Wildfowl 62

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Wildfowl 62: Editorial

This edition of *Wildfowl* is of particular interest for the new information provided on two endangered species – Madagascar Teal *Anas bernieri* and Brown Teal *Anas chlorotis* – and on the Auckland Islands Merganser *Mergus australis* which became extinct in 1902. The two merganser papers are particularly evocative; scrupulous attention to detail in a review of written records, use of modern techniques (stable isotope analysis) which throws further light on the birds' feeding habitat, and the author's biological insight into these birds throughout, helps to illustrate the distribution and habits of a species no longer with us. It is also touching that the review paper is dedicated to Janet Kear. She was remarkable not only for her pioneering studies of wildfowl and her work with waterbird conservation, but she inspired a generation of researchers and aviculturists, and for many years served as an eminent Editor of this journal. The Auckland Islands Merganser was a special interest of hers, and it is therefore hugely appropriate that these papers appear in *Wildfowl*.

In addition to the work on endangered and extinct species, I am very pleased to see the publication of a detailed paper on the effects of a wind farm on Bewick's Swans *Cygnus columbianus bewickii* wintering at Polder Wieringermeer in the Netherlands. Detailed post-construction studies of this kind are essential for assessing the effects of wind farm developments on waterbird populations. The journal also includes informative papers on, *inter alia*, the growth in numbers of Egyptian Geese *Alopochen aegyptiaca* in the Netherland, the latest population estimate for the Icelandic Whooper Swan *Cygnus cygnus* population and potential competition between Mallard *Anas platyrhynchos* and Black Duck *Anas rubripes* in New Brunswick. The threatened species focus also extended to North America, with a study providing evidence for the predation of Snowy Plover *Charadrius nivosus* eggs by Common Ravens *Corvus corax*. Insight into a more familiar species is provided through an assessment of whether feral Greylag Goose *Anser anser* feeding distribution in Stuttgart, Germany, is influenced by their being flightless during moult.

During the course of the year, scanning the *Wildfowl* back catalogue was taken forward speedily and effectively by Christine Orchard, and most papers published in the journal over the years are now in electronic (pdf) format. These are not yet readily available as some of the files are quite large (> 7 MB), but plans are underway to use OCR (optical character recognition) software to reduce file size, make the papers searchable, and ultimately to add them to the *Wildfowl* pages of the WWT website.

I remain indebted to Tony Fox for his time, effort and invaluable comments as Associate Editor for *Wildfowl*, and to Editorial Board members – Jeff Black, Bruce Dugger, Andy Green, Matt Guillemain and David Roshier – for continuing to provide the advice and support essential for maintaining the standards and interest of the journal. I thank the referees for their valuable comments on the papers, and Ellen Matthews (EM Typesetting) and the staff at MPG Biddles (which recently acquired the Cambridge University Press printing presses) for taking the papers forward to publication. My colleagues Maggie Sage, Linda Dickenson and Jane Gawthorne provided helpful support throughout, including in the distribution of *Wildfowl* 62.

Eileen Rees

Editor: *Wildfowl*
WWT Martin Mere

Photograph: Janet Kear during her time as Director of Centres at WWT and Editor of *Wildfowl*, by David Platt.

A merganser at Auckland Islands, New Zealand

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Dedicated to the late Janet Kear, a friend and colleague from afar, whose lifetime work enriched our knowledge and enjoyment of the world's waterfowl.

Abstract

The last population of the merganser *Mergus australis* persisted at Auckland Islands in New Zealand's Subantarctic until its extermination by specimen collectors in 1902. It is now represented by four duckling specimens, 23 skins of immatures and adults, three skeletons, and a partial cadaver stored in 11 museums. It was the smallest known *Mergus,* the males weighing *c.* 660 g and showing little plumage dimorphism from the smaller (*c.* 530 g) females. Only five published accounts report first-hand observations of its ecology, breeding or distribution. Most likely it occurred as year-round territorial pairs in the larger streams and along the coastal edge at the heads of Auckland Island's eastern inlets and in Carnley Harbour and fed on both marine and fresh water foods. Its population probably never exceeded 20–30 pairs. The scant records suggest it had a typical summer breeding season. Although its keel area and wing skeleton were reduced relative to its sternum length it was well capable of flapping flight.

Key words: Auckland Islands, Auckland Islands Merganser, *Mergus australis*.

A merganser (Family Anatidae, Tribe Mergini) once inhabited the Auckland Islands archipelago, 450 km south of New Zealand in the subantarctic Southern Ocean (Fig. 1). When Polynesians first settled New Zealand in the late 13th Century, mergansers were also present in New Zealand (North, South and Stewart Islands) and at Chatham Island 800 km to New Zealand's east (Holdaway *et al.* 2001; Worthy & Holdaway 2002). It was from Auckland Islands that the first specimen, in 1840 (Hombron & Jacquinot 1841), and the last, in 1902 (Alexander 1902; Ogilvie-Grant 1905) was obtained, Polynesians having earlier extirpated the New Zealand and Chatham Island populations. This biogeographic oddity, a merganser in New Zealand's waters, is today represented by 27 skins and bones thereof from Auckland Islands (Kear & Scarlett 1970; Kear 2005a) and a small but increasing collection of bones from midden and natural deposits from the other two populations (Worthy 1998a,b, 2004; Millener 1999).

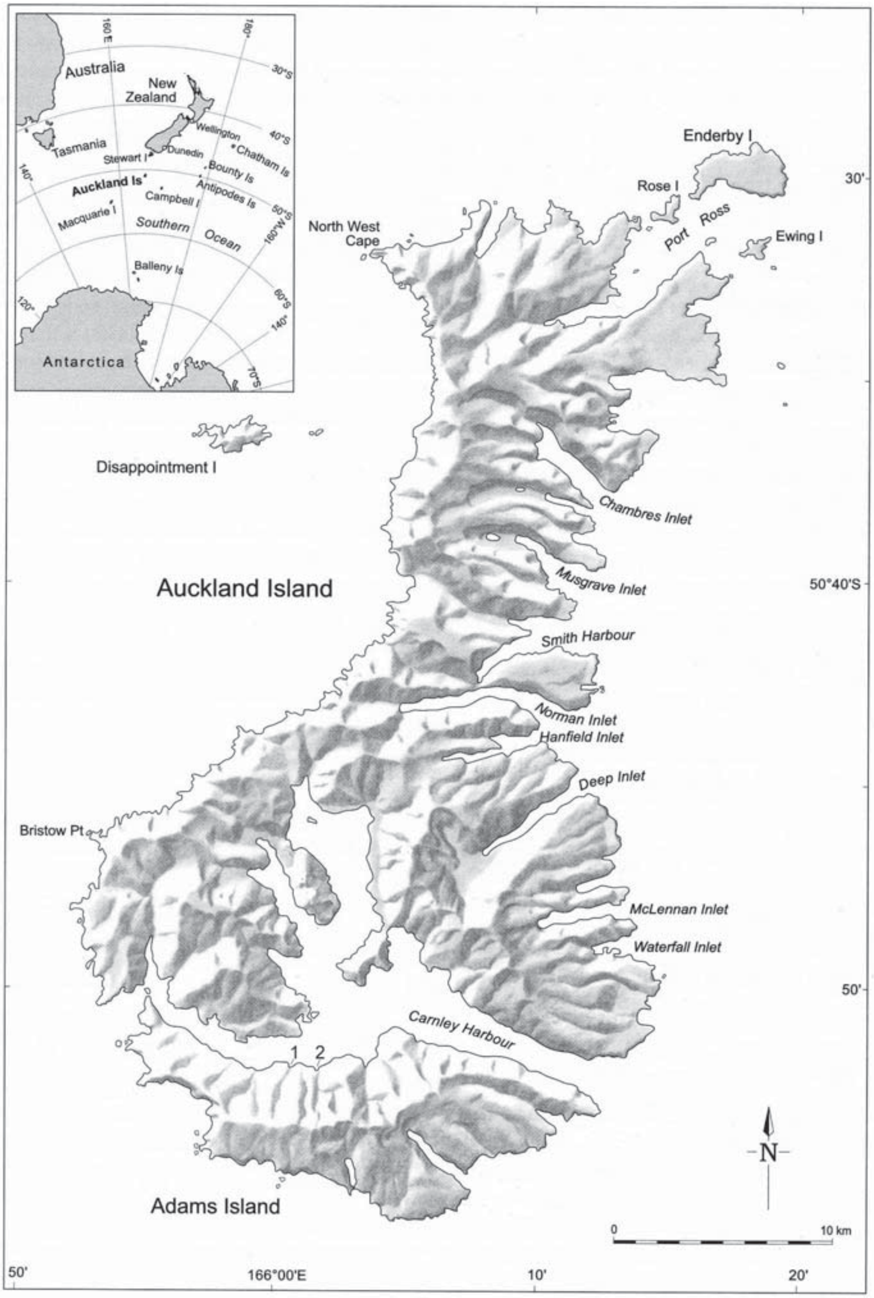


Figure 1. The Auckland Islands showing locations referred to in the text. 1= Magnetic Bay, 2 = Maclaren Bay.

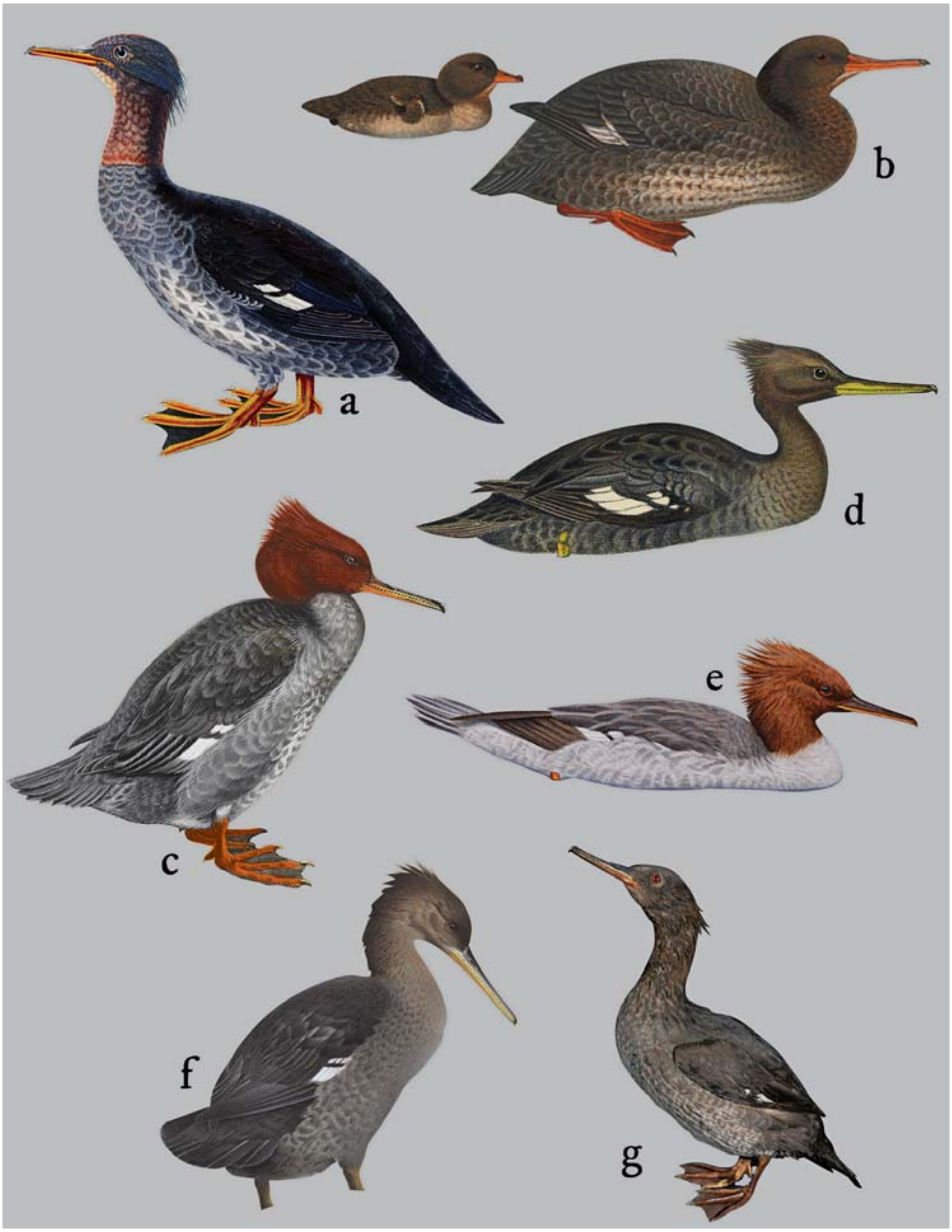
In this paper I review, and where appropriate reappraise, existing knowledge of *Mergus australis* at Auckland Islands, a bird commonly referred to as Auckland Island(s) Merganser (*e.g.* Buller 1882, 1905; Hutton & Drummond 1905; Kear & Scarlett 1970; Kear 2005a; Young & Kear 2006) but also as Southern Merganser (Tennyson & Martinson 2006) and New Zealand Merganser (Gill 2010). Scattered historical accounts and documentation of this merganser were assembled by Kear & Scarlett (1970) to provide a first synthesis. Livezey (1989) added an appraisal of its phylogenetic relationships and of its flightedness. These two publications provide the only substantive accounts of *M. australis* to date and have been the sources for all subsequent accounts (*e.g.* Marchant & Higgins 1990; Kear 2005a; Tennyson & Martinson 2006), much as Buller's (1905) account was the source for early treatises (*e.g.* Phillips 1926; Mathews 1936; Delacour 1959).

Since Kear & Scarlett's synthesis, a further skin has been reported in a museum collection (Sigwart *et al.* 2004, 2005), a partial skeleton reported (but erroneously identified; see Appendix 1) from Lyon, France (Wood *et al.* 1982), bones attributed to mergansers have been located at further sites on New Zealand's main islands (Worthy 1998a,b, 2004; Worthy & Holdaway 2002), and the smaller sizes of bones found in abundance in a cave on Chatham Island prompted Millener (1999) to suggest they may constitute a separate taxon. Morphometric distinctions between the three New Zealand Merganser populations await appraisal.

Description of plumage and soft parts

Kear & Scarlett (1970) described the plumages and soft parts of the adult, immature and duckling. The adult description was compiled from the authors' examinations of three skins in Canterbury Museum, Christchurch, New Zealand (CM) (see Appendix 1), six skins in the (British) Natural History Museum, Tring, England (NHM), and one skin in the Cambridge University Museum, Cambridge, England (J. Kear pers. comm.).

Their description was warranted because the original description (Hombron & Jacquinot 1841) had not been referred to in any publication other than in passing by von Hugel (1875), and most subsequent descriptions, commencing with Buller (1882, 1905), have been incremental modifications and abbreviations either of von Hugel's or of Buller's and have ignored Mathews' (1936) substantive re-description (based on specimens NHM 1901.10.21.57 and NHM 1901.10.21.58). Similarly, minor changes from the initial depiction (Hombron & Jacquinot 1853) have resulted in portrayals with plumage and soft part colourations that differ from original descriptions (*e.g.* Mathews 1936; Shirihai & Jarrett 2002; del Hoyo *et al.* 2002; Tennyson & Martinson 2006), and in the idiom of merganser species familiar to the artists (*e.g.* Fleming 1982). Some are more fanciful (*e.g.* Flannery & Schouten 2001). Depictions based on freshly collected specimens (*e.g.* Hombron & Jacquinot 1853; Buller 1905; Fleming 1982) best capture soft part and head colouration. A composite of some historic and contemporary illustrations is presented in Colour Plate 1.



Colour plate 1. Historic and contemporary depictions of *Mergus australis* from: a) Hombron & Jacquinot 1853; b) Buller 1905; c) Fleming 1982; d) Mathews 1936; e) Shirihai & Jarrett 2002; f) Tennyson & Martinson 2006; g) photograph of Otago Museum mount AV1110 (Rod Morris).

Kear & Scarlett (1970) did not discriminate the ages of the specimens they examined and, because some were newly-fledged young, their account is amended in the descriptions below.

Adult

Sexes alike but males are larger and have a longer head crest. Head, crest and neck dark brown, chin and throat a lighter brown. Crown and throat more rust-brown in male. Mantle, scapulars, back, rump and tail very dark brownish-black. Rust colouration of throat may descend onto upper breast (further in the male than female; Hutton 1901a). Entire ventral surface a dull grey liberally streaked brown to present an overall browny-mottled appearance (males paler on abdomen; Hutton 1901a); flanks are uniform dark brown. Wing coverts slate grey, like the sides of the breast, with the lower row darker and banded white. Middle secondaries white on the outer web and black on the inner web and tips. Primaries and inner secondaries blackish. Males have white sub-terminally on the outer web of 3–4 greater coverts to give the impression they have two white wing bars (Falla 1970). Underwing mottled and axillaries white.

Iris dark brown, culmen and tip of lower mandible black; cutting edge of upper mandible and rest of lower mandible yellowish-orange; legs and feet orange; webs, joints and soles dusky. This description of eye and soft parts is as written in F.W. Hutton's hand on the label of an adult female specimen (NHM 1901.10.21.58) and it is repeated on the label of the companion male specimen NHM 1901.10.21.57 (Appendix 1). The label to specimen NHM 1904.8.4.1, a female collected in July 1901 (mid winter), reads "Iris brown. Bill black on top, red underneath. Legs and feet light red".

Immature

This description is of birds newly-fledged and identified as such by a terminal notch in the rectrices or the persistence of the down feather stalk extending from the tip of the rachis (Larson & Taber 1980).

Sexes alike. Uniformly dark brownish-black on head, neck and throat. Entire dorsal surface, including rump and upper wing, dark grey. Entire ventral surface heavily mottled grey-brown. Developing head crest apparent.

Two specimens collected in July 1901 (NHM 1904.8.4.1; NHM 1902.8.6.1) whose rectrices have terminal notches, show a much darker dorsal surface, obvious rufous on head and throat and conspicuously elongated crest feathers. I interpret these as having undergone a post-juvenile body moult.

The dried legs of immature specimens indicate they were a reddish colour.

Duckling

Description taken from specimen CM AV1581 (Appendix 1). Dark brown-black above with only a trace of pale wing, scapular and dorsal rump spots. Chin, throat and upper breast rusty brown with a spot of chestnut beneath the eye (this chestnut may represent fading of a darker plumage). Remaining underparts yellowish-white. Bill, legs and feet dark olive-brown.

These descriptions indicate that *M. australis,* like the Brazilian Merganser *Mergus* *octosetaceus,* had little sexual dimorphism in plumage and the adult nuptial plumage was only a slight enhancement of the juvenile plumage. The patterns of the downy young were similar to all other mergansers but the uniformly dark appearance was most similar to *M. octosetaceus*.

Variation in body size

A size disparity between males and females occurs in all extant mergansers (Appendix 2). In general, female bills are approximately 10% shorter, their wings 6–10% shorter, and their weights approximately 15–20% less than males and these disparities are greatest in the three larger mergansers (Red-breasted Merganser *Mergus serrator,* Goosander *Mergus merganser,* Scaly-sided Merganser *Mergus squamatus*).

Two sets of standard measurements of *M. australis* skins have been compiled, by Livezey (1989) and this study. Neither set includes all skins. Livezey's 15 specimens included those in Otago, Museum of New Zealand(MNZ), Carnegie, American Museum of Natural History (AMNH), NHM and Dresden museums, and comprised seven adult, one juvenile males and four adult, three juvenile females (one of his males is now considered a female) although he did not discriminate between adults and juveniles. Table 1 below summarises measurements from 18 specimens measured by the author (thus excluding only Carnegie and AMNH museum specimens for which measurements are provided in Appendix 1) and comprises six adult, two juvenile males and five adult, five juvenile females.

Discriminating sex and age by measurement

Using measurements of culmen and wing there was a clear separation between birds labelled as males and females which helped indicate the likely sex of four unlabelled skins (Appendix 1). Culmen lengths and wing lengths of males did not overlap those of females and the widths of their nails at the bill-tips were wider; in combination any two of these three metrics separated the specimens into two groupings (Table 1, Fig. 2). Nares to bill tip measurements were also longer in males.

The wing lengths of juveniles were generally shorter than adults (Appendix 1) but all other standard measurements overlapped those of adults.

Four specimens whose sex was not recorded can be sexed by these measurements. The most problematic unsexed specimen was NHM 1875.11.6.14 (Appendix 1). It was collected in late November and has a short bill for a putative male but wing length and nail width both fall well within the male range; its well-developed head crest and rufous head and neck colouration suggest this bird was an adult, and a male.

Weight

No field weights of *M. australis* were recorded. Livezey (1989) regressed body weights of three merganser species (*M. serrator*, *M. merganser,* Hooded Merganser *Lophodytes culcullatus*) against the "body length" (skin length minus culmen and tail) of their museum skins. From the derived regression equation and inserting "body

Table 1. Measurements (mm) from all known *Mergus australis* skins except those at Carnegie Museum and AMNH (mean ± s.d., range). * Tarsus and mid toe & claw measurements are problematic on dried specimens; these were measured to nearest mm and the value recorded below is the mean of four separate measurements, presented to the nearest mm.

	Exposed culmen	**Width at nail**	**Nares to tip**	**Tarsus***	**MT&Cl***	**Tail**	**Wing**
Adult males	60.6 ± 0.5	6.6 ± 0.5	44.4 ± 1.5	42 ± 2	66 ± 5.1	73 ± 4	194 ± 6
(*n* = 6)							
All males	60.3 ± 0.9	6.6 ± 0.5	43.8 ± 1.7	41 ± 2.2	66 ± 4.2	72 ± 4	194 ± 6
(*n* = 8)	(58.4–61.3)	(5.8–7.1)	(41.6–45.9)	(39–45)	(57–70)	(68–78)	(185–202)
Adult females	54.5 ± 1.3	5.7 ± 0.2	39.4 ± 0.9	41 ± 1.6	63 ± 2.9	67 ± 4	180 ± 3
(*n* = 5)							
All females	54.6 ± 1.1	5.8 ± 0.2	39.3 ± 0.7	40 ± 2.2	61 ± 3.9	66 ± 4	179 ± 4
(*n* = 10)	(53.1–56.8)	(5.4–6.0)	(38.3–40.4)	(37–44)	(55–67)	(63–72)	(172–185)

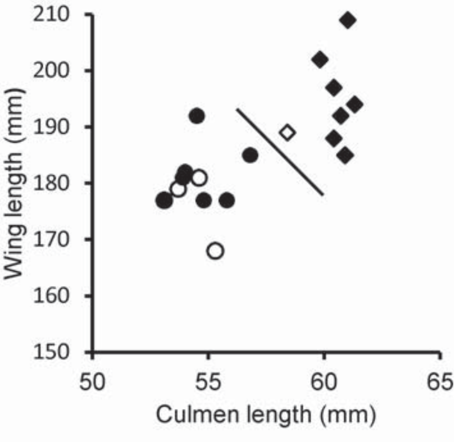


Figure 2. Scatterplot of wing and culmen lengths of *Mergus australis* museum specimens. Specimens labelled as males (◆), as females (●) and those unsexed (unfilled symbols) and indicating the sex now assigned to them.

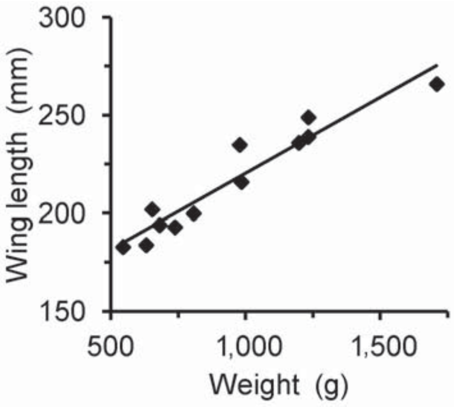


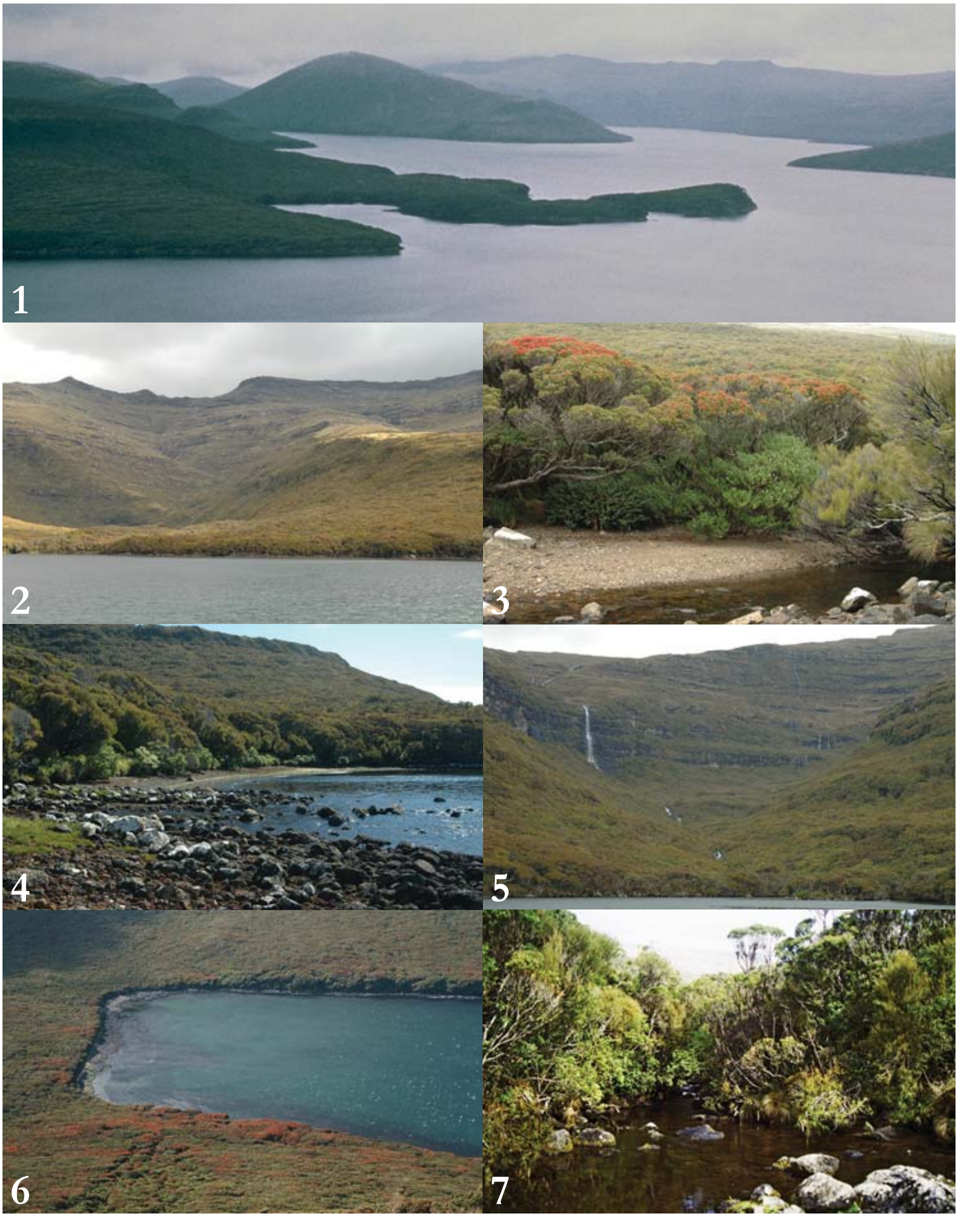
Figure 3. Relationship between mean wing lengths and mean weights for males and females of all extant merganser species. Data from Appendix 2. Regression equation is y = 0.095x + 133 ($R^2 = 0.95$, $n = 12$).

lengths" of *M. australis* and *M. octosetaceus* skins, he deduced a weight of 898 g for *M. australis* and 983 g for *M. octosetaceus.* Field weights for *M. octosetaceus* are now known (Appendix 2) and Livezey's estimated weight was approximately 20% too high (assuming it was for a male). Furthermore, 898 g for *M. australis* seems especially generous for what is undoubtedly a small merganser.

Across all extant mergansers, mean wing length and mean weight (of both sexes; Appendix 2) are strongly correlated ($R^2 = 0.95$, $P < 0.001$; Fig. 3). Using the regression equation (length = 0.095 * weight + 133) and the mean values of wing lengths of adult *M. australis* (Table 1) males may have weighed *c.* 660 g and females *c.* 530 g. Using the extremes of the range of adult wing measurements, the range of male weights may have been 550–800 g and females 460–620 g. These estimates imply a sexual size dimorphism similar to most other mergansers (Appendix 2).

Livezey (1989) suggested the wing lengths of *M. australis* were disproportionately shorter than those of other mergansers relative to their "body length". If so, estimated weights above will be conservative. However, as demonstrated later (see Flight) wing length is correlated with keel area which in turn reflects pectoral muscle mass, a major determinant of body weight. *M. australis* was capable of flight and wing length should still reflect weight in a way similar to other mergansers.

Using Livezey's "body length" for five merganser species (his Table 2) and relating them to the mean weights given in Appendix 2 produced a weaker correlation ($R^2 = 0.74$, $P = 0.05$) than the wing length : weight relationship above. Nevertheless, inserting Livezey's "body lengths" for *M. australis* into the equation describing the



Colour plate 2. Auckland Island landscapes and locations (2, 4) from which mergansers were collected. 1 = Carnley Harbour viewed from Adams Island; 2 = Maclaren Bay on Adams Island; 3 = stream at head of Magnetic Bay and typical of other streams on Adams Island; 4 = shoreline at head of Waterfall Inlet; 5 = Hanfield Inlet south branch; 6 = head of Musgrave Inlet; 7 = stream at head of Norman Inlet and typical of streams in most eastern inlets. (**Photographs:** K. Walker and G. Walls).

average relationship (length = 0.168 * weight + 348.5) derives a mean weight of 835 g for males and 757 g for females. Such a mean estimate remains too high, especially relative to known weights of *M. octocetaseus*, and indicates that "body length" of museum specimens is an unreliable measure of merganser size.

The estimated weights for *M. australis* seem appropriate when specimen skins and mounts are compared with the two smallest mergansers (Hooded Merganser and Smew *Mergellus albellus*) and with other New Zealand waterbirds of 500–700 g weight (*e.g.* Auckland Island Teal *Anas aucklandica*, Brown Teal *A. chlorotis* and Little Shag *Phalacrocorax melanoleucos*; see Marchant & Higgins 1990). Worthy (2004) noted that humerus, ulna and tarsometatarsus bones of *M. australis* were similar in size to, and readily confused with, those of Brown Teal, and that their carpometacarpi and scapulae approximated those of New Zealand Scaup *Aythya novaeseelandiae,* both species in the 500–700 g weight range.

Distribution and possible population size

Specimens were collected in Waterfall Inlet (Reischek 1889; Wilson 1959), McLennan Inlet (specimen NHM1901.10.21.57 label), Norman Inlet (Hutton 1901a) and Carnley Harbour (Maclaren or Magnetic Bay, Adams Island; Chapman 1891), possibly in Port Ross (Hombron & Jacquinot 1841), and at unspecified locations in Carnley Harbour (Alexander 1902, Fig. 1, Colour plate 2, Appendix 1). McCormick (1884) reported merganser present in Laurie Harbour at the head of Port Ross in 1840.

The absence of records from Auckland Island's other eastern inlets does not imply that suitable habitat elsewhere was lacking. The short and steep streams flowing into Waterfall, McLennan and Norman Inlets are replicated elsewhere (*e.g.* Hanfield Inlet and bays within Carnley Harbour) while at the heads of other inlets are larger streams flowing along flat valley floors (*e.g.* Deep and Chambers Inlets) and in two of which (Musgrave and Granger Inlets) are small lakes.

On riverine breeding habitat, other merganser species are generally dispersed at very low densities (< 0.2 pairs/km; species accounts in Kear 2005b). Most observations of their feeding are as pursuit feeders, chasing small fish prey underwater but they also grovel among stones and rocks in shallow water where snails and benthic invertebrates are captured (Hughes & Green 2005).

Auckland Island would have offered mergansers sheltered habitat only on its protected eastern side where, along its 42 km length, are 13 deep inlets (Fig. 1, Colour plate 2). At its southern end the drowned caldera of Carnley Harbour is flanked by Adams Island and within these confined waters lie 12–14 smaller bays into which short streams tumble from the steep surrounding hillsides (Fig 1, Colour plate 2); at least one, Maclaren or Magnetic Bay, provided habitat for a merganser pair and young (Chapman 1891).

A likely year-round territorial habit akin to *M. octosetaceus* suggests the head of each inlet or bay would probably have been occupied by just a single pair. Although in some larger inlets (*e.g.* Deep Inlet and

Chambres Inlet) two or more well-separated large streams emerge in close proximity, most likely these would have been occupied and defended by a single pair. Unpaired or juvenile birds may have been forced to live a more transitory life in smaller and more exposed bays or coves.

By this reasoning, a population of just 20–30 pairs, and a non-breeding component of perhaps 10 seems likely. Possibly mergansers persisted at the Auckland Islands in such low numbers because of the paucity of suitable feeding habitat in low gradient segments of streams at the heads of the inlets and bays. Their wider exploitation of more exposed marine environments may have been constrained by the high abundance of the coastal feeding Auckland Island Shag *Phalacrocorax colensoi.*

The paucity of merganser sightings remarked upon in the early writings (*e.g.* von Hugel 1875; Chapman 1891) suggests that, from the time of interest in collecting specimens, very few mergansers remained at the Auckland Islands. Contributing to this scarcity would have been early human depredation; from the time of the island's initial discovery (1806; Fraser 1986) to the collection of the first (and type) specimen (1840; Hombron & Jacquinot 1841) the heads of many inlets were occupied by sealers (Dingwall *et al.* 2007), and tame resident waterfowl would have provided ready fare. Furthermore predatory mammals, pigs *Sus scrofa* and cats *Felis catus*, had been introduced to Auckland Island. No historic account from prior to von Hugel obtaining the second specimen in 1874 (von Hugel 1875), either by shipwrecked mariners (*e.g.* Musgrave 1866; Smith 1866; Raynal 1874; Allen 2003), or settlers (*e.g.* Dingwall *et al.* 1999) refer to mergansers. Musgrave's and Raynal's accounts cover 20 month's life as castaways in Carnley Harbour and although Raynal, a Frenchman, recognisably described many birds including the flightless Auckland Island Teal ("young duck"), Auckland Island Shags ("widgeon") and Grey Duck *Anas superciliosa* ("canards sauvage"), he does not mention mergansers ("harle"). This lack of mention could suggest mergansers were already uncommon in the harbour and did not occur in bays near the castaway's camp. However, Krone (1900, pp. 26, 154), in an account commenting on fauna observed during his 140 days in Port Ross as a member of the German 1874 Transit of Venus expedition, refers to their presence in the harbour, and their possible capture "along the cliff- filled coast" (p. 26).

Breeding

The collection of four downy ducklings, approximately one week old, on 14 or 15 January 1890 in Maclaren or Magnetic Bay on Adams Island (Chapman 1891) is the single definitive record of the merganser's time of breeding. However, there are two other records that can be interpreted as indicating breeding.

Reischek (1889) reported that on 27 January (1888) in Waterfall Inlet (Colour plate 2) he "saw six mergansers, and shot two of them; the others concealed themselves among the rocks". Six mergansers together suggest a family group, and concealment among rocks is a likely response of unfledged young if caught on an exposed shoreline. Reischek's specimens were both adults (now in Vienna Museum, Austria; Appendix 1) and, because he did not indicate the others to have been conspicuously different, most likely they were near-fledged young.

New Zealand's then Governor-General, Lord Ranfurly, obtained four merganser specimens in early January 1901 (Alexander 1901). Two adult specimens, now in the Natural History Museum at Tring, were obtained on 5 January 1901 and two other specimens were probably collected on that or the following day – AV2944 (now in Canterbury Museum, Christchurch) and NMINH 1904.559.1 (now in National Museum of Ireland, Natural History, Dublin; Appendix 1). Both latter specimens have identical characteristics of newly-fledged birds, their tail feathers carrying down stalks, their primaries unfrayed and unworn compared to those of adult birds, and they have immature plumage and colouration. Possibly they were newly-fledged siblings and collected together although there are no records to confirm this.

These observations, of newly-hatched and almost-fledged young in January, imply a late October–November laying period. Other merganser species, none of which breed in their first year, lay eggs at 1.5–2 day intervals mostly in hole nests, incubate for about four weeks, and take 60–70 days to fledge their young (Cramp & Simmons 1977; species accounts in Kear 2005b).

That nesting sometimes was more protracted is indicated by a letter (dated 16 May 1895) from S.V. Dannefaerd (a New Zealand specimen collector/dealer) to Walter Rothschild at Tring (O'Rourke 1997) in which he referred to a female specimen collected in February containing an egg (specimen AMNH 734365; Appendix 1). Perhaps the merganser had a similar breeding period to Auckland Island Teal whose late re-nesting attempts can extend into January and February and whose ducklings can sometimes be observed in March and early April (Williams 1995).

Both Chapman (1891) and Reischek (1889) provide evidence of brood size, one soon after hatching and the other near fledging, and both are of four young. Neither can be interpreted as clutch size other than as a minimum. Other mergansers lay clutches of 8–10 eggs (species accounts in Kear 2005b).

Krone (1900, p. 154) provides an enigmatic reference to the merganser's choice of nesting site. Translated from his account, which was presented in poetic form .... "*We liked the meat of the hunted cormorants, tasting just like geese and ducks, with lemon yellow fat, also the rare Sage taucher (merganser), also called Entensager, with serrated duck beak, which is on the side sharply notched, to hold the fish which they catch while diving – those nest, always rare, on top of the steep cliff, facing north or north east, above the wild surf, around the big cliff gate (cave?), where they live together with the cormorants and also with the penguins, related through kinship.*"

Social structure

Observations of mergansers at Auckland Islands have been reported from October (Wilson 1959), late November (McCormick 1884) and January–February (Chapman 1891; Reischek 1889; Alexander 1901, 1902; Hutton 1901a,b). Specimens were collected at other times (November, March, July; Appendix 1) but I have not found notes associated with these that shed light on the birds' habits at these times.

There are no records of mergansers having been encountered other than as singles, as pairs, or as pairs with young; Reischek's (1889) encounter with six mergansers is interpreted as a family group. Wilson's encounter, when he shot a pair in a stream away from the coast (Falla 1970), is the only one that immediately precedes the assumed breeding period, and has the pair together.

All northern hemisphere mergansers are gregarious during winter and during migration and form monogamous pair bonds on breeding habitat. The females of some species have been recorded at the same breeding sites in consecutive years (species accounts in Kear 2005b). Brazilian Mergansers are dispersed as pairs on well-defended river territories year round (Silveira & Bartmann 2001) and a similar social dispersion seems likely for *M. australis.*

Foods and feeding habitat

There are two records of food taken by Auckland Island's mergansers.

A specimen shot in 1901 (NHM 1901.21.57) at Adams Island's Maclaren/ Magnetic Bay had a 90 mm ("3.5 in") Koaro *Galaxias brevipinnis* in its bill (Hutton 1901b). Although described by Hutton as a marine species, this is, like all *Galaxias* sp., a freshwater inhabitant and most likely the merganser would have caught it in the lower reaches of the bay's stream to which there would have been easy access from the shoreline for Hutton and his hunters.

Kear and Scarlett (1970) reported the gut contents of a preserved cadaver (NHM A/1999.1.124) as containing "macerated fish bones, mandibles of an errant polychaete and an unidentified gastropod". They added that "the presence of the polychaete tends to suggest a brackish water environment".

Some treatises (*e.g.* Phillips 1926; Delacour 1959; Greenway 1967) have reported *M. australis* taking freshwater shrimps, an observation attributed to Waite (1909) but Waite says no such thing.

There are no accounts of mergansers feeding at the Auckland Islands and few accounts from which their feeding habitat can be discerned with certainty. Reischek (1889) observed his group of six feeding among rocks on the shoreline of Waterfall Inlet (Colour plate 2); Waite (1909) quotes Capt. J. Bollons, master of the government ships regularly visiting the Subantarctic islands, as not having seen the bird on the coasts, but having found it at the heads of estuaries and especially on the island's watercourses "picking about in the creeks"; and Falla (1970) reports R.A. Wilson, the collector of two specimens in 1891, as having encountered his quarry up the stream bed some distance from the coast and in a deep pool where the stream was partly dammed on a rocky terrace.

Despite many streams on Auckland and Adams Islands being short and steep, *Galaxias brevipinnis* is common in all, and especially so where the streams' gradients flatten prior to flowing into the sea (M. Williams pers. obs.). These lower reaches would have offered suitable, albeit limited, feeding sites for mergansers in fresh water. However, given that human access up streams from the coastline is extremely difficult, it is not surprising that the merganser specimens were mostly seen and taken at the head of the bays, either in a stream's lower reaches or at the coastal edge (Colour plate 2).

Williams *et al.* (2012) examined stable isotopes of C and N in feathers and claws of some museum specimens. They concluded some of the birds sampled were feeding mostly on marine-sourced prey at the time of growing their feathers while others had included fresh water-sourced prey. However, they found no evidence of an exclusively fresh water feeding habit; feathers from one of Wilson's specimens collected from a stream provided evidence of a mixed-source diet.

Flight

M. australis was not flightless despite its depictions with short wings suggesting otherwise (*e.g.* Buller 1905; Fleming 1982). Ogilvie-Grant (1905) quotes F. W. Hutton's comment that the merganser "flies well". Elsewhere, Hutton reported that "an old drake merganser flew out from the shore to the steamer where it was anchored close in for the evening. It settled on the water within a few yards of the vessel and swam calmly about quacking like a duck" (Hutton & Drummond 1905).

Livezey (1989) suggested *M. australis* approached the threshold of flightlessness, a conclusion derived from his estimates of both body weight and wing area and the assumption that wing loading (wing area/weight) is a measure of flying ability. The latter is not so for flapping flight (Pennycuick 2008).

Livezey (1989) also identified *M. australis* as having a "weakly keeled" sternum and "disproportionately short mid-wing elements". The latter conclusion arose from his observation that the length of the wing skeleton was similar to that of Hooded Merganser, which he concluded was a smaller bird.

Relative to its sternum length, *M. australis* had a reduced keel. The keel area of all five specimens examined lie beyond the 50% prediction interval of a regression equation describing the average relationship between keel area and sternum length for four extant merganser species combined (see Fig. 4 in Appendix 3). On average, the keel area was 79% (75–84%; geometric mean and range) of that predicted by the regression equation. This implies a relative reduction in pectoral muscle mass, and of weight.

Similarly, relative to its sternum length, *M. australis* had shortened wing bones (humerus + ulna). The wing bone lengths of all three specimens examined lie beyond the 50% prediction interval of the regression equation describing the average relationship between wing bone length and sternum length for four extant merganser species combined (see Fig. 5 in Appendix 3). The combined lengths of the two wing bones of *M. australis* were 91% (89–93%; geometric mean and range) of that predicted by the regression equation.

Does having a reduced keel (and thus reduced pectoral muscle mass) and reduced wing bone length necessarily mean reduced flying ability? Pennycuick (2008) provides a model (PROGRAM *Flight 1.22*) for determining the merganser's likely flight characteristics (Table 2).

In simulations of *M. australis,* pectoral muscle mass as a percentage of total body mass was varied between the default value of 17% and 12% (to reflect the reduction in keel area), and body weight and wing span were also varied within the range of estimates and measurements obtained. Even when the most extreme values of maximum calculated weight (from Fig. 3), shortest wing length (Table 1) and 12% pectoral muscle mass were included together in a simulation the results suggest *M. australis* had similar flight characteristics to many other waterfowl (Table 2) and flew with the rapid wing beat typical of the two smaller mergansers (Hooded Merganser, Smew). The work required to maintain level flight at minimum power speed was about the same per unit weight of muscle as for a Mallard *Anas platyrhynchos* (Williamson *et al.* 2001; Pennycuick 2008).

Extinction

The merganser is the only bird known to have become extinct at the Auckland Islands following the islands' discovery by Europeans in 1806, after which people, predators and specimen collectors arrived.

Human occupation of the islands was brief and localised. Sealers were the earliest residents, establishing camps at the heads of several bays and inlets (Dingwall *et al.* 2007); tame waterfowl would almost certainly have been included in their fare. Maori and European settlement persisted for about a decade (1842–1854) in the Port Ross area (Fraser 1986) and presumably local waterfowl would have supplemented the residents' diets also.

The scale of successful alien animal introductions to Auckland Islands is modest by comparison to other islands in the New Zealand region (King 2006). While no rat *Rattus* sp. colonised any of the Auckland Islands and no alien mammals were released onto Adams Island, mice *Mus musculus*, goats *Capra hircus*, cats and pigs became well established on Auckland Island. Pigs, already numerous about Port Ross by 1840 (McCormick 1884), and cats have impacted many seabird colonies on Auckland Island and now restrict some petrel species to breeding only on the smaller and predator-free islands (Taylor 2000), just as they have Auckland Island Teal. Undoubtedly cats and pigs would have preyed upon any merganser nesting in an exposed site.

A third and final influence on the merganser's extinction was specimen collecting (see Appendix 1). Eighteen of the 23 skins of adults and fledglings now in the world's museums were collected during the 14 year period 1888–1902. More were undoubtedly collected but have subsequently disappeared, *e.g.* one of Wilson's pair from 1891, the 1882 Colonial Museum specimen (Appendix 1), and others that were collected for private dealers and collectors (including S.V. Dannefaerd, H.H. Travers and W.L. Buller) by crew of the government vessels *Hinemoa* and *Tutanekai* during twice-yearly visits to the islands.

Buller's (1892) insistence that "specimens of this interesting form in the adult stage should be obtained for our museums before it is too late" clearly found willing listeners and established willing buyers. For example, Ogilvie-Grant (1905) chronicles how, when at port in Bluff prior to Ranfurly's 1901

Table 2. Results of simulations using PROGRAM *Flight 1.22* (Pennycuick 2008) examining the flight characteristics of *M. australis* and selected other mergansers and waterfowl.

Species (sex)	**Weight (kg)**	**Wing span (m)**	**[1]V_{mp} = minimum power speed (m/s)**	**[2]Specific work at V_{mp} (J/kg)**	**[3]Wingbeat frequency (Hz)**	**Source; notes**
M. serrator (F)	0.908	0.86	14.8	10.6	7.61	Pennycuick 2008: *Program Flight 1.22*
M. australis (M)[4]	0.70	0.700	15.0	10.41	9.43	17% pectoral muscle mass
M. australis (M)	0.70	0.700	15.0	15.5	9.43	12% pectoral muscle mass
M. australis (M)	0.76	0.678	15.7	10.8	10.1	Maximum calculated weight, shortest male wing, 17% muscle mass
M. australis (M)	0.76	0.678	15.7	16.2	10.1	Maximum calculated weight, shortest male wing, 12% muscle mass
M. australis (F)[5]	0.55	0.658	14.3	9.46	9.53	17% pectoral muscle mass
M. australis (F)	0.55	0.658	14.3	14.1	9.53	12% pectoral muscle mass
M. australis (F)	0.63	0.652	15.0	9.97	10.2	Maximum calculated weight, shortest female wing, 17% muscle mass
M. australis (F)	0.63	0.652	15.0	14.9	10.2	Maximum calculated weight, shortest female wing, 12% muscle mass

L. cucullatus (JM)[6]	0.59	0.61	15.2	9.94	11.0	captive
L. cucullatus (M)	0.68	0.63	15.7	10.9	10.4	Mean male wt, mid range of wingspan from Cramp & Simmons (1977)
M. albellus (JM)[6]	0.58	0.57	15.6	12.1	11.4	captive
M. albellus (M)	0.65	0.62	15.6	10.9	10.4	Mean male wt, mid range of wingspan from Cramp & Simmons (1977)
Anas platyrhynchos	1.09	0.885	15.5	14.3	7.14	Pennycuick 2008: *Program Flight 1.22*
A. penelope	0.81	0.842	14.4	11.7	7.16	Pennycuick 2008: *Program Flight 1.22*

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[1] V_{mp} = minimum power speed, the velocity at which the power required to fly is less than at either slower or faster speeds. If the muscles cannot produce this level of power, then the bird cannot fly horizontally, and if the heart and lungs cannot sustain the minimum power aerobically, then it can only fly in short bursts, if at all (from Pennycuick 2008: Chapter 1).

[2] Specific work at V_{mp} = the work done in each contraction by unit mass of muscle when flying level at V_{mp}.

[3] Wingbeat frequency = wingbeat frequency expected in level flight at V_{mp}.

[4] All *M. australis* male simulations based on estimated body weight (Fig. 3), and wingspan (distance between glenoid fossae (54 mm) from NHM A/1999.1.124, humerus + ulna length (128 mm) from NHM 1904.8.4.3, mean adult wing length (194 mm), aspect ratio 9).

[5] All *M. australis* female simulations based on estimated body weight (Fig. 3), and wingspan (estimated distance between glenoid fossae (50 mm), humerus + ulna length (124 mm) from NHM 1904.8.4.4, mean adult wing length (180 mm), aspect ratio 9).

[6] Fledged juvenile male in captivity, Wildfowl & Wetlands Trust, Slimbridge, UK.

collecting trip on *Hinemoa*, a bystander offered the ship's crew £3 10s for any merganser skin from the island. Ranfurly's very deliberate pursuit of mergansers in every inlet of Auckland Island for the British Museum (Alexander 1901, 1902; Ogilvie-Grant 1905) yielded the last nine specimens in 1901–1902. None was seen subsequently despite a determined search by members of a 1907 scientific expedition to the islands (Waite 1909). It is hard not to conclude that a naturally small merganser population, already depleted by early human occupants and under pressure from two new mammalian predators, was tipped into premature extinction by rapacious collecting.

Overview

The persistence of a small and isolated population of mergansers at Auckland Islands at the time of European arrival in New Zealand provided a brief glimpse of a species that had already disappeared everywhere else.

This small fish-eating duck, the smallest *Mergus*, might be expected to show hints of the 'islandisation' conspicuous among waterfowl, and especially *Anas* ducks, on remote islands (Lack 1970; Weller 1980). These effects include reduction in body size, lower clutch sizes, larger eggs relative to body size, reduced flight capability, year-round territoriality, increased terrestrial habit, enhanced sexual size dimorphism and reduced plumage dimorphism, most of which may be viewed as energetic responses to limited but spatially predictable food on small islands (McNabb 1994a,b).

Breeding characteristics of mergansers at Auckland Islands may never be resolved but if mergansers had been long-established residents of Auckland Island a smaller clutch size than other merganser species is almost certain (Lack 1970; Weller 1980; Rohwer 1988). Perhaps Chapman's (1891) observation of four new hatchlings is indicative. A reduction of body mass relative to its New Zealand progenitor is also possible if the founders responded to their isolation in a manner similar to the antecedents of Auckland Island Teal (Williams *et al.* 1991). The reduction in pectoral muscle mass which a reduced keel area implies and the apparent shortening of wing bones are indicators of this response. Still to be resolved, however, is whether Auckland Islands' mergansers were smaller 'island' derivatives of those on mainland New Zealand or whether all mergansers in the New Zealand region were small derivatives of a larger common founder.

The Auckland Islands archipelago is such a small and restricted locality that it is difficult to interpret many of the snippets of merganser ecology assembled by Kear & Scarlett (1970) and in this presentation. This was a more widely distributed bird whose bones have been recovered in natural deposits and middens on New Zealand's main islands (from northern North Island to Stewart Island) and on Chatham Island (Millener 1999; Worthy 1998b; Worthy & Holdaway 2002). Although eight of the present nine sites at which *Mergus* bones have been found on New Zealand are coastal this does not necessarily imply the merganser was a marine or coastal species. To date, only two inland lacustrine sites have yielded Holocene avifaunal remains –

Pyramid Valley in North Canterbury from which no fish-eating birds were recovered (Holdaway & Worthy 1997), and Lake Poukawa in inland Hawkes Bay where *Mergus* and almost all other Holocene waterfowl and water-dependent birds were present (Worthy 2004). *M. australis* may have had a wider distribution which the few fossil sites under-represents and plausibly may have been a bird of New Zealand lakes and rivers, a habitat like that of most extant mergansers. The coastal edge habitat of mergansers at Auckland Islands may be more an example of a broader island niche than one confirming a ubiquitous habitat choice.

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Appendix 1. *Mergus australis* specimens from Auckland Islands in museum collections.

The late 19th century was a period of assiduous collecting of New Zealand's avifauna and specimens from its remote islands, like the Auckland Islands, were especially prized. This demand was driven by competition between Imperial museums in Europe to assemble premier collections of fauna, flora and anthropology from their nation's colonies, by New Zealand's new Colonial Museum and provincial museums in Auckland, Christchurch and Dunedin to do likewise, and by private collectors, most notably Walter Rothschild of Tring, England.

Baron Anatole von Hugel (1875), a travelling UK-based aristocrat returned the first mergansers to England having purchased his specimens from collectors in Invercargill. He placed one specimen each in the British Museum of Natural History and the Zoological Museum at Cambridge University. Hermann Krone, following participation in the German Transit of Venus expedition to Auckland Island in 1874

(Dawson & Duerbeck 2008) returned home with a pair of mergansers which he presented to the Dresden Museum. Between 1877–1889 Andreas Reischek assembled a prodigious collection of New Zealand's birds for the K.k. Naturhistorisches Hofmuseum (later Naturhistorisches Museum Wien) in Vienna (Reischek 1889, 1930) and was the first major collector to visit the Auckland Islands (in 1888) determined to secure a pair of mergansers.

Crew of government ships visiting the island twice yearly returned to port with bird specimens for sale and some of their merganser specimens are included among the existing museum specimens. Sir Walter Buller was a determined acquirer of these for both his own collection and for sale to Walter Rothschild (Bartle & Tennyson 2009). Although Rothschild acquired many bird specimens from other New Zealand collectors (*e.g.* Dannefaerd, Travers) he received all of his mergansers from Buller. Those specimens are now in the AMNH collection (Bartle & Tennyson 2009).

A last and most determined field collector was Lord Ranfurly, Governor-General of New Zealand 1897–1904, who collected a large number of New Zealand and Pacific birds at the request of the British Museum (Ogilvie-Grant 1905). He visited Auckland Islands in January 1901 (on NZGS *Hinemoa*) and January 1902 (on NZGS *Tutanekai*) (Alexander 1901, 1902), collecting four mergansers in 1901 (an adult pair going to the British Museum and a recent fledgling each to Dublin and Canterbury Museums) and another two birds in 1902 (the fates of which remain uncertain). At Ranfurly's request crew of the British naval vessel HMS *Archer* visiting Auckland Islands in July 1901 collected at least three other merganser specimens which were eventually lodged in the British Museum (Ogilvie-Grant 1905). Following Ranfurly's 1902 collecting no live mergansers were seen again despite earnest (Waite 1909) and forlorn (Williams & Weller 1978) searches.

Eleven museums, three in New Zealand, two in USA, three in Europe, two in UK and one in Ireland, hold between them four duckling specimens and 23 skins of immatures and adults. Near-complete skeletal remains of three birds and a partial cadaver from another are held at the Natural History Museum, Tring, and sternum and pelvic bones from skins are in Otago and Canterbury Museums. No merganser bones have yet been collected from natural deposits at Auckland Islands. The documented presence of two *M. australis* skulls in the Universitie d'Lyon Anatomy Department collection, France (Wood *et al.* 1982) is a case of *M. serrator* skulls being misidentified and wrongly labelled (A. Previato pers. comm.).

Not all specimens apparently received by museums can now be accounted for. For example, Buller (1892) refers to the British Museum then containing "a pair" but the current collection contains only one specimen pre-dating 1892. Buller also refers to a specimen in both Otago and the Colonial (= National) Museum collections (the latter deposited in 1880–81; *Evening Post* 25 April 1882) but their current collections contain no mergansers of that vintage. Mystery also surrounds the fate of both birds collected by Ranfurly in 1902, and of the skins of 2 skeletons and cadaver in the NMH (see below).

Listed below are details for each specimen, as originally provided by Kear & Scarlett (1970), with added comment and measurements (in mm). Measurements of tarsus (especially) and mid toe & claw on the dried specimens proved extremely problematic and rarely repeatable to within 1 mm; the means of four measurements are provided for each simply to indicate their approximate magnitude. Length of exposed culmen, width of bill at tip (widest part of nail), and wing length proved the most repeatable of standard measurements, the latter being of unflattened wing feathers from the distal portion of the carpus to the tip of the longest primary feather (usually the second). Rectrices of all specimens were examined for presence of terminal down stalks to indicate a recent fledgling (Larson & Taber 1980).

Canterbury Museum, Christchurch, New Zealand

Skin. AV1580. Collection date recorded as May 1894, collector not identified. Ex W.L. Buller collection. Original label has sex as male, changed (by R.M. Scarlett) to female. Measurements: culmen 54.5, bill width at tip 5.4, wing 178, tarsus 41, mid toe & claw 67, tail 63. Sex by measurement – female. Head crest poorly developed.

Skin. AV1583. Ex E.F. Stead collection. Collected by R.A. Wilson, 30 Oct 1891, probably at Waterfall Inlet (Wilson 1959). Unsexed. Measurements: culmen 61, bill width at tip 6.9, wing 199, tarsus 44, tail 73. Sex by measurement – male. Adult.

Skin (mount). AV2944. Collected by Lord Ranfurly's party 5 Jan 1901. Acquired by F.W. Hutton, Canterbury Museums' curator of the time who accompanied Ranfurly on *Hinemoa* and was later responsible for despatching Ranfurly's collection to the British Museum (Hutton 1901a; Ogilvie-Grant 1905). Labelled male. Measurements: culmen 55.8, bill width at tip 5.8, wing 177, tarsus 37, mid toe & claw 55, tail 62. Sex by measurement – female. Tips of its remiges and rectrices are unfrayed and the down stalk visible at tip of at least 3 rectrices. Recent fledgling. Identical in plumage to NMINH 1904.559.1 which was collected at the same time.

Skin. AV 1581. Duckling. Ex W.L. Buller collection. Downy, *c.* 1 week old. Kear & Scarlett (1970) suggest this to be one of the ducklings collected by crew of NZGS *Hinemoa* on or about 15 Jan. 1890 in Maclaren/Magnetic Bay, Adams island (Chapman 1891). Chapman collected 2 of these for Otago Museum (Chapman 1891) (see specimens A51.51) and another duckling from this brood is AMNH 744347, derived from Buller's collection (Buller 1892; Bartle & Tennyson 2009).

Bones. AV 1582. Head including part cranium, upper and lower mandibles and quadrate. Label states "from old skin skeletonised 23/10/53 R.J.Scarlett. Length of culmen 5.3 inches" Nares to tip 36.6 and comparable with females NHM 1904.8.4.2 and NHM 1904.8.4.4. No collection data or date recorded.

Bones AV 5176. Pelvis, sternum and 3 caudal vertebrae. Label reads "sternum and pelvis of male (O.1224.3) now AV 5176, Auckland Is, Jan 1901." Almost certainly from mounted specimen AV2944 in which case it is incorrectly sexed. Sternum + keel length (ventral) 85.7, sternum length (visceral/ dorsal) 71.1, sternum anterior width 41.9, sternum posterior width 47.3, keel area 6.01 cm^2, pelvis acetabulum width 28.6, pelvis posterior width 48.0. Measurements comparable with those of females NHM 1904.8.4.2 and NHM 1904.8.4.4.

Bones. AV 7157. L. corocoid, length 44.8. L. scapula. Both bones labelled "merganser". No other data.

Otago Museum, Dunedin, New Zealand

Skin (mount). AV 1110 (formerly A51.50). Labelled as "collected 1890, ex F.R. Chapman collection, sex female". Kear & Scarlett (1970) suggest this specimen may have been collected in January 1890 on Chapman's journey on NZGS *Hinemoa* but Chapman (1891) makes no such claim and specifically says that the parents of the ducklings collected then escaped. Rectrices still carrying the down stalk. Recent fledgling.

Measurements: culmen 54.8, wing 177, tarsus 38, mid toe & claw 56, tail 69. Sex by measurement – female. Kear and Scarlett (1970) report that the female of the adult pair shot by R.A. Wilson in October 1891 (Wilson 1959) was presented by Wilson to the Otago Museum, and Buller (1905) refers to "a pair in Otago Museum." This specimen (AV 1110), because of its age, is not Wilson's female.

Spirit. AV 8511 and AV 8512 (formerly A51.51). Ducklings (2). Ex F.R. Chapman collection. Downy, *c.* 1 week old. Collected Maclaren or Magnetic Bay, Adams Island on 18 January 1890 (Chapman 1891). Siblings of AV 1581 (Canterbury Museum) and AMNH 744347.

Bones. AV1436. Sternum with articulated corocoids, scapulae, furcula and portions of ribs. Presumed to belong to AV 1110. Sternum + keel length (ventral) 85.8, sternum length (visceral/dorsal) 71.9, sternum anterior width 41.9, sternum posterior width 47.8, keel area 5.93 cm^2.

Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand

Skin (mount). OR 001357 (formerly DM1357). Labelled as "collected June 1902, Auckland Islands, sex unknown, age unknown". No collector is identified. Measurements: culmen 53.7, bill width at tip 5.7, wing 179. Sex by measurement – female. This is a recent fledgling; a down stalk persists on several rectrices, the elongated nape feathers of the crest are barely discernible, the overall colouration is a dull brown (probably much darker in life) being only slightly lighter beneath than above, and no hint of rufous on head. Collection date (month) is clearly erroneous given the plumage characteristics of the specimen. Likewise the year and possible source is a matter of conjecture and confusion. Buller (1892, 1895, 1905) refers to a "good specimen" already in the Colonial Museum, presumably a reference to a specimen added to the museum's collection in 1880–81 (*Evening Post* 25 April 1882). The last known collection was of two specimens by Ranfurly on 9 January 1902 (Alexander 1902) but the fates of both are unknown; this specimen may be one of them.

National Museum of Ireland, Natural History, Dublin, Ireland

Skin (mount). NMINH 1904.559.1. Labelled as collected on 5 January 1901, Auckland Islands. Mounted by Rowland Ward, Piccadiliy, London. Lord Ranfurly collection. Unsexed. Measurements: culmen 54.6, bill width at tip 5.6, wing 181. Sex by measurement – female. This is a young bird with characteristics identical to those of Canterbury's AV 2944, its probable sibling. This specimen was not among those received by the British Museum (Ogilvie-Grant 1905).

Naturhistorisches Museum, Vienna, Austria

Skin. 50759. Collected 26 January 1886, Waterfall Inlet, Auckland Island. A. Reischek, collector (see Reischek 1889, 1930). Label sex – female. Measurements: culmen 56.8, bill width at tip 5.8, wing 185. Sex by measurement – female. Adult.

Skin. 50760. Collected 26 January 1886, Waterfall Inlet, Auckland Island. A. Reischek, collector (see Reischek 1889, 1930). Label sex – male. Measurements: culmen 59.8, bill width at tip 6.3, wing 202. Sex by measurement – male. Adult.

Museum Nationale d'Histoire Naturelle, Paris, France

Skin (Type). #28. Collected March 1840, M. Jacquinot, collector (Hombron & Jacquinot 1841, 1853). Label sex – male. Measurements: culmen 60.9, bill width at tip 5.8, wing 185.

Sex by measurement – male. Collected during Dumont D'Urville's expedition to Auckland Islands 10–20 March 1840. The collection locality is presumed to be Port Ross because D'Urville's two ships remained anchored there and later in that year McCormick (1884) saw mergansers there. However D'Urville's expedition scientists visited several of the island's eastern inlets on a visiting Portugese whaler *Speculacao* (McNab 1913).

Staatliches Museum fur Tierkunde, Dresden, Germany

Skin. C5730. Carnley Harbour, Auckland Island. 1874. H. Krone presented. Label sex – male. Measurements: culmen 61.3, bill width at tip 7.1, wing 194. Sex by measurement – male. The date and location cannot be verified. Kear & Scarlet (1970) list the specimen's entry as "H. Krone bought and pres." implying either its purchase by Krone or its purchase from Krone. Hermann Krone was a member of the five-month long 1874–75 German Transit of Venus expedition based at Terror Cove in Port Ross. Although the expedition assembled a substantial natural history collection, it did not include birds. The expedition members are not known to have journeyed beyond Port Ross and they travelled to and from Auckland Island on the *Alexandrine* directly to Melbourne, without calling at any New Zealand port (Elliot Dawson pers. comm.). However Krone (1900, pp. 24–26) lists seabirds at the island including small penguins in Carnley Harbour, perhaps indicative of an otherwise unrecorded visit.

Skin. C5731. Carnley Harbour, Auckland Island. 1874. Label sex – female. Measurements: culmen 54.1, bill width at tip 6.0, wing 182. Sex by measurement – female. Comments as above.

Zoology Museum, Cambridge University, Cambridge, England

Skin. 12/Ana/38/a/1. Von Hugel collection. Label sex – male. Measurements: culmen 60.7, bill width at tip 7.0, wing 192, tarsus 39, mid toe & claw 66, tail 73. Sex by measurement – male. Adult. Collection date on label given as 11 Dec. 1874; von Hugel (1875) indicates he purchased this and another specimen (BMNH 1875.11.6 14) in Invercargill, NZ and "the birds were killed the latter end of November..."

Natural History Museum, Tring, England

Skin. 1875.11.6.14. Presented by von Hugel, one of pair purchased in Invercargill (von Hugel 1875). Label sex – unrecorded. Measurements: culmen 58.4, bill width at tip 6.3, wing 189, tarsus 38, mid toe & claw 67, tail 68. Sex by measurement – probably male. Measurements of bill and wing are smallest for any "male" measured. Its well-developed head crest and rufous colour of head and throat suggest it to be an adult.

Skin. 1901.10.21.57. McClennands (= McLennan) Inlet, Auckland Island. 4 January 1901. Presented by Earl of Ranfurly. Label sex – "male certain". Label contains description of soft parts in hand of F. W. Hutton. Measurements: culmen 60.4, bill width at tip 6.5, wing 188, tarsus 45, mid toe & claw 68, tail 70. Sex by measurement – male. Adult.

Skin. 1901.10.21.58. McClennands (= McLennan) Inlet, Auckland Island. 4 January 1901. Presented by Earl of Ranfurly. Label sex – "female certain". Measurements: culmen 53.9, bill width at tip 5.7, wing 181, tarsus 43, mid toe & claw 63mm, tail 72. Sex by measurement – female. Adult.

The collection date for the above 2 specimens is incorrect by one day. On 4 January 1901, Ranfurly's party aboard NZGS *Hinemoa* spent all day in the Port Ross area of Auckland Island (Alexander 1901; Hutton 1901a). They journeyed to Carnley Harbour on 5 January visiting many of the eastern inlets, including Norman and McLennan Inlets, along the way. Hutton (1901a) records one merganser being obtained in Norman Inlet but makes no reference to any being retrieved from McLennan Inlet. His notebook entry for 5 January 1901 records "visited sounds on east coast" followed by a description of a merganser's bill, feet and eye and a reference to its short wings and "quacks like a duck". His notebook entry for 6 January is without reference to location (but the party was then in Carnley Harbour; Alexander 1901) and contains a description of a male merganser. Later in his notebook he comments that "A full-grown male flew from the shore to the *Hinemoa* and settled in the water within gunshot of the vessel where it remained swimming about and quacking until shot from on board". The 4 January 1901 collection date appears to have arisen from Hutton's notebook listing of small bird specimens collected that day on Enderby Island and the Port Ross shoreline and placed in a numbered specimen jar, to which he later added (in different pencil) "merganser australis 1 in Normans Inlet". Two other mergansers (CM 2944 and NMINH 1904.559.1.) are labelled as collected on 5 January 1901.

Skin. 1904.8.4.1. Collector J.P. Rolleston, Carnley Harbour, Auckland Island, 9 July 1901 (Ogilvie-Grant 1905). Label records soft part colouration. Labelled sex – female. Measurements: culmen 53.1, bill width at tip 5.8, wing 177, tarsus (most removed from skin), mid toe & claw 60, tail 68. Sex by measurement – female. Rolleston, commanding officer of HMS *Archer* responded to Ranfurly's request and obtained a range of bird specimens when patrolling New Zealand's Subantarctic islands. Culmen measurements are not reliable because the rhampotheca has been soaked and lifted from the underlying bone, the entire skull removed from the skin and retained as part of skeleton NHM 1904.8.4.2.

Skin. 1902.8.6.1. Collector Lt. Kennett Dixon, R.N. Auckland Island. No collection date. Labelled as male. Measurements: culmen 60.4, bill width at tip 7.1, wing 197, tarsus 42, mid toe & claw 68, tail 78. Sex by measurement – male. Age uncertain. Collector was officer on HMS *Archer* which visited Auckland Island July 1901.

Skin. 1904.4.30.1. Collector Lt. A.J. Stewart, R.N. No further details. Presumed to have been collected July 1901 during HMS *Archer* visit to Auckland Island. Measurements: culmen 55.3, bill width at tip 6.0, wing 172, tarsus 41, mid toe & claw 63, tail 68. Sex by measurement – female. Falla (1970) considered this specimen to have "indeterminate" plumage and could be a young bird, which I confirm from the presence of down stalks at the tips of the rectrices.

Skeleton. 1904.8.4.2. Female. From skin 1904.8.4.1 (Ogilvie-Grant 1905). Total skull length 102.6, nares to bill tip 35.8, sternum + keel length (ventral) 87.4, sternum length (visceral) 71.7, sternum anterior width 42.5, keel area 5.45 cm^2, pelvis acetabulum width 28.7, pelvis posterior width 47.1, humerus 67.8, ulna 54.7, femur 42.6, tibiotarsus 76.9, tarsus 40.4.

Skeleton. 1904.8.4.3. Label sex – male. Associated note reads "belongs to mounted specimen standing up". No such specimen can be traced. Total skull length 109.9, nares to bill tip 40.2, sternum + keel length (ventral) 94.8, sternum length (visceral/dorsal) 77.1, sternum anterior width 47.7, keel area 6.28 cm^2, pelvis acetabulum width

31.2, pelvis posterior width 49.9, humerus 72.1, ulna 57.7, femur 45.4. Tibia and tarsus presumably retained in the mount.

Skeleton. 1904.8.4.4. Label sex – female. Associated note reads "belongs to lying mounted specimen". No such specimen can be traced. Total skull length 103.6, nares to bill tip 37.3, sternum + keel length (ventral) 88.5, sternum length (visceral/dorsal) 72.3, sternum anterior width 43.1, keel area 5.60 cm^2, pelvis acetabulum width 29.0, pelvis posterior width 47.0, humerus 68.9, ulna 55.0, femur 43.1, tibiotarsus 77.7, tarsus 41.2.

Ogilvie-Grant (1905) refers to skeletons "of an adult pair in the possession of Lord Ranfurly"; 1904.8.4.3 and 1904.8.4.4 are presumably these. Since both retain complete skulls the rhampothecae must have been removed from the bills, as for 1904.8.4.2. The whereabouts of the mounts are unknown.

Spirit. A/1999.1.124. Cadaver of a male (based on sternum-keel length) that was initially labelled as female but subsequently re-labelled as male. All musculature and entrails remain but the gizzard has been opened and food contents reported in Kear & Scarlett (1970). Associated original labels offer no indication of origin but one states "belongs to the one standing on/upright. Tibia and tarsus left with stuffed specimen". Body width at shoulder joint (glenoid fossae) 54mm.

Ogilvie-Grant (1905) refers to the museum receiving in the "ranfurly collection" 3 skins (1901.10.21.57, 1901.10.21.58, 1904.8.4.1) a skeleton (1904.8.4.2) derived from one of the skins (1904.8.4.1), plus another two skeletons of "an adult pair in the possession of Lord Ranfurly", which presumably are the two birds he collected in Carnley Harbour on 9 January 1902 (Alexander 1902). The museum later received a male specimen (1902.8.6.1) followed by a female specimen (1904.4.30.1). Of the birds presently in the NHM collection, the spirit specimen could be derived from either of the two male skins 1902.8.6.1 or 1901.10.21.57. The reference to a standing mount could be a confusion should one of these two birds have originally been mounted and later relaxed and turned into a skin, or it could indicate the cadaver is not from any specimen now in the museum. In the latter case it would represent another, presently unknown, male specimen.

Carnegie Museum, Pittsburgh, USA

Skin. 24509. Male. This was purchased in 1905 with the "third Buller collection" (Bartle & Tennyson 2009; Appendix 5) and is thought to be the adult male mentioned in Buller (1905). A separate tag bears Buller's no. 125. Bartle & Tennyson (2009) record collection date as 1894 and possibly supplied to Buller by the collector A.W. Bethune. Measurements (supplied by S. Rogers, Carnegie Museum): culmen 53.8, nares to tip 40.1, bill width at tip 5.3, wing 181. Sex by measurement – female.

American Museum of Natural History, New York, USA

Skin. 734364. Male. No other data. Original label in the handwriting of commercial collector S.V. Dannefaerd. Measurements (supplied by M. LeCroy, AMNH): culmen 61.5, bill width at tip 5, wing 187. Sex by measurement – probably male.

Skin. 734365. Female. No other data. Dannefaerd's label gives collection date as 2/1895. Measurements (supplied by M. LeCroy, AMNH): culmen 60, nares to tip 40, bill width at tip 5, wing 178. Sex by measurement – female.

Skin. 734366. Labelled as female but a note by R.A. Falla dated 5 Aug. 1966 says "this is clearly a male". Falla (1970) adds this specimen is "bigger than 734364". Dannefaerd's label gives collection date as 2/1895. Measurements (supplied by M. LeCroy, AMNH): culmen 62, nares to tip 44, bill width at tip 5, wing 188. Sex by measurement – male.

Skin. 734367. Unsexed. December 1901 Travers collection. Falla (1970) writes "seems to be a male, wing 192mm, bill only 58mm but wide and deep like 734366". Measurements (supplied by M. LeCroy, AMNH): culmen 62, nares to tip 44, bill width at tip 5.5, wing 188. Sex by measurement – male.

Skin. 744347. Duckling. Presumably one of the brood of four collected by Chapman (1891). Others in Otago and Canterbury Museums.

These specimens were included in the AMNH's 1932 purchase of W.L. Rothschild's collection at Tring. According to Salvadori (1895) a male and female at Tring were immature birds in first plumage. Rothschild (1907) mentioned four specimens at Tring, one mounted and three skins.

Appendix 2. Comparative measurements (mm) and weights (g) of mergansers. Means are given ± s.d. with ranges in parentheses. Sources: 1 = Kear 2005b; 2 = Livezey 1989; 3 = Cramp & Simmons 1977; 4 = Kortright 1942; 5 = Solovieva & Shokhrin 2008; 6 = L. Lins (pers. comm.); 7 = this study.

Species	Sex	Culmen	Tarsus	Wing	Weight
Mergus australis	M	60.3 ± 0.9[7]	42 ± 2[7]	194 ± 6[7]	550–760[7]
		59.6 ± 3.8[2]	43.4 ± 1.7[2]	185 ± 5.2[2]	898[2]
	F	54.6 ± 1.1[7]	40 ± 2[7]	179 ± 4[7]	440–630[7]
		55.0 ± 2.8[2]	40.5 ± 1.2[2]	175 ± 3.5[2]	(80–83% of male weight)
		(91–93% of male size)		(93–94% of male size)	
Mergellus albellus	M	29.6 (27–32)[3]	34.0 (31–36)[3]	202 (197–208)[3]	652 (540–825)[3]
	F	26.8 (25–29)[3]	30.6 (29–32)[3]	184 (181–189)[3]	568 (515–630)[3]
		(90% of male size)		(91% of male size)	(87% of male weight)
Lophodytes cucullatus	M	39.6 (37–41)[1]	32.4 (30–34)[1]	198 (191–207)[1]	680 (595–879)[4]
		40.7 ± 1.2[2]	33.6 ± 1.6[2]	193 ± 4.2[2]	
	F	38.3 (35–40)[1]	31.3 (30–33)[1]	185 (180–191)[1]	544 (453–652)[4]
		39.0 ± 2.1[2]	32.2 ± 1.1[2]	183 ± 3.4[2]	(= 80% of male weight)
		(96% of male)		(93% of male)	617[2]
Mergus octosetaceus	M	51.6 ± 1.5[2]	44.4 ± 2.9[2]	200.2 ± 4.4[2]	828[6]
					983 (calculated)[2]
	F	48.6 ± 0.9[2]	40.8 ± 2.2[2]	193.0 ± 3.9[2]	753[6]
		(94% of male size)		(96% of male size)	(91% of male weight)

Appendix 2 (*continued*)

Species	Sex	Culmen	Tarsus	Wing	Weight
M. serrator	M	59.2 (56–64)[3]	47.0 (44–50)[3]	247 (235–255)[3]	1,197 (947–1,350)[3]
		58.1 ± 1.5[2]	46.6 ± 1.6[2]	236 ± 9.0[2]	984[2]
	F	52.1 (48–55)[3]	42.7(40–45)[3]	228 (216–239)[3]	984 (900–1,100)[3]
		54.4 ± 2.6[2]	45.1 ± 2.8[2]	216 ± 9.1[2]	(82% of male weight)
		(88–93% of male size)		(92% of male size)	
M. squamatus	M	52–57[1]	46–48[1]	250–265[1]	1,232(1,125–1,400)[1]
		55.6 ± 1.4[2]	46.8 ± 0.7[2]	249 ± 6.5[2]	1,234(calculated)[2]
	F	~45[1]	–	220–250[1]	977 (930–1,070)[5]
		50.5 ± 2.0[2]	45.7 ± 2.3[2]	235 ± 11.9[2]	(79% of male weight)
		(91% of male size)		(94% of male size)	
M. merganser	M	55.8 (52–60)[3]	51.7 (49–55)[3]	285 (275–295)[3]	1,709 (1,528–2,160)[3]
		55.5 ± 3.6[2]	51.9 ± 1.7[2]	267 ± 5.5[2]	1,382[2]
	F	48.7 (44–52)[3]	47.4 (44–51)[3]	262 (255–270)[3]	1,232 (1,050–1,362)[3]
		50.6 ± 2.3[2]	46.7 ± 1.3[2]	239 ± S 3.5[2]	(72% of male weight)
		(87–91% of male size)		(90–92% of male size)	

Appendix 3: Sternum lengths, keel areas and wing bone (humerus + ulna) lengths of mergansers.

Contributed by Stephen Hartley, School of Biological Sciences, Victoria University, P.O. Box 600, Wellington, New Zealand.

To examine whether the keel of *M. australis* was reduced and its wing short relative to its sternum length, linear regressions between $\log_e$(sternum length) and $\log_e$(keel area) and between $\log_e$(sternum length) and $\log_e$(wing bone length) were performed using data from four extant merganser species (Appendix 4). The results were back-transformed to the original scale for graphical display. In fitting the regressions, individuals were considered independent data points. 50% prediction intervals were constructed around the fitted regression lines; the area within the 50% prediction interval is expected to contain 50% of all future points following the same relationship used to build the model.

Data points for *M. australis* (Appendix 4) were then compared to the inter-specific relationship to determine whether they fell inside or outside the prediction interval more, or less, frequently than expected.

For the sternum – keel area relationship, all five points for *M. australis* fell below the 50% prediction interval (Fig. 4). The probability of this occurring if *M. australis* follows the same relationship as the other mergansers is $P = 0.0017$ ($0.5 * 0.25^4$). For a given sternum length, the keel area of *M. australis* was 0.792 (0.753–0.839) [geometric mean and range] times that predicted by the inter-specific relationship.

For the sternum – wing bone length relationship, all three points for *M. australis* fell below the 50% prediction interval (Fig. 5). The probability of this occurring if *M. australis* follows the same relationship as the other mergansers is $P = 0.029$ ($0.5 * 0.25^2$). For a given sternum length, the wing bones of *M. australis* were 0.913 (0.892–0.925) [geometric mean and range] times the length predicted by the inter-specific relationship of the other species.

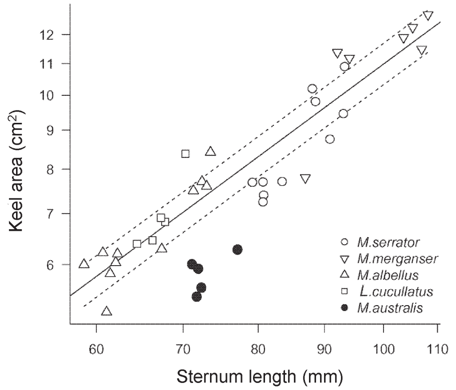

Figure 4. Interspecific allometric relationship (excluding *M. australis*) between sternum length and keel area for four species of merganser (open symbols) with 50% prediction interval (dashed line). $\log_e$(sternum) = $-3.377 + 1.254*\log_e$(keel area), $R^2 = 0.879$, $F_{1,31} = 224.2$, $P = 9.7*10^{-16}$. Data from Appendix 4.

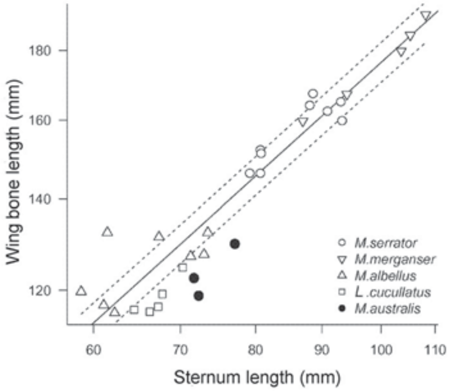

Figure 5. Interspecific allometric relationship (excluding *M. australis*) between sternum length and wing bone length for four species of merganser (open symbols) with 50% prediction interval (dashed line). $\log_e$(sternum) = $1.200 + 0.862*\log_e$(wing bone), $R^2 = 0.920$, $F_{1,25} = 288.5$, $P = 3.1*10^{-15}$. Data from Appendix 4.

Appendix 4. Sternum lengths, keel areas and wing bone (humerus, ulna) lengths of four extant merganser species and *M. australis*. Specimens sourced from National Museum of Ireland, Dublin (NMINH), Natural History Museum, Tring (NHM), Naturhistorisches Museum, Wien (Vienna), Staatliches Museum fur Tierkunde, Dresden (Dresden), Museum Nationale d'Histoire Naturelle, Paris (Paris), Otago Museum, Dunedin (Otago), Canterbury Museum, Christchurch (CM).

Species & specimen identity	**Sex**	**[1]Sternum length (mm)**	**[2]Keel area (cm^2)**	**Humerus length (mm)**	**Ulna length (mm)**
M. serrator					
NMINH 1932.13.1	F	80.7	7.70	83.1	69.0
NHM1930.3.24.242	F	80.8	7.40	82.7	68.5
NHM 1997.78.1	F	79.2	7.69	81.5	64.7
NMINH 1927.6.1	M	88.6	9.81	91.1	76.2
NMINH 2004.79.26	M	93.3	10.90	87.6	72.2
NHM 1898.2.12.5	M	93.1	9.46	90.5	74.5
NHM 1930.3.24.633	M	88.1	10.20	90.3	73.7
Vienna 4456	F	83.5	7.71		
Vienna 4827	M	90.9	8.76	89.3	73.1
Paris 1996/39	?	80.7	7.25	80.2	66.0
M. merganser					
NHM 1955.5.10	F	94.1	11.18	93.9	73.2
NHM 1866.12.30.5	F(?)	87.0	7.80	87.2	72.5
Dresden 3092	F	92.1	11.38	94.0	
Dresden 3022	M	107.0	11.49		
NHM 1930.3.24.239	M	103.6	11.90	98.2	81.6
NHM 1930.3.24.238	M	105.3	12.27	100.1	84.6
Vienna 2733	M?	108.2	12.75	104.0	87.2
M. albellus					
NHM 1930.3.24.236	F	58.7	6.00	65.2	54.5
NHM s/1986.32.1	F	62.3	6.20	62.9	52.6
Dresden unnumbered	F	60.7	6.22		

Appendix 4 (*continued*)

Species & specimen identity	Sex	[1]Sternum length (mm)	[2]Keel area (cm^2)	Humerus length (mm)	Ulna length (mm)
NHM 1930.3.24.235	M	73.5	8.42	71.3	61.0
NHM 1930.3.24.237	M	71.3	7.50	68.9	58.2
Dresden barhmann 110	M	72.4	7.71	71.5	
Vienna 8645	F	61.5	5.84	72.1	60.2
Paris 1977/1200	?	73.0	7.60	69.4	58.1
Paris 1977/1199	?	67.4	6.29	72.0	59.3
Paris 1997/679	?	61.1	5.20	63.5	53.5
Paris 1921-203	?	62.1	6.04		
L. cucullatus					
NHM 1986.60.8	M	70.3	8.38	69.1	55.6
NHM 1997.35.1	F	64.5	6.39	64.1	52.0
Vienna 4865 captive	M	67.3	6.91	64.2	52.5
Vienna 2207 captive	F	67.8	6.83	66.6	52.6
Vienna 4598 captive	?	66.3	6.46	64.0	51.7
M. australis					
NHM1904.8.4.4	F	72.3	5.60	68.9	55.0
NHM1904.8.4.2	F	71.7	5.45	67.8	54.7
NHM 1904.8.4.3	M	77.1	6.18	72.1	57.7
CM 5176	F	71.1	6.01		
Otago 1110	F	71.9	5.93		

[1] Sternum length is measured along the midline of its visceral (dorsal) surface.

[2] Keel area measured from a thin plasticine impression of the keel scanned against 1 mm grid graph paper background.

Impacts of wind farms on swans and geese: a review

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Abstract

This review considers data published on the effects of offshore and onshore windfarms on swans and geese and finds that the information available is patchy. Of 72 swans or geese reported as collision victims at 46 wind farms, most (39 birds) were reported at 23 wind farms in Germany where such data are collated. Post-construction monitoring was undertaken for ≤ 1 year at 67% of 33 sites, making it difficult to test for cumulative effects or annual variation in collision rates. Site use by the birds was measured at only nine of 46 wind farms where collisions by swans and geese were monitored or recorded. Displacement distances of feeding birds at wintering sites ranged from 100–600 m, but preliminary evidence suggested that large-scale displacement also occurs, with fewer swans and geese returning to areas after wind farms were installed. Eight studies of flight behaviour all reported changes in flight-lines for swans or geese initially seen heading towards the turbines, at distances ranging from a few hundred metres to 5 km; 50–100% of individuals/groups avoided entering the area between turbines, but in some cases the sample sizes were small. Key knowledge gaps remain, including whether wind farm installation has a consistently negative effect on the number of birds returning to a wintering area; whether flight avoidance behaviour varies with weather conditions, wind farm size, habituation and the alignment of the turbines; provision of robust avoidance rate measures; and the extent to which serial wind farm development has a cumulative impact on specific swan and goose populations. It is therefore recommended that: 1) post-construction monitoring and dissemination of results be undertaken routinely, 2) the extent to which wind farms cause larger-scale displacement of birds from traditional wintering areas be assessed more rigorously, 3) further detailed studies of flight-lines in the vicinity of wind farms should be undertaken, both during migration and for birds commuting between feeding areas and the roost, to provide a more rigorous assessment of collision and avoidance rates for inclusion in collision risk models, and 4) the combination of collision mortality and habitat loss at all wind farms in the species' range be analysed in determining whether they have a significant effect on the population.

Key words: avoidance, collisions, displacement, offshore wind farms, terrestrial wind farms.

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Wind farms have been installed increasingly across Europe during the late 20th and early 21st centuries, as governments seek to secure renewable energy supplies and reduce greenhouse gas emissions to combat climate change. The European Commission's Renewable Energy Roadmap (EU 2007) set a target of 20% of EU energy to be generated from renewable sources by 2020 (EU 2008). Wind energy accounted for 3.7% of EU electricity generation by early 2008, and the European Commission's goal of increasing that share to 12% by 2020 is regarded as achievable (European Wind Energy Association; EWEA 2008). Annual installations of wind power have increased steadily from 814 MW in 1995 to 93,957 MW installed across Europe in 2011, with the largest installed capacity in Germany, followed by Spain, Italy, France and the UK (EWEA 2012). Growth projections for wind-generated energy vary substantially depending on the analytical methods used and the scope for technological progress (EWEA 2009), but current capacity is expected to treble by 2020 (EWEA 2008). Within the UK, 348 wind farms (332 onshore, 16 offshore) were operational by July 2012, generating > 7,000 MW of wind power, with a further 64 under construction, 270 consented and 335 at the planning application stage (RenewableUK 2012). Planning applications for the large Round 3 offshore wind farms proposed for British coastal waters, and for further Scottish Territorial Water sites, will be forthcoming from late 2012 onwards, with the first Round 3 projects (if consented) operational after 2015.

The rapid development of renewable energy has been a challenge for environmental conservation organisations. Increasing evidence shows climate change having deleterious effects on wildlife (Parmesan & Yohe 2003; Root *et al.* 2003; Thomas *et al.* 2004) yet injudicious location of wind farms may have detrimental effects on some species, including birds (Langston & Pullan 2003; Barrios & Rodriguez 2004; Garthe & Hüppop 2004; Hötker *et al.* 2006; Sterner *et al.* 2007; Bright *et al.* 2008; EEA 2009). Adverse effects include direct collision mortality, habitat loss/degradation, displacement from feeding areas, barrier effects (birds flying around wind farms and thus potentially increasing energy expenditure), and disturbance (see reviews in Langston & Pullan 2003; Bright *et al.* 2006; Drewitt & Langston 2006; Fox *et al.* 2006; Inger *et al.* 2009). The risk of turbine collisions varies across species (perhaps dependent on visual acuity and depth perception at the time; Martin 2011), and wind farm location, with potential for there being population-level effects in some cases (Bright *et al.* 2008), and raptors being particularly at risk of colliding with the turbines (Sterner *et al.* 2007; Carrete *et al.* 2012).

Within the European Union, the planning application process for wind farm development requires wind farm companies to undertake environmental impact assessments (EIAs) under the terms of the EU's Environmental Impact Assessment Directive 85/335/EEC (as amended by Directive 97/11/EC) to determine whether the installation would have a significant effect on wildlife or other environmental features (Drewitt & Langston 2006). A

Strategic Environmental Assessment (SEA) is required for large scale developments or programmes under the SEA Directive 2001/42/EC, which integrates environmental considerations in the development of plans and programmes and builds on project-level EIAs by considering environmental issues earlier in the planning process (Drewitt & Langston 2006). Where proposals pose a threat to the integrity of protected areas, such as those designated by governments as Special Protection Areas (SPAs) for birds under the EU Birds Directive, the legislation requires that a Habitats Regulation Assessment (HRA) be undertaken. The HRA first assesses the impacts of the plan, against the objectives for conserving sites protected under European legislation, by considering whether there is a "Likely Significant Effect" (LSE) of the plan, either alone or in combination with other plans or projects. If there is considered likely to be a significant effect on the interests of the SPA, then the "Competent Authority" (*e.g.* the local council planning department for UK onshore sites; Marine Scotland/Scottish Government and the Marine Management Organisation (MMO) for offshore sites in Scottish territorial waters and in England) is required to undertake an "Appropriate Assessment" (AA) of a proposal, which should ascertain that there will be no adverse effects on the interests of the SPA before development can be consented. The question of how to assess the cumulative impacts on migratory bird populations of several wind farms being installed along the migration routes has been considered (de Lucas *et al.* 2007; Norman *et al.* 2007; Masden *et al.* 2010a) but has yet to be fully resolved. Information on the total number of wind farms along migration routes, and the cumulative effect of these on birds migrating to or from key sites for the population (*i.e.* SPAs and/or Ramsar sites), is still rarely (if ever) incorporated into AAs undertaken for new wind farm sites.

Although many wind farms are now operational or are currently under construction across Europe, and many more are proposed, available information on the effects of these developments is patchy. A review of bird abundance data analysed to assess wind farm impacts at 19 sites found that although wind farms may have significant biological impacts, particularly for Anseriformes (wildfowl) and Charadriiformes (waders), the evidence-base remains poor, largely because many studies are methodologically weak and of short duration (Stewart *et al.* 2007). Evidence is stronger for some avian species than for others; for instance, for wind turbines increasing raptor mortality (*e.g.* Thelander & Smallwood 2007; Dahl *et al.* 2012) and displacing upland birds (Pearce-Higgins *et al.* 2008, 2009), with greater displacement during construction than subsequent operation for a number of upland species (Pearce-Higgins *et al.* 2012). A spatially-explicit individual-based model of a population of Hen Harriers *Circus cyanea* on Orkney, which assessed the combined effects of collision rate, habitat loss and displacement from wind turbines, found that the larger spatial responses to turbines were from those located close to nest sites (Masden 2010). Removal of collision mortality from this model showed that the majority of population-level turbine impacts were associated with direct and indirect habitat loss in this particular circumstance, but few comparative studies of this kind exist to gain insight into the relative impacts of turbines on avian populations. At offshore wind farms, assessments have focussed mainly on their possible impacts on seabird populations (*e.g.* Garthe & Hüppop 2004; Langston & Boggio 2011; Cook *et al.* 2012; Furness & Wade 2012; Langston & Teuten 2012), which is appropriate given that these birds spend much of the year at sea, and tracking studies have recently been undertaken to provide detailed information on the potential for offshore wind farms to affect goose and swan populations at different stages of their migration (Griffin *et al.* 2010, 2011). But post-construction assessment of how wind farm development affects bird numbers and distribution is still generally lacking, despite post-construction monitoring being required at some sites, and such information being extremely useful for informing environmental impact assessments at new developments.

This paper aims to collate and assess published information on the observed effects of wind farms on swan and goose populations. As many of these populations breed at high latitudes, in areas currently not subject to wind farm development, the study focuses on observations made in the wintering range and during spring and autumn migration. The three main hazards that turbines pose to the birds (after Fox *et al.* 2006): 1) displacement/habitat loss (*e.g.* reduced use of prime feeding areas following construction of the turbines), 2) barrier effects (requiring a change in migration routes or local flight-lines to avoid wind farms, potentially increasing energy expenditure and disrupting links between sites), and 3) collision mortality (Desholm *et al.* 2006; Drewitt & Langston 2006) are all considered. Particular consideration is given to measures used to determine avoidance rates, which have been calculated as: 1) the number of birds changing their flight-lines to avoid a wind farm, and as 2) the number of collisions recorded for birds entering a wind farm (usually via carcass searches), as slight variations in avoidance rate measures result in significant variation in the bird mortality predictions made by wind turbine collision risk models (Chamberlain *et al.* 2006). Additionally the review aims to identify gaps in knowledge and to outline priorities for future assessment of the impacts of wind farm development on these species.

Methods

Detailed information on the responses of geese and swans to wind farms was obtained by checking original sources for swan and goose data in published reviews (including Bright *et al.* 2006, 2008; Drewitt & Langston 2006; Fernley *et al.* 2006; Hötker *et al.* 2006; Pendlebury 2006; de Lucas *et al.* 2007), and by internet searches for more recent scientific papers and grey literature reports. Of 16 constructed offshore wind farms in the UK, five are potentially on the flyways of migratory swans and geese (at Barrow, Lynn & Inner Dowsing, Robin Rigg, Scroby Sands and Walney Island); websites for these five sites were visited to check for information on swan and goose passage movements in post-construction monitoring reports. Bird casualties attributable to wind farm collisions in Germany have been collated by the State Office for Environment, Health and Consumer Protection of Brandenburg (LUGV) since 2002, and data recorded up to July 2012 were provided for this review (Staatlichen Vogelschutzwarte 2012 and T. Dürr pers. comm.). Observations reported in the literature of cases where the turbines did or did not affect swans and geese were grouped into the three main categories established as potentially influencing bird populations (*i.e.* displacement/habitat loss, barrier effects and collision mortality). Major studies of the effects of wind farms on waterbirds along the Baltic coast, such as Pettersson (2005) and Petersen *et al.* (2006) covered a range of species, particularly Common Eider *Somateria mollissima*; only observations made of swans and geese included in these studies are cited here.

For each of the wind farm studies, the number and alignment (linear/cluster) of turbines in the wind farm, its construction date, the swan/goose species potentially affected and the duration of post-construction monitoring was recorded. Methods were inspected to determine which studies rigorously assessed collision rates, as opposed to those where incidental collisions were recorded during observations of displacement and barrier effects. The former included ground surveys made for any turbine-related casualties (in the case of onshore wind farms), or where video cameras using infrared sensing, or further analysis of bird occurrences and flight trajectories were used to detect collisions (for the offshore sites). Thus cases where swans and geese were seen flying through a wind farm, but methods (*e.g.* aerial surveys or use of radar) did not permit, or analyses did not include, an assessment of collision frequency (*e.g.* Petersen *et al.* 2006; Plonczkier & Simms 2012), were omitted from the collision rate review (but included in the barrier effect review), as there was no evidence for collision rates being low or zero. For studies assessing barrier effects, the number of birds flying towards the wind farm, the number that changed their flight-path and the distance at which they did so was recorded. For those assessing displacement from feeding areas or roost sites, the distance to which the birds approached the wind farm footprint before and after construction was assessed, and whether the study recorded any changes in the total number of swans or geese staging or wintering in the vicinity (as a broader measure of displacement from the site) was also considered.

Collisions with turbines

The literature review and LUGV data found post-construction monitoring which reported or aimed to report on collision rates for swans and geese at 46 wind farm sites: three in Belgium, one in Bulgaria, 23 in Germany, six in the Netherlands, one in Norway, one in Poland, three in Spain, one in Sweden (Skåne being treated as a single site in the absence of information on individual wind farms in the county), two in the UK and five in the USA (Table 1, Appendix 1). Forty of these included carcass searches, and nine studies (at Sabinapolder, Waterkaaptocht and Energy Research Centre (ECN) in the Netherlands, at Hellrigg and Barrow Offshore in the UK, Saint Nikola in Bulgaria, Fehmarn in Germany and at Buffalo Ridge (Minnesota) and Stateline

Table 1. Summary of monitoring undertaken to determine swan and goose collisions with turbines (carcass searches and observed collisions) at wind farm sites, and the total number of collisions recorded, based on data presented in Appendix 1. Carcass searches were undertaken at all sites except for Barrow Offshore Wind, UK (where birds were observed entering and leaving the wind farm) and four sites in Germany where swans and geese were reported as accidental recoveries.

Country	No. wind farms with post-construction reports on collisions	No. where monitoring duration is known	No. with flight obs. (visual or radar)	No. with > 1 year monitoring	No. where monitoring linked to bird presence	Total no. swan or goose collisions recorded
Belgium	3	3	0	3	0	4
Bulgaria	1	1	1	1	1	0
Germany	23	14	1	1	1	39
Netherlands	6	6	3	2	4	13*
Norway	1	1	0	1	0	4
Poland	1	0	?	?	?	5
Spain	3	?	?	?	?	3
Sweden	1	1	0	0	0	1
UK	2	2	2	0	2	0
USA	5	5	2	3	1	3
TOTAL	**46**	**33**	**9**	**11**	**9**	**72**

*Two additional birds recovered near a wind farm are omitted, on the basis that they're not considered to be collision casualties.

(Washington/Oregon) in the USA) used radar or visual observations to record bird flights within the wind farm sites (Table 1). All were onshore sites except for Barrow Offshore Wind, UK, where observations were made of Pink-footed Geese *Anser brachyrhynchus* flying through the wind farm from an observation point 7–9.7 km from the site. Whilst this may seem too far for accurate collision rate assessment, it is included here as nine geese were seen both entering and leaving the wind farm at rotor height in autumn 2007 (Barrow Offshore Wind 2008). The Staatlichen

Vogelschutzwarte (2012) data reported 39 swan and goose casualties associated with 23 wind farms in Germany collated over a 12-year period (2002–July 2012) for an estimated 26 monitoring years (mostly ≤ 1 year of post-construction surveys per wind farm, including wind farms searched only once; see Appendix 1): 16 Mute Swans *Cygnus olor*, one Whooper Swan *Cygnus cygnus*, four swan sp., three goose sp., three Greylag Geese *Anser anser*, three White-fronted Geese *Anser albifrons*, three Bean Geese *Anser fabalis*, and six Barnacle Geese *Branta leucopsis*. Two more geese (either Bean Geese or White-fronted Geese) were seen colliding with a turbine at the Meyenburg wind farm, Germany, in October 2008 (in both cases the individuals were at the end of a flock of *c.* 100 geese passing through the site), but these were not included in the LNGV database because only feathers were found the following day (Honig pers. comm. in Langgemach & Dürr 2012). Overall, 34 swans and 37 geese (including two domestic geese) were recovered in the surveys across all countries. Two Bewick's Swans found near the Waterkaaptocht & ECN wind farms were not included in these totals because *post mortem* examination found no evidence for them being collision casualties (Fijn *et al.* 2012).

Of the 46 wind farms considered, 32 were known to have been in place for ≥ 5 years. Exceptions were Schlalach, Germany (built in 2010), Hellrigg , UK (2011), Saint Nikola, Bulgaria (2009) and 11 German wind farm sites where the construction date was not reported (T. Dürr pers. comm.). The duration of post-construction surveys for bird collisions was known for 33 sites, with 22 (67%) being undertaken for ≤ 1 year or winter to date, including four sites in Germany where collisions were reported following an accidental discovery rather than through frequent and systematic surveys of the turbines (Table 1). Of the eleven longer-term (≥ 2 year) surveys, swans or geese were recovered at seven sites (3 in Belgium, 2 in the Netherlands, 1 in Norway and 1 in the USA), but only the Buffalo Ridge (USA), St Nikola (Bulgaria), Urk (Netherlands) and Sabinapolder (Netherlands) wind farms provided information on the number of swans or geese in the study area. No swans or geese were found in carcass searches at St Nikola and Buffalo Ridge, but only a proportion of the turbines were checked in each case (Table 1) and variation in mortality for different turbines within the same wind farm was found to be more than double the variation among wind farms for raptors (Ferrer *et al.* 2012). Only nine of the studies which reported or aimed to record swan or goose collisions (by carcass searches and/or flight observations) assessed in any detail whether the wind farm was in an area used regularly by these species, either as a staging or wintering site (Saint Nikola, Fehmarn, Urk, Sabinapolder, Waterkaaptocht, ECN, Hellrigg and Buffalo Ridge) or on the birds' flight-path during migration (Barrow Offshore Wind, UK). Definite collisions (3 Mute Swans at Urk, 6 Greylags and 1 Canada Goose at Sabinapolder, and 6 Barnacle Geese at Fehmarn, Germany) were recorded at just three of these sites though the extent to which Buffalo Ridge coincided with goose habitat or flight-lines was unclear, and it would be difficult to determine collision frequency at Barrow using the methods reported there to date.

Bird monitoring data at the five sites in the USA reviewed by Fernley *et al.* (2006) and by Pendlebury (2006), led to Scottish Natural Heritage (SNH) advising that 99% avoidance rates be used in collision risk models developed to determine the impact of wind farms on goose species (SNH 2010). An accurate assessment of bird-use of these sites therefore is of particular importance, because collisions would need to be linked to the likelihood of birds flying through the array for determining the rate of collision with or avoidance of the turbines. At Buffalo Ridge, fortnightly bird counts and carcass searches were conducted for four years post-construction, during which there were 909 observations of Canada Geese *Branta canadensis*, 278 observations of Snow Geese *Anser caerulescens* and 92 observations of White-fronted Geese (the latter in 1997 only; Appendix 1) seen flying within the 354-turbine wind farm area – measured as being within 800 m of the array (Osborn *et al.* 2000; Johnson *et al.* 2000; Johnson *et al.* 2002a; Fernley *et al.* 2006). That no goose carcasses were found during the study is indicative of high avoidance by the birds using this site but, as noted by Fernley *et al.* (2006) corpse searches were not complete, with only 21–91 of the 354 Buffalo Ridge turbines searched each year (Johnson *et al.* 2000, 2002a). In such cases, it is important to ensure that the sample of searched turbines is not biased, particularly as some turbines within a wind farm pose a greater risk to the birds than others (Ferrer *et al.* 2012). Moreover, a test of search efficiency for goose carcasses placed under turbines in Scotland found that the proportion found during weekly searches ranged from 65% (assuming all missed geese had been removed by foxes) to 96%, with the most likely figure being 83% of geese present being found (Gill & Smith 2001).

There was little post-construction data on goose-use at the other wind farm sites considered in the USA. Pre-construction bird counts made at the Klondike wind farm (Oregon) found that the use of the study area by waterbirds was low; the only species observed was Canada Goose, with 43 flocks (4,845 individuals) seen flying over the study area in the year-long pre-construction survey in 2001 (Johnson *et al.* 2002b). Goose flights in the vicinity were not recorded post-construction when monitoring focussed on carcass searches, during which two Canada Goose carcasses were found (Johnson *et al.* 2003); Pendlebury (2006) mentions a 1-year post-construction bird survey at Klondike, but the results of this are not evident in the Johnson *et al.* (2003) report. At Nine Canyon (Washington), bird-use was likewise monitored only pre-construction; goose-use of the area at the time is unclear, use by waterbirds appeared to be lower than at Buffalo Ridge, Klondike and Stateline (Erickson *et al.* 2002), and post-construction carcass searches were again undertaken without any reference to the number of geese present in the area during the survey years (Erickson *et al.* 2003). At Top of Iowa, large numbers of Canada Geese were reported to occur on managed habitat 1–5 km from the wind farm in autumn, but except for carcass searches there were no detailed bird-use observations recorded at the wind farm

Table 2. Number of geese and swans of different species recorded as wind turbine casualties in different countries.

Species	**Belgium**	**Germany**	**Netherlands**	**Norway**	**Poland**	**Spain**	**Sweden**	**USA**	**TOTAL**
Mute Swan		16	3		5		1		25
Whooper Swan		1		1					2
Swan sp.		4							4
Bean Goose		3							3
Greylag Goose	1	3	8	3		3			18
White-fronted Goose		3							3
Canada Goose			1					3	4
Brent Goose			1						1
Barnacle Goose		6							6
Domestic Goose	3								3
Goose sp.		3							3
TOTAL	**4**	**39**	**13**	**4**	**5**	**3**	**1**	**3**	**72**

(Fernley *et al.* 2006), and goose flight in the collision-risk zone was said to be very rare (Jain 2005). Lastly, at Stateline, 11 groups of Canada Geese (363 birds) were recorded within the wind farm during bird counts, and one Canada Goose carcass was found in 6–7 searches made of the 454-turbine site post-construction in 2003 (Erickson *et al.* 2004). Fernley *et al.* (2006) and Pendlebury (2006) both noted the gaps in the data and Pendlebury (2006) went on to note that the studies could not be used to provide reliable estimates of avoidance rates (which were put at 96% for one site and > 99% for the other sites), but several years later this has not been re-evaluated with the benefit of new studies and 99% avoidance of wind farms by geese remains the recommended value for inclusion in collision risk models.

Despite there being only one wind farm in Germany where carcass searches are known to have continued for > 1 year, the number of swan and goose collisions with turbines in Germany (39 casualties) clearly outnumber those from all other countries considered (33 casualties; Tables 1, 2). The most commonly reported species was the Mute Swan, with 16 recovered in Germany, five in Poland, three in the Netherlands and one in Sweden (Winkelman 1989; Ahlén 2002; Hötker *et al.* 2006; Rodziewicz 2009; Staatlichen Vogelschutzwarte 2012), followed by the Greylag Goose (18 birds from different parts of Europe) and the Barnacle Goose (six recovered in Germany; Staatlichen Vogelschutzwarte 2012; Table 2), but in none of these cases was there any flight observation data, for determining frequency of bird-wind farm overlap, and thus avoidance rates for birds flying across the sites. Carcass searches were made for only 1–2 years at most sites (Table 1, Appendix 1), so these figures represent *c.* 1 season's additional mortality at best, rather than an assessment of mortality rate since each of the wind farms was constructed.

Observed barrier effects

The review by Hötker *et al.* (2006) found that seven of 127 wind farm studies (not all relating to swans or geese) assessed and found evidence for turbines having a barrier effect on goose movements during migration or whilst commuting more locally (*e.g.* between feeding and roosting sites), for: Bean Geese (1 study), White-fronted Geese (3), Greylag Geese (2) and Barnacle Geese (1). Single observations and extensive investigations were combined, and a barrier effect was assumed in quantitative studies if at least 5% of the individuals or flocks showed a measurable reaction by changing their flight direction to go around or over a wind farm (Hötker *et al.* 2006). These observations were made during daylight as there was insufficient information at the time (*e.g.* through radar studies) on the birds' flight-lines at night, when migration often occurs.

Eight published studies of swan or goose flight-lines in relation to wind farm location provided information on the birds' avoidance behaviour (Table 3). Of these, radar studies or a combination of radar and visual observations were undertaken for Bewick's Swans at Waterkaaptocht and at ECN, Netherlands (Fijn *et al.* 2007, 2012), Brent and Barnacle Geese at Olsäng, Sweden (Pettersson 2005), Barnacle Geese at Utgrunden, Sweden (Pettersson 2005), Pink-footed Geese at Lynn & Inner Dowsing, UK (Plonczkier & Simms 2012), and Greylag Geese at Horns Rev, Denmark (Petersen *et al.* 2006), with visual observations made of Pink-footed Geese at Barrow Offshore, UK (BOWind 2008) and at Hellrigg, UK (Ecology Consulting 2012) (Table 3). All reported some changes in flight-lines for swans or geese initially seen heading towards the turbines, with 50–100% of individuals or groups avoiding entering the wind farm site (Table 3). Avoidance distance varied from a few hundred metres (at Waterkaaptocht/ECN and at Hellrigg wintering sites, where the birds were commuting daily between feeding areas and the roost) up to 5 km for birds observed during migration (Table 3).

Desholm & Kahlert (2005) additionally found that the proportion of Common Eider and goose flocks entering the Nysted wind farm area decreased significantly from 40.4% (*n* = 1,406 flocks) during pre-construction (2000–2002) to 8.9% (*n* = 779) during the first year of operation (2003), but whether there was a difference in the proportion of geese compared with eiders entering the wind farm was not reported. Jain (2005) observed Canada Geese flying in between, around and above wind turbines at Top of Iowa, USA, but states that avian flight in the collision-risk zone was very rare across seasons. A study of Red-breasted Geese *Branta ruficollis*, White-fronted Geese and Greylag Geese at the Saint Nikola wind farm in Bulgaria reported on flight-lines and altitude of flight, and noted from radar data that 64% of the geese (*n* = 272,210 goose flights detected in winter 2010/11) were at rotor height (*c.* 50–150 m for this particular wind farm), with 1% of birds flying at below rotor height (0–49 m) and 36% above the turbines (Zehtindjiev & Whitfield 2011), but it was unclear whether the birds adjusted their flight-lines to pass around or over the wind farm, and thus exhibit avoidance behaviour.

Flight-lines might also shift at longer distances following wind farm construction; for instance, Petterssen (2005) noted that, once the turbines had been erected at Olsäng and Utgrunden, geese generally flew closer to the mainland (inside the line of the turbines), and Plonczkier & Simms (2012) likewise found that migrating Pink-footed Geese were more likely to fly inland of the Lynn & Inner Dowsing turbines in the third winter of their post-construction surveys. Earlier studies for other migratory waterbirds have demonstrated that even quite dramatic shifts in migration routes may have only small effects on total migration distance (Desholm 2003; Masden *et al.* 2009), but where birds show diurnal movements, such as between breeding colonies and food provisioning areas (Masden *et al.* 2010b) or night roosts and daytime feeding areas, the energetic consequences of avoidance could become significant.

The radar studies were unable to provide data on collision rates for birds flying within the wind farms because of the difficulty of following individuals within flocks (and thus identifying those that fail to leave the wind farm site) by radar. Visual observations of flight-lines made in conjunction with radar at Waterkaaptocht/ECN, Netherlands, and without radar at Barrow Offshore, UK and at Hellrigg, UK did not record any collisions,

Table 3. Records of swans and geese adjusting their flight-lines to avoid wind farms. Observation method: RAD = Radar; FL = flight observations. References: 1 = Fijn *et al.* 2007; 2 = Fijn *et al.* 2012; 3 = BOWind 2008; 4 = Ecology Consulting 2012; 5 = Plonczkier & Simms 2012; 6 = Christensen et al. 2004; 7 = Petersen et al. 2006; 8 = Pettersson 2005. Turbine alignment: * = linear alignment; ** = turbines in 2 lines; *** = cluster. Observation method: RAD = Radar; FL = flight observations.

Species	**No. flight-lines directly towards wind farm**	**No. flights within wind farm**	**% avoidance**	**Wind farm name/ location**	**Built**	**No. turbines (hub height m)**	**Obs. method**	**Avoidance dimension (V = vertical; H = horizontal)**	**Avoidance distance**	**Duration of post-construction monitoring**	**Ref.**
Bewick's Swan	364 birds	167 birds	54	Waterkaaptocht, Nths	2003	8* (78 m)	RAD & FL	H	Few hundred metres	3 days (winter 2006/07)	1, 2
Bewick's Swan	684 birds	308 birds	55	ECN test-park, Nths	2003–2006	9 ** (90 m)	RAD & FL	H	Few hundred metres	5 days (winter 2006/07)	1, 2
Pink-footed Goose	503 birds	9	98	Barrow Offshore, UK	2006	30*** (75 m)	FL[1]	V	2–3 km	21 days (2007)	3
Pink-footed Goose	1,022 birds within 200 m of turbines	4 groups	Unclear	Hellrigg, UK	2011	4*** (80 m)	FL	H	>200 m	38 h (22.12.11–09.03.12)	4
Whooper Swan	0 groups	0 groups	–	Hellrigg, UK	2011	4*** (80 m)	FL	H	>200 m		4

Pink-footed Goose	292 flocks	16 flocks[a]	94	Lynn & Inner Dowsing, UK	2006	54*** (70–100 m)	RAD	V[b] & H	Not reported	134 days (2008–2010)	6
Greylag Goose	8 flocks	3 flocks	63	Horns Rev, Denmark	2003	80*** (70 m)	RAD & FL	H & V	Not reported	69 days (244 h visual; 398 h radar; 2003–2005)	6, 7
Goose sp.	11 flocks	1 flock	91	Horns Rev, Denmark	2003	80*** (70 m)	RAD & FL	Not reported	Not reported		6, 7
Barnacle Goose	2 flocks	1 flock	50	Olsäng, Sweden	2001	5* (65 m)	RAD	Not reported	*c.* 5 km	52 days (2000–2002)	6. 7
Brent Goose	3 flocks (292 birds)	1 flock (17 birds)	94	Olsäng, Sweden	2001	5* (65 m)	FL	Not reported	*c.* 500 m		8
Barnacle Goose	2 flocks	0 flocks	100	Utgrunden, Sweden	2000	7* (65 m)	RAD	Not reported	*c.* 2 km	52 days (2000–2002)	8

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[a] Numbers based on 167 of the 292 flocks (tracked by radar) heading towards the array actually crossing the array, and 84 (94.46%) of 93 flocks seen (from visual observations) crossing the footprint seen to gain height and fly above the turbines as they did so.

[b] Initial flight height not reported, so unclear whether geese gained height to clear (avoid) the turbines or continued on their same flight-lines when passing over the footprint.

but it seemed that the birds were flying in good weather conditions: either conditions were said to be good (Fijn *et al.* 2012), or good visibility was required for the observations to be made (Barrow Offshore Wind 2008), or conditions during vantage point (flight-line) observations were not recorded (Ecology Consulting 2012).

None of the studies reported adverse weather conditions during observations. The effects of strong winds, heavy precipitation or fog on the birds' ability to avoid the wind farm or to negotiate the turbines if flying within the wind farm therefore remains unclear, albeit that the low number of casualties reported from carcass searches to date indicates that adverse weather may not increase the risk to swans and geese substantially at terrestrial sites. The six Barnacle Geese recorded as wind turbine casualties in Germany were all found under a single turbine the day after fog and a storm, but it is not known whether the weather contributed to these collisions (T. Dürr, pers. comm.). Whether the size of the wind farm affects avoidance behaviour, with swans and geese being more likely to fly around smaller wind farms but to pass between the turbines for wind farms covering a larger area should also be considered, as this is relevant to the construction of larger wind farm sites over the next decade. The largest wind farm included in this review of observed barrier effects – the Horns Rev offshore wind farm in Denmark (80 turbines) – had a relatively high proportion (21%) of geese which were flying towards the wind farm continue through it (three of eight Greylag Goose flocks and one of 11 flocks of unidentified goose species; Table 3), but the sample sizes are relatively small and the number of individual birds involved were not recorded. Accumulated knowledge of how a range of individuals from different species react to turbines are however helpful for populating models of avoidance behaviour, which can be insightful for predicting how geese and swans may respond to different sizes of wind farms and specific turbine configurations (Masden *et al.* 2012).

Displacement from feeding areas and roost sites

Displacement of birds from feeding areas and roost sites is an important consideration because migratory swans and geese tend to congregate at favoured (but frequently undesignated) feeding sites in winter, many of which are associated with roost sites that have been classified as Special Protection Areas (SPAs) under Article 4 of the Birds Directive (EC Directive on the Conservation of Wild Birds, 79/409/EEC) because of their importance for the species (Bright *et al.* 2008). Habitat quality in the non-breeding season has been shown to influence the timing of bird migration (Marra *et al.* 1998; Gill *et al.* 2001; Stirnemann *et al.* 2012), body condition during spring migration (Bearhop *et al.* 2004) and breeding success (Ebbinge & Spaans 1995; Madsen 1995; Norris *et al.* 2004; Inger *et al.* 2010). Loss of feeding or roosting habitats through disturbance or displacement by the turbines therefore could affect the birds' use of protected areas or result in them moving to suboptimal sites, with consequences for future survival and productivity (Gill *et al.* 2001; Norris & Taylor 2006; Ratikainen *et al.* 2008).

Birds' avoidance responses to wind farms vary within and between species, but swans and geese are considered sensitive to these developments because they frequent open landscapes (Hötker *et al.* 2006). The review by Hötker *et al.* (2006) indicated that the minimal distances to wind farms reported was 150 m (s.d. = 139 m, *n* = 8 studies) for swans and 373 m (s.d. = 226 m, *n* = 13) for geese, with the minimal distances recorded for geese during the non-breeding season ranging from 50–850 m. Papers considered in the current review likewise recorded displacement distances of 200–560 m for swans and 30–600 m for geese at terrestrial wind farms, and 2 km for one offshore site (Table 4), the latter estimated from maps illustrating Mute Swan displacement (Figure 51 in Petersen *et al.* 2006). For Pink-footed Geese, displacement was greater at wind farms where the turbines were arranged in clusters (200 m) than at linear or single turbine sites (100 m) (Larsen & Madsen 2000). Long-term post-construction studies, and thus information on whether birds adapt to the change in landscape, are rare. An exception is that of Madsen & Boertmann (2008), who found not only that Pink-footed Geese grazed closer to wind turbines *c.* 20 years after construction than 10 years previously (Table 4), but that the extent to which they habituate to the turbines varied across sites. Observations made at two sites – the Klim Fjordholme and Velling onshore wind farms in Denmark – indicated that the geese remained at a greater distance from the larger turbines (Madsen & Boertmann 2008), but more studies of potential habituation to different types of turbine are required to support these findings.

In addition to assessing the extent to which birds approach turbines at a local level, whether the construction of wind farms influences the extent to which swans and geese winter in an area should be considered. In her pioneering study of bird use of fields around the Urk wind farm, which consisted of 25 turbines (hub height = 30 m) positioned along a dyke bordering Lake IJsselmeer on the Noordoostpolder, the Netherlands, Winkelman (1989) found that, at the local level, Bewick's, Whooper and Mute Swans were displaced to feeding areas 200–400 m from the wind farm site post-construction, with pooled data for Bean Geese, White-fronted Geese and Barnacle Geese similarly suggesting 200–400 m displacement, albeit that this was a subjective assessment as the data did not permit a meaningful comparison of pre- and post-construction distances for the geese. Raw data indicated that more geese were counted in the study area pre- than post-construction; for the three swan species (combined), mean numbers were rather similar in comparison with the range of counts recorded (Table 4), but a significant negative impact was found for Whooper Swans in 1988/89, two years post-construction (Winkelman 1989). Goose counts were presented in a different manner, but these too indicated that, whilst the number of Bean Geese in the area increased substantially post-construction (mean values = 5,615 and 11,842, *n* = 10 years and 2 years pre- and post-construction, respectively; 111% increase), there was also a drop in

Table 4. Displacement distances recorded for swans and geese, measured as an absence or reduction in the number or density of birds in habitat near the wind farm. Observation methods: AS = aerial survey; DD = dropping densities; BC = bird counts. References: 1 = Petersen et al. 2006; 2 = Larsen & Madsen 2000; 3 = Madsen & Boertmann 2008; 4 = Kruckenberg & Jaene 1999; 5 = Kowallik 2002; 6 = T. Dürr pers. comm.; 7 = Bioconsult & Arsu 2010; 8 = Handke *et al.* 2004; 9 = Möckel & Wiesner 2007; 10 = Fijn *et al.* 2012; 11 = Fijn *et al.* 2007; 12 = Winkelman 1989; 13 = Ecological Consulting 2012. * = linear alignment; ** = turbines in 2 lines; *** = cluster.

Species	**Wind farm**	**No. turbines (hub height m)**	**No. birds in vicinity (pre-construction)**	**No. birds in vicinity (post-construction)**	**Obs. method**	**Displacement distance (m)**	**Refs**
Mute Swan	Nysted, Denmark	72*** (69 m)	8,662–10,604	2,882–3,478	AS	*c.* 2,000^{a}	1
Pink-foooted Geese	Klim Fjordholme, Denmark	1–35^{b} (25–50 m)	Not reported	Not reported	DD^{c}	100–200^{d}	2, 3
Pink-footed Goose	Thorup, Denmark	5* (31 m)	Not reported	Not reported	DD^{c}	50–125^{d}	3
Pink-footed Goose	Velling Maersk, Denmark	66*** (21–31 m)	Not reported	Not reported	DD^{c}	30–100^{d}	3
White-fronted Goose	Holtgaste, Germany	10* (50 m)	Not reported	Not reported	BC	400–600	4
Barnacle Goose	In Germany	??	??	??	DD	350–600	5, 6
Greylag Goose	Fehmarn, Germany	Various	??	??	BC	> 200	6, 7
Goose sp.	Krummhörn, Germany	??	??	??	??	300–400	6, 8
Greylag Goose	In Brandenburg, Germany	Various	??	??	??	250	6, 9
Bean Goose & White-front Goose	In Brandenburg, Germany	Various	??	??	??	500	6, 9

Bewick's Swan	ECN test-park, Nths	9** (90 m)	1,099	530	BC	560	10, 11
Bean Geese	ECN test-park, Nths	9** (90 m)	5,840	1,885	BC	464	11
Bean Goose	Urk, Nths	25* (30 m)	5,615	11,842	BC	200–400[e]	12
White-fronted Goose	Urk, Nths	25* (30 m)	8,570	7,697	BC	200–400[e]	12
Barnacle Goose	Urk, Nths	25* (30 m)	887	197	BC	200–400[e]	12
Mute Swan	Urk, Nths	25* (30 m)	129.2 (± 54.5; 81–246)	123.2 (± 85.7; 16–292)	BC	200–400[f]	12
Whooper Swan	Urk, Nths	25* (30 m)	102.3 (± 123.8; 0–519)	93.3 (± 104.8; 0–395)	BC	200–400[f]	12
Bewick's Swan	Urk, Nths	25* (30 m)	677.2 (± 629.7; 0–2,312)	614.9 (± 716.9; 0–2,402)	BC	200–400[f]	12
Pink-footed Goose	Hellrigg, UK	4*** (80 m)	3,950 (270–7,100)	2,175 (max = 9,320)	BC & DD	>600[g]	13

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[a] Displacement of Mute Swans on coastal waters near the offshore wind farm; all other displacement distances are for onshore sites.

[b] Total of 61 mostly medium-sized wind turbines within the study area in recent years; all wind farms ≤ 5 tubines (including single turbines) except for one cluster of 35 turbines.

[c] Avoidance distance = point at which dropping density reached 50% of the maximum density along a transect perpendicular to the object.

[d] Median displacement distances; upper value recorded in 1998–2000, upper value in 2008.

[e] Pooled data for goose species; estimated as it was not possible to make a meaningful comparison of pre- and post-construction distances (Winkelman 1989).

[f] Pooled data for swan species.

[g] Geese mostly 600–1,500 m from turbines, but one flock of 70 birds seen within the wind farm site during surveys made in the post-construction winter (2011/12).

numbers of White-fronted Geese (8,570 *vs.* 7,697; 10% decrease) and Barnacle Geese (887 *vs.* 197; 78% decrease) in the vicinity (from Table 18 in Winkelman 1989). There was an increase in the number of Bean Geese, stable numbers of White-fronted Geese and a decline in Barnacle Geese across the Noordoostpolder over the same years (mean annual totals =11,387 *vs.* 35,791 for Bean Geese; 34,162 *vs.* 31,580 for White-fronted Geese; 6,211 *vs.* 2,807 for Barnacle Geese; from Winkelman 1989), but the proportion of Noordoostpolder geese recorded in fields up to *c.* 3.5 km from wind farm was lower after than before construction for all three species (49% *vs.* 33% for Bean Geese, 25% *vs.* 24% for White-fronted Geese and 14% *vs.* 7% for Barnacle Geese, pre- and post-construction in each case).

Bird counts made at the Saint Nikola wind farm in Bulgaria found that numbers of geese were much lower in winter 2010/11 (two years post-construction) than in 2008/09 (pre-construction) and 2009/10 (Zehtindjiev & Whitfield 2011), but winter 2010/11 was relatively severe so longer-term monitoring is required to determine whether there is any large-scale displacement of geese from the area.

In the only study which specifically analysed the proportion of birds wintering in the vicinity of a wind farm site before and after construction, Fijn *et al.* (2012) likewise found a significant drop, post-construction, in the proportion of wintering Bewick's Swans using the area where wind turbines had been installed in Polder Wieringermeer. Like Madsen & Boertman (2008), they found evidence for habituation, with swans feeding closer to the turbines later in the study, but with fewer birds present in the study area (Fijn *et al.* 2012). Thus, although swans may be displaced by up to 600 m from field feeding areas, with larger-scale displacement (*c.* 2 km) in one case where swans were feeding in coastal waters (Table 4), whether the proportion of population using areas where wind farm development has occurred diminishes post-construction, and the extent to which this is attributable to displacement by the turbines still needs to be addressed. This is also important for determining whether any mitigation plans (*e.g.* habitat management) in conjunction with wind farm development are likely to be successful. The potential for cumulative displacement impacts attributable to the arrangement of wind farms in the landscape, through possible non-linear synergistic effects with other wind farms or other landscape elements, also needs to be explored (Larsen & Madsen 2000).

Gaps in knowledge

In addition to needing better linkage of avoidance rates to the birds' use of the site, and a robust assessment of whether wind farm installation results in fewer birds returning to a wintering area, outlined above, more specific information on how the positioning and structure of wind farms affect the birds would be useful to ensure that any impacts are kept to a minimum. For instance, turbines come in variable sizes, and may be installed singly, linearly or as a cluster, but there are few detailed studies of the effects of turbine height and alignment on swans and geese. Larsen & Clausen (2002) initially suggested, from pre-construction observations, that Whooper Swans might be more at risk from a park of medium-sized turbines than large turbines as typical flight heights (mostly at 5–35 m when flying between feeding areas and the roost) would put them in the collision risk zone more often. On the other hand, birds (including swans and geese) may be more likely to be displaced over longer distances by larger turbines: Hötker *et al.* (2006) estimated from six studies included in their review that there was a 6.22 m increase in minimal distance between birds and a wind farm for every 1 m increase in tower height, though this change was not statistically significant. The only studies which aimed to test the effects of turbine height on goose distribution similarly found that geese are less tolerant of larger turbines, and may also be less likely to habituate to them (Larsen & Madsen 2000; Madsen & Boertmann 2008), but it should be noted that alignment is also relevant (with geese displaced further by a cluster of turbines than single turbines or those in a line; Larsen & Madsen 2000) and the interactive effects of height and alignment has yet to be assessed. More recently, Krijgsveld *et al.* (2009) used radar and carcass searches to study the collision risk for birds with large modern turbines at three wind farms in the Netherlands (Waterkaaptocht, Groettocht and Jaap Rodenburg), and found that the risk was *c.* threefold lower than for the smaller turbines for the species (not including swan and geese) passing through the wind farm sites. They suggested that one possible reason for this was that the increased height of the turbine allowed more birds to fly under the rotors, and also proposed that the wider spacing allowed more birds to pass between the turbines. The relative costs and benefits of potentially lower collision rates but higher displacement distances for the larger wind farms therefore should be assessed more rigorously for onshore sites.

The cumulative impact on migratory bird populations of several wind farms being installed along the migration routes, or within a wintering area, is known to be an issue but has yet to be resolved. Written guidance has been produced to assist in the process of ornithological cumulative impact assessment (CIA) for offshore wind farms (since Norman *et al.* 2007), and Fox *et al.* (2006) emphasised the importance of undertaking full Strategic Environmental Assessments (SEAs) for offshore wind farm sites, not least to comply with European legislation. Masden *et al.* (2010a) went on to argue for the benefits of elevating CIA to a strategic level, as a component of spatially explicit planning. Yet although there is an increasing tendency for developers of the large offshore wind farms to take into account other wind farms nationally, collision risk assessments for all wind farms along international migration routes, and the cumulative effect of these on birds migrating to/from key sites for the population (*i.e.* Special Protection Areas and/or Ramsar sites), are still rarely (if ever) incorporated into Appropriate Assessments undertaken for new wind farm sites. For most European and North American goose and swan populations, there is sufficient information about the precise migration routes, other hazards encountered along these corridors and the demographics of these populations to be able to make preliminary assessments of cumulative effects. Ultimately, this knowledge should be used to support the construction of robust models of their population dynamics to establish the relative costs of collision, barrier effects and habitat loss from each new wind farm proposal, based on existing sources of mortality and given current population trajectories.

Moreover, there has been a general lack of post-construction monitoring work undertaken, both for the early offshore sites and for the numerous smaller terrestrial wind farms. For those studies that have been undertaken, the collision rate and displacement data are not collated centrally, nor are they readily available in accessible reports for assessing existing impacts. A Scottish Wind Farm Bird Steering Group (SWBSG) has recently been formed, with the aim of bringing together the onshore wind farm industry, government agencies and conservation organisations to collate and analyse post-construction monitoring data collected in Scotland, but this is not (yet) being extended across the UK. Even in Germany, where collision data has been collated since 2002, in most cases monitoring is undertaken and reported to LUGV for only one year post-construction. Developers are reluctant to undertake post-construction monitoring (particularly for > 1 year) because of the cost involved, and up to now it has not been an automatic requirement of the planning process, although longer-term monitoring is recommended by SNH (SNH 2009). Data therefore are lacking for assessing cumulative impacts of existing wind farms, making it currently impossible to determine the extent to which each new wind farm would serially reduce the attractiveness of a site for swans and geese.

One drawback of undertaking post-construction monitoring for only one year is that this reduces the scope for determining the effects of weather conditions and poor visibility on the birds' flight-lines and large-scale avoidance of wind farm sites. Because wind speeds and birds' airspeeds are often of a similar magnitude, wind strength and direction has a major influence on the orientation and energy expenditure of migrating birds, but the extent to which birds are susceptible to wind drift appears to vary (*e.g.* Thorup *et al.* 2003; Green *et al.* 2004). Satellite-tracking and radar studies of swans and geese on migration indicate that migration routes may shift between years (Pettersson 2005; Griffin *et al.* 2011; Plonczkier & Simms 2012), and the extent to which this varies with weather conditions (especially wind drift) has yet to be determined. Variation in wind conditions was one explanation given for a lack of correlation between raptor abundance and collision rates at wind farms in Spain (Ferrer *et al.* 2012). Radar studies have demonstrated that birds continue to fly over or around wind farms after dark (Desholm & Kahlert 2005; Fijn *et al.* 2012), but one study also noted that the proportion entering the wind farm is higher at night (Desholm & Kahlert 2005). Whether familiarity with the wind farms will result in an increasing tendency for birds to pass through rather than over or around a site, the extent to which this increases their susceptibility to collisions with the turbines, and the effects of poor visibility (including night-time flights and fog) on their ability to avoid the rotors on flying within a wind farm has yet to be determined. Poor weather conditions, such as fog or low cloud, can affect visibility and studies of bird collisions with other structures (*e.g.* power lines) found that birds are much more susceptible to flying accidents under such circumstances (Brown 1992; Drewitt & Langston 2008; Jenkins *et al.* 2010; Prinsen *et al.* 2011; Barrientos *et al.* 2012). Additionally, strong winds (especially tail- or cross-winds) blunt the fine motor control of flying birds and consequently raise their susceptibility to collision (Bevanger 1994 and Crowder & Rhodes 2001 in Jenkins *et al.* 2010). Although difficult to assess, the frequency with which swans and geese encounter adverse weather during migration, and the extent to which this puts them at risk of large-scale losses at wind farms (through reduced ability to avoid the turbines), therefore should be considered and included in collision risk models, perhaps as a stochastic event in the modelling process. Likewise, geese and swans migrate at high speeds and at night (Griffin *et al.* 2010, 2011), so the ability of geese to avoid turbines under these circumstances should be assessed at existing wind farm sites, for instance by developing techniques for detecting collisions and measuring micro-avoidance rates within wind farms (Desholm *et al.* 2006; Collier *et al.* 2011).

Overview

Development of renewable energy has substantial benefits, notably reducing carbon dioxide emissions and the provision of a secure local energy supply, with wind power becoming a major contributor to this field over the past two decades. It has long been recognised that collisions with and displacement by the turbines could have a significant negative effect on birds, but the rate of wind farm development is still not matched by publication of rigorous peer-reviewed reports or papers from studies observing, carefully analysing and accurately reporting these effects (Stewart *et al.* 2007; Natural England 2010; this study). Before-after-control-impact (BACI) studies of the effects of wind farm development are not undertaken and reported routinely at onshore sites in the UK, despite these being recommended by statutory nature conservation bodies (*e.g.* Natural England 2010), yet such information would be invaluable for informing future wind farm development, including the preparation of EIAs and advising on height, alignment, and the effectiveness of mitigation programmes such as (in the case of swans and geese) habitat management to provide the birds with alternative feeding areas for the life-time of the turbines. Where post-construction surveys have been undertaken to date, they have usually been of short duration (1 year, although SNH guidance is for longer periods; SNH 2009) and treated as confidential (therefore not readily available) by the developer who commissioned the study. Moreover, except for the collation of collision data by LUGV in Germany and the new initiative (establishment of the SWBSG) in Scotland, there is no central national repository to assess whether post-construction surveys are being undertaken and reported appropriately, and to provide an information source to determine whether any significant impacts on birds (at the population or local level) are being addressed. Yet centralised post-construction monitoring data is crucial for determining actual impacts (as well as for validation and improvement of modelled predictions) and is required for cumulative impact assessments both for wind farm development along migration routes, and where turbines are installed in proximity to internationally important sites. Post-construction monitoring is undertaken more routinely for offshore wind farms, but again tends to be of short duration and not readily accessible, and within the UK the surveys have focussed more on the potential displacement of seabirds from feeding areas (which of course is an important issue) than on collision rates and barrier effects for birds on migration.

A species-specific approach is required in assessing the potential impact of wind farms on birds because, as noted by Jenkins *et al.* (2010) susceptibility to collision varies with morphology, as ocular structure and acuity affect a bird's ability to see structures and thus take evasive action (Bevanger 1994; Drewitt & Langston 2008), while size, mass and wing structure influence the time required to make the necessary adjustments (Brown 1992; Bevanger 1994; Rubolini *et al.* 2005). Reaction time is also affected by flight speed, which tends to be higher in heavy-bodied species, and a higher wing loading also reduces manoeuvrability (Bevanger 1994; Janss 2000). The highly social nature of swans and geese (where parent-offspring bonds may persist for many years, *e.g.* Warren *et al.* 1993) are also significant, since recent studies show that social interactions have a significant, non-linear and potentially large effects on collision risk (Croft *et al.* 2012). Hence, theoretically, relatively large, heavy and socially interactive birds (*e.g.* swans and geese) are more susceptible to collision than small, light and relatively large-winged birds with acute vision (Jenkins *et al.* 2010), and birds such as raptors which use predominantly downward (lateral) vision are particularly susceptible to collisions with turbines (Thelander & Smallwood 2007; Martin 2011; Dahl *et al.* 2012). Given our relatively weak ability to predict post-construction actual collision mortality (*e.g.* Ferrer *et al.* 2012) existing empirical and mechanistic methods of predicting collision risk at turbines should perhaps be augmented (Tucker 1996; Sugimoto & Matsuda 2011). One approach would be to gather more information about the underlying visual and behavioural processes of collision risk in particular species, in order to populate individual-based or agent-based simulation models that may provide more powerful predictive tools to supplement current approaches (*e.g.* Croft *et al.* 2012; Eichhorn *et al.* 2012).

This review found that 72 swans or geese were reported as collision victims at 46 wind farms, but most (39 birds) were reported at 23 German wind farms where such data are collated, and even there only usually for *c.* 1 year post-construction. Moreover, there was a lack of linkage of collision rates with the birds' use of a site; whether or not swans or geese occurred in the immediate area of the wind farm, or flew across/within the site, was considered at only nine of 46 wind farms where collisions by swans and geese were monitored or recorded. Likewise, avoidance of turbines should be related to whether or not flights were initially in line with the wind farm, rather than in relation to all bird movements in the area, as including the latter artificially boosts sample sizes used for calculating avoidance rates. Sample sizes for birds or flocks actually seen to change their flight-lines to avoid wind farms were available for only eight studies (Table 3); these gave a wide range for the proportion of birds that ultimately passed through the wind farm (2– 46%, for sample sizes of <5 birds or flocks) rather than going over or around the site, with interactive effects of wind farm size and visibility (day *versus* night-time flights and weather conditions) on large-scale avoidance yet to be assessed for swans and geese. Yet such information is important for collision risk models (Band *et al.* 2007; Band 2012), as minor changes in avoidance rates can have a major influence on the outcome of (and confidence in) the models (Chamberlain *et al.* 2006). Swans and geese have good eyesight and the review indicates that high levels of avoidance do occur. But avoidance rates of 98% for Whooper Swans and 99% for geese currently advocated by Scottish Natural Heritage for use for collision risk models (SNH 2010) should be revisited and based on better observational data than those available from the reviews (Fernley *et al.* 2006; Pendlebury 2006) which set the avoidance levels in the mid 2000s. Plans are underway to measure levels of micro-avoidance and collision rates by installing systems (using a variety of cameras and radar) within wind farms (Collier *et al.* 2011, 2012). Use of such technology would provide a major advance for contributing to model development and validation, as well as for determining whether wind farms are likely to have significant effects on survival rates for swan and goose populations.

This review has highlighted the relatively little attention paid in other studies to the potential for large-scale displacement of swans and geese from non-breeding feeding sites. Thus, although birds returning to an area may approach on average to 100–600 m from the turbines, closer (40–100 m) where habituation occurs (Madsen & Boertmann 2008), and were reported between turbines in two studies (Madsen & Boertmann 2008; Ecology Consulting 2012), count data provided in other studies suggest that fewer birds returned to study areas post-construction. In the one study that analysed this (Fijn *et al.* 2012), reductions in numbers were significant. Swans and geese favour open landscapes, and topographical features such as trees and hedge lines are known to have an adverse effect on site use (*e.g.* Madsen 1985). The combined effects of landscape (power lines, wind breaks, roads and settlements) caused an effective loss of 68% of the field feeding areas (40 km^2) available for Pink-footed Geese at Klim Fjordholme (Denmark), with the presence of 61 turbines (one farm of 35 turbines; the remainder of ≤5 turbines including single turbines) resulting in the loss of 13% of the remaining area (Larsen & Madsen 2000). The potential for wind farm development to cause large-scale displacement of geese and swans from internationally important wintering sites through habitat fragmentation and displacement from preferred feeding areas therefore should be analysed more rigorously and addressed more carefully in the planning process. This should include an assessment of small wind turbines (SWT), which like larger turbines, vary in size and scale. The only study to date aiming to quantify the effects of SWTs on bats and birds grouped three types of SWT (10 m high building-mounted, 6.5 m high free-standing, and 18 m high free-standing; Minderman *et al.* 2012) and did not consider swans and geese.

Several recommendations emerge from the information gathered in this review. Firstly, although several authors have emphasised in recent years the need for systematic post-construction monitoring, and dissemination of the results of these studies (*e.g.* Fox *et al.* 2006; Drewitt & Langston 2006; Natural England 2010) this information still seems to be lacking. Such monitoring programmes should be undertaken routinely, collated centrally, and adapted to quantify collision, barrier and displacement effects. Secondly, better information is required about the extent of large-scale and local displacement of geese and swans from feeding/drinking/roosting sites, and the effects of turbine number, size and alignment on such effective habitat loss. Thirdly, further detailed studies of the birds' flight-lines in the vicinity of wind farms are required, both during migration and for birds commuting between feeding areas and the roost, to provide a more rigorous assessment of collision and avoidance rates, and to quantify additional energy costs of any avoidance behaviour during regular local flights. Finally, the combination of collision mortality and habitat loss attributable to wind farms across a species' range should be analysed to determine whether the current sites and new developments will have a significant effect on the population. The development of new technology to determine collision rates for birds entering large wind farms should help to provide much more accurate assessments of the consequences of wind farm development for swans, geese and other avian species.

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Photograph: Bewick's Swans at the ECN wind farm, the Netherlands, by Wim Tijsen.

Appendix 1. Records of swans and geese found to have collided with wind turbines. References: 1 = Everaert 2008; 2 = Zehtindjiev & Whitfield 2010; 3 = Zehtindjiev & Whitfield 2011; 4 = Staatlichen Vogelschutzwarte 2012; 5 = Bioconsult & Arsu 2010; 6 = Musters *et al.* 1996; 7 = Winkelman 1989; 8 = Fijn *et al.* 2007, 9 = Fijn *et al.* 2012; 10 = Krijgsveld & Beuker 2009; 11 = Veerbeek *et al.* 2012; 12 = Bevanger *et al.* 2009; 13 = Rodziewicz 2009; 14 = Hötker *et al.* 2006; 15 = Ahlén 2002; 16 = BOWind 2008; 17 = Ecology Consulting 2012; 18 = Osborn *et al.* 2000; 19 = Johnson *et al.* 2000; 20 = Johnson *et al.* 2002a; 21 = Johnson *et al.* 2002b; 22 = Johnson *et al.* 2003; 23 = Fernley *et al.* 2006; 24 = Pendlebury 2006; 25 = Erickson *et al.* 2003; 26 = Erickson *et al.* 2004; 27 = Jain 2005. Countries: B = Belgium; NL = Netherlands; N = Norway; POL = Poland; S = Sweden; UK = United Kingdom; USA = United States of America. Observation methods: ACC = accidental finding; CS = carcass search; RAD = radar; FL = flight observations through/across wind farm; BC = bird counts. * = linear alignment; ** = turbines in 2 lines; *** = cluster.

Species	No. collisions	No. flights within wind farm	Wind farm name/location	Built	No. turbines (hub height)	Years/winters of post-construction monitoring	Obs. method	Duration of post-construction monitoring	CS linked to bird presence	Refs
Domestic Goose	2	Not recorded	Boudewijnkanaal, Belgium	2000–2001	14 * (60 m)	5	CS	*c.* 26 days/year (fortnightly; 2002–2006)	NO	1
Domestic Goose	1	Not recorded	Kluizendok, Belgium	2005	11** (98 m)	3	CS	*c.* 26 days/year (fortnightly; 2005–2007)	NO	1
Greylag Goose	1	Not recorded	Oostdam, Belgium	<2001	23** (23–55 m)	7	CS	*c.* 26 days/year (fortnightly; 2001–2007)	NO	1
Goose sp.	0	296,420 bird-flights in 2009/10; 70,450 in 2010/11^{a}	Saint Nikola, Bulgaria	2009	52*** (105 m)	2^{a}	CS, RAD FL & BC	78 days/winter (435 turbines searched in *c.* 50 days in 2010/11)	YES	2, 3
Whooper Swan	1	Not recorded	Niebull-Fahrehoft, Germany	Not known	?	ACC	ACC		NO	4
Mute Swan	1	Not recorded	Kossdorf, Germany	2004	15 (125 m)	1	1 CS	Only 1 search	NO	4
Mute Swan	1	Not recorded	Nauen-I, Germany	1999	22 (85–100 m)	1	CS	6 days (6–12 visits per turbine, in 2006)	NO	4

Appendix 1 (*continued*)

Species	No. collisions	No. flights within wind farm	Wind farm name/location	Built	No. turbines (hub height)	Years/winters of post-construction monitoring	Obs. method	Duration of post-construction monitoring	CS linked to bird presence	Refs
Mute Swan	1	Not recorded	Schlalach, Germany	2010	16 (179 m)	1	CS	*c.* 22 days (fortnightly Feb–Dec, in 2011)	NO	4
Mute Swan	1	Not recorded	Seelow, Germany	1996	1 + 13 (85–145 m)	ACC	ACC		NO	4
Mute Swan	1	Not recorded	Wittmannsdorf, Germany	1994–1997	7 (63–85)	1	CS	*c.* 52 days (2003–2004)	NO	4
Mute Swan	1	Not recorded	Zitz-Warchau, Germany	2003	20 (112 m)	4	CS	61–150 days/year (Nov 2003–Mar 2007)	NO	4
White-fronted Goose	2	Not recorded	Zitz-Warchau, Germany	1997–2003	20 (112 m)	4	CS		NO	4
Swan sp.	1	Not recorded	Klein Mutz, Germany	2003	8 (118 m)	ACC	ACC		NO	4
White-fronted Goose	1	Not recorded	Heidehof-Jüterbog, Germany	2007	31 (149 m)	?	CS	*c.* 22 days/year (fortnightly Feb–Dec)	NO	4
Bean Goose	1	Not recorded	Göllnitz, Germany	2001	6 (93–94 m)	ACC	ACC		NO	4
Goose sp.	1	Not recorded	Etzin-II, Germany	2006	3 (149 m)	1	1 CS	Only 1 search	NO	4
Goose sp.	1	Not recorded	Zachow-II, Germany	1994–1998	3 (55–85 m)	?	CS	Only 1 single search/year	NO	4
Mute Swan	1	Not recorded	Stuthof, Germany	?	*c.* 10 (<150 m)	?	CS	Only 1 single search/year	NO	4
Mute Swan	4	Not recorded	Dollart, Germany	?	Large wind farm (<100m)	?	CS	?	NO	4
Mute Swan	2	Not recorded	Wybelsumer, Germany	?	Large wind farm (<100m)	?	CS	?	NO	4
Swan sp.	3	Not recorded	Wybelsumer, Germany	?	?	?	CS	?	NO	4
Greylag Goose	1	Not recorded	Wybelsumer, Germany	?	?	?	CS	?	NO	4
Mute Swan	1	Not recorded	? (in Niedersachsen, Germany)	?	<10 (<100)	1	CS	52 days (weekly, 2001)	NO	4
Greylag Goose	1	Not recorded	Riepster Hamrich, Germany	??	?	?	?	?	?	4
Greylag Goose	1	Not recorded	Oevenum-Föhr, Germany	?	?	?	?	?	?	4

Bean Goose	1	Not recorded	Belgern, Germany	?	1	1	CS	Oct 1999–Mar 2000	NO	4
Bean Goose	1	Not recorded	Aschekippe Trattendorf-Zerre, Germany	?	1	?	CS	?	NO	4
Mute Swan	1	Not recorded	Krevese, Germany	?	1? (<100 m)	1	CS	52 days (weekly, 2000)	NO	4
Goose sp.	1									
Mute Swan	1	Not recorded	Westfehmarn, Germany	?	? (<100 m)	?	CS	1 search per week	NO	4
Barnacle Goose	6	Not recorded	Fehmarn, Germany	1990	>75*** (several sites) (<100 m)	1	CS & RAD	Autumn 2009	YES	4, 5
Brent Goose	1	Not recorded	Kreerak, Nths	1990	5 (30 m)	1	CS	*c.* 180 days (28.04.90–29.04.91)	NO	6
Mute Swan	3	Not recorded	Urk, Netherlands	1987	25* (30 m)	2	CS	Daily in autumn; 1–2 times/week in winter and spring	YES	7
Bewick's Swan	0–2	1,664+ (101 groups)	Waterkaaptocht, Nths	2003	8* (78 m)	1	CS & RAD	31 search-days (winter 2006/07)	YES	8, 9
			ECN test-park, Nths	2003–2006	9** (90 m)	1				
Greylag Goose	2	Not recorded	Anna Vosdijk, Nths	2007	5* (80 m)	1	CS	1–2 times/week	?	10
Greylag Goose	6	Not recorded	Sabinapolder, Nths	1995	6* (48 m)	2	CS & RAD	138 search-days in 2-year study	YES	11
Canada Goose	1	Not recorded	Sabinapolder, Nths	1995	6* (48 m)	2	CS & RAD	138 search-days in 2-year study	YES	11
Whooper Swan	1	Not recorded	Smøla, Norway	2002	68*** (70 m)	7	CS	52 days/year (weekly; 2003–2009)	NO	12
Greylag Goose	3	Not recorded	Smøla, Norway	2002	68*** (70 m)	7	CS	52 days/year (weekly; 2003–2009)	NO	12
Mute Swan	5	Not recorded	Kisielice-Łodygowo, Poland	2007	27*** (85 m)	?	CS	?	?	4, 13
Greylag Goose	1	Not recorded	Elgea Alava, Spain	<2003	???	?	CS	?	?	4
Greylag Goose	1	Not recorded	Elgea-Urkilla, Spain	2003	40***	?	CS	?	?	4
Greylag Goose	1	Not recorded	Guipúzcoa-Álava, Spain	<2009	???	?	CS	?	?	4
Mute Swan	1	Not recorded	Skåne (*c.* 20 sites), Sweden	<2002	51 (varied)	1	CS	1 visit/site (Aug–Oct 2002)	NO	14, 15
Pink-footed Goose	0	9	Barrow Offshore, UK	2006	30 *** (75 m)	1	FL^b	21 days (2007)	YES	16
Pink-footed Goose	0	4 groups	Hellrigg, UK	2011	4*** (80 m)	1	CS, BC & FL	12 search-days; 38 h flight observations (22.12.11–09.03.12)	YES	17

Appendix 1 (*continued*)

Species	No. collisions	No. flights within wind farm	Wind farm name/location	Built	No. turbines (hub height)	Years/winters of post-construction monitoring	Obs. method	Duration of post-construction monitoring	CS linked to bird presence	Refs
Canada Goose	0	909 observations	Buffalo Ridge, USA	1994–1999	354*** (36–50 m)	4	CS & BC	Fortnightly bird counts and searches (15 Mar–15 Nov); 21–91 turbines checked each year (1996–1999)	YES	18, 19, 20
Snow Goose	0	278 observations	Buffalo Ridge, USA	1994–1999	354*** (36–50 m)	4	CS & BC		YES	18, 19, 20
White-fronted Goose	0	92 observations (in 1997)	Buffalo Ridge, USA	1994–1999	354*** (36–50 m)	4	CS & BC		YES	18, 19, 20
Canada Goose	2	Not recorded	Klondike, USA	2002	16* (65 m)	1	CS & BC	BC mostly pre-construction; 13 searches (monthly, Mar 2002–Mar 2003	NO[c]	21, 22, 23, 24
Canada Goose	0	Not recorded (proximity not assessed)	Nine Canyon, USA	2002	300*** (60 m)	1	CS	19 searches (4–5 days each; Sep 2002–Aug 2003)	NO	25
Canada Goose	1	11 groups (363 birds)	Stateline, USA	2001–2002	454*** (50 m)	2	CS & BC	5–6 searches of 399 turbines in 2002; 6–7 searches of 454 turbines in 2003	UNCLEAR	26
Canada Goose	0	Not recorded	Top of Iowa, USA	2001	89*** (72 m)	2	CS	*c.* 150 searches/year (i.e. every 2–3 days) under 26 of 89 turbines in Apr–Dec 2003 and Mar–Dec 2004.	NO	23, 24, 27

[a] Carcass searches reported for one winter; flight-line data recorded in two winters. Number of flights said to be for flights within project area (*i.e.* not necessarily through the wind farm), though flights through/across the wind farm illustrated on maps in the report, and 64% of flights were at rotor height. Groups of turbines stopped in January to reduce collision risk (Zehtindjiev & Whitfield 2011).

[b] Observations made at a distance of 7–9 km.

[c] Use of Klondike study area by waterbirds said to be low; only species of waterfowl observed was Canada Geese, with 43 flocks (4,845 individuals) seen flying over the study area in the year-long pre-construction survey in 2001 (Johnson *et al.* 2002b).

Population size and breeding success of Icelandic Whooper Swans *Cygnus cygnus*: results of the 2010 international census

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Abstract

Trends in total population size and mid-winter distribution have been determined for the Icelandic Whooper Swan population through coordinated international censuses, undertaken in January across its wintering range in Britain, Ireland and Iceland, at *c.* 5-yearly intervals from 1986 onwards. A total of 29,232 swans recorded during the sixth international census in January 2010 represented an increase of 11% on the previous census in 2005 and is the highest census total to date. Overall, 35.8% of the population (10,452 swans) was recorded in the Republic of Ireland, 30.8% (8,999) in England, 15.8% (4,616) in Northern Ireland, 9.1% (2,659) in Scotland and 7.8% (2,278) in Iceland, with the combined total in Wales and the Isle of Man accounting for < 1% of birds counted. There was a significant increase across censuses (1986–2010) in the proportion of birds wintering in England, in comparison with the rest of the range, whereas the Republic of Ireland and Scotland saw a significant decline. This suggests an overall shift to the southeast in the swans' winter distribution, though a prolonged period of cold, snowy weather prior to the January 2010 census may have resulted in more birds moving south from Scotland, or potentially from mainland Europe, in this year. The majority of Whooper Swans in Ireland were recorded on pasture in 2010, whilst in Britain they were seen mainly on arable land. Although the frozen conditions in 2010 are likely to have influenced habitat choice, there has been a general increase in the use of arable land by Whooper Swans since 1995.

Key words: distribution, habitat, trends in numbers, Icelandic population, international census, productivity, Whooper Swans.

The Whooper Swan *Cygnus cygnus* has a widespread breeding distribution in the northern Palaearctic, extending from Iceland and northern Scandinavia, across Russia, to the Pacific coast (Brazil 2003; Rees *et al.* 2002). The Icelandic-breeding population of Whooper Swan is one of five populations described for this species (Brazil 2003; Wetlands International 2006); ringing and count programmes indicate that most of the Icelandic Whooper Swans migrate to winter in Britain and Ireland, with a small proportion (500–1,300 individuals) remaining to overwinter in Iceland (Black & Rees 1984; Gardarsson 1991; Rees *et al.* 2002). Satellite tracking studies have demonstrated that the swans may undertake the 1,400 km overseas flight between Ireland and Iceland either direct or via Scotland (Rees 2009), but there is a minimum 800 km overseas flight between Britain and Iceland, and the swans are vulnerable to being blown off course or unable to make landfall if they encounter strong head or side winds during the flight (Pennycuick *et al.* 1996; Rees 2009). In the early part of the 20th century, the swans fed mainly on aquatic vegetation during the winter months, but use of agricultural land became more frequent from the 1960s onwards, at a time of agricultural intensification in Britain and Ireland. The habitat switch on to cropped land (arable and agriculturally-improved pasture), together with an increase in the numbers of birds wintering in Britain and Ireland during the second half of the 20th century, has resulted in some conflict with agricultural interests, particularly in relation to re-seeded grasslands, winter cereals, root crops and oil seed rape (Robinson *et al.* 2004; Chisholm & Spray 2002).

Whooper Swans have been monitored annually in Britain since the 1950s, largely through the Wetland Bird Survey (WeBS; formerly the National Wildfowl Counts), undertaken each month during the winter, and extended to Northern Ireland in 1986. Similarly, the Irish Wetland Bird Survey (I-WeBS) has monitored waterbird numbers and distribution in the Republic of Ireland since winter 1994/95. Additional count data on Whooper Swans in Ireland have been collected by the Irish Whooper Swan Study Group (IWSSG) since the early 1990s. Numbers of Whooper Swans wintering in accessible areas of Iceland have been recorded as part of the annual winter bird census coordinated by the Icelandic Institute of Natural History (IINH) each year since 1952. Although coverage for WeBS and I-WeBS includes many wetland sites in Britain and Ireland, the daily dispersal of Whooper Swans away from wetland roost sites and their tendency to feed at temporary wetlands and in non-wetland (generally farmland) habitats means these surveys miss a substantial proportion of the population. Likewise, counts undertaken annually in Iceland may miss some overwintering birds because the swans are rather scattered at this time and accessing some areas by foot or car can be difficult in harsh weather conditions. Coordinated species-specific surveys that include these areas are, therefore, required to provide accurate estimates of population size, which are used to identify sites of national and international importance for the species, with regular counts of ≥ 1% of the total population being one of the criteria used for designating sites Special Protection Areas under the EU Birds Directive. Extensive coordinated surveys are also important for verifying trends in numbers identified by the national count programmes, and for describing any changes in feeding habitat as habitat is not usually recorded in the WeBS and I-WeBS programmes.

An international census of the Icelandic-breeding Whooper Swan population has been carried out in mid-January at *c.* 5-year intervals since 1986, as part of a wider census of wintering migratory swans in Europe, coordinated by the IUCN-SSC/Wetlands International Swan Specialist Group. Results from the early censuses show fluctuating numbers, with totals of 16,742, 18,035 and 15,842 individuals recorded in 1986, 1991 and 1995, respectively (Salmon & Black 1986; Kirby *et al.* 1992; Cranswick *et al.* 1997). More recent censuses have shown a growth in the population, with totals of 20,856 Whooper Swans in 2000 and 26,366 recorded in 2005 (Cranswick *et al.* 2002, Worden *et al.* 2009). As the number of Icelandic Whooper Swans has increased there has been a noticeable shift in the distribution of birds across countries, with an increasing proportion located in England (Worden *et al.* 2009). Additionally, there are indications that birds are moving to southern locations earlier in the winter than has previously been noted (Spray 2007). The number of swans remaining to overwinter in Iceland has also increased, although as a proportion of the total population there has been only small variation between censuses.

This paper presents the results of the sixth international census of Whooper Swans in Britain, Ireland and Iceland, which took place in January 2010. It aims to describe trends in the numbers and mid-winter distribution of the Icelandic Whooper Swan population from the first international census (in 1986) onwards and also to determine regional variation in the percentage of juveniles recorded. The habitats on which the birds were observed during each of the censuses since 1995 are analysed to assess any major changes in habitat use by the swans over time.

Methods

The 2010 international census of Icelandic Whooper Swans was coordinated by the Wildfowl & Wetlands Trust (WWT) and followed the methods used in previous years, as well as covering the same count areas (details in Worden *et al.* 2009). The census in Britain was organised by WWT, in Ireland by BirdWatch Ireland and the IWSSG, and in Iceland by Ólafur Einarsson and the IINH. Counts were undertaken by a network of volunteers (including WeBS and I-WeBS counters and IWSSG members) and professional staff.

The main census dates of 16–17 January 2010 were chosen to coincide with the WeBS and I-WeBS counts in that month. In addition, counters were asked to visit sites known to have held, currently hold or may potentially be suitable for Whooper Swans but are not regularly covered by these other surveys. An aerial survey was undertaken in Ireland on 22 January to ensure complete coverage of areas with limited accessibility: the Rivers Suck, Brosna and Shannon Callows (south of Athlone), Lough Derg and the Shannon and Fergus Estuary.

In Iceland, data were collected mainly through the annual winter bird census with ground counts undertaken in the northeast, southeast, southwest and west of the country between 26 December 2009 and 12 February 2010. An aerial survey of the southern lowlands, not covered by the winter bird census, was undertaken on 30 January 2010. The broad range of dates is considered acceptable as only small numbers of birds are recorded and there is probably little movement between sites in Iceland during midwinter.

Submitted data were checked to identify duplicate counts, due to sites being surveyed more than once or where birds were believed to have moved between adjacent sites. Where duplicate counts occurred, the criteria used to select data for inclusion in the analysis included the following: proximity to the census weekend, coordination with adjacent sites, and whether the count was said by the observer to be most representative of the number present at the site. Any counts considered to be duplicates were excluded from the census totals. For sites where no count was carried out on the census weekend, data were included for a week either side but only if it was deemed unlikely that birds may have moved in from other sites. Only in exceptional circumstances were counts from outside this time period included and only then if the risk of double counting was thought to be minimal.

Counts and age assessment data were grouped by country for analysis, namely: Iceland, Northern Ireland, the Republic of Ireland, Scotland, England/Isle of Man (only small numbers occurred on the Isle of Man so these data were combined with England) and Wales. This grouping helps facilitate comparison with earlier studies and also provides a north/south and east/west divide for assessing distribution. For some analysis of breeding success, countries were further divided into regions, definitions of which are given in Appendix 1 in Worden *et al.* (2009).

Chi-squared tests were used to determine whether there was any significant difference in the proportion of swans and number of flocks recorded across countries between the 2005 and 2010 censuses, and in the frequency of brood sizes recorded in each country compared to the rest of the range. Productivity data (*i.e.* the proportion of cygnets recorded in wintering flocks, arcsine transformed) were not normally distributed (Shapiro-Wilk test: $W = 0.7643$, $P < 0.001$); non-parametric Kruskal-Wallis tests therefore were used to assess differences between countries and regions in the proportion of young birds, and also in the brood sizes recorded. Mann-Whitney tests assessed differences in flock size within countries between the 2005 and 2010 censuses. Generalised linear models (GLMs), specifying a Poisson error distribution with log link function, investigated whether the total number of swans counted in each country during each of the censuses varied significantly between countries and across years. The dispersion parameter was not fixed, to control for overdispersion in the count data (Crawley 2002). Country (included as a factor), year (included as a variate with 1986 = year 1, to test for trends over time) and the quadratic function of year (*i.e.* year^2, to test for any curvilinearity in population trends) were included as explanatory variables in the initial maximal model. Two-way interaction terms were also tested for significant variables. Non-significant variables were omitted sequentially from the GLM, the least significant variable being omitted first, so that the final model was parsimonious. Linear regression analysis of the proportion of birds recorded in each country (arcsine transformed) in the international censuses from 1986 onwards further tested for trends in the mid-winter distribution of Whooper Swans over time.

Results

Coverage

The weekend of the census followed a period of very cold weather in Britain and Ireland, with the majority of the region covered in snow and many waterbodies completely frozen. Although a thaw had set in by the time the census was undertaken, some areas were still difficult to access.

In Britain, 64% of the counts (where swans were recorded, n = 247) were conducted on the core weekend, with a further 30% within three days either side. All counts were carried out between 12 and 24 January, with the exception of one at The Wash, Lincolnshire/Norfolk which was undertaken on 3 January. The counts carried out late in January were mainly in the Scottish Highlands where conditions were too poor to undertake surveys on the core weekend.

In Northern Ireland, counts were undertaken between 15 and 27 January, with 33% (where swans were recorded, n = 102) carried out on the core weekend and a further 45% within three days either side. Those sites covered outside this period included Upper Lough Erne, which could not be counted on the core weekend due to fog. In the Republic of Ireland, 62% of counts (where swans were recorded, n = 284) were conducted on the core weekend, whilst 23% were carried out within three days either side. The remaining counts were undertaken outside this period, but between 10 and 31 January.

Counts in Iceland were carried out between 26 December and 12 February. Coverage was good for most regions with the exception of the northeast where, based on numbers from previous years, it was thought that 20–50 swans may have been missed. It is also possible that 10–20 birds may have been missed in western areas, although coverage there was considered to be fairly good. An aerial survey of the southern lowlands did not cover an area between Skógar and Meðalland where up to 50 swans have been located in previous censuses.

Numbers and distribution

A total of 29,232 Whooper Swans was recorded in 755 flocks in Britain, Ireland and Iceland during the January 2010 census (Table 1), a 10.9% increase on the 26,366 swans recorded in 2005 (Fig. 1, Table 2). All countries except Scotland saw an increase in total numbers, with the rate of increase in Northern Ireland and the Republic of Ireland being less than that of the entire population (Table 2). Over 40% of the

Table 1. Numbers of Whooper Swans recorded in Iceland, Ireland and Britain during the international census in January 2010.

	Number of swans	Number of flocks
Iceland		
South	1,222	88
Southwest	654	20
Northeast	327	10
West	50	3
Southeast	25	1
Total	**2,278**	**122**
Northern Ireland		
Londonderry	1,673	29
Fermanagh	1,020	27
Down	548	10
Antrim	520	13
Armagh	508	13
Tyrone	347	10
Total	**4,616**	**102**
Republic of Ireland		
Galway	1,104	35
Mayo	966	33
Cavan	865	29
Donegal	854	18
Roscommon	774	24
Offaly	650	9
Wexford	641	5
Clare	639	17
Westmeath	566	7
Kerry	537	6
Waterford	485	11
Meath	416	7
Monaghan	414	23
Tipperary	276	8
Cork	215	10
Longford	210	8
Limerick	194	2
Sligo	186	9
Laois	151	2
Leitrim	130	12
Kildare	112	5
Wicklow	41	2
Louth	25	1
Kilkenny	1	1
Total	**10,452**	**284**
Isle of Man	**27**	**1**
England		
Cambridgeshire	4,546	27
Lancashire	2,405	14
Norfolk	1,426	11
Cumbria	313	10
Northumberland	100	5
Cheshire	71	2
Humberside	36	3
Lincolnshire	22	1
South Yorkshire	21	2
West Yorkshire	20	1
Shropshire	10	2
Gloucestershire	8	1
Bedfordshire	6	3
Kent	3	2
Devon	3	2
Somerset	2	1
Northamptonshire	2	2
Cornwall	2	1
Suffolk	1	1
Essex	1	1
Leicestershire	1	1
Total	**8,999**	**93**
Scotland		
Dumfries & Galloway	940	21
Highland	393	22
Strathclyde	265	23
Tayside	253	12
Orkney	166	11
Fife	139	3
Shetland	136	28
Lothians	122	2
Western Isles	118	16
Borders	66	2
Grampian	51	2
Central	10	3
Total	**2,659**	**145**
Wales		
Gwynedd	113	3
Dyfed	45	2
Clwyd	23	2
Powys	20	1
Total	**201**	**8**
Overall total	**29,232**	**755**

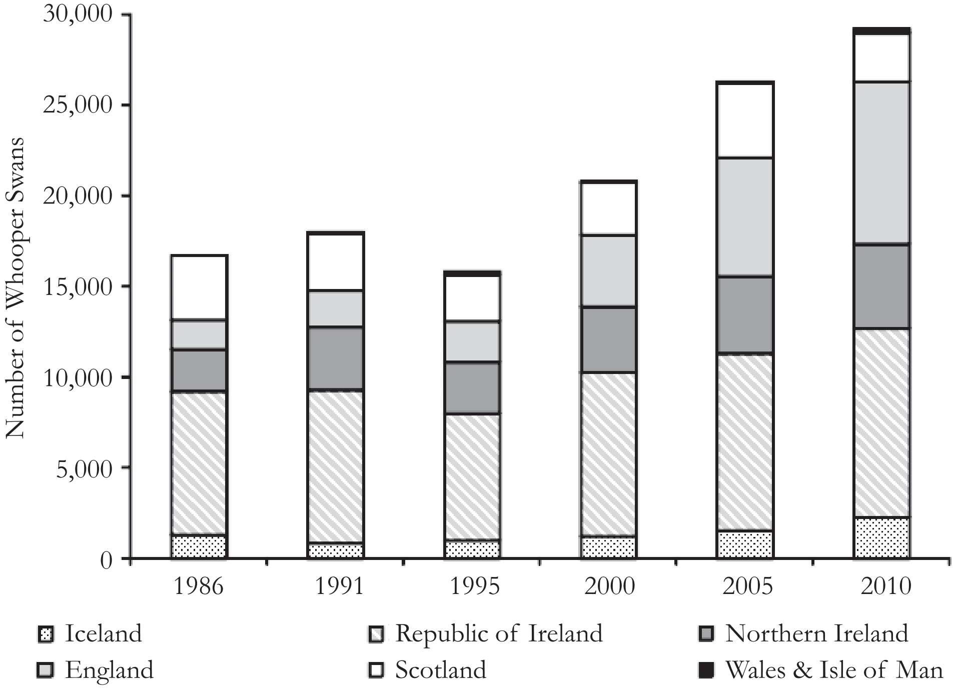

Figure 1. . Number of Whooper Swans recorded during the international censuses of the Icelandic-breeding populations from 1986–2010 inclusive.

swans were located in Britain, 51.5% in Ireland and 7.8% in Iceland. There was a significant shift in the distribution of swans across countries between 2005 and 2010 (χ^2_6 = 799.5, $P < 0.001$) (Table 2). The number of swans counted varied significantly both by country and over time (GLM: $F_{24,4} = 9.30$, $P < 0.001$ for country; $F_{24,1} = 9.25$, $P < 0.01$ for year^2). There was a significant increase in the proportion of the population recorded in England/Wales/Isle of Man across all censuses (1986 to 2010) (linear regression: $F_{5,1} = 143.41$, $t = 11.98$, $P < 0.001$), and a significant decrease in Scotland ($F_{5,1} = 19.23$, $t = -4.39$, $P < 0.05$) and the Republic of Ireland ($F_{5,1} = 45.78$, $t = -6.77$, $P < 0.01$), with the proportion recorded in Northern Ireland and in Iceland remaining relatively stable over this period ($F_{5,1} = 0$, $t = -0.03$ and $F_{5,1} = 0.1$, $t = 0.32$, respectively, n.s. in each case; Fig. 2).

In Britain, the majority of birds (30.8% of the overall population) were recorded in England; the proportion wintering there being notably higher than during the 2005 census (24.6%; Table 2 & Fig. 2). Swans were distributed from Northumberland to Devon, with the largest concentrations occurring at the Ouse Washes, Norfolk/Cambridgeshire, and Martin Mere, Lancashire, where flocks totalled 5,632 and

Table 2. Total numbers of Whooper Swans recorded in Iceland, Ireland and Britain during the international censuses in January 2005 and 2010, and the percentage change between the 2005 and 2010 censuses. Total numbers in 2010 were compared with 2005 using Chi-square tests with d.f. = 1 for comparison of each country with the rest of the range, and d.f. = 6 for overall comparison.

	Number of birds in 2005	**Number of birds in 2010**	**% change in number of birds**	**Comparison of total numbers**	
				χ^2	***P***
Iceland	1,556	2,278	46.4	77.2	<0.001
Northern Ireland	4,331	4,616	6.6	4.1	<0.05
Republic of Ireland	9,748	10,452	7.2	8.9	<0.005
England	6,480	8,999	39.3	265.9	<0.001
Scotland	4,142	2,659	–38.5	564.7	<0.001
Wales	94	201	113.8	28.8	<0.001
Isle of Man	15	27	80.0	2.3	n.s.
Overall	**26,366**	**29,232**	**10.9**	**799.5**	**<0.001**

2,052, respectively (Table 1, Fig. 3a). Whooper Swans were recorded at a further 45 sites, where total numbers ranged from a single bird to 337. Ten counties, which held birds in 2005 recorded no birds in 2010, although these accounted for < 2% of the previous census total for England and consisted mainly of flocks of one or two birds. Five counties recorded birds in 2010 where none were seen in 2005 but these contributed < 1% of the 2010 total.

Scotland held 9.1% of the population, a notably smaller proportion than in 2005 (15.7%; Table 2 & Fig. 2), and swans were located at 139 sites within Scotland, distributed across the country from the Shetland Isles to Dumfries & Galloway (Table 1, Fig. 2). Total numbers ranged from one individual to 271, with the largest flocks observed in Strathclyde, Highland and Dumfries & Galloway. Except for Dumfries & Galloway, all counties held considerably fewer birds compared with the numbers recorded in 2005.

Wales and the Isle of Man each held < 1% of the total population (Tables 1 & 2). Seven sites were found to have Whooper Swans in Wales, where 8–72 swans were counted, and one flock was seen on the Isle of Man (Fig. 3a).

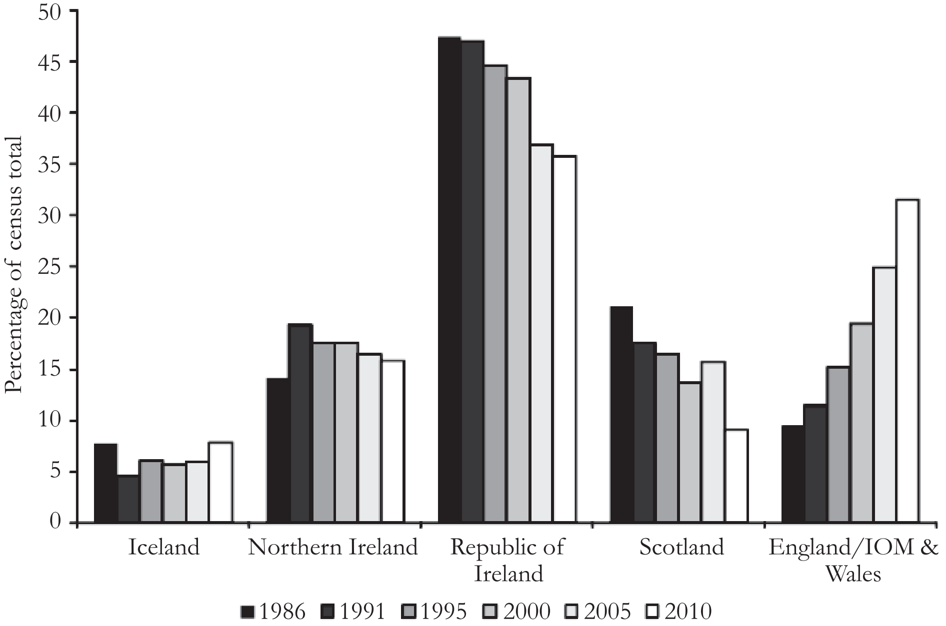

Figure 2. Changes in the distribution of Whooper Swans across Iceland, Ireland and Britain during the international censuses of 1986–2010. Note: Wales and Isle of Man have been combined with England as each only contributes <1% to the census totals each year.

In Ireland, 35.7% of the population was recorded in the Republic of Ireland whilst 15.8% were seen in Northern Ireland, a slight reduction on the proportion observed in each country during 2005 (37% and 16.4%, respectively) (Table 2, Fig. 2). Whooper Swans were recorded in all counties except Carlow and Dublin (Table 1). Londonderry, Fermanagh and Galway held the highest proportions of birds; Louth and Kilkenny had just 25 and one swan respectively, but no swans were recorded in these two counties during the previous census. Loughs Neagh & Beg (Antrim/Londonderry/Tyrone/Armagh/Down), Lough Foyle (Londonderry/Donegal) and Upper Lough Erne (Fermanagh) held the highest numbers, with 1,803, 883 and 799 individuals, respectively (Fig. 3a). A further 210 sites in Ireland held birds, with total numbers ranging from one to 506 swans.

A slightly higher proportion of the population overwintered in Iceland compared with 2005 (Fig. 2). Swans were predominantly seen in the south, southwest and northeast of the country (Table 1, Fig. 3b). The largest concentrations were located at Hólsá (290), Þykkvabæjarvatn (182), and Landbrot and Meðalland (131) in the south, and at Breiðan og Álar, Lake Mývatn (182) in the northeast. Elsewhere, birds were distributed in smaller flocks, ranging from one to 86 individuals. Whooper Swans were often observed along stretches of river or coastline, most notably

Figure 3. Distribution of Whooper Swans recorded during the international census in January 2010: a) Britain and Ireland; b) Iceland. Symbols represent total numbers recorded at a site.

along the southwest coast between Stafnes and Hvalfjörður, where a combined total of 419 birds was recorded.

There was a significant difference in the overall number of flocks across the range between the 2005 and 2010 censuses (Table 3), which is likely a consequence of the significant decrease in the number of flocks seen in Scotland and the increase in England/Isle of Man compared with the rest of the range. The latter, however, can be attributed to swans at the Ouse Washes being counted at numerous feeding sites in 2010 rather than at a single roost site as in 2005. This was confirmed on excluding the Ouse Washes from the analysis (one flock in 2005; 35 flocks in 2010), upon which there was no significant difference in the overall number of flocks across the range between censuses ($\chi^2_5 = 10.4$, n.s.) nor in England/Isle of Man compared with elsewhere ($\chi^2_1 = 0.0$, n.s.). There was still a significant difference in the number of flocks recorded in Scotland compared to the rest of the range, though to a lesser extent ($\chi^2_1 = 9.7$, $P < 0.005$), with fewer flocks than expected recorded.

The majority of flocks consisted of ≤ 25 birds, representing 65% of all flocks observed (Fig. 4). Only three flocks of > 500 individuals were recorded, these being found in England at the Ouse Washes in Cambridgeshire/Norfolk (two flocks consisting of 1,262 and 672 individuals) and at Martin Mere in Lancashire (one flock of 1,286 individuals). England/Isle of Man saw the widest range of flock sizes (Table 3), reflecting the large flocks recorded on the Ouse Washes and at Martin Mere, whilst in Scotland over 80% contained 25 or fewer birds and the majority of these held less than ten. Iceland also saw a large proportion of small flocks, but there the tendency is for Whooper Swans to disperse into very small groups.

There was a significant difference in flock size across the range between the 2005 and 2010 censuses ($W = 609065$, $P < 0.01$) (Table 3). Fewer flocks consisted of ≤ 25 individuals in 2010 (65.4%) compared with 2005 (74.5%), with a higher proportion of medium-sized flocks (26–100 birds; 19.7% in 2005 *cf.* 26.1% in 2010) and large flocks (101–500 birds; 5.8% in 2005 *cf.* 8.5% in 2010) in the most recent census. Comparing flock size within each country between the two censuses found a significant difference for Wales and England/Isle of Man (Table 3), with a higher proportion of medium-sized flocks (26–100 birds) in 2010 in both countries (0% in 2005 *cf.* 37.5% in 2010 for Wales; 18.5% *cf.* 27.6% for England/Isle of Man), and fewer with ≤ 25 birds (100% in 2005 *cf.* 62.5% in 2010 in Wales; 69.2% *cf.* 51.1% in England/Isle of Man). On excluding the Ouse Washes from this analysis, to test whether the numerous flocks recorded there in 2010 affected the results, there was still a significant difference in flock size across the range between censuses (though to a lesser extent; $W = 602574$, $P = <0.05$). No significant difference between years was found for England/Isle of Man ($W = 3949$, n.s.), however, indicating that a high proportion of the larger flocks in England were located at the Ouse Washes during the 2010 census.

Sites of conservation importance

During the census, 14 sites in Ireland and six in Britain supported numbers exceeding the

Table 3. Number of flocks and mean flock size of Whooper Swans recorded in Iceland, Ireland and Britain during the international censuses in January 2005 and 2010. The Isle of Man has been included with England for the purpose of this analysis as only one flock was observed in each year. The number of flocks recorded during the 2005 and 2010 censuses were compared using a Chi-square test with d.f. = 1 for comparison of each country with the rest of the range, and d.f. = 5 for overall comparison. Mann-Whitney tests were used to compare flock size within each country and overall between 2005 and 2010.

	2005		**2010**		**Flock number comparison**		**Flock size comparison**	
	Number of flocks	**Mean flock size ± s.e.**	**Number of flocks**	**Mean flock size ± s.e.**	χ^2	***P***	***W***	***P***
Iceland	126	12.3 ± 1.6	122	18.7 ± 3.4	0.1	n.s.	15402.5	n.s.
Northern Ireland	102	42.6 ± 8.5	102	45.3 ± 6.4	0.3	n.s.	10021.0	n.s.
Republic of Ireland	288	33.8 ± 3.2	284	36.8 ± 2.9	0.8	n.s.	79337.0	n.s.
England & Isle of Man	65	99.9 ± 55.1	94	96.0 ± 21.6	7.1	<0.01	4555.0	<0.05
Scotland	219	18.9 ± 2.4	145	18.3 ± 3.0	12.9	<0.001	40914.0	n.s.
Wales	11	8.5 ± 2.4	8	25.1 ± 7.1	0.3	n.s.	78.0	<0.01
Overall	**811**	**32.5 ± 4.8**	**755**	**38.7 ± 3.2**	**17.5**	**<0.005**	**609065.0**	**<0.01**

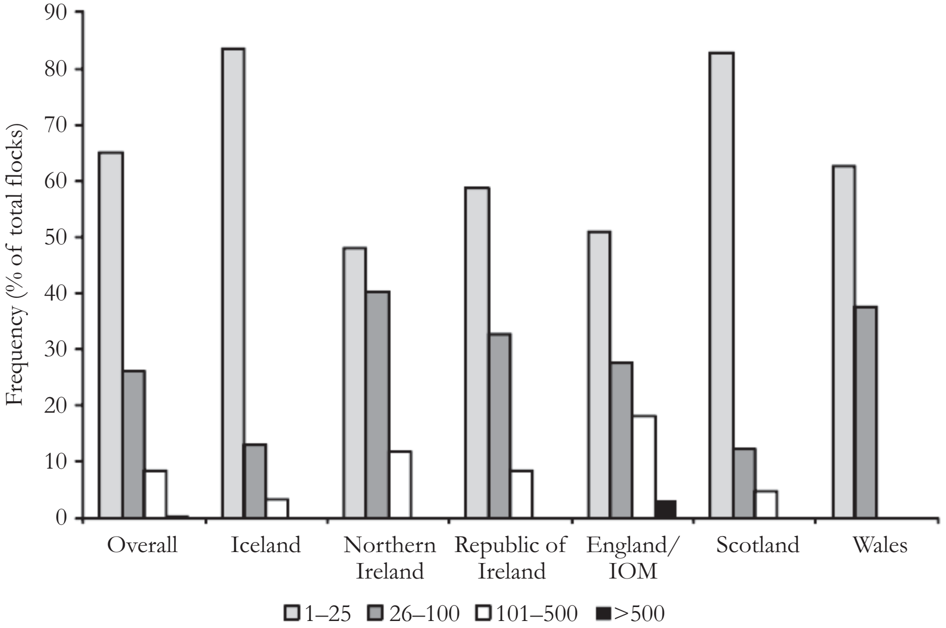

Figure 4. Frequency of flocks of each category recorded in Iceland, Ireland and Britain in January 2010. Number of flocks recorded in each country (n values) are: Iceland = 386, Northern Ireland = 102, Republic of Ireland = 284, England/Isle of Man = 94, Scotland 145, Wales = 8, Overall = 755.

current 1% threshold used to indicate sites of international importance (210 birds; Wetlands International 2006), including six that did not hold such numbers in 2005 (Appendix 1). Fifteen of these twenty sites supported at least 1% of the numbers recorded during the 2010 census (290 birds), of which four were in Britain and 11 in Ireland (Appendix 1). Ten sites that qualified in 2005 did not maintain internationally important numbers in 2010. Five sites in Britain held nationally important numbers (110; Musgrove *et al.* 2011), only two of which held these concentrations in 2005, including the Ribble Estuary which held numbers above the threshold for international importance during the previous census. Of the nine sites in Ireland which supported numbers greater than the all-Ireland threshold for site importance (130; Crowe *et al.* 2008), only Strangford Lough (which held internationally important numbers during the 2005 census) had previously qualified in 2005.

Age and brood size data

A total of 23,413 Whooper Swans was aged during the 2010 census, with the highest numbers aged in England and the Republic of Ireland (Table 4). The overall percentage of young was 16.3%, ranging from 13.8% in England/Isle of Man to 19.1% in Northern Ireland. The variation in the proportion of young differed significantly between

Table 4. Proportion of young, mean brood size and frequency of brood sizes of Whooper Swans in Iceland, Ireland and Britain in January 2010 (see Appendix 1 in Worden *et al.* 2009 for regional definitions).

	% young	Number aged	Mean brood size	Brood size					
				1	2	3	4	5	6
Iceland									
Northeast	11.6	259	1.00	2	–	–	–	–	–
South	17.0	871	2.34	16	21	10	10	2	–
Southwest	21.9	479	2.79	6	2	6	1	3	1
West	26.2	42	2.75	2	–	–	1	1	–
Total	**17.8**	**1,651**	**2.43**	**26**	**23**	**16**	**12**	**6**	**1**
Northern Ireland	**19.1**	**4,017**	**2.06**	**129**	**97**	**60**	**28**	**6**	**4**
Republic of Ireland									
Northeast	16.5	1,888	2.35	17	20	14	3	6	–
Northwest	17.6	3,224	2.22	56	52	25	22	6	1
Southeast	16.5	1,477	2.58	12	20	29	7	2	1
Southwest	15.7	1,363	2.33	26	21	18	7	4	2
Total	**16.8**	**7,952**	2.33	**111**	**113**	**86**	**39**	**18**	**4**
Ireland total	**17.6**	**11,969**	2.21	**240**	**210**	**146**	**67**	**24**	**8**
Scotland									
Northern Isles	25.6	133	2.13	6	4	4	2	–	–
Northwest	20.8	106	–	–	–	–	–	–	–
Northeast	12.3	65	1.17	5	1	–	–	–	–
Southwest	17.8	600	1.84	15	16	5	2	–	–
Southeast	18.3	360	2.04	8	8	6	–	1	–
Total	**18.8**	**1,264**	**1.90**	**34**	**29**	**15**	**4**	**1**	**–**
England									
Northwest	19.9	2,562	1.85	74	54	31	6	2	–
Northeast	21.4	56	4.00	–	–	–	1	–	–
East Central	11.0	5,714	1.89	137	98	59	15	2	2
South	0.0	10	–	–	–	–	–	–	–
Total	**13.8**	**8,342**	**1.88**	**211**	**152**	**90**	**22**	**4**	**2**
Wales	**18.2**	**187**	1.50	**2**	**2**	**–**	**–**	**–**	**–**
Britain total	**14.5**	**9,793**	**1.88**	**247**	**183**	**105**	**26**	**5**	**2**
Overall total	**16.3**	**23,413**	**2.08**	**513**	**416**	**267**	**105**	**35**	**11**

countries (Kruskal Wallis: H_5 = 12.06, $P < 0.05$), but there was no significant difference in the proportion of young between regions within each country (Kruskal Wallis: H_9 = 8.82, n.s, H_4 = 6.41, n.s., and H_3 = 3.07, n.s., for Britain, Ireland and Iceland, respectively; Table 4).

The overall mean brood size was 2.08 cygnets per successful pair amongst the 1,347 families assessed, only marginally lower than the previous census (2.3 cygnets), and ranged from 1.5 cygnets in Wales to 2.43 in Iceland (Table 4). Most families (69%) had relatively small broods of one or two cygnets, few (11%) were observed with four or more and no families had more than six cygnets (Table 4). A comparison of the frequency of small (1–2 cygnets) and larger (3–6 cygnets) brood sizes recorded for different countries found that a higher proportion of the larger broods were recorded in Iceland and the Republic of Ireland than elsewhere (Iceland: χ^2_1 = 4.7, $P < 0.05$; Republic of Ireland: χ^2_1 = 17.6, $P < 0.001$) whereas smaller brood sizes were more frequent in England (χ^2_1 = 14.8, $P < 0.001$).

Habitat use

Habitat data were collected for over 80% of all swans counted. The majority of birds were seen on pasture (51.2%) and arable land (37.5%), with relatively few seen on permanent standing water (Table 5, Fig. 5).

Table 5. Percentage of Whooper Swans recorded on different habitat types in January 2010.

	Iceland	Britain	Northern Ireland	Republic of Ireland
Number of swans (*n*)	2,278	8,762	4,616	7,883
Permanent standing water	38.7	6.0	3.3	7.8
River	29.1	0.5	0	6.3
Coastal	25.6	1.9	0.1	0.4
All pasture	0.1	11.5	77.9	79.9
Improved pasture (dry)	0	6.1	71.4	52.9
Improved pasture (wet)	0	1.8	6.0	15.2
Rough/unimproved pasture (dry)	0.1	3.4	0.5	5.7
Rough/unimproved pasture (wet)	0	0.2	0	6.1
All arable	3.3	76.6	18.7	5.0
Arable growing	3.3	38.8	0	0.2
Arable waste	0	37.8	18.7	4.8
Other	3.2	3.4	0	0.6

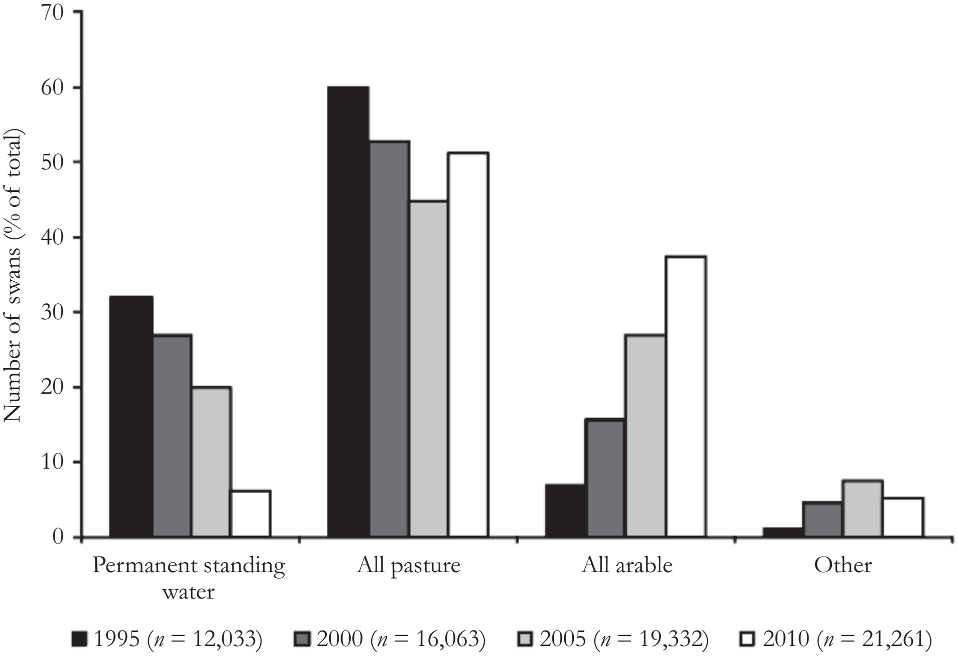

Figure 5. Distribution of Whooper Swans on permanent standing water, pasture, arable and 'other' habitats in Britain and Ireland in January 1995, 2000, 2005 and 2010.

Birds in Britain were mainly seen on arable land (with growing crops or waste) (76.6%) whilst in Ireland dry, improved pasture was the preferred habitat (71.4% in Northern Ireland and 52.9% in the Republic of Ireland). These habitat types were rarely used, if at all, in Iceland, where the majority of birds were recorded using permanent standing water (38.7%), rivers (29.1%) and coastal areas (25.5%).

Discussion

Despite the cold and snowy weather conditions experienced in Britain and Ireland prior to the January 2010 census, which made surveying conditions difficult in some areas, coverage of all sites known to be used by swans was thought to be good. A number of sites were visited in the week after the census, following a thaw across the country, and it is possible that bird movements occurred during this time. All attempts were made during data collation, however, to try to reduce the possibility of duplicate counts being included in the analysis. It has been suggested that swans may have been missed or undercounted in Ireland due to the wider distribution of birds away from their traditional sites as a result of the weather (Boland *et al.* 2010), which resulted in more effort being required to find some flocks. The number missed, however, is not believed to be notably more than during a typical season (O. Crowe pers.

comm.). It is possible that a similar situation occurred in Britain; however, indications from counters suggest coverage there was fairly extensive. Based on counts in previous years, around 120 birds may have been missed in Iceland due to a few areas not being surveyed. This represents just over 5% of the total recorded for Iceland in 2010 but only 0.4% of the overall census total. The total presented in this report, therefore, is thought to be an accurate estimate of the population size of Icelandic Whooper Swans in January 2010.

The total of 29,232 Whooper Swans was the highest to date, representing an 11% increase on the total counted in 2005. It continues the period of sustained growth that has occurred since the 1995 census although the rate of increase was lower than seen previously, with an increase of 31% recorded between the 1995 and 2000 censuses, and 26% between 2000 and 2005.

An increase in wintering numbers was evident in all countries across the range, except for Scotland where numbers were lower than in 2005. The rate of increase in Ireland and the Isle of Man was lower than that of the population as a whole. Conceivably, the cold weather in Britain and Ireland in December 2009 and January 2010 affected the distribution of swans, pushing birds southwards, although similar weather conditions were experienced across both islands. Some evidence for this could be inferred when comparing total numbers between the 2005 and 2010 censuses, with many northern counties in Scotland holding considerably fewer birds in 2010, while the southern county of Dumfries and Galloway saw a marked increase. The census total for England was also notably higher, mainly due to the large increase at the Ouse Washes (Cambridgeshire/Norfolk) but there was no major increase in any of the northern counties in England. As supplementary feeding occurs at WWT centres during the winter (located at Caerlaverock in Dumfries & Galloway, Martin Mere in Lancashire, and Welney in Norfolk) birds may have moved to these sites during cold weather as they can be assured of easy access to food. In Ireland, swans had moved away from their traditional areas and were absent from many regular sites and were reported in places where they had not been recorded before (Boland *et al.* 2010). This may also have been the case in Scotland, resulting in birds being missed, but it is thought unlikely that this would account for such a large difference in the census totals between 2005 and 2010.

There has been some evidence that other species of wildfowl, such as Bewick's Swan *Cygnus columbianus bewickii*, are tending to winter closer to their breeding grounds with the milder winters of the early 2000s (Worden *et al.* 2006). Since the 1991 census, however, there has been a significant increase in the proportion of the overall population of Whooper Swans wintering in England, with a corresponding decrease in Scotland, though to a lesser extent. There has also been a downward trend in the proportion recorded in Ireland, significantly in the Republic of Ireland. Only England has seen a consistently higher rate of increase in numbers when compared with the overall population increase. This would suggest that the population as a whole is shifting its range south and in 2010 this may have been exaggerated by cold weather movements. In Scotland and Ireland, Whooper Swans are widely distributed across many sites. In contrast, Whooper Swans in England continue to be concentrated at just a few sites, the majority at Martin Mere and the Ouse Washes. Both sites have seen a sustained increase in numbers since the 1995 census, with 1.8 and 5.4 fold increases occurring, respectively. The disproportionate increase seen in England is predominately a result of the increase at the Ouse Washes, where in 2010, the increase accounted for 89% of the rise in total numbers recorded in England. A similar southerly shift in the wintering distribution of the Iceland/Greenland population of Pink-footed Goose *Anser brachyrhynchus* has also occurred (Gill *et al.* 1997), with an increasing proportion of the population being recorded in Norfolk, the most southerly region in Britain where these birds winter. The most likely cause of this is the birds' preference for foraging on post-harvest sugar beet waste, a crop that was increasing in Norfolk at that time, partly because it is highly nutritious and partly because birds can feed largely undisturbed by farmers because this is a by-product of no commercial value. It is possible that Whooper Swans are moving south for similar reasons, though more investigation is required to determine whether habitat choice is the determining factor.

It is also possible that an influx of birds from the Northwest European population, which breeds from Fenno-Scandia to northwest Russia and winters in northwest and central mainland Europe, has added to the numbers recorded during the census. Laubek *et al.* (1999) suggested that the large increase in the Northwest European population since the 1980s has resulted in an increasing number of these birds wintering in Britain, particularly in southeast England, and these movements may be influenced by severe weather. In January 2010, mainland Europe also experienced very cold and snowy conditions. Numbers of Whooper Swans in the Netherlands (the southern end of the wintering range of the Northwest European population) were only slightly higher than during previous years of milder winters, however (2,212 in 2010 compared with 2,184 in 2009), and the monthly trend was also similar to that of previous years, with peak numbers recorded in January (Hornman *et al.* 2012). The highest numbers were observed in the east of the Netherlands, indicating that a small number of birds may have moved in from further east/northeast, as is often the case during colder winters (Ridgill & Fox 1990; M. Hornman pers. comm.), but there were no clear indications for an influx of swans from mainland Europe into southeast England (the area closest to Whooper Swans sites in mainland Europe) during winter 2009/10 winter. For instance, there were no reported sightings in Britain in winter 2009/10 of ringed Whooper Swans from the Northwest European population (K. Brides pers. comm.). A census of Whooper Swans in Iceland in the late summer/autumn prior to an international census may help to provide further insight into the level of influx of birds from the continent (estimated at a few hundred birds in the 1990s; Laubek *et al.* 1998), albeit that this may vary with annual variation in weather conditions. Undertaking the population censuses within

Iceland rather than on the wintering grounds would help to resolve the issue of whether immigration/emigration is occurring but, given that Whooper Swans are widely dispersed across Iceland during the summer, and move from moulting to staging areas in the autumn (Gardarsson & Skarphedinsson 1984), the practicalities of undertaking such a survey would need to be considered with care.

Many of the British and Irish sites supporting internationally important numbers in 2005 did so in 2010, although some saw considerable variation in total numbers. There was a marked change, however, in the list of sites supporting nationally important numbers. Only two sites in Britain maintained qualifying numbers between the two censuses, whilst all those holding more than the all-Ireland threshold did not do so in 2005, with the exception of Strangford Lough, which was formally internationally important. These differences are, in part, likely to relate to the change in distribution caused by the cold weather in January 2010, with swans in Ireland using areas away from their traditional sites and the possible shift south in Scotland. Given this, it is difficult to conclude whether the variation in qualifying sites is indicative of a genuine shift in wintering sites used.

The 2010 results show a small increase in the proportion of the population overwintering in Iceland following a period of stability between 1995 and 2005, with the rate of increase in total numbers between the 2005 and 2010 censuses being much higher than that of the overall population (46% in Iceland compared with 11% overall). This alone provides little evidence, however, of a shift in the distribution of the population, *i.e.* an increasing proportion wintering closer to their breeding grounds in Iceland, hence further monitoring is required to see whether this upward trend continues.

Although no significant difference was found in the proportion of young recorded across regions there was considerable variation, ranging from 26.2% in west Iceland (small sample size) to 11.0% in east-central England. In Britain and Ireland, the highest proportion of young was found amongst flocks in the Northern Isles of Scotland, northwest Scotland and northwest England (excluding northeast England where only a few birds were aged). There was a significant difference in the frequency of brood sizes between countries, with larger families observed in Iceland and Ireland, reflected in the mean brood size which was highest in various regions of these countries. This variation in breeding success may reflect the preference for Whooper Swan families to stay closer to their breeding grounds, with non-breeding birds travelling further south (Rees *et al.* 1997).

Analysis of habitat use by Whooper Swans during the international censuses suggest a steady decline since 1995 in the use of permanent standing water with a corresponding increase in the use of arable land. It should be noted, however, that weather conditions in 2010 are likely to have had a strong influence on habitat choice, with many waterbodies being frozen for a long period of time and, in some regions, swans were observed in areas away from their usual sites. Similarly, it was suggested that wet, often flooded conditions during the 2005 census may also have influenced habitat selection, away from permanent waterbodies towards flooded grassland (Worden *et al.* 2009). The difference in habitat use is, however, noticeable between all censuses since 1995 which would suggest that swans are potentially altering their choice of feeding habitat. Further investigation and research is, however, needed to assess to what extent this is truly occurring.

The WeBS 2010 January count recorded a total of 10,996 Whooper Swans in Britain and Northern Ireland (Holt *et al.* 2011), which represents 67% of the census total for the country, highlighting the fact that WeBS misses a proportion of the population. This, together with the possibility that more birds may be wintering in Iceland, emphasises that a species-specific census is necessary to produce an accurate estimate of population size. Annual indices derived from WeBS data follow a trend similar to that calculated from the international censuses, indicating a pronounced increase in numbers from the mid- 1990s to the early 2000s in Britain, followed by a more steady increase up to 2009/10 (*i.e.* the latest year for WeBS data Whooper Swan trends published to date), whilst for Northern Ireland the index shows a very gradual increase in wintering numbers. This suggests that WeBS currently provides a reasonable indication of the trend in the Icelandic Whooper Swan population.

Results from the 2010 census show a sustained growth in the Icelandic Whooper Swan population and provide further evidence of a southerly shift in its wintering distribution. The increase in numbers may be attributable to several good breeding seasons for the population in the early 21st century, with the proportion of young present in wintering flocks estimated at 15.4%, 20.7%, 16.8%, 15.4% and 16.3% in 2006/07–2010/11 inclusive (Wildfowl & Wetlands Trust 2011), but survival analyses are required to determine any changes in mortality rates over time. Continued monitoring is required, however, to clarify whether this shift is sustained and to what degree the cold weather in 2010 may have exaggerated the pattern of occurrence, particularly given that results from the 2005 census suggested the proportion of swans wintering in Scotland was starting to increase.

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Appendix 1. Sites in Britain and Ireland exceeding current 1% thresholds for international importance (210; Wetlands International 2006) and national importance for Britain (110; Musgrove *et al.* 2011) and Ireland (130; Crowe *et al.* 2008) in January 2010, with the percentage change in numbers compared with the 2005 census.

Site	County	No. of swans in 2010	% Change from 2005
Sites of international importance in Britain and Ireland			
Ouse Washes (arable)	Cambridgeshire, Norfolk	5,632	66
Martin Mere & surrounding area	Lancashire	2,052	19
Loughs Neagh and Beg	Antirm, Armagh, Down, Londonderry, Tyrone	1,803	19
Lough Foyle	Donegal, Londonderry	883	–7
Upper Lough Erne	Fermanagh	799	29
Cashen River & Estuary	Kerry	506	121
Wexford Harbour & Slobs†	Wexford	411	204
River Foyle	Donegal, Londonderry, Tyrone	389	–12
Shannon Callows	Galway, Offaly, Roscommon, Tipperary, Westmeath	364	–16
Lough Oughter Complex	Cavan	361	33
Shannon & Fergus Estuary	Clare, Kerry, Limerick	339	54
Lough Swilly	Donegal	338	–33
Nene Washes†	Cambridgeshire	337	327
River Suck (Aerial)	Galway, Roscommon	331	2

Appendix 1 (*continued*)

Site	County	No. of swans in 2010	% Change from 2005
Solway Estuary	Dumfries & Galoway, Cumbria	290	–43
Little Brosna Callows†	Offaly, Tipperary	279	1,016
Lough Iron†	Westmeath	261	+
Blackwater Callows	Cork, Waterford	225	–57
Pear Tree Grove, Pilling Moss†	Lancashire	215	+
Kelton Mains†	Dumfries & Galloway	210	+
Sites of national importance in Britain			
Wigtown Bay	Dumfries & Galloway	177	19
Ballone†	Highland	142	+
Ribble Estuary*	Lancashire	119	–67
Abbey House, Abbeytown†	Cumbria	116	+
Loch a`Phuill (Tiree)†	Strathclyde	115	1,050
Sites of All-Ireland importance in Ireland			
River Blackwater (Meath)†	Meath	207	+
River Lagan†	Antrim, Down	204	1,569
River Boyne†	Meath	190	+
The Cull & Killag†	Wexford	181	71
Mullaghmore (Moylough/ L. Nalarsagh)†	Galway	174	81
River Moy†	Mayo	169	635
Strangford Lough*	Down	138	–41
Foxhall/Cloghans Hill†	Galway	136	+
East Ballinamore Lakes†	Cavan, Leitrim	135	16

† Site did not qualify during the 2005 census.
* Site was of higher importance status during the 2005 census.
\+ Site held no birds during the 2005 census.

Sites that did not maintain either internationally or nationally important numbers between the 2005 and 2010 censuses: Farmland near South Kinkell (Perth & Kinross), Finn-Lacky Catchment (Monaghan Fermanagh), Glen Lough (Westmeath), Loans of Tullich/Cromarty Firth (Ross & Cromarty), Loch Insh & Spey Marshes (Inverness), Loch Leven (Fife), Loch of Strathbeg (Aberdeenshire), Lyonstown Stud Farm (Tipperary), North Central Galway Lakes (Galway), Rinn Lough Lakes (Leitrim), River Isla; Bridge of Crathies (Perth & Kinross), River Tweed Norham (Northumberland), Tacumshin Lake (Wexford), Tara Mines Tailings Ponds (Meath), Tralee Bay, Lough Gill & Akeragh Lough (Kerry), Turraun Nature Reserve (Offaly), Wetlands east of Ballinrobe (Mayo Galway).

Habitat use, disturbance and collision risks for Bewick's Swans *Cygnus columbianus bewickii* wintering near a wind farm in the Netherlands

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Abstract

Each winter ~ 30% of the Northwest European Bewick's Swan *Cygnus columbianus bewickii* population feeds in Polder Wieringermeer, the Netherlands, on waste crops left after the harvest. The area has also become important for generating energy as a result of wind farm development. This study analyses pre- and post-construction data on Bewick's Swan distribution, movements and foraging behaviour in the vicinity of a nine-turbine wind farm site, in order to determine the effects of wind turbines on wintering swans. The swans' flight-lines between feeding areas and the roost were recorded visually and using radar over 10 evenings in good weather conditions. Food availability on different agricultural plots appeared to be an important factor explaining swan numbers and distribution in the area. In circumstances with even food availability early in the season, swans showed a preference for foraging in areas further away from the turbines, indicating some displacement caused by the turbines. Nevertheless, swans increasingly fed closer to the wind turbines during the course of the season in response to food availability. The likelihood that a single Bewick's Swan passing through the wind farm will collide with a turbine (collision risk) at the nine-turbine site, determined from swan movements through the wind farm (number of swan flights per unit length per unit time) and from regular searches for carcasses, was estimated at 0–0.04% in winter 2006/2007. Avoidance behaviour was observed, with birds navigating around and between the lines of turbines. The observed disturbance of foraging birds early in the season, the acquired knowledge of avoidance responses, and the calculated collision rates in this study can be used for future assessments during planning and construction of new wind farms in wintering areas of Bewick's Swans, especially in areas where important congregations of world or flyway populations occur.

Key words: barrier effects, Bewick's Swan, collision, disturbance, Wieringermeer, wind turbines.

Government plans to reduce carbon emissions to slow down global climate change, include increasing the capacity to generate energy from renewable sources such as wind and tide. A primary area for the production of wind energy in the Netherlands is Polder Wieringermeer, in the northwest part of the country. Traditionally this area was cultivated agricultural land, but nowadays it is also increasingly used for generation of renewable energy. By 2010, several wind farms had been built in the area, with a total of 54 large turbines (>1 MW, hub height above 70 m) installed, along with 36 smaller solitary turbines (0.85 MW, hub height ~ 50 m). These ninety turbines generate a total of 106 MW of electricity but new turbines planned for the future will increase the capacity to 400 MW.

The Northwest European population of Bewick's Swans *Cygnus columbianus bewickii* has decreased substantially in numbers since the mid 1990s. It was estimated at 21,500 individuals in January 2005, and national trend indices indicate a further decline since then (Rees & Beekman 2010). The swans breed in arctic Russia and a large proportion of the population winters in the UK and the Netherlands. Polder Wieringermeer is an internationally important wintering area for the species, with counts indicating that 25–33% of the population use the site each winter. The polder provides feeding grounds in close proximity to roosting places, and the birds are able to feed on crop remains (mainly sugar beet) left after the harvest, typically from November onwards (van Gils & Tijsen 2007).

Previous studies have discussed three main ways in which wind turbines can affect bird populations: through the disturbance and displacement of foraging and resting birds, by flying birds colliding with the turbines, and by the turbines potentially acting as a barrier during flight (Langston & Pullan 2003; Dirksen *et al.* 2007; Percival 2007; Drewitt & Langston 2008). Wind farms are known to have negative effects on some species (*e.g.* Madders & Whitfield 2006; Thelander & Smallwood 2007), but more detailed understanding of species-specific responses to the turbines is required for an adequate assessment of the impact of the turbines on bird populations. Research into the disturbance and displacement of birds has mostly focussed on changes in numbers at turbine locations (*i.e.* calculated a species-specific 'disturbance distance', *e.g.* Winkelman 1989; Schreiber 1993; Kruckenberg & Jaene 1999), but disturbance of foraging and resting waterbirds can also result in changes in physiology, behaviour and habitat choice (*e.g.* Orloff & Flannery 1992; Kruckenberg & Jaene 1999). Swans are potentially at risk of collisions because Whooper Swans are known to fly at altitudes of 5–45 m during commuting flights to feeding areas (Larsen & Clausen 2002). The collision risk (*i.e.* the probability that a given bird flying through the wind farm will collide with a turbine) is a combination of the probability of collision and the movement of birds through the wind farm area (*cf.* Desholm *et al.* 2006; Band *et al.* 2007). In general, the number of birds that collide with a turbine in a specific wind farm per unit time (*i.e.* the collision rate) differs between studies. Across species and locations, previously found collision rates range from 3.7–58 birds per year per turbine (*e.g.* Winkelman 1989; Winkelman 1992; Everaert & Stienen 2007). This rate depends on a range of factors including the number of birds flying through the area, the location and lay-out of the wind farm, landscape features, and the behaviour and physiology of the species (Thelander *et al.* 2003; Dirksen *et al.* 2007; de Lucas *et al.* 2008; Drewitt & Langston 2008; Martin 2011). The mortality rate and collision risk for Bewick's Swans have been modelled previously for a wind farm at Cheyne Court in the UK. Here, collision risk was estimated at 0.145 % of bird passages, with a mortality rate of 0.06 swans over 180 days, but it should be noted that the study used an avoidance rate of 0.9962 from observations made mainly of gulls (Painter *et al.* 1999) which have different flight characteristics (Chamberlain *et al.* 2006).

To the best of our knowledge, the study presented here is the first before/after assessment of the possible impact of wind turbines on Bewick's Swans at a wintering site. We used pre- and post-construction data to study whether the installation of multiple new wind turbines coincided with a change in Bewick's Swan numbers, distribution and habitat choice in the area. Furthermore, collision risk was assessed for Bewick's Swans at the site from a calculated collision rate and from measures of flight intensity through the area covered by the wind farm.

Methods

Study area

Between February 2003 (start of first building activities) and July 2006 (opening and first month of full operation), the Energy Research Centre of the Netherlands (ECN) built a wind farm in the spring and summer months in Polder Wieringermeer (52°49'54"N, 5°04'50"E) in one of the agricultural areas used by large numbers of wintering Bewick's Swans. This farm consists of two lines of different types of turbines positioned west–east with a northern row of five and a southern row of four turbines. All turbines were rated > 2.3 MW with an average hub height of 90 m and a rotor diameter of 100 m (*i.e.* a rotor sweep area of 40–140 m above ground level). Turbines in the northern row are on average 300 m apart whereas turbines in the southern row are ~ 400 m apart, and the two rows are 1,600 m apart. Small red lights shine during darkness on top of the hub.

The study area (~ 1,860 ha) around the ECN turbines was divided into two contiguous parts: the wind farm area (~ 770 ha) in which the new wind farm was built, and an adjacent unchanged area (~ 1,090 ha) with no new turbines, hereafter referred to as the 'control' area (see Fig. 4 for an outline of the study area). Some solitary wind turbines were present near farms (3 in the wind farm area; 6 in the unchanged area) in the study area. These were installed several years before the study commenced and were smaller (maximum height reached by the rotors = ~ 80 m) than the new wind farm turbines.

Displacement of swans from their feeding areas

Surveys of the study area were conducted at around midday on a near daily basis in the winter, prior to construction (from 23 October 2000 until 7 March 2001), and again after construction (from 27 October 2006 until 25 January 2007), to determine whether the swans were displaced from some of their feeding areas. The number of wintering swans present was recorded on each occasion, together with their distribution across the site and foraging behaviour. Swan numbers and distribution were also recorded in winters 2003/04 to 2005/06 inclusive, but these surveys were part of the monthly waterbird counts undertaken in the Netherlands, so were less frequent than in winters 2000/2001 and 2006/2007. Nevertheless, they provide a good indication of the numbers of swans present for each winter between the two study seasons. The distance from each group of swans (taken from the centre of the group) to the nearest turbine was measured using ArcGIS for each of the count days.

The swans' favoured food in the Polder Wieringermeer (mainly waste sugar beet and, to a lesser extent, carrots and potatoes) was available only between harvest and ploughing, the length of this period being determined by the farmers (Dirksen *et al.* 1991; W. Tijsen unpubl. data). Food availability in the study area was recorded during 2006/2007 (but not in 2000/2001) by mapping the different crop types on a field-by-field basis, keeping track of the harvest and noting the ploughing dates. By doing so, the total number of hectares of sugar beet fields was recorded. From farming records the total number of hectares of sugar beet fields in the study area in 2000/2001 could be determined.

Quantification of Bewick's Swan flights

The movements of swans passing the wind farm area during flights to and from night-time roosts were recorded visually and with radar. The use of radar provided precise information on flight behaviour (flight-lines) through and around the wind farms, as well as quantifying the number of flights, particularly during hours of darkness when visual observations were not possible. The radar system used was an X-band marine surveillance radar with a peak power of 12 kW (Furuno FR1510 MARK–3, X-band pulse repeat frequency 9,410 ± 30 MHz, vertical beam width 20°, rotation speed 24 rpm, supplied by Radio Holland Rotterdam) mounted on a 2 m high tripod. Radar range was set to 2.8 km to cover the entire study area. Due to lower detection probability at the outer limit of the radar range, effectively a circle around the radar with a radius of 2.5 km (19.6 km^2) was sampled. The radar system was positioned 0.8–1.5 km from the turbines and the radar thus reached a minimum of ~ 1 km beyond the turbines.

Bewick's Swan movements in the study area were monitored using radar over five evenings and the following mornings in winter 2000/01 from four hours around sunset and four hours around sunrise (two hours before until two hours after, in each case), to provide the Environmental Impact Assessment (EIA) of the proposed wind farm with baseline data on the flight-paths taken by the birds. Fieldwork was also carried out on seven evenings in 2006/2007, in differing but albeit generally good weather conditions for the time of year (temperature = 6°–15°C, wind direction = S–SW; wind speed = 3–7 Bft; cloud cover = 4/8 to 8/8; precipitation = dry, with only occasional showers), from approximately 2 h before to 2 h after sunset. The departure of different groups of Bewick's Swans from the fields to roosting areas on nearby Lake IJsselmeer was highly synchronised and occurred over a relatively short period of time. Observations continued until all swans, as determined by the swan survey earlier that day, had left the study area for the roost. In case of poor visibility (due to darkness), species identification was determined from the birds' flight calls and the characteristic behaviour (size and speed) of echoes on the radar screen. If a potential group of swans seen on the radar was out of audible range, one of the field observers was directed towards the flying group to confirm species identification. Swan movements were also recorded on three additional evenings in 2006/2007 at a second wind farm in Polder Wieringermeer ('Waterkaaptocht'; 52°51'46"N, 5°02'22"E; ~ 4 km from the study area), which has eight similar 2.3 MW turbines in one line (see Krijgsveld *et al.* 2009), to increase the number of flight records.

All bird tracks observed in the field were digitised and, if positively identified by field observers, flight-path specifications (*i.e.* date, time, species, number of birds and altitude of flight) were stored in an ArcGIS database. This database was used to produce maps of the swans' flight-lines within and around the boundaries of the wind farms. The detailed flight data made it possible to calculate the proportion of the swans present in the study area and in adjacent feeding areas that passed through the wind farm during flights to the roost. About 30 min after sunset observers were not able to observe flying swans in the field; however, at close distances, structures such as wind turbines might still be visible to flying swans, especially when some background illumination is present. As the exact extent of this phenomenon is unknown, we decided in this study to set the boundary between dark and light at 30 min after sunset, in other words when observers encountered reduced visibility. A diversion from the intended flight-path was defined as occasions when a swan discontinued its flight direction, in either the horizontal or vertical plane. These avoidance records were used in calculating swan movement ('flux') through the wind farm, which in turn was used to determine collision risk as described below.

Collision risk

The collision risk for Bewick's Swans in the study area was calculated by dividing the collision rate by the flux (*i.e.* the number of Bewick's Swan per area [m^2] within the wind farm per unit time). Collision rate was investigated by regular searches for corpses combined with corpse disappearance rate experiments. Between 27 November 2006 and 2 February 2007, the area below the turbines in the study area and also at the Waterkaaptocht wind farm was searched for collision victims at 2–3 day intervals. The additional wind farm was included to increase the probability of finding collision victims, as earlier research found that the frequency with which birds collided with turbines was low (*e.g.* Winkelman 1992; Krijgsveld *et al.* 2009). The area within a radius of 100 m of each turbine was searched, on the basis that previous studies found that victims fall within a radius of up to 1.1 times the hub height of the turbine (Winkelman 1992; Grünkorn *et al.* 2009), *i.e.* up to 88 m in this study. Swans are expected to fall at even closer range due to their high body mass (Krijgsveld *et al.* 2009). The searched area (100 m radius) therefore was considered large enough to include all potential victims. We included only those turbines under which vegetation type and height did not obstruct visibility of potential victims. Nevertheless, the total searched area in the winter of 2006/2007 was 15,697,457 m^2 (98.6%) of a total area of 15,927,874 m^2 around the turbines in both wind farms. The area below a turbine was searched either with binoculars from the base of the turbine (ECN wind farm) or by walking in parallel lines 4–6 m apart (Waterkaaptocht, see Krijgsveld *et al.* 2009), depending on visibility of potential victims. Because swans are conspicuous, with their large size and white colour, a detection probability of 100% was assumed. All victims found during the searches were recorded, photographed and sent to the Dutch veterinary laboratory CIDC-Lelystad for *post mortem* examination (internally and externally) to determine the cause of death.

Scavenging predators, such as Common Buzzard *Buteo buteo* and Red Fox *Vulpes vulpes*, roam the study area and might remove swan corpses during the study period, resulting in underestimates of collision rates. To determine the disappearance rate, seven defrosted carcasses were laid out in the study area (1 Brent Goose *Branta bernicla*, 4 Bewick's Swans and 2 Mute Swans *Cygnus olor*), placed semi-randomly in all directions at distances of 1–100 m from the turbines. Turbines used for the disappearance test were not used in victim searches, to avoid predators and scavengers being attracted to the former, which could lead to an increase in disappearance of collision victims. Presence and condition (eaten, moved, buried) of carcasses were registered for two weeks after carcasses had been laid out. The probability that a carcass remained at a location was calculated as the probability that a carcass present on day t was still present at day $t + 1$, day $t + 2$, *etc.* Calculations were similar to those undertaken by Winkelman (1992) to facilitate comparison with other studies.

The number of collision victims, corrected for observer efficiency and disappearance rate (Nc), was determined by correcting the number of victims found (Nf), for the probability that a victim remains at the location rather than disappearing through scavenging (Pd), the probability of finding a victim (Pf), the fraction of the total area (100 m radius) underneath the turbine that was searched (Fs), and for the fraction of days of the research period that victims were searched for (Fd). The corrected number of collision victims used to calculate the collision rate for swans within the whole wind farm was thus calculated as follows (following Winkelman 1992): $N\text{c} = N\text{f} / (P\text{d} \times P\text{f} \times F\text{s} \times F\text{d})$.

Statistical analysis

Data were analysed using SPSS version 15.0. Changes in swan numbers wintering in the study area over the years were calculated as a proportion of the total number recorded across Polder Wieringermeer (Fig. 1). The numbers of swans in the wind farm area and the adjacent unchanged ('control') area did not follow a normal or a Poisson distribution (Figs. 1 & 2); non–parametric statistics (Chi-square test and Spearman Rank correlation) therefore were used to analyse these data. Distance to the nearest turbine in relation to date (Fig. 3) was analysed using a logarithmic regression. Linear regressions on arcsine transformed proportionate data were used to model the carcass disappearance rate (Fig. 5). Mean values are given ± s.d. unless otherwise stated.

Results

Swan numbers during the winter

Bewick's Swans were present in the study area from 23 October to 7 March in winter 2000/01 and from 1 November to 28 January in winter 2006/07. The maximum numbers counted in the study area (*i.e.* in both the 'control' and the wind farm areas) were significantly lower in 2006/07 than in 2000/01 ($\chi^2_1 = 36.9$, $P < 0.001$; Table 1). The shorter period that swans were present in the area, in combination with the lower peak counts, resulted in fewer swan-days being recorded in the year following construction than beforehand ($\chi^2_1 = 128.6$, $P < 0.001$). The wind farm area and the adjacent 'control' area showed a similar decrease in the total number of swan-days, but the seasonal maximum count decreased more substantially within the wind farm site (Table 1).

In contrast, the maximum number of birds present across the whole of Polder Wieringermeer was higher after construction (Table 1). Pre-construction, in 2000/2001, up to 89% of the winter's maximum number of swans counted across Polder Wieringermeer was found in the wind farm area and 70% in the adjacent 'control' area. Post-construction, in 2006/2007, these percentages decreased to 24% and 29% respectively. The proportion of the total number of birds in Polder Wieringermeer that visited the study area decreased significantly in the years between 2000/2001 and 2006/2007 ($r_s = –0.90$, $n = 5$, $P < 0.05$; Fig. 1).

The proportion of the Northwest European Bewick's Swan population wintering in Polder Wieringermeer has increased during the study, from 5% of the total population in 2000/2001 to 11% in 2006/2007 (Rees & Beekman 2010; Table 1). In contrast, the study area within Polder Wieringermeer appears to have become less attractive with 5% of the Northwest European population present in 2000/2001 and 3% in 2006/2007.

Swan feeding distribution

There was a within-winter shift in the distribution of swans across the study area in relation to variation in the availability of sugar beet remains following the harvest in the 2006/2007 season. Numbers in the 'control' area correlated significantly with the number of hectares of fields with food remains in that area during habitat assessments ($r_s = 0.38$, $n = 85$, $P < 0.01$), but there was no significant association between the number of swans and the number of hectares with food remains in the wind farm area ($r_s = 0.24$, $n = 64$, n.s.). In 2000/2001

Table 1. Numbers of swan-days (sum of number of swans on each day of the field season, on days when counts were missing, gaps in data were calculated as the average of the two counts spanning the missing count) and seasonal maximum numbers in the 'control' and wind farm areas in the two study seasons 2000/2001 and 2006/2007. Also shown are the proportions of the total number of birds wintering in the Wieringermeer and of the total Northwest European population. Changes in abundance between the two study seasons are expressed as a percentage.

	2000/2001	**2006/2007**	**Change**
Total number of swan-days			
'Control' area	20,714	4,546	– 78%
Wind farm area	34,586	9,526	– 72%
Seasonal maximum count			
'Control' area	860	550	– 36%
Wind farm area	1,099	530	– 52%
Polder Wieringermeer	1,230	2,233	+ 82%
Proportion of Wieringermeer birds			
'Control' area	0.70	0.29	– 59%
Wind farm area	0.89	0.24	– 73%
NW European population (Rees & Beekman 2010)			
	23,000	21,500*	– 7%
Proportion of NW European population			
Polder Wieringermeer	0.05	0.11	+ 120%
Entire study area	0.05	0.03	– 40%

*Note that the Northwest European population figure for Bewick's Swans described in Rees & Beekman (2010) is based on the census of January 2005 and not 2007.

such a shift was not observed and Bewick's Swans were present in both 'control' and wind farm areas throughout the season.

The number of birds in the wind farm area increased when the number of hectares with available food decreased in the 'control' area (r_s = –2.53, n = 85, P < 0.05; Fig. 2). These results imply that, when food was available on fields both with and without turbines, the swans generally foraged in the area without the newly-constructed turbines. Up to 530 birds (95% of the peak count for the study area in 2006/07) were recorded on fields within the area with new

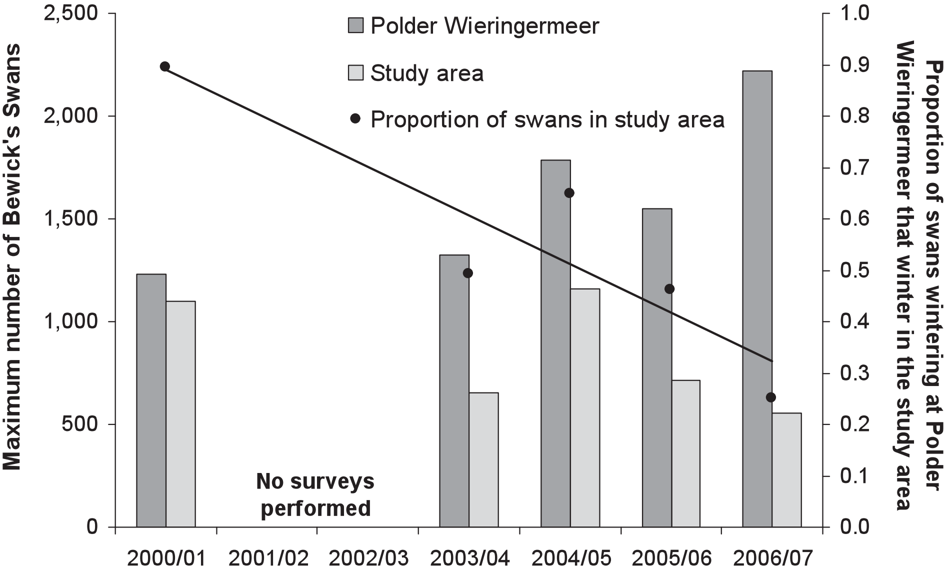

Figure 1. Maximum numbers of swans counted each winter in the study area and across the Polder Wieringermeer. The proportion of the Bewick's Swans wintering in Polder Wieringermeer recorded in the study area is also illustrated. The wind farm was built during the summer months between summer 2003 and summer 2006.

turbines on 12 individual days in November, but these were resting on grass and not foraging. At the beginning of the 2006/2007 season, when sugar beet remains were available in both areas, the swans foraged predominantly in the 'control' area. Later in the season when most of the fields in the 'control' area had been ploughed, the swans moved to the wind farm area and closer to the turbines to utilise the sugar beet remains that were still available there.

Bewick's Swans foraged significantly closer to the turbines as the season progressed (Fig. 3; logarithmic regression of distance of birds to the nearest turbine versus date: $F_{1,84} = 65.62$, $r^2 = 0.44$, $P < 0.001$). This effect was attributable mainly to a large number of birds feeding at greater distances from the turbines at the start of the season. Excluding these birds from the analysis still resulted in a significant, albeit smaller, decrease in the distance of the swans from the turbines as the winter progressed ($F_{1,77} = 21.05$, $r^2 = 0.22$, $P < 0.001$). The decrease in distance was not due to the distribution of harvested fields as the distance of harvested fields to the turbines did not decrease significantly during the course of the season (linear regression of distance of fields to the nearest turbine versus date: $F_{1,32} = 0.39$, $r^2 = 0.01$, P = n.s.). The distance between foraging and resting Bewick's Swans and the turbines was on average 560 m (s.e. = 57.9, n = 86), whereas the minimum recorded distance was 125 m.

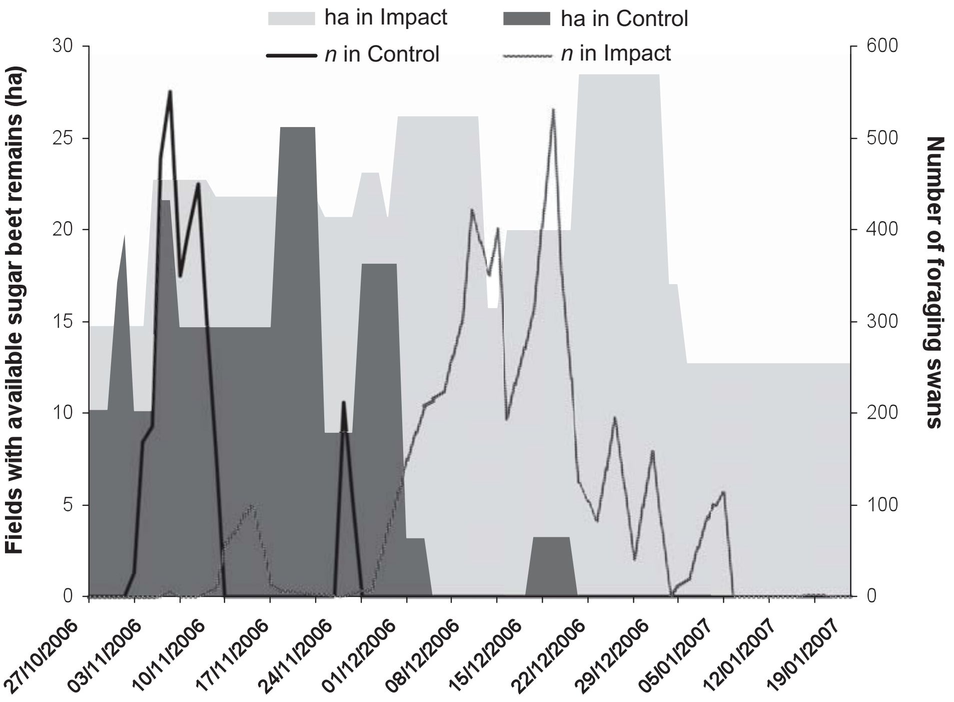

Figure 2. Numbers of swans in the 'Control' (no new large wind turbines) and wind farm 'Impact' (nine new large wind turbines) sections of the study area in relation to the availability of sugar beet remains. Early in the winter, when waste sugar beet was available in both areas, Bewick's Swans fed in areas away from the turbines.

Swan flights in the study area

Swans flew towards the roosting sites in the late evening and early night. At least 1,664 Bewick's Swan flight-paths for 101 groups flying to the roost were recorded in both wind farms during eight out of ten fieldwork evenings in 2006/2007 (flights were not recorded during two evenings as swans were absent from the study area and no swans flew past from adjacent areas). This is a minimum estimate of the total number of swan flights as 33 groups were recorded only as radar tracks in complete darkness, > 30 minutes after sunset. The birds giving these tracks could be identified as Bewick's Swans on the basis of flight calls but group size could not be determined. A minimum group size was estimated on these occasions, based on the number of birds counted by the field observer earlier in the day. There was substantial variation in the timing of the evening flights to the roost. Of all groups of swans, 61 ± 41% (range: 0–100%, $n = 7$ nights, 101 groups) flew after dark (> 30 min after sunset) each night in 2006/2007. Group size was limited to 16 ± 41 (range 1–300) birds at maximum. Of all

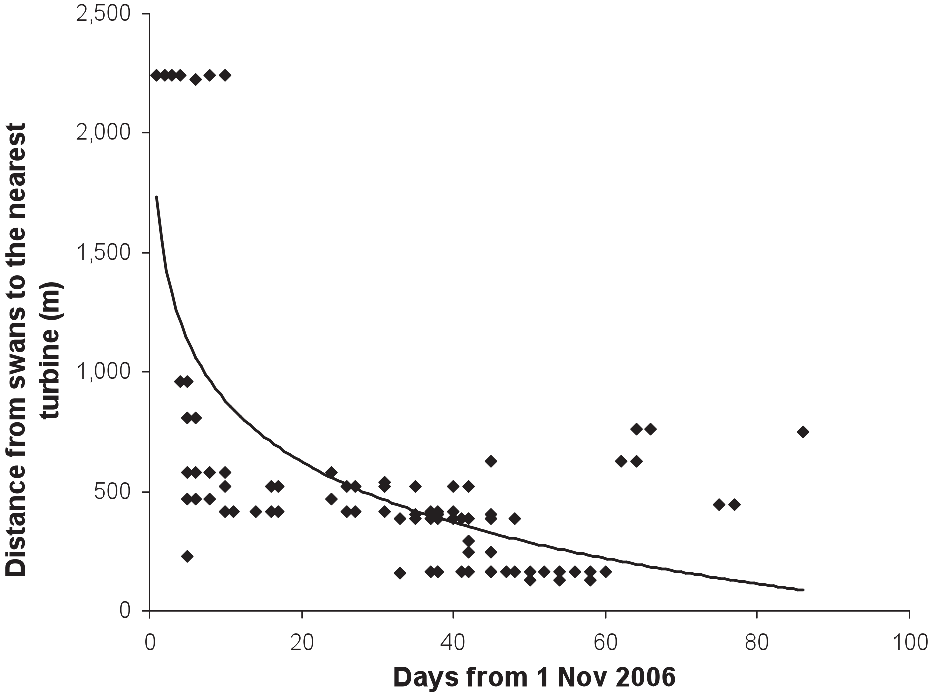

Figure 3. Distance of Bewick's Swan flocks in the study area to the nearest turbine during the course of winter 2006/07, from 1 November onwards (logarithmic regression with $r^2 = 0.44$).

individual swans flying towards the roosting sites, 75 ± 35% (range: 0–100%, *n* = 7 nights, 1,664 birds) flew after dark. Birds that flew past the outer edge of the wind farm adjusted their flight direction at a distance of a few hundred metres at maximum (*n* = 562 birds). Of all swans present in the area an average per day of 16 ± 22.5% (range: 0–65%) flew through the wind farm during commuting flights (Table 2).

In 2000/2001, Bewick's Swans generally flew in straight lines from fields where they had been feeding during the day towards the roost site (Lake IJsselmeer), although no fixed flight-paths through the landscape were identified. Foraging areas were similar in 2006/2007 (albeit not identical to those recorded in 2000/01, due to crop rotation and a decrease in the area of sugar beet available) and birds were seen to fly in a similar direction to the roost. In 2006/2007 birds adjusted their flight-paths to the presence of the wind turbines during both light and darkness; however, neither large deflections around the entire wind farm nor panic reactions in the air were observed. Birds avoided turbines by navigating around individual turbines and between rows of turbines (as illustrated for the evening of 24 November 2006 in Fig. 4).

Table 2. Bewick's Swan flights in the study area (ECN) and in the nearby Waterkaaptocht wind farm (WK), recorded as visual and radar observations of the swans' flight-paths. The number of swans that were present in, or flying through the study area is shown; the percentage of these birds that flew close to or through the wind farm during commuting flights (% head towards wind farm), and thus potentially at risk of collision, was calculated (*i.e.* number flying towards wind farm/number swans*100). Of the birds that flew toward the wind farm, some avoided the wind farm entirely (% deflecting, *i.e.* number deflecting/number swans*100) and some flew through the wind farm (% through wind farm, *i.e.* number through wind farm/number swans*100).

Date	Location	No. swans	% head to wind farm	% deflecting	% through wind farm
21 Nov 2006	ECN	94	18	14	4
24 Nov 2006	ECN	294	100	98	2
01 Dec 2006	ECN	51	100	100	0
07 Dec 2006	ECN	459	66	1	65
16 Jan 2007	ECN	9	100	100	0
01 Dec 2006	WK	351	43	12	32
03 Jan 2007	WK	227	70	53	16
10 Jan 2007	WK	206	26	17	9
Mean ± s.d.		211 ± 155.1	65 ± 33.6	49 ± 44.0	16 ± 22.5

Collision rate estimates

Two Bewick's Swans were found dead during > 2 months of searching for corpses in the study area (31 field days, average interval between searches = 2.3 days). Collision with the wind turbines could be ruled out as the cause of death in both cases for the following reasons: 1) there were no fractures or dislocations found during *post mortem* examinations, 2) the birds were found > 150 m from the turbines, and 3) the birds were found upwind of the wind farm and the wind force was strong (4–5 Bft) on both days. Dissection did not reveal a clear cause of death and it was assumed that the swans had died of natural causes or been killed by a predator. That no swans were found to have collided with the turbines during the study period does not however, mean that the collision rate was zero. In order to consider the potential consequences of collision–related mortality, a collision rate was determined based on the assumption that

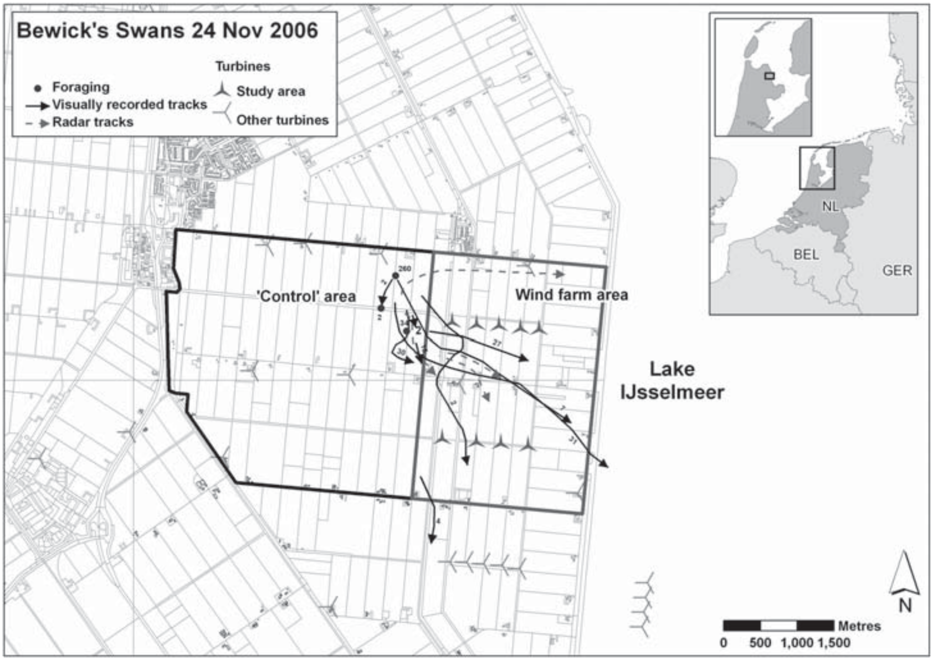

Figure 4. Map of the study area, showing the wind farm area (eastern part) and the adjacent 'control' area (western part), with Bewick's Swan flight-paths (arrows) from foraging fields to the Lake IJjsselmeer roost on 24 November 2006. Numbers adjacent to the arrows indicate group size. Insert shows the location of the study area within the Netherlands.

one turbine victim was found in this study. This does not provide an absolute measure of collision rate, but does give a maximum estimate of collision rate for the studied season. This figure can subsequently be used to estimate maximum collision risk (see next section). The probability that a victim was found (*P*f) was set to 1 (see Methods section).

The disappearance tests found that seven carcasses placed in the study area disappeared at a slow rate (Fig. 5). After four days, two were scavenged but all were still present and recognisable. Only one bird, a Mute Swan, totally disappeared during the 14-day trial; it was found to have been buried by a Red Fox at the foot of a turbine, six days after being laid out. The remaining six carcasses were still present and recognisable after fourteen days. A scavenging animal moved two birds, by 1 m and 25 m respectively. The probability (*P*d) that a bird was still present (after the average search interval in this study: 2.3 days) was 0.97 (linear regression: *P*d = –0.0255* number of days since placement + 1.026, $r^2 = 0.71$, Fig. 5). The proportion of the total area underneath the turbine that was searched (*F*s) was 0.986. The proportion of days over the search period that victims were searched for (*F*d) was set to 1 as the mean interval between searches was smaller than the quickest disappearance of laid-out corpses.

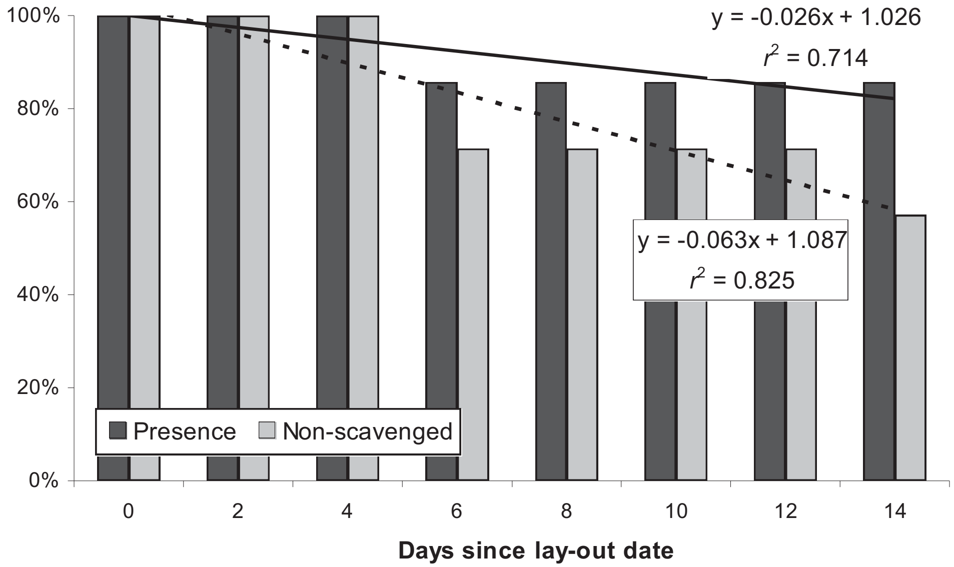

Figure 5. Status of seven carcasses for up to 14 days after being placed in the study area. Shown are the percentage of carcasses still present at the location after x days (black bars, closed line, linear regression r^2 = 0.71 and a slope of –0.026) and the percentage of carcasses remaining at the location without being scavenged by predators (grey bars, dotted line linear regression r^2 = 0.83 and a slope of –0.063).

Fitting the number of collision victims found (between zero and one) to the above parameters, gives an estimated collision rate of 0–1.05 swans colliding with the turbines each season for both wind farm sites. The study season consisted of 1,163 'turbine search days' (number of turbines * number of search days) so the estimated collision rate is 1.05/1,163 = 0.0009 per turbine per night. This collision rate implies a maximum of approximately 2–3 victims per winter (15 October – 15 March) in both wind farms considered in this study.

Collision risk

The near-daily swan counts gave an average of 132 Bewick's Swans present each evening during the 2006/2007 winter. Of these 132 birds, 16% flew through the wind farm area (see the swan flights section above). Assuming that the route to and from the roosting area is flown twice per day, and that dusk flights are as risky as dawn flights (noting that light levels are low in both cases), an average of 42 swan-flights pass the turbines every 24 h. With an estimated maximum collision rate of 0.0009 birds per turbine per night, the maximum collision risk can be calculated as: (17 (turbines) * 0.0009)/42 = 0.0004 (fraction), or 0.04% of all swans passing the two wind farms. Because no actual collision victims were found, this collision risk reflects the maximum risk; the actual risk estimate is of 0–0.04 % of Bewick's Swans passing these particular turbines colliding with them in each 24 h period.

Discussion

Disturbance of foraging swans

The proportion of the total number of Bewick's Swans wintering in Polder Wieringermeer that visited the study area was significantly lower after construction of the wind farm (2006/2007) than before it was built (2000/2001). This decrease was particularly evident in the wind farm area in comparison with the adjacent area, suggesting that the birds had been displaced by the newly-constructed turbines. Whilst the installation of the turbines seems to have made the wind farm area less attractive to the swans, the birds' use of the 'control' area (without newly-built turbines) also diminished, probably due to changes in food availability between the two study seasons. In particular, a smaller proportion of the study area was used for sugar beet cultivation in 2006/07 compared with 2000/2001 (100 ha *versus* 64 ha). On arrival in the Netherlands, Bewick's Swans start feeding on water plants in other parts of the country and only start feeding on crop remains in Polder Wieringermeer later in the season (Beekman *et al.* 1991; Dirksen *et al.* 1991). The timing of availability of harvest waste is thus important for wintering Bewick's Swans in the Netherlands and an absence or lower availability of crop remains might cause shifts to other foraging areas.

Our study found that displacement of Bewick's Swans from the wind farm area was most evident at the start of the season, when there appeared to be an abundant food supply for the birds. The swans were more likely to forage in areas without turbines while food was available in both the 'control' and wind farm areas. Only later in the season, when food sources were limited to just the wind farm area, swans increasingly fed in areas closer to the turbines. This decreasing distance between foraging swans and the turbines may be due to a lack of food further afield, to habituation to the wind farm, or a combination of these factors. Displacement by wind turbines has also been reported for Whooper Swan *Cygnus cygnus* and for several species of geese, with the displacement of birds evident up to 400 m of the turbines (Winkelman 1989; Kruckenberg & Jaene 1999). Habituation to wind turbines has also been found for the same species (Kruckenberg & Jaene 1999; Larsen & Madsen 2000; Madsen & Boertman 2008). Devereux *et al.* (2008) showed that wintering farmland birds (non–waterbirds) were not influenced by wind turbines; however, our results suggest that these results are not applicable across all species wintering in farmland areas.

Barrier effects

Although the swans appeared to be displaced from potential feeding areas, there was no evidence for the wind farm acting as a barrier during the evening flight; the birds navigated between and around the turbines during their flights to the roost. This ability to adjust their flight-paths is in line with studies made of other waterbird species (Dirksen *et al.* 1998; Tulp *et al.* 1999; Desholm & Kahlert 2005; Masden *et al.* 2009). The small size of the wind farm in this study (nine turbines in two rows) and the large spacing between turbines may have helped to ensure that these two lines did not act as a barrier to flying birds. The use of modern large wind turbines may help both to make the structures more obvious to the birds (thus reducing collision risk) and also perhaps reduce the chance that birds perceive the turbines as barriers because the larger spacing between individual turbines makes it easier for the birds to pass between them (Krijgsveld *et al.* 2009). The same reasoning can be applied to increasing the numbers of turbines within a wind farm, as more turbines will enhance the perceived barrier effect. The orientation of the turbine rows will also have an effect, since turbines constructed in rows parallel onto the dominant flight direction of birds commuting between foraging and sleeping areas will present less of a barrier than when perpendicular to it. In the extreme, such a barrier effect could potentially render roosting or foraging sites inaccessible, especially where the energetic costs of avoidance make significant additional contributions to energy budgets. Due to crop rotation, flight-paths could potentially change between years. In this study, tracking of flight-paths was limited to only one pre- and one post-construction year; adequate assessment of barrier effects requires monitoring in multiple pre- and post-construction years.

Collision risk

Avian turbine collision risk varies widely between species and also between habitats; for instance, raptors are often found to collide with turbines in mountainous areas (de Lucas *et al.* 2008; Smallwood & Thelander 2008). Swans and geese are rarely reported as turbine victims, although swan collisions with power-lines have been recorded frequently (*e.g.* Brown *et al.* 1992; Rees 2006). This study found no collision victims among Bewick's Swans during the research period, but the assumed one collision victim per season would equate to 0–0.04% of swans passing the wind farm turbines. These probabilities are very low but are similar to results from extensive research at two other turbine farms involving geese and swan in other parts of the Netherlands (Krijgsveld *et al.* 2009). The collision risk at this wind farm is lower than that calculated for Bewick's Swans in the UK (from Chamberlain *et al.* 2006) at a larger study site (26 *versus* 9 turbines), located near Romney Marsh, a proposed Ramsar site with nationally important numbers of Bewick's Swans for the UK. However, numbers of swans on Romney Marsh were much lower (mean maximum = 123 swans per winter during 2005–2009, Calbrade *et al.* 2010) than in the current study at the Polder Wieringermeer.

This study covered no evenings and mornings with fog or mist; on nights with poor visibility, collision risk for swans could be higher (Brown *et al.* 1992). However, evenings or mornings with poor visibility (< 300 m) were rare (five out of 114 dusks and dawns, Royal Netherlands Meteorological Institute, KNMI-station Berkhout, 21.11.2006–6.01.2007, downloaded from www.knmi.nl), so effects of fog or mist probably have negligible effects on the collision risks found in this study.

Given our various assumptions, we suggest a mortality rate of 0–3 swan victims per winter for the whole wind farm, of similar order of magnitude to 0.06 swans per 180 days found for the UK (from Chamberlain *et al.* 2006). Collision risk can be estimated, but where low, actual collision rates can be difficult to determine. In other studies, casualties are most frequent in bird-rich areas and on mountain ridges (Hötker *et al.* 2006; Thelander & Smallwood 2007; de Lucas *et al.* 2008), but elsewhere, chances of collision are much lower. To date, no clear avian population effects from wind turbines have been demonstrated, although these effects will be greater for long-lived species with low reproductive rates, such as seabirds and raptors (Thelander *et al.* 2003; Horch & Keller 2005; Hötker *et al.* 2006; Stienen *et al.* 2007). In the case of the Bewick's Swans in Polder Wieringermeer the collision risk calculated in this study is so low that it is not expected to cause negative effects on the locally wintering swans. However, as Polder Wieringermeer now supports large numbers of individual wind farms, the combined effects of all these wind turbines, together with changes in cropping and land use, could combine to reduce overall wintering numbers of swans even in the absence of collision mortality.

Implications for conservation and future developments

In conclusion, this study shows that although the collision risk for swans with turbines was low at the site, wind farms can result in a diminished use of foraging habitat. Increasing demand for renewable energy could result in more and larger turbines which could reduce the attractiveness and carrying capacity of Polder Wieringermeer for wintering Bewick's Swans. Polder Wieringermeer is a key wintering area for > 3% of the Northwest European Bewick's Swan population, whilst the adjacent Lake IJsselmeer roosts are of international importance under the EC Birds Directive and are designated as a Natura 2000 Specially Protected Area. This Birds' Directive Annex I species has declined in recent years (Wetlands International 2006; Rees & Beekman 2010) so changes to the potential carrying capacity of these important areas should be considered with caution. The increasing use of rural land in Polder Wieringermeer for the construction of wind turbines may have adverse impacts on the quality of the habitat for wintering waterbirds in the future.

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Photograph: Bewick's Swans on pasture in the Netherlands by Jelger Herder (www.digitalnature.org).

Limits of grazing area use by feral Greylag Geese *Anser anser* during moult

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Abstract

Use of grazing areas by feral Greylag Geese *Anser anser* was studied from May–September 2010 to compare grazing pressure at two feeding sites during and after moult. Grazing pressure was determined from weekly counts of goose droppings within random 5 m^2 plots; vegetation height and composition were measured to determine whether variation in food supply influenced the extent to which geese used the two sites. Distance from the water's edge explained much of the variation in goose grazing across sites, with birds less likely to use areas furthest from open water during moult.

Key words: distance to open water, grazing pressure, vegetation cover.

Foraging decisions can affect an animal's chances of survival (Alcock 1993) and reproductive success (Black *et al.* 2007). Geese tend to select food plants high in nutrients and low in fibre (Prop 1991; Black *et al.* 2007) and food quality is a major factor determining where they feed (Owen 1971; Van der Graaf 2006). When choosing a feeding site, geese balance their need for nutrients against the probability of disturbance and predation (Fox & Kahlert 2000; Kahlert 2006). Optimal feeding areas therefore need to be sufficiently open to detect approaching predators (Madsen 1985). The main reasons for geese leaving a feeding area are usually disturbance by a real predator (foxes or hunters), a quasi-predator stimulus (*e.g.* noise, helicopter or car) or a false alarm (Madsen 1985; Kahlert 2006). Disturbance that leads to physical escape is an energetically costly process, and additionally reduces the time available for feeding (Kahlert 2006).

In cities such as Stuttgart, disturbances are plentiful; people walk up to the geese, children try to catch them and dogs, cars or helicopters can cause the birds to retreat to the safety of an open water body. Geese usually flee by walking quickly or flying to water, which provides safety from most terrestrial predators (Schwarz 2010). During moult, geese are flightless for up to five weeks (Cramp & Simmons 1977; Taylor 1995) making them more vulnerable to interference and predation at this time. In principle, geese should prefer to graze at the water's edge when flightless, enabling retreat to safety from predators. If all geese were to do this, however, the vegetation close to the water would quickly become depleted or of reduced nutritional quality, and under these circumstances the geese may experience more agonistic behaviour as they compete for limited resources. Thus areas close to the water need not necessarily be preferred during the moult.

Detailed studies of habitat use by moulting geese have been carried out mostly in the birds' natural environment, for instance in Alaska for Black Brant *Branta bernicla nigricans* (Weller *et al.* 1994; Lewis *et al.* 2011), in Greenland for Pink-footed Geese *Anser brachyrhynchus* and Barnacle Geese *Branta leucopsis* (Madsen & Mortensen 1987) and on the Danish island of Saltholm or in the Oostvaarderplasen, the Netherlands, for Greylag Geese *Anser anser* (Fox & Kahlert 2000; Loonen *et al.* 1991). There have, however, been few studies of habitat use by geese in urban areas (Käßmann & Woog 2008), and to the best of our knowledge there have been no such studies to date made during the moulting period. Urban habitats may differ from more natural settings in that geese are more used to people, show lower flight distances, perceive predation risk differently and are exposed to other forms of disturbances. This study therefore analyses grazing pressure in relation to vegetation height, vegetation cover and distance to water at two feeding sites used by Greylag Geese in an urban environment (Stuttgart, Germany), and investigates whether the birds' use of these sites – particularly their proximity to water – varies depending on whether or not the birds are in moult.

Methods

Study area and study population

Since first breeding successfully in 1995, a population of feral Greylag Geese *Anser anser* has become established in Stuttgart, southwest Germany (48°46'N, 9°10'E; Woog *et al.* 2008). Numbers increased to 282 individuals by 2010 (Schwarz 2010; Woog *et al.* 2012), and birds also moult in the area, mostly from late May – late June. Woog *et al.* (2011) provide a more detailed description of this population.

Observations were made from 24 May – 5 September 2010 at two sites in Stuttgart, used by the geese throughout their annual cycle: 1) a system of three small lakes in a park close to the inner city ("Park"), which has a small flock of *c.* 30 moulting geese, and 2) a lake 7 km to the north along the river Neckar (Max-Eyth Lake, "MES"), heavily used for leisure activities, but also the most important breeding site for geese in the area, which has a flock of about 200 geese during moult (Woog *et al.* 2008). Regularly mowed pastures around the lakes offer year-round high quality grazing (Schwarz 2010; Woog *et al.* 2012) as repeated mowing increases the protein content of many grasses and herbs (Ydenberg & Prins 1981; Gadallah & Jefferies 1995). In Stuttgart, geese are used to humans and, when able to fly, most individuals walk away for only a few meters to avoid them. They strongly react towards dogs, however, especially large ones (Schwarz 2010). Dogs and people account for 30% of known causes of goose mortality ($n = 17$) in the city (F. Woog, unpubl. data). There has been no evidence for predation by nocturnal foxes or mustelids in the past decade (2002–2012), which may be attributable to the geese being mostly diurnal and spending the night on water or on islands.

Data collection

Grazing pressure was expressed as dropping density per 5 m^2, which is considered a better measure than observational data of how markedly different areas are used for grazing (Ebbinge *et al.* 1975; Ydenberg & Prins 1981; Woog & Black 2001; Black *et al.* 2007). Ninety two circular plots each covering 5 m^2 were placed along randomly selected transects (Park: n = 46, MES: n = 46) at varying, measured, distances from the water. Droppings were counted and removed weekly from the plots. Resting piles of droppings produced by loafing geese where counted but later excluded from the analysis, as were plots close to points where people feed the birds.

Vegetation height was measured each month, by placing a ruler at three random points within each plot, and recording (to the nearest mm) the maximum height of the vegetation. As the grass was of uniform length, this gave a good measure of the height of the sward. Vegetation cover was also estimated at the start of the field season by assessing, to the nearest 5%, the percentage cover for herbs, grasses, moss and soil within each plot.

Data analyses

Generalized linear models (GLMs) in program "R", version 2.11.1. (R Development Core Team 2010), were used to determine factors that had a significant influence on grazing pressure. The number of droppings per plot was used as the dependent variable and a quasi-Poisson error distribution with logarithm link function was used to fit these data in the GLM. To reduce the effects of data dependency between weekly measures, the number of droppings accumulated (*i.e.* grazing pressure) were analysed for different time periods. Firstly, the complete study period (from 24 May – 5 September 2010) was considered. Secondly, to test the effects of moult, we summed droppings accumulated over the four weeks when most birds were flightless (24 May – 20 June) and compared this with droppings accumulated during four weeks when all birds were capable of flight (9 August – 5 September).

Explanatory variables included in the model were field number, distance to the water, vegetation height, total vegetation cover, grass cover and herb cover. All explanatory variables were categorical. The distance to the edge of the water was classed as: 1) < 30 m, 2) 30–60 m, and 3) > 60 m; vegetation height as: 1) < 6 cm, and 2) 6–9 cm; vegetation cover as: 1) ≤ 120%, and 2) > 120%; and grass cover and herb cover were each classed as: 1) < 40%, 2) 40–80%, and 3) > 80%.

Variation in the dropping data was explored initially by testing the effects of each explanatory variable, independently, in an ANOVA. All explanatory variables were then fitted to one model (GLM) sequentially. As the cover parameters were correlated (vegetation cover and grass cover, $r = -0.3$, $P = 0.003$; vegetation cover and herb cover, $r = 0.57$, $P < 0.0001$; grass cover and herb cover, $r = -0.96$, $P < 0.0001$), only total vegetation cover was included in the

GLM. Thirdly, various models were tested against each other using *F*-tests, as recommended by Bolker *et al.* 2009 for quasi-Poisson models. Model testing followed the procedure proposed by Korner-Nievergelt & Hüppop (2010), in which a model containing one explanatory variable (*e.g.* "site") is compared with a model containing the same and an additional variable (*e.g.* "site" + "distance to water"), and a significant *F*-test indicates that the second variable has an additional explanatory value. This was done for all explanatory variables separately. The most significant explanatory variable was then included in the next model (thus controlling for it in subsequent tests), which was again compared against models containing an additional variable (*e.g.* the first model "site" + "distance to water" was tested against a second model containing "site" + "distance to water" + "vegetation cover"), until inclusion of additional variables no longer improved the explanatory power of the model.

Results

When testing single terms, grazing pressure varied most with site ($F_{1,90}$ = 18.68, $P < 0.001$; Fig. 1), with the Max-Eyth Lake having much higher dropping densities than the Park. Geese preferred plots with high grass cover (> 80%; $F_{2,89}$ = 11.45, $P < 0.001$), low herb cover (< 40%; $F_{2,89}$ = 7.0; $P < 0.01$) and that were close to the water's edge ($F_{2,89}$ = 13.78, $P < 0.001$; Fig. 2). Total vegetation cover and vegetation height tested as single factors had no influence on grazing pressure. There was little variation in vegetation height (of the 95

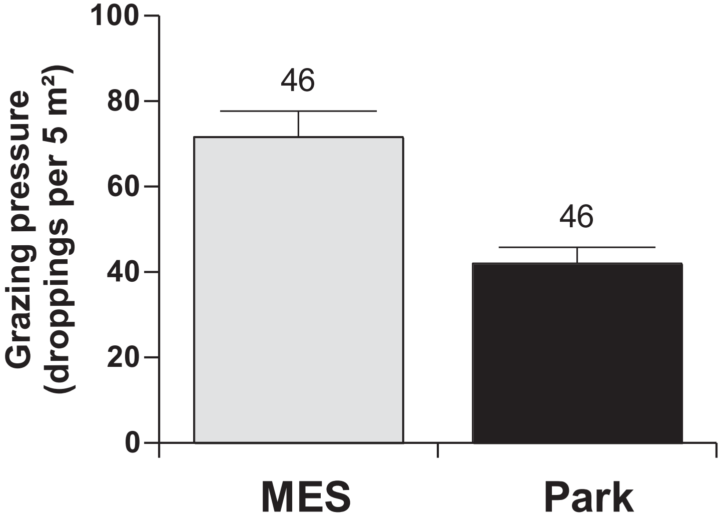

Figure 1: Mean grazing pressure (± s.e.) at the two study sites, measured as cumulative droppings from 24 May – 5 September 2010. "MES" = Max-Eyth Lake, "Park" = park close to the inner city, Stuttgart. Sample sizes indicate the number of plots per pasture.

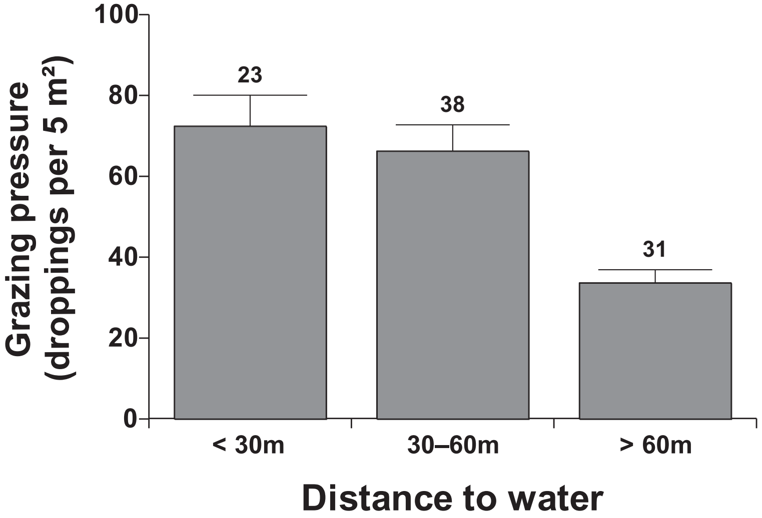

Figure 2: Mean grazing pressure (± s.e.) by Greylag Geese in Stuttgart (cumulative number of droppings between 24 May – 5 September 2010), in relation to the distance of the dropping plots from the water's edge. Sample sizes indicate the number of plots surveyed.

plots, 56% were < 6 cm and 34% were 6–9 cm).

On considering the entire study period, regardless of whether or not the birds were in moult, only "site" and "distance to water" had a significant effect on grazing pressure (GLM: $F_{1,90}$ = 34.0 and $F_{2,88}$ = 37.67 respectively, P < 0.001 in each case); vegetation height and vegetation cover did not prove significant ($F_{1,87}$ = 2.64 and $F_{1,86}$ = 0.87, n.s.) when included in the model. When controlling for "site", only "distance to water" and "grass cover" were significant, but when controlling "for distance to water" then "site", "grass cover" and "herb cover" had an influence (Table 1). On controlling for "site" and "distance to water" at the same time, none of the vegetation parameters remained significant (Table 1).

The data were grouped into the four weeks during moult (when birds were flightless) and four weeks during the period when birds were able to fly to test the effects of moult, on the birds' use of the different sites. For this reduced dataset, "site" and "distance to water" again had a significant effect on grazing pressure (GLM: $F_{1,182}$ = 26.94 and $F_{2,179}$ = 21.21 respectively, P < 0.001 in each case), with "moult" also proving significant ($F_{1,181}$ = 6.17, P < 0.05), but not vegetation cover and vegetation height ($F_{1,178}$ = 0.48, n.s. and $F_{1,177}$ = 2.12, n.s.) when these terms were included sequentially in the model. Because grazing pressure was significantly higher at the Max-Eyth Lake than at the Park (Fig. 1), changes in feeding distribution at the two sites were tested separately in subsequent analysis. During moult, grazing pressure

Table 1. Significance of explanatory variables added to three initial models, to test the effects of site, distance to water, vegetation height and vegetation cover on Greylag Goose grazing pressure (expressed as droppings/5m^2 accumulated over the entire study period). Each of the three models in the left column was tested against that model plus one of explanatory variables on top (*i.e.* Droppings~Distance to water was tested against Droppings~Distance to water+ % grass cover *etc.*). The site and the distance from open water explained most of the observed variation in grazing pressure. Significant results are given in bold.

Initial model	**Variables added to the model**					
	Site	**Distance to water**	**% Grass**	**% Vegetation**	**% Herbs**	**Vegetation height**
Droppings~Site	X	**$F_{2,88} = 37.55$** **$P < 0.001$**	**$F_{2,88} = 3.20$** **$P < 0.05$**	$F_{1,89} = 0.85$ $P = 0.36$, n.s.	$F_{2,88} = 0.88$ $P = 0.42$, n.s.	$F_{1,89} = 0.19$ $P = 0.66$, n.s.
Droppings~Distance to water	**$F_{1,89} = 62.74$** **$P < 0.001$**	X	**$F_{2,87} = 15.79$** **$P < 0.001$**	$F_{1,88} = 3.25$ $P = 0.07$, n.s.	**$F_{2,87} = 12.13$** **$P < 0.001$**	$F_{1,88} = 0.27$ $P = 0.60$, n.s.
Droppings~Site + Distance to water	X	X	$F_{2,86} = 0.76$ $P = 0.47$, n.s.	$F_{1,87} = 0.86$ $P = 0.36$, n.s.	$F_{2,86} = 0.60$ $P = 0.55$, n.s.	$F_{1,87} = 2.23$ $P = 0.14$, n.s.

decreased with distance to water at both sites, but this was more evident at Max-Eyth Lake (Fig. 3; Tables 2a,b). The geese used plots at distances of ≥ 30 m less during the moulting period. When birds were able to fly (*i.e.* not moulting), distance to water did not have a significant influence on grazing pressure ($F_{2,43}$ = 2.66, P = 0.08 and $F_{2,43}$ = 0.7, P = 0.5 for non-moulting geese at MES and the Park, respectively; n.s. in each case). Moreover, grazing pressure at the Max-Eyth Lake was much higher than at the Park during moult ($F_{1,90}$ = 70.1, P < 0.001), whereas outside the moulting period grazing pressure was similar between the two sites ($F_{1,90}$ = 0.21, P = 0.65, n.s.).

Discussion

During moult, feral Greylag Geese in Stuttgart preferred to graze closer to the water and this was not influenced by vegetation height or vegetation cover. Moulting geese used areas at greater distances from the water less, and this reduced the area available for foraging. Fox & Kahlert (2000) found a reduced feeding range of moulting Greylag Geese on the Danish island of Saltholm. This is a pattern also found for feral Greylag Geese in

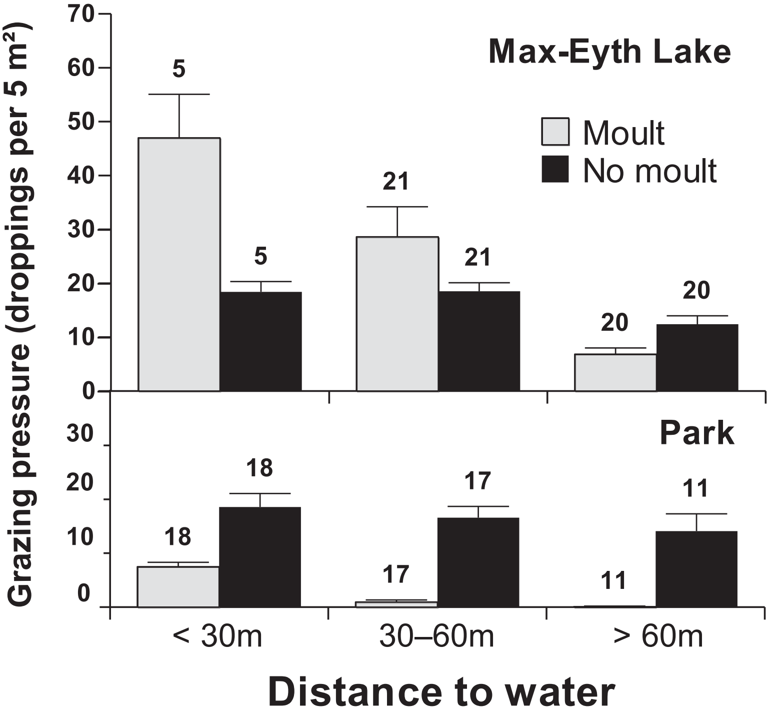

Figure 3: Mean grazing pressure (± s.e.) by Greylag Geese during moult (grey bars; 24 May –20 June) and after moult (black bars; 9 August – 5 September) at the Max-Eyth Lake and the "Park", in relation to the distance of the dropping plots from water. Sample sizes indicate the number of plots surveyed.

Table 2. Significance of explanatory variables added to two initial models, to test the effects of distance to water, moult, vegetation height and vegetation cover on Greylag Goose grazing pressure (expressed as droppings/5m^2) at: (a) Max-Eyth Lake, and (b) the Park. Each of the models in the left column was tested against that model plus one of explanatory variables listed (*i.e.* Droppings ~ Distance to water was tested against Droppings~Distance to water+Moult, *etc.*). Moult status explained most of the observed variation in grazing pressure, with distance to the water also proving significant. None of the vegetation parameters were significant.

Initial model	**Moult**	**Distance to water**	**% Grass**	**% Vegetation**	**% Herbs**	**Vegetation height**
(a) Max-Eyth Lake						
Droppings~Distance to water	**$F_{1,88} = 5.68$** **$P < 0.05$**	x	$F_{2,87} = 0.12$ $P = 0.89$	$F_{1,88} = 1.78$ $P = 0.19$	$F_{2,87} = 0.69$ $P = 0.51$	$F_{1,88} = 3.17$ $P = 0.08$
Droppings~Moult	x	**$F_{2,88} = 28.22$** **$P < 0.001$**	$F_{2,88} = 2.76$ $P = 0.07$	$F_{1,89} = 0.22$ $P = 0.64$	$\mathrm{F}_{2,88} = 1.41$ $P = 0.25$	$F_{1,89} = 0.05$ $P = 0.83$
(b) Park						
Droppings~Distance to water	**$F_{1,88} = 5.68$** **$P < 0.05$**	x	$F_{2,87} = 0.12$ $P = 0.89$	$F_{1,88} = 1.78$ $P = 0.19$	$F_{2,87} = 0.69$ $P = 0.51$	$F_{1,88} = 3.17$ $P = 0.08$
Droppings~Moult	x	**$F_{2,88} = 28.22$** **$P < 0.001$**	$F_{2,88} = 2.76$ $P = 0.07$	$F_{1,89} = 0.22$ $P = 0.64$	$\mathrm{F}_{2,88} = 1.41$ $P = 0.25$	$F_{1,89} = 0.05$ $P = 0.83$

Stuttgart. Fox & Kahlert (2000) suggest that the decrease in area use with distance from the shore was caused mainly by the predator escape mechanism, which is heightened during the flightless moulting period. The Greylags on Saltholm showed more frequent escape responses during moult, including escapes from "quasi predator stimuli" (Kahlert 2006), indicating that being flightless made the geese more "nervous". This was also observed in Stuttgart but detailed data are missing.

Moult is an energy demanding process (Bezzel & Prinzinger 1990; Singer *et al.* 2012). Geese become flightless for up to five weeks and during this time need to balance their need for food with that of predator and disturbance avoidance (Fox *et al.* 1995; Kahlert 2006). The importance of these needs varies between goose species and sites. Some goose species put on fat prior to moult and can at least partly rely on their body reserves during moult whereas others need to feed (Ankney 1984; Fox & Kahlert 2005), or else they lose weight (Loonen *et al.* 1991; Fox & Kahlert 2005; Singer *et al.* 2012), and some deplete food at a site to the extent that it is no longer suitable for moulting (Loonen *et al.* 1991). Predator density, perceived predation risk and probability of disturbance also vary between areas. Because these data have not yet been recorded for Stuttgart, evaluation of the importance of the different factors – *i.e.* the need to maintain proximity to water as opposed to improve food intake during the moult – must remain speculative.

Compared to moulting Pink-footed Geese in Greenland (which feed 200–220 m from water; Madsen & Mortensen 2008), and the Greylags on Saltholm (which roam up to 150 m; Fox & Kahlert 2000), Greylags in Stuttgart rarely ventured more than 30 m from the water's edge. There are several potential explanations for this difference. Birds in Stuttgart may have more endogenous energy stores to rely on, or find food sufficiently rich enough in nutrients close to the water. Alternatively, real or perceived predation risk may be higher in the urban habitat than in the arctic, encouraging the geese to stay close to water, to which they can retreat quickly for safety. The landscape in the parks of Stuttgart consists of small grasslands divided by paths, hedges and trees and as such contrasts with the vast open areas of the arctic, where the birds can see predators and take evasive action at relatively long distances. Flight distances of wintering Pink-footed Geese in Denmark were lower in areas with obstructions to open view (Madsen 1984). The perceived predation risk in Stuttgart therefore may be much higher than in more open landscapes, with a corresponding reduction in the area available for feeding.

Moult migrations to sites with favourable feeding conditions, described for many migratory geese (Owen & Black 1990; Weller *et al.* 1994), occur only locally amongst Greylag Geese in southwest Germany (F. Woog unpubl. ring re-sightings data). Grasses and herbs around the selected moulting sites in Stuttgart are likely to be rich in nutrients, however, through the regular management of the parkland, as repeated mowing generally increases the protein content of vegetation (Ydenberg &

Prins 1981; Gadallah & Jefferies 1995). Grazing pressure was highest in plots with a high grass and low herb cover, a pattern also found by Käßmann & Woog (2007) during the winter. More detailed studies are needed on the food plant taxa selected by the geese, including nutrient content and biomass in relation to observed grazing patterns, to inform and improve habitat management regimes for the birds (Bos *et al.* 2005).

Future studies on moulting geese in urban habitats should concentrate on the study of individuals, their decisions and consequences for their survival and subsequent reproductive success. Is the behaviour of the Greylags in Stuttgart dependent on their condition before and during moult? To what extent do they lose body reserves during moult and is this affected by their reaction towards disturbances? Such studies could also guide management recommendations to set aside areas for undisrupted foraging, especially during moult.

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Egyptian Goose *Alopochen aegyptiaca*: an introduced species spreading in and from the Netherlands

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Abstract

The Egyptian Goose *Alopochen aegyptiaca* was introduced as an ornamental species to parks in the Netherlands during the 20th century because of its exotic plumage. Escaped birds started to breed in the wild in 1967, and the species has now colonised most of the country. From the 1980s onwards the birds spread further to Germany, then to Denmark, while escapes from parks in Brussels established viable populations there and in France. This study summarises the latest available information on the numbers and distribution of free-living Egyptian Geese in the Netherlands and Europe. The population dynamics of the species were analysed to provide a better understanding of the development of the Dutch population over the past 40+ years, with special attention paid to the effects of culling, natural winter mortality and possible habitat preferences. Numbers breeding in the Netherlands were estimated at *c.* 10,000 pairs in 2010, and the total population at *c.* 45,000 individuals in winter 2010/11. Both breeding and non-breeding numbers increased exponentially (by 28% annually) from the establishment in the wild until 1999. However, the rate of increase has slowed in the last ten years, likely due to saturation of available breeding sites and an increase in culling activity. Within-season mortality in severe winters exceeded that during mild winters. The success of the Egyptian Goose in the Netherlands can likely be attributed to the abundance of freshwater areas available close to grasslands with few trees. Extrapolation up to 2010 of trends observed in Belgium and Germany until 2005 and 2006, respectively, suggests that these breeding populations together exceed 16,000 pairs, bringing the total numbers breeding in northwest Europe (including pairs in Britain, France and Denmark) to > 26,000 pairs.

Key words: exotic, feral, introduced, non-native, population dynamics.

The establishment and spread of alien introduced species often raises considerable public concern (Duncan *et al.* 2003). This mostly relates to potential ecological effects, such as hybridization with native species, or competition for breeding sites and limited food resources (Weller 1969). Lately, however, economic impacts including damage to agricultural crops (Conover 2002; Mangnall & Crowe 2002), social issues (*e.g.* defecating in recreational waters) and amenity effects (*e.g.* defecation in public areas) have all become matters of extensive public debate (Bomford 2003; Banks *et al.* 2008). A better understanding of the ecology and population dynamics of introduced species therefore is required to better support public discussion and provide adequate evidence upon which to base decision-making.

The Egyptian Goose *Alopochen aegyptiaca* is one of the non-native waterfowl species most rapidly spreading in Europe. It is widespread in its native range in Africa, south of the Sahara, numbering > 500,000 individuals (Brown *et al.* 1982; Banks *et al.* 2008). The species was introduced to England as an ornamental waterbird in the 17th century, and developed into a free-living, self-sustaining population in East Anglia, but has shown little growth in numbers in Britain over the centuries (Sutherland & Allport 1991).

In the second half of the 20th century, the species was kept in captivity at sites across Europe, including the Netherlands. Escaped individuals from parks in The Hague were reported breeding freely for the first time in 1967 (Teixeira 1979). Since then, the introduced population of Egyptian Geese has expanded and colonised all parts of the Netherlands (Lensink 1999a). During the compilation of the Dutch breeding bird atlas in 1999/2000, > 4,900 pairs were estimated breeding across 61% of the 1,674 atlas squares (5 × 5 km) monitored during the survey (Lensink 2002). From the 1980s onwards, the species has spread deep into Germany, with increasing numbers also reported from Switzerland and Denmark (Banks *et al.* 2008). Birds escaped from parks in Brussels in Belgium to establish another population, now spreading into France (Fouque *et al.* 2011), are perhaps supplemented by local escapes in both countries.

In contrast to the relatively slow growth of the English population since its establishment more than 300 years ago, rapid growth occurred on mainland Europe immediately after first breeding in the wild. Insight into the ecology of the Egyptian Goose is required, however, to ensure that models developed to predict future trends in the European population are scientifically sound (Kampe-Persson 2010; Rehfisch *et al.* 2010). We here present results of a study of the changes in distribution and abundance, habitat selection and winter mortality of the species in the Netherlands (the main source of the Northwest European population), to better understand the population dynamics of the Egyptian Goose in Europe and to predict its future distribution and abundance. Additionally, the current distribution and numbers of the Egyptian Goose in Europe are summarised and the possible ecological, economic and social impacts of the species are discussed.

Methods

Data

Numbers, trends and distribution of the Egyptian Goose in the Netherlands originate from data provided by the Dutch Centre for Field Ornithology (SOVON) based on observations recorded during:

1) the Dutch Breeding Bird Monitoring Project (BMP) from 1990–2009, 2) the Waterbird Monitoring Scheme (WAVO) from 1975–2008, and 3) the seven nationwide breeding pairs censuses of the period 1967–1999/2000 (in 1967, 1972, 1977, 1983, 1989, 1994, and 1999/2000).

The BMP survey in the Netherlands is designed to track trends in breeding bird numbers, based on intensive mapping of breeding bird territories. Between March and July, approximately 1,500 study plots (varying in size from *c.* 10–250 ha) are visited 5–10 times, depending on the type of habitat and species coverage, and all birds showing territorial or nesting behaviour are recorded (van Dijk 1993). Since the study plots do not reach 100% coverage nationally, SOVON presents annual changes in indices relative to the baseline year of 1990, estimated using log-linear Poisson regression models of time series corrected for missing data (Pannekoek & van Strien 2005). For our study, BMP data was available as totals for the Netherlands, and also separately for the 12 provinces and 13 different physical-geographical regions, for the period 1990–2008.

The WAVO censuses are carried out monthly from September to April at 86 important wetlands in the Netherlands, as well as at the staging sites of geese and swans (van Roomen *et al.* 2003). The counts are reported as monthly averages, and not as indices as in the BMP. Counts are carried out during daytime, and hence when Egyptian geese are at the foraging sites. Birds are only counted if present within the habitat (*i.e.* excluding birds flying over). Data from the Waterbird Monitoring Scheme was available for the period 1975–2008. During the regular WAVO survey in mid-January (which also provides the Netherlands counts for the International Waterbird Census (IWC) coordinated by Wetlands International), many additional canals and smaller waterbodies are visited, bringing the total size of the census area to approximately 1.95 million ha. Areas with missing counts are imputed by standardized methods (van Roomen *et al.* 2003), providing a robust and reliable estimate of waterbird numbers in the Netherlands. These data were available as totals and also separately for 16 physical-geographical regions.

The breeding pairs census of 1999/2000 provided the most recent nationwide count of the number of Egyptian Goose breeding pairs. For this census, the Netherlands was subdivided in 1,674 atlas squares (5 × 5 km), which all contained 25 kilometre squares. The goals of the census were to compile a list of breeding bird species and to estimate the number of breeding pairs per atlas square. All landscape types within an atlas square were visited several times during the breeding season. If breeding density was high, often only part of the atlas square was visited and the number of breeding pairs counted there was extrapolated proportionally to the amount of available habitats in the rest of the square. Like the WAVO censuses, breeding pairs census data were available for 16 physical-geographical regions.

Information on Egyptian Goose numbers outside the Netherlands was collected by personal communication with local experts and from published sources on the breeding population in Belgium (Devillers 1988; Anselin & Devos 1994;

Lensink 1999a; Banks *et al.* 2008) and Germany (Lensink 1996; Lensink 1998; Hüppeler 2000; Südbeck *et al.* 2007; Banks *et al.* 2008). The most recent data for Belgium and Germany were from 2005 and 2006, respectively.

Analysis

Population growth rates for Egyptian Geese in the Netherlands were calculated by taking the exponential of the slope of the natural log-transformed numbers plotted per year. The estimated number of breeding pairs in 2010 was calculated in two ways, both using the number of pairs reported in the Dutch breeding bird atlas as a starting point (SOVON 2002). This was the most recent complete nationwide census of breeding Egyptian Goose pairs, estimated as 4,950 pairs in 1999–2000 (Lensink 2002). One estimate for 2010 was based on the mean growth rate recorded per province by the BMP surveys in the period 2000–2009. These growth rates were applied per province, and were relative to the number of breeding pairs registered during the first year of the period (year 2000). The other method was also based on numbers registered in each province in 2000, but relied on the mean annual increase (*i.e.* 8.8% for the whole country) in bird numbers recorded by the WAVO censuses in the period 2000–2008. This growth rate was applied per province, and again relative to the numbers registered during the first year of the period (year 2000).

An estimate of the total population size (including both breeding and non-breeding birds) in the summer of 2010 was derived from the estimated number of breeding pairs. The estimate was based on Leslie matrix calculations (Caswell 2001), assuming that breeding commences after the first winter, a juvenile survival rate of 72%, adult survival of 83% and a production of 1.9 juveniles/pair/year (Table 1; values taken from Lensink 1998). However, the national database of the Royal Netherlands Shooting Association (Koninklijke Nederlandse Jagers Vereniging) shows that culling since the 1990s gradually increased to 20,000 Egyptian Geese shot in 2008, roughly equal to 1.5 geese per 100 ha, a removal of birds that has remained relatively stable since then (Montizaan & Siebenga 2010). In order to the test the effect of culling on growth rates, the model was run both with and without controlling for culling. In the former, the number of shot birds was corrected per age-class for the number of birds that would not have survived until next year.

The WAVO census data were used to test the effects of winter severity on Egyptian Goose numbers within and between years. IJnsen indices provided a measure for winter severity. This measure is the degree-sum, on a scale of 0–100, of the number of

Table 1. Leslie matrix of the vital population parameters used to model the effect of shooting on Egyptian Geese in the Netherlands.

	1st year	≥ 2nd year
Fecundity	0	0.684
Survival to 2nd year	0.720	0
Survival to > 2nd year	0	0.830

frost days (minimum temperature < 0°C), ice days (maximum temperature < 0°C) and very cold days (minimum temperature < –10°C) between November and March (Van Engelen *et al.* 2001). The IJnsen indices were used as the independent variable in a linear regression model to predict changes in the annual average number of birds counted in the winter half-year (November–March) during the years 1975–2008. A one-way ANOVA tested whether the annual changes in numbers differed significantly after severe winters (with an IJnsen index of > 30; $n = 7$), compared to after mild winters (with an IJnsen index of < 10; $n = 15$). In addition, an ANOVA assessed within-winter mortality by testing whether the difference between the average numbers of individuals counted during the waterfowl censuses in November–December and January–February were lower in severe than in mild winters. These periods are known to achieve the most extensive census coverage with the fewest imputed numbers for missing counts. Values were natural log-transformed to achieve normality.

In order to test statistically for changes in distribution, the count areas of the IWCs conducted in January each year were grouped into 16 different physical-geographical regions. Numbers counted in January 2000 and January 2008 were log-transformed and were subjected to simple linear correlation.

The habitat preference analysis relied on the habitat type classification (*i.e.* urban areas, orchards, forests, arable land, grassland, heath, water, sandy areas, and "other" habitats) of the SOVON survey areas ($n = 3{,}959$; mean ± s.d. surface area = 587 ± 955 ha) of the IWC January 2000 census. SOVON reports bird numbers per survey area but not specifically per habitat type within the area. Nevertheless, the number of Egyptian Geese varied greatly among survey areas (range = 0–299 birds). On omitting survey areas without Egyptian Geese, the mean number recorded was 12.1 birds per survey area. In order to compare the habitat types between preferred and non-preferred areas, survey areas were selected where no Egyptian Geese were observed and also where > 50 birds were observed. The surface areas of the nine habitat types were summed for these two groups. Subsequently, the arcsine transformed proportions of the habitat types within one group were compared with a paired t-test for unequal variances with the corresponding proportions of the other group.

Population growth rates outside the Netherlands were based on published data related to the breeding population in Belgium and Germany. The numbers of breeding pairs were natural log-transformed and exponential curves were fitted to the relationship between these and the year of observation. The resulting equations were then used to extrapolate the figures for Belgium and Germany up to 2010 which, when combined with data from other countries, provided a recent estimate of the total European population.

Results

Numbers in the Netherlands

Relating the most recent complete estimate of Egyptian Geese breeding in the Netherlands (4,944 breeding pairs in 1999–2000; Lensink 2002) to earlier nationwide breeding pair censuses undertaken since 1967 (reported in Lensink 1996, 2002; Table 2) gave a mean annual growth rate of 28.2% of the breeding population calculated over the whole period between 1967 and 1999. Nevertheless, the growth was not constant. The nationwide censuses and the breeding bird surveys provided similar estimates of mean annual rates of increase (*i.e.* 12.1% and 12.7%, respectively) in the period of 1990–1999 (BMP surveys were available only from 1990 onwards) but the values were lower than over the whole period, suggesting a slower growth rate during the 1990s. The increase in the number of Egyptian Goose pairs (N_{NL}) with year (t) in the period 1967–2000 could be best described by an exponential function ($\ln N_{NL} = 0.25t - 488$, $r^2_5 = 0.98$, $P < 0.0001$). Fitting a second order polynomial did not improve the relationship as the quadratic term remained 0.

There were no nationwide censuses of Egyptian Geese carried out after 1999–2000, but the BMP surveys indicated that the rate of increase slowed down further between 2000 and 2009 to an annual mean of 7.0% for the total Dutch population. The WAVO surveys (conducted between November and April) found a similar growth rate (8.8%) for the period 2000–2008. The BMP surveys also allowed an analysis at the level of the 12 Dutch provinces and 13 physical-geographical regions. The BMP surveys revealed a low growth rate of the number of breeding pairs in nine provinces, and a growth rate of > 10% in only three provinces during the period 2000–2009 (Table 2). The comparison of the growth rate of the number of breeding pairs between the periods 2000–2009 and 1990–1999, revealed a slower growth rate after 2000 in all provinces. At the scale of the 13 physical-geographical regions, slower growth rates occurred in eight, comparable growth rates were observed in two others and a higher rate only in three cases: 1) in dunes and tidal areas at the Wadden Sea islands, and the northern marine clay salt marshes; 2) higher sandy areas in the north of the Netherlands and 3) higher sandy areas in the middle and southern part of the country. A paired *t*-test analysis comparing the slopes of the growth rates in the 13 regions revealed a significantly lower increase in the last decade ($t_{11} = 2.48$, $P < 0.05$).

Based on the growth rate obtained per province from the BMP indices, the total size of breeding population in the 12 provinces was estimated at 10,171 breeding pairs in 2010 (Estimate 1 in Table 2). The WAVO surveys indicated a nationwide average annual growth rate of 8.8% between 2000 and 2008. Estimate 2 for 2010 in Table 2 is the product of extrapolating the number of breeding pairs recorded in 2000 per province by this value, resulting in numbers similar to Estimate 1. From Estimate 1 (10,171 breeding pairs), the Leslie matrix predicted the total population in the Netherlands (inclusive of breeding and non-breeding individuals and an ongoing culling of 20,000 individuals annually) at 45,523 birds in 2010 (Fig. 1a). Without accounting for culling, the growth of the population would have remained exponential, and the size of the population could have reached a theoretical maximum of 66,359 breeding pairs (Fig. 1b) or a total

Table 2. Number of breeding pairs per province in the period 1967–2000 (data from nationwide breeding censuses reported in Lensink 1996, 2002) and an estimate of the number of breeding pairs in the Netherlands in 2010. The rate of increase for the period 2000–2009 is derived from the breeding bird census (BMP). These rates provided Estimate 1 for 2010, whereas Estimate 2 is derived from the increase recorded by the waterfowl censuses (WAVO) during the period 2000–2008 (*i.e.* 8.8% per year at the national scale).

	Nationwide breeding pairs censuses							**BMP growth rate (%/year)**	**Estimate 1**	**Estimate 2**
	1967	**1972**	**1977**	**1983**	**1989**	**1994**	**1999–2000**	**2000–2009**	**2010**	**2010**
Groningen	0	0	0	0	10	28	133	10.3	355	308
Friesland	0	0	0	0	2	55	359	4.9	580	830
Drenthe	0	0	0	1	11	46	265	14.9	1,063	612
Overijssel	0	0	0	4	16	105	534	4.8	853	1,233
Gelderland	0	0	2	15	70	365	815	4.0	1,206	1,883
Utrecht	0	0	0	5	27	104	326	6.7	624	754
Flevoland	0	0	0	0	1	6	43	8.8	99	98
Noord Holland	0	0	3	16	59	190	620	11.8	1,890	1,431
Zuid Holland	1	7	43	72	128	290	891	6.4	1,656	2,058
Zeeland	0	0	0	0	1	10	119	5.0	194	275
Noord Brabant	0	0	0	2	19	60	510	7.3	1,031	1,177
Limburg	0	0	0	0	1	45	330	6.5	619	762
Netherlands	1	7	48	115	345	1,345	4,945	7.0	10,171	11,421

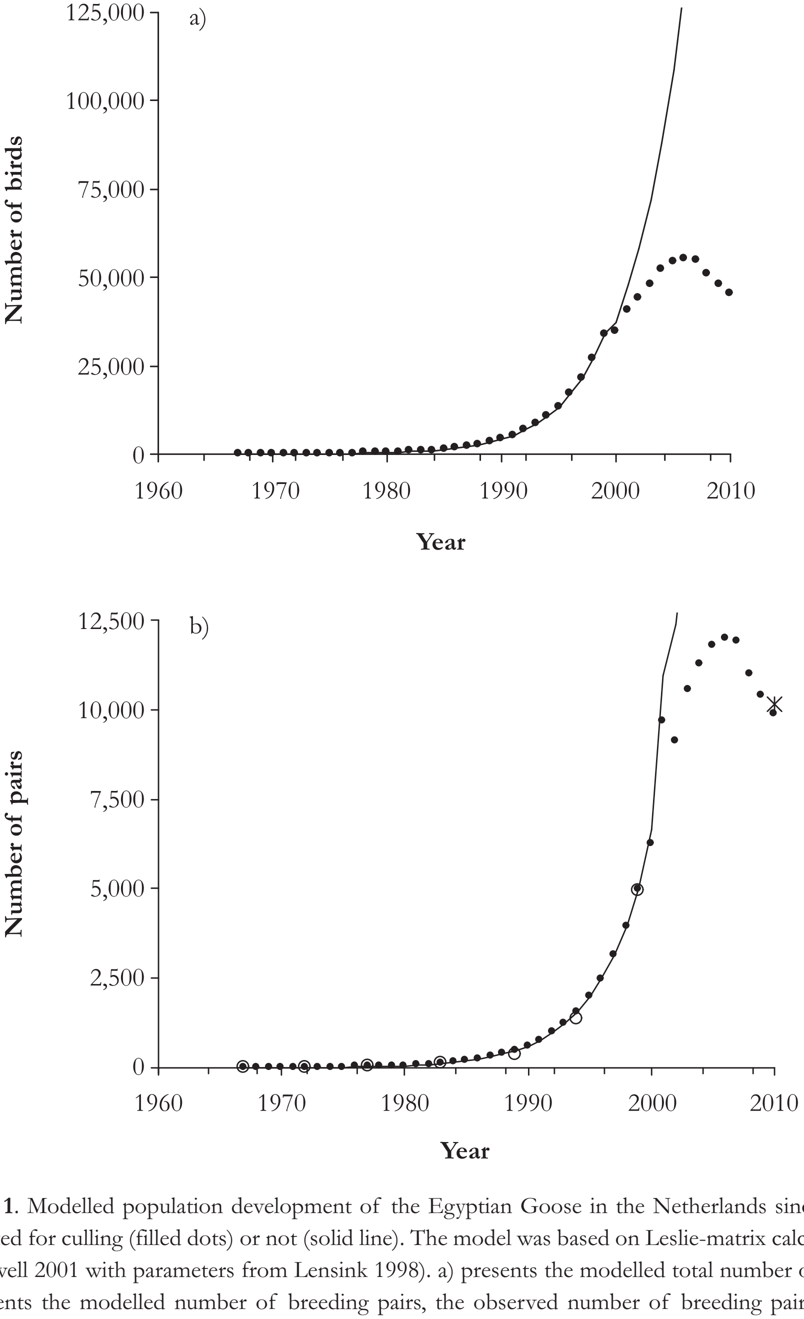

Figure 1. Modelled population development of the Egyptian Goose in the Netherlands since 1967, accounted for culling (filled dots) or not (solid line). The model was based on Leslie-matrix calculations (*cf.* Caswell 2001 with parameters from Lensink 1998). a) presents the modelled total number of birds; b) presents the modelled number of breeding pairs, the observed number of breeding pairs in the period 1967–2000 (open dots = data from Lensink 1996, 2002), and the estimated number of breeding pairs in 2010 (asterisk = data from this study; see Estimate 1 in Table 2).

population of 306,097 birds (assuming no effects of habitat limitation or other density dependent factors; Fig. 1a).

The within-year variation in the WAVO counts showed that the highest numbers were counted in September (*i.e.* after the end of the breeding season), followed by a sharp decreasing trend until January, and thereafter remaining roughly stable or slightly decreasing until March. There was no clear effect of winter severity (determined by IJnsen indices) on annual changes in abundance (linear regression: $r^2_{21} = 0.64$, n.s.), nor when comparing changes in numbers following severe and mild winters (ANOVA: $F_{1,20} = 0.26$, n.s.). However, the within-season analysis, with winter severity as categorical factor, revealed that the number of Egyptian Geese show a significantly stronger decrease during severe winters than during mild ones (ANOVA: $F_{1,20} = 9.58$, $P < 0.01$). Based on back-transformed data, in severe winters the mean number of individuals in January–February was approximately half of that in November–December (*i.e.* 54%). In contrast, in mild winters the reduction in numbers was < 8% (Fig. 2).

Distribution in the Netherlands

Habitat preferences

The annual IWCs carried out in January showed that Egyptian Geese can be found in all parts of the Netherlands, but the largest concentrations were recorded in the lower parts of the country (generally the western and northern provinces), mostly in riparian areas, where breeding density was highest (often > 10 pairs per 100 ha). The species was absent from heavily afforested areas and areas where water bodies are lacking. However, the analysis of the nationwide waterfowl census data conducted in January 2000 revealed no significant difference between the proportions of habitat types in count areas where no Egyptian Geese were counted compared to those with > 50 birds reported ($t_8 = 0.87$, n.s.). The only notable difference existed between the proportions of grasslands and arable areas: 51% of the census areas with > 50 Egyptian Geese ($n = 35$) was grassland (total = 12,728 ha), whereas of the survey areas where the species was absent ($n = 3{,}364$) only 35% was grassland (Fig. 3). In contrast, the proportion of arable land constituted 29% of the survey areas where the species was absent compared with 20% of the survey areas with > 50 Egyptian Geese (in total 5,008 ha).

Changes in distribution

A comparison of the numbers counted in January 2000 (*i.e.* including adults and sub-adults; N_0) and in January 2008 (N_8) for 16 physical-geographical regions revealed that total numbers increased in all areas ($\log N_8 = 0.77 \log N_0 + 0.96$, $r^2_{15} = 0.64$, $P < 0.001$; Fig. 4 a). However, the relative abundance in the regions changed, revealed by the slope of the relationship being significantly smaller than one (0.77 ± 0.15 s.e.). This resulted from regions with larger numbers in 2000 increasing proportionally less than regions with small numbers. A similar comparison to the number of birds counted in January 2000 (N_0) per physical-geographical region and the number of breeding pairs (*i.e.* only adult birds) in 2000

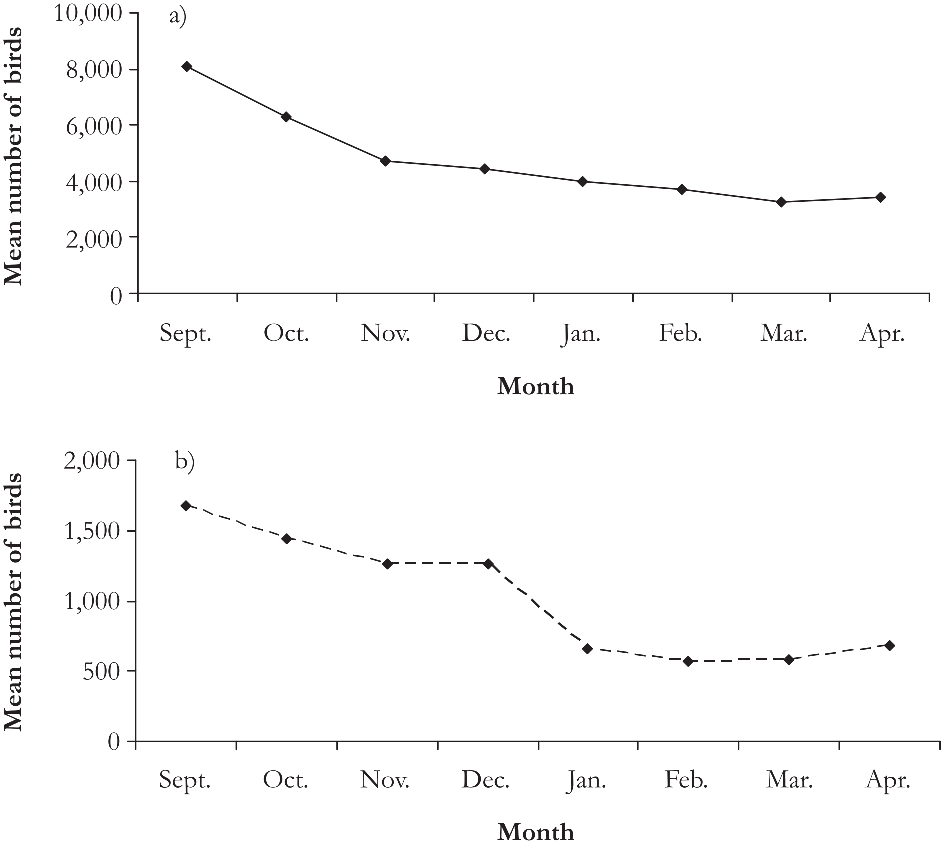

Figure 2. Mean number of Egyptian Geese per month in the winter half year during a) mild (n = 15) and b) severe winters (n = 7) during the period 1976–2008. During the last decade, when bird numbers were the highest, five mild winters but no severe winters occurred, causing generally higher mean numbers during mild winters (note the difference in the scale of the vertical axes).

(N_{0b}) in the same regions also showed a close relationship ($N_{0b} = 0.62\log N_0 + 0.98$, $r^2_{15} = 0.80$, $P < 0.001$; Fig. 4 b).

Introduced populations elsewhere in Europe

According to the latest estimates, 700 birds breed and at least 1,000 winter in England (Rehfisch *et al.* 2010). However, due to the patchy reporting of breeding Egyptian Geese, these figures could be underestimates and the real size of the breeding population could be much higher (2,500–3,000 individuals suggested by Banks *et al.* 2008).

In Belgium, the first successful feral breeding dates from 1982 (Segers 1984; Gabriels 1985). In 2002, the number of breeding pairs was estimated at 800–1,100 (Banks *et al.* 2008), at 1,300 pairs by 2005 in

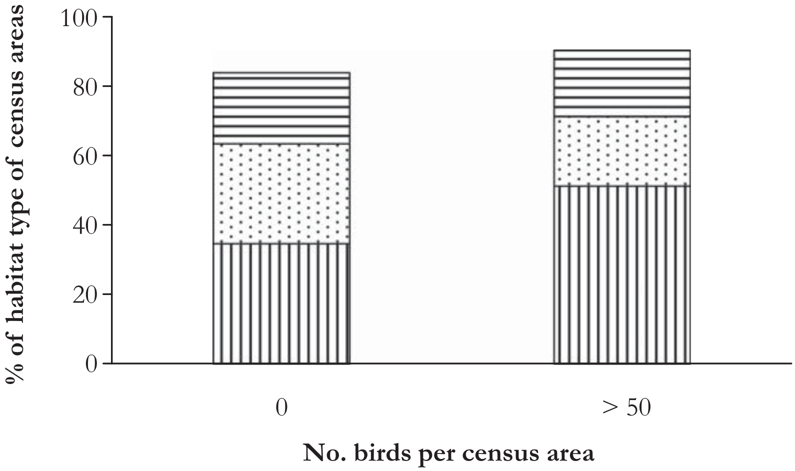

Figure 3. Proportion of the most important habitat types in waterfowl census areas where 0 (in total 3,364 areas with a surface area of 1,918,627 ha) and > 50 Egyptian Geese (in total 35 areas with a surface area of 24,866 ha) were observed in January 2000. Dotted area = arable land, vertical stripes = grassland and horizontal stripes = water. Habitat types of minor importance are omitted; hence proportions do not add up to 100%.

Flanders only (Anselin & Vermeersch 2005), and at 330–590 pairs by 2007 in Wallonia only (Jacob *et al.* in press). The population is still expanding its breeding range, especially in the western and central part of the country (Anselin *et al.* 2010). According to the latest counts, the population was estimated at around 3,000 individuals in winter 2009 (Huysentruyt *et al.* 2010). Based on available data on the breeding population in Belgium, the number of Egyptian Geese pairs (N_B) increased with year (t) on average by 35.9% between 1982 and 2005 ($\ln N_B = 0.32t - 630$, $r^2_4 = 0.95$, $P < 0.01$; Fig. 5).

In Germany, breeding of free-living birds started in 1981 along the river Rhine, originating from the introduced population in the Netherlands (Lensink 1996), building to an estimated 2,200–2,600 pairs in 2005 (Bauer & Woog 2008). Numbers in Germany (N_G), increased exponentially during 1981–2005 ($\ln N_G = 0.33t - 659$, $r^2_4 = 0.90$, $P < 0.02$; Fig. 5). By extrapolating the Belgian and German trends, the total breeding population in Belgium and Germany is estimated to have exceeded 16,000 pairs in 2010.

In France, 618 individuals were counted in 2009, with 125 breeding pairs observed in the summer (Fouque *et al.* 2011). In Denmark, at least 20 pairs were breeding in 2007 (Banks *et al.* 2008) and, according to the latest records in 2009, a total of 544 observations were listed of 1–63 individuals present throughout the year (Kampe-Persson 2010). A small number of birds occur in Switzerland; two pairs have bred in an urban park each year since 2003 (Banks *et al.* 2008), and in 2009 two new breeding sites were recorded (Verena Keller, unpubl. data).

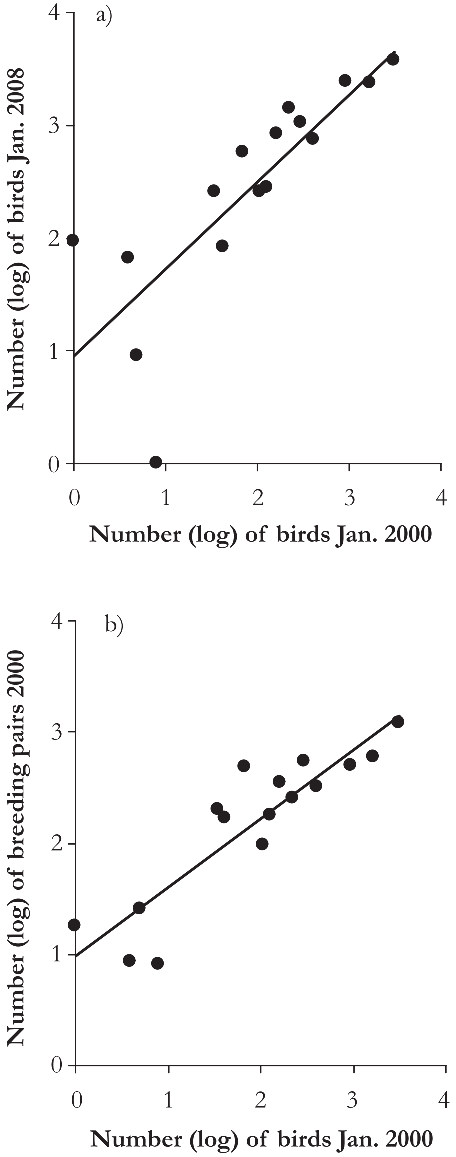

Figure 4. Comparison of the number of Egyptian Geese in: a) January 2000 and January 2008, and b) January 2000 with the number of breeding pairs in 2000 in the 16 physical-geographical regions of the Netherlands. All axes are log transformed.

Furthermore, some birds are regularly seen or occasionally known to breed in Spain, Italy, Sweden, Poland and the Czech Republic (Banks *et al.* 2008).

Discussion

The Egyptian Goose population in the Netherlands showed rapid exponential growth shortly after feral breeding was first recorded in 1967. By 2010, the breeding population was estimated at > 10,000 pairs, equivalent to over 45,000 individuals in the total mid-winter population. Breeding density was highest in riparian areas and 51% of the larger groups of Egyptian Geese were observed on grasslands in 2000. Our results suggest that the birds generally use the same habitats throughout the year. Winter severity seemed to have a negative effect on within-winter numbers. On summing the breeding pairs in the Netherlands, Belgium, Germany, Great Britain, France and Denmark we estimated the total number of breeding birds to be at least 26,000 pairs in 2010.

Despite the generally increasing trend in the Netherlands between 1967 and 2008, population growth has slowed in the past decade. In this latter period, the number of breeding pairs has increased only slightly in ten out of thirteen provinces. This could be due to increasing culling intensity, could imply that nearly all the suitable breeding sites had been occupied earlier, or be a combination of the two as a result of different factors acting locally. Up until 1994, the breeding range expanded at an average rate of 3.0 km per year (Lensink 1998), and the species was found breeding in

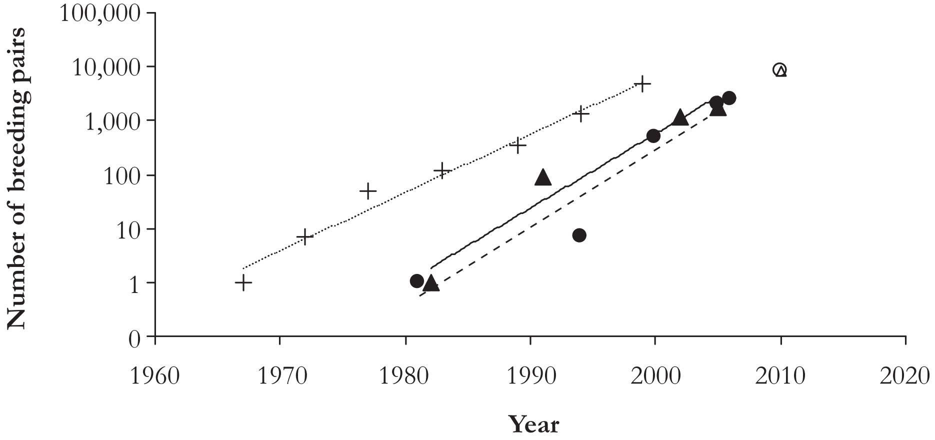

Figure 5. Growth of the Egyptian Goose population in western Europe. Filled triangles and solid line (lines are exponential trends) depict Belgium, filled dots and dashed line Germany. Open symbols indicate the extrapolated number of breeding pairs for these countries. The trend of the breeding population (based on nationwide counts) in the Netherlands between 1967 and 1999 is also provided (crosses and dotted line) for comparison. Note the log-scale of the vertical axis.

61% of the 1,674 atlas squares (5 × 5 km) in the Netherlands by 1999 (Lensink 2002). Exponential growth is frequent amongst populations of invasive species in newly colonised areas, often followed by a period of little or no increase (Lensink 1999a). In newly colonised areas, observed breeding success was much higher (60–70% of nests successful) than amongst earlier established populations (15–30% of nests successful; Lensink 1996), indicating density-dependent limitations on growth. One of the physical-geographical regions where the local population is still growing exponentially is located far from the sources of the escaped populations (*i.e.* the dunes and tidal areas of the Wadden Sea islands), whereas the other two regions provide lower quality habitats (*i.e.* sandy areas), which might reflect their lower preference by Egyptian Geese. Comparing all physical-geographical regions between 2000 and 2008 revealed that the numbers increased significantly in each of the different regions. However, the fact that the increases were greater in physical-geographical regions where numbers were relatively low in 2000, also suggests that density-dependent effects may be present.

In order to estimate the current size of the Dutch Egyptian Goose population, we relied on the observed growth rate of the breeding population (BMP indices). This trend seemed to be very similar to the one derived from nationwide censuses undertaken during the period 1990–1999, and was thus assumed to be trustworthy. In addition, estimates from the Royal Shooting Association on the size of the breeding population in each province of the Netherlands were close to the BMP estimates (Montizaan & Siebenga 2010). According to our modelled results, the size of the national population reached its maximum in 2006 at nearly 12,000 pairs, and more than 55,000 individuals in July. By assuming an annual culling of 20,000 individuals, the model predicted slightly decreasing or stagnating numbers since then. In contrast, according to the latest estimates on the number of breeding pairs in the Netherlands, the increasing trend continued until 2010 (Boele *et al.* 2012). The discrepancy may occur due to the culling figures also being estimates, and possibly varying annually. Moreover, the model relied on the assumption that the number of birds shot is equally divided among age-groups, which may not necessarily be the case. Furthermore, the parameter values on survival and reproduction originated from the early increasing phase of the population, and may be lower now through density-dependence. If so, this might also explain why the population has stabilised (even without culling). Nevertheless, the model clearly shows that without the gradually increasing culling since the 1990s the population size could have already reached 28,213 pairs, the potential maximum calculated based on the amount of suitable habitat available (SOVON unpubl. data).

Lensink (1996) reported adverse effects of winter severity on the rate of increase for the years 1975/76–1998/99. In our extended study period, such clear effects were not detected, although effects of winter severity on within-season changes in abundance were found. The species is not known to conduct regular, directed migration in the Netherlands, although smaller movements do occur outside the breeding season (Lensink 1996, 1999b). However, more dispersion could occur in severe winters. In its natural range the species moves large distances to moulting sites, and also in times of food scarcity (Del Hoyo *et al.* 1992; Maclean 1997). Moreover, recent ringing studies in the Netherlands, Belgium and Germany found that individuals of the introduced European populations also regularly disperse up to several hundred kilometres from the ringing site (Van Dijk & Majoor 2011). Nevertheless, severe winters occurred more frequently during the period 1975–1999 than in subsequent years, leading to greater winter movements, which may have caused the discrepancy in the results of this study compared with the earlier work of Lensink (1996). Alternatively, the increasing culling mortality since 1999 could have masked the effect of severe winters, or the larger population may be more capable of recovering after a severe winter by attaining higher reproductive success in the following breeding season (Lensink 1999a).

The similarity between the total numbers recorded in January 2000 and the number of breeding pairs in 2000 is striking, suggesting that the winter distribution of Egyptian Geese in the Netherlands reflects their breeding distribution. Although the species is well-known for its wide choice of breeding habitats (Harrison 1978), they mostly prefer to stay close to (< 1 km) freshwater bodies (Pitman 1963). Generally, Pleistocene soils are thought to provide lower quality breeding habitats (Lensink 2002), and in the Netherlands they breed most commonly in trees, old nests of other birds, or tree cavities (Lensink 1998). The Egyptian Goose feeds mainly on grass in the Netherlands, and areas with abundant grasslands appeared to be the preferred habitat. Our study found that the highest concentrations occurred close to water bodies in open grasslands with a few trees, which is also the typical habitat for the species in its natural range in Africa (Del Hoyo *et al.* 1992).

The population in England has grown slowly since its establishment more than 300 years ago, whereas in the Netherlands a rapid exponential growth was achieved shortly after the breeding started. Breeding success of the Egyptian Goose is low in England (1.5 fledglings per pair; Sutherland & Allport 1991), as well as in its native range (Eltringham 1974), compared with the Netherlands (4.5 fledglings per pair; Lensink 1996). Low predation pressure, and the abundantly available, fertilized grasslands adjacent to freshwaters that create outstanding habitats for herbivorous waterfowl (Van Eerden *et al.* 2005), may be the reason for the larger number of fledged chicks in the Netherlands.

The size of the Egyptian Goose population in northwest Europe has increased rapidly in the past decades and could have exceeded 26,000 breeding pairs by 2010. Supposing a similar population structure as in the Netherlands, this could translate to > 100,000 individuals including the non-breeding adults and sub-adults. Our extrapolations are based on the assumption that the rate of increase was constant until 2010. Based on the experiences in the Netherlands, and on the amount of suitable habitats in Belgium and Germany, it is not likely that the increase would have slowed since the latest published censuses. On the contrary, the species is expected to expand its breeding range further. Due to the negative effect of winter severity, the 0°C isocline could form the approximate border of the expansion range (Lensink 1998), and hence the species will likely spread mostly southwards.

The increase in abundance and distribution of such an introduced species commonly result in substantial public concern about their eventual ecological and economic impacts. Waterfowl species have a great propensity to hybridize with other species (Weller 1969). Hybridizations of Egyptian Geese mainly occur with other introduced goose and duck species (Lensink 1996; Harrop 1998; Banks *et al.* 2008), although these hybrids are usually infertile (Susanne Homma and Olaf Geiter, unpubl. data). As the birds' main food is grass, which is abundant throughout Europe, inter-specific competition for food is likely to be of minor significance. Although Egyptian Geese are often observed being aggressive towards other birds, the increasing population in the Netherlands seems not to have had a negative effect on the population development of native species so far (Lensink & van den Berk 1996). Only one study reported evidence on such an effect, where Black Sparrowhawks *Accipiter melanoleucus* raised fewer chicks due to usurpation of nests by Egyptian Geese (Curtis *et al.* 2007).

Economic impacts seem to be more profound. The increasing native population in South Africa is considered to be an agricultural pest, especially around water bodies used for moulting, where considerable damage to agricultural fields has been reported (Maclean 1993). Young wheat and barley shoots and leaves were mostly consumed, but Egyptian Geese also seem to select surface seeds (Mangnall & Crowe 2001, 2002). Egyptian Geese have likewise been reported feeding on agricultural fields in England (Sutherland & Allport 1991), the Netherlands (this study) and Belgium (Beck *et al.* 2002), although damage to crops has not yet been directly measured. Whilst a period of a few days grazing may encourage plant growth (Kear 1970), it is doubtful that this will ease the worries of European farmers when increasing numbers of Egyptian Geese appear on their land. In England, the Egyptian Goose is on the list of species that can be legally shot without a special permit (source: RSPB website). In Belgium, this holds for all exotic species, and in Germany for the period between 1 August and 15 January. Our study shows that, if necessary, such culling measures could be effective to stop or limit further growth of Egyptian Goose populations in Europe.

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Evidence for Mallard *Anas platyrhynchos* and American Black Duck *Anas rubripes* competition in western New Brunswick, Canada

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Abstract

The hypothesis that Mallard *Anas platyrhynchos* and American Black Duck *Anas rubripes* compete during the breeding period has generated considerable debate. To further evaluate this hypothesis, the following predictions were tested for sympatric Mallard and Black Duck breeding in New Brunswick: 1) Mallard and Black Duck do not partition breeding resources in space and/or time, 2) Mallard reduce the amount of breeding habitat available to Black Duck, and 3) production of Mallard and Black Duck is inversely related over time. Study results supported all predictions. Mallard and Black Duck pairs were distributed among wetland classes independent of species, though Black Duck were more likely to be observed alone or without Mallard on wetlands that were surrounded by > 75% upland forest. Mallard and Black Duck hatch dates did not differ, indicating they do not temporally partition breeding resources. Black Duck were more likely to be observed on wetlands where Mallard had been removed than on wetlands where they were not removed. This result supported the prediction that Mallard reduce the availability of breeding habitat for Black Duck through interference competition. To test the prediction that production of Mallard and Black Duck is inversely related over time, brood surveys were conducted from 1990 to 1994 to determine relative and absolute changes in numbers of Mallard and Black Duck broods. The ratio of Black Duck to Mallard broods declined from 0.938 in 1990 to 0.244 in 1994. Total number of Black Duck broods on 59 wetlands surveyed with equal effort in 1990 and 1994 declined from 45 in 1990 to 19 in 1994, while Mallard broods increased from 48 in 1990 to 78 in 1994. These findings support the hypothesis that Mallard and Black Duck compete.

Key words: *Anas platyrhynchos, Anas rubripes,* interspecific competition, niche overlap.

The hypothesis that competition with Mallard *Anas platyrhynchos* has contributed to a decline in Black Duck *Anas rubripes* has generated considerable debate. Several studies suggest that Mallard out-compete Black Duck for the most nutrient rich breeding habitat (Ankney *et al.* 1987; Merendino *et al.* 1993; Dwyer & Baldassare 1994; Merendino & Ankney 1994), yet there is little evidence for differences in reproductive success between the two species (Laperle 1974; Krementz *et al.* 1992; Dwyer & Baldassare 1993; Longcore *et al.* 1998; Petrie *et al.* 2000). Efforts to evaluate behavioural mechanisms have provided mixed results as Mallard were dominant under some study conditions (Brodsky & Weatherhead 1984; Brodsky *et al.* 1988; Seymour 1990), but not others (D'eon *et al.* 1984; Hoysak & Ankney 1996; McAuley *et al.* 1998). Black Duck populations have declined in some areas where Mallard increased (Dennis *et al.* 1989; Petrie 1998), but have remained stable in other areas of Mallard-Black Duck sympatry (Nudds *et al.* 1996). Zimpfer & Conroy (2006) found evidence for density effects of Mallard on Black Duck reproduction rates and suggested that this may be due to Mallard reducing Black Duck carrying capacity. However, others have argued that Mallard are simply filling a niche vacated by Black Duck (Maisonneuve *et al.* 2006).

Mallard and Black Duck defend wetland territories to protect paternity and allow females to forage undisturbed (Anderson & Titman 1992). In addition, the two species treat each other as conspecifics and exclude each other from established breeding territories (Seymour 1992). Black Duck numbers could be limited by this spacing behaviour if the two species fail to partition breeding resources and habitat is limiting. Although Black Duck and Mallard do not differ in bill morphology, foraging behaviour, or prey size selection (Eadie *et al.* 1979; Nudds & Bowlby 1984; Belanger *et al.* 1988), utilisation of different wetland types or differences in reproductive chronology may enable resources to be partitioned in time as opposed to space (Toft *et al.* 1982). Failure to partition macro-habitat may lead to declines in Black Duck if demands for breeding resources exceeds supply and Mallard reduce breeding habitat availability through interference competition. If competition coefficients are asymmetrical in favour of Mallard as suggested by the competition hypothesis (Merendino *et al.* 1993), population trends for the two species should be inversely related over time (Nudds 1992).

To evaluate the hypothesis that Mallard and Black Duck compete for breeding resources, three predictions were tested for Mallard and Black Duck breeding sympatrically in western New Brunswick: 1) Mallard and Black Duck do not partition breeding resources in space and/or time, 2) Mallard reduce the amount of breeding habitat available to Black Duck, and 3) production of Mallard and Black Duck is inversely related over time.

Methods

Study area

The study area was approximately 500 km^2 in the Woodstock-Florenceville area of Carleton County, mid-western New Brunswick, Canada (68°40' N 46°15' W).

The area lies in the Saint John River ecodistrict of the Continental Lowlands Ecoregion. Although stands of tolerant hardwood species once dominated the area, these forest types now mostly exist as small woodlots in an agricultural matrix as relatively dense human settlement has fragmented the forest. Major coniferous species include Red Spruce *Picea rubens* and Eastern Hemlock *Tsuga canadensis* that are generally confined to lower slopes and valley bottoms. Most of the ecodistrict is covered by deep non-compact soils derived from Ordovician rocks (Anonymous 1996). Approximately 45% of the land base in the study area had been cleared for agriculture. Potatoes are the primary cash crop, often in rotation with grain and livestock operations. The area contained a variety of wetland types including most classes of palustrine wetlands as well as riverine and lacustrine habitats (Cowardin *et al.* 1979).

Prediction 1: Resource partitioning in space and time

To test the prediction that Mallard and Black Duck do not partition breeding resources by using different habitat types, the distribution of breeding pairs was determined using helicopter surveys. Breeding pair counts from these aerial surveys were used in subsequent analyses of resource partitioning. Mallard and Black Duck pairs were surveyed on 58 wetlands in 1990 that were identified from aerial photographs. The number of wetlands surveyed for breeding pairs was increased to 72 in 1991 and to 80 in 1992 because we discovered wetlands not visible on aerial photographs. Two large rivers in the study area (St. John and Meduxnekeag) were also surveyed in all years.

Surveys were conducted in the first week of May 1990, 1991, and 1992 to minimise the probability of encountering migrant birds (Erskine *et al.* 1990). The same two observers conducted breeding pair surveys in all years. For both Mallard and Black Duck, breeding pairs were defined as a male and female observed together or a male or female observed alone. To reduce the probability that two male Black Duck would be recorded as a pair we distinguished sex of this species using bill colour and the appearance of scapular feathers (Ross & Fillman 1990). When one or more females were observed with two or more males the number of females was assumed to equal the number of breeding pairs. Groups of birds consisting of > 5 individuals, regardless of whether they included females, were assumed to be migrants and were not included in any analysis. In some surveys, groups of ≤ 5 males are considered equal to five breeding pairs (Dzubin 1969). However, groups of ≤ 5 males may consist of birds that have congregated on a wetland while females are laying or incubating (Dzubin 1969). The conservative definition of breeding pair adopted here increased the likelihood that birds were observed on wetlands used during establishment of breeding territories.

All wetlands surveyed for breeding pairs were classified according to Cowardin *et al.* (1979) at the class level. An additional category was created for eutrophic wetlands used in treating livestock waste. Riverine habitat in the St. John and Meduxnekeag rivers was classified to subsystem; however, a section of the St. John River was classified as lacustrine because of the presence of a dam (Cowardin *et al.* 1979). To further evaluate resource partitioning, 11 habitat characteristics were also measured for wetlands surveyed between 1990 and 1992 (Table 1). However, these characteristics were not measured for the St. John and Meduxnekeag rivers because their size precluded meaningful measurements (*e.g.* % upland forest cover varied widely along the length of these rivers).

To determine if Mallard and Black Duck partitioned habitat in time, brood surveys were conducted to compare reproductive chronology between species. Hatch dates for both species were estimated by back-dating duckling age. Mallard and Black Duck lay similar sized clutches and have similar incubation periods (Bellrose 1980). Thus, high overlap in hatch dates would indicate high overlap in reproductive chronology. Brood surveys were conducted once every 10–14 days between the last week of May and mid-July on 100 wetlands in both 1990 and 1991. Eighty of the same wetlands were surveyed in both 1990 and 1991, as were the St. John and Meduxnekeag Rivers. Twenty of the wetlands surveyed in 1990 were not surveyed in 1991 because they no longer existed (*e.g.* beaver dams had broken or been removed) or had proven extremely difficult to access. Twenty wetlands surveyed in 1991, but not 1990, were created by recent beaver activity or had been discovered but not surveyed in 1990. Surveys were conducted from shore areas that provided good visibility or by kayak depending on wetland size and were scheduled during periods of peak brood activity (06:00–09:00 h and 18:00–21:00 h; Parker *et al.* 1992). Information on duckling age (determined by plumage characteristics; Gollup & Marshall 1954) and number was used to identify broods that were observed on previous visits to a wetland, to avoid duplicating counts (Ringelman & Longcore 1982). Finally, a brood survey was conducted by helicopter shortly after completion of ground counts in mid-July in both 1990 and 1991. Helicopter surveys were conducted on all wetlands surveyed from the ground.

To determine if Mallard and Black Duck pairs partitioned macro-habitats, Fisher's exact test was used to examine the association between species and wetland class (SAS Institute Inc. 1990). Log-linear modelling was used to determine whether breeding pair surveys could be pooled across years when examining the association between species and wetland classes. For this analysis, wetland classes that had few observations were combined to meet sample size requirements. Finally, a chi-square test was used to examine the association between species and wetland class when results from all three years were combined (SAS Institute Inc. 1990).

In addition to wetland class, 11 habitat variables were evaluated on their ability to explain patterns of wetland use by Mallard and Black Duck (Table 1). Polytomous logistic regression (Hosmer & Lemeshow 1989) was used to determine which covariates were useful in distinguishing wetlands where both Mallard and Black Duck were present, only Black Duck were present, only Mallard were present, and wetlands where neither species was observed. This approach was used as an alternative to multivariate discriminate

Table 1. Habitat variables used to assess Mallard and Black Duck niche partitioning.

Variable	Description
WLCLASS[a]	Wetland Classification (Cowardin *et al.* 1979)
ORIGIN[a]	Natural *versus* man-made wetlands
BEAVER[a]	Water levels influenced by current or past beaver activity *versus* water levels not influenced by current or past beaver activity
AREA[b]	Wetland area (ha)
PER[b]	Wetland perimeter (m)
VDP[a]	Visible disturbance present *versus* visible disturbance not present. Visible disturbance is defined as an occupied dwelling or road travelled at least twice a day that was visible from any part of the wetland
DTD[b]	Distance to disturbance (m), where disturbance is defined as an occupied dwelling or road travelled twice a day but is not conditional on being visible from the wetland
UPLAND[b]	Percent of upland that is forested within 500 m of wetland perimeter. Four categories of UPLAND were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
VEG[a]	Percent of wetland surface area covered by emergent vegetation. Four categories of VEG were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
HERB[a]	Percent of wetland surface area that is herbaceous sp. vegetation. Four categories of HERB were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
ERIC[a]	Percent of wetland surface area that is ericaceous sp. vegetation. Four categories of ERIC were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%
FT[a]	Percent of wetland surface area that is flooded tree sp. vegetation. Four categories of FT were recognised: 1) 0–25%, 2) 26–50%, 3) 51–75%, 4) 75–100%

[a] Determined at wetland.

[b] Determined from aerial photographs.

analysis because it allows interactions between variables of interest to be incorporated, can easily accommodate more than two response levels, and does not require the assumption that predictor variables are normally distributed (Johnson 1998). Variables considered for inclusion in the model included those listed in Table 1, as well as wetland class. Data were combined across all 3 years (1990–1992), for a total of 186 wetland * year observations. Maximum number of wetland * year observations was 210 given that 58 wetlands were surveyed in 1990, 72 wetlands in 1991, and 80 wetlands in 1992. Preliminary descriptive analysis indicated that for some variables the number of classes would have to be reduced. Contingency tables were constructed of occupancy (both species present, Black Duck only, Mallard only, no ducks present) by each predictor variable. If there were empty cells or cells in these tables containing only one wetland, collapsing was necessary as the logistic regression models would fail to converge. The following modifications were made to the predictor variable classes: Wetland Class (WLCLASS) = Lacustrine unconsolidated bottom (L-UB), Palustrine emergent (PEM), Palustrine unconsolidated bottom (PUB) and Others (collapsed wetland classes); % Vegetative cover (VEG) = 0–25%, 26–100%; % Herbaceous cover (HERB) = 0–50%, 51–75%, 76–100%; % Ericaceous cover (ERIC) = 0–25%, 26–75%, 76–100%; % Forested upland (UPLAND) = 0–50%, 51–75%, 76–100%. Percent flooded tree cover (FT) was excluded from modelling as only 10 percent of the wetlands had any flooded trees, of which only one wetland hosted Mallard only.

Missing values were highest for Visible disturbance (VD) and UPLAND (30 wetland * year observations missing for each variable), with VEG, HERB, and ERIC missing 20 observations each. We analysed the complete data from 149 * year observations where the model was simplified via a backwards elimination procedure. A full model with main effects of all predictor variables was initially fitted. The variable yielding the smallest likelihood ratio statistic (least significant) was then eliminated and the model re-fitted until only significant variables remained (Agresti 1990).

To determine if Mallard and Black Duck partitioned habitat in time by relying on differences in reproductive chronology, hatch dates for both species were grouped into discrete 10-day intervals and the association between species and hatch date was evaluated using log-likelihood ratios for 1990 and 1991 (*G*-test: PROC FREQ: SAS Institute Inc. 1990). The start date for the first 10-day interval was the date on which the first Mallard or Black Duck brood was observed in each year. Hatch dates from 1990 and 1991 were used because sample sizes were large for both species during these years. This allowed contingency tables to be constructed with narrow hatch day intervals, while still meeting minimum cell requirements.

Prediction 2: Mallard reduce the amount of breeding habitat available for Black Duck

In 1993, Mallard pairs were removed from selected wetlands to test whether the probability of observing a Black Duck pair is greater on wetlands where Mallard pairs are removed. It was assumed that observing Black Duck at a higher rate on these removal wetlands would support the prediction that Mallard reduce the amount of habitat available to breeding Black Duck. Wetlands that were included in the removal experiment met the following criteria; 1) occupied by a single pair of Mallard over three consecutive days, and 2) less than 1 ha in size. The 1ha size restriction was imposed to minimise the probability of including wetlands that could accommodate more than one pair of breeding birds. Mallard and Black Duck pairs were observed together on larger wetlands in the study area and have been observed using the same wetlands elsewhere (Merendino *et al.* 1993; Merendino & Ankney 1994; McAuley *et al.* 1998; McAuley *et al.* 2004). Although these wetlands may have resources for several breeding pairs, intra and interspecific competition can still take place in these habitats (Merendino & Ankney 1994). However, including large wetlands in a removal experiment could require that multiple pairs be removed or confound bird response. For example, Black Duck pairs that are using the wetland when Mallard are shot might abandon it because of disturbance.

Daily surveys of wetlands meeting the size criterion began on 13 April along a pre-determined route. Prior to this date Mallard and Black Duck had only been observed in riverine habitats that were ice-free. Wetlands were either observed from a vehicle or approached on foot depending on distance from a road. To avoid observing wetlands at the same time each day, we alternated the direction along the survey route as well as the times of day surveys were initiated. Wetlands that met both the size and occupancy criteria were assigned to one of two treatments: 1) maintained free of Mallard, via removals, for the duration of the experiment, 2) Mallard remained undisturbed (control). Wetlands were assigned to one of these two treatment groups on the third consecutive day that a single pair of Mallard was observed on the wetland. Treatment assignments (removal *versus* control) were alternated among wetlands meeting the size and occupancy criteria. Between 16–22 April, seven and five wetlands were assigned to the removal and control treatments, respectively. Ten of these twelve wetlands were assigned a treatment on or before 19 April. A Fisher's Exact test was used to determine if the probability of observing a Black Duck pair on a wetland was independent of whether Mallard had or had not been removed from a wetland (SAS Institute Inc. 1990).

Prediction 3: Production of Mallard and Black Duck is inversely related over time

To test the prediction that Mallard and Black Duck production is inversely related over time, changes in the ratio and absolute number of Mallard and Black Duck broods from 1990 to 1994 were determined. To determine changes in the ratio of Mallard and Black Duck broods, brood surveys were conducted in all years between 1990 and 1994. The number of wetlands, as well as the frequency at which wetlands were surveyed, varied among years. One hundred wetlands were surveyed in 1990 and 1991 at 10–14 day intervals between the last week of

May and mid-July. Analysis of the 1990 and 1991 data indicated that Mallard and Black Duck broods did not differ in their distribution among wetland classes (Petrie 1992, 1998). The number of wetlands surveyed in 1992 and 1993 was reduced because of time constraints imposed by an ongoing study of Mallard and Black Duck reproductive success (Petrie *et al.* 2000). In 1992, 63 wetlands were sampled at two week intervals between 1–30 June, which was the time period in 1990 and 1991 when the majority of broods of both species were observed. Wetlands surveyed in 1992 and 1993 were taken from the pool of 80 wetlands sampled in both 1990 and 1991, and the 20 wetlands sampled in 1991 but not 1990 (see Prediction 1). In 1994, 74 wetlands were surveyed over the same time period and at the same frequency as in 1990 and 1991 with the exception that helicopter surveys were conducted in 1994. Fifty nine of these 74 wetlands had been surveyed in 1990 and 1991. The remaining 15 wetlands had been surveyed in 1991 but not 1990. All wetlands surveyed for Mallard and Black Duck broods between 1990 and 1994 were located in the original study area boundaries established in 1990.

Absolute changes in numbers of Mallard and Black Duck broods were examined to determine the underlying cause of any change in brood ratios. For example, Mallard : Black Duck brood ratios could increase over time solely as a result of increases in Mallard broods. To examine absolute changes in brood numbers, we compared the number of Mallard and Black Duck broods observed on the same 59 wetlands that were surveyed in both 1990 and 1994. These wetlands were ground-sampled with identical effort in 1990 and 1994; however, broods that were located only by helicopter in 1990 were excluded when comparing counts between the two years. Sixty four percent of Mallard and 64% of Black Duck broods in 1990 were observed on these 59 wetlands. In addition, the ratio of Mallard to Black Duck broods on these wetlands in 1990 was identical to that of the study area as whole. As a result, absolute changes in Mallard and Black Duck broods that occurred on these 59 wetlands were assumed to be representative of the study area.

To evaluate changes in the relative abundance of Mallard and Black Duck broods over time, linear regression was used to determine if the slope of the line describing changes in the ratio of Black Duck to Mallard broods between 1990 and 1994 differed significantly from zero (SAS Institute Inc. 1990). Because survey efforts were not constant among years, a least squares regression was conducted with weights proportional to the number of wetlands surveyed within a year (SAS Institute Inc. 1990). To assess changes in Mallard and Black Duck broods that occurred on the same 59 wetlands surveyed with the same effort in 1990 and 1994, we evaluated changes in the ratio of the two species using a *G*-test (SAS Institute Inc. 1990), and also examined changes in the absolute numbers of Mallard and Black Duck broods.

Results

Prediction 1

Distribution of breeding pairs among wetland classes (Table 2) was independent

Table 2. Distribution of Mallard (MAL) and Black Duck (BD) breeding pairs across wetland classes 1990–1992.

Wetland subsystem / class	**1990 BD**		**1990 MAL**		**1991 BD**		**1991 MAL**		**1992 BD**		**1992 MAL**	
	%	***n***	**%**	***n***	**%**	***N***	**%**	***n***	**%**	***n***	**%**	***n***
Riverine lower perennial	27.1	(19)	29.6	(16)	34.1	(30)	43.5	(27)	37.5	(30)	34.8	(24)
Lacustrine limnetic	25.7	(18)	27.8	(15)	25.0	(22)	25.8	(16)	17.5	(14)	28.9	(20)
Palustrine emergent	15.7	(11)	20.3	(11)	17.0	(15)	14.5	(9)	15.0	(12)	13.0	(9)
Palustrine unconsolidated bottom	27.1	(19)	13.0	(7)	12.5	(11)	8.1	(5)	15.0	(12)	11.6	(8)
Palustrine scrub shrub	2.9	(2)	0.0	(0)	2.3	(2)	0.0	(0)	1.3	(1)	0.0	(0)
Palustrine forested	0.0	(0)	1.9	(1)	4.6	(4)	3.2	(2)	7.5	(6)	1.4	(1)
Palustrine aquatic bed	0.0	(0)	1.9	(1)	2.3	(2)	1.6	(1)	1.3	(1)	2.9	(2)
Eutrophic	1.4	(1)	5.6	(3)	2.3	(2)	3.2	(2)	5.0	(4)	7.2	(5)
TOTAL		70		54		88		62		80		69

of species in 1990 ($P = 0.22$, n.s.), 1991 ($P = 0.90$, n.s.), and 1992 ($P = 0.41$, n.s.). Comparison of log linear models to test for conditional independence of year with species and combined wetland classes, indicated that information on breeding pair distribution could be pooled across years (likelihood ratio: $\chi^2_{18} = 17.21$, $P = 0.51$, n.s.). Using this conditional independence model as a basis and contrasting it with a model characterised by further independence of species and combined wetland class, we found that Mallard and Black Duck distribution across wetland classes did not differ when surveys were combined across years (likelihood ratio: $\chi^2_4 = 4.75$, $P = 0.31$, n.s.). Four variables (WLCLASS, ORIGIN, PER, UPLAND) were retained in the model associating habitat characteristics with observations of Black Duck only, Mallard only, both species present, and no ducks present (Table 3). Mallard, alone or with Black Duck, were observed in greater proportion

Table 3. Variables retained in a model associating habitat characteristics with the presence of Mallard and Black Duck. L-UB = Lacustrine unconsolidated bottom; P-EM = Palustrine emergent; P-UB = Palustrine unconsolidated bottom; Other = Palustrine scrub shrub, Palustrine forested, Palustrine aquatic bed and Eutrophic.

Variable	**Wetlands with Mallard and Black Duck**		**Wetlands with Black Duck only**		**Wetlands with Mallard only**		**Wetlands with neither Mallard nor Black Duck**	
	%	(*n*)	%	(*n*)	%	(*n*)	%	(*n*)
L-UB[a]	7.1	(2)	32.2	(9)	7.1	(2)	53.6	(15)
P-EM[a]	17.3	(9)	21.2	(11)	11.5	(6)	50.0	(26)
P-UB[a]	7.0	(3)	23.3	(10)	20.9	(9)	48.8	(21)
Other[a]	23.1	(6)	34.6	(9)	15.4	(4)	26.9	(7)
Natural[b]	8.3	(11)	28.6	(38)	15.0	(20)	48.1	(64)
Man-made[b]	56.2	(9)	6.3	(1)	6.3	(1)	31.2	(5)
< 50% Forest[c]	16.2	(6)	13.5	(5)	21.6	(8)	48.7	(18)
50–75% Forest[c]	13.3	(8)	26.7	(16)	8.3	(5)	51.7	(31)
> 75% Forest[c]	11.5	(6)	34.6	(18)	15.4	(8)	38.5	(20)

[a]WLCLASS; [b]ORIGIN; [c]UPLAND

on Palustrine Unconsolidated *vs.* Lacustrine Unconsolidated wetlands, and were more likely to be observed on wetlands with shorter perimeters. Black Duck only or with Mallards were likely to be observed in greater proportion on Other wetlands than on Palustrine Unconsolidated wetlands. Both species together were more likely to be observed on man-made *versus* natural wetlands: however, few man-made wetlands were present in the study area (16 of 149 wetland-years used in modelling). Of the four variables retained in the model, only UPLAND was associated with the presence of one species. Black Duck only were more likely to be present on wetlands that had > 75% upland forest cover than wetlands that had < 50% upland forest cover (Table 4).

Hatch dates determined for Mallard and Black Duck broods in 1990 and 1991 (Fig. 1) showed that the two species failed to partition breeding resources in either time or space. Hatch dates were independent of species in both 1990 ($G^2_4 = 4.72$, $P = 0.32$) and 1991($G^2_3 = 1.70$, $P = 0.64$).

Prediction 2

Black Duck were more likely to be observed on wetlands where Mallard had been

Table 4. Polytomous logistic regression results of modelling Mallard and/or Black Duck presence as a function of 10 habitat variables, wetland class, and year.

Variable	Likelihood ratio (χ^2)	d.f.	*P* value
HERB[a]	4.53	9	0.87
VEG[a]	1.65	3	0.65
VD[a]	1.92	3	0.59
DTD[a]	2.04	3	0.56
YEAR[a]	6.59	6	0.36
AREA[a]	3.06	3	0.38
ERIC[a]	10.84	6	0.09
BEAVER[a]	4.41	3	0.22
WLCLASS[b]	16.78	9	0.05
ORIGIN[b]	8.80	3	0.03
PER[b]	14.33	3	0.01
UPLAND[b]	12.14	6	0.05

[a] Variables not retained in model based on sequential backwards elimination procedure
[b] Variables remaining in final model

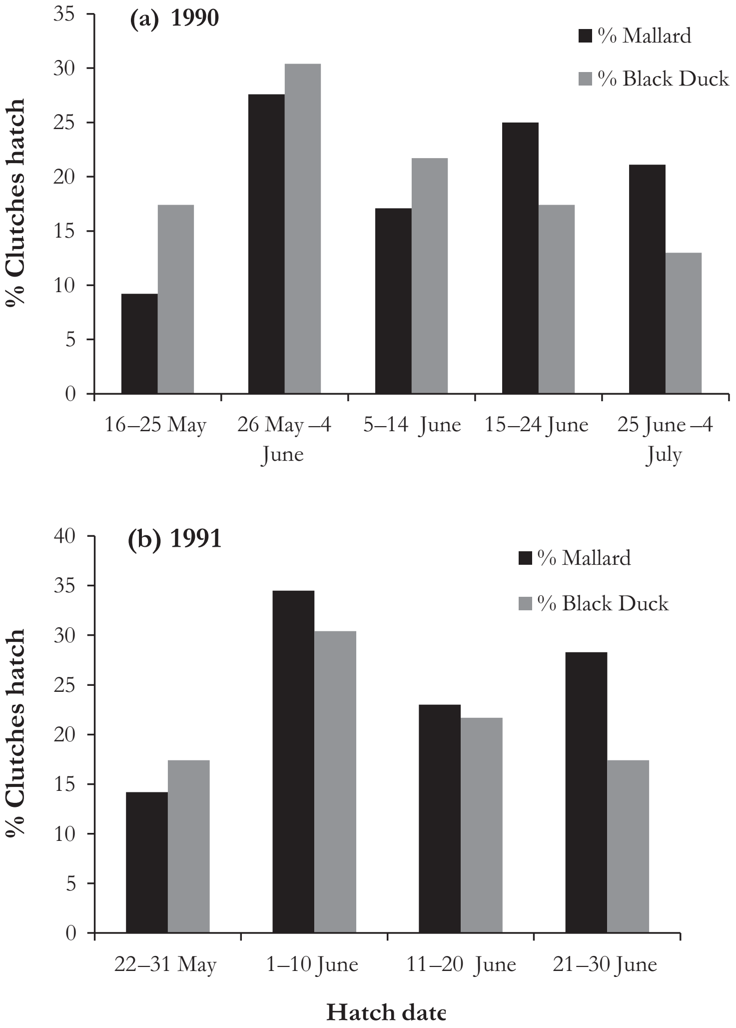

Figure 1. Timing of Mallard and Black Duck hatch dates over 10-day intervals in: (a) 1990 (n = 76 Mallard and n = 69 Black Duck clutches seen to hatch), and (b) 1991 (n = 113 and n = 77 for Mallard and Black Duck, respectively). The start date for the first 10-day interval was the date on which the first Mallard or Black Duck brood was observed in each year.

removed than on control wetlands where Mallard were not removed (P = 0.03). Black Duck pairs were observed on five of seven removal wetlands. On all five of these wetlands a Black Duck pair was observed within a day of removing Mallard (Table 5a). No Black Duck were observed on any of the five control wetlands for the duration of the experiment (Table 5b).

Table 5. Daily observations of wildfowl on: (a) removal wetlands (where Mallard were removed), and (b) control wetlands (where Mallard were not removed). MP = Mallard pair; MP-COL = Mallard pair collected; MP-NC = Mallard pair observed but failed to collect; NWO = no wildfowl observed; MM = Mallard male; MBD = male Black Duck; BDP = Black Duck pair.

	(a) Removal wetland number						
Observation day	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	MP	MP	MP	MP	MP	MP	MP
2	MP	MP	MP	MP	MP	MP	MP
3	MP-COL	MP-COL	MP-COL	MP-COL	MP-COL	MP-COL	MP-COL
4	NWO	BDP	BDP	NWO	BDP, MBD	BDP	BDP
5	MP-NC	MP-NC	BDP	NWO	MBD	NWO	MM
6	NWO	MP-NC	BDP	MM	BDP, MBM	MP-NC	NWO
7	MP-NC	MP-COL	MP-NC	MM	MBD, 2MM	NWO	BDP
8	MP-COL	MP-NC	MP-NC	NWO	MBD	MM	MBD
9	MBD	MP-COL	NWO	NWO	MM	NWO	BDP
10	NWO	BDP	MP-NC	MM	BDP, MBD	NWO	NWO
11	NWO	BDP	NWO	NWO	BDP, MM	NWO	2MM
12	NWO	NWO	MP-COL	MM	MBD, 2MM	NWO	NWO
13	NWO	3MM, MBD	NWO	NWO	NWO	NWO	
14	NWO	NWO	NWO	MM		NWO	
15	NWO						
16	NWO						
17	NWO						
18	NWO						

	(b) Control wetland number				
	1	**2**	**3**	**4**	**5**
1	MP	MP	MP	MP	MP
2	MP	MP	MP	MP	MP
3	MP	MP	MP	MP	MP
4	MP	MP	MP	NWO	MP
5	MP	NWO	NWO	NWO	MP
6	MP	MM	MP	MM	MP
7	MP	MM	MP	NWO	MP
8	MP	MM	MM	MP	NWO
9	MP	MM	MM	MM	NWO
10	MM	MM	MM	MM	NWO
11	MM	MM	MM	MM	NWO
12	MM	MM	MM	NWO	
13	MM	MM			
14					

Removal wetlands varied in numbers of times Black Duck were observed. On none of the wetlands were Black Duck pairs observed for the duration of the experiment. Black Duck were intermittently observed on removal wetlands, or a Mallard pair was observed at the site after observing Black Duck the previous day. Additional Mallard pairs were shot on three removal wetlands after the initial pair had been removed, as dictated by the treatment. We failed to collect Mallard pairs that were observed on some removal wetlands after the initial pair had been shot (Table 5a). On control wetlands, Mallard pairs or a single male Mallard were consistently observed throughout the experiment (Table 5b).

Prediction 3

The ratio of Black Duck to Mallard broods decreased significantly from 0.92 in 1990 to 0.22 in 1994 ($F_{1,3}$ = 24.74, r^2 = 0.89, P = 0.02), with decreases being most apparent after 1991 (Table 6). The ratio of Black Duck to Mallard broods also declined significantly over this five-year period when ratios were weighted by the number of wetlands sampled in a year ($F_{1,3}$ = 27.26, r^2 = 0.87, P = 0.01). Black Duck to Mallard brood ratios also declined significantly for 59 wetlands that were surveyed with equal effort in 1990 and 1994, from 0.94 to 0.24 (G^2_1 = 18.0, $P < 0.01$). The number of Black Duck broods observed on these 59 wetlands declined from 45 in 1990 to 19 in 1994, whereas the number of Mallard broods increased from 48 in 1990 to 78 in 1994. Total broods of both species increased by < 5%, from 93 in 1990 to 97 in 1994.

Discussion

Increasing Mallard populations in eastern North America have been accompanied by major declines in Black Duck abundance (Collins 1974; Dennis *et al.* 1989; Merendino *et al.* 1993). Consequently, some authors have attributed the decline of Black Duck to competition and/or hybridisation with Mallard (Ankney *et al.* 1987; Dennis *et al.* 1989; Merendino *et al.* 1993). Results of our study supported the hypothesis that Mallard and Black Duck compete for breeding resources.

Table 6. Changes in the ratio of Black Duck to Mallard broods in 1990–1994.

Year	No. of wetlands surveyed (n)	No. Black Duck broods	No. Mallard broods	Black Duck/ Mallard ratio
1990	100	70	76	0.921
1991	100	77	116	0.664
1992	63	29	83	0.349
1993	42	17	53	0.321
1994	74	23	106	0.217

Past attempts to document niche partitioning among sympatric species of waterfowl have usually revealed differences in macro-habitat use, diet, or morphological adaptations associated with foraging and micro-habitat use (Nudds 1992). Although resource partitioning appears to be widespread in the waterfowl community (Nudds 1992), we detected no interspecific differences in the distribution of breeding Mallard and Black Duck among wetland classes for any year. We also found no evidence that Mallard and Black Duck partitioned breeding habitat through differences in reproductive chronology.

Earlier studies also failed to find evidence of resource partitioning by Mallard and Black Duck. Mallard and Black Duck breeding in the western Adirondack Mountains of New York did not differ in proportional use of four wetland habitat types (Dwyer & Baldassare 1994). Merendino & Ankney (1994) found that Mallard and Black Duck breeding in central Ontario preferred wetlands of similar size, shape, fertility, and open water, and concluded that competition for breeding habitat was likely. Although these studies generally focused on macro-habitat characteristics, the two species also fail to partition habitat through differences in micro-habitat use or foraging ecology (Eadie *et al.* 1979; Nudds & Bowlby 1984; Tremblay & Couture 1986; Belanger *et al.* 1988).

Although distribution of Mallard and Black Duck among wetland classes was independent of species, log linear modelling revealed that wetlands surrounded by greater than 75% upland forest cover were more likely to be occupied by Black Duck only than by Mallard only or by both species together. However, Mallard do breed within heavily forested regions of the Black Duck's range (Porter 1993; Dwyer & Baldassare 1994; Merendino & Ankney 1994; Maisonneuve *et al.* 2006), so intact forests do not function as an indefinite isolating mechanism for Black Duck (Dwyer & Baldassare 1994; Nudds *et al.* 1996). While these results suggest that Black Duck prefer more heavily forested landscapes than do Mallard, Mallard were also documented breeding in these landscapes (*i.e.* 26.9% of all Mallard pairs were observed in wetlands surrounded by > 75% upland forest cover).

Failure to partition breeding resources should not affect Black Duck if Mallard do not prevent Black Duck from using these resources, or if breeding habitat is not limited. However, Black Duck were observed at a significantly higher rate on wetlands where Mallard were removed. Although sample sizes were small, no Black Duck were observed at any time on control wetlands where Mallard were not collected. The presence of Mallard on control wetlands appeared to limit the use of these wetlands by Black Duck and supports the prediction that Mallard reduce the amount of breeding habitat available to Black Duck. These results also support Seymour's (1992) conclusion that the two species treat each other as conspecifics when defending breeding territories.

Although Mallard and Black Duck were never observed together on either treatment or control wetlands, the two species can occur together on the same wetland. For example, McAuley *et al.* (2004) observed Mallard and

Black Duck pairs using the same wetlands in northeast Maine. The average size of wetlands in their study was much larger than wetlands included in our removal experiment (all < 1 ha), however, and included wetlands up to 113 ha in size. Larger wetlands are more likely to offer visual obstructions, which can allow pairs to isolate themselves from conspecifics. We purposely chose small treatment and control wetlands to avoid this possibility. However, breeding pair densities on larger wetlands must eventually be limited by spacing behaviour regardless of the greater opportunity to achieve visual isolation in these habitats. It seems that Mallard occupying the same wetlands as Black Duck may ultimately reduce the potential of those wetlands to support Black Duck because the two species treat each other as conspecifics (Seymour 1992). Even if competition coefficients for the two species are symmetrical, Mallard would represent an additional source of intraspecific density dependence for Black Duck.

Recent efforts to model production rates of Black Duck populations have found evidence of intraspecific density dependence on the breeding grounds (Zimpfer & Conroy 2006). The authors suggested that evidence for density dependence in Black Duck reproduction could mean that Black Duck are near habitat carrying capacity and that Mallard could further reduce carrying capacity. Competition between Mallard and Black Duck is conditional on breeding habitat limitation. If Black Duck populations are near carrying capacity, then the likelihood for competition seems high given the failure of these two species to partition resources in time or space.

Inverse changes in population sizes over time are consistent with the hypothesis that waterfowl species compete (Pöysä 1984; Nudds 1992). Within our study area there was evidence that production of Mallard and Black Duck was inversely related. Ratios of Black Duck to Mallard broods declined steadily between 1990 and 1994, and surveys on the same 59 wetlands in 1990 and 1994 documented large declines in numbers of Black Duck broods. This decline was entirely offset by increases in Mallard broods. There were no interspecific differences in distribution of Mallard and Black Duck broods among wetland classes (Petrie 1998). Thus, even if changes in relative abundance of wetland types occurred between years (and there was no evidence that they did), we would expect Mallard and Black Duck broods to respond similarly. Moreover, our conclusions are not dependent on the assumption that all broods are observed, or that Mallard and Black Duck broods are observed with equal probability. We only assume that the probability of observing Mallard and Black Duck broods did not change over time. Changes in relative mortality rates of Mallards and Black Duck young between 1990 and 1994 could have produced changes in brood ratios, especially if these mortality changes occurred shortly after hatch. However, work on the study area between 1992 and 1994 indicated no differences in duckling survival between the two species (Petrie *et al.* 2000).

Inverse changes in Mallard and Black Duck populations have been documented elsewhere. Mallard increased by 600% in southern Ontario between 1951 and 1971, while Black Duck increased by 50% (Collins 1974; Merendino *et al.* 1993). From 1971 to 1985, Mallard increased by another 51%, while Black Duck decreased by 38% (Ankney *et al.* 1987; Merendino *et al.* 1993). However, we concur with Nudds *et al.* (1996) that Mallard are not certain to cause declines in Black Duck. Black Duck populations remained stable in northwest Ontario over a 40-year period despite large numbers of Mallard breeding in the region (Nudds *et al.* 1996). Perhaps breeding habitat in northwest Ontario is sufficient to meet the needs of both species and Black Duck have experienced no population effects as a result of competition with Mallard. We conclude that Mallard and Black Duck will compete where breeding resources are limiting, and concur with Zimpfer and Conroy (2006) that efforts to manage Black Duck using an adaptive management framework should include the possible effects of Mallard.

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Measurements and movements of Madagascar Teal *Anas bernieri* captured and ringed at Lake Antsamaka in central-western Madagascar

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Abstract

Madagascar Teal *Anas bernieri* were captured at Lake Antsamaka, central-western Madagascar, during the species' annual wing moult to test whether the sexes could be differentiated on morphometrics and report on a little-known species. A total of 345 birds were caught, measured and ringed over a 13 year period (1997–2009), of which 73 were recaptured. Males and females did not differ significantly in body mass; for other body measurements (tarsus, culmen and skull) males were significantly larger. Body mass did not change significantly with wing length for moulting birds re-growing their feathers, implying an adequate food supply to maintain mass during moult at the site. Wing length increased linearly at a rate of 5.72 mm/day in individuals recaptured 1–8 days after first being caught, indicative of feather growth over this period, with growth rates stabilising and diminishing thereafter. One adult female (aged at least 2 years) was caught eight years after first capture, indicating that Madagascar Teal can reach an age of at least 10 years in the wild. Individuals caught and ringed during moult moved up to *c*. 200 km from the ringing site. Declines in numbers moulting at Lake Antsamaka during our study were linked to water depth at the site, which is in turn apparently linked to annual precipitation. Conservation of this species requires protection of the population in several watersheds and at moulting sites where it is very vulnerable to disturbance, capture for food by local people and predation.

Key words: biometrics, longevity, Madagascar Teal, ringing.

The Madagascar Teal *Anas bernieri* is a little-known species of Anatidae, endemic to Madagascar, with a range limited principally to the western coastal wetlands between the Mangoky Delta and Antsiranana and also the extreme northeast of the country (Safford & Hawkins in press). Prior to 1990, it was known to occur only in the

Manambolomaty Delta wetlands of the Antsalova region of Madagascar, where the population was estimated at 100–500 birds in 1993 (Safford 1993). The species was not included in the IUCN red data book before 1986, but was listed as "Vulnerable" from 1986–2000 (Green 1996; Collar & Stuart 1985). Madagascar Teal have been observed only on shallow fresh and brackish water, including marshes, river mouths, small lakes, estuaries and mangroves at around sea level (Morris & Hawkins 1998). It is thought that they may move only a few kilometres between nesting, moulting and dry-season sites (Young 2006). The most recent population estimate is of just 1,500–2,500 birds (Delany & Scott 2006) and the species is now classified as "Endangered" (BirdLife International 2012).

As with all Anatidae species, Madagascar Teal typically regrow flight feathers (especially the primary and secondary wing feathers) after the breeding season, becoming flightless for at least two weeks at this time. In common with close relatives such as the Grey Teal *Anas gracilis*, both members of the pair accompany the brood after hatching (Young *et al*. 1998). Madagascar Teal ducklings fledge in *c*. 45–49 days, and the adults moult following departure of the young (Young 2006). The breeding sites become dry at the start of Madagascar's west coast dry season (April–December), when young teal move to dry season refugia and the adults to safe moult sites such as Lake Antsamaka before also transferring to the refugia (Young 2006). Birds have been captured at one moulting site, Lake Antsamaka in central-western Madagascar, since the late 1990s to improve knowledge on the species' ecology and individual movements. All caught birds are ringed, measured and weighed, with rainfall and lake depth also being recorded. This paper aims to: 1) increase the information available on body measurements for non-captive Madagascar Teal (including feather growth rates), 2) investigate whether the birds' body mass varies with moult stage, 3) describe for the first time the dispersal of individual birds after moulting, and 4) provide preliminary information on the birds' life-span in the wild.

Study site

Lake Antsamaka, in the Antsalova district of central-western Madagascar (19°02'S, 44°22'E; Fig. 1) is part of the larger Manambolomaty Ramsar site. It is shallow and saline, *c*. 7m above sea level, with an area of *c*. 174 ha in the wet season. The lake is ephemeral, typically without standing water from October–December inclusive, but may become dry much earlier (from July), depending on the amount of rainfall in the area and also on the extent of flooding from River Manambolomaty. Lake vegetation is dominated by water lilies *Nymphea stellata*, *N. lotus* and *Logorosipho madaggascariensis*, with patches of Purple Nutsedge *Cyperus rotundus* and rushes *Juncus* sp. The lake is an important habitat for waterbirds in central-western Madagascar, and two endangered duck species – the Madagascar Teal and the White-backed Duck *Thalassornis leuconotus insularis* – occur at the site (Woolaver & Nichols 2006).

Methods

Since 1997, regular attempts have been made to catch Madagascar Teal at Lake

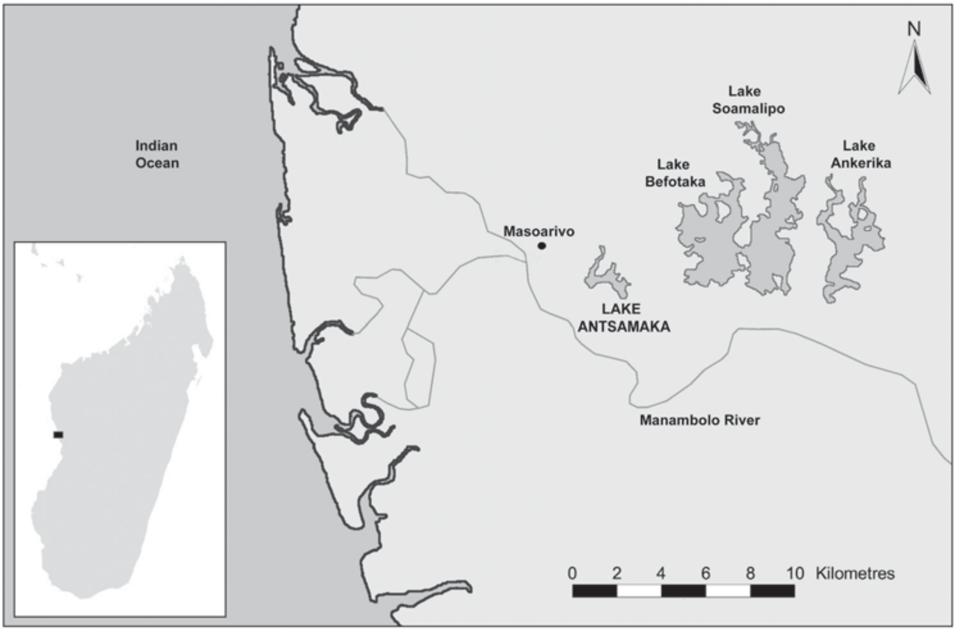

Figure 1. Location of the Madagascar Teal ringing site, Lake Antsamaka, in Madagascar.

Antsamaka during the moulting period (mid-April to mid-June), although in some years the lake dried early and the birds departed. In the first two years, the birds were caught using nets 6 m long and 2 m wide, placed in the lake with a support at each end and with the bottom 50 cm of the net submerged. Moulting ducks were pushed slowly toward the net and corralled. In subsequent years the catching technique was changed and ducks were pushed toward the vegetated edge of the lake. Once out of the water the ducks hid under the vegetation where they remained motionless and were easily caught by hand. For each bird captured a variety of measurements were taken including skull length (mm; from top of the head to tip of the bill); culmen (mm; from the un-feathered base of the bill to its tip), tarso-metatarsus (mm; from the tarsal joint to the base of foot) and body mass (to the nearest 1.0 g). Wing length (to the nearest mm; from carpal joint to the end of longest primary feather) was also recorded to determine the stage of the moult. Finally, birds were ringed with coloured plastic rings fitted to one leg and a numbered metal ring fitted to the other leg. The metal rings were all provided by The Société Jersiaise in Jersey through the Durrell Wildlife Conservation Trust. It is not possible to sex Madagascar Teal by external characters and, as field workers were not trained in cloacal sexing, this was not undertaken to avoid undue stress to the birds. The sexes differ in their calls, however, with males having multi-syllabic whistles and females a harsh, croaking quack (Young 2005; Safford & Hawkins in press) and this was noted for each bird on release after ringing. Sex was not assigned for those birds that did not call on release. The birds were all adults and considered to be at least 2 years old because wing moult does not occur until at least one year old (*i.e.* after the first breeding attempt) and Madagascar Teal do not breed at the Lake Antsamaka moulting site.

Rainfall and lake depth were recorded at Lake Antsamaka from 2000–2009 inclusive. A rain gauge, installed and placed 1 m above the ground, was read at 07:00 h each day throughout the year. Lake depth was monitored by weekly readings of water levels on a wooden post (marked at 1 cm intervals) installed in the lake. An annual count of teal was conducted each July across all areas of open water in the study area: three main lakes and 3–6 small ponds among the mangroves, depending on drought. The counts were coordinated (made near-simultaneously) at all sites by field workers using binoculars and spotting scopes. Differences between males and females for each of the body size measures (body mass, tarsus, culmen and skull length) were analysed using Mann-Whitney U tests. Spearman's rank correlations assessed whether there was a trend in the numbers of birds: 1) counted, and 2) captured over time, and also tested for an association between the depth of the lake and the number of birds counted and caught. Linear regression analysis was used to determine changes in wing length (indicative of feather growth) between initial capture and recapture.

Results

A total of 345 individuals was caught between 1997 and 2009, of which 73 were recaptured in subsequent years (Table 1). The number of birds caught was very low during the first year because the capture session was too late in the season compared to the moulting period. Numbers caught were higher in years 2, 3 and 4 but decreased and fluctuated thereafter; no individuals were caught in 2006, 2008 and 2009 (Table 1). There was no correlation between number of individuals captured and number of individuals counted ($r_S = 0.46$, $n = 13$, $P = 0.15$, n.s.), but there was a significant decline over time both in the number of individuals caught ($r_S = -0.66$, $n = 13$, $P = 0.01$) and in the numbers counted each year ($r_S = -0.64$, $n = 13$, $P = 0.04$; Fig. 2). The sex ratio of captured birds which vocalised on release was 1.8 males to each female ($n = 210$); 135 (39%) of the 345 birds caught did not call. The maximum interval between capture and recapture was eight years, for a teal originally ringed as an adult (*i.e.* at least 2 years old) in 1999 and recaptured in 2007.

Biometrics data recorded for 119 male and 64 female Madagascar Teal during the moulting period are presented in Table 2. Although males were marginally heavier than females, sex differences in body mass were not statistically significant ($U = 3205.5$, $P = 0.07$, n.s.). Other measurements did differ significantly, with males having longer tarsus ($U = 2270$, $P < 0.001$), culmen ($U = 1780$, $P < 0.001$) and skull lengths ($U = 1223$, $P < 0.001$) than females, albeit that there was substantial overlap in the

Table 1: Number of individual Madagascar Teal caught, ringed and recaptured from 1997–2009.

Year first ringed	**No. ringed**	**No. recaptured in each year**											
		1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
1997	15	3	13	–	–	–	–	–	–	–	–	–	–
1998	89	–	19	4	–	–	–	–	–	–	–	–	–
1999	66	–	–	20	–	–	5	3	–	–	1	–	–
2000	94	–	–	–	–	–	3	2	–	–	–	–	–
2001	7	–	–	–	–	1	–	–	–	–	–	–	–
2002	3	–	–	–	–	–	–	–	–	–	–	–	–
2003	26	–	–	–	–	–	–	3	1	–	3	–	–
2004	27	–	–	–	–	–	–	–	–	–	2	–	–
2005	6	–	–	–	–	–	–	–	–	–	1	–	–
2006	0	–	–	–	–	–	–	–	–	–	–	–	–
2007	12	–	–	–	–	–	–	–	–	–	–	–	–
2008	0	–	–	–	–	–	–	–	–	–	–	–	–
2009	0	–	–	–	–	–	–	–	–	–	–	–	–
TOTAL	345	3	21	24	0	1	8	8	1	0	7	0	0

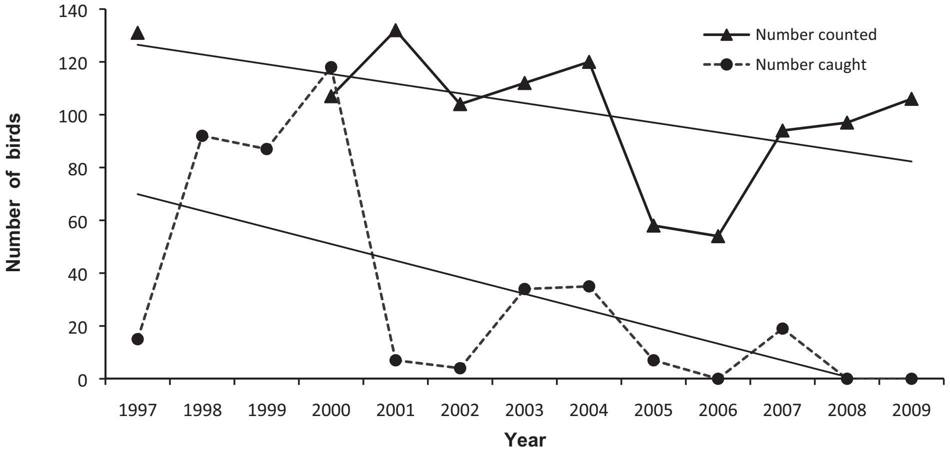

Figure 2. The number of individual Madagascar Teal caught each year at Lake Antsamaka, and the maximum annual count at the site.

ranges recorded for each sex (Table 2). For 27 birds caught twice which were re-growing their feathers, wing length (including primary length) correlated significantly with the duration between catches ($r_s = 0.428$, $n = 27$, $P = 0.006$). Wing length increased linearly at a rate of 5.72 mm/day in individuals recaptured 1–8 days after first being caught (linear regression: $R^2 = 0.75$, $t_{1,20} = 8.33$, $P < 0.01$), indicative of feather growth over this period, with growth rates stabilising and diminishing thereafter (Fig. 3). Body mass recorded for birds caught for the first time in a season (*i.e.* omitting birds that might have lost mass because of capture a few days earlier) appeared to be higher towards the end of the moult (indicated by longer wing lengths, for birds known from subsequent capture to be re-growing their feathers) but

Table 2. Measurements and weight of Madagascar Teal during moult.

	Male	**Female**
	$n = 119$	$n = 64$
Body mass (g)	378 ± 36 (290–490)	368 ± 34 (300–450)
Wing (mm)	129 ± 25 (80–210)	117 ± 28 (82–205)
Tarsus (mm)	46 ± 2 (41–50)	45 ± 2 (41–95)
Culmen (mm)	38 ± 3 (34–49)	36 ± 2 (32–48)
Skull (mm)	82 ± 2 (77–90)	79 ± 3 (75–90)

the correlation between mass and wing length did not prove statistically significant ($R^2 = 0.29$, $t_{1,25} = 1.86$, $P = 0.08$, n.s.; Fig. 4).

Annual rainfall ranged from 44 cm (in 2005) to 329 cm (in 2004), with mean of 109 cm over the years 2000–2009. The lake depth varied between 240 cm in 2004, corresponding with the period of highest rainfall, and 50 cm (in 2006 and 2009). Lake depth was positively correlated with the number of teal captured across years ($r_S = 0.77$, $n = 10$, $P = 0.009$).

Four individuals ringed during the study were re-sighted and two recovered elsewhere in Madagascar. All observations were at coastal locations (Fig. 5). Two birds were caught in fishing nets at Bemia Lake (30 km from the study area) and two were seen at Lake Bedo during a waterbird survey in the Menabe central coastal wetlands, about 100 km south of the ringing site. One bird was killed by hunters at Lake Bedo and a second by local people at Behoria, 200 km north of Lake Antsamaka.

Discussion

The number of individuals captured fluctuated among years during our study, but declined overall. This decrease may be partly but not totally related to a decline in the overall number of Madagascar Teal at the site, as there was no significant correlation between the number of individuals captured and the number of individuals counted. Fewer birds were caught in years when the lake was shallower, which suggests that

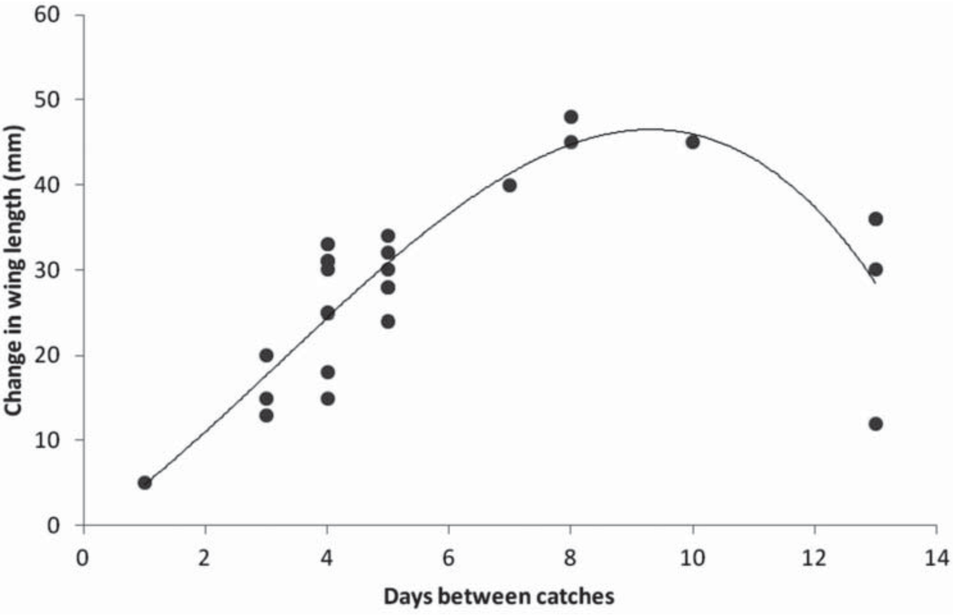

Figure 3. Increase in wing length (reflecting increase in feather length) recorded for individual Madagascar Teal captured and recaptured within a moulting season.

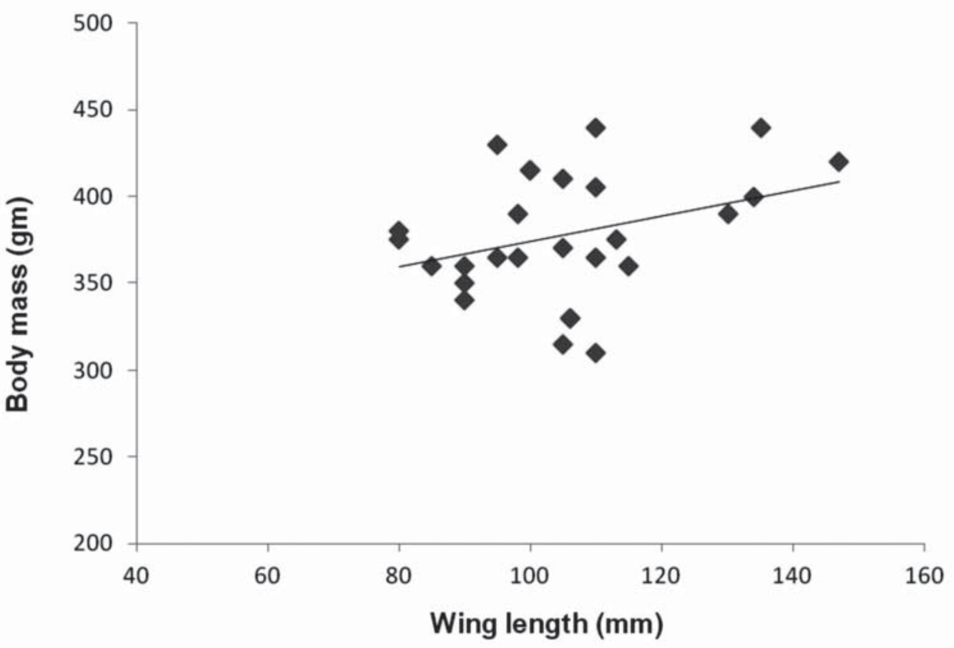

Figure 4. Madagascar Teal body mass in relation to moult stage, indicated by wing length. Measurements are for first capture dates, for birds re-growing their feathers.

variation in lake depth may influence ability to catch teal moulting at Lake Antsamaka. It is also possible, however, that the decline in numbers counted and caught over time is due to birds using other sites to moult, due to human disturbance at the lake. The reduced catching success therefore may be due to a combination of several factors including the lake depth, vegetation cover which serves to ensure flightless ducks' safety (the extent of vegetation was not specifically recorded at site, but was consistent with lake depth in that emergent vegetation suitable for cover disappears as the lake dries) and human disturbance including capture effects. As of 2010, we have stopped the catching and ringing programme for five years while continuing to monitor the number of moulting birds at Lake Antsamaka. This will help to clarify the reason for the decline in the number of teal moulting in the site.

Like their close relative the Grey Teal (Marchant & Higgins 1990), male and female Madagascar Teal are similar in body mass; males are larger on average, but there is substantial overlap in the range of measures recorded (Safford & Hawkins in press). For the other body size measures considered here, males were significantly larger than females, but again there was substantial overlap in the ranges. Madagascar Teal therefore does not seem to show a large degree of sexual dimorphism, and consequently it seems that body size cannot be used to identify males and females reliably in the field.

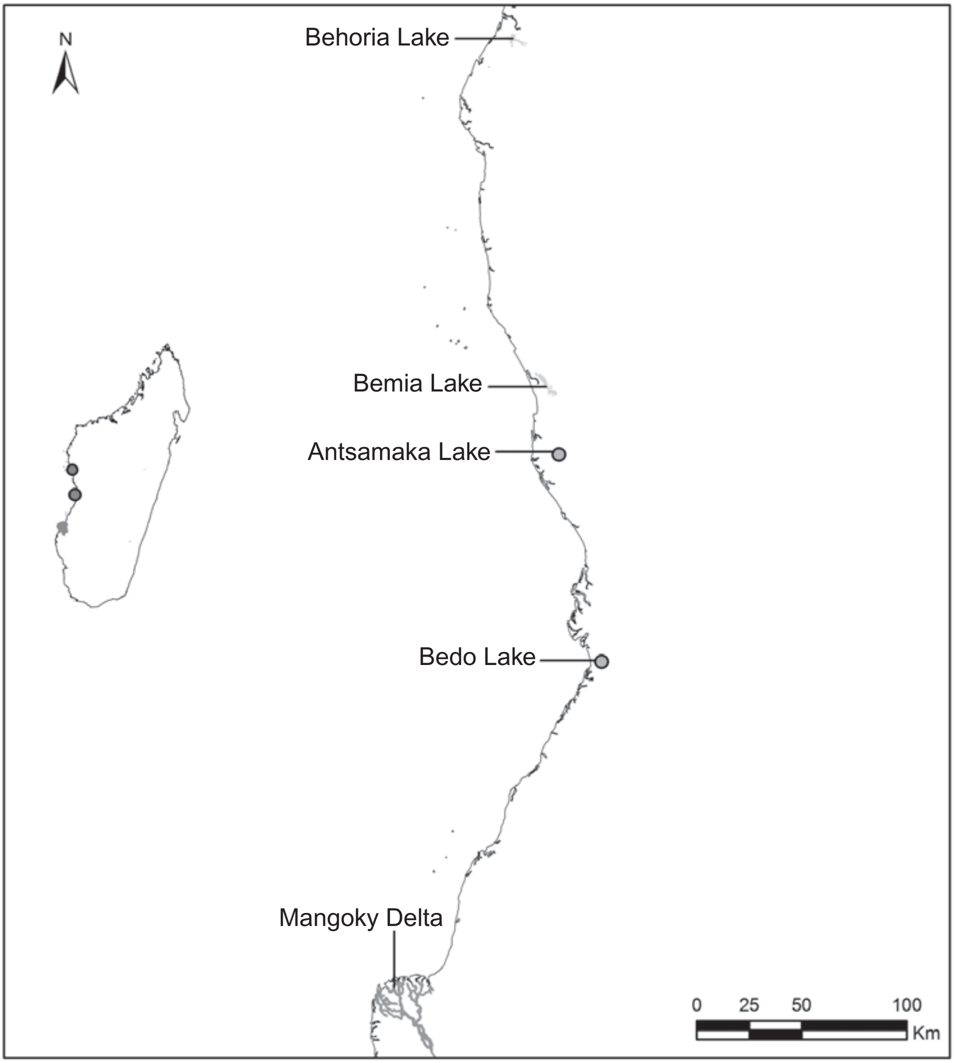

Figure 5. Sites where ringed Madagascar Teal were re-sighted, along the coast of western Madagascar.

An individual female was recaptured in 2007, eight years after first being caught. As birds of ≤ 1 year are thought not to occur at Lake Antsamaka, and captured birds therefore were at least two years old on ringing, it seems that Madagascar Teal can reach at least 10 years of age in the wild. Additionally, one male caught in the wild in 1993 lived until 2004 (aged 13 years) in captivity (Young *in litt.*), indicating that both wild and captive Madagascar Teal can have long life-spans. The sex ratio recorded for Madagascar Teal moulting at Lake Antsamaka (that called during handling and could be sexed) was 1.8 : 1, with males being nearly twice as numerous as females. Sex ratios may vary within a species' range; for instance, if males compete with females for food resources in the non-breeding season or smaller-bodied females require a more temperate climate (Owen & Dix 1986; Carbone & Owen 1995). Given that sex was determined by the birds' calls, however, and that 135 (39%) of the 345 birds caught did not call, cloacal sexing should be undertaken for Madagascar Teal at Lake Antsamaka to determine whether the apparent preponderance of males is attributable to males being more likely than females to vocalise on release.

Primary feather growth rates of 5.8 mm/day are similar to those of Mallard (5.5–6.7 mm/day; Panek & Majewski 1990) and the similarly sized Teal *Anas crecca* (4.8 mm/day; Sjöberg 1988) in Europe. However, unlike many dabbling duck species in Europe (*e.g.* King & Fox 2012) and in Africa (*e.g.* Ndlovu *et al.* 2011), Madagascar Teal did not lose mass during wing moult, suggesting that Lake Antasmaka not only provides a safe refuge from potential predators during the flightless period, but that it also supplies sufficient sources of exogenous energy to meet the energy demands of individuals throughout the moult.

Sightings of ringed individuals indicate that Madagascar Teal can move at least 220 km from their moult site; the furthest distance between re-sighted birds was > 400 km within *c.* 1,500 km of Madagascar coastline with wetlands potentially suitable for the birds. These sightings suggest that the teal disperse between different breeding areas and that individuals may travel over large annual ranges. Lake Antsamaka is an important moulting site for Madagascar Teal, but after the moult some birds move to other areas. These results indicate that long-distance movements occur, possibly due to the birds taking advantage of differing conditions between watersheds. The fluctuation in numbers recorded moulting at Lake Antsamaka also suggests that Madagascar Teal use of a site is not stable; for instance, teal may be forced to move to other sites when Lake Antsamaka is too dry. Ensuring the future survival of the endangered Madagascar Teal therefore requires conservation of wetlands across several watersheds, including the shallow, well-vegetated inland wetlands used during the moult.

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Captive breeding and release diminishes genetic diversity in Brown Teal *Anas chlorotis*, an endangered New Zealand duck

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Abstract

We examined levels of mitochondrial DNA (mtDNA) and DNA microsatellite genetic variation in Brown Teal (*Anas chlorotis*), mainland New Zealand's rarest waterfowl. Samples were taken from the two remaining wild populations, a captive population, and four new populations established by released captive offspring. The larger wild population on Great Barrier Island (GBI) had two mtDNA haplotypes, one very rare, perhaps indicative of a historic bottleneck. The captive population was founded exclusively from GBI individuals; it and all new populations contained only the common GBI haplotype. In contrast, the smaller wild population at Mimiwhangata (MIW), Northland, contained 11 mtDNA haplotypes, including the common GBI haplotype which was probably introduced by captive-sourced releases 18–20 years ago. Microsatellite allelic richness was high in wild populations compared with captive and new populations. We suggest that genetic supplementation should be considered for the captive and new populations, and that the long-term goals of the Brown Teal recovery programme would benefit from assiduous and persistent genetic management and monitoring.

Key words: *Anas chlorotis*, Brown Teal, captive breeding, genetic diversity, reintroduction.

Captive breeding programmes are invariably crisis responses to extensive population declines and fragmentation, and to threatening circumstances in the wild. They are used to maintain the demographic viability of endangered populations and, to a lesser extent, to counteract the loss of genetic diversity, which is a feature of small remnant or recently founded populations. Captive breeding contributes to on-going conservation when the progeny of any successful breeding are released into the wild, either to establish a new population or to supplement an existing one. Wellpublicised captive breeding successes for Peregrine Falcon *Falco peregrinus* (Cade & Burnham 2003), Nene *Branta sandvicensis* (Black 1995; Blanco *et al.* 1999) and Arabian Oryx *Oryx leucoryx* (Rahbek 1993) among many others, raise the profile and publicly reinforce the value of this conservation technique.

Captive breeding programmes are often established with low levels of genetic variation because they are a crisis response to a seriously depleted population. The captive populations are typically small and have restricted gene flow with any other populations, conditions that cause strong genetic drift and which eventually erode genetic diversity. Genetic issues associated with captive breeding are now better understood (Ebenhard 1995; Allendorf & Luikart 2007) and include the possibility of inbreeding depression, long-term captivity causing undesirable adaptation (Frankham 2008), and concerns for the long-term viability of populations founded or supplemented from genetically depauperate captive-raised progeny (O'Brian *et al.* 1985; Caro & Laurenson 1994; Frankham *et al.* 2002). A long-term management perspective is necessary in captive breeding programmes to avoid these unintended genetic consequences for small and confined populations.

Captive breeding programmes have featured in historic and contemporary responses to the conservation plight of many New Zealand birds including Takahe *Porphyrio hochstetteri* (Lee & Jamieson 2001), Kiwi *Apteryx* sp. (Anon 2004), Black Stilt *Himantopus novaezeelandiae* (Reed *et al.* 1993) and Brown Teal *Anas chlorotis* (Williams & Dumbell 1996; O'Connor *et al.* 2007). While modern management guidelines for these programmes include statements about the management of genetic diversity among captive animals (Dumbell 2000; Anon 2004), limited consideration is given to how representative released individuals are of the genetic diversity remaining in the wild populations.

Historically the Brown Teal was distributed throughout lowland forests and on the freshwaters of New Zealand's three main islands, and on several near-shore islands (Worthy 2002). It is now the rarest and most endangered waterfowl on mainland New Zealand (Miskelly 2008) with just two natural populations remaining, on Great Barrier Island (GBI) and surrounding Mimiwhangata (MIW) on Northland's east coast (Fig. 1).

A captive breeding programme commenced in 1973, founded by 22 birds then in captivity, to which a further 42 were added within three years (Williams & Dumbell 1996). An additional 15 wild birds entered the captive population in 1987–1988; they, like all others, were sourced from GBI, the larger of two remaining wild populations. By 2000 approximately 1,700 captive-raised birds had been dispersed as 66 releases to 15 regional sites, including supplementing the smaller wild MIW population (Dumbell 2000). At only one site, mammal-free Tiritiri Matangi Island, was a new population successfully established. Between 2000–2008 another 16 birds from GBI were added opportunistically to the captive population and 474 captive-raised birds released at seven sites (K. Evans, pers. comm.).

Figure 1. Map of New Zealand and the locations of Brown Teal populations that were sampled. Waipu Gorge and Helena Bay were the locations at which the sampled museum specimens were collected.

Presently, "new" populations derived from these releases persist at Mana Island, Kapiti Island, Tiritiri Matangi Island, Karori Wildlife Sanctuary (now called "Zealandia") and Moehau (Fig. 1), although the Moehau population originates from a tiny remnant wild population supplemented by releases of captive-raised teal.

Little was known about the genetic diversity remaining in the wild populations (Dumbell 1987) and nothing of that within the captive and new populations. This study sought to use mitochondrial and microsatellite DNA markers to determine the levels of genetic diversity in the two remaining wild Brown Teal populations, the present captive breeding stock, and in four populations newly established by releases of captive-raised teal. We use the results of our genetic analysis to make several recommendations for the future genetic management of the Brown Teal captive breeding and recovery programme (O'Connor *et al.* 2007).

Methods

Brown Teal feathers were collected from GBI (36°11'S, 175°25'E), MIW (35°43'S, 174°21'E), the captive breeding population, and new populations at Moehau (36°45'S, 175°31'E), Karori Wildlife Sanctuary (41°19'S, 174°46'E), Tiritiri Matangi Island (36°52'S, 174°46'E) and Mana Island (40°57'S, 175°03'E). Feathers were taken between 2001 and 2007 inclusive and stored individually in dry paper envelopes labelled with the banding code of the bird and the area caught. In addition, we obtained foot pad tissue from two museum skins from the Museum of New Zealand and collected in Northland at locations where Brown Teal no longer occur; Helena Bay in 1978 (35°43'S, 174°21'E) adjacent to the MIW population, and Waipu River gorge in 1935 (36°54'S, 174°47'E) (Bell 1959).

The base of each feather (approximately 3 mm) was excised with a sterilised scalpel and DNA was purified using the standard phenol-chloroform extraction procedure followed by ethanol precipitation (Sambrook *et al.* 1989). A portion of the mitochondrial DNA (mtDNA) control region (636 bp) was amplified using polymerase chain reaction (PCR) and the primers L78 (5'-GTTATTTGGTTATGCATATCGTG-3') and H774 (5'-CCATATACGCCAACCGTCTC-3'), taken from Sorenson *et al.* (1999). Five microsatellite DNA markers were selected from the studies of Huang *et al.* 2005 (*caudo24*, *caudo19*, *caudo13*, and *caudo1*) and Maak *et al.* 2003 (*adph13*) based on their high levels of observed heterozygosity (H_O ranged from 0.68 to 0.97) and allelic diversity (5–13 alleles per locus) in Mallard *Anas platyrhynchos*. The M13 sequence method (Schuelke 2000) was used to label one of the microsatellite primers in each pair with the fluorescent marker 6FAM or VIC (Applied Biosystems).

PCR amplifications were performed in 25μL volumes using 1–2 μL of DNA template, 10 mM Tris pH 8.0, 50 mM KCl, 1.5 mM $MgCl_2$, 0.4 μg/ml BSA, 0.4 μM of each of the forward and reverse primer, 200μM of each dNTP, and 0.5–1 units of BIOTAQ DNA polymerase (Bioline). For the mtDNA control region, thermal cycling was carried out for 30 s at 94°C, 30 s at 54°C, and 60 s at 72°C, each repeated for 35 cycles. For the microsatellite markers, the same conditions were used with the addition of an M13 attachment cycle added to the end of the thermal cycling conditions.

The resultant PCR products were electrophoresised in agarose gel and a molecular weight standard was used to determine the size of the amplified DNA fragments. For the mtDNA control region, PCR products were purified using either column purification (Roche) or ExoSAP-IT (GE Healthcare Lifesciences), and their

DNA sequence was determined using dye-terminator reaction chemistry and analysed on an Applied Biosystems 3730 Genetic Analyzer. For the microsatellite markers, PCR products of the correct size were diluted depending on their concentration and the allele sizes were determined using an Applied Biosystems 3730 Genetic Analyzer.

Mitochondrial DNA sequences were edited by eye and then aligned using Clustal W in MEGA v4.0 (Kumar *et al.* 2004). Overall levels of nucleotide diversity (π) for each population were calculated in MEGA v4.0 (Kumar *et al.* 2004) and standard errors were estimated using a bootstrap method with 500 replicates. DNA base frequencies and the appropriate model of sequence evolution were estimated using Modeltest 3.7 (Posada & Crandall 1998). The level of sequence divergence within and between populations was determined using a pair-wise analysis in DnaSP v 4.10.9 (Rozas *et al.* 2003). TCS v1.21 (Clement *et al.* 2000) was used to estimate a phylogenetic network of haplotypes using statistical parsimony. A homogolous DNA sequence from Mallard was retrieved from Genbank (accession number AY928900; Kulikova *et al.* 2005) and added to the data set as the outgroup taxon.

Microsatellite allele sizes were determined using the GeneMapper® v4.0 software (Applied Biosystems). Calculations of allelic richness and tests for null alleles were implemented in HP-RARE 1.0 (Kalinowksi 2005) using the rarefraction method to standardise for sample size. Allele and genotype frequencies, Observed (H_O) and Expected (H_E) heterozygosities, F_{IS}, tests for Hardy-Weinberg Equilibrium (HWE), and linkage disequilibrium (LD) were calculated using GENEPOP v4.0 (Raymond & Rousset 1995). Deviations from HWE were tested using global tests for heterozygosity deficit and excess within each population by means of the exact probability test with Markov chain parameters (with Bonferroni correction). Linkage disequilibrium was tested for using Fisher's exact test.

Results

Mitochondrial haplotype diversity

The DNA sequence of the mtDNA control region was determined for a total of 150 individual Brown Teal: 49 from MIW, 39 from GBI, 20 from the captive population, 19 from Moehau, 12 from Karori Wildlife Sanctuary, eight from Tiritiri Matangi Island and three from Mana Island (Table 1). The aligned sequence data set was 636 base pairs long, and contained 18 variable sites (2.8%) of which eight were parsimony-informative (1.3%). The pooled sample contained 12 haplotypes (labelled A to L), with a haplotype diversity (h) of 0.3900 and nucleotide diversity (π) of 0.0044 (Table 1). The highest level of mtDNA diversity was found within the MIW population, which contained 11 haplotypes (10 unique), with $h = 0.6990$ and $\pi = 0.0088$. Within the GBI population, only one sample had a unique haplotype (labelled L) and all other samples were haplotype A. Haplotype ($h = 0.0645$) and nucleotide ($\pi = 0.0003$) diversity were low within the GBI sample compared with MIW. Within the captive and all new populations only a single haplotype (A) was found. Considering all populations together, the most common haplotypes were A

Table 1. The sampled Brown Teal populations and summary statistics of genetic diversity. Column headings: n_{ms} = microsatellite sample size; A = mean number of alleles per locus; *Arich* = mean allelic richness; H_{O} = observed heterozygosity; H_{E} = expected heterozygosity; n_{mt} = mtDNA sample size; H = the number of haplotypes (H); h = haplotypic diversity; S = number of segregating sites; π = nucleotide diversity; and the haplotypes present.

	Microsatellite loci							*Mitochondrial DNA*					
Population	n_{ms}	A	***Arich***	***Ho***	H_{E}	**Private alleles**	F_{IS}	n_{mt}	**H**	h	S	π	**Haplotype**
Mimiwhangata (MIW)	39	11	4.366	0.782	0.833	2	0.0177	49	11	0.6990	12	0.0088	A, B, C, D, E, F, G, H, I, J, K
Great Barrier Island (GBI)	28	9	4.222	0.773	0.788	1	0.2498	39	2	0.0645	1	0.0003	A, L
Captive breeding	36	9	4.075	0.571	0.751	1	0.1629	20	1	0	0	0	A
Moehau	24	7.5	3.322	0.521	0.637	0	0.1864	19	1	0	0	0	A
Karori Wildlife Sanctuary	12	6	3.369	0.500	0.745	0	0.3393	12	1	0	0	0	A
Tiritiri Matangi Island	8	3	2.441	0.313	0.515	0	0.4118	8	1	0	0	0	A
Mana Island	3	1	1.000	n/a	n/a	0	–	3	1	0	0	0	A
Pooled samples	150							150	12	0.3900	12	0.0044	

(*n* = 118; 79%), B (*n* = 16; 11%) and C (*n* = 5; 3%). No DNA sequence differences were found between the GBI, captive and new populations. However, a genetic distance of 0.7% was found between the MIW population and all other populations. The network of mtDNA haplotypes is presented in Fig. 2.

When the DNA sequences of the outgroup and two museum samples were included, the data set contained 80 variable sites (12.8%) and 50 parsimony-informative sites (7.8%). The Waipu River gorge sample had a haplotype (labelled M) that was not found in any of the contemporary samples, whereas the Helena Bay sample had

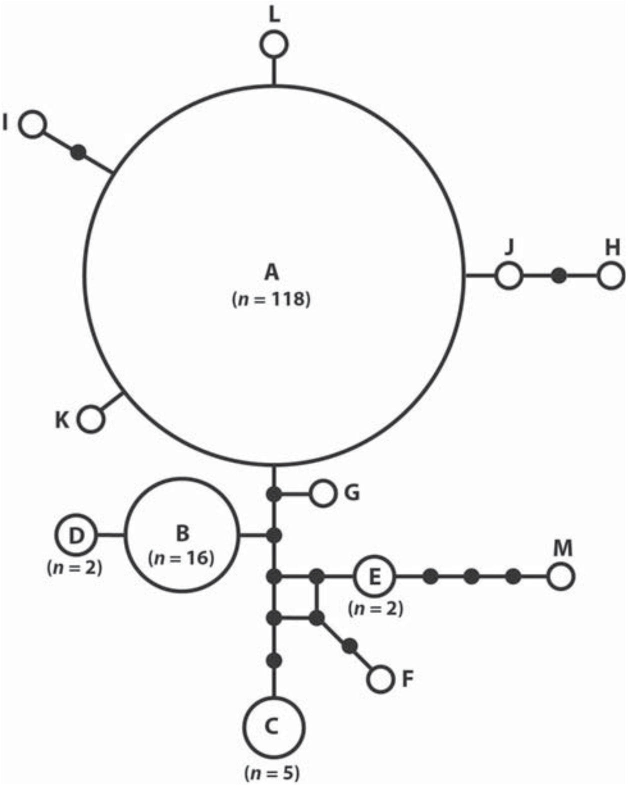

Figure 2. A phylogenetic network showing evolutionary relationships among the Brown Teal mtDNA haplotypes found in the seven extant populations (Mimiwhangata, Great Barrier Island, the captive breeding population, Moehau, Karori Wildlife Sanctuary, Tiritiri Matangi Island and Mana Island) and the two sequences from museum samples (Helena Bay and Waipu River gorge). Letters denote the haplotype identifier for samples (see Table 1 for the populations that contained haplotypes A–L). Circles denote the relative number of samples represented in each haplotype, and when more than one individual had a haplotype the total number is shown. The lines between haplotypes denote mutational steps between each DNA sequence, and closed circles indicate the inferred, unsampled haplotypes.

haplotype C that was present in the contemporary MIW population. The genetic distance between the Helena Bay museum sample and the GBI, captive and new populations was 1.8% whereas that between the Waipu River gorge museum sample and the GBI, captive and new populations was 2.3%. The genetic distance between the Helena Bay and Waipu River gorge samples was 3.2%.

Microsatellite diversity

One hundred and fifty samples were genotyped for five microsatellite loci, 39 were from MIW, 28 from GBI, 36 from the captive population, 24 from Moehau, 12 from Karori Wildlife Sanctuary, eight from Tiritiri Matangi Island and three from Mana Island (Table 1). Of the five loci used, two were polymorphic (*caudo24* and *caudo13*) and three monomorphic (*caudo19*, *caudo1* and *adph13*). A total of 14 alleles were identified at the *caudo24* locus and eight at the *caudo13* locus. The test for null alleles was non-significant over both polymorphic loci. The inbreeding coefficient (F_{IS}) was positive and significant within GBI, the captive population, and new populations but not within the MIW population. No evidence of linkage disequilibrium was found within any population ($P > 0.05$).

MIW was in Hardy-Weinberg equilibrium (HWE) for both loci ($P > 0.05$), but all other populations deviated from HWE at either one or both loci ($P < 0.05$). The departure from HWE observed in the GBI samples was due to a (non-significant) heterozygote deficit (global $P = 0.145$) at the *caudo13* locus. The captive population was in HWE for *caudo24* only and a heterozygote deficit was found at the *caudo13* locus (global $P < 0.05$). The new populations showed significant departures from HWE, due mainly to heterozygote deficit at both loci (global $P < 0.001$). Because of small sample size, tests for HWE could not be performed on the Mana Island sample.

Overall the two wild populations had greater genetic diversity than the captive and new populations (Table 1). Expected heterozygosity (H_E), allelic richness, and number of alleles per locus were highest within the MIW population and lowest in the Mana Island population. Two unique alleles were found within the MIW population, one in the GBI population and another in the captive population (Table 1). However, the unique allele found at the *caudo24* locus within the captive population (not found in either wild population) could be due to the limited sampling size, and if more samples from GBI were taken, this allele might be detected in the wild.

Discussion

Our study found different levels of genetic diversity among the populations of Brown Teal and the captive-raised birds had the lowest levels of diversity. The mtDNA analysis showed that there was a lack of genetic diversity within the GBI wild population, the source of all captive stock. Such low diversity indicates that the population may have experienced a historical bottleneck and/or founder effect (Arrendal *et al.* 2004; Leonard *et al.* 2005; Munoz-Fuentes *et al.* 2005; Ogden *et al.* 2005). A previous study on GBI Brown Teal using 14 allozyme markers also found no genetic diversity within 58 individuals

(Daugherty *et al.* 1999; Dumbell 1987). Furthermore, historic field observations suggest the species may once have been scarce on GBI (Bell & Braithwaite 1964; Dumbell 1987), and a mid-1800s survey of birds on the island failed to report Brown Teal (Hutton 1868).

In contrast to GBI, the samples from MIW revealed extensive mtDNA diversity. The high frequency of the common GBI haplotype A (33%) in the MIW population most likely arose from the releases of 321 captive-bred teal there between 1984–1991 (Dumbell 2000). Although more extensive DNA sampling of historic museum specimens might show haplotype A was once present elsewhere within the Northland region, it is now at a high frequency at MIW and further releases of captive-raised (GBI-sourced) birds into MIW, or elsewhere in Northland, will only result in raising its frequency and diluting the population's remaining genetic diversity. The MIW population, alone, represents almost all of the haplotype diversity now remaining in Brown Teal.

Low levels of microsatellite DNA variation and no mtDNA haplotype variation were found within the new populations at Moehau, Karori Wildlife Sanctuary, Tiritiri Matangi Island and Mana Island. The latter three populations were founded by small numbers of individuals (<20) and they have persisted thereafter in even smaller numbers (Anderson 2005; Dumbell 2000; G. Timlin, pers. comm.), which means the founder effect and/or genetic drift were likely to have been strong. Inbreeding is also a concern for the new populations; those at Karori Wildlife Sanctuary and Mana Island are now dominated by descendants of a single pair (Anderson 2005; R. Empson & G. Timlin, pers. comm.). We accept that having used only two microsatellite loci may lead to an under-estimate of the number of private alleles per population. When more loci become available for this species a re-analysis would be prudent.

Captive breeding and release has long been the sole pathway for advancing the numerical and range expansion of Brown Teal (Williams & Dumbell 1996; O'Connor *et al.* 2007). Brown Teal have struggled in the face of mammalian (especially mustelid) predation and, despite extensive releases (Dumbell 2000), new populations have been established only recently on mustelid-free islands (Tiritiri Matangi, Mana, Kapiti) or in mustelid-free enclaves (Karori Wildlife Sanctuary, Moehau). With the exception of Moehau, all new populations remain small (<20 birds) and are unlikely to persist without regular supplementation. The remaining wild populations have declined (between 1997–2007) despite concerted trapping of predatory mammals (Parrish & Williams 2001; Ferreira & Taylor 2003). Direct wild-to-wild transfers to establish new populations, or to augment the tenuous small populations, are not included in current management plans (O'Connor *et al.* 2007).

Our study highlights that: (i) the captive population does not represent the full range of genetic diversity present in the two wild populations, and (ii) the new populations do not encapsulate the full genetic diversity within the present captive-breeding population. Two serial genetic bottlenecks have been introduced by the establishment of the captive breeding programme and, again, during the release phase. There is mounting evidence that genetic bottlenecks are a concern for the long-term persistence of newly-established populations. Empirical studies have emphasised the negative consequences of low levels of genetic variation including inbreeding depression and an inability to respond to environmental challenges (*e.g.* disease or climate change) (Allendorf & Luikart 2007; Amos & Balmford 2001; Frankham 1995, 1996, 2005; Frankham *et al.* 2002).

The low levels of genetic diversity in populations associated with small founder sizes, whether established by wild-to-wild transfers or by captive-raised releases, as evidenced by inbreeding depression (*e.g.* Hendrik & Kalinowski 2000; Briskie & Macintosh 2004) or reduced immunocompetence (*e.g.* Hale & Briskie 2007), can be traced to the inadequate genetic sampling from the source population. From an evaluation of theory and case examples, Frankham (2005) considered the importance of genetic factors in the persistence of small isolated populations to be undeniable, a viewpoint re-examined and reinforced by Jamieson (2007). In effect, the debate has now largely moved on, to a consideration of how the genetic diversity remaining in small populations of threatened species can be managed and maintained, and to make "genetic diversity be a fundamental component in long-term management strategies for threatened species" (Jamieson *et al.* 2008). Management strategies that include a captive breeding component must take into account, in addition to genetic representation, the negative effects of adaptation to captivity and the accumulation of rare alleles which are deleterious but partially recessive in the wild (Frankham 2008). Furthermore, mixing genetically impoverished captive-raised stock with wild populations may also produce offspring of reduced fitness (Araki *et al.* 2007).

Without assiduous genetic management, conservation strategies which rely exclusively on captive breeding to establish new populations or to supplement declining ones, may well achieve short-term gain by establishing new populations, but over the long-term produce populations with limited evolutionary potential and which are vulnerable to any environmental change. If captive breeding and release has to remain the sole conservation pathway for Brown Teal, as O'Connor *et al.* (2007) outlined, we suggest that the present captive breeding stock should be augmented to capture the full genetic diversity remaining in the wild populations. By this means the adaptive potential within each wild population becomes available to all populations henceforth. However, because so many generations have elapsed since the captive population was established a complete renewal of the breeding stock should also be considered, especially while the more genetically diverse wild population at MIW remains (potentially) large enough to supply new captive recruits. Occasional or *ad hoc* additions to the existing breeding stock could simply perpetuate the existing genetic under-representation.

Furthermore, we suggest that additional genetic diversity be introduced to all new populations, but especially to the larger Moehau population, by wild-to-wild transfers from MIW or via a reconstituted captive breeding programme. These transfers may need to be repeated and certainly closely monitored, to ensure that those individuals added successfully reproduce. Protocols like those suggested by Haig *et al.* (1990) may be able to guide this approach. After genetic supplementation, the small populations established where habitat is limited and where single families have become dominant (*e.g.* Karori Wildlife Sanctuary, Mana, Kapiti, Tiritiri Matangi Islands) could be managed as a meta-population simply by rotating breeding individuals between them and monitoring the outcomes.

The conservation status of Brown Teal is still assessed solely on numbers (Hitchmough *et al.* 2007; Birdlife International 2008; Miskelly *et al.* 2008), but this perspective ignores the important long-term role of genetic diversity. By incorporating genetic information where available, conservation assessments could be viewed as less about number of populations or minimum overall numbers and more about "equipping populations" with the adaptive potential to respond to the future's inevitable environmental challenges.

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Photograph: Brown Teal with brood, courtesy of New Zealand Herald/Gerard Johnson.

Feeding environments of New Zealand's extinct merganser revealed by stable isotope analyses

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Abstract

The likely feeding environments of individuals from each of the three populations of New Zealand's extinct merganser *Mergus australis* were interpreted from stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) in fossil bones and tissue from preserved skins. Analyses of feather and claws from 10 specimens from Auckland Islands indicated the birds fed predominantly on marine prey but that some freshwater-sourced foods may also have been consumed. Stable isotope values from three bones of mergansers from Chatham Island strongly suggest a marine feeding habit while those from two mainland New Zealand bones indicated the birds fed mostly in fresh water. Merganser bones found at a New Zealand lake (Poukawa) suggest this species occupied mainland New Zealand's fresh waters at the time of first human settlement.

Key words: feeding, feeding environment, *Mergus australis*, New Zealand Merganser, stable isotope analysis.

The now-extinct New Zealand Merganser *Mergus australis* once occurred on New Zealand's three main islands (North, South, and Stewart Islands) and on two distant archipelagos, Chatham Islands *c.* 800 km to New Zealand's east and Auckland Islands *c.* 450km to its south (Holdaway *et al.* 2001; Worthy & Holdaway 2002). Early Polynesian settlers extirpated the New Zealand and Chatham Island populations and the last sighting from the Auckland Islands was in 1902 (Kear & Scarlett 1970; Williams 2012). Today this enigmatic waterfowl is represented by just 27 skins from Auckland Islands and small numbers of bones of the other two populations derived from Polynesian's middens and natural deposits.

Deposits containing bones from New Zealand's merganser population are few and, with but one exception, have all been at coastal locations (Kear & Scarlett 1970; Worthy & Holdaway 2002). This distribution prompted Worthy (2004) to regard four merganser bones retrieved from an extensive natural deposit at North Island's Lake Poukawa as being from "vagrants" rather than being indicative of the merganser's possible wider distribution. Collection localities specified for Auckland Islands' specimens generally refer to the heads of sheltered bays or inlets, locations at which the island's short and steep watercourses debouch (Kear & Scarlett 1970; Williams 2012). On Chatham Island, merganser bones have been retrieved from coastal dune deposits and, most abundantly, from a cave alongside the island's extensive saltwater Te Whanga Lagoon (Millener 1999; Worthy & Holdaway 2002).

Mergansers (Family Anatidae, Tribe Mergini) are specialist fish-eating waterfowl. Five of the six extant species have Holarctic distributions and primarily or exclusively inhabit lakes and rivers whereas the sixth, the now very rare Brazilian Merganser *Mergus octosetaceus*, once occurred more widely on Brazilian and Argentine rivers (Callaghan 2005). The coastal and marine habitat ascribed to mergansers of the New Zealand region (Worthy & Holdaway 2002; Worthy 2004) contrasts with that of other mergansers notwithstanding the Red-breasted Merganser's *Mergus serrator* use of sheltered coastal bays, coves and estuaries (Cramp & Simmons 1977).

In this study we sought to identify the primary feeding environments of individuals from all three New Zealand Merganser populations. We have attempted this by interpreting carbon and nitrogen stable isotopes values obtained from New Zealand and Chatham Island fossil bones and from feathers and claws from 10 Auckland Island specimen skins. Stable isotope ratios of carbon ($^{13}C/^{12}C$) are used to indicate the primary feeding environment (marine or fresh water) (Bearhop *et al.* 1999; Fry 2006) and of nitrogen ($^{15}N/^{14}N$) to indicate comparative trophic levels at which birds within each population fed. The results are compared with carbon and nitrogen isotope values obtained from feather and bones of other merganser species.

Methods

Specimens and tissue analysed

We were permitted to sample undertail covert feathers, entire hind claws and a rib bone from 10 museum skins of Auckland Island's mergansers and bone from New Zealand and Chatham Island-sourced mergansers (Appendix 1). From one Auckland Island specimen (NHM 1904.8.4.1; 1904.8.4.2) we obtained feather, claw and bone and from four others, feather and claw (Appendix 1) which allowed us to present isotope ratios from different tissues of an individual. Two specimens providing feather and claw samples (NHM 1904.8.4.1; samples 9, 10 and NHM 1901.10.21.58; samples 13, 14, Appendix 1) were initially preserved in formalin (Ogilvie-Grant 1905). Two feather (7, 25) and one claw (8) samples came from young birds in juvenile plumage whereas all others samples were from adult birds (see Appendix 1 in Williams 2012).

The two fossil New Zealand-sourced limb bones were from Polynesian middens on Old Neck, Stewart Island and at Marfells Beach, Lake Grassmere, South Island

(Worthy 1998a,b). The three Chatham Island bones were fragments of sterna retrieved from the natural deposit in Te Ana a Moe cave near Te Whanga Lagoon (Millener 1999; Appendix 1).

Feather and bone samples from other merganser species were obtained from specimens in the collections of the Natural History Museum, Tring, UK (Appendix 2) and mean isotope values from feathers of living Scaly-sided Merganser *Mergus squamatus* were provided by Diana Solovieva and Tony Fox (pers. comm.).

Analytical techniques

Feather and claw samples were prepared at the Stable Isotope Laboratory, GNS Science, New Zealand. They were cleaned in 2:1 chloroform/methanol v/v and air dried for 48 h to remove surface oils (Wassenaar & Hobson 2006) and any residual museum conservation treatments, and then finely ground. The five fossil bones (samples 27–31; Appendix 1) were prepared and analysed by IsoTrace New Zealand Ltd (Dunedin, New Zealand) and the remainder by the Stable Isotope Laboratory, GNS Science, New Zealand. Extraction of bone collagen at both laboratories followed the procedure described by Holdaway & Beavan (1999). The cleaned bones were ground and demineralised in 1N HCl for 24 h to remove carbonates and all organic traces, then neutralised and rinsed with deionised water. The collagen extract was gelatinised, ultra-filtered and freeze-dried. Ground feather and claw subsamples (1.5 ± 0.1 mg near their tip) and dried bone powders (1.5 mg) were weighed into tin capsules for isotopic analysis.

The samples were combusted in an ANCA SL elemental analyser (Europa Scientific, Crewe, UK) and measured in a GEO 20–20 isotope ratio mass spectrometer (Europa Scientific, Crewe, UK). Results are reported as %C and %N by dry mass and as $\delta^{13}C$ or $\delta^{15}N$ (‰) = $(R_{SAMPLE}/R_{STANDARD} - 1)*1{,}000$ with $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ relative to VPDB (Vienna PeeDee Belemnite) and N_2 gas in air standards (Rogers 2003; Sharp 2007).

Results

New Zealand Merganser

Auckland Islands

Carbon ($\delta^{13}C$) isotope values of feathers extended from –10.6‰ to –18.0‰ (*n* = 10), claw values from –11.6‰ to –19.8‰ (*n* = 5) and the single bone value was –11.6‰ (Appendix 1, Fig. 1).

The $\delta^{13}C$ values for two of the five claws sampled (Appendix 1, Fig 1) were *c.* 2‰ more negative than corresponding feather values from the same specimens (samples 9–10, 13–14), there was little difference for another two (samples 2–3, 5–6) whereas the difference for the fifth, a newly-fledged bird, was *c.* 5‰ (samples 7–8). From the single specimen providing bone (11), feather (10) and claw (9) samples, the $\delta^{13}C$ values of feather and bone were similar (Fig. 1).

The $\delta^{13}C$ values from all tissues combined were not distributed evenly throughout their range (–10.6‰ to –19.8‰) but appear distributed as two groupings (Fig. 1): –10.6‰ to –15.2‰ and from –16.5‰ to –19.8‰. Notwithstanding that different fractionation rates will apply

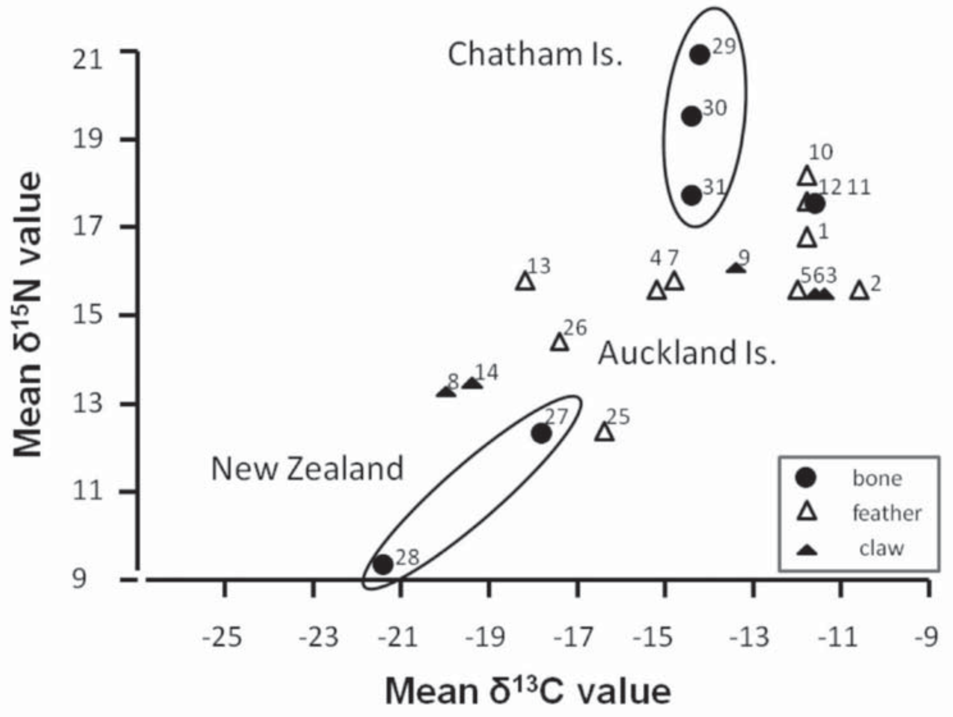

Figure 1. Distribution of δ15N and δ15C isotope values of *Mergus australis* bone, feather and claw samples sourced from Auckland Islands, Chatham Island (encircled) and New Zealand (encircled). Sample numbers are those indicated in Appendix 1.

between prey and the tissues sampled, and the large difference between feather and claw values from one specimen (1904.559.1; samples 7, 8), this distribution is suggestive of two different feeding strategies among these individuals.

Most (12 of 16) nitrogen ($\delta^{15}N$) isotope values were within the range 15‰–18‰. The four samples providing lowest $\delta^{15}N$ values were also those with the lowest $\delta^{13}C$ values. The $\delta^{15}N$ values from three of the five claws sampled (Appendix 1, Fig 1) were *c.* 2‰ lower than corresponding feather values from the same specimens (samples 7–8, 9–10, 13–14) but there was little difference for the other two (samples 2–3, 5–6). From the single specimen providing bone (11), feather (10) and claw (9) samples, the $\delta^{15}N$ values of feather and bone were similar (Fig. 1) but almost 2‰ higher than for its claw. These results suggest all mergansers were feeding on similar prey.

New Zealand

Bones from the two New Zealand specimens (samples 27, 28; Fig. 1), both derived from middens, had considerably lower $\delta^{15}N$ and $\delta^{13}C$ values than the Auckland Island and Chatham Island birds.

Chatham Islands

Three Chatham Island merganser bones (samples 29, 30, 31; Fig. 1), all sampled from the same natural site, had similar $\delta^{13}C$ values and these were similar to some of the Auckland Island-sourced specimens. As a group their $\delta^{15}N$ values were higher than those obtained from all other *M. australis* specimens.

Other mergansers

Feathers from two Brazilian Mergansers (samples 15, 16; Appendix 2) had $\delta^{13}C$ values that were 1–3‰ lower than any of the Auckland Island specimens. However, they were in turn 1–2‰ higher than the Smew *Mergellus albellus* feather (sample 19), and considerably higher than the range recorded for Scaly-sided Merganser (Appendix 2). The single feather (sample 17) of Goosander *Mergus merganser* had similar isotopic values to those of two Auckland Island birds (samples 25, 26). The Red-breasted Merganser feather (sample 21; Appendix 2) had higher $\delta^{15}N$ and $\delta^{13}C$ values than any of the other merganser samples, perhaps emphasising this species' considerable use of marine environments (Cramp & Simmons 1977).

Discussion

Observations of merganser food and feeding at Auckland Islands

There are two records of merganser foods at Auckland Islands. A specimen shot in 1901 (NHM 1901.21.57) at McLennan Inlet had a 90 mm ("3.5 in") Koaro *Galaxias brevipinnis*, a fresh water fish, in its bill (Hutton 1901). Kear and Scarlett (1970) reported the gut contents of a preserved partial cadaver (NHM A/1999.1.124) whose collection details are unknown comprised "macerated fish bones, mandibles of an errant polychaete and an unidentified gastropod". They added that "the presence of the polychaete tends to suggest a brackish water environment".

There are no recorded observations of mergansers feeding at the Auckland Islands and few from which their habitat can be discerned with certainty. Reischek (1889) refers to a group of six mergansers (probably adults and fledglings) among rocks on the shoreline of Waterfall Inlet. Waite (1909) quotes Captain J. Bollons (master of the government ships regularly visiting the subantarctic islands) as not having seen the bird on the coasts, but having found them at the heads of estuaries and especially on the island's watercourses "picking about in the creeks". Falla (1970) reports R.A Wilson, the collector of two specimens in 1891 (sample 26 is from one), as having "encountered his quarry up the stream bed some distance from the coast and in a deep pool where the stream was partly dammed on a rocky terrace."

Despite streams on Auckland and Adams Islands being short and mostly very steep, *G. brevipinnis* is common along their lengths and especially so where the stream gradients ease prior to reaching the sea (M. Williams pers. obs.). Human access up streams from the coastline is extremely difficult so it is not surprising that mergansers were seen only on the sea at the heads of bays and inlets (see Williams 2012).

Interpreting isotope values

Influence of formalin preservation and midden effects

All *M. australis* specimens sampled from Natural History Museum (NHM), Tring (samples 9–14, Appendix 1) had been transported to England in formalin (Ogilvie-Grant 1905) and possibly the Dublin Museum specimen also (samples 7, 8; see Williams 2012). Formalin lowers $\delta^{13}C$ values by up to 2‰ but has little effect on $\delta^{15}N$ (Barrow *et al.* 2008 and references therein). From three specimens we obtained both feather and claw samples (7–8, 9–10, 13–14; Appendix 1, Fig 1); claw $\delta^{15}N$ and $\delta^{13}C$ values were *c.* 2‰ lower than feather values from all which suggests a possible differential effect even though both tissues are keratin. There was little difference between feather and claw measurements from the other two specimens (2–3, 5–6) which are thought to have been transported as dry skins (Kear & Scarlett 1970). In our interpretation of merganser feeding environments at Auckland Island we assume a formalin effect of lowering $\delta^{13}C$ values by *c.* 2‰.

The two New Zealand fossil bones (samples 27, 28; Appendix 1) were from middens (Worthy 1998a,b). Temperatures at which Polynesians cooked birds in ground ovens appear not have been high enough to have altered the carbon and nitrogen isotopic ratios in the bone collagen (see de Niro *et al.* 1985) and biomolecules have been extracted from some midden eggshell fragments (*e.g.* Oskam *et al.* 2011).

Isotope turnover and fractionation

The tissues analysed accumulate and retain dietary carbon and nitrogen over different time periods. Feathers capture dietary carbon and nitrogen during their short period (2–4 weeks) of growth. Claws, however, grow continuously; Bearhop *et al.* (2003) found that claws have similar isotope values to feathers and in some passerines the whole claw contained a record of the bird's diet over the *c.* 3–5 months of its growth. The growth rate of merganser claws is unknown. Bone collagen retains a dietary isotope record for considerably longer, with perhaps a dietary carbon turnover of 50% after about 6 months (Hobson & Clark 1992).

Conversion of prey tissue to body tissue is accompanied by change in isotope ratios. In general there is a stepwise increase of approximately 4‰ in $\delta^{15}N$ and ≈1‰ for $\delta^{13}C$ (*e.g.* de Niro & Epstein 1978; McCutchan *et al.* 2003). However Bearhop *et al.* 1999 identified a consistent $\delta^{13}C$ fractionation from fish prey to Cormorant *Phalacrocorax carbo* and Goosander feather of 2.3‰, Mitzutani *et al.* (1992) recorded an average $\delta^{13}C$ fractionation from prey to feather for fish-eating birds of 3.3‰ in an experimental study, and Becker *et al.* (2007) reported fractionation of $\delta^{13}C$ was 2.5‰ ± 0.2‰ from delipidated fish muscle to breast feather of the marine-feeding Common Murres *Uria aalge*. Furthermore, Mitzutani *et al.* (1991) demonstrated considerable variation in $\delta^{13}C$ fractionation from fish prey to different Cormorant tissues and Hobson & Clark (1992) reported a diet to bone collagen $\delta^{13}C$ fractionation of 2.6 ± 1.1‰ for gulls fed solely on fish.

To assist our interpretations of merganser feeding environments we assume a $\delta^{13}C$ fractionation of 2.5‰ from prey to each of the merganser tissues sampled.

Carbon isotope values indicative of marine and fresh water feeding

No isotope measurements of likely marine and fresh water prey of *M. australis* at Auckland and Chatham Islands are known to us. From the literature (*e.g.* Bearhop *et al.* 1999 and references therein; Bushula *et al.* 2005; Crow *et al.* 2010) we derived an approximate $\delta^{13}C$ isotope value for merganser tissue which, taking into account the fractionation estimate above, could indicate mixed marine–fresh water feeding (–17‰) and predominantly fresh water feeding (–21‰).

Feeding environment of Auckland Islands' mergansers

Mergansers at the Auckland Islands undoubtedly fed in fresh water; Bollons and Wilson (*loc. cit.*) saw them there, Wilson shot one there (sample 26; Williams 2012) and Hutton (1901) prised an exclusively freshwater fish from a cadaver's bill. However, the $\delta^{13}C$ isotope values, most of which exceed –16‰, do not indicate fresh water having been a significant feeding habitat. The range of $\delta^{13}C$ values lies within the range of values recorded for many marine birds, including piscivorous (*e.g.* Bearhop *et al.* 1999; Hobson *et al.* 1994) and squid-eating species (*e.g.* Phillips *et al.* 2009).

Sample 26 (Appendix 1), a feather of the bird collected "up the stream bed some distance from the coast and in a deep pool where the stream was partly dammed on a rocky terrace" (Falla 1970) had a $\delta^{13}C$ value of –17.5‰. Allowing 2.5‰ fractionation from prey to predator suggests that, during feather growth, the merganser consumed prey with an average $\delta^{13}C$ value of *c.* –20‰. This is consistent with feeding in both fresh water and marine environments (see Fig. 3 in Bearhop *et al.* 1999). There are three other samples (8, 13, 14) which returned similar $\delta^{13}C$ values; these samples were obtained from two specimens initially preserved in formalin. If applying a +2‰ correction to their $\delta^{13}C$ values (Barrow *et al.* 2008) is appropriate, then they too indicate mixed fresh water and marine feeding.

The $\delta^{15}N$ values from feathers of all but one of the mergansers lie within a narrow 4‰ range, indicative of the mergansers feeding on similar prey at the time of feather growth. The most likely nearshore marine prey for mergansers would have been the abundant small omnivorous and predatory Nototheniidae fishes (Williams 1988; Paulin & Roberts 1992), while fresh water streams contained *Galaxias brevipinnis,* an invertebrate predator.

Feeding environments of New Zealand's and Chatham Islands' mergansers

The isotope values of sample 28 (Appendix 1, Fig. 1), from a midden on Stewart Island, suggests that this merganser fed primarily in fresh water. The midden is at the mouth of Paterson Inlet, a large sheltered coastal inlet into which two major rivers (Rakeahua, Freshwater), and many smaller streams, flow. These waterways drain extensive, low relief, peat-filled basins and although their waters are typically stained brown by tannins they support an abundant fish fauna, including diadromous and non-diadromous *Galaxias* species *(*McDowall & Chadderton 1999). The $\delta^{15}N$ value of sample 28 (9.0‰) is low relative to that for other *M. australis* samples but consistent with a diet of non-diadromous *Galaxias* sp. with isotope values similar to those of *G. gollumoides* from streams in nearby Southland streams ($\delta^{15}N$ = 5.15 to 6.59‰; $\delta^{13}C$ = –21.63 to –26.76‰; Crow *et al.* 2010).

We interpret the $\delta^{13}C$ isotope from sample 27 (Appendix 1, Fig. 1) as indicative of a diet of mixed fresh water and salt water prey. This bone is from a midden at Marfells Beach, a natural gravel and sand bar separating Lake Grassmere from the sea: natural fossil deposits in the dunes also contain many merganser bones (Worthy 1998a). The compositions of those deposits clearly indicate a rich freshwater avifauna at Lake Grassmere after it was separated from the sea *c.* 1800 years ago (Ota *et al.* 1995, Worthy 1998a). As with other barrier-bar lakes such as Ellesmere and Wainono (eastern South Island) and Onoke (southern North Island) Grassmere would have been connected to the sea periodically, its water then becoming increasingly saline and allowing a variety of estuarine fish (*e.g.* Flounder *Rhombosolea plebeia*, Mullet *Aldrichetta forsteri)* as well as diadromous galaxiids to enter and thrive. We consider this bone was from a bird that fed predominantly in Lake Grassmere, not in the adjacent marine environment.

Chatham Island mergansers had access to a distinctive feeding environment, a large saltwater lagoon. The high $\delta^{15}N$ values of the three Chatham Island samples probably reflects a prey fauna consisting largely of piscivorous fishes with $\delta^{15}N$ enrichments similar to or higher than those reported in other seabird trophic studies (Hobson *et al.* 1994; Thompson & Furness 1995; Bearhop 1999). That the Chatham Islands' mergansers were primarily marine is emphasised by the presence of conspicuous salt gland impressions on the skulls of all 44 merganser crania examined at the Museum of New Zealand (see Fig. 7.2 in Worthy & Holdaway 2002). Impressions of salt glands are barely discernible on three crania of mergansers from Auckland Island examined at the Natural History Museum, Tring, UK. (M. Williams unpubl. data).

Comparing *Mergus australis* with other mergansers

The $\delta^{15}N$ and $\delta^{13}C$ values of tissues of mergansers from the Auckland Islands were higher than those of samples from almost all other merganser species. Isotope values of Auckland Islands' mergansers indicate they fed in the marine environment more than other mergansers, except Red-breasted Merganser. More negative $\delta^{13}C$ values for Goosander (Bearhop *et al.* 1999; Morrissey *et al.* 2004) confirm their strong freshwater isotopic signatures. The $\delta^{13}C$ values for the two mergansers from mainland New Zealand, however, are close to or within the range reported from other freshwater mergansers (Appendix 2).

Could New Zealand's merganser have been more widespread than existing bone deposits suggest?

With the exception of the Red-breasted Merganser, all extant mergansers occupy primarily or exclusively freshwater habitats. Brazilian Mergansers are year-round inhabitants, and Scaly-sided Mergansers seasonal inhabitants, of mountain foothill rivers whose physical characteristics are similar to those of many New Zealand rivers. Could New Zealand's mergansers also have lived in rivers or lakes beyond the coastal fringe?

The isotopic measurements and historic observations suggest that fresh waters were part of, but not the exclusive, feeding environment of mergansers at Auckland Islands, which is unsurprising given the short and steep nature of the islands' watercourses. The Chatham Island birds had isotope values indicating a marine-sourced diet which, too, is unsurprising given the presence of the extensive Te Whaanga Lagoon and the lack of anything other than small slow-flowing streams and peat lakes on the island. However, the isotope values from both New Zealand bones are suggestive of fresh water feeding. The view that New Zealand's merganser was a "coastal species" (Worthy & Holdaway 2002; Worthy 2004) is not disproved, especially if by "coastal" was meant estuaries and coastal dune lakes. However, the Stewart Island bone (sample 28) indicates that some New Zealand mergansers may have fed mostly in fresh waters, and if that was possible on Stewart Island then it could also have been so on North and South Islands where, historically, their numerous rivers and lakes contained an abundant small fish fauna (McDowall 2010).

Lacustrine avian bone deposits in New Zealand are rare (Worthy 2004) so the presence of a *Mergus* bone at two of the three sites excavated is significant. Although the Marfells Beach site is "coastal" it is also on the shore of an extensive lake (Grassmere; Worthy 1998a) while the other, at Lake Poukawa in Hawkes Bay (Worthy 2004), is 25 km inland. Isotopic examination of a Lake Poukawa bone would advance ecological understanding of the New Zealand population, especially if assessed in relation to isotope measurements of other species from the deposit which would have consumed similar prey from the lake's water column (*e.g.* New Zealand Scaup *Aythya novaeseelandiae*, New Zealand Dabchick *Poliocephalus rufopectus,* Great Crested Grebe *Podiceps cristatus,* and shags *Phalacrocorax* sp.). The other major lacustrine site, Pyramid Valley in North Canterbury, is 30 km inland and although it contained the remains of most endemic waterfowl and wetland birds (Holdaway & Worthy 1997) it lacked mergansers and other piscivorous birds.

The general lack of piscivorous birds in New Zealand rivers – perhaps only Black Shag *Phalacrocorax carbo* represents this guild in the present avifauna – suggests that the merganser could have had little direct competition, whereas the estuaries and coasts of New Zealand, as well as at the Auckland and Chatham Islands, would have been occupied, as they still are, by a range of individual and group-feeding species of shags (Family Phalacrocoracidae). Taken together, the evidence that some Auckland Island's mergansers fed in fresh water, that a Stewart Island bird fed mostly or exclusively in fresh water, that the $\delta^{13}C$ value of the Marfells Beach specimen suggests it fed in a brackish lake, that mergansers were present on Lake Poukawa, and that all other merganser species inhabit rivers and lakes, suggests New Zealand's merganser was a hitherto unrecognised occupant of its fresh waters at the time of first human settlement.

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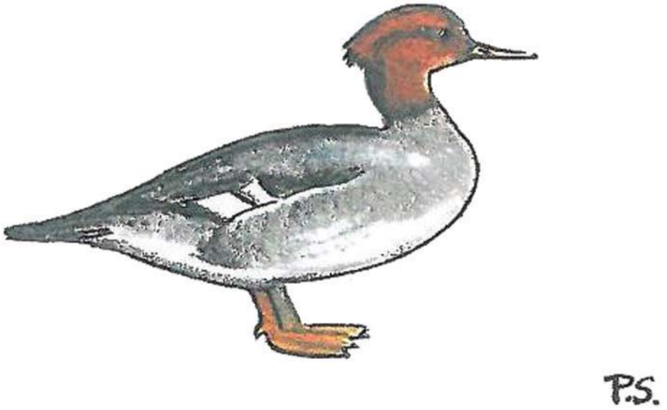

Drawing: Auckland Islands Merganser by Peter Scott.

Appendix 1. New Zealand Merganser specimens and tissues sampled, and their mean (± s.d.) δ^{15}N and δ^{15}C isotope values. Bones from Museum of New Zealand (MONZ) are from Chatham Island cave deposits, both bones from Canterbury Museum are from South Island, New Zealand Polynesian midden deposits, all other specimens are from Auckland Island. All feathers were undertail coverts and all claws were entire hind claws.

Museum*	**Collection no.**	**Tissue sampled**	**Sample no.**	**δ^{15}N ± s.d.**	**δ^{13}C ± s.d.**
Dresden	3092	Feather	1	16.5 ± 0.08	–11.8 ± 0.03
	3022	Feather	2	15.7 ± 0.04	–10.6 ± 0.20
	3022	Claw	3	15.6 ± 0.01	–11.8 ± 0.27
Vienna	50760	Feather	4	15.5 ± 0.06	–15.2 ± 0.34
Cambridge	12/Ana/38/a/1	Feather	5	15.6 ± 0.08	–11.9 ± 0.08
	12/Ana/38/a/1	Claw	6	15.8 ± 0.20	–11.6 ± 0.08
Dublin	1904.559.1	Feather	7	15.8 ± 0.09	–14.9 ± 0.12
	1904.559.1	Claw	8	13.2 ± 0.11	–19.8 ± 0.06
NHM	1904.8.4.1	Claw	9	16.0 ± 0.74	–13.4 ± 0.38
	1904.8.4.1	Feather	10	18.0 ± 0.04	–11.9 ± 0.01
	1904.8.4.2	Bone (rib)	11	17.7	–11.6
	1902.8.6.1	Feather	12	17.7 ± 0.00	–11.8 ± 0.00
	1901.10.21.58	Feather	13	15.5 ± 0.05	–18.0 ± 0.10
	1901.10.21.58	Claw	14	13.6 ± 0.02	–19.4 ± 0.04
Canterbury	AV1580	Feather	25	12.1	–16.5
	AV1583	Feather	26	14.1	–17.5
	AV37111	Bone (humerus)	27	12.0	–18.0
	AV13512B	Bone (tibiotarsus)	28	9.0	–21.5
MONZ	S/30036/1	Bone (sternum)	29	21.1	–13.8
	S/30046/2	Bone (sternum)	30	19.4	–14.2
	S/30046/3	Bone (sternum)	31	17.3	–14.4

*Museums are: Dresden = Staatliches Museum fur Tierkunde, Dresden, Germany; Vienna = Naturhistorisches Museum, Vienna, Austria; Cambridge = Zoology Museum, Cambridge University, Cambridge, England; Dublin = National Museum of Ireland, Natural History, Dublin, Ireland; NHM = Natural History Museum, Tring, UK; Canterbury = Canterbury Museum, Christchurch, New Zealand; MONZ = National Museum of New Zealand, Wellington, New Zealand.

Appendix 2. Mean (± s.d.) δ^{15}N and δ^{15}C isotope values of merganser species and tissues sampled. All tissues were obtained from Natural History Museum, Tring, UK; the Smew, Red-breasted Merganser and Goosander specimens were collected in United Kingdom and Brazilian Merganser from Argentina (15) and Brazil (16). The Scaly-sided Merganser data are from the South Primorye region of eastern Russia (D. Solovieva, unpubl. data and A.D. Fox, unpubl. data).

Species	Collection no.	Tissue sampled	Sample no.	δ^{15}N ± s.d.	δ^{13}C ± s.d.
Brazilian Merganser	1892.2.1.22	Feather	15	14.8 ± 0.04	–20.4 ± 0.02
	1966.24.2	Feather	16	13.9 ± 0.03	–18.5 ± 0.01
Goosander	1934.1.1.1752	Feather	17	13.4 ± 0.01	–15.8 ± 0.32
	1919.12.10.319	Bone	18	14.8 ± 0.06	–20.1 ± 0.21
Smew	1941.5.30.9241	Feather	19	13.8 ± 0.69	–21.7 ± 0.31
	S/1986.32.1	Bone	20	12.4 ± 0.10	–24.7 ± 0.24
Red-breasted Merganser	1955.3.40	Feather	21	16.8 ± 0.03	–13.3 ± 0.19
	S/1997.78.1	Bone	22	9.9 ± 0.04	–9.6 ± 0.27
Scaly-sided Merganser	D. Solovieva, unpubl. data and A.D. Fox, unpubl. data.	Feather (n = 18)		12.1 ± 1.00	–23.5 ± 1.60

Direct and indirect evidence that productivity of Snowy Plovers *Charadrius nivosus* varies with occurrence of a nest predator

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Abstract

The Snowy Plover *Charadrius nivosus* is a threatened species of shorebird that breeds along the Pacific coast of North America where predation of eggs and chicks is thought to be a principal cause of low productivity and small population size. Data were collated over nine years (2001–2009) at 19 breeding locations in northern California to evaluate relationships between the activity of the main predator (Common Raven *Corvus corax*) suspected to compromise plover reproductive success and *per capita* fledging success of plovers, including video camera evidence. An index of raven activity correlated negatively with plover productivity and appeared in the five most-competitive models, accounting for 88% of corrected-Akaike weights explaining variation in *per capita* fledging success. Activity of humans and American Crows *Corvus brachyrhynchos* was weakly correlated with plover reproductive success. Video cameras (deployed in the last two years of the study at the site where corvid activity was highest and most plovers bred) showed that ravens caused 70% of nest failures at an average of 12 (± 2.82 s.e.) days after clutch initiation; humans (20%) or drifting sand/tidal overwash (10%) caused remaining losses. Video recordings suggested that the departure of an incubating plover prompted raven predation of eggs. These results substantiate the notion that the Common Raven is an important factor limiting plover productivity in northern California, which emphasises the need for more effective management measures for predators.

Key words: Common Raven, human disturbance, predation, reproductive success, video cameras.

Worldwide, wader populations are declining (Morrison *et al.* 2001; Delany *et al.* 2009). A variety of causes have been implicated in these declines, including degradation and loss of wetland habitats in non-breeding areas (Myers *et al.* 1987), which affects adult survival (*e.g.* Burton *et al.* 2006), and low productivity on breeding grounds

(MacDonald & Bolton 2008; Teunissen *et al.* 2008). In arctic and boreal regions, low breeding productivity has been linked to elevated rates of nest predation, especially in human-altered landscapes (Evans 2004; MacDonald & Bolton 2008) that enhance populations of synanthropic species (Perry & Henry 2010). A variety of studies have implicated corvids (Family: Corvidae) as principal predators responsible for low reproductive success (see MacDonald & Bolton 2008), although evidence differs regarding the extent to which variation in corvid abundance is correlated with changes in wader productivity. For instance, Bolton *et al.* (2007) showed experimentally that Lapwing *Vanellus vanellus* nesting success was highly variable and largely unaffected (except at sites with highest predator densities) by lethal control of two predators (Red Fox *Vulpes vulpes* and Carrion Crow *Corvus corone*).

In North America, temperate latitude populations of waders that breed on ocean beaches face a variety of threats that compromise their productivity (Brown *et al.* 2001), including habitat loss (*e.g.* Aiello-Lammens *et al.* 2011), human disturbance (Lafferty *et al.* 2006) and predation of eggs and chicks by corvids (Colwell *et al.* 2010). In these habitats, negative effects of predation on wader productivity may be magnified at sites where anthropogenic refuse attracts corvids that subsequently depredate eggs and chicks. Additionally, human disturbance may lead indirectly to increased levels of nest predation, through human proximity displacing incubating birds from nests. This scenario has been exacerbated by increases in corvid populations (Marzluff *et al.* 1994; Kelly *et al.* 2002; Perry & Henry 2010). Little evidence exists, however, for an evaluation of relationships between corvids and wader reproductive success, which are critical for the recovery of some populations of species listed under the U.S. Endangered Species Act (ESA).

In 1993, the United States Fish and Wildlife Service (hereafter USFWS) listed the Pacific coast population segment of the Snowy Plover *Charadrius nivosus* (hereafter plover) as threatened under the ESA (USFWS 1993), following evidence of a reduction in number of breeding locations and a declining population (Page & Stenzel 1981; Page *et al.* 1991). The plover's recovery plan (USFWS 2007) identified three factors that are thought to have led to its small population size by reducing reproductive success: 1) loss and degradation of breeding habitats stemming from the spread of invasive vegetation (*e.g.* European Marram Grass *Ammophila arenaria*), which converts sparsely vegetated coastal habitats that are favoured by plovers (Muir & Colwell 2010) to dense vegetative cover; 2) direct and indirect impacts imposed by human activity (Lafferty *et al.* 2006); and 3) direct mortality of eggs and chicks arising from predation by native and non-native (*e.g.* Red Fox) vertebrates (Neuman *et al.* 2004; Colwell *et al.* 2011). While there is evidence that some mammalian predators occasionally depredate Snowy Plover nests, corvids (Common Raven *Corvus corax* and American Crow *Corvus brachyrhynchos*) are thought to be the most important predators of eggs and chicks throughout the plover's range

(USFWS 2007; Demers & Robinson-Nilsen 2012). Yet quantitative evidence for assessing the relationships between corvid abundance and plover productivity is limited.

Since the plover's listing under the ESA, efforts have increased to quantify factors affecting the species' demography, especially those compromising reproductive success. To date: 1) the population continues to be stable, yet depressed (*i.e.* < 2,000 breeding adults; USFWS 2007); 2) reproductive success is often low as a result of high predation of eggs and chicks (Neuman *et al.* 2004; Colwell *et al.* 2010; Demers & Robinson-Nilsen 2012), despite efforts to manage predators using non-lethal (Hardy & Colwell 2008) and lethal means (Neuman *et al.* 2004); and 3) at least one subpopulation with chronically low productivity is maintained by immigration from more productive areas (Mullin *et al.* 2010). However, precise relationships between low productivity and predator identity and abundance are generally lacking. Corvid populations have increased dramatically in the western United States (Robbins *et al.* 1986; Marzluff *et al.* 1994, 2001; Kelly *et al.* 2002; Perry & Henry 2010). Given the above, we undertook a multi-year study to evaluate relationships between Snowy Plover reproductive success and two potentially important causes of breeding failure: predators and humans. We use direct (*e.g.* video camera) and indirect (*e.g.* correlational analyses) evidence to determine whether predation of eggs by Common Ravens is an important factor limiting productivity of plovers in our study area.

Methods

Study area

Researchers studied breeding plovers at 19 sites in Humboldt County, California from mid-March to early September over a nine year period, from 2001–2009 inclusive. Eight sites were ocean-fronting beaches and 11 sites were gravel bars on the lower 15 km of the Eel River (Fig. 1; Colwell *et al.* 2010). A breeding site was defined as a beach or gravel bar, separated from other sites by unsuitable habitat (*e.g.* river channel, estuary, rocky headland) or distances of several km of unoccupied habitat (Colwell *et al.* 2007a), which exceeds the average home range size and movements of individuals (Pearson 2011). For example, adults tending broods rarely crossed river channels between sites and adults infrequently moved among sites within a reproductive attempt. In most instances, different county, state and federal agencies managed sites.

The two habitat types, sandy beach and riverine gravel bar, differed greatly in substrate and vegetation. Coarse, heterogeneous substrates varying in size from sand and pea-sized gravel to large cobble and sparse vegetation (sedges *Salix* sp., White Sweetclover *Melilotus alba*) characterised gravel bars (Colwell *et al.* 2010, 2011). Ocean-fronting beaches had relatively homogeneous sandy substrates interspersed with dense stands of Marram Grass. On beaches, plovers tended to nest in expansive, unvegetated patches of sand (Muir & Colwell 2010) with debris fields of wood, shells and crustacean carapaces, small tufts of vegetation (*e.g.* Marram Grass and Sea Rocket *Cakile* sp.)

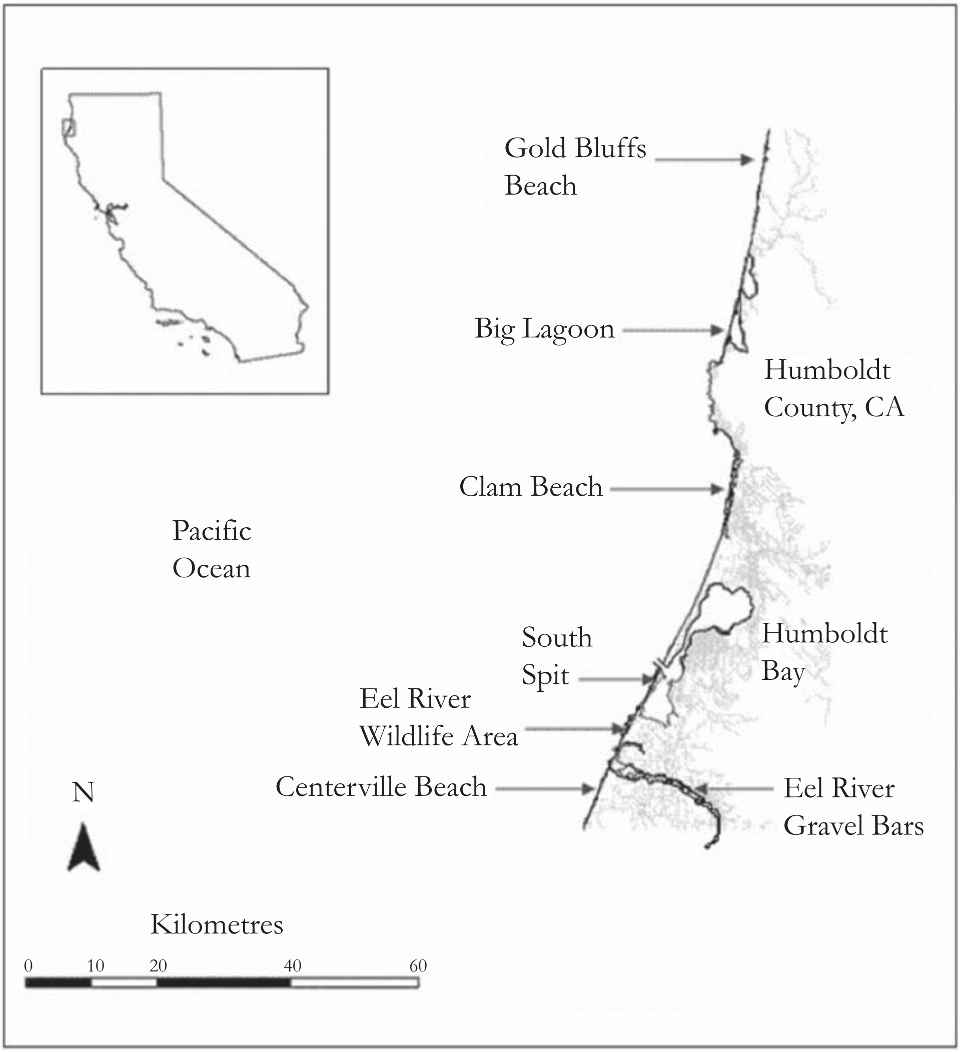

Figure 1. Location of the main study area where Western Snowy Plovers bred in Humboldt County, California from 2001–2009.

and miscellaneous refuse (Colwell *et al.* 2010).

Field methods

Intensive monitoring of plovers in Humboldt County commenced in 2001 (Colwell *et al.* 2010, 2011; Mullin *et al.* 2010). Each year, researchers captured and banded nearly all unmarked breeding plovers and newly hatched chicks in the study area. Adult plovers were marked with a unique combination of three coloured leg bands and a USFWS metal band wrapped with coloured tape; newly hatched chicks were marked with a single metal band wrapped with brood-specific coloured tape to distinguish between chicks of similar age in a common area (Colwell *et al.* 2007b).

Each year, observers surveyed the 19 sites at 7–10 day intervals from 15 March until late August or early September to locate nests, monitor broods and re-sight banded birds. Observers often surveyed sites occupied by breeding plovers more frequently (at 1–4 day intervals). Site visits continued until the last young fledged at 28 days old. Observers conducted nearly all surveys between dawn and 12:00 h. During surveys, observers stopped frequently to search for plovers using binoculars and spotting scopes. Observers recorded the location of courtship scrapes, nests, broods and adults using a global positioning system (GPS; WGS 84 datum) in ArcPad 6 and a Dell Axim X50 Personal Digital Assistant (PDA) fitted with an auxiliary GPS unit (GPS Ultra Holux). From 2004–2009, observers also used this automated system to record instantaneous 500 m point counts, determined by an alarm at fixed 20 min intervals (*i.e.* at 07:00 h, 07:20 h, *etc.*), during regular surveys at 18 of 19 sites (Colwell *et al.* 2010). During a point count, observers counted the number of pedestrians, dogs, vehicles, horses and corvids (Common Ravens and American Crows separately) within 500 m of their location.

In 2008 and 2009, a video camera system was used to monitor a subset (*n* = 25) of plover nests at the breeding site (Clam Beach) where corvid activity was known to be comparatively high and the highest concentration of plovers bred (Appendix 1). Upon discovery of a nest, two individuals (*i.e.* camera crew) set up the video system late in the evening so as to minimise attracting corvids and humans to the site. The system consisted of a video camera, 100 m of cable, digital video recorder and 12 V deep-cycle battery. The camera had 15 large 850 nm infrared light-emitting diodes to facilitate recording at night up to 80 m away. The digital video recorder operated at 30 frames per second, 24 h a day. The camera crew placed the system in a protective container, buried in the sand, to protect it during inclement weather and to prevent damage when camouflaging necessitated partial burial of the camera. The camera was installed 15–90 m from the nest, camouflaged with vegetation, driftwood and sand so as to disguise its presence from predators and humans. The camera system was close enough to the nest to provide adequate illumination at night, but sufficiently distant to ensure that any effects on nest survival were kept to a minimum. That cameras did not influence plover nesting success was shown by similar daily survival rates of nests with (mean = 0.915, 95% CI = 0.875–0.944, *n* = 25) and without (mean = 0.862, 95% CI = 0.813–0.899, *n* = 39) cameras. Control nests were selected at random from within the study area using Geographical Information System (GIS) software.

The video cameras were used to evaluate: 1) the success with which field observers could determine accurately the cause of nest failure, by identifying a predator via the nest camera, and 2) the behaviour of predators that depredated eggs. Specifically, researchers were interested in whether or not corvids found nests based on the contrast of eggs with surrounding sandy substrates (and plover tracks that were often visible in the sand), or by the behavioural response of adults (*i.e.* corvids observed an incubating adult leave the nest). Events surrounding nest failure therefore were reviewed to determine: 1) the interval (in seconds) between departure of the incubating plover from the nest and arrival at the nest cup of a corvid, and 2) proximity to the nest (< 1 m; 1–5 m; > 5 m) of the corvid when it landed.

Data summary and analyses

For each year (2004–2009), data from point counts were collated to develop an index of corvid and human activity at each site (Appendix 1). Incidence was defined as the proportion of *n* point counts during which observers detected at least one form of human activity or at least one corvid. Plover productivity was indexed each year at a site as the average number of young fledged (*i.e.* reaching 28 days) per male.

Measures of corvid incidence and abundance from point counts were highly correlated for beach ($r_6 = 0.93$, $P < 0.01$) and river ($r_{10} = 0.95$, $P < 0.01$) sites individually and for all sites combined ($r_{17} = 0.97$, $P < 0.01$). Similarly, incidence and abundance of human activity on point counts was positively correlated for beach ($r_6 = 0.46$, $P < 0.01$) and river ($r_{10} = 0.99$, $P < 0.01$) sites individually and for all sites combined ($r_{17} = 0.99$, $P < 0.01$). Consequently, two covariates (*ravens* and *crows*) were used based on the incidence of these two potential predators derived from point counts to characterise the predation threat to plover chicks and eggs. Similarly, three additional covariates (*pedestrians*, *dogs* and *vehicles*) were based on their incidences on point counts to characterise the potential negative impacts of humans to breeding plovers. Thirteen *a priori* models were developed based on these five covariates, representing independent hypotheses of the relationship between these variables and productivity. The same analyses undertaken using abundance rather than incidence measures gave near-identical model outputs; only models using incidence data are presented here, however, to simplify presentation of the results.

An information theoretic approach (Burnham & Anderson 2002) was used to evaluate relationships between predator activity and human activity (independent variables) and *per capita* fledging success (dependent variables) at the 19 breeding sites. Multiple linear regression models were evaluated using *a priori* parsimonious model selection and inference strategies based on Akaike's Information Criterion corrected for small sample size (AIC_c) in programme R (R Development Core Team 2005; Burnham and Anderson 2002). Akaike weights (w_i), based on the scaled-likelihoods for each model given the collection of models and dataset analysed, were derived for all candidate models (Burnham & Anderson 2002). There was no evidence of spatial autocorrelation among independent variables based on Moran's I (Burrell 2010).

Tests were conducted for model goodness-of-fit using residual standard error, adjusted *R*-squared and *F*-tests for all candidate models. Comparisons of the differences in plover occupancy between beach and river habitats, as well as the cause of nest failure, were conducted using *t*-tests of untransformed data and Spearman's rank correlation. The estimates for all covariates used in models were obtained for all breeding sites in the last six years of the study (2004–2009; *i.e.* site-year). Plover breeding site-year was used as the sample unit and sample dispersion is represented with standard error (s.e.) for all analyses. We excluded all site-years in which predator exclosures were used. The relative importance of covariates of the individual predictor (x_k) based on Akaike weight was estimated, derived from: (x_k) = Σw_i, where x_k is in model_j. Model averaging was applied to the most competitive models accounting for 90% of Akaike weights (Burnham & Anderson 2002), to derive unconditional beta coefficient estimates and associated 95% confidence intervals.

Results

Plover breeding activity varied greatly among the 19 sites (Appendix 1). Two sites (CB and GW) were occupied consistently by breeding plovers and these locations had the highest breeding densities (plovers per km). Overall, occupancy correlated positively with breeding density ($r^2_{17} = 0.52$, $P < 0.01$). On average, breeding density was lower on beaches (0.75 ± 0.04) than on gravel bars (1.64 ± 0.27), but this difference did not reach statistical significance ($t_{15} = 2.07$, $P = 0.06$, n.s.; Fig. 2a).

Observers detected corvids on 40% of 10,745 point counts (Appendix 1), with an average of 1.41 ± 0.06 corvids per observation. Most (87%) observations were of Common Ravens. Human activity (*i.e.* pedestrian, dog, vehicle, horse) occurred on a quarter of all point counts (Fig. 2b; Appendix 1).

Plover productivity and activity of humans and corvids

Per capita fledging success varied greatly among sites (Appendix 1). The best-fitting model, accounting for 37.4% of corrected Akaike weights, had fledging success correlate negatively with *ravens* and positively with *crows* (Table 1). The most competitive model performed well on goodness-of-fit tests, with a comparatively low residual standard error (0.80), a significant *F*-test ($F_{27} = 6.94$, $P = 0.004$) and an adjusted $R^2_{27} = 0.31$. Estimates for the beta coefficients indicate that *per capita* fledging success correlated negatively with *raven* incidence (–2.40 ± 1.59) and positively with *crow* incidence (3.41 ± 3.63), although the 95% CI for *crows* overlapped with zero.

The covariate *ravens* occurred in the top five competitive models and had the highest importance (0.88) based on corrected-Akaike weights. The covariate *crows*, which appeared in two of the six most-competitive models, had comparatively low covariate importance (0.26). Four of the top six models, accounting for the top 90% of all Akaike weights, included covariates *vehicles*, *dogs* or *pedestrians*, but the 95% confidence intervals all broadly overlapped zero. The top six models all had relatively good

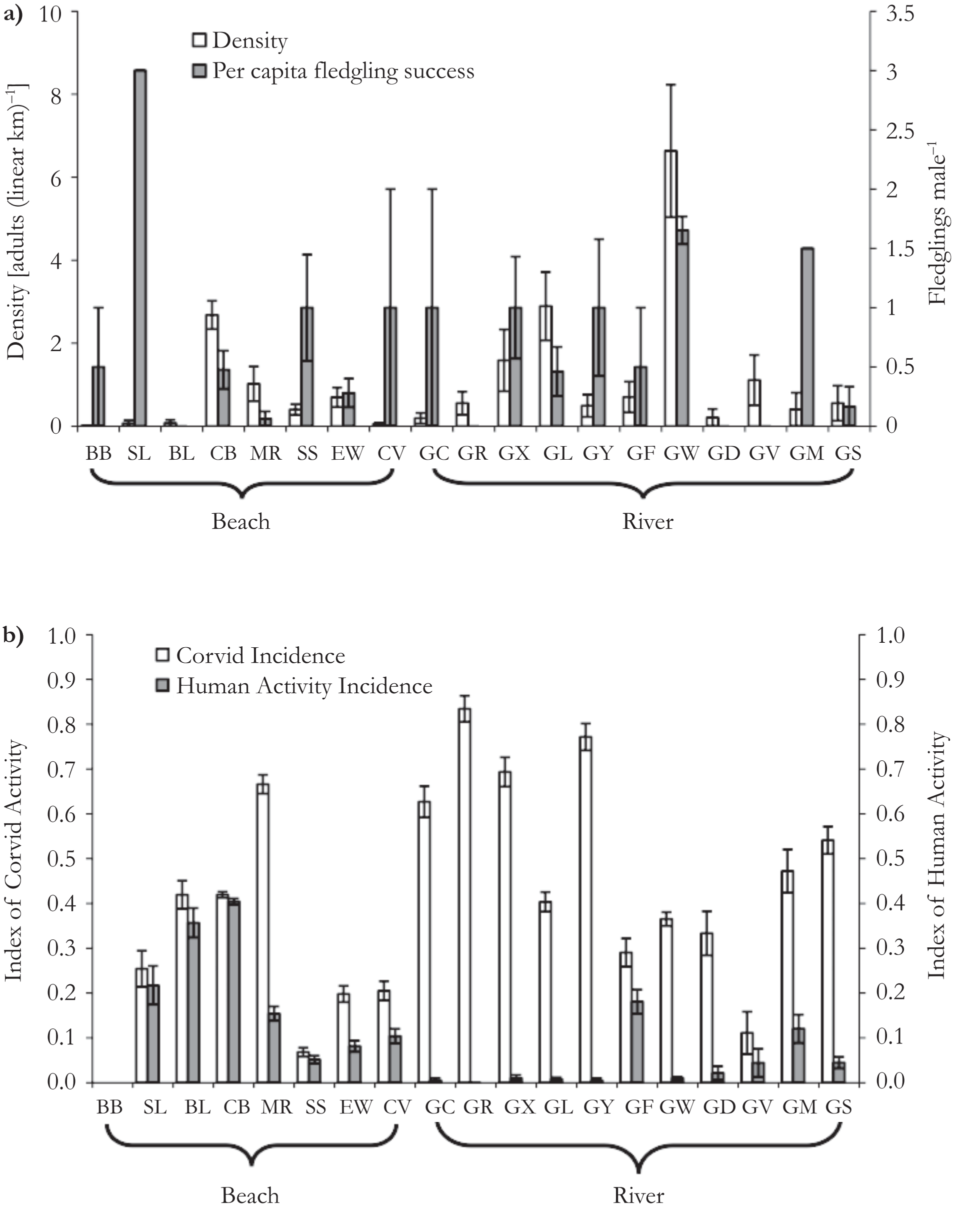

Figure 2. a) Variation in average (± s.e.) density and *per capita* fledging success (2001–2009) and, b) average (± s.e.) incidence of corvid and human (*i.e.* pedestrians, dogs, vehicles, horses) activity detected on 500 m point counts at 19 Snowy Plover breeding sites in Humboldt County, California (2004–2009). Two-letter codes represent breeding sites.

Table 1. Model covariates, parameters (k), adjusted R^2, ΔAIC_c, and Akaike weights for the six most competitive candidate linear regression models predicting *per capita* fledging success of male Snowy Plovers in Humboldt County, California (2004–2009).

Model covariates	k	**Adjusted R^2**	**ΔAIC_c[a]**	**Akaike weights**
Ravens + crows	3	0.31	–	0.37
Ravens	2	0.24	1.05	0.22
Ravens + vehicles	3	0.25	2.05	0.13
Ravens + dogs	3	0.23	2.86	0.09
Ravens + pedestrians	3	0.21	3.48	0.07
Crows + dogs	3	0.19	4.40	0.04
Null model	1	–	7.52	0.01

[a] Change in AIC_c from the most competitive, best-fitting model.

model fit based on significant F tests, low residual standard errors and a moderately high adjusted R^2. To obtain unconditional beta estimates, we averaged the top six most competitive models, which accounted for 92.53% of Akaike weights (Table 2), and found that the covariate *ravens* (–1.77 ± 0.08) was negatively correlated with fledging success.

Evidence from video cameras

Video cameras monitored 25 nests over two years (Appendix 2). Cameras operated successfully at 21 nests, 7 in 2008 and 14 in 2009, which represented 18% and 56% of nests each year, respectively, at Clam Beach. Nests monitored by camera were initiated by at least 14 different birds (6 males and 8 females; see Appendix 2). Four cameras did not record video evidence at the time of clutch failure because the system failed ($n = 3$) or the camera system was vandalised ($n = 1$).

Cameras provided conclusive evidence of two main causes of clutch failure at 20 nests (Appendix 2), with Common Ravens depredating eggs at 14 (70%) of the nests. Ravens ate eggs at an average of 12 (± 2.82 s.e.) days after clutch initiation (*i.e.* within a week of the start of incubation), which was similar in duration ($t_{17} = 0.58$, $P = 0.57$, n.s.) to six nests that failed for other reasons (± 2.12 s.e.). Humans (or dogs) destroyed four (20%) clutches; two additional nests failed because a high tide washed over the nest or wind-driven sand buried eggs prior to clutch completion and the start of incubation.

Each year, field observers often categorised the cause of failure as

Table 2. Unconditional β estimates with 95% confidence intervals and covariate weights based on corrected-Akaike (AIC_c) weights for models examining relationships between corvid and human occurrence and *per capita* fledging success of Snowy Plovers.

		Model averages		
			95% CI	
Covariate	w_i	**Estimate**	**Lower**	**Upper**
Intercept	–	1.1125	0.9931	1.2319
Ravens	0.8840	–1.7660	–1.8464	–1.6856
Crows	0.2645	1.5746	–0.0624	3.2116
Dogs	0.1944	–0.3210	–0.8610	0.2190
Pedestrians	0.1127	–0.0251	–0.2003	0.1501
Vehicles	0.0781	–0.6148	–1.6352	0.4056

[a] Covariate weight (x_k) = Σw_i, where x_k is in model.

"unknown" (Appendix 2), including 69% and 24% of nests in 2008 and 2009, respectively. For the 20 failed nests that were monitored by cameras, 10 (77%) of the 13 "unknowns" resulted from raven predation; three additional "unknowns" failed due to human activity. In one noteworthy case, eggs disappeared from a plover nest and an absence of tracks and other evidence led field observers to classify the cause of failure as "unknown", but video recordings showed that two humans removed the eggs from the nest. At another nest, eventually destroyed by high tide, a woman flushed the incubating adult, manipulated eggs, and photographed the nest. Unleashed dogs destroyed two incomplete clutches when they stepped on nests. Field observers correctly labelled one nest destroyed by tide, but they did not determine that wind-driven sand had buried another nest.

Behaviour of corvids

Common Ravens were the only nest predator detected by cameras. Most predation (31%) occurred shortly after sunrise or later in the afternoon (44%) (Fig. 3a). In 50% of losses to ravens, it appeared that departure of an incubating adult plover from the nest prompted predation by a raven flying nearby. This was based on the observation that in 64% of predation events, ravens landed within 1 m of the nest (Fig. 3b) and that 50% walked directly to the nest within 1 min of landing (Fig. 3c). In two instances, the

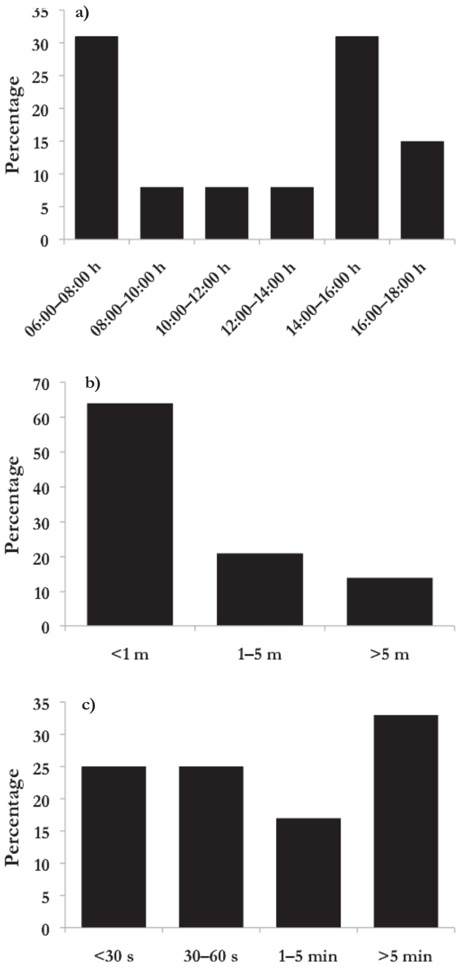

Figure 3. Percentage of Common Ravens predating Snowy Plover nests (*n* = 20): a) across all daylight hours, b) on landing near the nest, and c) on walking to the nest relative to the departure of the incubating plover.

plovers had already left the nest when ravens landed and took the eggs, illustrated by the long (> 10 min) intervals between departure of the incubating adult and arrival of a raven.

Discussion

Our results offer important insights for correlative studies investigating variation in the reproductive success of waders, and have strong management implications for the threatened Snowy Plover population. Plovers in northern California generally have experienced low reproductive success attributable to predation, although at some sites plovers are occasionally highly successful (Burrell 2010; Colwell *et al.* 2010, 2011). This variation has been linked to Common Raven abundance, and ravens were also suspected as being the most important nest predator in our study area and elsewhere (USFWS 2007; Demers & Robinson-Nilsen 2012). The video evidence gives strong evidence for this association at the most important breeding site in our study area, and provides a foundation for implementing more effective management measures to control predation of Snowy Plover eggs by ravens and other predators (MacDonald & Bolton 2008).

Variation in reproductive success

MacDonald and Bolton (2008) reviewed an extensive literature on European waders to show that nesting success (*i.e.* daily predation rate; DPR) was highly variable across species, years and habitats. Similarly, our results demonstrate that Snowy Plovers exhibited considerable variation in *per capita* fledging success (which correlated strongly and produced nearly identical modelling results as DPR of nests; Burrell 2010) among sites and across years. Interestingly, DPR for Snowy Plover nests at the one site (Clam Beach), occupied consistently by a large proportion of the population in northern California (Burrell 2010; Mark A. Colwell, unpubl. data), is much higher than values reported for nearly all waders with the exception of the closely related Kentish Plover *Charadrius alexandrinus*, which also breeds on coastal beaches (MacDonald & Bolton 2008).

Predation has been implicated as a cause of low nesting success and a principal driver of declining wader populations worldwide (MacDonald & Bolton 2008), and for some threatened and endangered taxa. In Europe, evidence suggests that many wader populations have experienced unsustainably high nest losses to predators. In a large sample (*n* = 544 site-years sampled across 57 studies), MacDonald and Bolton (2008) reported that >50% of nests were depredated in 55% of site-years or studies reviewed. Moreover, population viability analyses suggest a linkage between chronically high nest failure and population declines in Temminck's Stint *Calidris temminckii* (Rönkä *et al.* 2006) and Northern Lapwing *Vanellus vanellus* (MacDonald & Bolton 2008). Extending this reasoning, several authors have suggested that the southern extent of breeding range for Palearctic waders may be limited by predation (Pienkowski 1984; Koivula & Rönkä 1998). Waders with low population size and at the limits of their range may be especially vulnerable to the effects of predation. Interestingly, it is widely recognised that high rates of nest predation continue to limit recovery of the listed Snowy Plover population (Neuman *et al.* 2004; USFWS 2007; Colwell *et al.* 2010, 2011).

Snowy Plovers have experienced chronically low nesting success in our study area, averaging 0.71 (± 0.28 s.e.) fledged young per breeding male per year (*n* = 9 years ending 2009; M. Colwell, unpubl. data), with predators causing the majority of nest failures. Adult numbers are sustained by immigration of birds from sites elsewhere along the Pacific coast of North America (Mullin *et al.* 2010). The negative correlation between plover productivity and Common Raven occurrence across multiple breeding sites and multiple years adds further evidence for the detrimental effects of ravens, as abundant, synanthropic omnivores (Perry & Henry 2010). Video camera evidence collected over two years where Common Ravens were strongly suspected to be a significant nest predator reinforced this view, with ravens consuming eggs at nearly all nests where observers classed the cause of failure as "unknown" (*i.e.* eggs had disappeared from the nest cup and there was no clear sign to indicate that a predator had visited the nest).

Predation by ravens

Our videos showing that Common Ravens were the only nest predator at the site where plovers have experienced chronically low breeding success contrasts with evidence from European studies (MacDonald & Bolton 2008) and for the listed population of the Snowy Plover (USFWS 2007). In Europe, nest predation is commonly attributed to mammals, with occasional mention of corvids and gulls (MacDonald & Bolton 2008). For Snowy Plovers, a diversity of predators has been suspected as the cause of poor reproductive success, resulting in occasional lethal control (Neuman *et al.* 2004). In the San Francisco Bay area, where corvid populations have grown rapidly (Kelly *et al.* 2002), a raven was one of five species of bird detected by video cameras eating plover eggs (Demers & Robinson-Nilsen 2012). After more than a decade of studying plovers in northern California, we have only rarely observed or determined (*e.g.* based on tracks at nest) that other species (American Crow *Corvus brachyrhynchos*, Ring-billed Gull *Larus delawarensis* and Grey Fox *Urocyon cinereoargenteus*) have caused reproductive failure by eating plover eggs and occasionally chicks.

Per capita fledging success was inversely correlated with an index of raven abundance, which was the only covariate of importance in the analyses. Moreover, at the most important breeding site (*i.e.* Clam Beach, where >50% of the local population has bred in recent years, albeit with consistently low success; Colwell *et al.* 2010), video cameras showed that ravens caused 70% of nest failures, and that most (77%) of the "unknown" causes of nest loss were attributable to ravens. Additional evidence supports this interpretation. For instance, apparent nesting success in the population has varied annually between 14–68%, although success has decreased with time (r_8 = –0.89) coincident with a shift in the population away from high quality riverine gravel bars (Colwell *et al.* 2011) to ocean beaches (Colwell *et al.* 2010). On gravel bars, survival of nests and chicks is significantly higher than on ocean beaches because rocky substrates afford greater crypsis (Colwell *et al.* 2011). Collectively, these observations strongly indicate that egg predation by Common Ravens is a major cause of low plover productivity in our study area.

Overall, our results underestimated the impact of corvids as egg predators for several reasons related to field methods. First, our classification of causes of nest failure included an "unknown" category, which accounted for the majority of failed nests (*e.g.* Colwell *et al.* 2011). These "unknowns" occurred when eggs disappeared prior to the predicted hatch date for a clutch and observers lacked clear evidence (*e.g.* corvid tracks in the sand) at the nest cup to determine the cause of failure. Video cameras showed that 77% of these "unknowns" failed owing to corvid predation. A second reason why our data from early in the study (2001–2006) underestimate the importance of egg predation is because we used exclosures to protect many nests, especially at sites with high raven activity. As a result, apparent nesting success was artificially high. After 2006, when we ceased using exclosures owing to an episode of high predation on incubating adults by an unknown avian predator, nesting success and *per capita* fledging success dropped to the lowest values recorded in 11 years (Colwell *et al.* 2011).

We used cameras to monitor nests at Clam Beach because this site had the majority of breeding plovers (Appendix 1) that experienced low nest survival and fledging success (Hardy & Colwell 2008; Colwell *et al.* 2010); it was also the location where corvid activity was relatively high (see Appendix 1). In most cases, ravens depredated eggs by landing near the nest shortly after departure of an incubating adult. This suggests that the initial cue possibly used by ravens to find a nest was the movement of the incubating adult. However, without detailed information on the behaviour of ravens (both those that did and did not depredate eggs) as they moved about the study area, it is difficult to ascertain conclusively the circumstances that led to nest predation events. Only a detailed study of the behaviour of ravens foraging in the vicinity of plover nests will increase our understanding of how predators detect nests. At this same site, variation in survival of plover nests was not enhanced by varying degrees of crypsis afforded to eggs by natural habitat features in the vicinity of the nest (Hardy & Colwell 2012). Collectively, these observations suggest that abundant corvids overwhelmed the capacity of the physical habitat to sustain plover reproductive success. Moreover, if this phenomenon is widespread, then some management practices (*e.g.* spreading shell hash; Colwell 2010) intended to ameliorate high predation rates by enhancing the crypsis of nesting substrates are likely to fail.

Human disturbance

Worldwide, waders frequenting ocean beaches are subject to high levels of disturbance owing close proximity to centres of human population that favour coastal habitats for recreation and development (Brown *et al.* 2001). Human disturbance is one of three main factors affecting the threatened status of the plover. In our study area, reproductive success was weakly correlated with human activity. Most models that included vehicles, dogs or pedestrians contributed little to improving model fit. This probably resulted from the comparatively low percentage of nest or brood failure that was caused by humans compared to losses inflicted by corvids (Colwell *et al.* 2010, 2011). Nevertheless, videos showed that humans did cause reproductive failure at Clam Beach (20% of nest attempts videoed) where human recreational activity was highest, either directly (*e.g.* eggs stolen, vehicle strike) or indirectly (dogs taking the eggs or chicks) (Fig. 2b; Appendix 2). On riverine gravel bars, vehicle strikes accounted for 14% of nest losses during 2001–2009 (Colwell *et al.* 2011). These observations: 1) show that plover reproductive success may be compromised at some sites by human activity, and 2) argue that some types of recreational use are incompatible with plover conservation goals and require active management. Finally, it is noteworthy that we conducted our study in a region of low human population size and often at remote sites not often frequented by humans. Elsewhere in the species' range data suggest that restrictions (*e.g.* fencing that provides a refuge for breeding plovers in areas of high human use) on recreational activity in close proximity to plovers can promote breeding (Lafferty *et al.* 2006). Furthermore, in our study area, use of fencing resulted in an increase in breeding success at the site with highest human activity (Wilson & Colwell 2010).

Management implications

The results show that Common Ravens are the most important factor influencing reproductive success of plovers in our study area. This result is not universal within the range of the listed population (Demers & Robinson-Nilsen 2012). The population of plovers in northern California is a demographic sink plagued by low reproductive rates (Colwell *et al.* 2010; Mullin *et al.* 2010) and sustained by immigration (Mullin *et al.* 2010). As a result, we suggest that enhanced predator management should be considered for our study area. Plovers initially (2001–2006) had higher *per capita* reproductive success in our study area when: 1) a larger proportion of birds nested amidst gravel substrates that offered camouflage for eggs and chicks (Colwell *et al.* 2011), and 2) nest exclosures were used to boost hatching success at sites where ravens were especially problematic (Hardy & Colwell 2008). We stopped using exclosures after an episode of high adult mortality in 2006 (Mullin *et al.* 2010; Hardy & Colwell 2008). In the subsequent 6 years, exclosures were used to protect only two of 250+ nests. As a result, *per capita* fledging success has continued to decline to a low of 0.45 fledged chicks per male in 2011. Renewed interest in predator management is therefore warranted, with the aim of boosting plover productivity and facilitating population recovery in northern California and elsewhere in the species' range.

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Appendix 1. Number of years that each site was occupied, estimates of average density and *per capita* fledgling success with associated standard error (s.e.) for Snowy Plover breeding locations in Humboldt County over a nine year study (2001–2009). Incidence of corvid and human recreational activity based on 500 m point counts conducted at Snowy Plover breeding locations in Humboldt County (2004–2009).

Site[a]	Occupancy	Density	Fledging success[b]	Corvid incidence[c]						Human activity incidence[d]					
				2004	2005	2006	2007	2008	2009	2004	2005	2006	2007	2008	2009
BB	2	0.01 ± 0.01	0.50 ± 0.50	–	–	–	–	–	–	–	–	–	–	–	–
SL	1	0.07 ± 0.07	3.00 ± 0.00	–	–	0.12	0.62	0.18	0.22	–	–	–	0.10	0.30	0.19
BL	1	0.08 ± 0.08	0.00 ± 0.00	–	–	0.33	0.51	0.42	0.32	–	–	0.00	0.35	0.34	0.51
CB	9	2.68 ± 0.34	0.48 ± 0.16	0.26	0.41	0.41	0.50	0.48	0.47	0.29	0.39	0.40	0.50	0.36	0.48
MR	4	1.02 ± 0.42	0.06 ± 0.06	–	–	–	0.69	0.69	0.62	–	–	–	0.22	0.13	0.12
SS	6	0.40 ± 0.13	1.00 ± 0.45	0.05	–	–	0.18	0.02	0.20	0.04	–	–	0.09	0.04	0.00
EW	7	0.70 ± 0.24	0.28 ± 0.12	0.16	–	0.11	0.11	0.24	0.27	0.02	–	0.17	0.06	0.09	0.09
CV	2	0.05 ± 0.03	1.00 ± 1.00	0.09	–	0.32	0.37	0.15	0.14	0.00	–	0.04	0.14	0.16	0.06
GC	2	0.19 ± 0.13	1.00 ± 1.00	0.24	0.29	0.64	0.76	0.75	0.75	0.00	0.14	0.00	0.00	0.00	0.00
GR	3	0.56 ± 0.28	0.00 ± 0.00	0.55	–	1.00	0.97	0.96	0.88	0.00	–	0.00	0.00	0.00	0.00

Appendix 1 (*continued*)

Site[a]	Occupancy	Density	Fledging success[b]	Corvid incidence[c]						Human activity incidence[d]					
				2004	2005	2006	2007	2008	2009	2004	2005	2006	2007	2008	2009
BGX	4	1.59 ± 0.74	1.00 ± 0.43	0.34	–	0.82	0.88	0.71	0.77	0.00	–	0.00	0.00	0.02	0.03
GL	6	2.89 ± 0.82	0.46 ± 0.21	0.20	0.44	0.43	0.70	0.60	0.58	0.00	0.00	0.03	0.00	0.00	0.04
GY	3	0.49 ± 0.27	1.00 ± 0.58	0.48	0.72	0.88	0.92	0.91	0.93	0.00	0.00	0.00	0.00	0.02	0.00
GF	3	0.70 ± 0.37	0.50 ± 0.50	0.19	0.14	0.33	0.32	0.22	0.41	0.13	0.00	0.08	0.19	0.32	0.12
GW	9	6.63 ± 1.6	1.65 ± 0.12	0.25	0.27	0.38	0.50	0.44	0.38	0.00	0.03	0.01	0.01	0.01	0.01
GD	1	0.21 ± 0.21	0.00 ± 0.00	0.27	–	0.40	0.48	0.31	0.29	0.00	–	0.00	0.05	0.04	0.00
GV	3	1.11 ± 0.61	0.00 ± 0.00	0.08	–	0.25	–	–	–	0.00	–	0.25	–	–	–
GM	1	0.40 ± 0.40	1.50 ± 0.00	0.40	–	0.00	0.59	0.50	0.42	0.10	–	0.00	0.19	0.13	0.08
GS	2	0.56 ± 0.42	0.17 ± 0.17	0.20	0.25	0.52	0.74	0.69	0.42	0.00	0.00	0.00	0.02	0.06	0.12

[a] Two-letter codes represent breeding locations (*i.e.* sites); they are listed north to south (beaches) and down- to upstream (gravel bars; *i.e.* those codes beginning with a "G").

[b] *Per capita* fledging success (fledged chicks male^{-1}).

[c] Incidence (proportion) of all point counts in which corvids were detected within a 500 m radius of an observer.

[d] Incidence (proportion) of all point counts in which pedestrians, dogs, vehicles and/or horses were detected within a 500 m radius of an observer.

(–) indicates site was not surveyed in given season.

Appendix 2. Summary of video-monitored Snowy Plover nests at Clam Beach, Humboldt County, California (2008–2009).

				Date			**Determined outcome of nest attempt**	
Year	**Nest Identity**	**Male**	**Female**	**Clutch initiated**	**Camera installed**	**Failed or hatched**	**Field observation**	**Video camera**
2008	CN06	GV:GB	VW:GW	25-Apr	26-Apr	1-May	Unknown	Common Raven
	CS07	OR:RY	VW:YY	28-Apr	2-May	2-May	Unknown	Common Raven
	CS13	GV:GB	BP:OG	9-May	22-May	29-May	Unknown	Common Raven
	CS18	VW:OW	GL:WO	25-May	7-Jun	23-Jun	Unknown	Common Raven
	CS19	OR:YR	WW:YG	26-May	30-May	1-Jun	Unknown	Common Raven
	CS26	OR:YR	RY:YW	27-Jun	30-Jun	20 & 29 Jul	Vehicle[a]	Vehicle[a]
	CS27	VW:OW	GL:WO	30-Jun	30-Jun	21-Jul	Unknown	Common Raven
2009	CN02	OR:YR	OR:RR	17-Mar	20-Mar	21-Mar	Unknown	Dog
	CN03	Unknown	Unknown	20-Mar	24-Mar	24-Mar	Common Raven	Common Raven
	CN04	VW:BR	VW:GW	23-Mar	24-Mar	25-Mar	Unknown	Common Raven
	CN09	WW:YB	BP:OG	29-May	29-May	30-May	Common Raven	Dog
	CN10	WW:YB	BP:OG	6-Jun	12-Jun	26-Jun	Tidal overwash	Tidal overwash
	CN11	WW:YB	BP:OG	5-Jul	8-Jul	15-Jul	Common Raven	Common Raven
	CN12	VW:BR	VW:YY	11-Jul	16-Jul	1-Aug	Unknown	Common Raven
	CS04	OR:YR	OR:RR	17-Apr	19-Apr	3-May	Unknown	Common Raven
	CS05	VW:OW	VW:YY	25-Apr	2-May	29-May	Hatched	Hatched
	CS07	VW:BR	VW:GW	2-May	8-May	9-May	Unknown	Human
	CS08	WW:YB	BP:OG	12-May	15-May	17-May	Common Raven	Common Raven
	CS10	GV:GB	X:R	17-May	18-May	20-May	Unknown	Buried by sand
	CS11	VW:BR	VW:YY	5-Jun	8-Jun	9-Jun	Common Raven	Common Raven
	CS12	VW:BR	VW:YY	13-Jun	16-Jun	2-Jul	Unknown	Common Raven

[a] Truck crushed 2 eggs; 3rd egg hatched.

Ducks foraging on swan faeces

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Abstract

Foraging on avian faeces by birds is uncommon apart from the consumption of nestling faeces by songbird parents. Here, observations made of five Mallard *Anas platyrhynchos*, three Green-winged Teal *A. crecca* and one Baikal Teal *A. formosa* seen feeding on Whooper Swan *Cygnus cygnus* faeces, on the ice in Lake Izunuma, Japan, on 10 February 2010, are described. The faeces of herbivorous Whooper Swans contained undigested vegetation which, when dissolved in water on top of the ice, was available for consumption by the ducks.

Key words: Coprophagy, ducks, faeces, Whooper Swans.

Coprophagy is rare in birds in comparison with other animals such as mammals and insects. Gallant (2004) reported that White-winged Crossbills *Loxia leucoptera* foraged on River Otter *Lontra canadensis* faeces, perhaps consuming fish bones or undigested fish present in the droppings. Faeces can be used as a source of carotenoids by birds; for instance, the brightly coloured yellow on the head of the Egyptian Vulture *Neophron percnopterus* is obtained by ingesting carotenoid pigments from the excrement of ungulates (Negro *et al.* 2002). In wildfowl, Whooper Swans *Cygnus cygnus* have been observed in aggressive confrontations over their own and their neighbours' faeces, which contained large amounts of undigested barley (Black & Rees 1984). Foraging on avian faeces by birds is uncommon, however, apart from the consumption of nestling faeces by songbird parents (Hurd 1991).

I had an opportunity to observe ducks foraging on swans faeces when their lake was covered with ice in February 2010. The observations are presented here as a further contribution to knowledge on avian coprophagy.

Methods

Field observations were conducted at Lake Izunuma (369 ha area; 38°47'N, 141°07'E) in Tome City, Miyagi Prefecture, Japan, a well-known wintering area for wildfowl, supporting Greater White-fronted Goose *Anser albifrons*, Whooper Swan, Mallard *Anas platyrhynchos*, Northern Pintail *A. acuta*, Green-winged Teal *A. crecca* and Goosander *Mergus merganser*.

Cold weather conditions generally occur at Lake Izunuma from late December to early February each year, and the lake is covered with ice for longer periods in more severe winters. In winter 2009/10, the lake was covered in ice from mid January onwards. I used binoculars (8× magnification) and a spotting scope (30×) to observe ducks foraging on swan faeces on the ice for a 2 h period during the morning of 10 February 2010. A total of 4,743 swans and ducks were counted on the lake the previous day (9 February 2010), including 1,153 Whooper Swans, 403 Green-winged Teal and 18 Baikal Teal.

Results and Discussion

Five Mallard were seen feeding on Whooper Swan faeces at Lake Izunuma on 10 February 2010, when part of the lake was frozen (Fig. 1a,b). The swans and ducks were resting on the ice, and swan faeces were close to the resting swans. Three Green-winged Teal and one Baikal Teal *A. formosa* were also seen feeding on the swan faeces.

When the lake was covered in ice, the Whooper Swans were unable to access aquatic vegetation in the lake, and therefore, fed on grasses and on waste grain in rice fields in the surrounding area. The faeces of herbivorous Whooper Swans contained

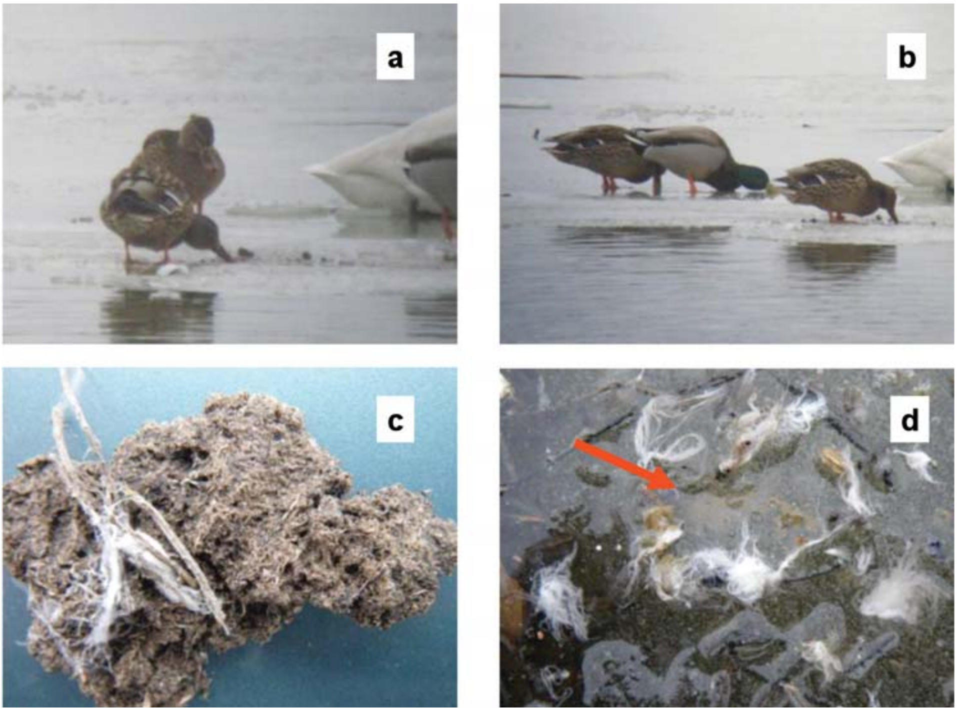

Figure1. Swan faeces ingested by ducks: (a) and (b) = Mallard foraging on Whooper Swans faeces, (c) = Whooper Swan dropping, and (d) = dissolved faeces on ice (red arrow).

undigested fibrous vegetation (Fig. 1c) which when dissolved in water on top of the ice (Fig. 1d) was available to be filtered and consumed by the ducks. The three duck species observed (Mallard, Green-winged Teal and Baikal Teal) are omnivorous (Young 2005; Fox 2005; Moores 2005) and in Japan they include rice grain, wild cereal seeds, herbs, submerged plant and aquatic insects in their diet (Haneda 1962). The undigested fibre would likely have been the primary nutrient derived from the swan faeces by the ducks, but the quantity of swan faeces consumed by the ducks and the nutritional value of the faeces was unknown.

Anatidae have been found to digest a low proportion of the organic matter in vegetation ingested; estimates generally range from 18–40% for leaf material, but vary with the type of food being taken (Buchsbaum *et al.* 1986; Gadallah & Jefferies 1995; Van der Wal *et al.* 1998; Durant *et al.* 2002). For all vegetable foods, a large proportion of the undigested material excreted in the birds' droppings is fibre. Nevertheless, for some other organisms, such remains in faeces can offer some food value. For example, Barnacle Goose *Branta leucopsis* droppings were consumed by Svalbard Reindeer *Rangifer tardandus platyrhynchus*, with the Reindeer selecting goose droppings containing grass fragments, as these were more profitable as a food source than grazing on the sparse forage generally available in the local environment (van der Wal & Loonen 1998).

In early February, waste grain in the fields around Lake Izunuma is usually depleted due to the intense foraging activity by Greater White-fronted Geese (Shimada & Mizota 2008). Food resources for ducks around the lake therefore were low, added to which the ice and snow cover in this severe weather would have covered feeding sites, further decreasing food availability. The period of time that swan faeces were accessible on the ice was restricted to a few weeks, until the ice melted. Nevertheless, swan faeces may have offered a relatively profitable food resource for the ducks during this time of low food availability, high thermoregulatory costs and highly restricted foraging conditions.

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Photograph: Whooper Swans foraging in rice fields by Rikio Ito.

Announcement

The 9th Conference of the European Ornithologists' Union (28–31 August 2013, Norwich, UK)

The European Ornithologists' Union (EOU) has been founded as an equal partnership among avian biologists across Europe to provide an international forum for the advancement of European ornithology in all its aspects. The bi-annual conferences provide ideal platforms to get in contact, exchange ideas and disseminate knowledge. The Council of the EOU and the local organisers cordially invite you to join the 9th EOU conference to be held in Norwich, UK, from 28–31 August 2013.

This event will be organised jointly by the University of East Anglia (UEA) and the British Trust for Ornithology (BTO), Royal Society for the Protection of Birds (RSPB), British Ornithologists' Union (BOU), and the Edward Grey Institute of Oxford University (EGI). The conference will cover the full range of ornithological research, including both basic and applied aspects. The programme will be composed of plenaries, symposia, contributed oral presentations and poster sessions.

Information on the scientific programme, conference venue, deadlines, registration fees, contact details for the organisers, and excursions are available and will be updated on the conference website at http://wwww.norwich.eounion.org/index.php.

For information about previous conferences (including pdfs of abstract books) and the EOU in general, please visit the EOU website on http://www.eounion.org.

Wildfowl

Instructions for Authors

This information can also be found at http://www.wwt.org.uk/conservation/saving-wetlands-and-wildlife/publications/wildfowl, together with PDF files of papers from earlier editions of *Wildfowl*.

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Wildfowl is an international scientific journal published annually by the Wildfowl & Wetlands Trust (WWT). It disseminates original material on the ecology, biology and conservation of wildfowl (*Anseriformes*) and ecologically-associated birds (such as waders, rails and flamingos), and on their wetland habitats. Research and review articles related to policy development and application are welcome. Material on habitat management is also sought, particularly where this is directed to the conservation of wildfowl and other wetland birds.

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Research projects submitted as papers for publication in *Wildfowl* must have proper regard for animal welfare and habitat conservation, and employ humane practices. Attention is drawn to the guidelines published in *Animal Behaviour* 61: 271–275 and on the journal's website: www.elsevier.com/wps/find/journaldescription.cws_home/622782/authorinstructions#6002. The impact of a particular study should be evaluated in terms of the possible gains in knowledge (and the practical use of this knowledge), weighed against potential adverse consequences for individuals, habitats or populations. Papers are considered for publication in *Wildfowl* solely on the condition that the work reported was undertaken within relevant legal statutes, or where work is carried out in areas lacking legislation or regulation, the work should conform to ethical standards expected in the UK.

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Title page – this should contain:
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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.

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

ntroduction – 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.

References – when mentioned in the text, references should be listed in chronological order, separated by a semi-colon. Citation of work by one or two authors should be in full (Owen 1980; Bannister & Walker 1998), but where there are more than two authors, the citation should be abbreviated to *et al.* (Worden *et al.*) in the text. When different groups of authors with the same first author and date occur, they should be cited as (Thomson *et al.* 1991a, b).

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Baldassarre, G.A. & Bolen, E.G. 1994. *Waterfowl Ecology and Management.* Wiley & Sons, New York, USA.

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.]

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Each table should be on a separate page, numbered and titled. Table headings should be concise and tables should be numbered consecutively in the text as Table 1, *etc.* Data should not be duplicated in both figure and table form. Footnotes should be listed as letters not numbers.

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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>
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>
> "The difference between the samples is not significant ($t_{17} = 1.2$, n.s.)."
>
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