Differential flight responses of spring staging Teal *Anas crecca* and Wigeon *A. penelope* to human *versus* natural disturbance

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Abstract

Observations made of disturbance to spring staging Wigeon *Anas penelope* and Teal *A. crecca* by human and "natural" (non-human) stimuli at a restored wetland in the Skjern River delta, Denmark, were analysed to inform future management of human access to the site. The effects of human activity (anglers, cyclists, farming activity) on the flight responses and displacement distances of ducks within uniform habitat along a public path were compared with the birds' reaction to natural stimuli such as mammals or birds of prey. Excluding the controlled disturbance by a pedestrian, undertaken as part of the study, the main cause of flushing in Wigeon was a response to the movements of birds of prey and other birds, especially Lapwings *Vanellus vanellus* performing flight displays. For Teal, birds of prey accounted for around half of the flushes, with other birds accounting for one third of the flushes. Wigeon and Teal were displaced significantly farther by human activities than by natural causes. We tested whether the ducks reacted differently to natural disturbances shortly after disturbance by a pedestrian by comparing response patterns to natural stimuli within the first hour following disturbance from a passing pedestrian with their response patterns in the absence of pedestrians, but found no evidence to suggest that they did so. In our study area, Wigeon used land for feeding and water as predator-escape habitat; 23% of the 144 observed take-offs of Wigeon were from water but 68% of the landings were on water. Of the 83 observations of flushed Teal, 56% flushed from water and 51% landed on water.

Key words: displacement distance, disturbance, human disturbance, public footpath, waterbirds, waterfowl refuges, wetland.

Despite domestic and international legislation to protect wetland habitats, rates of loss and degradation of wetlands have been rapid during the 20th and early 21st centuries (Davidson 2014). Even well-protected wetlands are facing pressures from multiple competing uses, especially from increasing urban human populations that wish recreational access to such areas. Many features of modern recreational use and nature conservation interests are directly incompatible with each other. For instance, many recreational activities cause waterbirds to suffer increased vigilance, loss of feeding, enhanced energy expenditure, or a combination of these to the extent that they desert a site or suffer reductions in reproductive success or survival (Madsen & Fox 1995, 1997; Livezey *et al.* 2016). On the other hand, it is essential that there is public access to protected wetlands to ensure societal support for their protection. International legislation also enshrines the sustainable use of such areas and includes non-destructive recreational use of wetlands as part of their guiding principles (*e.g.* in the Ramsar Convention; UNESCO 1994). One important mechanism for reducing conflict is to zone recreational activities on protected wetlands, thus providing birds with refuge areas from loci of major disturbance, but this requires an understanding of the distances at which waterbirds react to sources of disturbance and the distances over which they are displaced (*e.g.* Fox & Madsen 1997; Livezey *et al.* 2016).

Such an understanding is especially important with regard to restored wetlands, where large investments of public and/or private money to recreate habitats heighten the expectations of local communities with regard to the potential recreation and other demands placed upon a new and novel resource. Fostering public support for wetland restoration is essential for the long-term sustainable management and use of such restored wetlands because of the loss of traditional activities (such as waterbird hunting or fishing) prior to reinstatement (Scholte *et al.* 2016). Many case studies have demonstrated that a lack of effective coordination between responsible managing organisations often leads to direct competition that favours cultural ecosystem services (especially public access and tourism) to the detriment of habitat services (*i.e.* biodiversity conservation; Cohen-Shacham *et al.* 2015). Because of such pressures to integrate human access requirements with nature conservation management objectives on restored wetlands, it is vital that we have a good understanding of how individual waterbird species respond to pedestrian human access, and precisely how these may interact with natural sources of disturbance to affect the attractiveness to wildlife of a reinstated wetland.

Here we present the results of a study on the causes of displacement (*i.e.* flushes) of Wigeon and Teal, including an assessment of how these two species respond to human activities within or on the periphery of the wetland. The study was carried out in the lower Skjern River in Denmark, which consists of 22 km^2 of restored wetlands including lakes, shallow wetlands and flooded wet grassland (Petersen *et al.* 2007; Bregnballe *et al.* 2014). Our objectives were to describe responses of spring-staging dabbling ducks to natural disturbance stimuli before and after the passage of a single person walking on a path along habitat used by these birds. Specifically, we wished to test the hypothesis that Wigeon *Anas penelope* and Teal *A. crecca* (the commonest spring-staging wetland species at the site) responded by flying greater distances to settle after being disturbed by human activities than in response to natural sources of disturbance. Secondly, we sought to find whether these two species responded differently to disturbance soon after having been disturbed by a passing pedestrian, compared to their responses in the absence of pedestrians (see Smit & Visser 1993), for informing policy on future human access to such areas of a restored wetland complex.

Study area and methods

The study area was a section of continuous wet grassland habitat within a much larger wetland restoration complex along the lower River Skjern, west Jutland, Denmark (55°55'N, 8°25'E; Bregnballe *et al.* 2009, 2014). The human activities that in some cases caused disturbance to Wigeon and Teal included anglers walking along the river, cyclists (biking outside the footpath) and noise originating from agricultural activities on adjacent farmland. The behavioural response of dabbling ducks to the controlled disturbance from a pedestrian using the public footpath in the study area was described in Bregnballe *et al.* (2009). The study site could be overlooked from a fixed observation point on a dike (without disturbing the birds) and most dabbling ducks present could see pedestrians on the footpath which runs 450 m along the study site (see map in Bregnballe *et al.* 2009). When undisturbed, dabbling ducks feed throughout most parts of the study area, so we assumed that the entire area offered suitable habitat. A very detailed map of the studied part of the wetland was drawn from aerial photographs, with visible water edges and vegetation features used to divide the study site into a large number of sub-areas. Displacement distances were measured as the distance from the centre of the birds' take-off sub-area to the centre of their landing sub-area. Each displacement distance recorded was then grouped into one of six intervals: 0–50 m, 50–100 m, 100–150 m, 150–200 m, 200–300 m and > 300 m. We observed daytime reactions of Wigeon and Teal to human activity and to the presence of other birds and mammals, during 25 mornings in March and April of 2003 and 2004. The path along the study site was closed to public access during these times to reduce uncontrolled disturbance of the ducks by pedestrians. The public had free access to the path along the study site throughout the day on days when no experiments were undertaken, as well as during the rest of the day after the observations associated with the controlled disturbance had ended. One person acted as the pedestrian whilst a second person, concealed from the birds' view, made behavioural observations from the dike. The behavioural observations were made using binoculars and a telescope and dictated onto a recorder. After the observer had mapped the waterbirds present at the study site, the pedestrian approached the study site, walking at normal speed interspersed by short stops lasting up to approximately 3 min, simulating someone observing wildlife. As soon as the pedestrian was at least 100 m from the study area, they were rendered invisible to the birds because of tall vegetation.

Causes of Wigeon or Teal taking flight (hereafter called "flushing") were grouped into six categories: human (anglers, cyclists elsewhere than on the footpath, farmers), birds of prey, Lapwing *Vanellus vanellus*, other birds (larger than *c.* 100 g, so omitting the smaller passerines), mammals and "unknown". Birds of prey which the ducks always or sometimes flushed from included Osprey *Pandion haliaetus*, Marsh Harrier *Circus aeruginosus*, Hen Harrier *C. cyanus*, Buzzard *Buteo buteo*, Sparrowhawk *Accipiter nisus*, Goshawk *A. gentilis*, Kestrel *Falco tinnunculus*, Merlin *F. columbarius* and Short-eared Owl *Otus flammeus*. Other birds included Cormorant *Phalacrocorax carbo*, Grey Heron *Ardea cinerea*, Spoonbill *Platalea leucorodia*, geese *Anser* sp., Curlew *Numenius arquata* and two gull *Larus* species (Herring Gull *Larus argentatus* and Great Black-backed Gull *L. marinus*). Mammals were Red Fox *Vulpes vulpes* and Roe Deer *Capreolus capreolus* (ducks did flush from deer on occasion). We compared the frequency distribution of the causes of flushing in the non-disturbed situation with the frequency distribution of causes within 15–70 min after the manipulated disturbance by the pedestrian had ended (*i.e.* the human was no longer visible to the birds), using two-sample Z tests to test for differences between these two sets of data for each response category. Only one controlled disturbance event was carried out per day.

Wilcoxon two-sample tests were used to compare displacement distances for flushing caused by human disturbance with those caused by natural disturbances, across each of the six distance categories described above. The natural disturbance category consisted of flushing caused by "birds of prey", "other birds", "mammals" or "Lapwing".

Results

In the flight-response test, Wigeon often flushed without any evident cause, both before and after the controlled human disturbance (26% and 32% of all flushing events, respectively, $n = 93$; Fig. 1a). Lapwing, other birds and birds of prey each contributed 15–26% of flushes, whereas humans (present further away than the public footpath) and mammals together accounted for 8% of the flushes by Wigeon both before and after the controlled disturbance from the footpath. For Teal, birds of prey accounted for 54% of the flushes ($n = 93$) before the controlled disturbance but only 25% after the disturbance (Fig. 1b), whereas other birds accounted for 29% of the flushes both before and after disturbance. The number of flushes attributable to Lapwings more than doubled from 8% to 21% before and after the disturbance event. There were no significant differences (at $P < 0.05$) between the proportions of flushes in each category before and after manipulated human disturbances for Wigeon, but Teal reacted significantly more frequently before the controlled disturbance from the pedestrian than afterwards ($Z = 1.98$, $P = 0.027$; Fig. 1).

Displacement distances for Wigeon and Teal were significantly longer when flushes were induced by human disturbance than when flushes were the result of natural causes (Fig. 2). In the 74% of cases where Wigeon were displaced by natural causes they landed within 50 m of their original

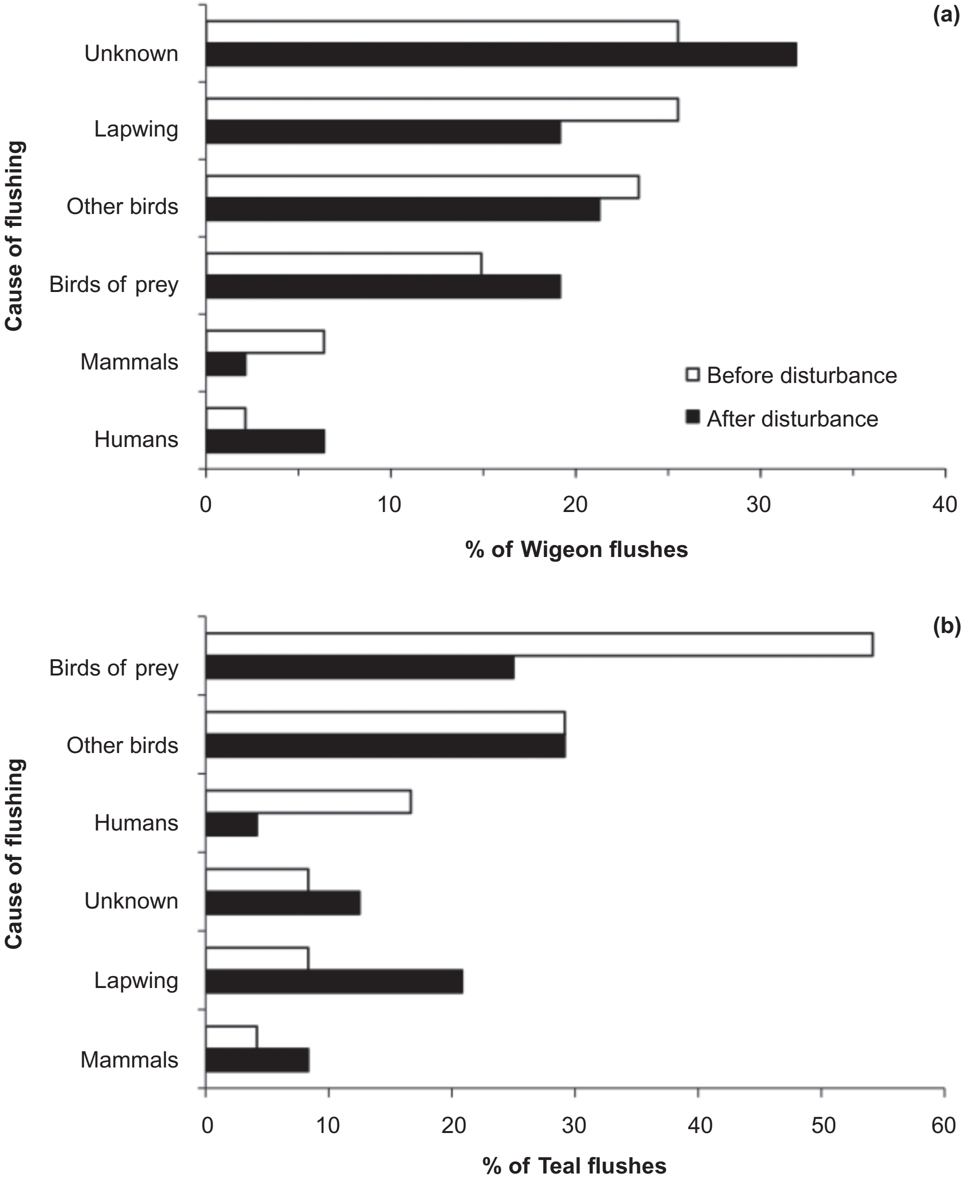

Figure 1. Cause of flushes for (a) Wigeon (n = 93 incidents) and (b) Teal (n = 93) observed at Skjern River, western Jutland, Denmark both prior to and following controlled disturbance by a human walking along a footpath adjacent to the feeding area. Differences in the response of Teal to "birds of prey" before and after the human disturbance were statistically significant (Wilcoxon two-sample test: $Z = 1.98$, $P = 0.027$).

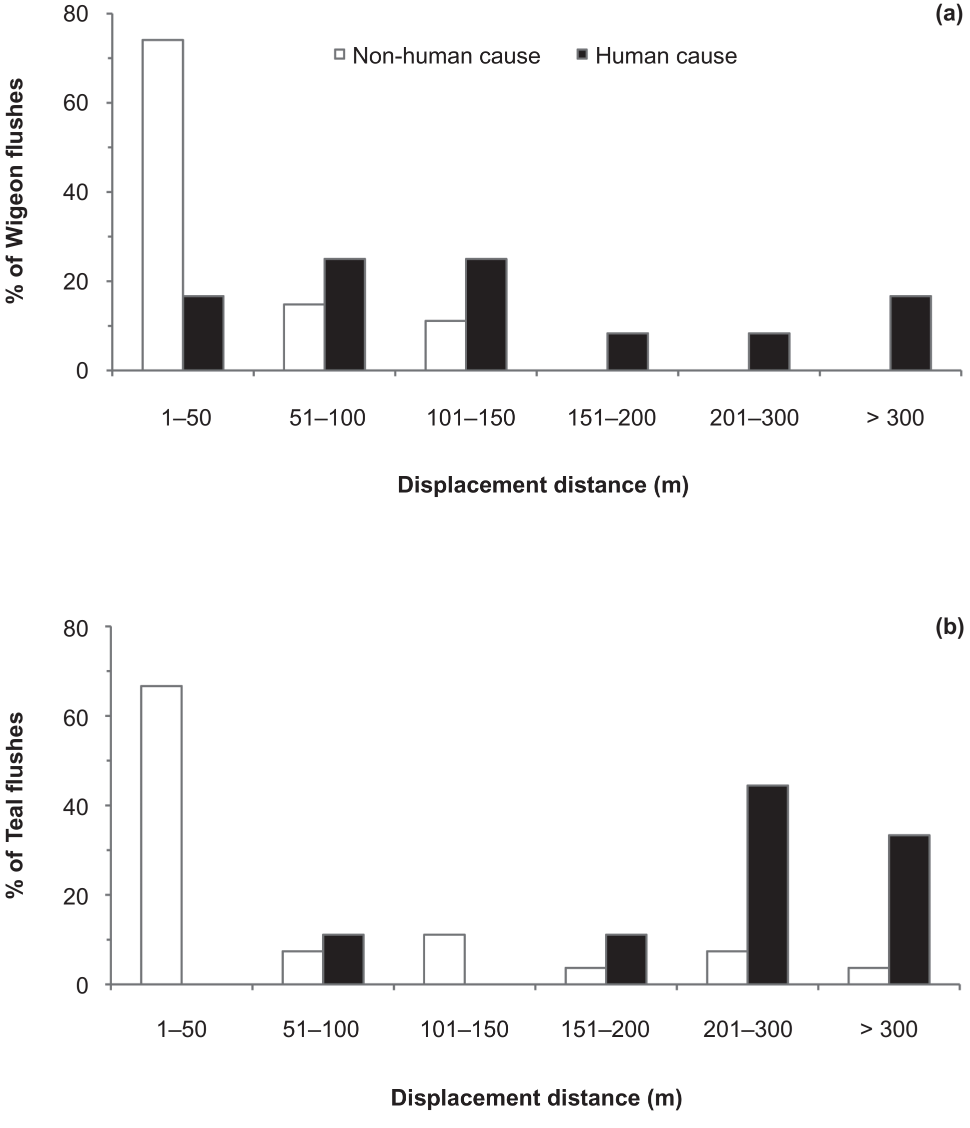

Figure 2. Frequency distributions of displacement distances following flushes induced by human disturbance and from natural causes for (a) Wigeon, and (b) Teal at the Skjern River study site in western Jutland, Denmark. For Wigeon sample sizes were 12 records of displacement distance for flushes caused by humans and 27 records for flushes caused by natural causes. For Teal sample sizes were 9 and 27, respectively. Displacement distances were significantly greater for human disturbance than for "natural" disturbance in both Wigeon (Wilcoxon two-sample test: $U_s = 189.5$, $P < 0.01$) and Teal ($U_s = 199$, $P < 0.01$).

location, whereas they did so on only 17% of the occasions when flushed by human disturbance (Fig. 2a; see figure caption for sample sizes). Wigeon flushed by human disturbance flew > 150 m in 33% of all cases, but flights of > 150 m were never recorded when Wigeon were flushed by natural causes. Similar flight responses were apparent for Teal (Fig. 2b), where 67% of flushes induced by natural causes were short (< 50 m), and flights were always longer than this in response to human disturbance. Long flights (> 200 m) were recorded in > 78% of the cases when flushes of Teal were caused by human disturbance compared to only 11% of the cases when flushes were induced by natural causes. There were also indications that "birds of prey" elicited shorter displacement distances at our study site than human disturbance despite harriers attacking and pursuing Teal. For instance, for Teal 75% of 16 displacement distances caused by raptors were of < 100 m, whereas only 11% of nine displacement distances caused by humans were < 100 m. For Wigeon the proportions were 70% (n = 12) and 42% (n = 10), respectively.

Amongst all 144 observations of Wigeon flushed from all causes combined, 23% were from water, since most active feeding by this species occurred on terrestrial wet grassland. However, 68% of the time they landed on water after being flushed. Of the 83 observations of flushed Teal, 56% flushed from water and 51% landed on water.

Discussion

These results indicated that there was no difference in the response of Wigeon to different sources of disturbance before and after disturbance by a pedestrian, and that Teal were more likely to react prior to such disturbance, which suggests there was no elevated response to particular sources of disturbance after birds were exposed to manipulated disturbance from a pedestrian. The results showed significantly longer flushing distances before resettling after human disturbance (excluding the manipulated disturbance caused by the pedestrian) compared to those generated by all natural sources of disturbance, suggesting both an enhanced energetic cost and possibly also a greater displacement from favoured feeding areas when disturbed by humans compared to other stimuli.

The majority of Teal flushes were responses to birds of prey, other birds and "human activity" (*e.g.* anglers, cyclists). Marsh Harrier and Hen Harrier induced most predator flushes; we observed several attacks on Teal by harriers and both species of harriers attack ducks, despite their established preference for smaller prey (Génsbøl 2004). More specialised avian duck predators such as Peregrine *Falco peregrinus* and White-tailed Eagle *Haliaetus albicilla* were not observed during our observation period, but both species were present in the area. The main stimulus in the "other birds" category was the Great Black-backed Gull, a species observed attacking ducks along Skjern River (J.P. Hounisen, pers. comm.) and a probable explanation for why "other birds" induced flushing amongst Teal. Unlike Wigeon, "Lapwing" accounted for a small proportion of flushes in Teal. This difference may reflect the tendency for Wigeon to feed on land to a greater extent than Teal (Bregnballe *et al.* 2009), where they may be more sensitive to disturbance and perhaps have a lower stimulus threshold, making them more apt to take off in response to stimuli that we failed to detect (Mayhew & Houston 1987). Wigeon often flushed in response to "Lapwing" and many "unknown cause" flushes probably were associated with "Lapwings" where we failed to detect the true stimulus. There may be several explanations for this, including the fact that Lapwing silhouettes are somewhat similar to that of a broad-winged bird of prey and that displaying Lapwings are noisy in spring when their erratic display flights (with many rapid turns and dives) present sudden and unpredictable movements. It has been suggested that birds have evolved anti-predator responses to generalised, threatening stimuli such as loud noises and rapidly approaching objects (Frid & Dill 2002). Secondly, foraging Wigeon were often seen near Lapwings, since both species select for shorter grass swards, whereas Teal remained in shallow waters where they rarely encountered displaying Lapwings. Thirdly, Wigeon occurred in large flocks, whereas Teal often were observed foraging in small groups and flushing probability and flushing distance from disturbance has been shown to be positively associated with increasing flock size (review in Smit & Visser 1993; Bregnballe *et al.* 2009).

Waterbirds are subject to multiple sources of disruption to their daily activities, so responses to a specific locus of disturbance is likely to be a function of the presence and activity of other sources of disturbance and their frequency. The relative importance of any one source of disturbance is likely to be highly site-specific because of the array of disruptive activities to which birds are exposed at a given site. Hence, these findings may not apply to other locations, other times of year, or even to other times of the day. We also conclude that Teal flushes were, to a large extent in this study, restricted to situations where the source of the disturbance posed a threat to the birds, whereas Wigeon seemed to take off more frequently when the source of disturbance did not necessarily appear to pose a threat to the individuals concerned.

In this study, Wigeon and Teal flew significantly farther following human disturbances than after natural disturbances, but sample sizes were small. This was similar to the results presented by Béchet *et al.* (2004), who found that distances flown by spring staging Greater Snow Geese *Anser caerulescens atlantica* were longer after scaring and hunting than after natural forms of disturbances (including raptors and other predators). In our study area most types of human activities that caused disturbance could be characterised as occasional, unpredictable events, such as a sudden loud noise from farming activity, a cyclist appearing where cyclist would not normally appear, or an angler suddenly becoming visible. It therefore seems likely that, given the likely high turnover of individuals during spring staging, such groups of dabbling ducks experience difficulties in rapidly adapting to such unpredictable potential disturbance stimuli in situations where they do not remain long enough to be able to predict the likely mortality risks associated with them.

The energy expenditure associated with escape flights increases with the distance flown and time spent flying (*e.g.* Birt-Friesen *et al.* 1989; Nolet *et al.* 2016). Waterbirds consume around 10–12 times the energy at basal metabolic rate when flying (*e.g.* Mooij 1992 for flying geese), which represents a four-fold increase over the energetic costs of foraging and a six-fold increase compared to roosting. Furthermore, the cost of sudden locomotion requires the rapid attainment of escape velocity and manoeuvrable flight to avoid capture (Blumstein 2003). In addition to the energetic costs of escape, flushed birds lose foraging time and net energy gain during displacement from optimal foraging areas.

Overall, despite small sample sizes, our results suggest that flushes caused by human disturbance are associated with a greater energetic cost than flushes from natural causes due to flight costs. Furthermore, costs of escape may be even higher for Wigeon, since our results showed they tended to land in habitat unsuitable for foraging (water) and consequently have to return to their foraging habitat before resuming feeding. For instance, human disturbance displaced Wigeon and Teal over longer distances before they resettled than was the case following flushes attributable to natural stimuli, and the choice of habitat to which they were displaced (*i.e.* open water) also suggested a greater loss of feeding time, in addition to the greater energetic costs of such a disturbance event when caused by humans. These results clearly show that human activities can have a disproportionate energetic cost for staging waterbirds, in this case during the prelude to breeding. This suggests that if the primary site management objectives are to protect staging waterbirds (for example over strictly amenity interests), then human access should be managed in a sympathetic manner at the site (*e.g.* through the screening of public footpaths and creation of viewing hides) to achieve public access to wetlands and waterbirds without disruption to the birds' normal activities.

On a broader level, it is difficult to judge how likely the energetic costs of human displacement are to extend to influencing the survival and breeding success of the individuals affected. Other studies of waterbirds suggest that these birds may respond more rigorously to disturbance when the foraging costs are lower (*e.g.* Yasué 2006), which may suggest that behavioural responses may not directly reflect the potential fitness costs of human disturbance (see Gill *et al.* 2001 for a broader discussion). Nevertheless, there is abundant evidence that persistent human disturbance to dabbling duck and other waterbirds leads to permanent local displacement that represents a net loss to the "carrying capacity" of this part of the site (*e.g.* Madsen 1998). It is therefore important to establish clear conservation management planning priorities when designing future wetland restoration schemes to recognise the relative importance of protecting such staging waterbird populations in relation to other management priorities for the site after reinstatement. More results from studies of other species than those considered here would further support such development of management priorities and provide potential methods to avoid conflicts between management objectives.

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Photograph: Wigeon flushing, by Niels J.H. Andersen.