For these reasons, we consider it is necessary to plan the effective conservation of this species in the Carpathians and to monitor further its expansion in the region.

Acknowledgements

We would like to express our acknowledgements to Verena Keller, Tony Fox and Łukasz Ławicki for their helpful comments and to all who share their observations and information about breeding Goosanders in the Carpathians: A.-T. Bashta, A. Bokotey, V.N. Grishchenko, I.K. Istvan, D. Karaska, M. Kociuba, P. Kunysz, Sz. Mazgaj, P. Lešo, J. Ridzoň, P. Tamas, T. Wilk, K. Wojciechowski. P. Choróbski, K. Czajowski, M. Dyduch, J. Gil, J. Hasny, A. Hudy, P. Kauzal, M. Kukla, M. Legutko, T. Mazurkiewicz, S. Springer, P. Stolarz, A. Szulczyński, M. Twardowski, M. Wayda. Part of the study (the KIK/24 project) was supported by a grant from Switzerland, awarded through the Swiss Contribution to the enlarged European Union.

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Within and between year phenology of calling Spotted Crakes *Porzana porzana* in Denmark

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Abstract

Analysis of data relating to calling Spotted Crakes *Porzana porzana*, input to the Danish Citizen Science portal DOFbasen, suggested that on controlling for observer effort, national numbers reported annually have remained reasonably stable during 1981–2013, but with large influxes in a very few years, mostly due to large arrivals late in the season in June/July. Standard annual mapping of calling birds at Vejlerne, numerically the most important breeding area for the species in Denmark, correlated well with annual national indices over the same period of years. Calling birds mapped at Vejlerne and those reported to DOFbasen both showed a consistent bimodal pattern, with peaks in April/May and June/July, although the relative size of the second peak in particular varied between years. We speculate on the causes of these two peaks in calling activity which both potentially relate to birds defending territories and intending to breed. The often large late influx, and the occupancy of different territories during the second peak compared to the first, suggested the second wave of birds were different individuals to those recorded earlier in the season. Radio telemetry showed early breeding birds to be still present but silent during the second peak in calling activity, suggesting a new wave of late arriving birds in July (possibly from areas to the south or elsewhere where they may previously have attempted to breed) which potentially also attempt to breed in Denmark. We recommend continuing radio telemetry studies to confirm whether the same individuals call in both periods, supplemented by high quality sound recordings to differentiate individuals on the basis of their calls and assess the existence of any recognisable dialects across Europe. Stable isotope analysis of feathers grown outside the breeding areas would also help to provide a better understanding of the breeding status, origins and relative abundance of calling birds in these two waves.

Key words: annual abundance, Lille Vildmose, migration phenology, Vejlerne.

Despite being listed on Annex I of the European Birds Directive as a species of high conservation concern, very little is known about the abundance, distribution, habits and habitat requirements of the Spotted Crake *Porzana porzana* in Europe during the breeding period. Two major reasons for the lack of knowledge are: (i) the species' use of extensive wetland habitats which are difficult to access, and (ii) its generally highly secretive and silent nature, excepting the remarkable whiplash advertisement call given largely at night during the breeding season, mostly by males, but also by females which may duet with males (Cramp & Simmons 1980). Population estimates rely almost entirely on reports of calling birds, yet we still understand very little about how calling relates to breeding activity and abundance, not least because the calling period can extend between early April and early September (Stroud *et al.* 2012), can vary in timing during the night (Bengston 1962; Mortensen 1972; Mallord 1999; Schäffer 1999; Mackenzie 2000) and birds do not call every night, with calling activity potentially influenced by prevailing weather conditions (Stroud *et al.* 2012; Fox *et al.* 2013).

The Spotted Crake was considered a widespread and common summer breeding species in Denmark in the 1800s (Winge 1906), but had begun to decline even by the early 1900s (Løppenthin 1967). By 1960, it was considered that 45–115 pairs bred across 18 sites in Denmark (Ferdinand 1980) and that 32–55 pairs were nesting in the country by 1978–1981 (Dybbro 1985). The most recent breeding bird atlas found 22–61 breeding pairs at 15 sites during the 1990s (Grell 1998) and regular monitoring during 1999–2008 located numbers ranging from just over 200 to fewer than 25 pairs present each year (Bruun & Christensen 2008). The criterion for Spotted Crake to attain favourable conservation status within Denmark is that the breeding population should be stable or increasing from a minimal level of 35 pairs (Søgaard *et al.* 2007). Hence it is important when assessing the national conservation status of the species to be able to know what calling birds represent and how their number may fluctuate from year to year.

In this analysis, we attempt to assess the annual fluctuations in summer abundance of the species in Denmark based upon annual reporting of Spotted Crakes to the DOFbasen Citizen Science portal, supplemented by detailed mapping of calling birds at the single most important breeding concentration of the species, at Vejlerne in the northwest of the country, since 1978. Information about the timing and distribution of calling birds is used to interpret its phenology of migration and breeding status.

Methods

Annual numbers of reported Spotted Crake observations

We collated all reports of Spotted Crakes from the Danish Ornithological Society's (DOF) Citizen Science web portal "DOFbasen" (http://www.dofbasen.dk/), which amounted to 2,467 observations made between 8 May 1960 and 28 August 2013. Spotted Crake has been included in DOF's Rare and Threatened Species Programme since 1999 which encouraged all records to be entered into DOFbasen (Bruun & Christensen 2008). Total numbers of all bird observations entered into DOFbasen has increased steadily over the years, so we attempted to control the increase in observer effort and/or reporting rates by generating a calibrated assessment of annual relative abundance. To do so, we first truncated the data series to remove all years when the national numbers of Spotted Crakes reported (n) was less than 10 (effectively prior to but including 1981). We then adjusted for the reporting effort to DOFbasen associated with breeding birds, by dividing n by the annual number of reports of all breeding bird records (d) in that year, to give an index of relative abundance for Spotted Crakes (i):

$$i = n/d$$

Annual abundance of Spotted Crakes at Vejlerne

Reporting of observations may however be limited by the fact that similar numbers of observers visit only the same known sites for Spotted Crakes each year. To attempt to control for this effect, we also compared the national index with the annual standard monitoring census data generated at the most important site for the species in Denmark. Vejlerne (56°59'–57°07'N, 8°52'–9°08'E) in northwest Jutland is one of Denmark's outstanding freshwater wetlands and is a National Nature Reserve, a Special Protection Area and a Ramsar site, owned and managed by the Aage V. Jensen Foundation since 1993. The reserve comprises an embanked area of some 6,000 ha of grazed meadows, marshland, reedbeds and open water areas, that were until 1880 part of the Limfjord, now managed for the conservation of the high wetland biodiversity of the area. It has long been recognised as the most important area in Denmark for its breeding Spotted Crakes (Dybbro 1976; Grell 1998; Kjeldsen 2008) which are mainly found in the wet zones between meadows and reedbeds (Bruun & Christensen 2008). In recognition of its national and international importance, the breeding birds of the reserve have been monitored since 1978, although the individual records from this scheme are not entered into DOFbasen. The monitoring programme undertakes a regular assessment of breeding numbers present of nocturnally active Spotted Crakes, which includes regular night-time transects to count calling birds, following standardised routes and count techniques used from 1978 onwards. The presence of calling birds is mapped by determining angles to calling individuals from more than one observation position and plotted to determine occupancy of territories as the basis for estimating numbers of territory holders present in each year (Kjeldsen 2008). Given its importance and the fact that the numbers recorded there are not regularly entered in DOFbasen, we consider the annual abundance of Spotted Crakes at Vejlerne as an independent estimate of annual fluctuations in abundance at this important site. No counts were made at Vejlerne in 2004.

Annual variation in patterns of reports of calling observations

Each DOFbasen entry consists of the number of individuals recorded, their behaviour and information about the nature of the observations. For the purposes of this analysis, we are most interested in calling birds because it is generally considered that these in some way constitute birds advertising their presence in relation to breeding (either territorial defence and/or mate attraction). To filter this dataset for birds only making advertisement calls, we retained all records: (i) for which any part of the behaviour was recorded as “calling”, “staging and singing”, “staging, only heard” or “territory defence”, (ii) all records without behaviours where there was some indication in the comments or observation circumstances that showed the birds were heard, and (iii) all records made between 23.00–04.00 h for which there was no other information, assuming that these were of calling individuals. For each year, from 1998 to 2013 inclusive (years for which we considered there were sufficient data, where numbers of reports were > 50) we extracted all observations corresponding to these criteria and plotted them in 10-day periods from 1 January in each year as a percentage of the total observations of calling birds in that year to correct for annual variations in abundance.

Radio telemetry and mapping of calling individuals

In summer 2013, three males and one female (the latter paired to one of the males) were caught in the northern part of Lille Vildmose in north eastern Jutland (56°55’N, 10°11’E) using playback calls, mist nets, hand nets and walk-in traps (see Fox *et al.* 2013). Birds were fitted with 1.38 Biotrack Pip AG 392 VHF radios and tracked until the battery power was exhausted (see Fox *et al.* 2013 for full description). Positions at times through the day and night were determined by triangulation from more than one observation point on 18 dates between 31 May and 16 August 2013 (as presented in Fox *et al.* 2013). This method was used to determine the presence of the tagged (and potentially silent) birds in relation to the presence of calling birds which were monitored throughout Lille Vildmose on 16 nights between 16 April and 9 July (see Fox *et al.* 2013 for details).

Results

Annual number of Spotted Crake observations

The average annual number of Spotted Crakes reported to DOFbasen from 1982 to 2013 inclusive was 122 (ranging from 10 in 1985, up to 465 in 2003). When corrected for observer effort by dividing the number of Spotted Crakes reported by the number of reports of all breeding bird species, there was considerable annual variation in numbers (Fig. 1), but it can be seen that there has been no significant change in relative abundance over the time series

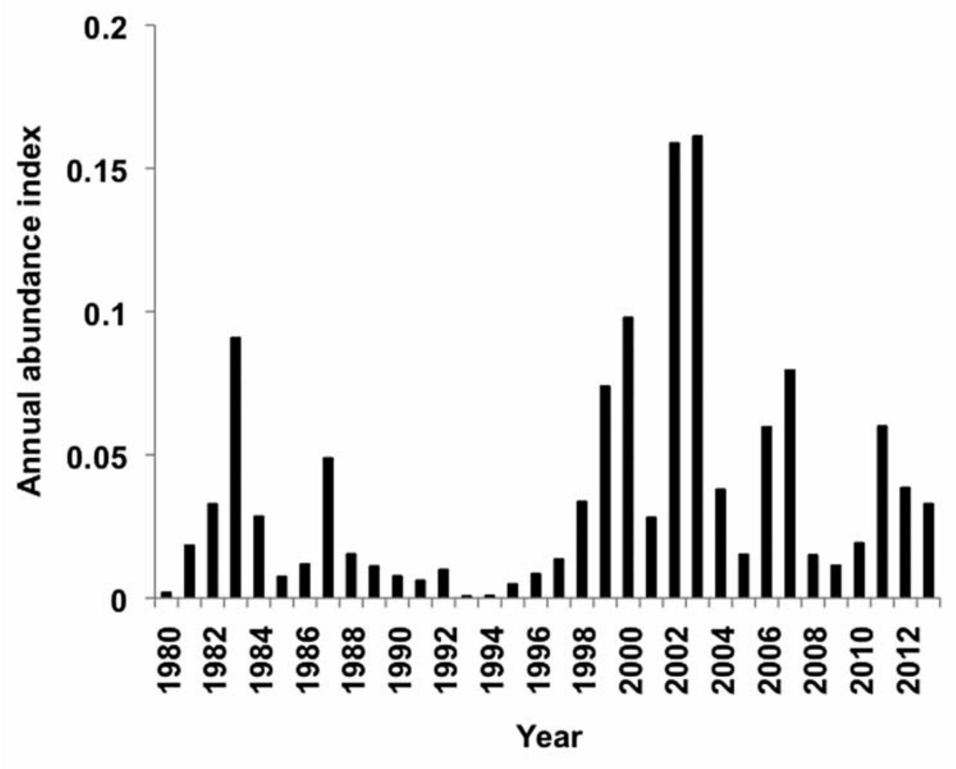

Figure 1. Annual index of the numbers of Spotted Crakes in Denmark reported to the Danish avian Citizen Science Portal DOFbasen during 1980–2013. The index adjusts for observer effort by dividing the total numbers of individual Spotted Crakes registered by the numbers of all breeding bird reports in each calendar year (*i.e.* as a measure of breeding bird reporting effort). Data from 1980 and 1981 are shown for completeness, but not included in the analysis because < 10 birds were reported in both years.

($y, i = 0.0011y - 2.175$, $F_{1,32} = 2.52$, $r^2 = 0.07$, $P = 0.12$, n.s.), although there have been a series of years with exceptional numbers (1983, 1999, 2000, 2002, 2003 and 2007) when numbers exceeded 0.0733, double the mean index value. Interestingly, the annual indices for Corncrake *Crex crex* and Common Quail *Cortunix cortunix* (calculated in the same way, weighing reports for annual breeding records submitted to DOFbasen) were highly significantly correlated with Spotted Crake indices for the years 1980–2013 ($r^2_{32} = 0.77$, $P < 0.0001$ and $r^2_{32} = 0.34$, $P < 0.0001$, respectively). There was no correlation between annual breeding abundance in the UK (data from Stroud *et al.* 2012) and the Danish indices presented here (both data natural log transformed during 1980–2009; $r^2_{30} = 0.02$, $P = 0.51$, n.s.) to suggest major flyway level fluctuations in annual abundance affecting numbers in both countries.

Annual abundance of Spotted Crakes at Vejlerne

The annual abundance of calling Spotted Crakes mapped on territories at Vejlerne is shown in Fig. 2, where it can be seen that there were similar trends in annual abundance to those generated from DOFbasen reports, although with lower numbers since 2003. Numbers correlate well between the adjusted DOFbasen observations and annual numbers monitored at Vejlerne ($r^2_{33} = 0.60$, $P < 0.001$ for 1978–2013 inclusive), which suggests that in years with many reports from throughout Denmark, there were also many registrations of calling birds at Vejlerne.

Annual variation in reports of calling observations

The reports of calling birds throughout Denmark showed a conspicuous bimodal distribution through the summer (Fig. 3) as did the mapped calling birds recorded at Vejlerne during 1978–2003 (Fig. 4, although differences in the relative size of the two peaks were much less there) with a clear peak from mid–April to mid–May but another, even greater peak from the last week of June until the last week of July. This general pattern of song phenology masks considerable year to year variation however, although the bimodal pattern of song is relatively constant. In some years, there is an evident dominant early peak (as in 1998, 2005, 2006 and 2008, see Fig. 5); in other years the later peak is the dominant feature (as in 1999, 2000, 2002, 2003 and 2007, Fig. 5), whilst in yet other years, the two peaks are even and are very similar between years (2001, 2004, 2011 and 2012, Fig. 5). In two recent years, the spring arrival has been relatively delayed and the bimodal pattern dampened but still evident (2009 and 2013, Fig. 5). Interestingly, four of five years with conspicuously large proportions of calling birds in the June/July peak (1999, 2000, 2002 and 2003) were years of very high overall numbers of reports of calling birds. It would thus appear that in most years between 1998 and 2013, there was a mean of 50 (s.e ± 7.9, range = 11–111) reports of calling Spotted Crakes during April/May, but greater and more variable numbers (mean 91 ± 19.9, range 2–248) of calling birds in the second peak in June/July.

Do birds in the two peaks sing in the same areas?

Based on mapping of calling birds at Vejlerne, there was evidence from the major influx in 1983 that although some birds arrived and set up territories in April/May of that year (8 individuals), the major numbers (31) arrived in June/July and began calling in areas not previously occupied by calling birds (Christensen & Engelstoft 1984). In summer 1984, exceptional numbers occurred again, although the main arrival was in the first peak (44 territories) with fewer in the second (22, Rasmussen 1987). In 1986, when more normal numbers occurred, the first peak (23) again exceeded the second (9) and their distributions were again mutually exclusive (Danielsen 1989) and the same was the case in 1988 when 51 and 32 territories were mapped, with the birds in the second wave occupying different areas to the first (Petersen 1990). Similar patterns were reported in summer

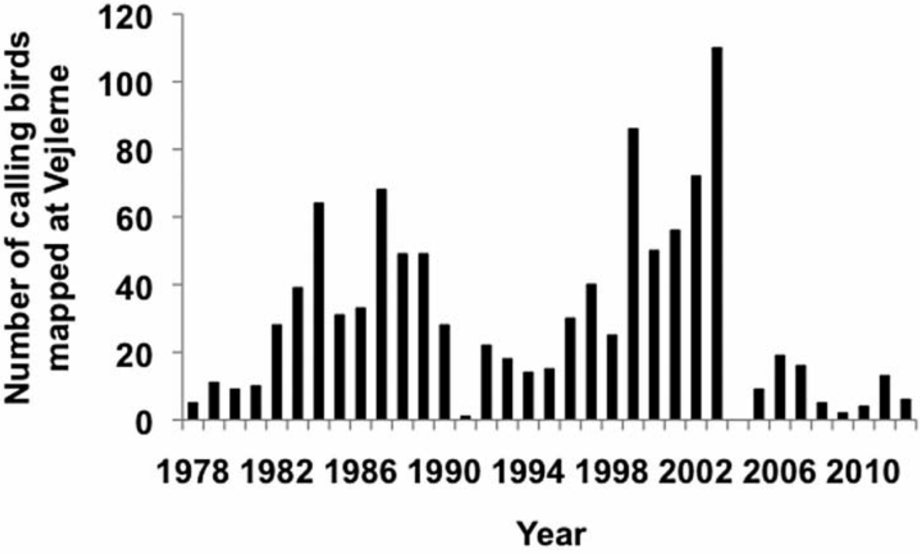

Figure 2. Estimated annual number of calling birds at Vejlerne, north Jutland during 1978–2012, based on mapping of birds' distribution, using the same census methods each year. Data from Kjeldsen (2008) and Nielsen & Kjeldsen (2013).

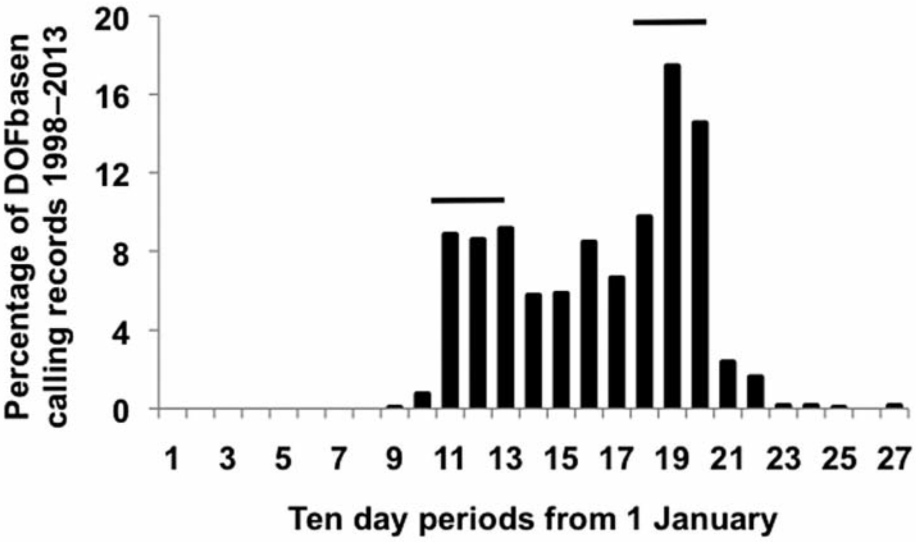

Figure 3. Frequency distribution of all calling Spotted Crakes reported to DOFbasen during the years 1998–2013 inclusive, in 10 day periods from 1 January. Horizontal lines above histogram columns indicate the two peaks in reporting of calling birds in April/May and June/July.

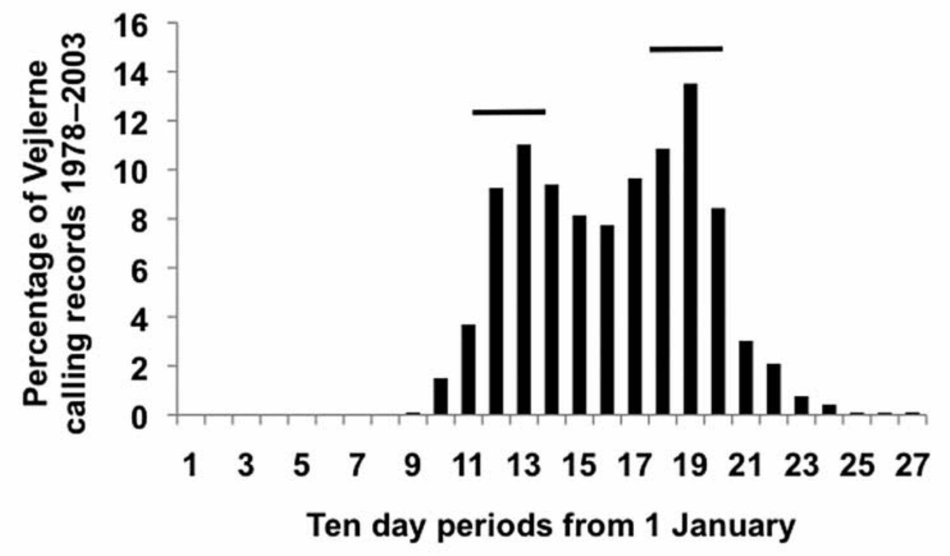

Figure 4. Frequency distribution of all calling Spotted Crakes mapped at Vejlerne during the years 1978–2003 inclusive, in 10 day periods starting 1 January. Horizontal lines above histogram columns indicate the two peaks in reporting of calling birds in April/May and June/July.

1989 and 1990 (Seidenfaden 1991; Petersen 1993). Based on intensive observations at Lille Vildmose in 2013 (reported in Fox *et al.* 2013), three territory-holding radio-tagged males were exclusively vocally active in the first peak, while "new" birds were heard in two other areas in the later peak, but in three other areas, birds were heard calling during both periods.

Are the birds calling in the two peaks the same individuals?

Tracking data from the three radio-tagged males and one female at Lille Vildmose during summer 2013 showed not only that all four birds arrived during the first peak, but that the males commenced calling in the first peak that year. All four tagged birds were present from the time they were caught in late May until the end of June (*n* = 1) and late July/early August (*n* = 3 included the male and female of the pair) when the transmitter batteries ran out (Fox *et al.* 2013). In one case, a nest was found, but the constant presence of these birds throughout the second peak when birds were calling elsewhere at Lille Vildmose suggest that the three tagged males remained on site to raise their young in the area at or near where they defended their territory, having ceased calling in late May. Their silent presence during the second peak confirms that these individuals are still present on their existing territories, but did not start to call as part of the second peak and also that they did not move to contribute to the second wave of calling on site or at wetlands elsewhere.

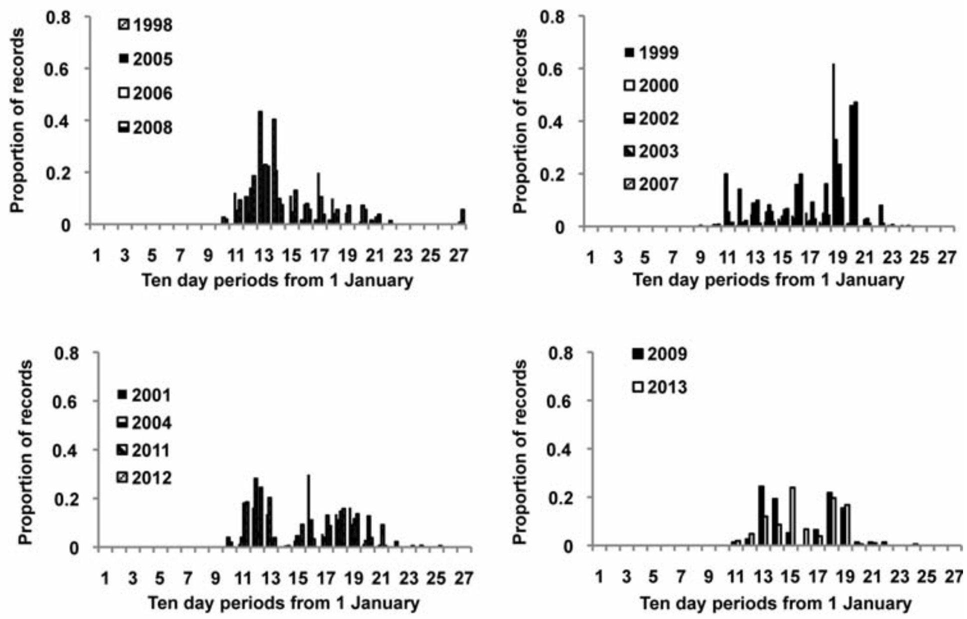

Figure 5. Annual frequency distribution of all records of calling Spotted Crakes reported to DOFbasen during the years 1998–2013 inclusive, broken down by 10 day periods starting 1 January as shown in Fig. 3. Years are aggregated by the nature of the frequency distributions – top left shows a dominant arrival peak in April/May, top right a dominant arrival peak in June/July, bottom left shows even bimodal peaks in both periods and bottom right shows a similar distribution but after a delayed arrival in spring.

Discussion

Controlling for observer effort, DOFbasen registrations suggest that despite wide fluctuations between years, the numbers of reported Spotted Crakes have remained reasonably stable during 1981–2013. The greatest source of inter-annual variation appears to arise from the periodic influx of birds as happened in large numbers in 1983, 1998, 1999, 2002 and 2003 and to a lesser extent in 1984, 1987 and 2000. Based on standard mapped distributions of calling birds since 1978 at the numerically most important site in Denmark, Vejlerne, the annual abundance there was highly correlated with the corrected national abundance and showed the same peaks in abundance in the same years. These results suggest that it may be extrinsic factors that affect the annual numbers in Denmark, or that macro-environmental factors (such as winter and spring precipitation and the subsequent effect on water tables) affect overall settlement of calling birds. Studies elsewhere in the range show that breeding birds abandon breeding areas when the habitat dries out and water level can affect the abundance of settling birds (for example in Poland; Schäffer 1999) and some earlier analyses showed correspondance between higher water levels at Vejlerne and numbers of calling Spotted Crakes in individual management units (Kjeldsen 2008) although others did not (Clausen *et al.* 2006). Hence, the condition of wetlands in Denmark in spring does likely contribute to the numbers of Spotted Crakes in the first peak remaining and breeding successfully.

Temporal analysis showed that there was a conspicuous bimodal distribution in the abundance of calling Spotted Crakes through the summer with clear peaks during mid-April to mid-May and from late June to late July. Although this pattern was not evident from a similar analysis of British data of calling Spotted Crakes (see Fig. 13 in Stroud *et al.* 2012), those authors stated that there was a peak in activity from mid-April to mid-June "with peaks in early and late May". Song phenology in Denmark showed considerable year to year variation, which subjectively could be summarised into the four classes shown in Fig. 5, namely a dominant early peak, a dominant later peak or two similarly sized peaks, with a variant of the latter resulting from a late spring arrival, but retaining a bimodal distribution. What is perhaps most interesting is that the major influxes of 1983 (based on data from Vejlerne), 1999, 2000, 2002 and 2003 (DOFbasen elsewhere in Denmark) were all associated with exceptional numbers of calling birds reported in the second peak during July, whilst those of 1984 (Vejlerne) and 1998 (DOFbasen) were associated with an early peak in calling birds and those in 1987 (Vejlerne) were equally distributed between early and later peaks.

What do the two peaks in calling birds represent? There could be several explanations, of which the simplest two are that: (i) two groups of Spotted Crakes arrive sequentially in Denmark and begin to establish territories at different times, or (ii) after an initial period of arrival, pairing and reproduction, the same birds restart territorial advertisement once investment in the first brood is completed. The data presented here tend to suggest that the second of these hypotheses is not supported, firstly because the second peak can be numerically far superior to the earlier peak in numbers, which suggests more territory holders are present later in the season, although we cannot exclude the possibility that many birds establish territories, pair successfully and reproduce in both periods without detection. The radio-tracking results suggested birds may stop calling soon after attracting a mate. Furthermore, data from Vejlerne in several years and to some extent Lille Vildmose in 2013 suggest that birds that begin to call late on in the season occupy different areas to those occupied during the first peak in abundance. Without tracking more individuals, we cannot exclude the possibility that this is merely because the same birds shift in relation to habitat change (for example water table recession; Schäffer 1999; Fox *et al.* 2013) and so exploit two different areas within the same year to raise broods in ephemeral hydrological conditions as these change through the course of the summer. The limited radio-tagging of individuals at Lille Vildmose in 2013 suggest this was not the case – all three males fell silent soon after marking, but remained active in the same general areas throughout the period when they were likely involved in brood rearing, from whence no further calling was heard (including during the second peak in calling at this site in July, see Fig. 2 in Fox *et al.* 2013).

These lines of evidence suggest that at least some of the birds at this site were single brooded at Lille Vildmose, remained on the territory which they had defended in the early phase after arrival to raise young, and did not take part in the second period of territorial advertisement in July 2013. Although we cannot prove this to be the case, the presence of new birds calling in previously unoccupied areas during July suggests new immigrants into the area. This raises the intriguing prospect as to whether this second wave of Spotted Crakes calling in July (and which are thought also to breed, because newly hatched young continue to be seen at Vejlerne well into August; Kjeldsen 2008) are new arrivals coming from areas further south and east within the breeding range having attempted to nest elsewhere, as is suspected to occur amongst Quail *Corturnix coturnix* (Guyomarc'h *et al.* 1998). This seems a likely possibility, given the apparent need of the species for stable shallow water with dense emergent vegetation in which to breed (Mallord 1999; Mackenzie 2000; Fox *et al.* 2013). Unless spring-fed to maintain water tables, the type of shallow water wetland vegetation favoured by the species (Schäffer 1999) is the very type of wetland habitat most likely to dry out, especially in the warm and semi-arid areas of North Africa, and of southern and eastern Europe where this species also breeds. Hence, it is not impossible to conceive of Spotted Crakes attempting and potentially succeeding in breeding in the south and east of the nesting range and individuals continuing north to attempt a second clutch in areas such as Denmark. The variable nature of the climate in the south may also account for the very large differences in numbers occurring here between years, although there was no clear correlation between the calibrated numbers entered into DOFbasen and spring/summer temperatures or hydrological drought condition in southern Europe in year *n* or *n*–1 (using data from Kavalieratou *et al.* 2012 for Greece; Sinoga & Gross 2012 for Spain) or precipitation in Poland (unpublished data). Kjeldsen (2008) also found no correlation between June temperature in Denmark and abundance at Vejlerne. Nevertheless the species is known to move locally during the breeding season in relation to local drying of groundwater conditions (Fox *et al.* 2013) and in extreme cases abandon others due to loss of shallow water (Schäffer 1999), which could provide an explanation for the arrival of a second wave of birds in July still with time to establish territories, pair and raise young before the autumn (Kjeldsen 2008). It would be interesting to see if the second wave appears in the avian observation portals of neighbouring countries such as the UK and Sweden.

It is intriguing that numbers of reported Corncrake and Quail reported to DOFbasen show highly variable abundance indices, with conspciuous influxes of Corncrake in 2000, 2002, 2003 and 2007, and of Quail in 2000–2003, 2006–8 inclusive, 2010 and 2011, and that their annual abundance indices are highly correlated with those of Spotted Crake. Whilst this could reflect suitability of settling and breeding conditions in Denmark or some factor (such as weather conditions) that makes one or other set of birds in these peaks more detectable to observers in those years, we favour the hypothesis that conditions elsewhere in the range of these species result in greater numbers moving to Denmark. To find further support for the latter hypothesis, we recommend that radio-tracking of Spotted Crakes in both peaks continue in order to further understand the movements, habitat use and nesting phenology of individuals associated with both waves. We also suggest that a combination of radio telemetry and high quality sound recording should be implemented to determine the ability to detect individual birds from their calls (as has been demonstrated for Corncrake; Peake *et al.* 1998; Peake & McGregor 2001). This would further confirm the contributions of individuals to the two peaks in calling as well as potentially test for differences in dialect between birds calling in the two periods if they are geographically separated in most years (again as has been demonstrated for Corncrake; Peake & McGregor 1999; Mikkelsen *et al.* 2013). These approaches could usefully be supported by genetic and stable isotope analysis using tissues from birds calling in both periods to attempt to assess any genetic separation or evidence of using different habitats in spring that could contribute to a better understanding of this perplexing phenomenon. The ability to track year on year changes in abundance locally and nationally is dependent on understanding how calling birds relate to potentially breeding individuals. It is therefore important that we understand the birds' movements in order to avoid double-counting, by attempting to differentiate origins and individuals amongst calling birds at a site.

Acknowledgements

We are deeply grateful to all the many birdwatchers that enter their records onto DOFbasen without whom such analysis would be impossible, to the Danish Nature Agency for the active support and funding to carry out this project, and to them, the Municipality of Aalborg and the Aage V. Jensen Fond for kindly granting permission to work on the area during the Life + Nature restoration programme on Lille Vildmose. We are very grateful to the many experts that shared their knowledge about the site and Spotted Crakes, but especially acknowledge the contributions made by John Mallord, Thorkild Lund, Jan Skriver, Ian Francis, David Stroud, Eileen Rees and two anonymous referees and our grateful thanks also to Lars Dalby and Kevin Clausen for assisting with the capture of crakes.

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Photograph: Spotted crake fitted with a metal ring, geolocator and radio antenna at Lille Vildmose, Denmark on 15 May 2014, by Mark Desholm.

The status of Ferruginous Duck *Aythya nyroca* breeding and wintering in China

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Abstract

Analysis of data published in the China Bird Report (CBR) and other literature between 1979 and 2013, along with our own field observations, found that the Ferruginous Duck *Aythya nyroca* now occurs throughout most of China. This contrasts with the situation in 1979, when the species was restricted to a few areas in the west of the country. Ferruginous Duck is predominately a winter visitor to China; up to 850 birds have been counted in Yunnan Province, 4,000 in Sichuan Province, and the wintering population is estimated at 6,000–8,000 individuals. In summer, the breeding population is estimated at 3,000–4,000 individuals (1,500–2,000 pairs), with highest concentrations in Xinjiang (*c.* 900–1,700 individuals) and Inner Mongolia (750–1,400 individuals). In China, females lay 6–11 eggs, which hatch in early June. The present population in China is likely to have spread from neighbouring central Asia (Kazakhstan, Kyrgyzstan or Mongolia). Since 1980, the climate had gradually changed from warm-dry conditions to a wetter climate in northwest China, making it a more suitable breeding area for this species and providing corridors for their expansion to the east. If the present trend continues, southern China could in the near future become an important wintering area for a duck species that is now increasingly common elsewhere in China.

Key words: *Aythya nyroca*, breeding, distribution, Ferruginous Duck, habitat, population size, range expansion, Xinjiang.

The Ferruginous Duck *Aythya nyroca* is listed as “Near Threatened” on the IUCN Red List and is also a priority species on three prominent international conservation treaties: the European Union Birds Directive, the Bern Convention and the Bonn Convention (under the African-Eurasian Migratory Waterbird Agreement; AEWA) (BirdLife International 2012). There have been international concerns about population declines and range contraction in the western Palearctic, and an international species action plan has been developed to help to conserve the species (Robinson & Hughes 2006).

The Ferruginous Duck breeds principally

in southwest Asia (from the west to China and the south to Pakistan and India), central and eastern Europe, and North Africa (Callaghan 1999; Vinicombe 2000; Kear 2005). Four populations are currently recognised by Wetlands International and the one encompassing China is described as the "S, E and SE Asia" population. The wintering range of the East European population partly overlaps with the breeding range and extends to the Middle East, northeast and west Africa (mainly Mali and Nigeria) and southeast Asia (Kear 2005). Currently the global population is estimated at *c.* 177,400–252,600 individuals (Wetlands International 2014). The duck has undergone declines in its population size and changes in distribution over the past few decades (Ali & Ripley 1978; Perennou *et al.* 1994; Lopez & Mundkur 1997; Grimmett *et al.* 1999). Primary reasons for its decline are thought to be unsustainable levels of hunting, habitat degradation and loss (Callaghan 1997). Recent surveys have found high numbers, perhaps into the tens of thousands, in Asia (Li *et al.* 2009). In China, it was known to be a summer visitor to the northwest and a migrant through the central provinces, with winter records from the middle reaches of Yangtze floodplain reported during the mid–late 20th century (Cheng 1987). More recently, Ferruginous Duck accounted for *c.* 0.13% of all wildfowl recorded as taken by hunters between 2009–2012 (MaMing *et al.* 2012), though recent photos of ducks recovered from hunters suggest that this proportion could be higher at around 5–10% (Fig. 1). There is much suitable habitat in the country, and this species is now thought to be common in China, although quantitative data are lacking. This study is the first review of the available data to assess the population, distribution and breeding ecology of this species in China.

Methods

In order to assess breeding and wintering abundance and distribution, and to describe

Figure 1. Eighty six Ferruginous Duck in *c.* 580 wild duck seized from poachers by the Xinjiang police on 9th July 2014. (Photograph by Roller MaMing).

the breeding ecology of the Ferruginous Duck in China, we reviewed about ten years of data published in the China Bird Report (CBR, checking *c.* 438 reports from across the country) along with reference literature from 1979 to 2013, including international waterbird census (IWC) data collated by Wetlands International and previously by the International Waterfowl & Wetlands Research Bureau and the Asian Wetland Bureau (Cheng 1979; Lopez & Mundkur 1997; Delany & Scott 2002; National Forestry Bureau, NFB 2009; Li *et al.* 2009; Ma 2011; Zhao *et al.* 2013). CBR data are collected by volunteers who differ in levels of skill in identifying species and making counts; therefore it is likely that, although Ferruginous Duck are relatively easy to identify in the field, there are some errors in the data, and an increased interest in ornithology within China has biased towards increased reporting rates in more recent years. In collating records, we have attempted to verify the data received from coordinators and observers, and have checked with coordinators the validity of some of the information. No information has been provided to the China Bird Report for Hong Kong and Taiwan, so literature searches and information from key researchers provided the best overview of the status of Ferruginous Duck in these two regions.

In addition, from 2011–2013 inclusive, we carried out field surveys of the breeding ecology, number of breeding pairs and migration of Ferruginous Duck in the Xinjiang Uygur Autonomous Region of China, using fixed route surveys, direct counts and interview surveys (Zhao *et al.* 2013).

The distribution of sites where Ferruginous Duck have been recorded in China since 1979 is shown in Fig. 2. Information on the location of each site was derived from the site forms submitted by observers. Although it was not feasible to check the accuracy of all information recorded, an attempt was made to check the location of all sites known to be important for the species. Some sites where only local names were recorded and numbers were relatively low could not be located precisely; sites illustrated in Fig. 2 therefore account for only *c.* 60% of all records of Ferruginous Duck sites from the review.

Results

Population size

From published winter count data (Rose & Scott 1994; China Bird Report 2001–2013; Delany & Scott 2002; National Forestry Bureau, NFB 2009; Li *et al.* 2009; Ma 2011) we estimated that there is a non-breeding population of 6,000–8,000 Ferruginous Duck in China (Table 1). In general, the species occurs at elevations ranging from 0–3,900 m above sea level, but is mostly found at 600–1,500 m. Maximum numbers occurred in January (about 6,000 individuals), although significant numbers (between 3,300–5,400) are also reported in February, November and December, with smaller numbers (380–1,700) in March–October (Fig. 3). From these data it appears that Ferruginous Duck is mainly a wintering species in southern China, where it occurs from early October to March.

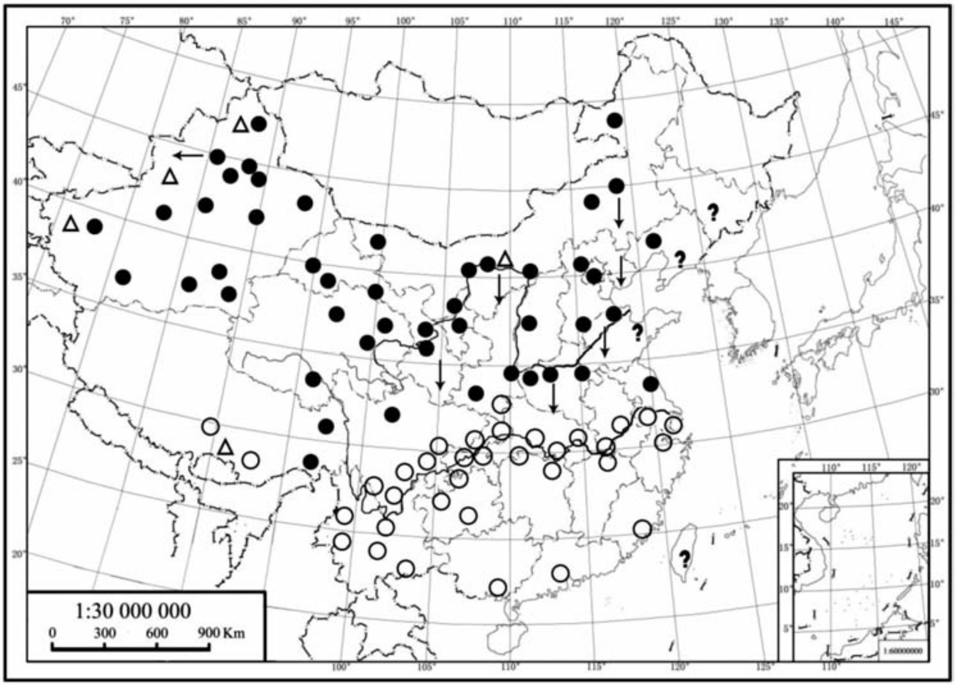

Figure 2. Distribution of Ferruginous Duck in China from 1979 to 2013. Note: ○ = wintering concentrations (recorded in the last ten years); ● = summer concentrations (recorded in the last ten years); △ = historical records (pre-1979); ↓ = migration route; **?** = vagrant.

The species also breeds in northern and northwest China. In spring (early March to late April) the species migrates to northern China and only small numbers remain in the wintering areas to which they return between late October and mid-November.

Distribution

The range of this species appears to have changed considerably over the last 40 years, although the extent to which it has done so is difficult to ascertain, as observer coverage and reporting has increased with the recent development of the CBR and bird-watching societies in China. In the 1970s, the species bred principally in northern and western Xinjiang, at Wuliangsuhai Lake in Inner Mongolia, and in southern Tibet. During migration, it was found at a few places such as Gansu, southern Shaanxi, northern Sichuan, Yunnan and southwest Guangxi. In winter it was occasionally reported from Shandong and Hunan provinces and less frequently elsewhere (Cheng 1979). More recently, the ornithological literature and the CBR indicate that ducks have extended their range to most of China, and the species has been recorded in *c.* 94% of all provinces over the past decade, including Xinjiang, Tibet, Qinghai, Gansu, Inner Mongolia, Liaoning, Hebei, Beijing, Tianjin, Ningxia, Shanxi, Shaanxi, Shandong, Jiangsu, Anhui,

Table 1. Maximum numbers of Ferruginous Duck recorded in various parts of China in a single year between 1979 and 2012, broken down by season. Estimated numbers present during the peak season are also given for each region.

Province	**Site**	**Altitude (m)**	**Number of observation records (times)**	**Maximum number of ducks recorded (individuals)**				**References**
				Summer	**Winter**	**Passage**	**Estimate**	
Anhui	Hefei	20–30	1	–	5	–	< 100	CBR
Beijing	Changping, Huairou, Miyun, Beijing & Yanqing	30–500	68	6	3	165	300–400	CBR
Fujian	Fuzhou	30–220	1	–	50	–	< 100	NFB 2009
Gansu	Baiyin, Dunhuang, Lanzhou, Subei, Luqu &Yongjing	1,000–2,000	24	218	1	124	400–500	CBR
Guangdong	Guangzhou	30–50	2	–	6	2	< 100	CBR
Guangxi	Beihai	10–20	1	–	3	–	< 100	CBR
Guizhou	Guiyang & Weining	1,000–2,300	15		274	50	500–600	CBR
Hebei	Huailai, Qinghuangdao, Huanghua & Hengshui	20–80	12	15	–	44	< 100	CBR
Henan	Kaifeng, Lingbao, Luoyang, Sanmenxia, Mengjin, & Zhongmou	60–500	15	6	118	2	200–300	CBR
Hubei	Honghu, Yangxin, Wuhan & Lingzihu	20–130	5	220	–	–	300–400	Ge *et al.* 2004

Hunan	Yueyang	20–50	1	–	6		100–200	CBR
Hong Kong	Hong Kong	0–500	6	–	4	–	50	Carey *et al.* 2001
Jiangsu	Sheyang	10–50	4	–	3	–	< 100	CBR
Jiangxi	Xinjian	30–130	1	–	190		400–500	CBR
Liaoning	Dandong, Faku &	90–100	4	–	–	6	150–250	CBR, IWC
Inner Mongolia	Baotou, Chifeng, Gulinhe & Ejinaqi	600–1,100	10	1,238	–	52	1,500–2,800	NFB 2009
Ningxia	Qingtongxia, Shizuishan, Zhongwei & Yinchuan	1,000–2,000	4	14	–	94	150–200	NFB 2009
Qinghai	Delingha, Gonghe, Guide & Yushu	1,500–2,500	12	45	–	20	150–200	CBR
Shandong	Dongying, Kenli	20–90	2	–	–	2	10–20	CBR
Shanxi	Taiyuan	500–1,000	1	–	–		50–100	CBR
Shaanxi	Heyang, Huxian, Xian & Xianyang	300–1,100	10	5	355	12	400–500	CBR
Shanghai	Chongming & Nanhui	0–5	2	1	6	–	< 100	CBR
Sichuan	Throughout Sichuan	500–2,500	93	57	4,000	–	2,000–4,000	NFB 2009
Tianjin	Jinghai & Tianjin	0–5	2	–	–	6	< 100	CBR
Taiwan	Tainan	0–1000	8	–	8	–	8	Liu *et al.* 2010
Tibet	Changdou & Linzhi	3,000–3,900	1	2	–	–	< 100	CBR
Xinjiang	Throughout Xinjiang	50–3,900	97	1,032	141	–	1,800–3,400	Field survey
Yunnan	Throughout Yunan	500–2,000	34	13	850	61	1,500–2,000	NFB 2009
Zhejiang	Haining & Hangzhou	0–100	2	5	10		< 100	CBR
Total			**438**	**2,877**	**6,033**	**640**	**6,000–8,000**	

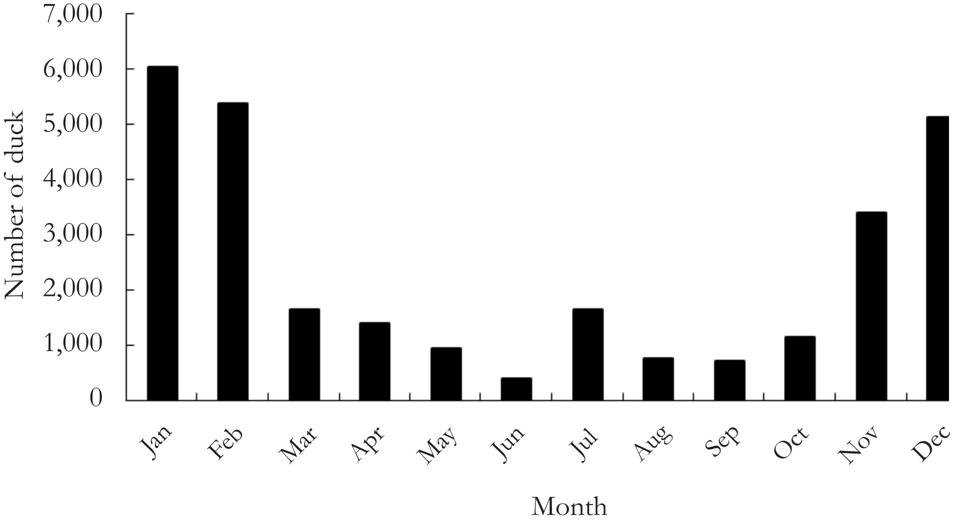

Figure 3. Maximum monthly counts of Ferruginous Duck reported to the China Bird Report and other ornithological publications.

Hubei, Hunan, Zhejiang, Shanghai, Jiangxi, Sichuan, Guizhou, Yunnan, Fujian and Guangdong. The breeding population is still mainly restricted to Xinjiang, Inner Mongolia and with scattered breeding in Gansu, Shanxi, Shaanxi, Hebei, Beijing, Henan and Tibet. In winter, the species appears to concentrate in Sichuan, Guizhou, Yunnan and Jiangxi, but also occurs regularly in Hunan and Hubei, with small numbers in Zhejiang, Fujian, Guangdong, Guangxi and Southern Anhui. Small numbers or vagrants occur on passage in Qinghai, Liaoning and Shandong. Despite the lack of early coverage and more limited reports before 1979, it would seem that the species has expanded from wintering in very few provinces 35 years ago to 30 provinces throughout the country at present, a range expansion of 2,000–3,000 km, or an average of 50–60 km per year (Ma 2010).

Breeding

Based on literature sources, the numbers breeding in China are estimated at 3,000–4,000 individuals (1,500–2,000 pairs), with most occurring in Xinjiang (900–1,700 individuals) followed by Inner Mongolia (750–1,400 individuals; from counts in Table 1). In the last 10 years, > 200 Ferruginous Duck have also been recorded in Gansu and Hubei during the summer, where they are likely to be breeding, with smaller numbers in other provinces of northern and central China including Qinghai and Sichuan (Table 1). The species is mainly migratory although little is known about its migratory routes. Spring migration begins as the birds leave their wintering grounds in mid-March. It breeds from early May to mid-June in single pairs or loose groups. It shows a preference for well-vegetated, closed, small and comparatively shallow wetlands in arid regions, such as fishponds, sewage pools, artificial reservoirs, natural lakes, slow flowing rivers, paddy fields, seasonal wetlands and salt lakes with low salinity. The female lays 6–11 eggs, which hatch in early June in Xinjiang. Departure from the breeding grounds begins in early October with most birds gone by mid-November, although our observations showed that some individuals in southern Xinjiang may remain on the breeding grounds there throughout the year. During migration, the species is usually encountered in small groups of 20–50 individuals (Zhao *et al.* 2013).

Discussion

Given that the range of the Ferruginous Duck may fluctuate considerably with wetland availability from year to year, it is unclear what proportion of the Asian population is currently counted (Petkov *et al.* 2003). There have been declines in Europe, but evidence of a decline in the larger Asian populations is sparse, and sometimes contradictory (Collar *et al.* 2001; Cao *et al.* 2008; Li *et al.* 2009). For instance, according to Li *et al.* (2009), there has been substantial variation in winter numbers in southern Asia, with estimates ranging from 6,512–12,863 individuals in 1987–1997 and from 31,280–97,205 individuals in the years 1998–2007. During the 1970s, the species bred mainly in northern and western Xinjiang, at Wuliangsuhai Lake (Inner Mongolia) and in southern Tibet, and these remain the main breeding areas within China. However, the species has been increasingly reported in a number of other provinces in northern and central China during the summer over the past 10 years. Pre-1979 records indicated that the winter distribution was limited to Shandong and Hunan. Now, Ferruginous Duck have been observed at wintering sites across central and southern China, and the numbers present in mid-winter are estimated at *c.* 6,000–8,000 individuals. We consider this estimate to be very conservative, particularly in comparison with the *c.* 100,000 thought to be over-wintering in southern Asia (Li *et al.* 2009). The most likely potential explanation for this apparent range expansion is that there is now more suitable habitat in China than in former times. Furthermore, since strict gun controls were imposed in China in the 1990s, there has been a reduction in hunting pressure on this species, though this has been offset by the illegal trapping and poisoning of waterbirds within China in recent years. Some of China's wintering population is likely to come from neighbouring parts of central Asia (notably Kazakhstan and Kyrgyzstan) where there are large numbers of breeding pairs (Petkov *et al.* 2003). Since 1980, the climate has changed from relatively warm-dry to a wetter climate in northwest China providing this species with more suitable habitat and corridors for expansion to the east (Shi *et al.* 2002, 2003; Ma 2010). There is also some evidence for population declines in India and Kazakhstan in recent decades (BirdLife International 2012).

Traditionally it was thought that individuals from Central Asia wintered in the Middle East and northeast Africa (mainly Sudan and Ethiopia) and southeast Asia (Vinicombe 2000). In former times, the

Ferruginous Duck was mainly a wintering species in south China, where the population size in winter was always greater than in summer, as now. It remains chiefly a migratory winter visitor to China, although little is known about its migration routes. It is widely distributed and very rarely aggregates into large groups. Based on our studies, the Ferruginous Duck mainly winters in southern China from where it migrates to northern China or potentially to countries further north (*e.g.* western Mongolia; Kear 2005), leaving only small numbers in the Chinese wintering areas in spring. We also still know little about the migratory routes of birds breeding in Xinjiang, in the west of China, which may travel to India or central Asia in winter. Although more data is required to obtain a better understanding of the abundance, distribution and migration routes of the species in China, there is little doubt that wetlands in southern China that were once only used as migratory stopover sites have become important wintering grounds for Ferruginous Duck in Asia.

Acknowledgements

The study had been supported by the National Natural Science Foundation of China (31272291, 30970340) and the Science Supporting Project of the National Ministry of Science & Technology (2008BAC39B04). Special thanks to the groups of the China Bird Report and China Bird Watch, and members of bird watching societies around the country, including the Xinjiang Bird Watching Society and the Hong Kong Bird Watching Society. We also thank H.F. Cheung, Go Jun, Zhang Tong, Xing Rui, Huang Yahui, Xu Feng, Ding Peng, Eileen C. Rees, Richard Hearn, Wang Xin, Cao Lei, Anthony David Fox, Paul Holt and some international birdwatchers for their help in the field and in reviewing this paper.

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Sex-specific dive characteristics in a sexually size dimorphic duck

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Abstract

Dive duration generally increases with body size in animals including wildfowl. Therefore, diving behaviour may vary between the sexes in sexually size dimorphic species, such as the extremely sexually size dimorphic Musk Duck *Biziura lobata*. However, a previous study reports longer dives in the smaller sex (females) when breeding. In this study, non-breeding male Musk Ducks dived for significantly longer periods than females and tended to have longer inter-dive intervals, conforming to the general patterns described for other species. The differences in dive behaviour we describe may be explained by niche partitioning or differential oxygen requirements or uptake rates by the sexes.

Key words: *Biziura lobata*, diving physiology, Musk Duck, niche partitioning.

Dive duration is influenced by many factors, including extrinsic factors such as prey distribution, depth and climatic conditions, and intrinsic factors such as duration of preceding and subsequent inter-dive intervals (Sjöberg & Danell 1982; Stephenson *et al.* 1986; Kramer 1988; Beauchamp 1992; Halsey *et al.* 2006; Michot *et al.* 2006). Body size also influences dive duration and inter-dive interval. Due to the greater capacity of oxygen storage, larger animals are able to make deeper and longer dives (*e.g.* Beauchamp 1992; Boyd & Croxall 1996; Mori 2002), but stay at the surface for longer than smaller divers because the partial pressure between lungs and tissue is lower meaning oxygen uptake is slower (Mori 2002; Halsey *et al.* 2006). The relationship between body size and dive duration suggests that in sexually dimorphic species, the larger sex should have longer dives and inter-dive intervals due to their greater oxygen storage capacity.

Interestingly, the influence of sexual dimorphism on diving has not often been discussed. Differences in diving patterns between the sexes within size dimorphic species have been observed in marine mammals (*e.g.* Boyd & Croxall 1996; Page *et al.* 2005; Page *et al.* 2006; Staniland & Robinson 2008; McIntyre *et al.* 2010; Weise *et al.* 2010), penguins (Rey *et al.* 2013) and cormorants (*e.g.* Gómez Laich *et al.* 2012), but only rarely among highly size dimorphic wildfowl. We investigated dive and inter-dive interval durations between the sexes of an extreme sexually size dimorphic duck, the Musk Duck *Biziura lobata*. In particular, we wish to reconcile the prediction that the larger sex (males) will have longer dives and inter-dive intervals, with a previous report (McCracken 1999) of breeding members of the smaller sex having longer dives.

Methods

Musk Ducks forage mainly by diving to the bottom of lakes. Their diet differs between the sexes and consists of insects, their larvae and to a lesser extent molluscs, crustaceans, frogs and plant material (Marchant & Higgins 1990). Musk Ducks are extremely sexually size dimorphic with some males (1,700–3,100 g) being almost three times heavier than females (1,150–1,910 g) (McCracken *et al.* 2000). We conducted observations at the Western Treatment Plant (WTP; 38°00'S, 144°34'E), Victoria, Australia. Three ponds were used (115E-8, 115E-9, and 115E-10) for observations because of their heavy use by Musk Ducks (Loyn *et al.* 2002), their homogenous depth (2 m), temperatures and steep sides (see Halsey *et al.* 2006).

Observations

We conducted focal animal sampling on a haphazardly selected, mature ducks which could be unambiguously assigned a sex (n = 550; 7–10 min; total = 91.5 h), between March 2006 and February 2007. We divided the time of day into: morning (3.5 h after sunrise), mid-day (3.0 h around midday) and afternoon (3.5 h before sunset). Dive duration and inter-dive interval(s) were measured for each dive; observation bouts contained at least five consecutive dives and interbout intervals were excluded. Given the hundreds of ducks on the ponds (Guay 2008), and our efforts to avoid repeat-sampling, pseudo-replication is unlikely to be a major feature of our sampling.

Statistical analysis

We analysed the effects of sex, time of day and pond on dive duration and inter-dive interval using saturated linear mixed effects models (implemented in SPSS version 19) with each duck having a random intercept. Separate models were run for the dependent variables. In one model, dive duration was the dependant variable and preceding inter-dive interval duration was included as a covariate. In a second model, inter-dive interval was the dependant variable and the preceding dive duration was included as a covariate. Means are presented ± one s.d.

Results

A total of 608 dives were measured from 65 foraging ducks (36 females and 29 males). Dive duration was: males 35.2 ± 6.2 s and females 32.0 ± 5.4 s. Inter-dive intervals were: males 13.8 ± 5.6 s and females 11.5 ±

3.1 s. Males conducted 10% longer dives and 20% longer inter-dive intervals than females (Table 1). Dive duration also varied between ponds (115-P8: 35.4 ± 5.2 s, 115-P9: 31.2 ± 5.1 s, 115-P10: 34.0 ± 6.5 s) and was longer during the morning (34.5 ± 7.3 s) than other times of day (midday: 33.8 ± 5.8 s, afternoon: 32.3 ± 5.1 s); inter-dive interval was not influenced by time of day or pond (Table 1). Dive duration was not correlated with the preceding inter-dive interval nor was inter-dive interval correlated to the preceding dive duration (Table 1).

Discussion

Male Musk Ducks conducted significantly longer dives than females; similar but less pronounced patterns occur in some cormorants (Gómez Laich *et al.* 2012) and the opposite pattern was recorded among breeding Musk Duck (McCracken 1999). Breeding female Musk Ducks increase their body weight by > 20% before egg laying (Briggs 1988) and so may intensify their foraging effort by increasing their dive duration (McCracken 1999; Falk *et al.* 2000). The ducks we measured were not breeding, so breeding status could explain this discrepancy. The link reported here between sexual size dimorphism and diving behaviour can be explained by either differences in oxygen storage and uptake capacities (Kooyman 1989; but see Weise & Costa 2007), diet differentiation or niche partitioning between the sexes (*e.g.* Casaux *et al.* 2001; Ishikawa & Watanuki 2002; Beck *et al.* 2005; Cherel *et al.* 2007). Interestingly, differences in diet and foraging behaviour are reported for diving species exhibiting only small sexual size dimorphism (*e.g.*

Table 1. Results of the mixed model analyses. Influences of sex, time period, season, and pond on the dive duration (“Dive”) and inter-dive intervals (“Inter-dive”) of Musk Ducks as well as the variation by dive duration on the inter-dive interval and vice versa.

Term (subscript identifies the model)	***F***	**d.f.**	***P***
Sex_{Dive}	9.35	1, 58.7	**0.003**
$\text{Observer}_{\text{Dive}}$	0.06	1, 57.2	0.804
$\text{Time period}_{\text{Dive}}$	3.34	2, 58.0	**0.042**
$\text{Pond}_{\text{Dive}}$	5.31	2, 58.2	**0.008**
$\text{Inter-dive}_{\text{Dive}}$	3.26	1, 563.2	0.072
$\text{Sex}_{\text{Inter-dive}}$	4.73	1, 51.9	**0.034**
$\text{Observer}_{\text{Inter-dive}}$	0.69	1, 43.4	0.410
$\text{Time period}_{\text{Inter-dive}}$	1.42	2, 46.1	0.253
$\text{Pond}_{\text{Inter-dive}}$	6.38	2, 47.4	**0.004**
$\text{Dive duration}_{\text{Inter-dive}}$	1.36	1, 245.1	0.244

Lewis *et al.* 2002). Due to the extreme sexual size dimorphism, Musk Duck males have much larger mandibles than females, and the sexes exhibit preferences for certain dietary items (Gamble 1966; Frith *et al.* 1969; McCracken *et al.* 2000).

The mean dive durations we recorded for Musk Ducks were 103% longer and 37% shorter respectively than those reported for both sexes by McCracken (1999) and for a single non-breeding male by Sedgwick (1954). These differences can apparently be explained by depth differences (McCracken 1999, 0.2–2.0 m; Sedgwick 1954, ca 12.2 m) as dive duration is positively correlated with depth in diving ducks (*e.g.* Halsey *et al.* 2006). We observed increased dive duration, but not longer inter-dive intervals, during the morning (*contra* McCracken 1999). Increased diving effort in the morning may represent the need for food after a longer foraging break during the night (this species may not forage at night; Guay 2008) or perhaps be due to increased prey availability then. Diurnal variation in foraging behaviour is common in ducks, with many displaying foraging peaks at dawn and dusk (*e.g.* Green *et al.* 1999). The observed differences in dive duration and inter-dive intervals between ponds may reflect differences in prey availability (Folk 1971).

Studies in various species of diving ducks report a correlation between dive duration and the following inter-dive interval (*e.g.* Beauchamp 1992; Malhorta *et al.* 1996; Parkes *et al.* 2002). However, we found no such correlation for Musk Ducks, perhaps because Musk Ducks did not dive close to their aerobic limits at the WTP or used the inter-dive interval for other activities like scanning for predators or prey handling (see Hamilton & Taylor 2006).

In conclusion, this study indicates that Musk Duck conform to the general principle that the larger sex makes longer dives and inter-dive intervals. It also suggests that the previous report of the smaller sex having longer dives may be explained by the influence of breeding on female dive behaviour.

Acknowledgements

Funding was provided by Melbourne Water and a Victoria University Fellowship to P. J. Guay. We thank William Steele for his support and advice and Stefan Bräger and Thomas C. Michot for comments on an earlier version. Work was conducted under Animal Experimentation and Ethics Committee Register 02088 (UoM).

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Photograph: Male Musk Dusk (foreground) between dives, while another (background) rests, by Sylvia Osterrieder.

Delineation of Tundra Swan *Cygnus c. columbianus* populations in North America: geographic boundaries and interchange

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Abstract

North American Tundra Swans *Cygnus c. columbianus* are composed of two well-recognised populations: an Eastern Population (EP) that breeds across northern Canada and north of the Brooks Range in Alaska, which migrates to the eastern seaboard of the United States, and a Western Population (WP) that breeds in coastal regions of Alaska south of the Brooks Range and migrates to western North America. We present results of a recent major ringing effort from across the breeding range in Alaska to provide a better definition of the geographic extent of the migratory divide in Alaska. We also reassess the staging and winter distributions of these populations based on locations of birds tracked using satellite transmitters, and recent recoveries and sightings of neck-collared birds. Summer sympatry of EP and WP Tundra Swans is very limited, and largely confined to a small area in northwest Alaska. Autumn migration pathways of EP and WP Tundra swans abut in southwest Saskatchewan, a region where migrating WP birds turn west, and EP birds deviate abruptly eastward. Overall, from 1989 to 2013 inclusive, 2.6% of recoveries or resightings reported to the USGS Bird Banding Laboratory were of birds that moved from the domain of the population in which they were initially captured to within the range of the other population; a proportion roughly comparable to the results of Limpert *et al.* (1991) for years before 1990. Of the 70 cross-boundary movements reported since 1989, 39% were of birds marked on breeding areas and 61% were of birds marked on wintering areas. Dispersing swans *(i.e.* those that made cross-boundary movements) did not differ with respect to age or sex from those that did not move between populations. The Brooks Range in northern Alaska effectively separates the two populations within Alaska, but climate-induced changes in tundra breeding habitats and losses of wetlands on staging areas may alter the distribution for both of these populations.

Key words: *Cygnus columbianus*, distribution, North America, population, Tundra Swan.

Tundra Swans *Cygnus columbianus* breed in arctic tundra habitat across the Holarctic. The nesting distribution of the North American subspecies *C. c. columbianus* is nearly continuous from the tip of the Alaska Peninsula in southwest Alaska to the east side of Hudson Bay, Canada, and the swans also occur in far eastern Chukotka (Limpert & Earnst 1994; Kear 2005). Tundra Swans in North America have two distinct wintering distributions: swans breeding in northern Alaska and across northern Canada winter in the Atlantic Flyway along the east coast of North America, whereas swans breeding in western and southwest Alaska winter along the Pacific Flyway of western North America (Sladen 1973; Bellrose 1980). Tundra Swans wintering on the east coast are managed as Eastern Population (EP) Tundra Swans (Eastern Population Tundra Swan Committee 2007), and those wintering in western states and provinces as the Western Population (WP; Pacific Flyway Council 2001). There has been considerable interest in the precise distribution of WP and EP swans in northwest Alaska, where the two populations are thought to abut (Sladen 1973; Bellrose 1980; Limpert *et al.* 1991). Early reports showed the distribution of EP swans extending south of Point Hope to the Seward Peninsula (Sladen 1973; Bellrose 1980; Fig. 1), whereas later investigations portrayed the WP occupying breeding habitats as far north as Point Hope, with some possible overlap between the two populations based on recoveries and sightings of northwest Alaska swans in the domain of the EP (Limpert *et al.* 1991). However, the overlap documented by Limpert *et al.* (1991) in northwest Alaska was based on a very small sample of recoveries, and they called for additional marking to verify the wintering affinities of birds breeding and moulting in northwest Alaska. Limpert *et al.* (1991) also summarised the incidence of cross-population recoveries through 1989; a topic which we reassess for recoveries and resightings of Tundra Swans from 1990 through 2013. Our reprise of the work of Limpert *et al.* (1991) is based on nearly 4,000 recent observations of > 1,800 Tundra Swans fitted with neck collars in Alaska from 2006–2010. We interpret our findings in the context of climate change and past vicariance events that likely shaped the extant distribution of the two populations.

Study area and methods

Flightless Tundra Swans were caught during wing moult in July–August 2006–2010 and fitted with coded plastic neck collars (Sherwood 1966; Sladen 1973) at five major breeding areas throughout the range of the species in Alaska (Fig. 1). The sex of the birds was determined from their cloacal characteristics (Bellrose 1980) and age was classed as either locals (*i.e.* unfledged cygnets), second year birds (SY; birds hatched the previous year) or after second year birds (ASY). Second year birds were distinguished from older birds by the presence of grey feathering on their head and neck and, sometimes, on the back (Bellrose 1980). We generally captured swans without cygnets, to reduce disturbance, except in 2008 when a small number (< 10) of breeding birds with cygnets from each area were implanted with satellite transmitters (see below) to obtain

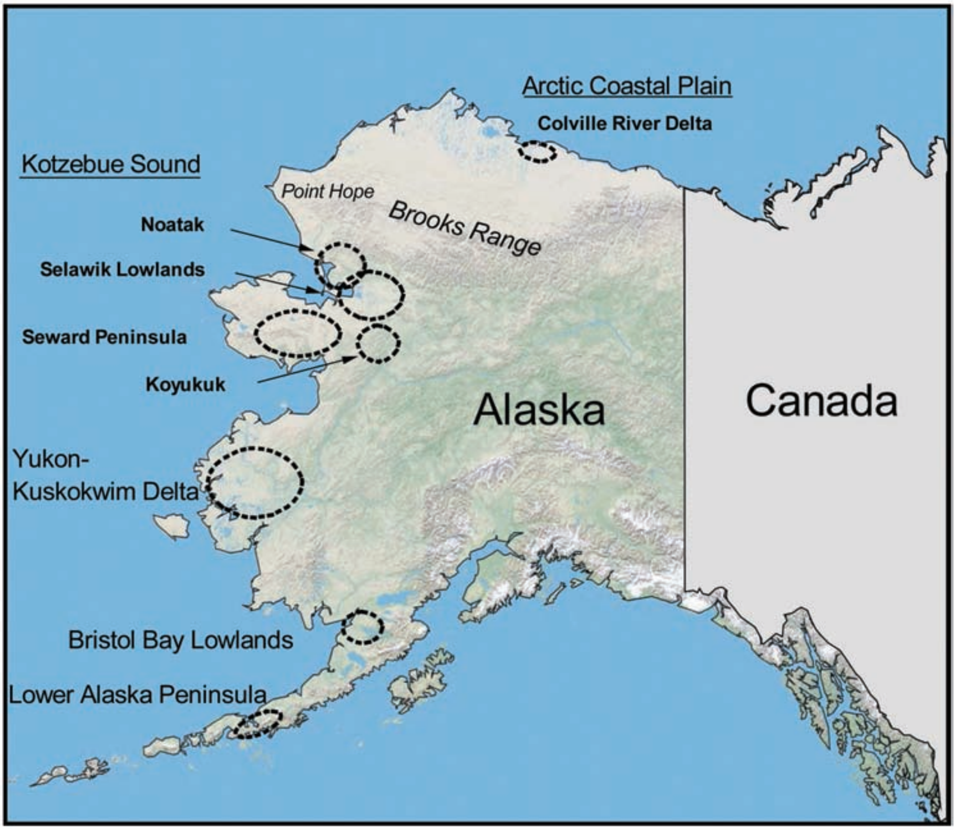

Figure 1. Areas where Tundra Swans were captured and marked in Alaska, 2006–2010.

distribution information on breeding individuals. Recovery and observation information reported to the USGS Bird Banding Laboratory (BBL) through to December 2013 were analysed to assess the overall distribution of Tundra Swans in North America. We also obtained observation data from marked swans contributed by participants in our Western Tundra Swan Observation Network, which included sightings by untrained volunteers (public), as well as trained observers who recorded marked birds at main staging and wintering areas used by the swans throughout the western states and provinces of the Pacific Flyway of North America. Sightings made by the public were frequently corroborated by examination of digital photographs sent by observers of the marked swans.

Satellite-marked swans

Satellite transmitters (platform transmitting terminals (PTTs), supplied by Microwave Telemetry, Maryland, USA) were implanted in the abdomen of 10 birds from each of five breeding locations in Alaska, following the procedure described by Korschgen *et al.* (1996). PTTs were programmed to transmit once every 1–4 days, depending on the season over a two-year period; if the two-year period was exceeded, the duty cycle reverted to data transmissions once every 3 days (Ramey *et al.* 2012). The Argos Data Collection and Location System (CLS America 2007) recorded information on latitude and longitude, date, time and the quality of the location data. We filtered unlikely locations based on rate and angle of movement (Douglas *et al.* 2012) and the highest quality locations were used to represent daily position.

Population affinities of marked swans

To assess overlap in the range of WP and EP Tundra Swans, we combined determination of their normal breeding and wintering ranges from earlier work (Sladen 1973; Limpert *et al.* 1991; Ely *et al.* 1997; Moermond & Spindler 1997; Petrie & Wilcox 2003) with data from the movements of the PTT-marked swans (see below). Limpert *et al.* (1991) showed that birds nesting north of the Brooks Range and across northern Canada generally wintered on the east coast of the United States and birds that nested south of the Brooks Range in Alaska wintered in coastal states and provinces along the west coast of the United States. Sladen (1973) and Bellrose (1980) considered locations in, or west of, the Rocky Mountain states and provinces to be within the range of the WP and locations east of the Rocky Mountains to be part of the EP. We used location information from our PTT-marked swans to further define the provenance of EP and WP swans, especially in southern Canada where their migratory pathways were in close proximity.

Possible changes in distribution of WP *vs.* EP swans marked in Alaska were assessed by comparing recent (≥ 1990) distribution information with that presented by Limpert *et al.* (1991) for Alaska-marked (< 1990) swans. The analysis by Limpert *et al.* (1991) included BBL recovery data, as well as observations of marked birds made by observers throughout the Atlantic Flyway, many of which were not reported to the BBL. For our overall assessment of population delineation we included recoveries or resightings of birds marked on breeding and wintering areas that were reported to the BBL or observed by our western observation network. In south-central Canada, where the migration corridors of EP and WP Tundra Swans are in close proximity (Sladen 1973), spring and autumn migration tracks from the PTT-marked swans were used to define the areas used by EP and WP swans and thus to assign recoveries and observations of neck-collared birds to the Eastern or Western Population. Recaptures or observations of Tundra Swans in Alaska were not included in analysis of population interchange, as most observations were on southern staging areas which could be used by either population. To compare cross-boundary movements of EP and WP Tundra Swans over two time periods we slightly modified the marking groups used by Limpert *et al.* (1991) by combining all recoveries from across the Arctic Coastal Plain of Alaska (which is represented by the Colville River Delta in our sample), grouping their two Yukon-Kuskokwim Delta samples into one, and adding new sampling locations in the Koyukuk River Valley and on the Lower Alaska Peninsula (Fig. 2).

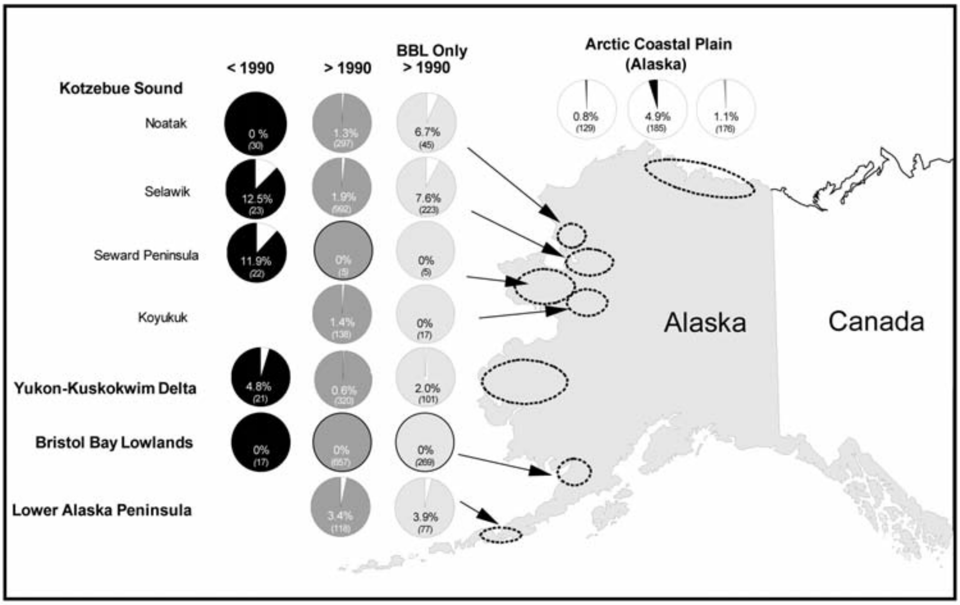

Figure 2. Recovery distribution of Tundra Swans in relation to the area where they were ringed in Alaska during two time intervals: before 1990 (Limpert *et al.* 1991; black circles), and from1990–2013 inclusive (this study; dark grey circles). Pie diagrams depict the proportion of birds marked in each area recovered in the range of the Western Population (solid colour), or Eastern Population (white colour). Values in parentheses are the number of recoveries. The light grey circles show the percent recovery of birds reported to the USGS Bird Banding Laboratory.

Resighting effort

The observation network established by Limpert *et al.* (1991) was in the Atlantic Flyway and some mid-western states along the flyway for EP Tundra Swans. Because of the general lack of observers in western states and provinces during their study, Limpert *et al.* (1991) largely relied on reports to the BBL for determining the distribution of WP Tundra Swans. Our current effort represents the reciprocal approach, with an established network of observers in the western states and provinces, but an absence of trained observers along the eastern seaboard. Hence for the distribution analyses presented here we rely almost exclusively on reports to the BBL for an assessment of the current winter distribution of EP Tundra Swans. To overcome potential geographical biases in observation effort, for analysis of winter distribution relative to marking location in Alaska, we include an analysis of recovery distribution based solely on reports to the BBL.

Results

Over 1,800 Tundra Swans were caught and fitted with neck collars at five different breeding areas across the range of the species in Alaska during 2006–2010; a further 367 were fitted with metal leg rings only (Table 1, Fig. 1). Nearly half the neck collars were put on birds from the Kotzebue Sound Lowlands (*n* = 850) whereas the fewest number of birds were neck-collared on the Colville River Delta (*n* = 76) because of an expected low resighting rate due to the absence of an established observation network in the eastern United States.

Recovery distribution of swans marked in Alaska

Our results show that there were few cross-population recoveries of Alaska-ringed Tundra Swans during either of the two time periods, and the recovery distributions were similar across years (Fig. 2). There was, however, evidence that observation effort may have affected the proportion of cross-population recoveries detected. An analysis of all post-1989 encounters (including data from BBL and the western observation network) revealed very little (< 2%) west-to-east population movement. However, when the analysis was restricted to just recoveries reported to the BBL (thereby removing the high observation bias in the west in recent years) the proportion of WP-ringed birds recovered in the east increased substantially and was highest for birds marked in the valleys of the Selawik River (7.6%) and the Noatak River (6.7%) of northwest Alaska (Fig. 2). A similar bias in observation effort was noted for our assessment of the distribution of Tundra Swans ringed in northern Alaska, as the proportion of EP-marked swans detected at WP sites post-1989 was substantially lower when restricting the analysis to BBL reports (1.1% *vs.* 4.9%).

Overall distribution of marked swans

The majority of recoveries and resightings of Tundra Swans since 1989 occurred within the geographic regions expected (Fig. 3). WP swans were generally found south of the Brooks Range in summer and within and west of the Rocky Mountain states and provinces in winter, whereas EP Tundra Swans were primarily found north of the

Table 1. Number of Tundra Swans fitted with neck collars and metal leg rings in Alaska, 2006–2010. (Numbers in parentheses refer to birds fitted with only a ring).

	Year											
Location	**2006**		**2007**		**2008**		**2009**		**2010**		**Total**	
Colville River Delta	58		8	(42)	10	(30)	0	(100)	0	(86)	76	(258)
Kotzebue Sound												
Noatak	17	(28)	0	(31)	65	(1)	57		62		201	(60)
Selawik	82	(1)	90	(7)	135	(25)	141	(1)	134	(1)	582	(35)
Koyukuk	16		10		41		0		0		67	
Yukon-Kuskokwim Delta	30		99		97		100		0		326	
Bristol Bay Lowlands	91	(4)	47		5	(10)	105		104		352	(14)
Lower Alaska Peninsula	62		59		31		0		101		253	
Total	356	(33)	313	(80)	384	(66)	403	(101)	401	(87)	1,857	(367)

Brooks Range in Alaska and east of the Rocky Mountain states and provinces during the winter months. There were some obvious exceptions however, with cross-boundary movements being particularly evident on wintering areas adjacent to the east and west coasts of North America. Since 1989, 70 of 2,711 (2.6%) unique recoveries of Tundra Swans reported to the BBL have been of birds that moved across population boundaries, with an average of 2.7% ± 0.54 s.e. (n = 24) out-of-range recoveries per year (Table 2, Fig. 3). The proportion of dispersing birds was fairly evenly represented across capture locations, with the possible exception of birds ringed at wintering areas in the west being somewhat more likely to be recovered in the east (4.2%) than other capture-wintering comparisons (Table 2). Overall, of the 70 birds reported to the BBL that crossed flyways since 1989, 39 moved from east to west, and 31 went from west to east.

Refinement of EP-WP boundary in Saskatchewan

Movements of PTT-marked Tundra Swans from the two populations showed a nearly parallel northwest-to-southeast movement across Alberta and Saskatchewan during autumn, with EP swans being on the northern and WP swans on the southern edge of this movement. The region of closest contact between WP and EP swans was in southwest Saskatchewan (Fig. 4), where EP and WP swans used adjacent areas during autumn. Both populations also migrated through southern Saskatchewan in

Table 2. Distribution of recoveries and resightings of Tundra Swans in North America reported to the USGS Bird Banding Laboratory, 1990–2013, in relation to ringing location. Eastern Population Tundra Swans generally breed in northern Alaska and Canada and winter on the east coast, whereas Western Population Tundra Swans usually breed in western Alaska and winter in western North America.

	Recovery Location			
Capture Location	**Eastern Population**	**Western Population**	**Total**	**Move (%)**
Northern breeding areas				
N. Alaska/Canada	176	2	178	1.1
Western Alaska	25	642	667	3.7
Southern wintering areas				
East coast	1,700	37	1,737	2.2
West coast	6	123	129	4.9

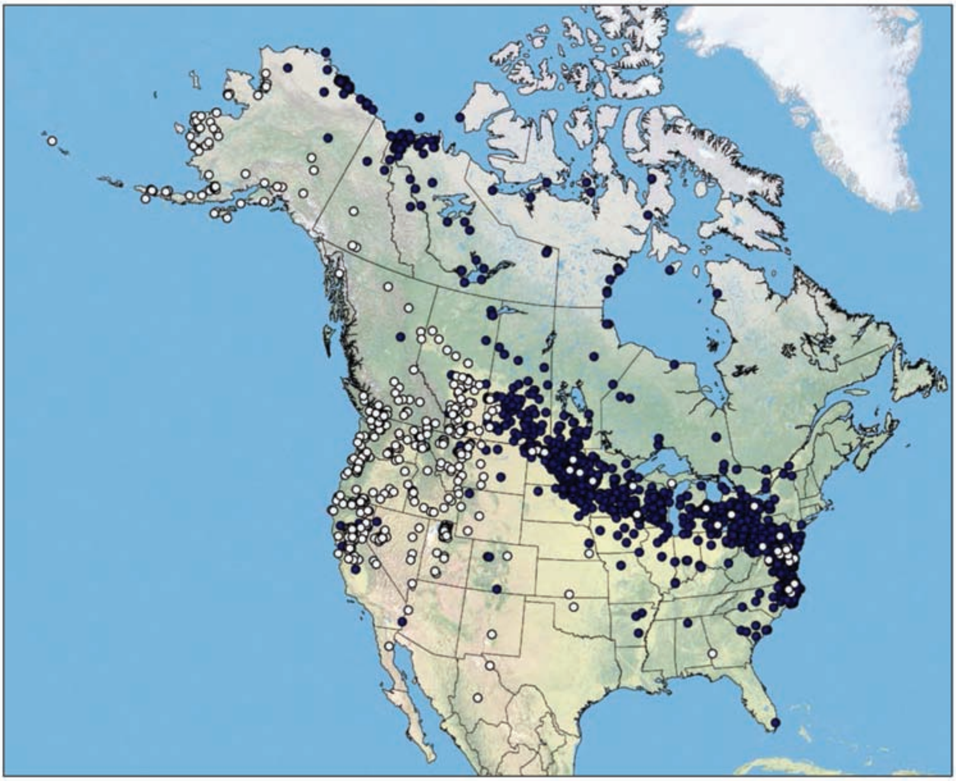

Figure 3. Resighting and recovery distribution for Tundra Swans fitted with rings and/or neck collars in North America. Data includes all reports to the USGS Bird Banding Laboratory (BBL) up to and including 2013, and 3,900 observations of neck-collared birds made by the Western Population Tundra Swan Observation Network. White circles represent recovery locations of birds marked in the range of the Western Population; dark circles represent locations of birds marked at sites normally used by Eastern Population Tundra Swans.

spring, but WP swans preceded EP swans by 1–3 weeks.

Characteristics of dispersing swans

The majority (89.2%) of Tundra Swans that switched flyways in recent years were marked as adults, with the remainder being second year birds or cygnets at the time of marking (Table 3). Females were slightly more likely than males to be recovered in the range of the other population (Table 3). However, the age and sex ratios of Tundra Swans that did not cross the population boundary were nearly identical to the ratios of the dispersing birds (Table 3; $\chi^2_1 = 0.99$, n.s. for age (first and second year age classes combined for analysis), and $\chi^2_1 = 1.22$, n.s. for sex), thereby indicating that there was not a propensity for Tundra Swans of a given age or sex class to disperse. The sex

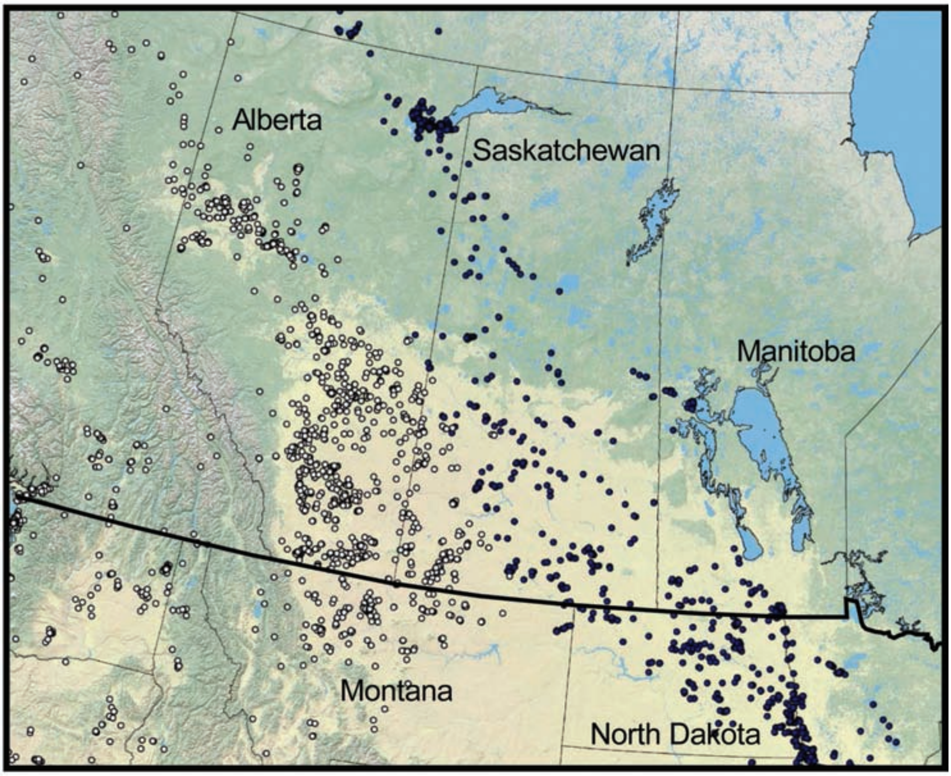

Figure 4. Distribution of satellite (PTT)-implanted Tundra Swans during autumn and spring while migrating through southern Canada and the northern United States, 2008–2012. White circles represent locations of birds marked south of the Brooks Range in Alaska (*n* = 28) and dark circles represent locations of birds marked north of the Brooks Range in Alaska (*n* = 10). Not portrayed are locations of two PTT-implanted swans that died on breeding areas in 2008 before migration and 10 birds implanted with PTTs on the lower Alaska Peninsula that either did not migrate or migrated only along the Pacific coast.

and age ratios of dispersing birds initially marked on summering and wintering areas did not substantially differ.

Discussion

Distribution of Eastern and Western Population Tundra Swans

The focus of this study was to determine the frequency that Tundra Swans cross-over between the Eastern and Western Populations, and whether there has been a change in cross-boundary movements since a similar summary by Limpert *et al.* (1991). In order to assess movement, the normal geographic range of each population was first established from earlier published studies (Sladen 1973; Bellrose 1980; Petrie & Wilcox 2003) and also from the locations of our PTT-marked birds migrating through

Table 3. Age and sex of all Tundra Swans recovered or observed in North America and reported to the USGS Bird Banding Laboratory relative to whether or not they crossed population domains, 1990–2013[a].

	Sex			
Age	**Female**	**Male**	**Total**	**%**
Swans that did not cross flyways				
Adult	1,112	1,082	2,194	85.4
Second year	198	128	326	12.8
First year[b]	27	22	49	1.9
Total	1,337	1,232	2,569	100.0
	(52.0%)	(48.0%)		
Swans that crossed flyways				
Adult	35	26	61	89.7
Second year	5	1	6	8.8
First year	0	1	1	1.5
Total	40	28	68[c]	100.0
	(58.8%)	(41.2%)		

[a]Does not include 73 birds of unknown age or sex; [b]includes cygnets ringed as locals (not yet flighted) and hatch-year birds (flighted); [c]age or sex of two birds was not determined.

southern Canada. However, there has not been complete agreement among earlier studies on the geographic extent of each population, particularly in northeast Alberta. Our ringing and telemetry data, combined with encounter data reported to the BBL corroborates earlier work by Sladen (1973) and Petrie & Wilcox (2003) in demonstrating that the Peace-Athabasca Delta region of northeast Alberta is a staging area used solely by EP birds (Fig. 3, Fig. 4), whereas Bellrose (1980) and Paullin & Kridler (1988) reported that the area was also used by WP Tundra Swans during spring. Bellrose (1980) likely presumed the region was a staging area for WP swans based on the timing and magnitude of use by unmarked birds, whereas Paullin & Kridler (1988) reported that several of the Tundra Swans they colour-marked in eastern Oregon were later observed in the Peace-Athabasca Delta region. Paullin & Kridler (1988) also reported that some of their dyed swans were observed during May and June 1962 on the

Mackenzie River Delta in the North West Territories, Canada, a breeding area for EP Tundra Swans. If WP Tundra Swans do stage in the Peace-Athabasca Delta and then move on to the Mackenzie River Delta, our data suggest it is likely an uncommonly used route, or the region is used by a subset of swans that has been poorly sampled to date. For our analyses, we considered northeast Alberta and the Mackenzie River Delta to be part of the EP flyway.

Distributional overlap between populations

The degree of spatial separation we document between EP and WP Tundra Swans in North America since 1989 is quite high, with over 97% of birds being resighted or recovered within the range of the population in which they were initially captured. Limpert *et al.* (1991) reported similarly high fidelity rates for swans encountered before 1990, with 94.5% of WP Alaska-ringed swans and 99.5% of EP Alaska-ringed swans being observed or recovered within their respective flyways, and < 1% of winter-ringed swans switching from one population to the other. Direct comparisons between the two studies should be undertaken with caution, given the extremely small sample sizes in the earlier work when only six Alaska-ringed WP swans were encountered (out of 110 total recoveries) in the range of EP swans, and two EP Alaska-ringed swans were encountered in the west (out of 416 ringed in northern Alaska and Canada; Limpert *et al.* 1991). Also, the analysis by Limpert *et al.* (1991) of Alaska-ringed swans was based primarily on birds captured as cygnets, which remain with their parents their first year of life and hence should initially have complete fidelity to the wintering area of their parents. Only if cygnets survive into their second summer could they possibly be expected to disperse to new wintering or breeding areas.

Our estimates of cross-population movement could be biased high if the swans we initially marked at northern areas were birds that were moult migrants from elsewhere. However PTT-marked swans from each of the five breeding areas in Alaska showed high summer site fidelity, with the exception of a subadult captured on the Colville River Delta that subsequently roamed across northern areas of Alaska and far western Canada within the range of the EP. Our finding that 2.6% of the resightings or recoveries per year were of cross-boundary movements is likely an underestimate of true movement given the relatively low resighting rate of marked birds during this study, particularly along the eastern seaboard. However, even low estimates of cross-population movement may be adequate to facilitate gene flow (Mills & Allendorf 1996), but only if dispersing birds mate with birds in the new population (Rockwell & Barrowclough 1987). A genetic analysis will be necessary to assess definitively the degree of gene flow between these two groups, as undertaken for Trumpeter Swans *Cygnus buccinator* in North America where two populations with overlapping ranges were found to differ genetically due to restricted gene flow (Oyler-McCance *et al.* 2007).

There are several scenarios that could lead to an overlap in staging and wintering distribution of EP and WP Tundra Swans. If EP and WP birds nest sympatrically in northwest Alaska, then nesting pairs and their offspring would naturally migrate back to the wintering area from which they came. However, simple overlap in breeding distribution does not explain the out-of-range occurrences of our Colville River Delta birds (Fig. 2), as these birds nest well within the breeding range of the Eastern Population. Overlap in population distribution could also be affected if pair formation occurs on staging areas or during winter, as reported for some geese (Ganter *et al.* 2005). In such an instance, birds pairing with individuals from another population at a common staging or wintering area might follow them back north to their natal area, as speculated by Limpert *et al.* (1991). However, our data show high fidelity of both males and females to wintering areas, so most males available for a female to pair with would be from the same population. In addition, the only non-summer area shared by EP and WP swans is in southwest Saskatchewan, where they are only sympatric during autumn (Fig. 4).

Movement of individuals across flyways has been reported for other populations of northern swans, but marking programmes and observation networks have generally been too patchy to quantify the degree of actual movement (Rees 1991). Rees (1991) reported the movement of marked Bewick's Swans, *C. c. bewickii*, between wintering areas in NW Europe and the Caspian Sea and also described the sighting of a Bewick's Swan in eastern Europe, that was initially marked in eastern Siberia. Hence it is apparent that although movement between flyways is unusual in Tundra Swans, it is not unprecedented. Such pioneering behaviour is a beneficial attribute for exploiting variable environments, and may prove necessary if the birds are to adjust to climate-induced changes in habitats.

Stability of WP-EP migratory divide in Alaska

Our analysis of the recovery distribution of Alaska-ringed Tundra Swans shows that there has been little change over time in the population affinities of birds from different breeding areas, with swans breeding on the south side of the Brooks Range distributed nearly exclusively in the Pacific Flyway, and Tundra Swans breeding north and east of the Brooks Range staging and wintering in the Atlantic Flyway, within the realm of the EP. The Brooks Range appears to be an effective barrier separating breeding populations of EP and WP Tundra Swans in Alaska. The proximity of the two populations in southwest Saskatchewan, with little appreciable overlap, is fascinating, especially since the two populations migrate through the area at approximately the same time during autumn (Fig. 3, Fig. 4). The degree of segregation is somewhat surprising, especially in a region without pronounced topographic barriers, given the mobility of migratory waterfowl and their propensity to seek out limited wetlands. Climate-induced changes in wetland dynamics, particularly in south-central Canada could affect population interchange. If wetland drying occurs, and EP and WP swans staging across southwest Saskatchewan are constrained into using the same wetlands, then increased population exchange could result; this would be particularly likely if disturbance events (often associated with over-crowded conditions and human activity) increase. The latter could lead to the break-up of families and pair bonds which might also promote population exchange.

Characteristics of dispersing swans

We expected that birds moving to a different migration pathway would differ with respect to age and sex relative to swans that did not move. In waterfowl, unlike most other birds, males generally disperse while females are typically more site faithful in the breeding range (Greenwood 1987), whereas the reverse pattern has been reported in winter, with male Bewick's Swans being more likely than females to return to their traditional wintering sites (Rees 1987). We therefore surmised that females would predominate in our sample of dispersing birds. We also suspected that young (second year) swans might be disproportionately represented in our sample of dispersing swans, as young birds have been reported to be more likely to disperse than older birds (Greenwood & Harvey 1982). However, the age and sex composition of dispersing birds was nearly identical to that of the birds that remained in the flyway where they were originally marked. Hence the tendency to emigrate in swans may be somewhat haphazard, although Rees (1991) did find that two of the three Bewick's Swans that moved among flyways in her study were subadults.

Origin of the migratory divide

Many parts of Alaska were unglaciated during much of the Pleistocene, but most of northern and central Canada was covered by ice up to 3500 m thick (Marshall *et al.* 2002; Dyke *et al.* 2002; Clark *et al.* 2009). There have been numerous expansions and contractions of Nearctic ice fields during the last 450,000 years, and during glacial retreats an ice-free corridor extended from eastern Alaska across Alberta and Saskatchewan to the Great Lakes (Marshall *et al.* 2002). The location of this corridor aligns very closely with the migration route of Tundra Swans from northern Alaska (Figs. 3, 4). It seems plausible that Tundra Swans nesting in tundra regions of eastern Canada during glacial minimums were restricted to nesting in far western Canada and northern Alaska when northern Canada became glaciated during glacial maximums, but maintained their wintering areas on the East Coast of North America. Previous authors have also speculated that Pleistocene glaciations may have dictated the nesting range of Tundra Swans (Ploeger 1968; Limpert *et al.* 1991).

It is apparent that Tundra Swans in North America have changed their migratory paths many times over millennia. Hence it is feasible that in a changing hydrological landscape driven by climate change they will once again be able to adapt. However, while adapting to changing climate cycles in the past Tundra Swans have not had to compete for wetlands with humans; their future fate will likely depend on the extent to which anthropogenic factors influence the landscape and the degree to which humans are able to mitigate such factors.

Acknowledgements

This work was funded primarily by the U.S. Geological Survey and the U.S. Fish &

Wildlife Service as part of a programme to monitor avian influenza viruses in wild migratory birds and identify factors related to the transmission of the viruses in North America. We appreciate the support of Dirk Derksen (USGS), Debra Rocque (USFWS), and Kimberly Trust (USFWS) who arranged funding for the study. Caryn Rea (Conoco Phillips) kindly supplied financial assistance for capturing swans on the Colville River Delta. Field assistance was provided by John Terenzi, Julian Fischer, Tyrone Donnelly, Domonique Watts, John Shook, John Whissel, Jim Helmericks, Michael Wege, George Walters, Kevin Fox, Adam Ahonen, Mathew Sorem and many other biologists at remote locations throughout Alaska, including Tina Moran, Dennis Marks, Karen Bollinger, Brad Scotton, Eric Sieh, Jennifer Bryant, Paul Anderson, Bill Larned, Rod King, Nathan Olson, Rob MacDonald, Denby Lloyd, George Walters, Chuck Steffen, Gene Peltola, Jennifer Steffen, Isaac Bedingfield and Robert Sundown. We are also indebted to the members of our Western Tundra Swan Observation Network, as well as all the interested members of the public who provided resighting information. Thomas Wood (Airlie Swan Research Group) and Danny Bystrak (USGS) helped track down elusive ringing records. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The authors declare they have no conflict of interest. We appreciate manuscript reviews by Larry Griffin, Brandt Meixell, John Pearce, Tony Fox, Eileen Rees and an anonymous reviewer, who helped with the clarity and quality of the paper.

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Aspects of the breeding biology of Bewick's Swans *Cygnus columbianus bewickii* nesting in high densities in the Chaun River delta, Chukotka, east Russia

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Abstract

The breeding biology of Bewick's Swans *Cygnus columbianus bewickii* nesting on Ayopechan Island in the Chaun River delta, Chukotka, northeast Russia was monitored from 2002–2013 inclusive, which coincided with a marked increase in the number of swans in the Eastern Population. A total of 535 nests were located during the study, and nest density, clutch size, egg dimensions, earliest hatch dates and nest success (*i.e.* whether at least one egg hatched) were recorded. Average nest density was 2.07 ± 0.25 nests/km^2 (range = 0.98–3.33 nests/km^2) and nest density appeared to increase over the study period, although the trend was not statistically significant. The minimum distance between two swan nests was 82 m, and average clutch size was 3.60 eggs (s.d. = 1.05; range = 1–7 eggs, n = 410 clutches). Nest success, recorded in 2009–2013, ranged from 32.2–72.2% and averaged 46.5%. Weather variables, such as the date on which temperatures rose above zero, the timing of snow melt, late May and early June temperatures, and a general (integrated) measure of spring weather conditions, were not significantly associated with nest density. Mean clutch size decreased during the study, through there being a decreasing proportion of large clutches of 5 and 6 eggs. Results are discussed in relation to a separate study of the breeding biology of Bewick's Swans in the Northwest European Population, which increased in numbers between the mid 1970s and the mid 1990s but is currently in decline.

Key words: Bewick's Swan, breeding biology, Chaun River delta, Chukotka, clutch size, *Cygnus bewickii,* nest density, nest success.

Long-term data on the breeding biology of the Bewick's Swan *Cygnus colombianus bewickii* have been reported for birds nesting on the Bolshezemel'skaya and

Malozemel'skaya Tundras and the Yugorskiy Peninsula (Mineev 1987, 1991, 2003), on Vaygach Island (Syroechkovsky *et al.* 2002; Syroechkovsky 2013) and in the Nenetskiy National Nature Reserve (*zapovednik*) (Shchadilov *et al.* 1998, 2002; Rees 2006), all in the western part of arctic Russia. These study areas had high densities of territorial and breeding Bewick's Swans during the late 20th century; nest density varied among sites and years but peaked at 1.40 nests/km^2 on the Malozemel'skaya Tundra and 1.60 nests/km^2 in the area around Khabuicka in the Nenetskiy *zapovednik* (Mineev 1991; Rees 2006). The observations made in European Russia from the early 1970s to 2000 coincided with an increase in the Northwest European Bewick's Swan Population until the mid-1990s, after which numbers declined (Rees & Beekman 2010). Ringing and satellite-tracking studies indicate that the Northwest European Population breeds in western Russia (Beekman *et al.* 2002; Rees 1991, 2006) and thus the studies were carried out on an increasing population, which was possibly reaching saturation level.

Bewick's Swans breeding in the Chaun River delta, Chukotka, in the eastern part of the range, were studied in 1971–1989 (summarised in Krechmar *et al.* 1991; Krechmar & Kondratiev 2006). The delta of the Chaun River was thought to be an important breeding area for Bewick's Swans from the Eastern Population, which migrate to winter in China, Japan and Korea, although the maximum nesting densities there in the second half of the 20th century (0.25 nests/km^2, Krechmar & Kondratiev 1986; Rees 2006) did not approach values similar to those recorded in the western part of Russia. Some of the Bewick's Swans breeding in the Chaun Delta in the late 1970s and early 1980s were found to winter in Japan (Kondratiev 1984). There was a significant increase in the number of Bewick's Swans wintering in Japan during the 1990s (Albertsen & Kanazawa 2002), and more recently there was no discernible trend for Bewick's Swans reported wintering in China (which vary substantially in number between years) in the early 2000s (Cong *et al.* 2011a,b). By 2007, the Eastern Population was estimated to number 92,000–110,000 birds, compared with 21,500 swans reported in the Northwest European Population in 2005 (Wetlands International 2012). Unfortunately, information is lacking for the period during which the Eastern Population was increasing (*c.* 1990–2001). Our study commenced in 2002, by which time population levels were considered relatively high.

An increase in bird abundance is generally to be welcomed, particularly when the species is one of conservation concern. The Chukotian-breeding population of the endangered Lesser White-fronted Geese *Anser erythropus* has increased recently, as have numbers of Bewick's Swans in the same area (Solovyeva & Vartanyan 2011). The Bewick's Swan and its habitats have long received protection through both national and international legislation, and the species was listed under The Red Data Book of the Russian Federation (2001). Amongst large herbivorous birds, such as the Anserini, however, increasing density can affect species interactions and their food supply on the breeding grounds. Overgrazing by the Lesser Snow Goose *Anser* *caerulescens caerulescens* has been found to damage tundra habitats in arctic Canada (Batt 1997), and local increases in abundance have long been thought to affect Barnacle Geese *Branta leucopsis* in some of the breeding areas on Spitsbergen (Drent *et al.* 1998), and the Greater White-fronted Goose *Anser albifrons* nesting on Kolguev Island, Russia (Zainagutdinova *et al.* 2011). The paper by Drent *et al.* (1998) found a density-dependent reduction in all reproductive parameters, namely: breeding propensity, nest success and the number of fledged young per pair. Decreasing production of young has also been reported for the increasing Greater White-fronted Goose population wintering in Europe (Mooij 2005).

This paper describes observations of the breeding biology of Bewick's Swans nesting in the Chaun River delta, at a time when numbers in the Eastern Population, and thus also local nest densities, are thought to be high. Results are considered in relation to similar observations made in the same area during the 1970s and 1980s, and also in comparison to those for swans breeding in western parts of the range during the late 20th century.

Methods

Study area

Ayopechan Island (68°50'N, 170°30'E; covering 91 km^2 and with a maximal elevation of 5–6 m a.s.l.; Fig. 1) is the largest island within the delta formed at the confluence of the Chun, Puchveem and Palyavaam Rivers, where they enter Chaun Bay in the East-Siberian Sea. The island was formed by alluvial and coastal marine sediments 3,000–4,000 years ago, with the highest points situated on the south and southeast parts of the island. Well-developed peat bog, thermokarst lakes and alas depressions (*i.e.* shallow temporary lakes formed by freeze-thaw cycles) constitute the main habitat types in areas of higher ground. A coastal strip of maritime marshes is regularly flooded by the sea. The island contains many lakes and ponds which are of different size (up to 2 km^2) and depth (but all are shallower than 5 m). Lakes of small and medium size, with indented shorelines and several islands, are typical of the area. Drained lake beds, covered with grassy meadows, also cover a significant portion of the island. Ayopechan Island is regularly flooded by wind-induced tides and the water in most of the lakes is brackish. A well-developed network of brackish channels is located on the north side of the island. Sub-arctic grass tundra is the predominated vegetation type with Hare's-tail Cottongrass *Eriophorum vaginatum*, several species of sedges *Carex* sp. and willow *Salix* sp., Arctic Dwarf Birch *Betula nana exilis*, and mosses dominating the plant community (Krechmar *et al.* 1991). The southern part of Ayopechan Island is covered by Shrubby Alder *Duschekia fruticosa* and willow bushes, while the northern part represents maritime tundra on salt marshes. Shallow parts of lakes were overgrown with horsetails *Equisetum* sp., mare's tail *Hippurus* sp., Arctic Marsh Grass *Arctophila fulva* and Pallas' Buttercup *Ranunculus pallasii*.

The coastal climate is typical of the Siberian arctic, strongly influenced by Atlantic cyclones during the summer. The

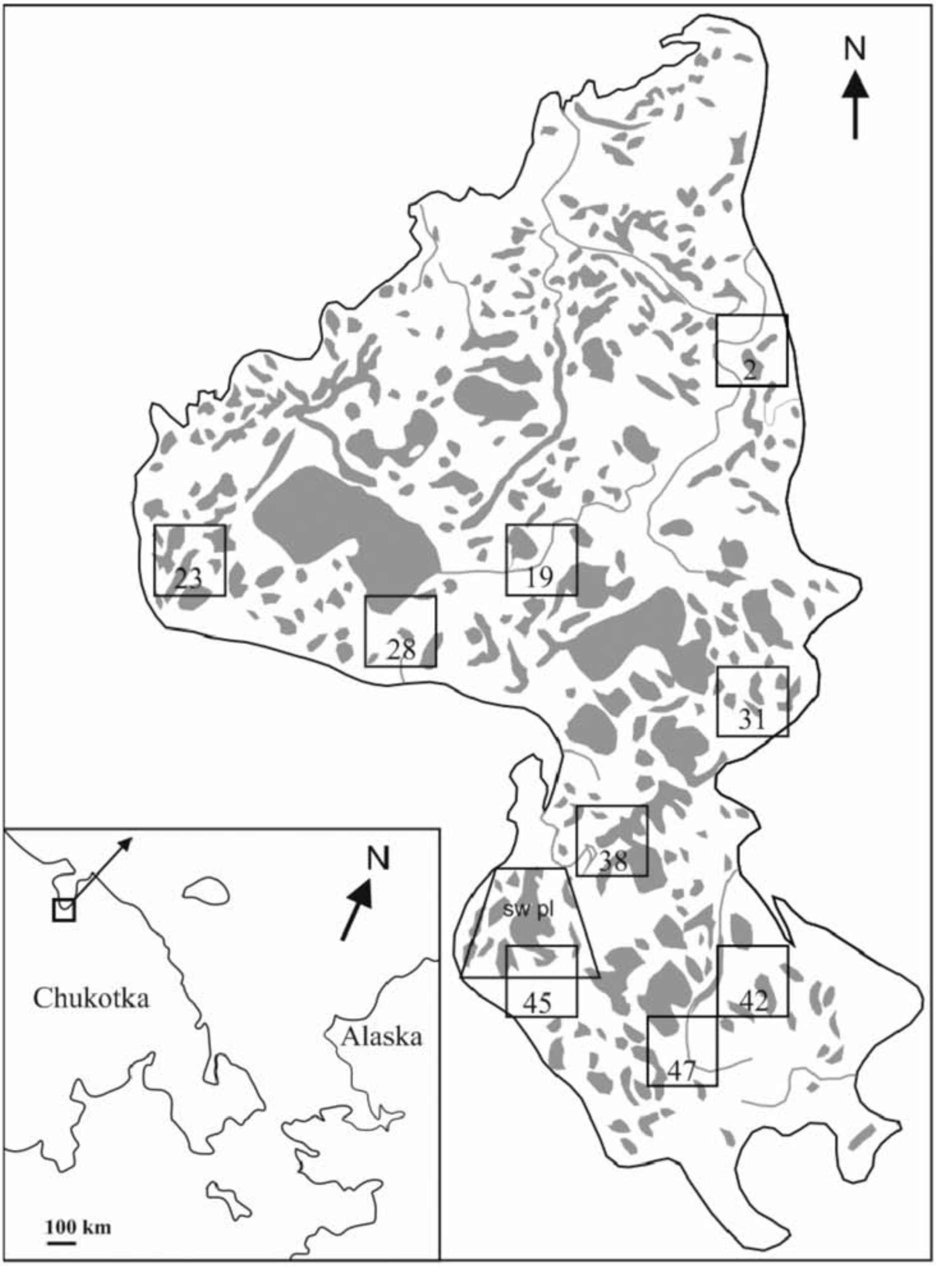

Figure 1. Map of Ayopechan Island, Chaun Delta. Nine 1 km^2 nest plots are shown and identified by their number codes according to a Spectacled Eider nest plot grid. The quadrilateral swan plot of 3.06 km^2 is shown and marked as **"sw pl"**.

coldest month is January (mean temperature = –34°C) and the warmest is July (12°C). Average temperatures recorded for the last 10 days of May and the first 10 days of June, and durations of frost-free season over the study period, are given in Table 1. Duration of the frost-free season, measured as the number of days between the date of the last frost in spring (when temperatures are consistently above zero) and the date of the first frost in autumn, indicates the period of vegetation growth during the summer months.

The Chaun Delta, and Ayopechan Island in particular, is an important breeding area for several waterfowl species in addition to the Bewick's Swan, notably for Long-tailed Duck *Clangula hyemalis* and Spectacled Eider *Somateria fischeri*. Other breeding waterfowl, such as Greater White-fronted Goose, Northern Pintail *Anas acuta*, Greater Scaup *Aythia marila* and King Eider *S. spectabilis* were less abundant, with densities of < 0.1 nests/km^2. Predators of eggs and chicks included the Arctic Fox *Alopex lagopus* (five dens on the island, 1–3 of them active per season), Red Fox *Vulpes vulpes* (one den used irregularly) and nesting Glaucous Gulls *Larus hyperboreus* and Vega Gulls *L. vegae*. Tundra birds of prey (Falconiformes) and owls (Strigiformes) were irregular summer visitors and did not reproduce on the island. About 500 people live at Rytkuchi, the only settlement in Chaun Delta. The village is situated *c.* 4 km inland from the east coast and its economy is based mainly on Reindeer *Rangifer tarandus* herding.

Data collection

The Bewick's Swan study was undertaken during fieldwork on Spectacled Eider in the Chaun Delta. Fifty-one eider nest plots, each of 1 km^2, were set up for this project, equally distributed across Ayopechan Island except for the northern maritime part and the southern shrub-tundra area. There was little additional effort invested in surveying swan nests in the years 2002–2010, except for establishing and monitoring a Bewick's Swan nest search plot, 3.06 km^2 in size (area "sw pl" on Fig. 1). In 2011–2013, the focus of the fieldwork shifted to monitoring bird communities in the Chaun Delta in relation to climate change and anthropogenic factors, which included searching for and locating all "large" bird nests (*i.e.* for all nesting species excepting shorebirds and passerines) within nine of our previous 51 eider plots (Fig. 1). Bewick's Swan nesting density therefore was estimated for the "sw pl" area during 2002–2010 (except in 2008) and for nine 1 km^2 plots (9 km^2 in total) in 2011–2013. In 2002–2010 (excepting 2008), a single search by 3–4 people for all swan nests was made in late June–early July each year, searching the swan plot during a 9–10 h day and mapping all swan nests, both active and predated. In 2011–2013, two people each searched one of the nine "large bird" plots each day; no searches of the "sw pl" area occurred after 2010. At each of the nine plots from 2011 onwards the first search was made in mid-June, the second 10 days later, and subsequent surveys aimed to located lately-built nests and to follow the fate of eggs in previously found nests. Only nests recorded on the plots were used to calculate the density of breeding pairs each year.

In addition to observations made at the swan nest plot, swan nests were also located

Table 1. Spring weather characteristics measured at the Chaun Delta, Siberia, each year during the study period (2002–2013). Years with a late spring (*n* = 3) are shaded in dark grey; years with "normal" spring (*n* = 6) are unshaded; years with an early spring (*n* = 3) are shaded in light grey. dd = data deficient.

Year	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**
Days from 1 January when mean daily temperatures first remain above 0°C	138	137	141	143	140	134	136	129	138	142	137	145
Days from 1 January when snow cover was completely melted	153	155	155	147	154	145	155	140	152	159	147	148
Duration of frost-free season (days)	74	57	dd	97	74	115	85	70	112	85	68	82
Daily average temperature: 20–31 May	4.27	0.42	1.33	0.92	3.47	3.91	1.18	2.74	1.53	–0.35	1.85	–2.04
Daily average temperature: 1–10 June	6.27	7.69	9.81	7.50	4.57	8.33	1.50	4.47	7.55	4.55	7.86	5.45

Table 2. Nest abundance, density and the earliest hatch dates (dd.mm) amongst Bewick's Swans nesting on Ayopechan Island, Chaun Delta, Siberia, in 2002–2013. dd = data deficient.

	2002	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**Total/ average**
No. of nests located	16	20	27	43	5	58	23	43	65	48	100	92	535
Nest density, nests/km^2	1.96	2.94	0.98	1.31	1.31	0.98	dd	2.61	2.61	2.00	3.33	2.78	2.07
Earliest hatch date	29.06	04.07	dd	06.07	dd	07.07	06.07	29.06	04.07	11.07	28.06	03.07	03.07

during searches for eider nests at all the eider plots from 2002–2013 inclusive. Fieldworkers were asked to report swan clutch sizes for these less regularly located nests, but as swan monitoring was not an aim of the eider study, whether they did so was at the discretion of the observer. Information therefore was missed for many swan nests, but the data collected are still considered representative for estimating annual variation in clutch size. Only complete clutches (*i.e.* those found after the onset of incubation, determined either by floating eggs in water (Westerkov 1950) or from a known hatch date) were included in the clutch size analyses; partial nest depredation was not measured, and thus the observed clutch size could be an underestimate due to the partial depredation of eggs. In 2009–2013 the teams were asked to report on all hatching success by reporting the presence of egg membranes at the nest. Nests without membranes and eggs were considered as depredated. Clutches where at least one young hatched were classed as having been successful. In 2011–2013, hatching success was documented for all clutches found on the nine "large bird" plots. Swan eggs were measured with calipers to the nearest 0.1 mm in 2011–2013. The date on which the first birds hatched each year ("earliest hatch date") was determined by recording when swan broods were first seen on the tundra (in which case hatch date was taken as the date on which the cygnets were first observed minus one day) or in the nests. We used seven Reconyx camera-traps to record the outcome of swan nesting activity in 2013. Cameras were set up in 5–8 m from the nests. The behaviour of nesting pairs was recorded for 24 different nesting pairs in 2013, with behaviour grouped somewhat subjectively into three categories: (1) aggressive to observer, (2) escaped when humans at a distance of 300 m ("shy"), and (3) intermediate behaviour (*e.g.* hiding behind the nest).

Weather data

Weather data, including daily temperatures and the timing of the snow melt, were obtained from the nearest weather station, Chaun, 8 km from the centre of the island (www.rp.5.ru). The onset of warmer (above zero) temperatures was estimated as the earliest date after which average temperatures remained above zero for at least three consecutive days (subsequent days with negative temperatures during summer weren't considered). Spring weather conditions were classified as either: 1 = warm (2002, 2007 and 2009), 2 = normal (all other years), or 3 = cold (2008, 2011 and 2013), on the basis of their overall characteristics (Table 1), depending on the date of onset of warmer weather (*i.e.* temperatures above zero), the date of complete melt of the snow cover and the average temperature from 20–31 May and into June. This method for describing spring weather conditions has been used in other Bewick's Swan studies (Syroechkovsky *et al.* 2002; Syroechkovsky 2013), and is used here to permit comparisons with observations made elsewhere in the swans' breeding range. Duration of the frost-free season was not analysed as an explanatory variable because it is relevant to fledging success, rather than to the early stages of the breeding season considered in this paper, but is included in Table 1 to provide an overview of weather conditions in the study area during the 2002–2013 breeding seasons.

Data analysis

The associations between spring weather conditions and biological parameters were analysed using statistic functions in Excel software. Overall nesting period was *c.* 37 days (*e.g.* sum of a 7-day laying period for a clutch of 4 eggs and a 30-day incubation period, Rees 2006). The total number of eggs laid by Bewick's Swans on Ayopechan Island each year was estimated by multiplying the average clutch size by nest density and by the area of the island (91 km^2). Partial loss of clutches was not controlled for in this calculation.

Results

Nest density

A total of 535 Bewick's Swan nests was located on Ayopechan Island over the 2002–2013 study period. The number of nests under observation varied among years because of different attention paid to swans in each year. Nest densities also varied among years and averaged 2.07 nests/km^2 (s.d. = 0.61, range = 0.98–3.33 nests/km^2) in 2002–2013 (Table 2, Fig. 2). In 2011–2013, when densities were recorded for 73 nests across nine plots, annual variation in nesting density in these plots was non-significant (ANOVA: $F_{2,24} = 2.13$; $P = 0.14$, n.s.). Nest densities looked bimodal, with high densities in 2003, lower numbers in 2004–2007, and relatively high densities again during 2009–2013. Minimal distances between swan nests on Ayopechan Island were recorded in 2012, the three lowest being 82 m, 84 m and 110 m apart. The minimum distance between nests in 2003 was 231 m; this parameter was not recorded in other years.

Clutch and egg sizes

Average Bewick's Swan clutch size was 3.60 eggs (s.d. = 1.05, n = 410 clutches) during 2002–2013. The frequency of different clutch sizes across years is illustrated in Table 3, together with the annual average and median values. The decrease in average clutch size over the years (Fig. 2) did not reach statistical significance (linear regression: $F_{1,9} = 4.42$, $P = 0.065$, n.s.). Unusually, a clutch of 7 eggs was found in 2003, and a second clutch of 7 eggs was reported by local people in 2005 (A. Kashina, pers. comm.). Clutches of 6 eggs were found in 5 years of our 11-year study and only in 2002–2010 (Table 3; Fig. 3). We found that the proportion of large clutches of 5 or more eggs and of 6 or more eggs also declined during the study (linear regression: $F_{1,10} = 7.20$, $P = 0.03$ and $F_{1,10} = 9.62$, $P = 0.01$, respectively; Fig. 3). Despite the common opinion among local people that the Bewick's Swans never incubate a clutch of 1 egg, incubation of single egg clutches was often reported (Table 3). In the cases where nest histories had been monitored, these were found to be clutches where some eggs had been taken by predators (see nest success and hatch dates for details of nest predation).

Egg dimensions recorded in 2011–2013 are given in Table 4 together with historical sizes from the same site. Small sample size in 1988–89 (n = 22 eggs) did not permit

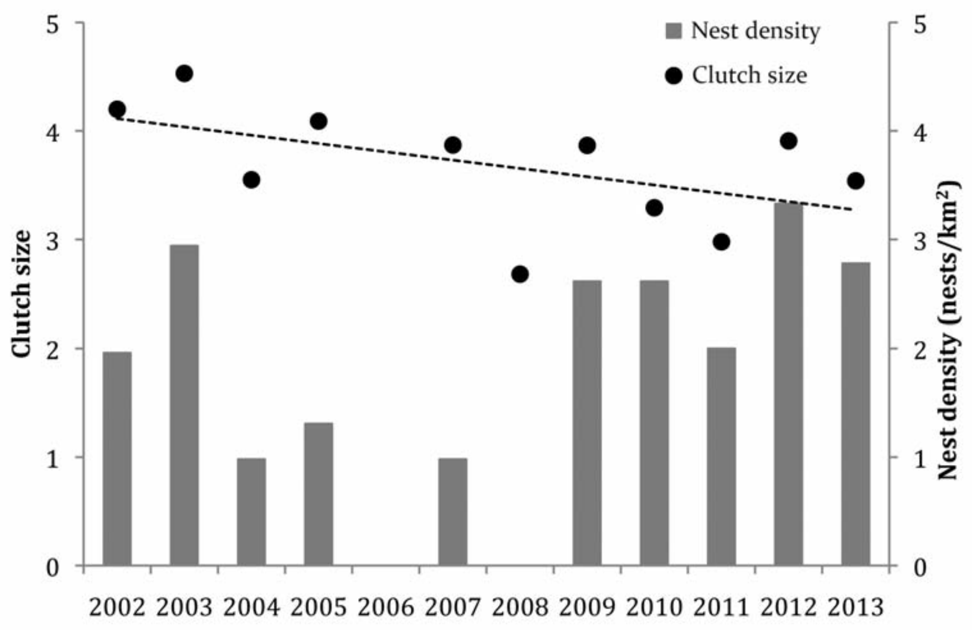

Figure 2. Between year changes in the nest density and mean clutch size of the Bewick's Swan nesting on Ayopechan Island, Chaun Delta, in 2002–2012. Nest density trend (not significant) is represented by the dotted line; clutch size trend (not significant) is represented by the dashed line.

comparisons with the egg size data recorded more recently. A sample size of 104 eggs for the years 1975–1977 and 1980–1984 was similar to our sample sizes; however, neither s.d. nor s.e. values for the egg size measures were given for this time period in Krechmar *et al.* (1991), and the data therefore again could not be compared statistically. In considering the extreme measures, the largest ranges both for egg length (85.1–116.9 mm) and for egg diameter (61.4–78.7 mm) were recorded in 2012. An abortive egg with no yolk was reported once in a Bewick's Swan nest in 2011: it measured 66.1 × 48.2 mm in size. About 1,538 eggs were encountered during the 2002–2013 study (Table 3), so the proportion of abortive eggs was very low in this population, at 0.07%.

Nesting success

Nesting success ranged between 32.2–72.2% in the years 2009–2013 and averaged 46.5% (Table 5). We observed Arctic Foxes successfully depredating clutches in all years, and a dead adult swan was found in an active Red Fox den in 2008. Significant predation of eggs by gulls *Larus* sp. was reported. Seven camera-traps recorded the outcome of Bewick's Swan nesting attempts in 2013. Of these, the clutches hatched in two nests, three were depredated by Arctic Fox and two were depredated by an unknown predator, most likely by gulls (the predation was not recorded on camera). Bewick's Swan pairs showed a variety of reactions to the observer: some strongly defended their

Table 3. Clutch sizes recorded for Bewick's Swan nesting on Ayopechan Island, Chaun Delta, Siberia, in 2002–2005 and 2007–2013.

Years	**No. of clutches of each clutch size**							**No. of nests**	**Average clutch size (± s.d.)**	**Median clutch size**
	1	2	3	4	5	6	7			
2002	0	0	0	3	8	2	0	13	4.92 (0.41)	5
2003	1	2	1	6	4	2	1	17	4.18 (2.40)	4
2004	0	3	7	6	4	0	0	20	3.55 (1.00)	3.5
2005	1	1	4	17	9	2	0	34	4.12 (1.02)	4
2007	1	5	6	16	10	0	0	38	3.76 (1.16)	4
2008	0	9	11	2	0	0	0	22	2.68 (0.42)	3
2009	2	1	6	12	8	1	0	30	3.87 (1.36)	4
2010	0	8	23	13	3	1	0	48	3.29 (0.81)	3
2011	4	7	21	12	1	0	0	45	2.98 (0.89)	3
2012	2	4	18	40	24	0	0	88	3.91 (0.87)	4
2013	1	6	24	27	9	0	0	67	3.54 (0.89)	4

nests, even threatening the observer (Fig. 4) while others escaped from the nest when the observer approached to within 300 m. The latter always left a nest uncovered, didn't return to the nest for several hours, and their nests were subjected to gull depredation. Intermediate behaviour, which fell between these two extremes, involved female swans hiding behind the nest and leaving only when the observer approached to within 10–20 m. Such females returned to their nests soon after the observer left the vicinity of the nest. This last type of behaviour has also been described for Bewick's Swans in other areas (Krechmar & Kondratiev 2006; Rees 2006; our observations in the Lena Delta, Siberia), whereas their active protection of nests from humans is known only from studies on the Chaun Delta in 1988–1989 and in the 2000s (A. Kondratiev, pers. comm.) and from observations on the Kolyma Delta in the 2000s (http://ibpc.ysn.ru/?page_id=386). In 2013, for 24 nesting pairs, in which behaviour at the nest was reported, three pairs were aggressive to observers, eight pairs were "shy" and thirteen pairs showed intermediate behaviour.

Nesting chronology

Bewick's Swans were first observed in the study area on average on 13 May (range = 10–17 May) in 2011–2013, earlier than the mean arrival date of 27 May recorded in 1971–1984 (range = 20 May – 2 June; Krechmar *et al.* 1991). The onset

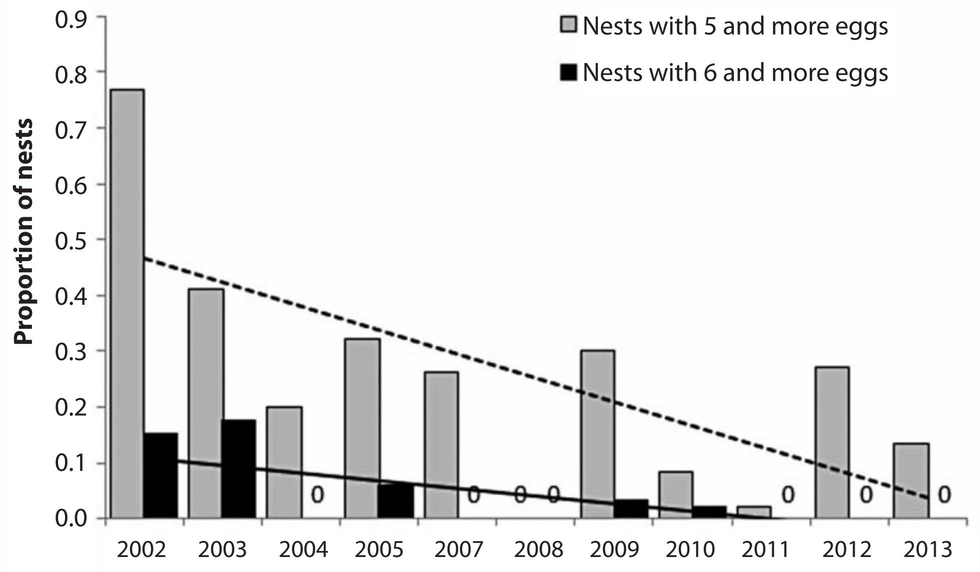

Figure 3. Between year changes in the proportion of large clutches in Bewick's Swan nesting on Ayopechan Island, Chaun Delta, 2002–2012. Clutches with 5 or more eggs and clutches with 6 or more eggs are considered as separate rows, although 6+ clutches are included in 5+ clutch row. Trend of 5+ clutch proportion is shown by dash line; trend of 6+ clutch proportion is shown by solid line.

of egg-laying occurred between 29 May and 8 June in 1975–1977 and 1980–1984 (Krechmar & Kondratiev 2006) and between 23 May and 4 June in 2002–2013.

Daily field observations made by the team on Ayopechan Island enabled us to record the dates on which the earliest Bewick's Swan broods first appeared on the tundra each year (except in 2004 and 2006), and the estimated earliest hatch dates ranged from 28 June (in 2012) to 11 July (in 2011) (Table 2).

Influence of weather characteristics

Most measures of spring weather conditions each year (*i.e.* the date of consistently above zero temperatures, snow melt date and temperatures in late May and early June) did not correlate significantly with nesting density, clutch size and hatch date (Table 6). Average clutch size increased with average temperature during 1–10 June (when most clutches were initiated), but this was not statistically significant (Spearman Rank correlation: r_{10} = 0.445, n.s., Table 6). Clutch size varied according to the spring classification, however, with larger clutches laid during early springs (mean ± s.d. = 3.99 ± 1.12) than in normal springs (3.79 ± 1.04) or late springs (3.22 ± 0.94) (ANOVA: $F_{2,419}$ = 18.15, P < 0.001), and average clutch size also varied according to whether the spring was early, normal or late each year (Spearman Rank correlation: r_{10} = 0.662, P < 0.05, Table 6). Although

Table 4. Historic and recent mean egg size measurements recorded for Bewick's Swans nesting on Ayopechan Island, Chaun Delta, Siberia between 1975 and 2013, in comparison with those for Bewick's Swans from Northwest European Population nesting at Khabuicka, Nenetskiy *zapovednik*, Archangelsk Okrug. (1) = Krechmar *et al.* 1991; (2) = Krechmar & Kondratiev 2006; (3) = Rees 2006; n/a = not available. Egg size measurements are in mm in each case.

Parameter/Year	**2011**	**2012**	**2013**	**1975–1977 and 1980–1984(1)**	**1988–89(2)**	**Khabuicka(3)**
Average egg length	103.78	104.20	105.09	104.6	107.1	102.7
(± s.d.)	(4.24)	(5.13)	(3.91)	(n/a)	(2.91)	(n/a)
Maximal egg length	114.1	116.9	113.5	113.8	111.5	117.4
Minimal egg length	96.6	85.1	95.6	93.5	100.5	89
Average egg diameter	66.74	67.51	67.04	67.7	67.9	66.4
(± s.d.)	(1.44)	(2.38)	(1.82)	(n/a)	(2.02)	(n/a)
Maximal egg diameter	69.9	78.7	70.4	70	71.1	72
Minimal egg diameter	60.5	61.4	63.2	63.3	63	60.5
Sample size (no. of eggs)	72	102	44	104	22	342

nesting chronology (expressed as the date on which the first broods were seen to have hatched) appeared to increase with the snow melt date, and also to be earlier in springs where the weather conditions were classed as early, these associations were not statistically significant (n.s., Table 6).

Discussion

Before this study, the highest reported average nest density of the Bewick's Swan was 1.1 nests/km^2 (peak density = 1.6 nests/km^2), reported from Zakhar'in Bereg near the Pechora Delta, northeast Russia, and at the time this was considered one of the highest throughout the entire range (Rees 2006). During 2002–2013, nest density in Chaun Delta averaged 2.07 nests/km^2 with peak densities of 3.3 nests/km^2, *i.e.* twice that of Zakhar'in Bereg and ten times higher than that reported at the same site in the 1970s and 1980s (0.2 nests/km^2 Krechmar *et al.* 1991). There was tentative evidence for an increase in Bewick's Swan nesting density during the study, though the trend would be better described as bimodal, and the increase was not significant. A break in monitoring occurred here between 1984 and 2002 and thus the increase in nest density throughout this time period was not fully documented.

Table 5. Proportion of clutches where at least one egg hatched, for Bewick's Swan nesting on Ayopechan Island, Chaun Delta, Siberia in 2009–2013.

Year	**2009**	**2010**	**2011**	**2012**	**2013**	**Average**
Nest success (≥ 1 egg hatched)	0.353	0.333	0.722	0.595	0.322	0.465
No. nests where nest success was known (*n*)	17	15	18	41	62	

Despite the Bewick's Swans' territorial behaviour, birds were found breeding in close proximity to each other on the Chaun Delta in the year of highest nest densities (2012). An increase in nest density in the Chaun Delta between the 1970s and 2010s corresponds with the reported growth in numbers wintering in Japan over this period, which increased from < 2,000 birds in the 1970s to > 30,000 birds by 2000 (Albertsen & Kanazawa 2002; see also Kondratiev 1984 for confirmation that at least some swans breeding on the Chaun Delta winter in Japan), representing a ten-fold increase on

Figure 4. Bewick's Swan actively protecting a nest from an observer, June 2013. (Photograph by A. Krechmar).

Table 6. Spearman rank correlations for weather conditions in relation to clutch size, nest density and the earliest hatch date amongst Bewick's Swans nesting on Ayopechan Island, Chaun Delta, Siberia, 2002–2013. Significant correlations ($n = 10$, $P < 0.05$) are highlighted in grey.

Weather variable	Clutch size	Nest density	Earliest hatch date
Days after 1 January when above zero temperatures commenced	–0.113	–0.133	0.186
Days after 1 January when snow had fully melted	–0.345	–0.056	0.407
Daily average temperature for 20–31 May	0.394	–0.360	–0.342
Daily average temperature for 1–10 June	0.376	–0.192	–0.092
Integrated spring characteristic	–0.662	0.303	0.340

both breeding and wintering grounds. Given the discovery of a large Chinese-wintering population in recent years (Cong *et al.* 2011a) a new ringing programme would help to establish contemporary migratory ties within the Eastern Bewick's Swan Population.

Recent warming has been especially pronounced in the Bering sector of the Russian arctic, resulting in unprecedented conditions for nesting birds which may have contributed to the dramatic increase in the Bewick's Swan in this area. Warm climate and the associated verdant vegetation were known to enable Bewick's Swan to extend their breeding range as far north as Zhokhov Island (76°N), in the New Siberian Archipelago, during the Holocene period 8,500 years ago (Makeev *et al* 2003). The median date for the onset of above-zero temperatures in spring has shifted from 1 June in 1975–1984 to 20 May in 2002–2013, and the median date of snow melt likewise advanced from 15 June to 2 June over the same period (Kondratiev 1979; Krechmar *et al.* 1991). The duration of the frost-free season has almost doubled from 35–60 days in the 1950s–1970s (Krechmar & Kondratiev 2006) to an average of 83.5 days during 2002–2013 (Table 1). We suggest these dramatic changes in the duration of the frost-free season, and a resulting increase in plant biomass production, may provide favourable conditions for breeding herbivorous swans (Rustad *et al.* 2001).

It seems reasonable to attribute variation in Bewick's Swan nest density, clutch size and nesting phenology to weather conditions within each nesting season, and several attempts have been made to this in different parts of the swans' breeding range (see summary in Rees 2006; Syroechkovsky 2013). We found that nest density in 2002–2013 was not correlated to any weather characteristics, but this period was relatively warm throughout. During a study on Vaygach Island, Syroechkovsky and co-workers found that Bewick's Swan nesting density was strongly associated with spring weather conditions, with reduced breeding propensity in cold springs (Syroechkovsky *et al.* 2002; Syroechkovsky 2013). This was for swans breeding in the high Arctic (latitude of the middle point of the Vaygach Island is 70°00'N, compared with 68°50'N at our study site), however, and during a run of relatively cold springs in 1986–1997. We suggest that the recent prevailing weather conditions were favourable for breeding even during the colder years, and that this could explain why nest density was independent of any weather variables.

Clutch size was influenced by spring weather conditions, with larger clutches laid in relatively warm "early" springs. Warmer June temperatures have previously been shown to be correlated with higher breeding productivity in arctic waterfowl (Barry 1962; Summers & Underhill 1987), but the mean annual clutch size did not vary significantly with June temperatures during the present study. No nests with 6 eggs were recorded during 2012, despite the large sample of nests checked and June temperatures being warmer than in 2003, when the highest proportion of very large clutches (*i.e.* with 6 or 7 eggs) was reported. The decline in the proportion of large clutches could be the first indication of density dependence on the island, perhaps as a consequence of overexploitation of local food resources at a critical period. With increasing nest density, female swans may have been unable to obtain sufficient reserves to produce clutches of 6 or more eggs in more recent years. During the earlier studies of A.Y. Kondratiev in 1975–1977 and 1980–1984, one clutch of 6 eggs was reported amongst 118 clutches (0.85%, Krechmar *et al.* 1991) compared to 2–17% in early years of this study. The unusual clutch of 7 eggs in 2003 could be a result of the food supply in that year, but we cannot exclude the possibility that this was one or more eggs dumped in another swan's clutch, the product of more than one female. The possibility of nest parasitism is difficult to reconcile with the Bewick's Swans' territorial behaviour, but it may be possible amongst closely related females, and has been demonstrated elsewhere (Syroechkovsky 2003). The minimal distance between nests (82 m) was also much lower than found in previous studies, for instance in comparison with 860 m reported on Vaygach Island (Syroechkovsky *et al* 2002).

There was a marked difference in clutch sizes between the Northwest European and the Eastern Bewick's Swan Populations, with a higher average clutch size of 3.6 eggs (range = 1–7 eggs; annual mean clutch size = 2.7–4.9 eggs) in the present study than the 3.4 eggs (range = 1–6; annual mean clutch size = 2.6–3.9 eggs) recorded at Khabuicka during 1991–2000, at a time when numbers in the Northwest European Bewick's Swan Population were peaking (Rees 2006). Bewick's Swan clutch size may be related to the latitude of the breeding site (Rees 2006), but Khabuicka in the Nenetskiy *zapovednik* is at a similar latitude to the Chaun Delta (N 68°15'). There was no obvious difference in the egg dimensions recorded for the Eastern and Northwest European Populations, although eggs from Chaun Delta appeared to be slightly larger. Thus, it seems that the Bewick's Swans in the Chaun Delta not only nested at higher densities than those at Khabuicka (average = 2.07 nests/km^2 and 1.1 nests/km^2 respectively), but also had larger clutches, perhaps reflecting higher quality breeding habitats for the species in the two study areas.

The average nesting success of 46.5% (range = 32.2–72.2%) recorded in this study was lower than the 67.2 % (range = 20–94%) reported on Vaygach Island (Syroechkovsky *et al* 2002). Annual nest success was not fully documented at Khabuicka but it averaged at least 54.9% during 1992–2000 (Rees 2006). Whether nesting density influences nest protection behaviour by Bewick's Swans is unclear. Following the findings of Drent *et al.* (1998) we suggest that low nesting success in this study may reflect density-dependent regulation of swans breeding at what seems to be a prime site, though the level of human activity in the region may also be a contributing factor. Some 33.3% of pairs in 2013 left the nest in response to human activity, rather than actively defending their clutch or hiding nearby, and egg depredation by gulls was recorded primarily amongst these "shy" pairs. Illegal shooting by villagers during the breeding season has been reported in the Chaun Delta, making nest protection dangerous for swans. Nevertheless, in contrast to this behaviour, at 12.5% of nests at least one pair member showed aggression to observers in 2013. All three nests with aggressive swans were situated close to the Chaun Biostation (average distance from these three nests to the station was 883 m, range = 490–1,500 m), and a territorial swan is also known to have nested near the Biostation in 1988–1989. The average distance from the station to "shy" swan nests was 5,233 m and to "intermediate" swan nests was 5,543 m in 2013, and none of these birds nested close to the Biostation. It therefore seems that the more territorial swans may have become habituated to the presence of researchers, who do not present any real danger to birds.

Overall, we consider that conditions in the Chaun Delta have become increasingly conducive as a breeding area for Bewick's Swans and that it has become a "swan paradise" in recent years. As the swans' feeding behaviour and food supply in the Chaun Delta have not been studied to date, we are unable to assess the extent to which the increasing density of nesting pairs observed in 2002–2013 can continue without affecting their food resources on the island and thus increase intra-specific competition for food. The Northwest European Population of the Bewick's Swan started to decline from 1996 onwards, after nesting density in at least one important breeding area had peaked (Rees 2006). It remains to be seen if the same pattern occurs for swans in the Eastern Population, possibly as a result of local density dependence regulation of one or more breeding parameters, such as nesting density, clutch size and fledging success.

Acknowledgments

We thank our field assistants in 2002 to 2013 whose hard work made this publication possible. The various transportation and logistic support (including helicopter flights to the remote study area) was kindly provided by Chukotka Mining and Geological Company (Kupol) of Kinross Gold Corporation in 2010–2013 and we express our great thanks to the managers. The Spectacled Eider study was financially supported by the U.S. Fish and Wildlife Service, Alaska, during all years of the research. The bird community monitoring project was funded by the Beringia Programme of the Wildlife Conservation Society in 2011–2013. Advice on statistical analysis was kindly provided by Eileen Rees from the Wildfowl and Wetlands Trust and by Anthony Fox from Aarhus University. Special thanks to Eileen Rees, Tony Fox and to two anonymous referees for helpful comments on an earlier draft of the text.

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Photograph: Bewick's Swan nesting habitat in Chuckotka, Russia, by Gleb Danilov.

Awareness and opinions of Maryland citizens toward Chesapeake Bay Mute Swans *Cygnus olor* and management alternatives

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Abstract

Concerns surrounding the ecological impacts from increasing numbers of non-native Mute Swans *Cygnus olor* have led some management agencies in the United States to implement control efforts directed at reducing populations of this invasive species. By 2001, concerns regarding the rapid increase in Mute Swan numbers in Maryland (USA) and their negative impacts upon Chesapeake Bay living resources (*e.g.* submerged aquatic vegetation, native waterfowl and colonial waterbirds) had become acute. An understanding of citizens' attitudes toward Mute Swans and potential management alternatives is necessary before wildlife agencies can enact socially acceptable measures to control these populations. A random telephone survey of Maryland registered voters therefore was conducted in February 2005 to assess public awareness (knowledge and attitudes) of Mute Swans in Chesapeake Bay, including the size of the swan population, preferences for swan management options and confidence in the ability of the Maryland Department of Natural Resources (MDNR) to control their numbers. A total of 625 completed surveys were obtained from respondents in seven geographical regions. Nearly all respondents (86%, *n* = 539) indicated they would support Mute Swan population control after they were provided evidence that this species was harmful to the Chesapeake Bay ecosystem; they felt the health of Chesapeake Bay was more important than sustaining a non-native swan population. Of the respondents that supported aggressive control measures, 62% (*n* = 387) supported the use of lethal methods of control, and a majority supported hunting over egg addling as a control method. Most respondents were also confident that the MDNR would implement control methods that were both humane and effective in solving the overabundance of Mute Swans in the region. The results provide useful information to wildlife professionals for management planning and communication when considering control of Mute Swan populations.

Key words: control, *Cygnus olor*, management, Maryland, Mute Swan.

Maryland's feral Mute Swan population originated from the escape of five captive birds in 1962 (Reese 1975). The population grew slowly through the 1960s and 1970s but then underwent rapid growth from *c.* 264 birds recorded in 1986 to *c.* 3,955 in 1999 (Hindman & Harvey 2004). As this population grew, so did concerns about their ecological impact on native bird populations and their habitats. In Chesapeake Bay (hereafter Bay), Mute Swans caused the abandonment of nesting areas by "state-threatened" waterbirds (likely to become endangered within the foreseeable future in the State) such as the Least Tern *Sterna antillarum* and Black Skimmer *Rynchops niger* (Therres & Brinker 2004). Large flocks of non-breeding swans also reduced submerged aquatic vegetation (SAV) at the local level (Naylor 2004; Tatu *et al.* 2007). The rise in breeding Mute Swan pairs also increased conflicts between people and breeding swans defending their nest territory and young (Hindman & Harvey 2004). Examples of conflicts include threat displays and direct attacks toward swimmers and people in small watercraft. This aggressive behaviour deters people from using riparian shorelines. Although no serious injuries to people have been reported in Maryland, there are two recorded cases of drowning involving attacks by Mute Swans elsewhere in the United States (Wisconsin Dept. of Natural Resources 2014; Steckling 2012).

In response to these increasing threats, the Maryland legislature adopted a law that in 2001 directed the Maryland Department of Natural Resources (MDNR) to control the Mute Swan population and to consider regulated hunting as a management tool (Maryland Annotated Code 2001). The Chesapeake 2000 Agreement identified the Mute Swan as one of the top priority invasive species requiring regional management (U.S. Environmental Protection Agency 2000). The agreement charged signatory agencies with developing and implementing management plans for those species deemed problematic to the restoration and integrity of the Bay's ecosystem.

In 2003 the MDNR developed a Mute Swan management plan to address the problems caused by this species (MDNR 2003). The agency recognised that any effort to control Mute Swans must occur concurrently with an effort to raise public awareness and advise Maryland citizens about potential threats posed by Mute Swans. One of the objectives in the management plan was to increase public awareness about Mute Swans and their impact to the Bay's living resources (MDNR 2003). The plan included a strategy to conduct a state-wide, random survey of citizens to determine their knowledge, perceptions and values regarding Mute Swans in Maryland (MDNR 2003). A companion strategy was to develop and implement a comprehensive Mute Swan communication programme that targeted specific demographic groups, particularly riparian shoreline owners and watershed community residents. Our survey contributed to this objective by obtaining an understanding of attitudes of Maryland citizens toward Mute Swans and their level of support for a range of management alternatives and methods required to control the swan population.

We tested the hypothesis that people who had contact with the Chesapeake Bay, defined by living and working near the Bay, were more likely to be aware of issues attributed to Mute Swans than people who did not have direct contact with the Bay. Given an awareness of issues about the Mute Swan, we predicted that a respondent from a region adjacent to the Bay was more likely to name a negative attribute of the Mute Swan than a respondent from a geographic region not adjacent to the Bay. We also predicted that respondents who were made aware of facts about the Mute Swan were more likely to support efforts to control the population. We predicted that supporters of Mute Swan population control were more likely to favour non-lethal methods of control over the use of lethal methods.

This survey was conducted to help the MDNR assess the public's awareness (knowledge and attitudes) of Mute Swans in Chesapeake Bay, including the size of the population, preferences for swan management alternatives and control methods, and also the public's confidence in the MDNR to manage the population.

Methods

In 2005, we contracted Mason-Dixon Polling and Research, Inc. (MDPR) to conduct a random telephone survey of registered voters in Maryland. The survey was developed to measure the voting public's awareness and opinions about: 1) the economic and environmental value of Chesapeake Bay to the State of Maryland, 2) the existence of various swan species in the Bay, 3) their knowledge of Mute Swans and the species impacts to Chesapeake Bay living resources (*e.g.*. submerged aquatic vegetation, native waterfowl and colonial waterbirds), 4) their support for population management alternatives to control this invasive species, and 5) the use of different control methods for reducing the swan population. An additional objective was to determine basic demographic information so the survey results could be used to inform communication efforts directed toward the public. The survey questions were reviewed by a panel of scientists from the University of Maryland (UMD), MDPR and MDNR and the survey was approved by the UMD Institutional Review Board.

Professional interviewers with the MDPR completed 625 telephone interviews during 23–25 February 2005. The population for this survey was all Maryland voters. The survey respondents were selected through a random digital telephone dialling procedure with a targeted sample that was stratified based on the demographic distribution of all registered voters, from the seven geographical regions of Maryland (Baltimore City, Central Maryland, Washington D.C. Suburbs, Southern Maryland, Upper Eastern Shore, Lower Eastern Shore, Western Maryland) (Fig. 1). Pearson chi-square tests were used to test for regional differences in knowledge of Mute Swans and support for population control (Snedecor & Cochran 1989). A chi-square test was also used to compare respondent characteristics, their opinions on the desired population level, and support for a range of management alternatives and population control methods.

The telephone survey consisted of 33 questions and each interview lasted *c.* 15

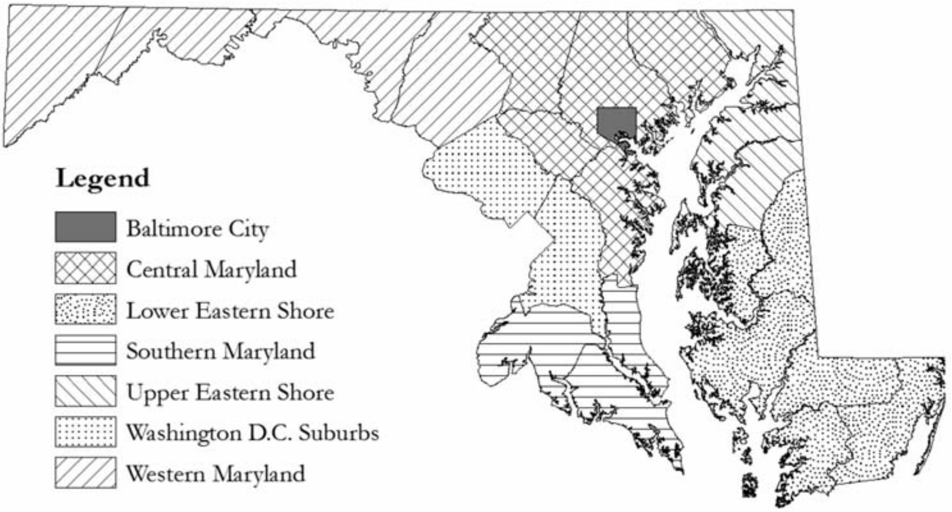

Figure 1. Geographic regions of Maryland used in a telephone survey of Maryland voters ($n = 625$) to assess citizen awareness of the Mute Swan population in Chesapeake Bay.

minutes. Survey interview questions included multiple choice, yes/no, Likert scale (1–5) and open-ended comments. The first section of the questionnaire measured respondents' opinions towards the importance of a healthy Bay to the State's economy and ecological health. In addition, this section established the respondents' personal experience with and participation in outdoor recreation activities related to the Bay. These activities included hunting, fishing, watching wildlife around their home, travelling at least one mile to view wildlife, camping and boating. Demographic information provided an opportunity to compare the findings by region, *i.e.* those living in proximity to the Bay regions, as opposed to those from the Central and Western regions of the State.

The second section of the questionnaire assessed the respondents' knowledge of Mute Swans and other swan species in the Bay. It also assessed the public's overall awareness of Mute Swan issues and conflicts. However, awareness in itself is difficult to measure because there are varying degrees of awareness. Some individuals may be completely unaware of the Mute Swan's existence; others may be able to recognise a Mute Swan, while others may be able to list the Mute Swan's defining features and role in the Bay ecosystem. To assess more accurately the true level of awareness, respondents were first asked if they could name any swan species in the Bay. They were then asked whether they had heard anything in the news or other information about Mute Swans and what was the source of the information (*e.g.* newspaper, television, radio, animal rights organisation, *etc.*). They were then asked about what they specifically had heard or knew about the Mute Swan (*e.g.* feeding on submerged aquatic vegetation, effects on other wildlife, public safety concerns) (Appendix 1, question (Q) 16). Respondents were also asked about their familiarity with issues related to the Mute Swan. Finally, in this section respondents were asked about the size of the Mute Swan population on the Bay (Appendix 1, Q 19).

In the third section, respondents were read information about the Mute Swan population in Maryland that included: 1) biological facts about the species, 2) their historical introduction into the Bay, 3) the increase in population size, 4) harmful impacts of Mute Swans to SAV and certain native wildlife species, and 5) their aesthetic values. After hearing the science behind the Mute Swan issues in the Bay, respondents were asked about their level of support for different management alternatives: 1) allow the population to expand naturally, 2) control or manage the population at a reasonable level (*e.g.* minimal impact to Chesapeake Bay living resources), or 3) eliminate Mute Swans from Chesapeake Bay (Appendix 1, Q 20). Respondents were then asked about their support for aggressive action to control the swan population, and support for lethal methods including regulated hunting and egg addling (Appendix 1, Q 21–24), using a 5-point Likert scale (strongly support, moderately support, moderately oppose, strongly support, not sure) (Likert 1932).

In the fourth section of the questionnaire, respondents were asked which of two statements best described their view of Mute Swans: "The MDNR should regulate the Mute Swan population…" or "Mute Swans should be protected from any control measures…" (Appendix 1, Q 25). The order of the statements was rotated with each interview.

The fifth section of the questionnaire measured respondents' confidence in the MDNR to implement a humane and effective Mute Swan population control programme and their support for dedicating resources to advise the public about Mute Swan issues in the Bay. The questionnaire ended with six demographic questions concerning: 1) respondent's type of residential area (city/urban, suburban, small town, rural), 2) race or ethnicity, 3) education, 4) age, 5) gender, and 6) geographic region of residence within the State. Responses to these questions were used to determine if there were differences or similarities in respondents' responses based upon the demographic information they provided.

Results

Respondent awareness and opinions of Chesapeake Bay Mute Swans and opinions on the value of the Bay to the State

A total of 625 completed surveys were obtained from seven geographical regions of the State (Fig. 1) out of approximately 1,000 telephone contacts.

Environmental and economical value of the Bay to the State. Nearly all respondents (99.6%, *n* = 622) felt that the Chesapeake Bay was either very important or somewhat important to Maryland's economy and ecological health.

Awareness and opinions of Mute Swans. Less than one third of survey respondents (28%, *n* = 174) said they were able to name a

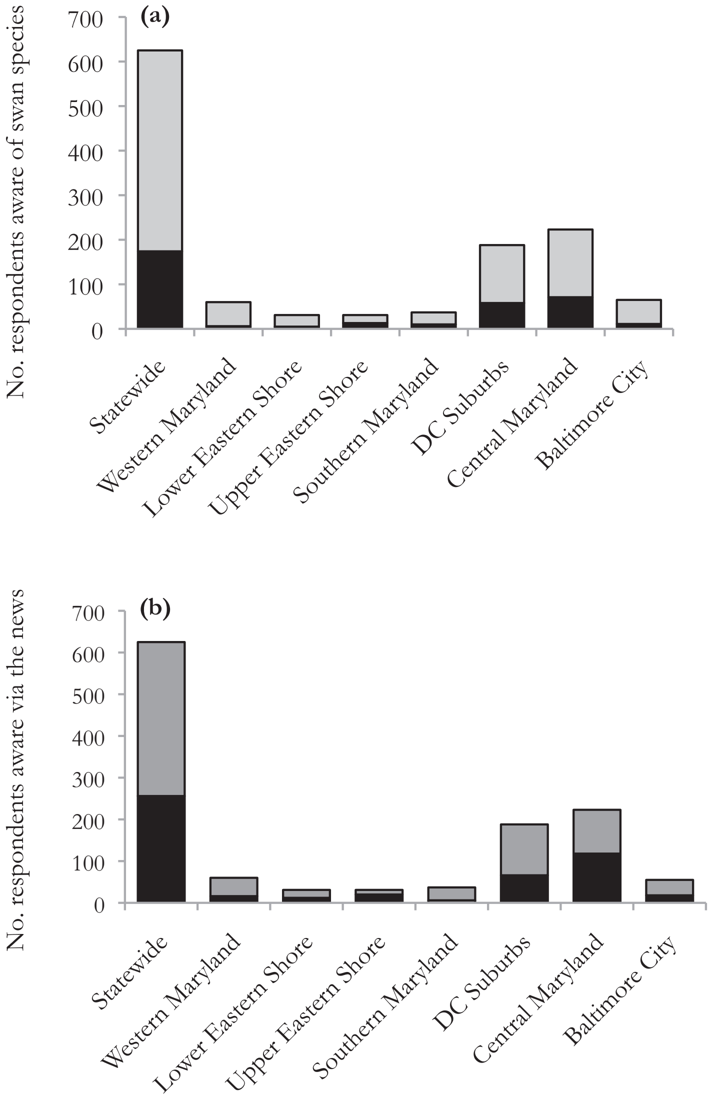

Figure 2. Statewide and regional responses of a random sample of Maryland voters ($n = 625$) to assess citizen awareness of swans in Chesapeake Bay. Respondents were asked if (a) they were aware of any specific swan species that live in Chesapeake Bay, and (b) if they had heard anything in the news regarding the Mute Swan? Black columns = yes responses; grey columns = no.

specific swan species inhabiting the Bay (Fig. 2). Of this group, more (49%, $n = 85$) were able to name the Mute Swan than any other swan species. Interestingly, more respondents (28%, $n = 49$) were able to name the Trumpeter Swan *C. buccinator* (rare winter transient) than the Tundra Swan *C. columbianus* (3%, *n* = 6), the most abundant swan species (wintering) in the Bay.

Overall, our geographic analysis proved to be inconclusive. While geographic region proved to be significant in regards to awareness of a swan species (defined by the ability of respondents to identify swan species) ($\chi^2_6 = 19.01$, $P = 0.004$), adjacency to the Bay was not a significant factor ($\chi^2_1 = 0.59$, $P = 0.44$, n.s.). About 42% (*n* = 13) of Upper Eastern Shore citizens claimed that they could name a swan species inhabiting the Bay, whereas only about 10% (*n* = 6) of Western Maryland respondents could name a swan species (Fig. 2a). The Upper Eastern Shore respondents also had the highest percentage of respondents who could name the Mute Swan (39%), followed by Trumpeter Swan (10%), and Tundra Swan (7%).

Perceived impacts of Mute Swans. About 41% (*n* = 256) of the state-wide respondents had heard something in the news regarding the Mute Swan (Fig. 2b). They obtained this information largely from newspapers (54%, *n* = 137) and television (39%, *n* = 99). When asked what they had heard about the Mute Swan, 62% (*n* = 159) of the responses were considered negative (Fig. 3). The most common facts expressed were Mute Swans are invasive (29%, *n* = 74) and destructive to agriculture (18%, *n* = 47).

Citizens who lived adjacent to the Bay, while unable to name any swan species better than their non-adjacent counterparts, had in fact heard more about Mute Swans ($\chi^2_6 = 39.00$, $P = < 0.001$). When asked to cite a negative fact they had heard about the Mute Swan, geographic region was unrelated to the respondent's awareness of Mute Swans ($\chi^2_1 = 1.15$, $P = 0.76$, n.s.).

Other factors influencing awareness of Mute Swans and related issues. Overall, involvement in outdoor recreational activities involving the Bay had a strong, positive relationship with swan awareness. There was a strong distinction between responses involving awareness of Mute Swan issues with those respondents who participate regularly in 0 (3%, *n* = 5), 1–3 (67%, *n* = 106), or 4–6 (30%, *n* = 48) outdoor activities ($\chi^2_2 = 9.90$, $P = 0.007$). Those who participated in more activities had a higher level of awareness of swans. In general, the more activities respondents participated in, the more likely they believed that the Mute Swan population was too high ($\chi^2_4 = 16.69$, $P = 0.002$).

Respondent's level of education was also correlated with their awareness of Mute Swan-related issues. There was a significant difference in awareness between those who had graduated college and those who had not ($\chi^2_1 = 18.20$, $P = < 0.001$. Only 22% (*n* = 54) of those who had not graduated college were able to name a swan species, whereas 33% (*n* = 120) of college graduates could name a swan species in the Bay. Those who had completed higher education levels (*e.g.* college, graduate school) were more aware of Mute Swan issues than those who had not.

Opinions about the Mute Swan population and management alternatives

Opinions about the Mute Swan population. Most survey respondents (57%, *n* = 356) were not

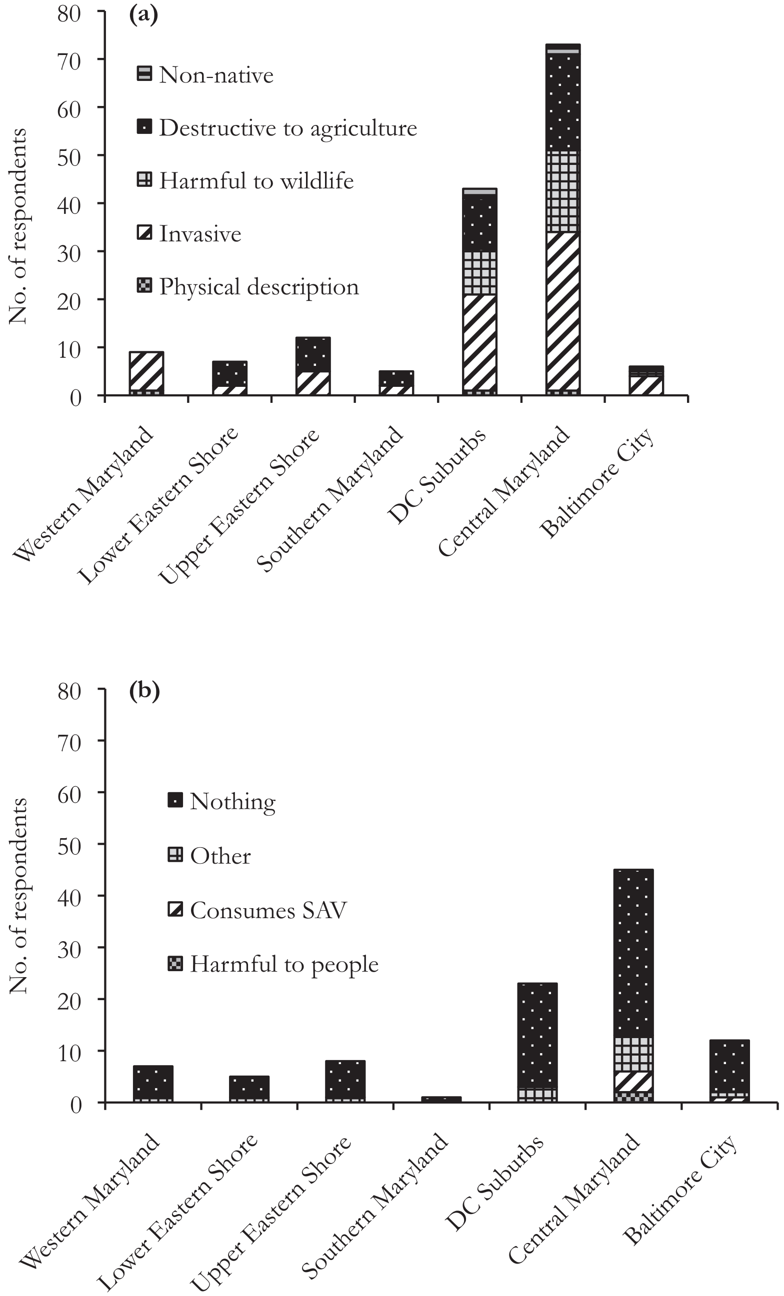

Figure 3. Regional and statewide responses (*n* = 256) of Maryland voters who had heard something about Mute Swans and what they had heard.

sure if the Mute Swan population was close to the optimum population size (Fig. 4). However, 26% (n = 163) of the respondents felt the Mute Swan population in the State was too high. A higher proportion (52%, n = 16) of Upper Eastern Shore respondents indicated that the population was too high compared to the overall, state-wide response.

Opinions about management options. After hearing information regarding the Mute Swan from an interviewer, the majority of respondents (79%, n = 486) felt the MDNR should take aggressive steps to control the Mute Swan population. A high proportion (86%, n = 539) felt that Mute Swans should either be controlled (n = 432) or eliminated

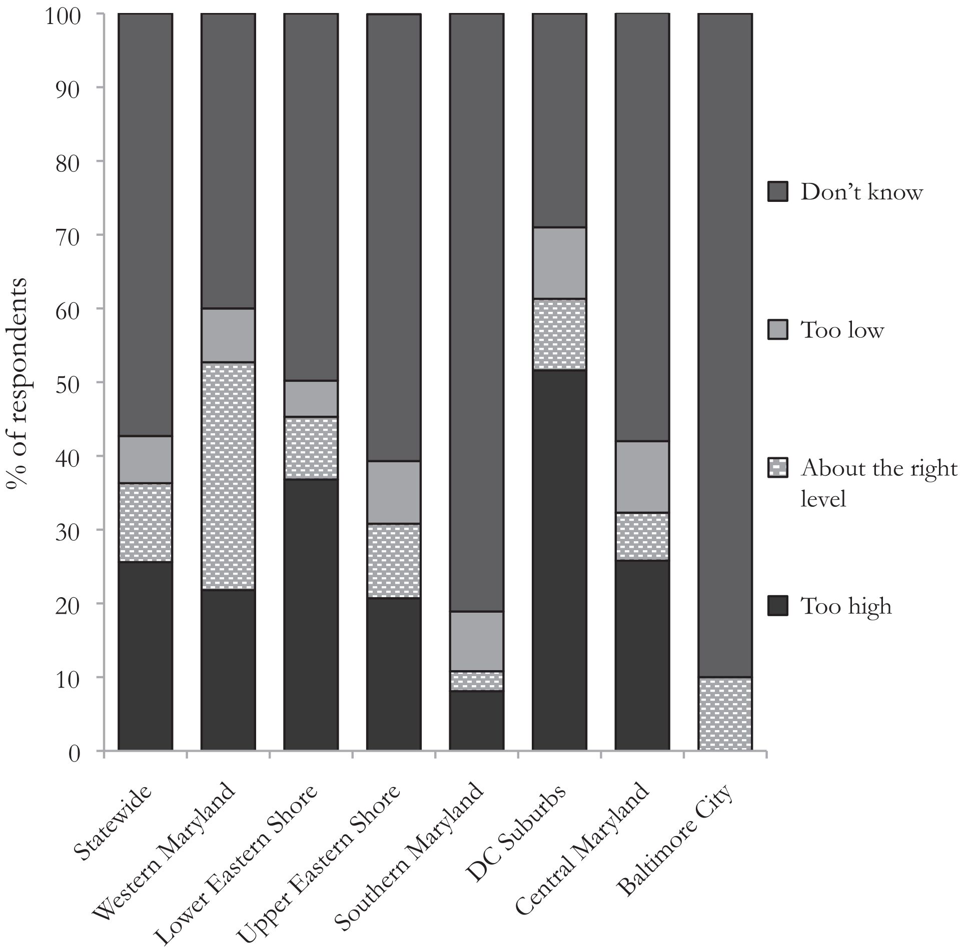

Figure 4. Statewide and regional responses (%) of a random sample of Maryland voters (n = 625) to assess citizen awareness of Mute Swan population size in Chesapeake Bay. Respondents were asked if the population was too high, about the right level or too low?

from the Bay (*n* = 107; Fig. 5). No one surveyed strongly opposed the MDNR taking aggressive measures to control Mute Swans.

Overall, the majority of survey respondents (62%, *n* = 387) supported the MDNR using lethal methods to control the Mute Swan population (Fig. 6). Of the 86% (*n* = 539) of respondents who opted for swan control, 65% (*n* = 350) supported the use of lethal methods. Of those who supported the elimination of Mute Swans in the Bay, 77% (*n* = 82) opted for lethal methods. The region with the largest percentage of respondents opposed to lethal control methods was Western Maryland (50%, *n* = 30) (Fig. 6). The region with the least percentage of respondents opposed to lethal methods was Central Maryland (18%, *n* = 40).

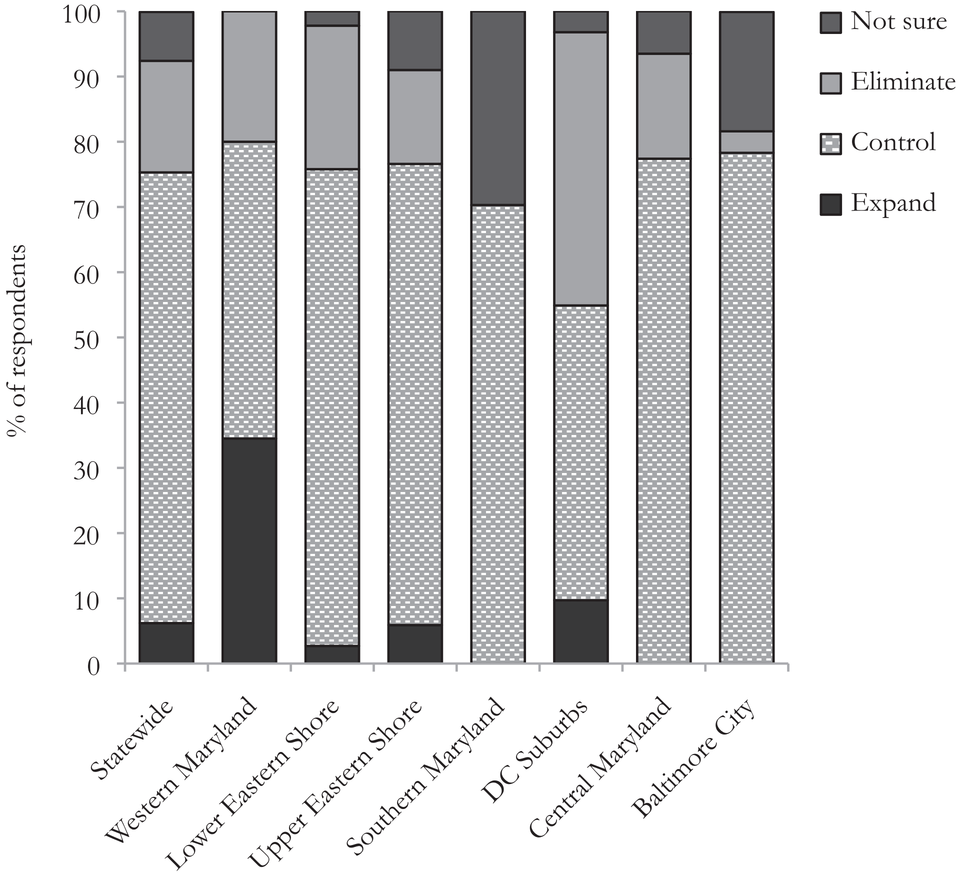

Figure 5. Statewide and regional responses (%) of a random sample of Maryland voters (*n* = 625) to Mute Swan management alternatives in Chesapeake Bay. Respondents were asked if they believed the Mute Swan population should be allowed to expand naturally, controlled by MDNR or eliminated?

Regulated hunting received the highest approval (76%, *n* = 476) as a Mute Swan control method (Fig. 6). The percentage of respondents from Baltimore City (*i.e.* urban) who strongly opposed hunting was more than three times the state-wide response (27%, *n* = 15 *vs.* 9%, *n* = 55). No respondent who had participated in hunting during the past year opposed hunting as a control method. Ironically, a large proportion of respondents (44%, *n* = 17) who stated the Mute Swan population should be allowed to expand naturally also felt hunting should be used as a swan control method.

A majority of respondents (64%, *n* = 402) supported egg addling as a control method (Fig. 6). Upper and Lower Eastern Shore citizens expressed the strongest regional response, strongly supporting egg addling (58% and 43%, respectively).

Attitudes toward the MDNR in managing the Mute Swan population

The majority of respondents (83%, *n* = 519) believed that the MDNR should manage the

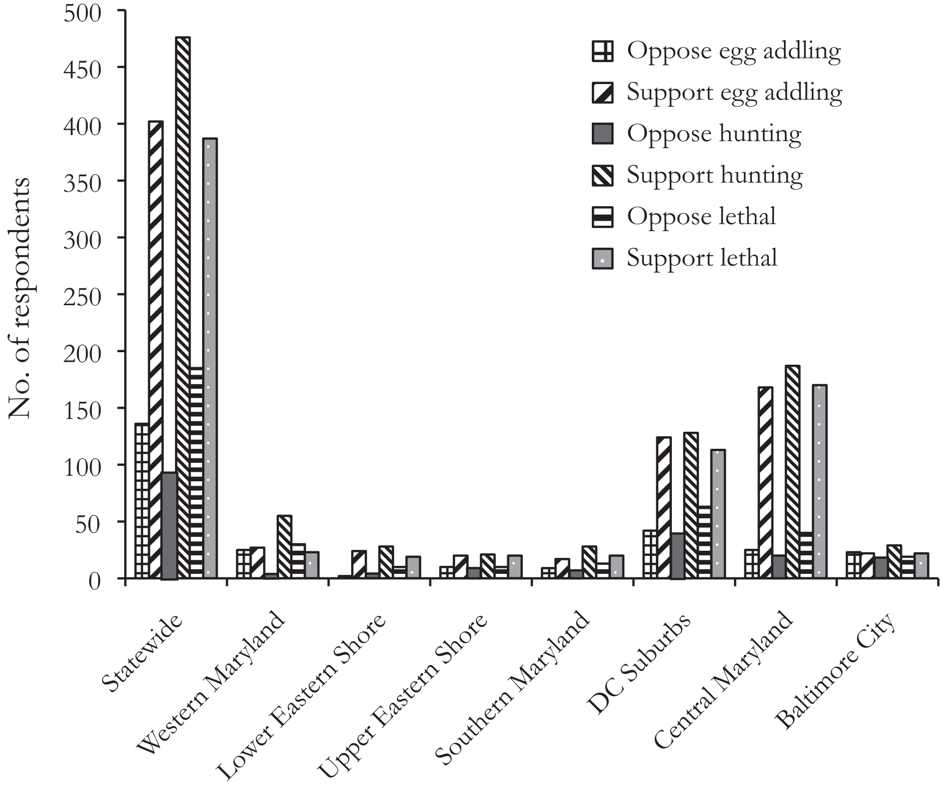

Figure 6. Statewide and regional responses (*n* = 625) of a random sample of Maryland voters concerning their support for the use of lethal contol, regulated hunting and egg addling to control the Mute Swan population in Chesapeake Bay.

Mute Swan population. Most respondents (72%, *n* = 449) indicated that they were confident that the MDNR could implement a humane and effective Mute Swan population control programme. Further, a high proportion of respondents (90%, *n* = 565) also supported the MDNR dedicating resources to raise public awareness about the Mute Swan issues in Chesapeake Bay.

Discussion

This is the first study to measure citizen knowledge of Mute Swans, their ecological impact and citizen support for Mute Swan population management and control methods on Chesapeake Bay. Survey findings revealed that most of Maryland's citizens felt that a healthy Bay was important. However, despite the Bay being one of the most important wintering areas for migratory waterfowl, they generally were not familiar with swan species found in the Bay. Given the news media attention Mute Swans have received in recent years (Baltimore Sun 2002), it was not surprising to learn that respondents were more familiar with Mute Swans than other swan species. However, most citizens knew very little about Mute Swans and their impact on the Bay's living resources. Respondents identified damage to agriculture as one of the negative impacts linked to Mute Swans; however, this species does not forage in agricultural fields in the Bay region (L. Hindman, pers. obs.). The ecological impact most often attributed to this species in the Bay by published research is their consumption and destruction of SAV (Naylor 2004; Perry *et al* 2004; Tatu *et al.* 2007; Sousa *et al.* 2008).

Our analysis indicated that people who had lived and worked near the Bay, were more aware of issues attributed to Mute Swans than those who did not have direct contact with the Bay. This awareness, in part, was likely to be the result of local media coverage (television and newspaper) from communities around the Bay. Two items that provided the focus of media coverage were: 1) the MDNR Mute Swan Management Plan objective of removing swans from important Bay habitats and 2) the legal challenges in federal courts concerning the legal status and management of Mute Swans in Maryland and the Atlantic Flyway (Cucuzzella 2004). Respondents' ability to name a negative attribute of Mute Swans was not linked to the distance from the Bay at which they lived or worked. Once respondents were provided with information about the ecological impact of Mute Swans and, most respondents supported the management of the swan population by MDNR and supported the use of lethal control, including hunting.

Mute Swan control efforts have often been initiated by wildlife management agencies without basic knowledge of public opinion about rising Mute Swan numbers, their effects on natural resources and how they view population control actions. These control programmes have often been met with strong objection by animal rights organisations and a vocal portion of the general public. More recently, management agencies have made attempts to inform and raise public awareness about the impacts of Mute Swans on native plant and animal species prior to reducing Mute Swan numbers (Michigan Dept. Natural

Resources 2014; Ohio Division of Wildlife 2014). However, local news media plays a significant role in constructing perceptions of wildlife problems and how they are best resolved, with people often becoming more aware of Mute Swan-related issues through widespread media attention.

The idea of controlling or using lethal methods to reduce or eliminate Mute Swans in various areas in the United States (U.S.) has elicited considerable public reaction (Odonell 2003; Moody 2014). Most control efforts have been met with opposition: 1) in the form of petitions (New Jersey, New York and Toronto, Canada: Change.org. Inc. 2014), 2) legislation (New York: Moody 2014; Blain 2014), and 3) legal challenges (U.S. Court of Appeals, U.S. District Court, Maryland: McGhee 2004; Cucuzzella 2004). However, in 2001, the Maryland General Assembly (legislature) directed the MDNR to control the State's Mute Swan population (Maryland Annotated Code 2001). The MDNR encountered legal action when the programme was initiated and control was suspended in 2004 (McGhee 2004). It was resumed on the litigation being resolved and on the U.S. Congress enacting the Migratory Bird Treaty Reform Act of 2004 (Wisch 2005), which removed federal protection for Mute Swans in the U.S.

As people experience negative encounters or perceive problems with wildlife, they often become more supportive of management actions to address these conflicts, including use of invasive or lethal techniques (Zinn *et al.* 1998). In addition, support for lethal control techniques often becomes stronger, depending upon the type and severity of the problem (Loker *et al.* 1999; Coluccy *et al.* 2001; Koval & Mertig 2004). Coluccy *et al.* (2001) found that landowners who reported property damage caused by Canada Geese *Branta canadensis* were more supportive of lethal alternatives. As in most situations involving native wildlife, many variables may account for conflicting attitudes toward Mute Swans. Public opinion may change with the amount and type of information that people receive on the issues and the circumstances within wildlife populations – particularly when the populations of certain species greatly increase (Duda & Jones 2008).

Opinions expressed during surveys can be influenced even when a small amount of information is included (Reiling *et al.* 1988; Fishkin 1995; Bright & Manfredo 1997; McComas & Scherer 1999; Lauber & Knuth 2000). With most of the Maryland public unaware of Mute Swans and their impacts, the information presented about Mute Swans during the survey interviews clearly influenced respondents' opinions. However, it was extremely valuable to learn how respondents felt about Mute Swan management and alternative management scenarios and control methods. We had predicted that supporters of Mute Swan population control were more likely to favour non-lethal methods of control over the use of lethal methods. However, the survey suggested that support for lethal control of Mute Swans, including regulated hunting, was greater among survey respondents than for non-lethal control methods like egg addling. The results suggested that it would be possible for MDNR waterfowl managers to implement some form of control management with few conflicts.

In 2003, when Maryland's Mute Swan management plan (MDNR 2003) was made available for public review, there was some limited interest in hunting Mute Swans (L. Hindman, pers. obs.). Though waterfowl hunting is a major outdoor activity in the area, there has been no recent history of hunting swans in the State; swans were last hunted in Maryland prior to the passage of the Migratory Bird Treaty Act in 1918. Although Mute Swans are unprotected in many areas of the U.S., and may be legally taken by hunters, no U.S. state or Canadian province (the swans are protected in Canada) has proposed a hunting season for the species. Many states allow the legal take of Mute Swans where the species is considered a deleterious, invasive or unprotected species (Atlantic Flyway Council 2003). In adjoining states (*e.g.* Delaware, Pennsylvania, Virginia) where Mute Swans are "unprotected", the number of Mute Swans harvested by hunters is very low (R. Hossler in Delaware, unpubl. data; I. Gregg in Pennsylvania, unpubl. data). A small, incidental harvest (< 50) of Mute Swans occurs each year in Virginia during legal Tundra Swans hunting seasons (G. Costanzo, unpubl. data).

Although the Maryland legislature had directed the MDNR to implement a Mute Swan control programme and to consider hunting as a management tool (Maryland Annotated Code 2001), a Mute Swan hunting season in Maryland would most certainly have elicited public opposition from within the State and other regions of the U.S. Further, with *c.* 16,000 Tundra Swans wintering in Maryland's portion of the Bay (U.S. Fish and Wildlife Service 2014), allowing the legal take of Mute Swans during regular waterfowl hunting seasons would likely result in misidentification and incidental, illegal kill of some Tundra Swans which are protected along the Atlantic Flyway except in North Carolina and Virginia (Serie *et al.* 2002).

We had hypothesized that respondents to the survey who supported population control would express greater support of non-lethal forms such as egg addling. The results however showed that they were generally less supportive of addling swan eggs than of regulated hunting (64% *vs.* 76% respectively). Lower support for egg addling may be linked to the public being less familiar with this method as a population control tool. Although egg addling is more socially accepted (*i.e.* considered humane) than lethal control for overabundant species such as Canada Geese (Laycock 1982), lower support for egg addling by Maryland citizens was likely to be influenced by differences in news media coverage. Citizens are more likely to experience and recall news media coverage of swan control involving the lethal removal of swans rather than egg addling (L. Hindman, pers. obs.). Another possible explanation for lower support for egg addling could be that the exact meaning of egg addling, even after being given a definition, was not clearly understood and therefore avoided by respondents.

Support for using hunting to control the Mute Swan population in Maryland may also have been influenced by the public's support for using hunting to control other overabundant species like White-tailed Deer *Odocoileus virginianus* (Responsive Management 1993, 2004). White-tailed Deer also carry the tick responsible for Lyme disease; thus, public concern for Lyme disease could lead to more positive attitudes toward hunting. In recent years the news media in Maryland has covered special managed deer hunts and the expansion of deer hunting on Sundays is being considered by the Maryland legislature (Herald-Mail Media 2014). Recent evidence suggests that people living near abundant wildlife populations may be more supportive of lethal management alternatives (Loker *et al.* 1999).

Application of the survey's findings to management of Mute Swans

Although respondents to the survey and the Maryland legislature expressed support for hunting as a method of Mute Swan control in the Bay, the MDNR declined to use hunting as a lethal management alternative in its swan management. Rather, the agency used an integrated programme of combining oiling swans eggs with the culling of adult swans by shooting, supplemented with euthanasia by mechanical cervical dislocation (using an emasculatome) to reduce the State's Mute Swan population (MDNR 2011; Hindman *et al.* 2014; American Veterinary Medical Association 2000, 2007). Numbers were thus reduced from *c.* 3,995 birds in 1999 to *c.* 41 in 2014. This management alternative was consistent with survey respondent support for control of Mute Swans in the Bay using both lethal (shooting) and non-lethal methods, and there was very little public opposition to the methods and level of control during the years (2005 through 2014) that the MDNR implemented its swan control programme.

This survey demonstrated that most people felt that a healthy Bay was essential to the economic and ecological well-being of the State and more important than maintaining a feral population of Mute Swans. The survey provided substantial evidence that the Maryland public would support lethal methods of control implemented by MDNR to reduce the State's Mute Swans population. Since public support for lethal wildlife management varies by management situation, managers need to consider public attitudes in specific lethal management situations. The survey findings and the management of the Bay's Mute Swans as a result of this survey provides useful information to wildlife professionals for planning communication and management alternatives when considering control of introduced (non-native) Mute Swan populations in other areas.

Acknowledgments

We thank Larry Harris, Mason Dixon Polling and Research Inc., and Lori Lynch and Susan Walker, University of Maryland, for their review of the survey questions. We also thank Bill Harvey and two anonymous referees for critical reviews of an earlier draft of the manuscript. We also thank members of the University of Maryland Gemstone Program for their contribution to this project: Jacob Bachmaier, Sarah Fixsen, Hannah Freymeyer, Stephen Herwig, Ryan Hoffmaster, Christina Johnson, David Sosnowski and Charles Wu. We are also particularly grateful to those Maryland citizens who agreed to be interviewed as part of this research project. This research was supported by the Maryland

Department of Natural Resources though Federal Aid in Wildlife Restoration Grant W-61-R. The University of Maryland Gemstone Program and Mason-Dixon Polling & Research, Inc. provided additional funding and in-kind services.

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Appendix 1. Prominent questions asked of Maryland voters (*n* = 625) about Mute Swans and their support for management alternative and population control methods in Chesapeake Bay Maryland, 2005. Question numbers correspond to the order in which they were read to respondents during telephone interviews.

Question 16. What have you heard or do you know about the Mute Swan? (first mention).
Is there anything else you know or have heard about the Mute Swan? (second mention).

Question 19. Based on what you do know, would you say the Mute Swan population in Maryland is too high, too low, about the right level or not sure?

The following questions were asked of survey respondents after they were read information about Mute Swans in Chesapeake Bay:

Question 20. Now that you have been presented with the scientific facts about Mute Swans in the Chesapeake Bay, do you believe the Mute Swan should be allowed to expand naturally, controlled to a reasonable population by the Maryland Department of Natural Resources (MDNR), eliminated from the Chesapeake Bay or don't know?

Question 21. In Maryland, there are legal hunting seasons for native waterfowl like Canada Geese and Black Ducks. Do you support or oppose regulated hunting as a way to control Mute Swan populations in Maryland? Is that strongly support, moderately support, moderately oppose, strongly oppose or not sure?

Question 22. Egg addling terminates the development of an embryo by shaking, oiling or freezing the eggs. Egg addling ensures that the female continues to incubate, thus preventing re-nesting. Do you support or oppose addling Mute Swan eggs as a population management option? Is that strongly support, moderately support, moderately oppose, strongly oppose or not sure?

Question 23. Do you support or oppose the MDNR taking aggressive steps to control the invasive Mute Swan population in the Chesapeake Bay?

Question 24. Do you support or oppose the MDNR using lethal methods to control the Mute Swan population in Maryland? Is that strongly support, moderately support, moderately oppose, strongly oppose or not sure?

Question 25. Please choose the statement that most closely describes your view: 1) The MDNR should regulate the Mute Swan population. Based on scientific evidence, the invasive, non-native Mute Swan is contributing to the decline of the health of the Chesapeake Bay and the issue of population control should be appropriately addressed, or 2) Mute Swans are a part of the Chesapeake Bay ecosystem and should be protected from any population control measures. Mute Swans have intrinsic and aesthetic value which adds to the beauty of the Chesapeake Bay. These birds have an innate right to reside in the Chesapeake Bay, or 3) not sure.

Spraying corn oil on Mute Swan *Cygnus olor* eggs to prevent hatching

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Abstract

During the 1980s and 1990s, non-native Mute Swans *Cygnus olor* increased dramatically in the Maryland (USA) portion of the Chesapeake Bay. As a method to slow further population growth, we tested the effectiveness of coating eggs in incubation with 100% food-grade corn oil to prevent hatching. During April to June 1996 and 1997, hatching success and nest abandonment was monitored in 26 control and 28 treatment nests. Whereas all full-term control nests hatched at least one egg, with an overall hatching success of 82.8% (111/134 eggs in 22 nests), no eggs in treated nests (0/118 eggs in 19 nests) hatched. Abandonment of oiled nests did not differ from that of controls, nor did abandonment among treated nests differ from controls between those treated early (first half of incubation) or late (last half of incubation). Treated nests carried full term were incubated on average an additional 16 ± 2.63 days (mean ± s.e.) beyond estimated hatching date. These experimental results were applied to a large-scale, integrated control programme initiated by the Maryland Department of Natural Resources (MDNR) aimed at reducing Mute Swan numbers in Maryland. In 2002, a fact sheet about the deleterious effects of Mute Swans and the agency's plan to treat nests was mailed to > 4,000 shoreline property owners who had previously licensed offshore waterfowl hunting blinds. Property owners who had known Mute Swan nests on their lands were contacted to seek multiple year permission to access their property to oil swan eggs. Over a 13-year period (2002–2003, 2005–2014), 1,689 Mute Swan nests containing 9,438 eggs were treated. Egg treatment was especially effective in reducing the number of swans that required culling by preventing an estimated additional *c.* 6,200 Mute Swans from entering the non-breeding population. Egg treatment was combined with the culling of adult swans (2005–2013) as part of the MDNR control programme that resulted in a reduction of the non-native Mute Swan population from *c.* 3,995 in 1999 to *c.* 41 in 2014. Corn oil provides resource managers with an effective, nontoxic method of reducing Mute Swan hatching success. While egg oiling can reduce the production of cygnets, however, merely treating eggs does little to reduce the swan population. If managers desire to reduce a

Mute Swan population quickly (< 5–10 years), an integrated strategy of treating swan nests and culling swans (*i.e.* reducing annual survival) by humane lethal means should be considered.

Key words: *Cygnus olor*, hatching success, invasive species, oiling, swan control.

A breeding population of Mute Swans *Cygnus olor* originating from the escape of two captive pairs in 1962 increased to > 4,000 birds in the Maryland portion of Chesapeake Bay by 2002 (Reese 1975, 1996; Hindman & Harvey 2004). Population growth and range expansion of this non-native species increased the number of swan-related problems. One of the most serious occurred in the early 1990s when a large moulting flock (*c.* 600) of Mute Swans disrupted nesting by Least Terns *Sterna antillarum* and Black Skimmers *Rynchops niger*, both state-threatened species, on shell bars and beaches in Tar Bay, Dorchester County (Therres & Brinker 2004). Mute Swans also sometimes injure or kill young waterfowl in the Bay (Hindman & Harvey 2004; Therres & Brinker 2004). Because of their foraging upon submerged aquatic vegetation (SAV) like Widgeon Grass *Ruppia maritima* and Eelgrass *Zostera marina* (Perry *et al.* 2004), Mute Swans reduce the availability of SAV to native wildlife (Reese 1996; Allin & Husband 2004; Naylor 2004; Tatu *et al.* 2007). Some breeding Mute Swans are aggressive and will threaten and even attack people and pets that come too close to their nest or young. Although the potential for injury is low, their territorial behaviour sometimes renders riparian waters inaccessible to people during the nesting season (Hindman & Harvey 2004).

In the absence of aggressive population control, the number of Mute Swans in Maryland was expected to continue growing rapidly and eventually could have become established throughout most of the Chesapeake Bay region (MDNR 2003). The MDNR's 2003 plan for managing the State's population of Mute Swans included an objective to reduce recruitment of young by > 60% and reduce the population size to < 500 birds (*i.e.* to mid-1970s levels) (MDNR 2003). In 2011, the MDNR modified its Mute Swan population objective to reduce the population to as few birds as possible to protect Chesapeake Bay living resources (*i.e.* submerged aquatic vegetation, native waterfowl and colonial waterbirds) (MDNR 2011). Thus, effective techniques were needed to reduce Mute Swan hatching success that could be applied in combination with the culling of adult birds to achieve the agency's management objective.

Several oils, including liquid paraffin (Baker *et al.* 1993), vegetable oil and mineral oil are effective at reducing hatching success of bird eggs (Pochop *et al.* 1998). Of these, only corn oil is considered non-toxic to the environment and thus is exempt from U.S. Environmental Protection Agency (EPA) regulations and is the only oil that may be used to treat eggs of free-ranging waterfowl without a Federal Experimental Use Permit. Guidelines for oiling eggs of over-abundant or injurious avian species such as temperate breeding Canada Geese *Branta canadensis*

(Smith *et al.* 1999) and Double-crested Cormorants *Phalacrocorax auritus* (Johnson *et al.* 2000; U.S. Department of Agriculture 2001) have recommended the use of corn oil.

A critical assumption of any egg-treatment programme is that the treatment technique does not cause incubating females to abandon the nest and provide opportunity for re-nesting. This assumption has been tested for temperate-breeding Canada Geese (Baker *et al.* 1993), but has not been established for Mute Swans, a species that will re-nest (Reese 1975, 1996) and for which widespread control, including egg treatment, has been advocated (Atlantic Flyway Council 2003; Mississippi Flyway Council 2012). Mute Swan eggs are larger with a thicker shell and possibly a different shell conductance and pore structure than the eggs of Canada Geese and other birds that have been used to test hatching success after treating with oils. In this study we therefore tested the effectiveness of spraying corn oil on Mute Swan eggs to reduce hatching success and monitor the rate of nest abandonment for free-ranging Mute Swans in Chesapeake Bay. The findings were applied to a large-scale control programme, which from 2005–2014 included a combination of reducing swan hatching success (treating eggs with oil) and adult survival (culling adult swans) to reduce the Mute Swan population in the Maryland portion of Chesapeake Bay.

Methods

This study was conducted in the brackish estuarine wetlands of Kent, Queen Annes, Talbot and Dorchester counties along the eastern shore of Chesapeake Bay, Maryland, USA (between 39°N and 38°N, 76°W). The study area supported about 70% of the State's Mute Swans that were distributed as large non-breeding flocks, located generally wherever SAV is abundant, and as breeding pairs within nesting territories. Mute Swan nests occurred in estuarine bay marshes dominated by Smooth Cordgrass *Spartina alternaflora* and Saltmeadow Cordgrass *S. patens* marshes and Common Reed *Phragmites australis* stands about 0.5 m above the high tide mark. Salinity was high (> 15 ppm) and tidal amplitude ranged from 21–24 cm.

This study was conducted over two breeding seasons from 29 April to 20 June 1996 and 14 April to 18 June 1997. Swan nests were spotted from fixed-wing aircraft from a survey altitude of 90–152 m and later visited either on foot or by boat. Each nest location was marked on maps (scale 2.54 cm = 2,000 m) and assigned randomly to either a control or treatment group. Three eggs from each nest were floated to estimate the stage of embryo development using the techniques described by Westerkov (1950) and Walter & Rusch (1997), and their incubation stage adjusted for a 36-day incubation period (*i.e.* full-term incubation for Mute Swans; Scott & The Wildfowl Trust 1972; Reese 1975; Ciaranca *et al.* 1997). The estimated hatching date (EHD) for each clutch was thus calculated by adding 36 days to the estimated date of clutch completion and clutches were then classed as being at the early (18–36 days before EHD) or late incubation stage (1–17 days before EHD).

Eggs in treatment nests were addled (*i.e.* embryo development curtailed) by coating with 100% food-grade corn oil. Oil was applied with a one-litre, hand-held spray bottle with an adjustable nozzle. Eggs were removed from the nest, and thoroughly spray coated with *c.* 60–100 ml of oil at a distance of *c.* 12 cm. Eggs in treatment nests that were wet from floating were wiped dry prior to oiling. Eggs in control nests were floated, wiped dry and returned to the nest. All eggs in treated and control nests were visually monitored every 1–4 days until nest termination to determine the fate of nests and eggs, *i.e.* whether the eggs were hatched, unhatched, predated or abandoned. For nests that terminated without hatching, we searched for signs of re-nesting within 300 m of the original nest site for a period of 30 days following abandonment. In Chesapeake Bay, Reese (1980) reported that re-nesting ranged from 11–30 days and averaged 18 days after loss of the first clutch.

To test whether there was an increase in pre-EHD nest abandonment for oil-treated versus untreated nests, we performed a chi-square test of proportions. A chi-square test was also used to compare pre-EHD nest abandonment between nests treated early and late in incubation (Snedecor & Cochran 1967). Differences in clutch size between years and between control and treated nests were tested by a 2-sample *t*-test at $\alpha = 0.05$.

Beginning in April 2002, the MDNR applied test results of treating Mute Swan eggs with corn oil to a large-scale, integrated control programme aimed at reducing the Mute Swan population in Maryland. The objective was to treat > 60% of the Mute Swan nests in the State (MDNR 2003). In March 2002, the MDNR sent a fact sheet to > 4,000 shoreline property owners who had previously licensed waterfowl hunting blinds offshore of their property. The fact sheet contained information about the deleterious effects of Mute Swans and the agency's plans to oil the eggs in Mute Swan nests. Property owners who had known Mute Swan nests on their properties were also contacted by the MDNR to seek multiple year permission to access their property for the purpose of oiling swan eggs.

Swan nests were located by aerial surveys in mid-April in 2002 through 2014. Following the aerial surveys, swan nests observed from the air were visited either by boat or on foot and all eggs were treated with corn oil. Nearly all (*c.* 98%) property owners with Mute Swan nests on their lands allowed nests to be treated (L. Hindman, unpubl. data). No nests were treated in 2004 as a U.S. District Court order prevented the U.S. Fish and Wildlife Service from issuing the MDNR, the required federal depredation permit (McGhee 2004). The following year the resolution of legal actions and the adoption of federal legislation (*i.e.* Migratory Bird Treaty Reform Act of 2004) resulted in regulatory authority for Mute Swans being returned to the U.S. states. Thus, beginning on 28 July 2005, the MDNR initiated its integrated swan control programme of combining egg oiling with the culling of adult swans by ethical lethal methods (American Veterinary Medical Association 2000, 2007). Lethal methods to reduce the Maryland Mute Swan population involved euthanasia by shooting and by mechanical cervical dislocation using an emasculatome.

Using vital rates of 1,689 nests treated × 6.07 (mean clutch size) × 82.8% (mean hatching success) × 88% (survival to fledgling; Reese 1975) × 83% (post fledging survival rate; Reese 1996) for Mute Swans, we calculated the number of swans that would have entered the non-breeding population that would have required culling if the MDNR had not undertaken a large-scale egg oiling effort. The calculations assumed no emigration or immigration of swans into the population, which we believe to be the case.

Results

We monitored 26 nests (11 control and 15 treated) in 1996 and 28 nests (15 control and 13 treated) in 1997. Mean clutch size did not differ between years (1996: mean ± s.e = 5.5 ± 0.43 eggs; 1997: 6.5 ± 0.43 eggs; t_{52} = 1.59, n.s.) and overall averaged 6.0 eggs (s.e. = 0.31; *n* = 54). Clutch size for both years combined did not vary between control (mean = 6.1 ± 0.44 eggs, *n* = 26) and treated nests (mean = 6.0 ± 0.43 eggs, *n* = 28) (t_{52} = 0.12, n.s.). Nest data from both years was combined for statistical analysis.

All control nests that reached EHD (*n* = 21) hatched at least one egg and overall 82.8% or 111 of 134 eggs hatched. In contrast, no eggs (0/118) in oil-treated nests that reached EHD (*n* = 19) hatched regardless of whether they were treated early (*n* = 5) or late (*n* = 14).

A similar proportion of control and treated nests reached EHD (control: 21 of 26 nests; treatment: 19 of 28 nests) (χ^2_1 = 1.17, n.s.). Furthermore, although samples were small, a similar proportion of control and treated nests reached EHD for both early-treated (control: 7 of 10 nests; treatment: 5 of 10 nests) (χ^2_1 = 0.83, n.s.) or late-treated (control: 14 of 16 nests; treatment: 14 of 18 nests) (χ^2_1 = 0.55, n.s.) nests. Nest loss was attributed solely to nest abandonment; there was no evidence that any active nest was predated. Additionally, no new nests were found within a 300 m radius of the original nests. Swans incubating treated clutches that reached EHD continued incubating *c.* 2 weeks (mean = 16.4 ± 2.63 days; range: 1–46 days, *n* = 18) past EHD.

Starting on 8 April 2002, the MDNR applied the test results of treating Mute Swan eggs with corn oil to a large-scale, integrated control programme aimed at reducing the Mute Swan population in Maryland. Over a 13-year period (2002–2003, 2005–2014) the MDNR treated 1,689 Mute Swan nests containing 9,438 eggs (Fig. 1). The number of treated nests per year ranged from 382 in 2005 to 3 in 2013 (Fig. 1). The egg-oiling effort prevented an estimated *c.* 6,200 Mute Swans from entering the non-breeding population. Thus, egg oiling not only reduced annual productivity of the swan population but it also reduced the related manpower, animal welfare concerns and expense that would have been required to cull these additional swans. Legal action (Cucuzella 2004) precluded the use of lethal methods of swan control until the summer of 2005. Between 2005 and 2014, the MDNR combined swan nest treatment with the culling of adult swans (*n* = 5,056) to reduce the Mute Swan population in Maryland from *c.* 3,995 in 1999 to *c.* 41 in 2014 (L. Hindman, unpubl. data).

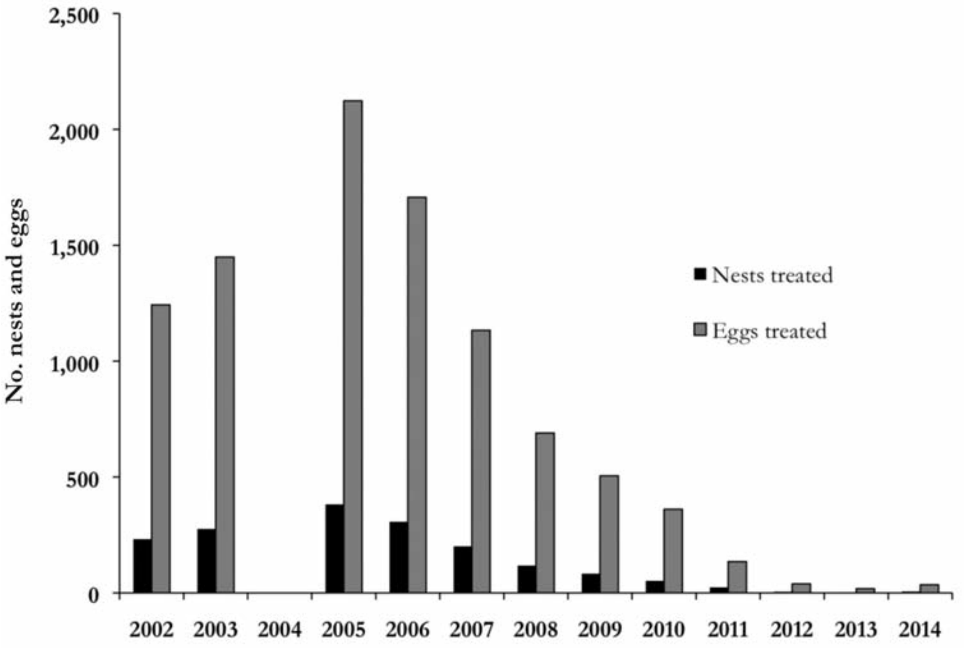

Figure 1. Number of Mute Swan nests and eggs treated with corn oil in Chesapeake Bay, Maryland, USA, during 2002–2003 and 2005–2014. No nests were treated in 2004.

Discussion

Corn oil proved 100% effective in preventing hatching of Mute Swan eggs and was equally as effective early in incubation as it was late in incubation. Although the Humane Society of the United States suggests that egg oiling for overabundant Canada Geese be undertaken during early incubation, the American Veterinarian Medical Association (AVMA) does not provide guidance on the addling of eggs under field circumstances (AVMA 2000, 2007). Nonetheless, there are no federal (U.S.) or Maryland regulations that prohibit the oiling of Mute Swan or other bird eggs for population control at any stage of incubation (U.S. Department of Agriculture 2001). Management agencies, such as the U.S. Department of Agriculture (USDA) Wildlife Services, now commonly use corn oil to reduce hatching success of overabundant bird species and apply the oil without regard to incubation stage, (USDA 2001). Treatment that provides effective control at a wide range of incubation stages reduces manpower and programme costs by eliminating the need for multiple flights and surveys to locate nests at specific stages of incubation. Moreover treating nests did not prompt early abandonment and re-nesting. We conclude that the effectiveness of corn oil displayed in this study would limit any need for nest searches for re-nests. We do not know if swans that abandoned their clutches before EHD re-nested; but if they did, they did not re-nest in the immediate vicinity of the original nests, *i.e.* no new nests were found within a 300 m radius of the original nests. Furthermore, Reese (1996) suggested that Chesapeake Bay Mute Swans lay a second clutch only if the first is lost before 10 May. Because the peak of hatching for Mute Swan eggs in Maryland is the first week in May, most swans incubating oiled eggs would continue incubation well past the threshold for re-nesting identified by Reese (1996), thus further limiting the possibility of re-nesting.

Alternative control measures, such as the removal and disposal of eggs, usually requires more labour than oiling eggs because the swans may re-nest at a high rate. In areas with small discrete breeding populations, egg shaking has been shown to be an inexpensive and effective method of limiting swan reproduction (Eltringham 1966). In Rhode Island (USA), shaking was the most practical method of controlling Mute Swan productivity because no additional tools and materials needed to be carried to the nest (J. Meyers, unpubl. data). However, shaking may not be as effective in inducing embryo mortality late in incubation (Cleary 1994), and if large numbers of eggs are involved may result in physical exhaustion of field personnel (Christens *et al.* 1995), which would also reduce its efficacy.

Pricking swan eggs with a sharp-pointed instrument has also been shown to be a practical method of terminating embryo development (Eltringham 1966; Allin *et al.* 1987). However, if puncture holes are not sealed, decomposition may accelerate and produce egg odour that may contribute to increased mammalian predation and nest abandonment. Pricking needs to be done carefully, because if the female detects that the eggs are damaged she may desert the nest and re-nest and lay another clutch elsewhere (Natural England 2001). Because abandonment in early or mid incubations prompts re-nesting, this method of egg control may simply lead to greater effort to find and treat new nests.

Spraying eggs of Ring-billed Gulls *Larus delawarensis* (Blokpoel & Hamilton 1989; Christens & Blokpoel 1991), Double-crested Cormorants, and Canada Geese (Christens *et al.* 1995) with white mineral oil prevented them from hatching. Coating Mute Swan eggs with penetrating oil, formalin or clear lacquer also prevented hatching (Allin *et al.* 1987). However, mineral oil, other petroleum-based oils and other toxic materials may not be used as an avicide without obtaining either federal registration or a permit from the EPA. In contrast, corn oil (a non-toxic, vegetable by-product) may be applied to incubating eggs of nesting gulls, waterfowl and other birds without a federal registration by virtue of an EPA exemption authorized by the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA; Section 25b). However, the appropriate state regulatory agency should be contacted to ensure that corn oil could be used under the FIFRA exemption. Further, government authorization may be required to treat swan eggs as Mute Swans are regulated in most states and provinces in North America.

Egg oiling is widely accepted by the

public as a method of population control for overabundant species, such as resident Canada Geese (Laycock 1982). A telephone survey of 625 Maryland citizens in 2005 revealed that a majority (62%, *n* = 388) supported lethal control of the Mute Swan population at Chesapeake Bay and 63% (*n* = 402) supported egg addling as a population control tool (Hindman & Tjaden 2014). Spraying Mute Swan eggs with corn oil reduces the proportion of nests that successfully produce cygnets (*i.e.* hatching success). This has a direct benefit by reducing the number of swans that must be culled if lethal control is part of an integrated control strategy to reduce a Mute Swan population. Egg oiling also reduces the manpower and expense required to cull additional swans.

While egg oiling can reduce the production of cygnets, however, merely treating eggs does little to reduce the swan population. Egg oiling targets that portion of the population with the greatest natural mortality rate and, thus, has the least effect on population control or reduction (Cooper & Keefe 1997). Ellis & Elphick (2007) determined that management that reduces reproductive rates, without changing survival rates, is unlikely to be an efficient strategy for reducing Mute Swan populations. Similarly in Rhode Island, Mute Swan breeding output was limited by aggressive egg addling; 79% of all active nests were addled between 1979 and 1998 but the population continued to rise by 5–6% per year between 1986 and 1999 (Allin & Husband 2004). In long-lived species, like Mute Swans, population growth is most sensitive to adult survival (Alisauskas *et al.* 2011; Lebreton & Clobert 1991). Thus, reducing hatching success must be combined with reducing adult survival to reduce swan population growth.

Egg oiling is also a labour intensive and time-consuming operation which must be maintained for several years to affect population growth. Model simulations of Maryland's Mute Swan population have shown that it would require reducing hatching success by 80% over a 10-year period to reduce the population by *c.* 10% (Hindman & Harvey 2004).

In most instances, it is impractical to locate and treat enough nests over a multiple year period to reduce the population. Thus, if managers desire to reduce a Mute Swan population quickly (*i.e.* < 5–10 years), an integrated strategy of treating swan nests and culling adult swans (*i.e.* reducing annual survival) by lethal means should be considered. Nevertheless, our findings provide resource managers desiring to control Mute Swan population growth with a safe, nontoxic method of effectively reducing Mute Swan productivity.

Acknowledgments

We are grateful to M. Keaney, U.S. Fish and Wildlife Service, Eastern Neck National Wildlife Refuge, and R. Miller and M. Pratt, MDNR for field assistance. We extend sincere appreciation to property owners who allow us access to their land. We also thank G.M. Haramis, B.L. Swift and two anonymous referees for critical reviews of an earlier draft of the manuscript. The MDNR, Wildlife and Heritage Service, Federal Aid in Wildlife Restoration Project W-61-R provided funding.

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Photograph: Female Mute Swan on her nest at Harris Creek, Chesapeake Bay, Maryland, USA, by Larry Hindman.

Long-term trends in the number of Whooper Swans *Cygnus cygnus* breeding and wintering in Sweden

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Abstract

The Whooper Swan *Cygnus cygnus* was a rare breeding species in Sweden during the early years of the 20th century, when total numbers likely consisted of only 20 pairs. Recent decades have however seen a marked increase in numbers and a spread in the swans' distribution, with the number of pairs breeding in the two northernmost provinces rising from 310 to 2,700 pairs between two main surveys, in 1972–75 and 1997. This paper documents continued long-term (1967–2014) increases in numbers of Whooper Swans breeding and wintering in Sweden, based on data collected by the Swedish Bird Monitoring Programme and during the mid-winter International Waterbird Counts (IWC). Most recent estimates for the country indicate that there are now 5,400 breeding pairs during the summer and close to 10,000 individuals present in normal or mild winters.

Key words: breeding, *Cygnus cygnus*, field feeding, population trends, Whooper Swan, wintering.

During the first decades of the 20th century the Whooper Swan *Cygnus cygnus* was considered to be a rare breeding species in Sweden, with about 20 pairs restricted to large but isolated mires in the northernmost part of the country (Nilsson *et al.* 1998). The species was a widespread breeding bird in Sweden during the early 19th century, but was heavily hunted to the brink of extinction during the latter part of the century (Fjeldså 1972; Nilsson *et al.* 1998).

In 1927 the Whooper Swan was protected from hunting in Sweden, which led to a slow reoccupation of its former breeding distribution as it spread to nesting sites in the inner parts of Swedish Lapland. After 1950, the rate of dispersal increased and the species was even found breeding in the southern parts of the country. It was not until 1972–1975, however, that large-scale counts of the species were undertaken for the first time, when the main breeding areas of northern Sweden (provinces of Västerbotten and Norrbotten) were covered by aerial surveys during the North Calot survey (Haapanen & Nilsson 1979). In 1985, Birdlife Sweden organised the first nationwide survey of breeding Whooper Swans (Arvidsson 1987) which was followed by a second national survey in 1997. During the latter census, aerial surveys were once more made in the two northernmost provinces of the country (Nilsson *et al.* 1998). Between 1972–75 and 1997, the number of Whooper Swans recorded in the two northern provinces Västerbotten and Norrbotten increased from 310 to 2,775 breeding pairs, and the species became more widely distributed across these provinces.

Sweden is also important for the species in winter, with 14% of the Northwest Mainland European Whooper Swans present during the international census of January 1995 (Laubek *et al.* 1999). Moreover, large numbers of Whooper Swans stage in the country during migration. The status of the Northwest Mainland Europe population, which includes swans breeding and wintering in Sweden, has been monitored since 1967 through the annual mid-winter International Waterfowl Counts (IWC) coordinated by Wetlands International (see Nilsson 1997, 2002, 2008). A marked increase in this wintering population has been recorded during the second half of the 20th century (Monval & Pirot 1989; Rose & Scott 1994), and this is thought to have continued into the 21st century (Wetlands International 2014).

This paper provides an update on the current status and long-term trends for Whooper Swans in Sweden since the last national review of the species in 2001 (Nilsson 2002). The number and distribution of swans breeding in the country is described and the swans' winter distribution is also considered in relation to habitat and winter weather conditions.

Materials and methods

Counts have been undertaken in Sweden in January on an annual basis since the start of the IWC in January 1967. In most years, counts were made at a set number of sites across the southern part of the country in order to provide data for calculating annual population indices (Nilsson 2008). The sites were grouped into a number of reference areas counted in the same way every year. Counts were also provided from a number of sites selected by the counters, which were covered to a varying degree between years (for details see Nilsson 2008). In addition to these annual counts at IWC sites, country-wide mid-winter surveys under the auspices of the IWC were undertaken in January 1971–73, 1987–89 and 2004. These larger surveys were thought sufficiently representative to reflect changes in the total numbers of Whooper Swans wintering in Sweden and can be compared with the specific swan count programmes started in 1995 (see below). Over the years, it was increasingly the case that Whooper Swans were using terrestrial areas which were less well covered than wetland or coastal areas by the IWC site network. More comprehensive surveys of wintering Whooper Swans across Europe therefore were organised by the Wetlands International/IUCN-SSC Swan Specialist Group, and these have been conducted at five-year intervals from 1995 onwards (Laubek *et al.* 1999). During these coordinated international censuses, all potential Whooper Swan sites were covered together with sites covered by the national goose counts. Many observations were also obtained through an information campaign in the local press in these years. As well as recording total numbers, observers were asked to count the number of swans present on different field types, to describe any changes in habitat use over time. Other data on wintering Whooper Swans were available from winter counts submitted to the Swedish Bird Monitoring programme, recorded during annual point counts made along selected routes in the country, which aims to produce annual national indices for different species (Green & Lindström 2014). The analyses presented here use only the mid-winter Whooper Swan data from this programme.

In addition, national waterbird counts have also been organised in Sweden in September since 1973. These counts are used here for a separate analysis of trends in swan numbers recorded during the autumn migration period.

Information on the expansion in numbers of Whooper Swans breeding in Sweden was obtained from the Swedish Breeding Bird Monitoring Programme (Green & Lindström 2014). Within this programme a system of summer point counts has been conducted along routes selected by the observers since 1975. The same routes were covered each year. In 1996, a system of fixed count routes systematically distributed over the country was introduced to get better and more consistent coverage. The observer walked a distance of 8 km stopping to make point counts eight times (at 1 km intervals) along the route, and observations of swans during line transects between the points were also recorded (for details see Green & Lindström 2014). A combination of the transect counts and point counts are included in the analyses.

Trends in numbers were calculated using TRIM ("TRends and Indices for Monitoring data") software (Green & Lindström 2014). The method has a GLM approach that fits log-linear regression models to individual counts data with Poission error terms, accounting for overdispersion and autocorrelation where these are detected, and accounts for missing values in the time series. The TRIM analyses give the percentage change along with significance levels for these changes over the duration of the monitoring programme.

Results

Breeding population

The breeding bird surveys (Fig. 1) show significantly increasing trends both for data recorded during the summer point counts (1987–2012: mean annual change = 8.3%, $P < 0.001$) and for the fixed route counts (1998–2012: mean annual change = 2.6%, $P < 0.01$). Unfortunately it was not possible to split the data into regions, to determine trends in the number of breeding pairs for different parts of Sweden.

Counts made in the main autumn staging areas in south-central Sweden (*i.e.* the arrival sites for swans migrating to Sweden from areas further east) indicate that wintering Whooper Swans have not yet reached Sweden from more easterly breeding areas by September. There has however been a

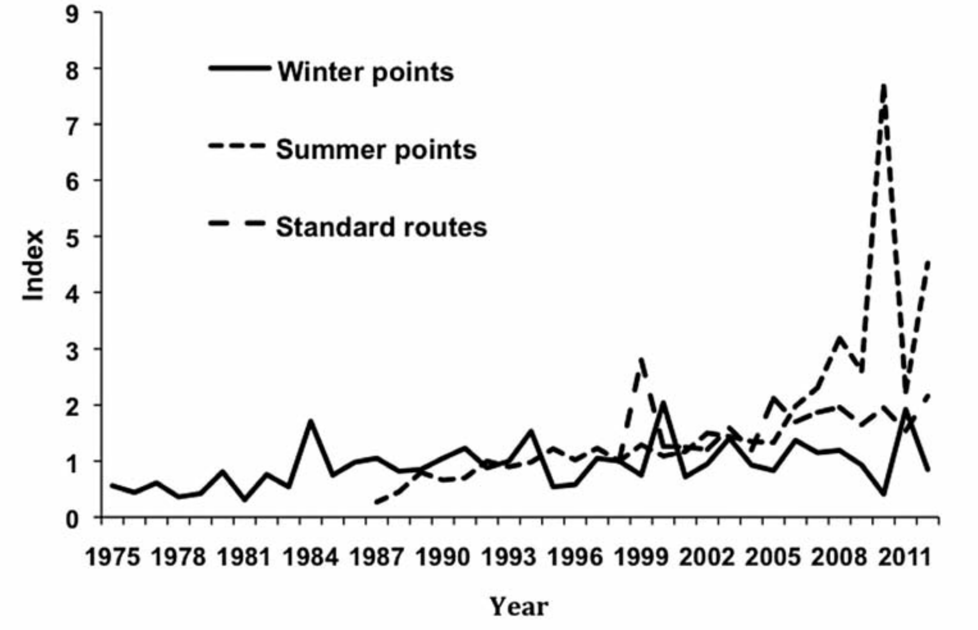

Figure 1. TRIM indices for Whooper Swans from the Swedish Bird Monitoring Programme (Green & Lindström 2014).

marked increase in the numbers of birds counted in Sweden in September since the late 1980s (1973–2013: mean annual change = 9.9%, $P < 0.001$; Fig. 2). The rate of increase in the September counts and the summer point counts are very similar, as might have been expected given that they both largely reflect numbers breeding in Sweden, although there are some annual differences as the September counts also reflect breeding success (*i.e.* they include young produced in that year).

In 1985, the number of Whooper Swans breeding in Sweden was estimated at 490 pairs (Arvidsson 1986).There has been no national survey of the breeding population since 1997, when the total for the country was estimated at 3,780 birds (Axbrink 1999). A compilation of local and regional estimates, and updates of older surveys in line with the trend estimates, suggested that there were 5,400 pairs of Whooper Swans breeding in the country by 2010 (Ottosson *et al.* 2012). This compilation also showed the species to be well distributed across the entire country with an important proportion of the increase taking place in southern Sweden compared with little recent change in numbers in the former core breeding areas in the north.

Wintering population

Numbers wintering in south Sweden have increased significantly over the full series of mid-winter counts, but there is no clear trend for the last ten years of the series (for

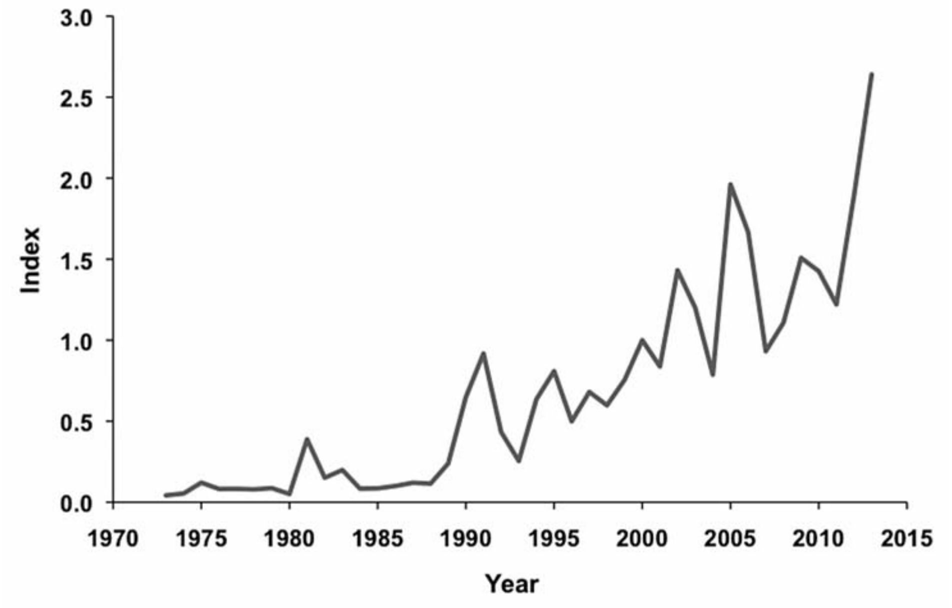

Figure 2. TRIM indices for Whooper Swans from the September counts of waterbirds in Sweden 1973–2013.

the whole series, 1967–2014: mean annual change = 1.3%, $P < 0.001$; for the last ten years, 2005–2014: mean annual change = 1.1%, n.s.; Fig. 3). The winter point counts from the Swedish Bird Monitoring also show an increasing trend over the years (1975–2012: mean annual change = 1.9%, $P < 0.001$; Fig. 1).

As the IWC do not cover key terrestrial areas used by wintering Whooper Swans in Sweden, data from these counts do not reflect the true status of the population within Sweden or trends for the population as a whole (Laubek *et al.* 1999; Nilsson 1997). However, the proportion of Whooper Swans feeding on fields in Sweden was low in the early 1970s, and thus the countrywide surveys undertaken for the IWC are likely to have reflected the total numbers of wintering birds in the country during this period. There were estimated to be around 2,000 Whooper Swans occurring in Sweden at this time (Fig. 4). When the first coordinated international count of Whooper Swans was made in 1995, between 7,000–8,000 birds were found in the country, increasing to 9,000–10,000 recorded during the 2005 census. In 2010, much smaller numbers were counted in the country due to a very hard winter as there was a substantial emigration from Sweden to countries to the southwest, *e.g.* Denmark.

The Whooper Swans were found wintering over most of the southern third of Sweden, both during mild and cold winters (Fig. 5a,b). However, swans were concentrated into the west and southwest parts of the country during the cold 2010

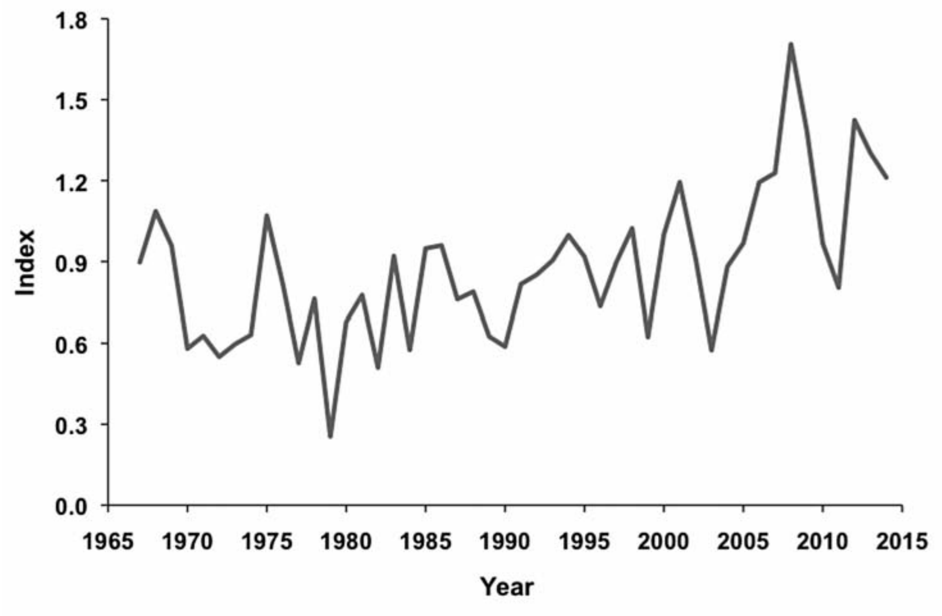

Figure 3. TRIM indices for Whooper Swans from the January counts (IWC) of waterbirds in Sweden, 1967–2014.

winter, when feeding conditions were more favourable there due to less snow. Most sites in inland and eastern Sweden also had wintering Whooper Swans in the cold winter, but numbers at these sites were much smaller.

Field choice in winter

When Nilsson (1997) analysed the results from the first International Whooper Swan Count in 1995, *c.* 70% of the swans were still found on wetlands, predominantly on water, both in coastal and inland areas. There were also marked regional differences with < 40% on water in Scania, the southernmost province of the country.

The proportion of swans feeding on fields increased markedly between the two international Whooper Swan surveys in 1995 and 2000 with *c.* 40% found on water during the latter survey (Fig. 6), this proportion being even less in 2005 (*c.* 35%). No habitat data are available for 2010 as most areas were covered by snow and thus the field types used by the flocks could not be established.

The main field types used by the Whooper Swans during the three surveys presented in Fig. 6 were grasslands, autumn-sown cereals, stubble and rape. On arrival in Scania, southern Sweden, the majority of Whooper Swans, along with staging geese, fed on the remains of the sugar beet harvest. These fields were generally ploughed before the mid-winter counts, although it is likely that many fields classified as "ploughed" were harvested sugar beet fields with some beet remaining on the land.

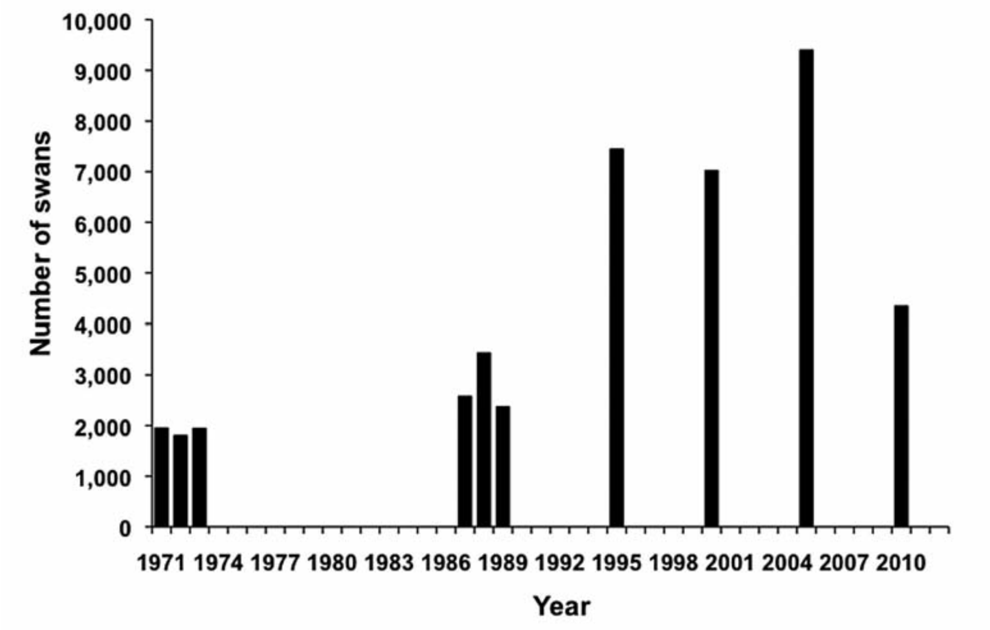

Figure 4. Number of Whooper Swans counted at the country-wide surveys in Sweden during 1971–2010.

Discussion

The breeding population of Whooper Swans in Sweden has increased exponentially during the last century from an estimate of about 20 pairs in the 1920s to about 5,400 pairs in recent years. The main reason for the marked increase was the protection afforded to the species in 1927. Initially the rate of increase was slow and in the early 1970s, Haapanen & Nilsson (1979) estimated the population for the two northernmost provinces in Sweden to about 300 pairs. However a few pairs were also found in the southern part of the country (Arvidsson 1987). After the 1970s, there was a marked increase and spread of the species and the population in the two northern provinces increased to 2,700 pairs (Nilsson *et al.* 1998). The rate of increase in the north levelled off during the 2000s and a survey of part of the northern provinces in 2009 found only small changes compared to the 1997 survey (Nilsson & Nilsson 2012).

There is a clear parallel with the Greylag Goose *Anser anser* breeding in Sweden, which also increased after protection from a few hundred pairs in the 1960s to about 41,000 pairs in recent years (Ottosson *et al.* 2012). For both the Whooper Swan and the Greylag Geese, changes in agriculture was most probably an important factor behind the increase in addition to the protection from hunting, providing much larger food resources on the staging and wintering areas than before. Additionally, the distribution of staging and wintering geese has been studied in relation to changes in agriculture in the late 20th and early 21st centuries (Nilsson &

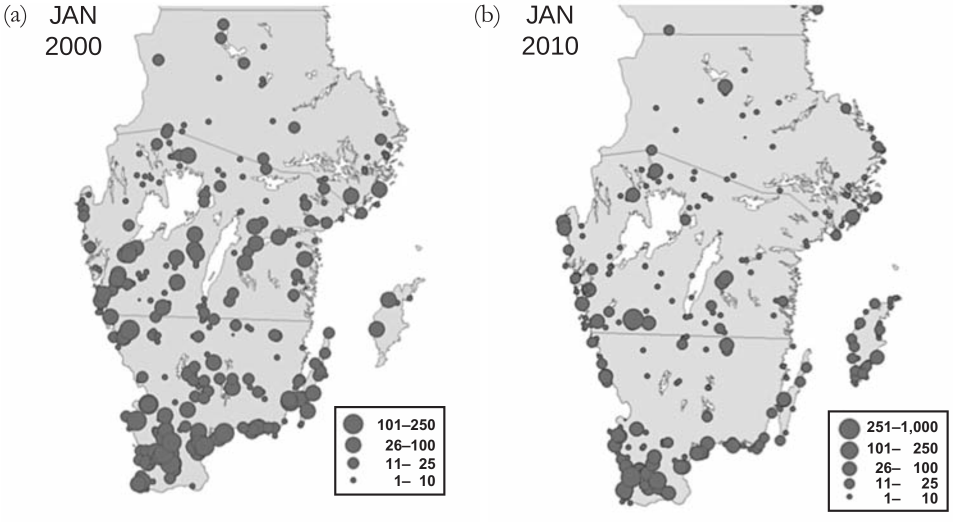

Figure 5. Distribution of wintering Whooper Swans at country-wide surveys during a mild (January 2000) and a cold (January 2010) winter.

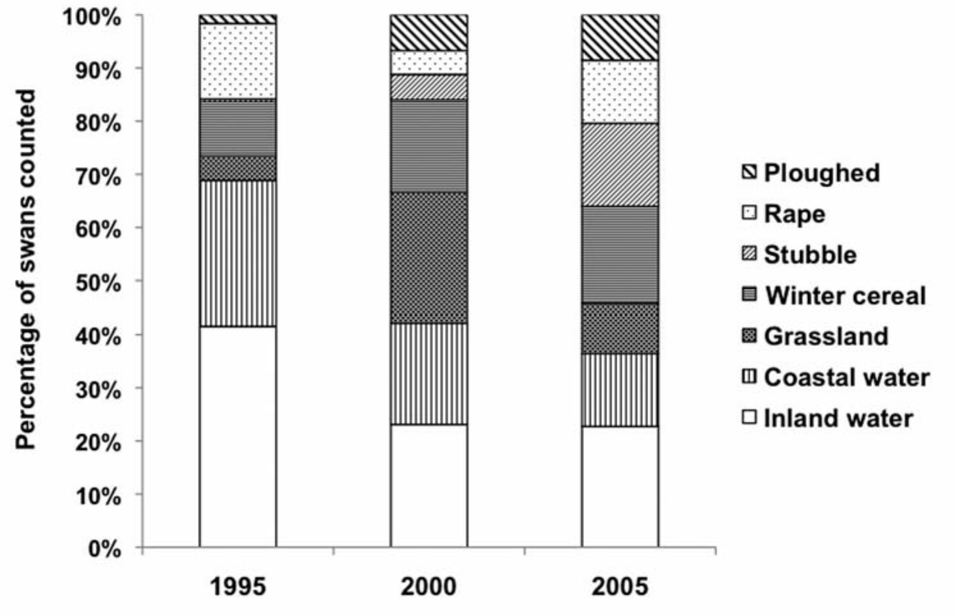

Figure 6. Field choice by Whooper Swans in January recorded during three country-wide surveys, in 1995, 2000 and 2005.

Kampe-Persson 2013), and results indicate shifts in habitat use in relation both to changes in crops grown and in harvesting methods (which may leave variable amounts of harvest waste as food for the birds) over the decades. The main changes in agriculture which are of importance both for Whooper Swans and for geese are the increases in the area of autumn-sown cereals. Moreover, there has been a change in the variety of oilseed rape grown, making the rape more palatable to wildlife since many of the alkaloids present in tissues have been removed. Over the years, geese have increasingly exploited waste left behind after the harvest of sugar beet (and potatoes) for food (Nilsson & Kampe-Persson 2013). Field use by Whooper Swans in Sweden has only been studied during the winter (present study) but it is clear from observations made in connection with the goose studies that waste sugar beet is also an important food source for Whooper Swans in south Sweden in autumn.

A large proportion of the Whooper Swans wintering in Sweden emanate from Finland and/or Russia, whereas many Swedish-breeding birds winter along the Norwegian coast. The increase in wintering numbers in southern Sweden therefore probably reflects general increases in breeding populations not only in the south of Sweden but also further east, with the mild winters in recent years likely also resulting in higher numbers wintering in the country.

Acknowledgements

Data from the national Bird Monitoring Programme were supplied by Åke Lindström. The International Waterfowl Counts (IWC) in Sweden was supported by grants from the Swedish Environment Protection Agency (as a part of the National Monitoring Programme).

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Photograph: Whooper Swan breeding pair at Dalarna, Sweden, by Bernd Zoller/Imagebroker/FLPA.

Breeding Whooper Swans *Cygnus cygnus* in the Baltic states, 1973–2013: result of a re-colonisation

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Abstract

A review of the literature on Whooper Swans *Cygnus cygnus* breeding in the Baltic states indicates that the swans are recolonising areas where they once bred historically. In recent years, the number of breeding birds has increased from two pairs in 1973 to 600–670 pairs in 2013, though the growth rate has slowed in Latvia, and maybe also in Estonia and Lithuania. There was a clear latitudinal difference in the choice of breeding habitats: in Estonia, the Whooper Swans preferred bogs, lakes and coastal waters, while the vast majority of all pairs in Latvia and Lithuania were found in fish-pond complexes and wetlands associated with beaver dams.

Key words: breeding habitat, fish-pond complexes, latitudinal differences, population increase.

Intense year-round persecution through hunting, trapping and egg collection had a major adverse impact on Whooper Swans *Cygnus cygnus* in Europe until the early 20th century (Brusewitz 1971). Regional and national breeding populations became extinct or were pushed close to extinction in many countries, except in Iceland and Russia (Cramp & Simmons 1977). The Whooper Swan was exterminated as a breeding species in Greenland and the Faroe Islands in the early 18th century (Winge 1898; Salomonsen 1963) and in south Sweden in the 1840s (Wallengren 1849). Legal protection of the Whooper Swan throughout Europe has halted and reversed the decline, and numbers of breeding pairs in the Northwest Mainland Europe population have increased since the 1950s (Lammi 1983; Svensson *et al.* 1999).

The Whooper Swan started to regain former breeding grounds, sometimes aided by releases and escapes, during the second half of the 20th century (Svensson *et al.* 1999). The southward expansion of the breeding range eventually attracted interest into the question of whether the species was colonising new areas or re-colonising historical breeding grounds. This question became topical in the Baltic states (Estonia, Latvia and Lithuania) as the swans started breeding in these three countries. Bauer & Glutz von Blotzheim (1968) stated that there was no evidence for the species breeding historically in East Prussia (*i.e.* in southern Lithuania, Kaliningrad and northeast Poland), but gave no data for other parts of the Baltic region. The Whooper Swan has bred regularly in Latvia and Lithuania since 1973 (Lipsbergs 2000; Švažas *et al.* 1997) and in Estonia since 1979 (Luigujõe *et al.* 2002), but whether or not the species re-colonised a former breeding area was still an open question.

In this paper we therefore review published information on the incidence of Whooper Swans breeding in the Baltic states, with a view to assessing whether the Whooper Swan is recolonising its historic breeding range in these countries. National reports from Estonia, Latvia and Lithuania on Whooper Swans breeding in the Baltic states in recent years (Nedzinskas 1980; Švažas 2001; Luigujõe *et al.* 2002; Boiko & Kampe-Persson 2010) are also reviewed and up-dated to 2013, for a preliminary assessment of the current status of Whooper Swans breeding in the region. Similarities and differences between the three countries in the swans' distribution and choice of breeding habitats are also described.

Material and Methods

We made a thorough literature search for records of Whooper Swans breeding in the Baltic states before 1973. The search focussed on books and articles about the bird fauna of this part of Europe published in the 18th, 19th and 20th centuries, but also included a few biographies by Balt-German authors and all published drawings and descriptions by Johann Christoph Brotze (1742–1823); travel reports were not included in the search. Additionally, recent publications providing national estimates of the number of Whooper Swans breeding in Estonia, Latvia and Lithuania from the 1970s onwards were reviewed, along with unpublished records for 2013, to assess the development of the breeding populations in the Baltic states since the late 20th century. Ten estimates each for Estonia and Latvia and eight for Lithuania were available for the period 1973–2013, although none were based on a nation-wide survey. Population estimates were available for all three countries in only two years, in 1973 and 2013.

Whooper Swans may defend a new territory for one or two summers and not breed until the third or fourth year (Haapanen & Hautala 1991). This gives rise to two different estimates of breeding population size, namely: "territorial pairs" (occupying a site) and "nesting pairs" (those specifically with a nest). Throughout, estimates presented here refer to the number of pairs recorded with a nest during the national surveys in the Baltic states.

Whooper Swan breeding habitats in the Baltic states were grouped into five main categories: fish-ponds (including multipurpose ponds), bogs, lakes, beaver dams and coastal water bodies (for further descriptions of the different habitats, see Luigujõe *et al.* 2002; Boiko & Kampe-Persson 2010). Breeding habitats of lesser importance included flooded gravel pit workings, flooded meadows, drainage ditches and rivers. Habitat data were recorded for all nesting sites found in Estonia in 1979–2000, in Latvia in 2000–2013 and in Lithuania in 2008–2013.

Mean annual increases in the number of nesting pairs were calculated using the estimates at the beginning and end of the given time period. When the annual count estimate was given as an interval, the mid-point of the interval was used in calculating the rate of increase in numbers over time.

Results

Historic records

When the Whooper Swan ceased to breed in the Baltic states is not known. The species still bred in Lithuania in the 16th century; the Statutes of Lithuania (originally known as the Statutes of the Grand Duchy of Lithuania), which consisted of three legal codes published in 1529, 1566 and 1588, stipulated a penalty or a fine for destroying a Whooper Swan nest (the documents mention "swan", but the species was identified by Nedzinskas 1980). Without specifying the species swans were reported to breed in the western parts of Estonia and Latvia in the late 18th and early 19th centuries, locally in large numbers (Fischer 1778, 1791; Beseke 1792; Brotze 1996). Descriptions and colour plates show that the Mute Swan *Cygnus olor* was a well-known breeding species (Fischer 1778, 1791; Meyer 1815) but from the descriptions some of the breeding pairs might have been Whooper Swans (Fischer 1778, 1791). Later, the Whooper Swan appears to have bred at Lake Pape in southwest Latvia in the mid 19th century (Löwis 1893), probably at Lake Lubāns in eastern Latvia in the 19th century (Lamsters 1932), very likely at Lake Tāši in western Latvia in 1944 (Tauriņš & Vilks 1949) and certainly in the Nemunas River delta in Lithuania in 1965, 1967 and 1968 (Nedzinskas 1980).

Recent breeding numbers and distribution

More recently, four Whooper Swan nest sites were found in Latvia during the 1970s, with the first located in the western part of the country in 1973 (Baumanis 1975, 1980). Subsequent estimates of the number of breeding pairs indicate a steady increase in the Latvian population from 1979 onwards: 10–20 pairs in 1984, 20–30 in 1993, 50–100 in 1998, *c.* 150 in 2004, 170–200 in 2006, *c.* 200 in 2007, *c.* 260 in 2009 and *c.* 320 in 2013 (Priednieks *et al.* 1994; Strazds *et al.* 1994; Latvian Ornithological Society 1999; Boiko 2005, 2008, Boiko & Kampe-Persson 2010, and D. Boiko, unpubl. data).

The development of the breeding population in Lithuania differed markedly from that in Latvia. Despite Whooper Swans recommencing breeding in Lithuania in 1973, the same year as in Latvia, there was still only one breeding pair in the country 14 years later in 1987 (Butkauskas *et al.* 2012). During the following decade, the species started to breed in a number of fishponds, inland lakes and peat-lands (Švažas *et al.* 1997, Jusys *et al.* 1999, Stratford 1999) but the total breeding population still numbered < 10 pairs (Švažas *et al.* 1997). It reached 15 pairs during the following three years (Švažas 2001). The main increase in the size of the Lithuanian breeding population took place after the turn of the millennium, from 15–20 pairs in 2001 to at least 30 pairs in 2007, at least 70 pairs in 2010 and 130–150 pairs in 2013 (Morkūnas *et al.* 2010, J. Morkūnas, unpubl. data).

Initially, the Whooper Swan population increased rapidly in Estonia, from one breeding pair in 1979 to at least five pairs three years later (Luigujõe *et al.* 2002). As no breeding was recorded in the years 1984–1986 and 1993–1994, Luigujõe *et al.* (2002) assumed that the development of the Estonian breeding population probably took place in waves. Available estimates of the number of breeding pairs might therefore give a slightly biased picture of the true development: about five pairs in 1982, 1991 and 1992, 10–20 pairs in 1997, 20–30 in 2000, 40–60 in 2002, 70–100 in 2009 and 150–200 in 2012 and 2013 (Lilleleht & Leibak 1993; Rees *et al.* 1997; Lõhmus *et al.* 1998; Luigujõe *et al.* 2002; Elts *et al.* 2003, 2009; Leho Luigujõe, *in litt.*).

Thus by 2013, the breeding population of Whooper Swans in the Baltic states was estimated to number 600–670 pairs in total: 150–200 pairs in Estonia, *c.* 320 pairs in Latvia and 130–150 pairs in Lithuania. The development to reach these numbers differed markedly among the three countries. From just 2 pairs recorded in 1973, the mean annual increase in the number of nesting pairs in the Baltic states during the period 1973–2013 therefore was 15.5%. The corresponding increase rates for each of the countries were 16.4% in Estonia (for the period 1979–2013), 15.5% in Latvia and 13.1% in Lithuania. The current rate of increase, expressed as the mean annual increase in the number of nesting pairs during the last "decade" (exact period within brackets), differ markedly among the countries: 12.5% in Estonia (2002–2012), 8.8% in Latvia (2004–2013) and 18.9% in Lithuania (2001–2013). In parts of Lithuania that were surveyed every year during the period 2008–2013, an even higher growth rate was recorded, though the year-to-year rate has declined, as it has in Latvia (Table 1).

In Latvia, the first pair of Whooper Swans bred in the western part of the country (Baumanis 1975), and this area has remained a stronghold for the species within Latvia (Boiko & Kampe-Persson 2010), supporting 87% of 278 sites where breeding

Table 1. Number of nesting pairs in parts of Lithuana that were surveyed annually and in the whole of Latvia in the years 2008–2013. Increase (%) in the number of nesting pairs from the year before is given in brackets.

Year	Lithuania	Latvia
2008	29	220 (10.0)
2009	45 (55.2)	260 (11.8)
2010	67 (48.9)	272 (4.6)
2011	79 (17.9)	294 (8.1)
2012	89 (12.7)	304 (3.4)
2013	101 (13.5)	320 (5.3)

was confirmed during the years 2000–2013, with 58% of pairs found in the districts of Liepāja, Talsi and Kuldīga. In Estonia and Lithuania, on the other hand, the Whooper Swan breeding sites are more widely dispersed across the country (Luigujõe *et al.* 2002; Kurlavičius 2006). The highest breeding densities in Lithuania are associated with the location of fish-ponds (Fig. 1) and a low rate of urbanisation. Apparently, it is mere chance that the species did not start to breed in other parts of Latvia much earlier.

All but a few Whooper Swan pairs in the Baltic states breed on small waters but the choice of habitats differs markedly among the countries (Fig. 1). The vast majority of all pairs in Latvia and Lithuania were found in fish-pond complexes and wetlands associated with beaver dams, whereas these habitats were rarely used in Estonia. Instead, the swans in Estonia preferred bogs, lakes and coastal water bodies. The choice of breeding habitat in Estonia today is quite similar to that in 2000 (L. Luigujõe, pers. comm.). The proportion of the sites situated at man-made waters was 21% in Estonia, 75% in Latvia and 78% in Lithuania.

Discussion

The review suggests that Baltic states were once a part of the historical breeding range of the Whooper Swan, but it seems that the species started to disappear from these countries before it was recognised as being separate from the Mute Swan. Both species were persecuted and disappeared from the region at around the same time, with local populations of wild Mute Swans hunted to extinction in the Baltic states during the 18th–19th centuries (Ivanauskas 1959). The Whooper Swan might have survived as a

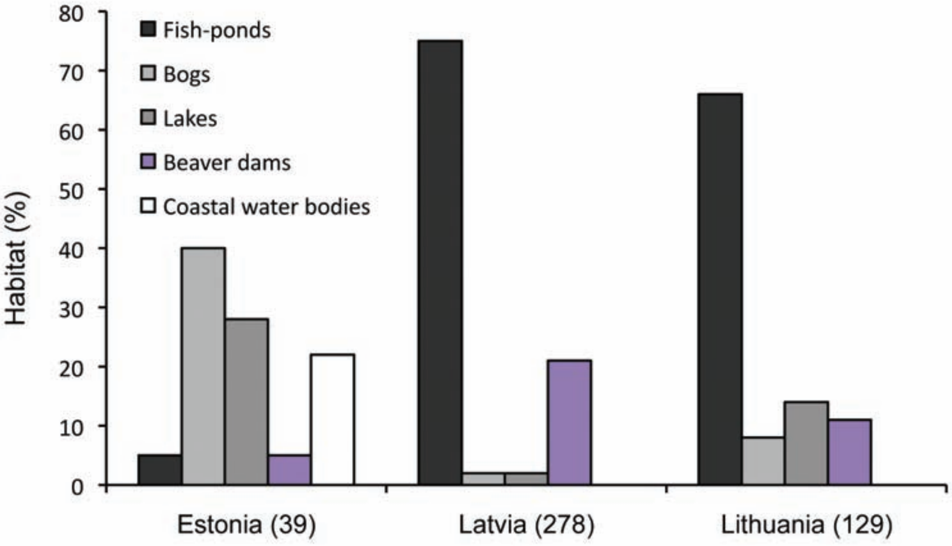

Figure 1. Nesting habitats recorded for Whooper Swans in Estonia (in 2000), Latvia (in 2013) and Lithuania (in 2013). Sample sizes are given within brackets in each case.

breeding species in a few inaccessible areas after the Mute Swan disappeared, but most likely the two species became extinct in the region at about the same time.

The Whooper Swan breeds on small water bodies in a wide range of habitats (Rees *et al.* 1997; Brazil 2003) but, around the Baltic Sea, they show large difference in habitat selection between countries. They are found mostly on small lakes with lush vegetation or in peat-lands and mesotrophic areas, especially in wet mires of the aapa fen type, in northern Sweden (Nilsson *et al.* 1998), Finland (Haapanen *et al.* 1977) and northwest Russia (Bianki 1981). The Whooper Swans show a strong preference for natural habitats, often nesting on small water bodies surrounded by forest in mid and southern Sweden (Holmgren & Karlsson 1982; Svensson *et al.* 1999) and also in Estonia (Luigujõe *et al.* 2002). In Latvia, Lithuania, Belarus, Poland and Germany, on the other hand, they mostly breed in fish-ponds or other small man-made water bodies (Vintchevski & Yasevitch 2003; Sikora *et al.* 2012; Axel Degen, pers. comm.; and this study). Small natural water bodies in Latvia and Lithuania are usually heavily overgrown and are therefore unsuitable for Whooper Swans. These water bodies have partly been replaced by artificial ponds and, in areas with intense agriculture, large fish-pond complexes provide the only wetland habitat suitable for breeding (Švažas & Stanevičius 2000). Fish-pond complexes provide good breeding and feeding conditions for Whooper Swans because they are extensive, comparatively shallow (depth of 1–2 m), fringed with scrub outgrowth of varying width, are subject to low human disturbance levels, and food distributed for the fish is also taken by the birds (Boiko & Kampe-Persson 2010; J. Morkūnas, S. Švažas & R. Morkūnė, unpubl. data). The marked difference in habitat choice between Estonia and the other two Baltic states can partly be explained by a shortage of fish-ponds in Estonia. Due to the shorter growing season for vegetation, conditions for fish-farming, especially the growing of Common Carp *Cyprinus carpio*, are less favourable in Estonia compared to countries situated further south. The area used for fish-ponds is therefore much smaller in Estonia than in Latvia and Lithuania (530 ha, compared to 5,600 ha and > 10,500 ha, respectively; www.fao.org, www.zm.gov.lv, www.aquafima.eu). In contrast, with a Eurasian Beaver *Castor fiber* population of *c.* 20,000 individuals in Estonia (Glazko & Ulevičius 2011) there is no lack of beaver dams for the Whooper Swans to breed at in Estonia, and 5% of Estonian-breeding Whooper Swans nested at these sites (L. Luigujõe, *in litt*). The Eurasian Beaver populations in Latvia and Lithuania are even larger, numbering > 100,000 individuals and *c.* 120,000 individuals, respectively (Glazko & Ulevičius 2011), and their dams may create further breeding habitats for the swans in these countries.

Since the Whooper Swan began to increase in numbers and regain former breeding grounds in northwest Europe in the 1950s (Lammi 1983; Svensson *et al.* 1999) it has started to breed in Latvia, Lithuania and Poland in 1973 (Baumanis 1975; Nedzinskas 1980; Tomiałojc & Stawyrczyk 2003), in Estonia in 1979 (Luigujõe *et al.* 2002), in Germany in 1995 (Bauer & Woog

2008), in Belarus and Denmark in 2002 (Abramchuk *et al.* 2003; Grell *et el.* 2004) and in Hungary in 2005 (Szinai 2009). Mean annual rates of population increase ranging from 10.5–15.5% have been reported from most parts of this breeding range: in Finland 1950–1977 (Haapanen 1991), the Baltic states 1973–2013 (this study), northern Sweden 1975–1997 (Nilsson *et al.* 1998), mid and southern Sweden 1985–1997 (Axbrink 1999), and Poland 2007–2012 (Sikora *et al.* 2012).

Notwithstanding a substantial growth in the Northwest Mainland Europe population of Whooper Swans since the 1950s (Laubek *et al.* 1999), the number of breeding pairs in the countries of northwestern Europe is still increasing, though the growth rate might be slower than earlier, for instance in the core area of northern Sweden (Leif Nilsson, *in litt.*), in Latvia (this study), maybe also in Estonia and Lithuania (this study). The Latvian breeding population reached a period of marked increase much earlier than the other Baltic states, which may be one reason underlying the difference between countries in mean annual growth rate over the last decade, for instance if there is a shortage of suitable breeding sites in the core area of western Latvia. A marking programme from 2004 onwards, in which 672 cygnets from the core area were fitted with neck collars by 2012, has yielded only one case of dispersal abroad, however, a bird that bred in Lithuania (Dmitrijs Boiko, unpubl. data).

Axbrink (1999) suggests that the Swedish breeding population could reach 10,000 pairs, and the most recent estimate of the Swedish population is 5,400 pairs (Ottosson *et al.* 2012). The Finnish breeding population, estimated at 5,000–7,000 pairs, is also still growing (Väisänen *et al.* 2011). Similarly, the Latvian breeding population will very likely continue to increase; given the availability of suitable breeding sites, especially in the eastern part of the country, the population has the potential to increase to 600 pairs (Boiko & Kampe-Persson 2010). Taking into account the current growth rate and the availability of suitable breeding sites, the Lithuanian population may reach 250–300 pairs in about ten years time. We therefore consider that programmes monitoring the numbers of breeding Whooper Swans should be maintained, ideally with future counts coordinated across the region, to provide further insights into the contribution made by breeding birds from different countries to the trends and distribution of Whooper Swans in the Northwest Mainland European population.

Acknowledgements

We thank Jaanis Lodjak and Leho Luigujõe for providing supplementary data on the Whooper Swans in Estonia. Comments by Leif Nilsson on an earlier version significantly improved the presentation of this paper.

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Breeding biology of the Black Swan *Cygnus atratus* in southeast Queensland, Australia

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Abstract

The breeding biology of Black Swans *Cygnus atratus* ringed on the Gold Coast of southeast Queensland, Australia, was studied from 2007–2012. Numbers breeding ranged from 13–23 pairs *per annum* and included between 23–39 recorded breeding attempts by marked birds each year (total = 185 attempts over the 6-year study), of which 36% of all breeding attempts were unsuccessful. In years of high rainfall, total numbers of breeding pairs and breeding attempts were higher, as was the percentage of breeding failures. Of 119 instances of pairs recorded breeding, 63% bred once per year, 26% bred twice, 31, 6% three times, 3% four times and 3% bred five times in one year. Over half of all follow-on breeding attempts were preceded by a successful breeding attempt; in four cases, three broods of cygnets were hatched in a single year. On average, birds nesting 3–5 times per year had no better productivity per breeding attempt than those nesting only once or twice, although they did produce more cygnets each year. Birds were first recorded pairing at 2–4 years of age, and first recorded breeding at 2–5 years (most at three years old). The mean number of cygnets hatched per breeding attempt varied between 1.61–2.61 cygnets for each year of the study and the mean number of cygnets reared to fledging varied from 0.96–2.20 cygnets per breeding attempt. Cygnets hatched in every month of the year except for November, with the highest numbers hatched in March–April and August–September. Results from this study of Black Swans breeding territorially are compared with earlier observations of Black Swans nesting colonially in Australia and New Zealand.

Key words: Australia, Black Swan, colonial breeding, territorial breeding, Queensland.

The Black Swan *Cygnus atratus* is endemic to Australia and is widespread along the east coast from Cairns to as far south as Tasmania, and in the southwest part of the country (Marchant & Higgins 1990). The species was introduced to New Zealand in the 1800s (Miers & Williams 1969), where it now occurs across both the north and south islands. Studies of the swans' breeding biology have been undertaken in several of Australia's states including Tasmania (Guiler 1966), central New South Wales (Braithwaite 1981a,b) and tropical north Queensland (Lavery 1964, 1971), and detailed observations have also been conducted in New Zealand (Miers & Williams 1969; Williams 1981a). The species nests both colonially and territorially (Marchant & Higgins 1990), with the majority of work published to date focusing on swans nesting in breeding colonies (*e.g.* Williams 1981a; Guiler 1966; Braithwaite 1982). Few have considered territorial breeding pairs, however, or compared the success of territorial *versus* colonial nesting strategies. Preliminary analyses by Williams (1981a) indicated that more cygnets are reared successfully by territorial rather than by colonial breeders, but this appears to be one of few comparative studies available.

Information on the timing of Black Swans' breeding season suggests that this may vary across the range. In New South Wales, breeding attempts have been recorded in every month of the year, albeit most frequently between April and August (Frith 1982), whereas there appears to be greater seasonal variation in breeding elsewhere. In Northern Queensland, for instance, there was a marked February–June breeding season, and breeding pairs were found to have only one clutch per year (Lavery 1971). However, Guiler (1966) found that some birds may nest more than once if the first nesting attempts fails, and both single and multiple breeding attempts by pairs in a single calendar year have been documented in southeast Queensland (Coleman 2010). Moreover, Braithwaite (1981a) demonstrated that captive Black Swans have the ability to breed several times during a single breeding season. Circumstances under which single or multiple breeding attempts per year occur, however, have yet to be clarified.

Few data are available on hatching and rearing success for Black Swans in their natural habitats, although Frith (1982) documented an average of 4.1 cygnets hatched per pair (with 2.7 fledged) and Miers and Williams (1969) recorded between 3.2–3.9 cygnets hatched over a 3-year study period (published information is summarised in Table 1). Breeding success has been linked to rainfall, with birds in New South Wales having a breeding success rate of ≤ 47% in drought years compared to 68% in non-drought years (White 1986), and water levels have a significant effect both on breeding success and the extent of the breeding season. (Guiler 1966; Miers & Williams 1969).

This paper presents new information from Black Swans breeding territorially in sub-tropical southeast Queensland. It compares data on the duration of the breeding season, hatching and rearing success, and the number of breeding attempts each year, with previously published data for the species nesting in temperate and tropical regions. Variation between breeding seasons is considered in relation to local weather conditions (*i.e.* whether these are wet or dry years). Additionally, the paper compares breeding success recorded for territorial pairs observed during this study with records for the more widely documented colonial-nesting Black Swans studied in other parts of Australia and New Zealand, to make a preliminary assessment the success of the different breeding strategies. The relative

Table 1. Available data on breeding seasons, hatching success and rearing success from Black Swan studies in Australia and New Zealand.

Study Site	Breeding Season	Breeding Strategy	Mean cygnets hatched	Mean cygnets reared	Percentage cygnets reared from total hatched	Reference
New Zealand (South Island)	July–Oct	Territorial	no data	no data	65%	Williams 1981a
New Zealand (South Island)	Sept–Nov (but variable between years)	Colonial	3.2–3.9	no data	42%	Miers & Williams 1969; Williams 1981a
North Queensland	Feb–June	Territorial	4.4	no data	no data	Lavery 1964, 1971
Western Australia	May–Oct	Territorial	no data	no data	no data	Halse & Jaensch 1989
Tasmania	June–Oct	Colonial	4.8	3.7	77%	Guiler 1966
Central New South Wales	Dec–Feb (but highly variable)	Colonial	4.1	2.7	66%	Frith 1982
Southern Queensland	All year	Territorial	1.0–2.6	1.0–2.2	69%	This study

merits of breeding once *versus* several times in a single year are considered, and the ages at which territorial Black Swans first pair and breed are also described.

Methods

Study area

Black Swans have been studied in southeast Queensland since 2006, in an area ranging from the New South Wales border in the south to Brisbane River in the north (Fig. 1). The study area has a wide range of freshwater and marine sites, with breeding and non-breeding swans occurring throughout the region. Large flocks of up to 900 non-breeding birds can be seen offshore, feeding in the shallow coastal waters of Moreton Bay, with smaller flocks of 10–100 birds frequenting freshwater sites

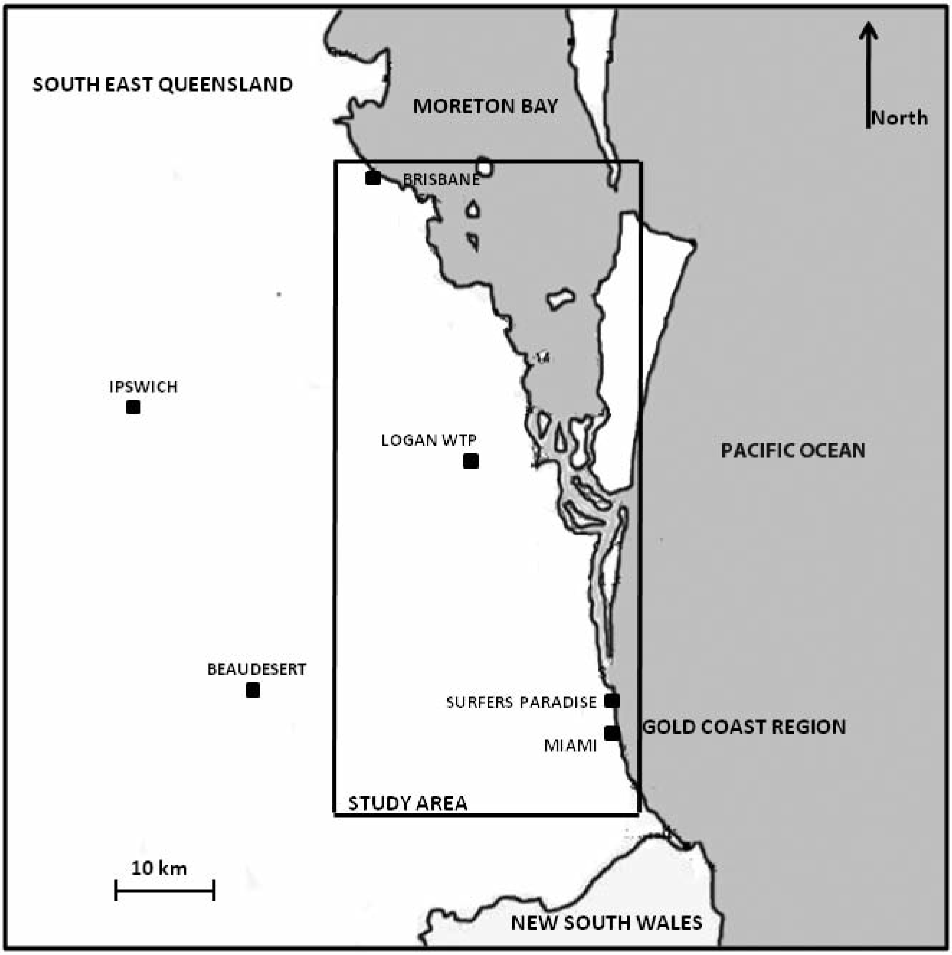

Figure 1. The Black Swan study area in southeast Queensland, Australia.

in the study area. Although some freshwater sites used by non-breeding birds are near the Brisbane area, most are further south, on man-made pools and canals 1–2 km inland from the Surfers Paradise and Miami. Breeding birds are found throughout the study area but the highest numbers are found on the Gold Coast. Almost all nests occur on man-made water bodies, on pools or larger lakes surrounded by houses or on golf courses. In addition to their natural food, the majority of Black Swans take food provided by humans, and supplementary feeding of bread and grain is now commonplace.

Climate in the study area is subtropical, with warm humid summers and cooler drier winters. Monthly rainfall and temperature data and annual rainfall totals recorded at the Logan Water Treatment Plant weather station (–27.71°S, 153.23°E; station no. 040854), which is mid-point in the study area, were downloaded from the Bureau of Meteorology website (www.bom.gov.au) for analysing the effects of weather conditions on the Black Swans' breeding season.

Catching and ringing

Birds were caught by hand throughout the year, using bread or grain to attract them close enough to be captured. Each bird caught was then aged from its plumage characteristics, sexed cloacally, and fitted with two rings: a standard Australian Bird and Bat Banding Society metal leg-ring and a red plastic leg-ring engraved with a unique white alphanumeric code readable in the field. The swans were also measured (skull and tarsal lengths) and weighed to the nearest 0.1 kg. The parentage of birds ringed as cygnets was recorded whenever possible, in order to determine the fate of offspring for known individuals.

Monitoring techniques

One to two days each month, a fixed route was travelled through the study area, visiting all sites where Black Swans were known to occur. Surveys were made in the mornings, between 06:00–12:00 h Australian Eastern Standard Time (AEST), during which the numbers of birds at each site were counted and their status recorded: as non-breeding, paired, breeding or cygnet. A juvenile bird still associating with its parents was classed as a cygnet, and a paired bird that had attempted to nest during that year was classed as a breeding bird. Breeding attempt was defined as the pair building a nest and incubating eggs. Swans obviously associating and exhibiting territorial behaviour were considered to be paired; any birds, alone or in small groups and flocks, were considered to be non-breeders.

Each month the swans' ring numbers were read using binoculars (in some cases using bread and grain to attract birds closer), to build-up life history data for known individuals. Attempts were also made to catch and ring as many unringed birds as possible during the monthly surveys. Associations data were recorded for marked individuals (especially whether they were with a ringed or an unringed mate), to determine the age of first pairing and breeding, mate fidelity and the number of cygnets hatched and reared to fledging for each breeding attempt. For paired birds, the month of breeding was also noted, to describe the timing of the breeding season

Results

A total of 341 swans were caught and ringed in the study area between 2007–2012, of which 42 were first ringed as paired birds and 36 caught as cygnets or non-breeders and subsequently paired or bred at least once during the study. A further 103 birds ringed as cygnets and 196 birds ringed as non-breeding flock birds were not seen with mates or young.

Age of first pairing and breeding

Of 15 males of known age subsequently recorded as paired, five (33.3%), eight (53.3%) and two (13.3%) were first seen to be paired at 2, 3 and 4 years old, respectively. Likewise, for 11 known age females, five (45.5%), four (36.4%) and two (18.2%) were first recorded as paired at 2, 3 and 4 years old.

Eleven males were of known age when seen breeding for the first time, of which two (18.2%), seven (63.6%), one (9.1%) and one (9.1%) first bred in their 2nd to 5th year of life. Females showed a similar pattern, with eight known age birds first seen breeding at age 2 years (2 individuals), 3 years (4 individuals) and 4 years (2 individuals). No birds were recorded either pairing or breeding for the first time at ≥ 5 years old, though this may reflect the relatively short study period (6 years to date) for a long-lived species. Despite males apparently pairing and breeding slightly later than females, there was no significant difference between the sexes in the age of first pairing or first breeding (Mann-Whitney U tests: U = 76.5, n = 15, 11, $P = 0.66$ and U = 43, n = 11, 8, $P = 0.92$).

Of the 139 birds banded as cygnets or first year birds, 67 were males and 72 were females of which a further 6 males (8.9%) and 11 females (15.2%) were subsequently recorded, either as paired or breeding, in subsequent years. However, it could not be confirmed that other birds in this group had not at some point paired or bred and remained undetected, as in almost all cases swans remained undetected for several months at a time at some point in the study.

Breeding season

Between 2007–2012, 118 successful breeding attempts were recorded, with the month of hatching recorded reliably for 93 of those attempts. Birds hatched cygnets in every month of the year except for November (Table 2), but hatching incidence did vary significantly across months ($\chi^2_{11} = 22.91$, $P < 0.02$). Peaks in hatching activity were recorded in January, March–April and August–September with fewer clutches hatched in February, May, October and December. The months in which cygnets hatched also appeared to vary between years. January was the only month in which broods hatched in every year of the study, and cygnets also hatched in March, April, July and September in 5 of the 6 years (Table 2).

Table 2 also suggests annual variation in the duration of the breeding season, with cygnets hatching in 9 months of the year in 2010 and 2012, compared to only 5 months in 2011. Nevertheless, this apparent difference in the number of months in which cygnets hatched did not vary significantly between years ($\chi^2_5 = 4.68$, $P > 0.05$).

Table 2. Number of Black Swan pairs that hatched cygnets each month in southeast Queensland, for each year of the study.

Month/Year	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**Years breeding recorded**
Jan	3	1	4	1	1	1	**6**
Feb			1	1		1	**3**
Mar	1		6	1	2	1	**5**
Apr	2	5		2	1	3	**5**
May		1		1		1	**3**
Jun	1	3	3	2			**4**
Jul		1	1	3	3	2	**5**
Aug	2	6		3		4	**4**
Sep	3		4	1	4	1	**5**
Oct	1	2					**2**
Nov							**0**
Dec	1					1	**2**
Months in which breeding was recorded	**8**	**7**	**6**	**9**	**5**	**9**	

Number of breeding attempts

A total of 185 breeding attempts were recorded over the duration of the study (Fig. 2). There was a significant positive correlation between total annual rainfall and the number of breeding pairs and the number of breeding attempts in each year, with the largest number of breeding pairs and breeding attempts in the years with highest rainfall (Spearman Rank correlation: $r_{11} = 0.81$, $P = 0.05$ and $r_{11} = 0.81$, $P = 0.05$ respectively). Of 119 pairs identified and recorded breeding, 75 (63.0%) nested only once in any calendar year, and a further 31(26.1%) bred twice in some years. There were seven examples where breeding pairs bred three times (5.9%), three pairs bred four times (2.5%) and three pairs bred five times (2.5%) during the year (Fig. 3). Forty (63.5%) of the 63 follow-on breeding attempts recorded followed successful breeding, where cygnets were seen to have hatched. The remaining 36.5% of follow-on breeding attempts following a failed breeding attempt.

Of the 44 cases where pairs nested more than once per year, 19 (43.2%) resulted in a

Figure 2. Number of breeding pairs and breeding attempts per year for Black Swan pairs monitored in southeast Queensland between 2007 and 2012.

second brood being hatched in that year and four (9.1%) resulted in three broods being hatched in a single year. Six (13.6%) of those pairs nesting more than once in a year (including one case of five breeding attempts in a single year) resulted in no cygnets being hatched; the remainder produced just one brood, despite multiple breeding attempts.

Productivity

The number of breeding pairs ranged from 13–23 and the number of breeding attempts from 23–39 each year (Fig. 2). Of the 185 breeding attempts recorded from 119 annual breeding events by pairs, 118 of those breeding attempts resulted in a total of 364 cygnets hatched and 254 reared. In only 25 (21.2%) of the 118 cases where cygnets hatched did the young fail to survive to fledging.

Of all breeding attempts recorded, 36.2% failed to produce cygnets, and this varied between years with only 25.0% of breeding attempts failing to hatch cygnets in 2008 compared to 53.9% in 2010, which was also the wettest year of the study (Fig. 2).

The mean number of cygnets hatched per breeding attempt varied between 1.61 and 2.61 over the years, and the mean numbers reared ranged from 0.96–2.20 cygnets. There was no significant difference in the average number of cygnets hatched or reared per breeding attempt between years ($\chi^2_5 = 0.3$ and $\chi^2_5 = 0.7$ respectively, $P > 0.05$ in each case), despite there apparently being fewer cygnets per breeding attempt in years of higher rainfall.

The average number of cygnets hatched and reared per breeding attempt did not differ significantly between birds that nested once as opposed to those that nested several times per year (ANOVA: $F_{4,177} = 0.92$, $P > 0.05$ and $F_{4,114} = 0.99$, $P > 0.05$, respectively). However, birds nesting more than once per year hatched and reared significantly more cygnets in a year than their counterparts which made fewer nesting attempts (Fig. 4, ANOVA: $F_{4,113} = 9.65$, $P < 0.01$ and $F_{4,114} = 5.34$, $P < 0.01$,

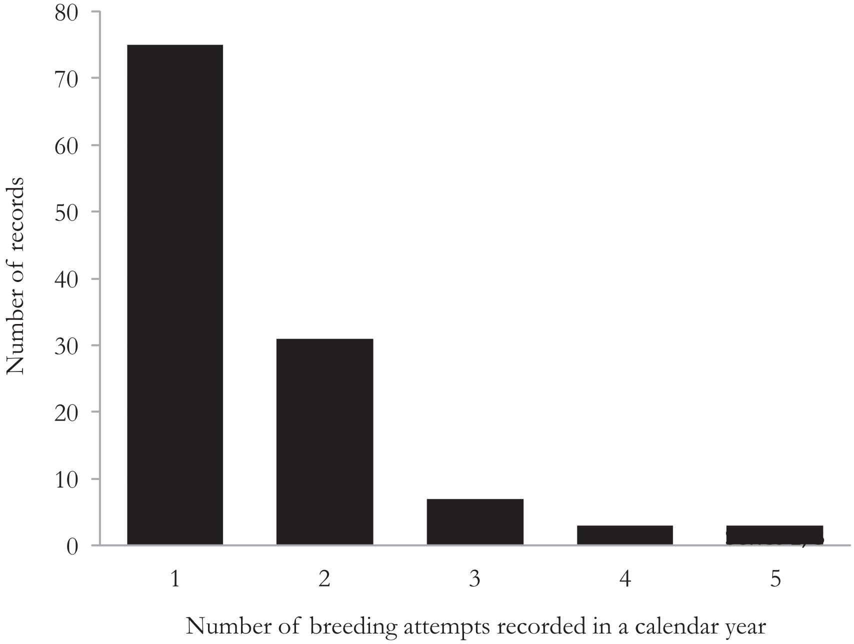

Figure 3. Number of breeding attempts recorded per year by Black Swan pairs in southeast Queensland between 2007 and 2012.

respectively), with means of 2.19 and 1.57 cygnets hatched and reared per annum for pairs breeding once per year compared to means of 6.50 and 4.00 cygnets hatched and reared per annum for those nesting 4–5 times per annum.

Discussion

Data collected on Black Swans breeding territorially in sub-tropical Queensland indicated that the species has a very broad breeding season, with cygnets hatched in almost every month of the year. This contrasts observations of more seasonal breeding amongst territorial pairs in more tropical (Lavery 1971) and temperate study areas (Guiler 1966; Miers & Williams 1969; Table 1).

Although most pairs (63%) observed in Queensland bred only once per annum, the remainder bred up to five times each year. Such levels of breeding activity have not been documented for Black Swans in studies elsewhere, although multiple breeding is known for birds in captivity (Braithwaite 1981a). Over half of the subsequent within-year breeding attempts followed successful breeding in which cygnets hatched, resulting in pairs sometimes defending two, or even three generations of cygnets simultaneously.

Age of first pairing and breeding

Only 8.9% of males and 15.2% of birds banded as cygnets or one-year-old birds were recorded as either pairing or breeding. However, in almost all cases the other

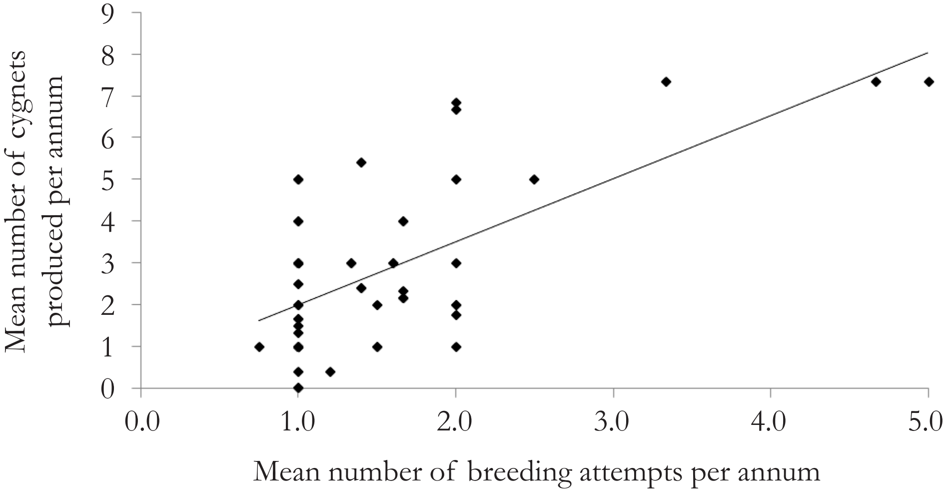

Figure 4. The effect of number of breeding attempts on the number of cygnets produced by breeding Black Swans in southeast Queensland between 2007 and 2012.

birds in this cohort were not recorded continuously throughout the study, and therefore others could have paired or bred and remained undetected. The median age of first pairing and first breeding was 3 years for both males and females monitored during the 6-year study. Anecdotal evidence from New Zealand (Williams 1981b) suggests that juvenile birds return to their breeding sites in their fourth year, suggesting that they commenced breeding at that time, and the age of first pairing and breeding is also similar to other swan species with most not breeding till more than 2 years old (Scott 1972; Rees *et al.* 1996). This is despite the fact that in at least some swan species, including the Black Swan (Braithwaite & Frith 1969; Braithwaite 1981a) and Mute Swan (Dawson & Coleman 1991), individuals are capable of breeding at an earlier age. The reasons for a delayed onset of breeding is likely to be behavioural, with juvenile birds in other swan species relying on non-breeding flocks to learn required behaviours in relation to social interactions and pairing (Minton 1971), and time constraints on the annual migratory and breeding cycle may result in deferred onset of breeding for migratory species (Rees *et al.* 1996). Non-breeding Black Swans are routinely territorial towards each other in flocks (Tingay 1974), so it is likely that the majority of subadult Black Swans lack the social- and dominance-related attributes required to pair, hold a territory and breed successfully in their first years of life.

Breeding season

There was little evidence for seasonality in breeding, with pairs hatching cygnets in almost all months of the year, contrasting with other published studies. While Black

Swan nests have been recorded all year round in New South Wales, much of this variation was between years and linked to rainfall, with breeding occurring after heavy rainfall periods and a marked breeding season within years (Frith 1982). Elsewhere the breeding season is less variable with breeding in June–August in Western Australia (Halse & Jaensch 1989), February–May in Northern Queensland (Lavery 1967) and August to October in the south island of New Zealand (Miers & Williams 1969; Table 1). In New Zealand the timing of breeding was also related to water levels and the season varied slightly between years in relation to availability of breeding habitat. However, once breeding began it was highly synchronised (Williams 1981a). Williams also showed that territorial breeders on sites with stable water levels had a much more predictable breeding season.

The lack of clear breeding seasonality in south-east Queensland is therefore unusual and difficult to explain. Southeast Queensland does not experience extremes of seasonal temperature variation or extended periods of tropical rainfall, despite having warm wet summers and drier colder winters, so climate is unlikely to inhibit year-round breeding. Additionally, almost all the breeding sites monitored in this study are man-made and the land around them actively managed as parks and gardens or for sport such as golf courses. The management practises on these sites may artificially increase the nutrient load in these territories, encouraging extended plant growth. Additionally, supplementary feeding by humans is also common (J. Coleman, pers. obs.). Both of these factors may also help in extending the breeding season.

Number of breeding attempts

Although > 60% of pairs in this study bred only once in a calendar year, the remainder bred two or more times and follow-on breeding attempts followed successful cygnet hatchings in almost half of recorded cases. While Braithwaite (1981b) demonstrated that, in captive birds, females had the ability to lay up to eight clutches in a year and rear three broods in a 12 month period, none of the published studies to date on Black Swans in their natural habitats have highlighted repeat breeding on this scale, although re-nesting following failed breeding attempts has been noted (Miers & Williams 1969; Guiler 1966). Several studies (*e.g.* Frith 1969; Guiler 1966) have however demonstrated opportunistic breeding in this species, with re-nesting and breeding delayed or commencing earlier, in response to local conditions. Data from this study suggest that, at least in some territories, conditions are suitable enough to allow birds to breed repeatedly throughout the year and the lack of seasonal extremes may remove the environmental constraints on breeding seasonality.

The energetics of breeding multiple times in a year require far more investigation, but was not attempted here because it was impossible to compare body condition of birds that nested once per year with those nesting multiple times, or to compare the relative habitat qualities of the territories involved. To lay an average clutch of 5 eggs (Miers & Williams 1969) at a rate of one egg every 1–3 days (Braithwaite 1977) and then incubate those eggs to hatching for an average period of 41 days (Braithwaite 1977) would mean that a female laying five clutches and hatching three broods in a year would spend at least 200 days per annum engaged in nesting activities, a significant investment.

Year round supplementary feeding by the public could have a significant influence on the condition of breeding birds, allowing them to breed multiple times in a year by removing some natural constraints such as food availability. The Black Swan is also one of the few Anatidae in which males assist with incubation (Braithwaite 1977) and Brugger & Taborsky (1994) hypothesised that this behaviour may have evolved to support opportunistic breeding allowing birds to breed quickly, when conditions are suitable and potentially more than once, by reducing the reproductive costs of incubation on females. In this study it is highly likely that this, combined with the favourable climate and abundant year-round food, all contribute to the multiple breeding attempts that some pairs undertake.

Productivity

Hatching rates (1.6–2.6 cygnets) and rearing rates (1.0–2.3 cygnets) in this study appear to be lower than Black Swan breeding success data from New South Wales (4.2 and 2.7 respectively; Frith 1982), and also for colonial nesters over a three year period (3.2 and 3.9; Miers & Williams 1969). The majority of territories in the study area were impoundments used for stormwater drainage, with summer storms or years of high rainfall causing water levels at these sites to fluctuate as a result of runoff (J. Coleman, pers. obs.), which in turn resulted in nests and clutches being lost to flooding (J. Coleman, pers. obs). Similar observations were made by Tingay *et al.* (1977) where agricultural runoff into lakes and dams results in nesting failures. Such artificial conditions may therefore provide apparently good habitats for feeding but be poor habitats for breeding as a result.

The number of follow-on breeding attempts in relation to productivity has not been documented before. Whether this is a response to the apparently low productivity in the study area, or simply a function of year-round suitable breeding conditions is not possible to answer with the available data. However it is clear from the results in this study that the number of cygnets both hatched and reared each year is significantly increased for birds breeding multiple times *per annum*.

Despite apparently poor productivity, 69.8% of the cygnets hatched in south-east Queensland were reared to fledging which compared well with 65% amongst territorial families but only 52.2% amongst crèches from colonial pairs in New Zealand (Williams 1981a). Williams (1981a) noted that colonial breeding was opportunistic and associated large flocks of birds in the breeding season potentially limiting territorial breeding opportunities. Nowhere in the Queensland study were there large flocks of non-breeders utilising suitable breeding habitats and each year, there appear to be a number of apparently suitable territories vacant suggesting that availability of breeding sites is not a constraint on territorial breeding in this study.

The results from southeast Queensland raise a number of questions about the Black Swan's breeding biology, and further work is needed to explore these. Data on the ages of breeding birds and annual body condition should be compared between single and multiple breeders. Comparing the frequency of supplementary feeding at sites with differing breeding strategies, as well as sampling of natural food resources in different territories, would also help to establish whether reproductive output is related to natural or human-supplemented food supply. Comparing breeding season extent and numbers of breeding attempts between the suburban and rural birds breeding on farm dams and lakes in southeast Queensland would further help towards explaining factors affecting these breeding strategies.

Acknowledgements

The author would like to thank Gold Coast City Council, Logan City Council and The Port of Brisbane Corporation for access to their land for the purposes of monitoring and capturing swans for banding. In addition, David Edwards and Stephen Macdonald have helped with many hours of fieldwork, for which the author is grateful. Murray Williams and an anonymous referee made helpful suggestions for improving the paper.

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Photograph: Nesting Black Swan at Pacific Pines, Gold Coast City, Queensland, Australia, by Jon Coleman.

Wildfowl

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Manuscripts should be typed in double line spacing with a generous margin (*c.* 3.25 cm) each side. Pages should be numbered consecutively, including those containing acknowledgements, references, tables and figure legends. It is preferable that authors prepare their main text in Microsoft Word (Garamond or Arial font) and graphs in Microsoft Excel. Manuscripts must be in English and spelling should conform to the *Concise Oxford Dictionary of Current English*. The passive voice is preferred; the active voice may be used only occasionally, typically to emphasize a personal opinion in the Introduction or Discussion.

Title page – this should contain:
A concise and informative title (as short as possible). Do not include the authorities for taxonomic names in the title.

A list of authors' names (commencing with the correspondence author), along with their contact address details that should be valid for the coming year. Use first names and subsequent initials, not just initials, for authors. For instance, Adrian D. Smith, not A. D. Smith. An E-mail address should be included for the first or corresponding author.

A running header of not more than 45 characters.

Abstract – this should state the main purpose of the paper and give the key results, conclusions and recommendations. The Abstract should not include references or speculation, and should not exceed 340 words. Please note that all text should be written in the "third person"; *i.e.* "A study was carried out ..." and not "I carried out a study of ...".

Key words – a list, in alphabetical order, of five words or short phrases, excluding words used in the title.

Introduction – this should give the background to the study, including the hypotheses being tested and the reasons why the study is thought to be worthwhile.

Methods – a concise description of data collection, analytical methods, and equipment used (where appropriate), in sufficient detail for the work to be repeated.

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Discussion – highlight the significance of the results in relation to the objectives for the work, and place them in the context of the broader scientific field. Where appropriate, resulting recommendations, *e.g.* for future management or research, should be clearly set out.

Acknowledgements – should be concise and appropriate.

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Béchet, A., Giroux, J.-F., Gauthier, G., Nichols, J.D. & Hines, J.E. 2003. Spring hunting changes the regional movements of migratory Greater Snow Geese. *Journal of Applied Ecology* 40: 553–564.

Follestad, A. 1994. Background for a management plan for geese in Norway. *NINA Utredning* 65: 1–78. [In Norwegian with English summary.]

Frederiksen, M., Fox, A.D., Madsen, J. & Colhoun, K. 2001. Estimating the total number of birds using a staging site. *Journal of Wildlife Management* 65: 282–289.

Nudds, T.D. 1992. Patterns in breeding waterfowl communities. *In* B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu (eds.), *Ecology and Management of Breeding Waterfowl*, pp. 540–567. University of Minnesota Press, Minneapolis, USA.

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Horizontal rules should be used in the tables themselves; use vertical rules only when absolutely necessary. The horizontal lines should be kept to a minimum, ideally limited to single horizontal lines before and after column headings and at end of table (*e.g.* Simple 1 format in Microsoft Word), with blank rows used to separate information presented within a table where needed to help interpretation. Keep tables in portrait format if possible, to fit one column (width: 6 cm) or 1 page (width: 13 cm) of *Wildfowl.*

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Apply capitals as follows: Bewick's Swan, Pink-footed Goose *etc.*; but swans or geese. Follow an appropriate authority for common names, e.g. *Checklist of Birds in Britain and Ireland, Birds of the Western Palearctic* etc. Give the scientific (Latin) name of each species in full, in italics, at first mention in the main text, not separated by a comma or brackets, *e.g.* ...Red-throated Diver *Gavia stellata* was... . If there are many species, cite a check-list which may be consulted for authorities instead of listing them in the text. Do not give authorities for species cited from published references. Where appropriate, follow the Voous order of species.

Presentation of statistical information

Most statistical tests result in an estimate of the likelihood that a particular result could have arisen by chance. This probability is denoted by *P*. Authors are encouraged to follow the normal convention of indicating the probability of the result having arisen by chance and should be indicated by the use of < (less than) followed by the appropriate level (0.05, 0.02, 0.01, 0.001) taken from a set of statistical tables. Any result with a probability greater than 0.05 should be regarded as not significant and denoted by n.s. in the text, (not by $P > 0.05$). Authors are strongly recommended to follow the practice of using a null hypothesis before carrying out a test. In all cases, present the degrees of freedom, using a post-fix to the statistic symbol, for instance: $\chi^2{}_4$, $r^2{}_8$, t_{28}.

Authors should ensure that the test they carry out is appropriate and the data are acceptable for the particular test. Ensure that the statistic is calculated correctly when small samples are involved (this includes the use of Yates' correction for the calculation of $\chi^2{}_1$).

Examples of the style in which to present results are:

> "... and the difference is significant ($\chi^2{}_1 = 6.9$, $P < 0.01$)."
> "... the correlation between A and B is significant ($r_{28} = 0.79$, $P < 0.001$)."
> "The difference between the samples is not significant ($t_{17} = 1.2$, n.s.)."
> "Examination of the data using an ANOVA gives $F_{12,23} = 29.1$, $P < 0.001$."

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