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## Impacts of hunting disturbance on waterbirds - a review

Jesper Madsen & Anthony D. Fox

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Waterbird hunting is a widespread activity in wetlands throughout Europe and constitutes one of the most significant sources of disturbance during autumn and winter. The biological evidence for effects of hunting disturbance on the behaviour and distribution of migratory and wintering waterbirds and its possible impacts on population dynamics is reviewed. Most of the literature has been concerned with local effects of disturbance, focussing on quarry geese and dabbling ducks. Comparatively little is known about effects on diving ducks and waders, while there is no direct evidence for impacts at the population level for any waterbird species. Hunting disturbance can cause temporary disruption of normal activities of waterbirds, alter their diurnal rhythms and increase escape flight distances. It can displace waterbirds from preferred feeding and roosting habitats at local or regional level and increase turnover, so that the carrying capacity of a site is not reached. Quarry waterbirds, and those occurring in large in-shore concentrations, such as many dabbling ducks, geese and waders, are potentially most sensitive to disturbance. Hunting disturbance can disrupt pair-bonds and family structures which may affect reproductive output. Evidence is provided that many waterbird populations are limited by winter conditions and that the majority of studied waterbird species lose body reserves during winter. Because hunting disturbance causes under-exploitation of potential feeding grounds where population limitation is considered to occur, such disturbance will, by definition, have an impact at the population level. However, the magnitude of this impact has not been quantified and requires a modelling approach.

*Key words:* disturbance, hunting, waterbirds, population, condition, behaviour, habitat

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Hunting affects waterbird population dynamics as a direct result of the harvest kill (e.g. Anderson & Burnham 1976, Nichols 1991, Ebbinge 1991), but the indirect results of disturbance caused by shooting activity remain controversial. It has proved relatively simple to demonstrate that hunting activity can have an effect on waterbirds, i.e. that shooting activity can affect the behaviour, numbers and distribution of waterbirds using a wetland

area (see reviews by Meltote 1982 and Bell & Owen 1990). However, because most waterbirds are migratory, the impacts of hunting disturbance, i.e. the long-term consequences for a population measured in terms of changes in mortality or recruitment processes, have proved comparatively difficult to demonstrate (Bell & Owen 1990). Many confounding factors other than disturbance affect population dynamics making key variables difficult to



isolate (Cayford 1993), and impacts may only become manifest thousands of kilometres away from the point of disturbance (Davidson & Rothwell 1993).

This review uses scientific publications and reports to evaluate current knowledge of the impact of hunting disturbance on waterbirds. We review a hierarchy of demonstrated effects and impacts, ranging from behavioural and distributional responses to consequences for body condition and, ultimately, survival and fecundity (*sensu* Cole & Knight 1991, Stock et al. 1994). Since it is difficult to demonstrate direct impacts of disturbance on population dynamics, we examine the indirect evidence to support the hypothesis that such impacts occur. Hence, we look for evidence that 1) hunting disturbance causes a significant displacement of birds from potential food resources which would otherwise have been exploited and, 2) waterbird populations are limited by food resources during winter. If populations are primarily limited by factors operating on the breeding grounds, hunting disturbance during autumn and winter is unlikely to exert a major influence on population change. Implicit in these assumptions is the fact that birds face energetic bottlenecks during this period of their life cycle, a feature that can only be measured indirectly by changes in individual body condition. In addition, this review addresses other factors that may impact upon individual survival or fecundity probabilities.

## Behavioural effects of hunting disturbance

### Escape flight distances

The escape flight distance, i.e. the distance at which a bird or a flock of birds takes flight approached by a disturbance stimulus, is often used as a measure of the effect of disturbance. However, the measure is highly variable, depending on the species, flock size, the type, frequency, predictability and previous experience of stimuli, the site and weather conditions (Madsen 1985, Keller 1989, Madsen et al. 1992a, Keller 1992, Smit & Visser 1993).

An increase in escape flight distance in response to hunting has often been claimed, but the evidence is restricted to few controlled studies where distances have been measured before and during the open season or in shot-over sites versus areas not shot-over. Most work has been carried out on geese (brent geese *Branta bernicla*: Owens 1977, Madsen 1988; bean geese *Anser fabalis* and white-fronted geese *Anser albifrons*: Gerdes & Reepmayer 1983; pink-footed geese *Anser brachyrhynchus*: Madsen 1985) while information is very restricted on ducks (dabbling ducks: Arctander et al. 1984) and waders (common snipe *Gallinago gallinago*: Arctander et al. 1984).

Generally, escape flight distances approximately doubled after hunting seasons opened, amongst geese increasing from 150-211 metres to 367-500 metres. In most studies, the controlled stimulus eliciting escape flight was human approach, which indirectly shows that hunting activity has a synergistic disturbance effect, enhancing bird responses to other forms of human activity in the absence of hunting.

### Activity patterns

Usually, waterbirds are shot at in flight and birds not killed fly away from the hunter or dive. However, shooting may affect birds feeding or resting nearby, including non-target species. Their reactions may range from no reaction to escape flight, with intermediate reactions such as increased alertness and walking/swimming away from the hunter.

The disturbance period, i.e. the time it takes for a flock of birds to resume the activity performed before escaping from a source of disturbance, varies according to species and stimulus, and hunting activity can elicit a stronger response than other activities (greater snow geese *Anser caerulescens atlanticus*: Bélanger & Bedard 1989, wigeon *Anas penelope* and mute swan *Cygnus olor*: Madsen et al. 1992a). Stationary shooting punts caused an eight-minute disruption to feeding wigeon (no different from a spontaneous flight), whereas mobile shooting punts pursuing the ducks caused 46 minutes of disturbance, significantly longer than that caused by fishing boats (20 minutes). Wigeon disturbed a second time by a mobile punt took 168 minutes to resume feeding (Madsen et al. 1992a). In protected mute swans, the disturbance period elicited by mobile punts was on average 95 minutes.

The ability of waterbirds to compensate for lost foraging time depends on the energetic cost incurred by the disturbance, measured in terms of the increased flight time and the disturbance period, as well as feeding strategy of the species. Generally, the longer feeding time a species requires to fulfill its daily energy demands, the less able it is to compensate. The wigeon mentioned above spent most of the daytime foraging in autumn and winter, and were thus unable to compensate for lost feeding time, even if only disturbed by one mobile punt per day. They lost up to 25% of foraging time on days with repeated disturbance. By comparison, mute swans spent less time foraging, and compensated for the lost feeding time within the same day (Madsen et al. 1992a). Bell et al. (1991) found that wigeon and brent geese foraging in an estuary outside refuges together lost 14% of the daily feeding time due to disturbance. In the refuge part of the estuary, the birds lost 7% of the foraging time. Furthermore, because access to their inter-tidal feeding resource is already



restricted by tidal inundation, such birds have little opportunity to compensate by increasing feeding time throughout the daily cycle (Mudge 1989, Fox et al. 1993). Likewise, greater snow geese which spend most of the daytime foraging were unable to compensate for time lost to disturbance, especially by low-flying aircraft and hunting (Bélanger & Bedard 1989, 1990).

Hunting activity may modify diurnal activity of waterbirds: in British refuge areas, wigeon mostly feed by day, but are night-time foragers on most sites outside the refuges (Owen & Williams 1976). A similar pattern occurs amongst wigeon in the Danish Wadden Sea (Madsen 1988) and black ducks *Anas rubripes*, mallards *Anas platyrhynchos* and diving ducks in North America (Conroy et al. 1987, Girard 1941, Thornburg 1973). In Greece, undisturbed wigeon, shoveler *Anas clypeata*, pintail *Anas acuta* and coot *Fulica atra* actively fed by day, when teal *Anas crecca* roosted. On shooting days, shoveler and pintail completely stopped feeding, while wigeon and coot continued feeding, although at lower intensity. Some wigeon ceased foraging by day altogether, solely foraging at night (Joensen & Madsen 1985).

## Distributional effects of hunting disturbance

### Local distribution

Local redistribution, i.e. a temporary spatial displacement of waterbirds when hunters are present, not necessarily resulting in an under-use of resources, has been shown for cormorant *Phalacrocorax carbo sinensis* (Madsen et al. 1992b), mute swan (Madsen et al. 1992a,b), snow geese (Burton & Hudson 1975) brent geese (Denson & Murrell 1962, Kramer et al. 1979, Madsen 1988), wigeon (Joensen & Madsen 1985, Bell et al. 1991), black duck (Conroy et al. 1987), Anatidae (Bossenmaier & Marshall 1958, Thomas 1976, Gomes cited in Hirons & Thomas 1993, Gerhard 1994), eider *Somateria mollissima* (Salvig et al. 1994), waders (Meltotte 1980, Gomes cited in Hirons & Thomas 1993), lapwing *Vanellus vanellus* and golden plover *Pluvialis apricaria* (Meltotte 1981), whooper swan *Cygnus cygnus* and curlew *Numenius arquata* (Schneider-Jacoby et al. 1991, Meile 1991).

Several accounts report reductions in waterbird numbers, representing an under-use of local food resources either by comparing ecologically similar areas with intensive shooting to areas with low shooting intensities (Anatidae: Reichholf 1973, Schneider 1986, Frenzel & Schneider 1987, Ziegler 1987, Ziegler & Hanke 1988, Meile 1991, Frikke & Laursen 1994a; wigeon and teal: Madsen 1988) or by comparison of years with different shooting intensities (wigeon: Townsend & O'Connor 1993).

In 18 cases, the number and distribution of birds have been compared before and after reserve creation. In 14 of these, dramatic increases in numbers were reported (Anatidae: Geroudet 1967, Andersson 1977, Jepsen 1983, Owen & Salmon 1984, Frenzel & Schneider 1987, Hirons & Thomas 1993; greylag geese *Anser anser*: Roos & Lindskog 1976, Hirons & Thomas 1993, Rasmussen 1994, waders: Campredon 1979); in the remaining four cases, no effects were observed (Anatidae: Owen & Salmon 1984).

The above studies suffer from the lack of experimental study of disturbance effects and lack of monitoring of confounding environmental variables (e.g. available food stocks). Experimental reserves were established on two Danish wetlands to test whether hunting activity caused disturbance. It was hypothesised that, if hunting caused disturbance, reserve creation would cause a local redistribution and overall increase in bird numbers, especially quarry species. Following four years of base-line observations, refuge positions were changed each year for three hunting seasons, after which permanent refuge areas were established. Local food stocks (mainly submerged vegetation), weather and water levels, hunting pressure and overall population levels were monitored throughout (Madsen et al. 1992a,b,c,d, 1995, Madsen 1995). In both areas, waterbird numbers increased following reserve creation and the highest bird concentrations occurred in the shooting-free zones. Quarry species responded most strongly (by three to forty fold increases compared to base-line years), but some protected species (especially lapwing and golden plover) also increased. None of the local increases could be explained by changes in food stocks, weather or water level conditions or human use of the areas inside and adjacent to the reserves; only in few species could the increases be explained by changes in overall flyway population levels (Madsen et al. 1995).

The consequence of long escape flight distances or increased wariness induced by hunting disturbance as described above, is a restriction of local site use (Owen 1972, Owens 1977, Madsen 1985, Smit & Visser 1993). For example, pink-footed geese staging at a refuge in Denmark during autumn were unable to effectively exploit approximately one third of the refuge grassland area because hunting took place along the borders (Madsen 1980). In some cases, the birds may be able to compensate and use the unexploited resource at times of the 24-hour cycle when human activity ceases or at other times of the season (Owens 1977, Gerdes & Reepmayer 1983, Madsen 1988). However, in other cases this is not possible, either because the resource has dropped in quality or has disappeared at the time of closure of shooting (Madsen 1985, 1988).



## Regional distribution

There have been some attempts to look at the wider-scale effects of hunting disturbance on waterbird distribution, comparing numbers and distribution of birds in relation to regional/national patterns of hunting practises (Tamsier & Saint-Gerand 1981) or refuge distribution (Jepsen 1983, Bell et al. 1991). The results of these studies can, however, be disputed either because they did not take into account the available habitat resources, or because the scale of the habitat areas were too crudely determined to address the problem effectively.

In Britain, Owen & Salmon (1984) showed that during a 23-year period, numbers of dabbling ducks increased significantly in refuge areas but not in shot-over areas. Wigeon numbers greatly increased on reserves and decreased outside. Outside the open season this relationship was not apparent, suggesting that it was primarily disturbance and not improved habitat quality on the reserves that was the cause. The study suggested that the observed developments were due to redistributions. However, it is unknown to what extent improved survival and body condition (which may affect breeding output) of birds using the protected areas contributed to the increase in numbers. In Denmark, the autumn staging population of wigeon was almost doubled following the creation of two reserves; the increase happened within 3-4 years, excluding a general population increase being the main cause but suggesting a redistribution within the northwest European flyway (Madsen 1995).

In geese, progressive protection of feeding areas and ultimately a full shooting ban was followed by a gradual increase in numbers and expansion in range of *Anser* geese in Belgium and the Lower Rhine area in Germany (Meire & Kuijken 1991, Mooij 1991), the rate of increase exceeding the general rate of increase in the overall northwest European wintering population levels. In Denmark, autumn staging populations of pink-footed geese and greylag geese are concentrated on sites with low shooting intensities; outside the shooting season both species have a much wider distribution (Madsen 1982, 1986). Similarly, despite the fact that geese are protected in Italy, they are concentrated in few sites which have some protection from hunting (Perco 1991). Shooting of pink-footed geese in the two major autumn staging sites in Denmark can result in an exodus of almost the entire population to the Netherlands within one day (Madsen & Jepsen 1992, Jakobsen 1993). Similarly, most of the Norwegian greylag geese emigrate southwards to staging grounds in Denmark and the Netherlands prior to or during the first days of the open season, and the early mass-departure is ascribed to the disturbance associated with the hunting (Lorentsen 1988, Follestad 1994).

In golden plovers and curlews staging in Denmark, Møltøfte (1981) described a differential distribution in

spring compared to autumn; in autumn, proportionally fewer birds occurred in areas with high shooting intensity compared to areas with no or moderate shooting intensity. In other species of waders, there was no clear relationship.

## Turnover

The number of birds present in an area is obviously determined by the numbers immigrating and emigrating at any one time. Both these parameters are affected by intrinsic (e.g. the food resource, predation risk) and extrinsic factors (e.g. the quality of known sites further along the flyway), but together they produce an observed rate of turnover amongst birds using a site. If we assume stable population size and regular duration of migration periods between years, the most important parameter affecting the number of birds using a site is the average length of stay of individuals at that site (Thompson 1993). Whilst assessment of the mean length of stay is difficult (e.g. requiring intensive capture/recapture programmes), daily counts provide phenology data which enable calculation of total number of bird days at a site. This provides an indirect measure of the effects of disturbance on mean length of stay.

Three papers document prolonged staging periods following refuge creation, based upon phenology curves and the numbers of bird days (Anatidae: Geroudet 1967, dabbling ducks and waders: Madsen et al. 1992c,d). In the Danish experimental reserves, some spring- and autumn-staging migrants have started to overwinter. While the numbers of birds grew in the two study sites, there were no concurrent reductions in neighbouring staging areas. This suggests that, rather than 'draining' birds from adjacent areas, increases were due to the cumulative effect of increasing numbers of birds prolonging their stay, hence birds were 'captured' by the refuges and 'lost' from areas farther down the flyway (Madsen et al. 1995).

While increases in turnover can be demonstrated as a result of hunting disturbance, the scale of this effect is more difficult to determine. How many birds are lost to a site as a result of disturbance relative to the number actually killed? By using a multifactorial simulation model, Frederick et al. (1987) attempted to describe lesser snow goose *Anser caerulescens caerulescens* use of refuge areas, based on many parameters using data gathered from real-life situations. Data input to the model included food availability, numbers of geese, feeding behaviour, energetics and migration patterns, as well as details of human hunting activities, although some of these parameters were not derived empirically. The results of the model showed that increasing hunting activity not only increased the kill, but induced greater numbers of geese to move out of the refuges to other sites on the basis of re-



duced feeding efficiency caused by disruption from the hunting activity. The main conclusion from the work was that the direct effect of hunting mortality was far less important in reducing numbers within a managed area than the associated disturbance which greatly enhanced emigration. Similarly, field investigations of the effects of hunting on mallard in Germany showed that out of an initial 650 ducks, 256 were shot during one day of intensive shooting, but only 100 birds remained in the lake system, implying that 300 ducks emigrated as a result of hunting disturbance (Jettka 1986). In one of the Danish experimental reserves, the annual hunting kill of widgeon was ca 3,000, compared to an increase in peak counts of more than 21,000 after creation of refuge areas (Madsen et al. 1992a, 1995).

### Species-specific sensitivity to disturbance

Outside the breeding season most waterbird species exhibit ecological characteristics which are reflected in their distribution, food choice and behaviour, and which have implications for the sensitivity of each species to disturbance. It is therefore important to be able to determine the differential vulnerability to disturbance of the different species.

Bell & Owen (1990, based on Mayhew 1988) used the proportion of the 24 hours a species has to feed to meet its energetic demands as a prime indicator of vulnerability, which seems plausible as birds which have to feed much, e.g. widgeon, have less time to compensate for disturbance. Species with distributions restricted to the intertidal zone were also classified as vulnerable, because this is the zone where hunting is most prevalent and where tidal inundation of feeding areas may further restrict access to feeding opportunity.

Madsen & Pihl (1993) devised a multifactorial classification of sensitivity of wildfowl and coot to disturbance, based on their potential risk of being affected by disturbance. From this analysis the following species were regarded as potentially most sensitive to disturbance: whooper swans and Bewick's swans *Cygnus bewickii*, geese (all species), dabbling ducks (all species except mallard), pochard *Aythya ferina*, tufted duck *Aythya fuligula* and scaup *Aythya marila*. Generally, these species stay close to the coast or inland, and are concentrated, mostly in relatively large flocks. Most are herbivorous and are popular quarry species, except whooper and Bewick's swans which are protected and often feed on arable land in isolated flocks, hence making them less susceptible to hunting disturbance. Larger diving ducks and sawbills were regarded as being the least sensitive.

Generally, quarry species are the most sensitive to hunting disturbance (Madsen et al. 1995). However, as protected species often mix on the roost or feeding grounds with quarry species, these also suffer disturbance (Madsen 1988, Meile 1991, Madsen et al. 1992a,b, 1995, Schneider-Jacoby et al. 1993).

### The scale of the problem

Hunting of waterbirds is a popular recreational activity; in Europe and the Mediterranean basin, 10-15 million ducks and geese are shot annually by approximately 3.2 million hunters (Scott 1982). However, shooting is only one of many human activities which may cause disturbance to waterbirds and it is relevant to judge the importance of other sources as well. Furthermore, whilst other activities operating in isolation may not be as disturbing as hunting, the effects of multiple disturbance from different sources can have a synergistic or cumulative effect on birds. All sources of disturbance have the same net effect: the presence of human activity denies access to resources (be it loafing, sleeping, feeding or other areas used by waterbirds) and this may reduce exploitation rates below those which would be attained in the absence of such activity. In this respect, all disturbance activities can be considered to equate to net habitat loss.

Few field studies have quantified the intensities, distribution, phenology, diurnal patterns and hence the potential disturbance effects of the various human activities operating in areas used by waterbirds. In two Danish coastal wetlands of international importance for waterbirds, Madsen et al. (1992a,b) found that hunting and fishing were the most frequent human activities during the open season, whereas leisure activities, such as boating, windsurfing and beach walking, were primarily confined to the summer period. In autumn, fishing gradually stopped, while hunting continued whilst quarry waterbird species were present. Hunting took place in the core feeding areas of the waterbirds, i.e., in shallow water zones with submerged vegetation or in adjacent marshes, while fishing was mainly restricted to deeper water, outside core waterbird feeding areas. In intertidal areas, beach activities, including bait digging, are more frequent and year-round (e.g. Kirby et al. 1993, Laursen 1982, Salvig et al. 1994). However, hunting activity was under-represented in those studies, because most hunting takes place at dawn and dusk (e.g. Frikke & Laursen 1994a,b).

In the non-refuge part of the Exe Estuary in southern England, a variety of human activities occurred throughout the winter season. Free-roaming dogs, bait diggers, windsurfers and walkers were the most frequent potential disturbance sources; however, in terms of the frequency and duration by which brent geese and widgeon were dis-



turbed, hunters represented quantitatively the most important source of disturbance (Bell et al. 1991).

In the Greek Amvrakikos wetlands, hunting was the most frequent winter activity, followed by boat fishing (Joensen & Madsen 1985). Most hunting took place from the shore during dawn and dusk, but motorised punts were also used.

At Lake Constance (Germany/Switzerland) waterbird hunting is only one of several human activities causing disturbance to wintering waterbirds, of which canoeing, boating, wind-surfing and walking on the lake shores, together with hunting, are the most disturbing (Schneider 1986, Frenzel & Schneider 1987, Bauer et al. 1992, Schneider-Jacoby et al. 1993).

The available information is too patchy to allow an extrapolation of the above studies to a wider European scale. There is a great need for more information about the distribution of human activities and their spatial and temporal overlap with roosting and feeding areas of waterbirds in wetlands. A comparison of the disturbance effects of hunting versus other activities can only be achieved effectively against such a background. Judging from the few examples available, hunting activity seems to be more disruptive in terms of interruption of feeding activity than other studied surface activities, comparable only with the effects of low-flying aircraft (Bélanger & Bedard 1990, Bell et al. 1991, Madsen et al. 1992a). The increase in escape flight distances of geese and dabbling ducks during the open season indicates that hunting activity is the critical source of disturbance affecting the strength of that response, which in turn implies that in the absence of hunting, escape flight distances would be shorter.

## Impacts on body condition, survival and reproduction

Support for the hypothesis that waterbird populations are limited by factors away from the breeding areas can be derived from two sources; firstly, from evidence of population limitation during winter and secondly, from identification of particular energetic bottlenecks in the life cycle of the animals which offer clues to the likely role of key factors affecting survival and reproduction.

## Migration and regulation of populations

The mobility of birds facilitates their exploitation of different habitats, including some unsuitable for reproduction. The relative availability of resources remote from a populations' breeding area may therefore affect overall breeding success and survival. Waterbirds exhibit a range of migratory strategies adapted to different circumstances (e.g. Alerstam & Högstedt 1982).

Several studies suggest that wintering habitat limits wader and duck populations. Loss of wintering habitat has been shown to reduce the numbers of overwintering waterbirds (e.g. Teesmouth in the UK, Evans 1980), and reductions in wintering dunlin *Calidris alpina* numbers in the UK have coincided with loss of mudflat habitat due to *Spartina* encroachment (Goss-Custard & Moser 1988). Baltic-breeding eider and tufted duck numbers varied with changes in winter food supply (Pehrsson 1978, 1984), and studies suggest that mallard overwinter mortality determines breeding population size in the United States (Anderson & Burnham 1976, Bergan & Smith 1993, although Reinecke et al. 1987 and Blohm et al. 1987 do not support this suggestion) and in the UK (Hill 1984). Cavity-nesting goldeneyes *Bucephala clangula* are primarily limited by availability of nest sites, since provision of artificial nestboxes initially increased breeding numbers. However, when supplied with an over-abundance of artificial nest sites, above a certain threshold, the population varied in a way unattributable to any factor related to breeding population or habitat (Fredga & Dow 1984). Finnish studies of dabbling duck assemblages show that most species are not in competitive equilibrium, since densities are well below potential carrying capacities of the environment in most years (Pöysä 1984).

Factors influencing bird numbers using an area may vary in time and space, which confounds attempts to understand such processes at a single point in time. For example, the grey plover *Pluvialis squatarola* increase on UK estuaries was attributed to factors outside of wintering areas, where there was a sequential expansion in numbers using different wintering sites. Preferred habitats were already "filled" prior to the increase and showed no change during the period of increase (Moser 1988). Similarly, protection from hunting of Greenland white-fronted geese *Anser albifrons flavirostris* at Wexford in south-east Ireland resulted in a rapid increase in wintering numbers, which has since stabilised at a higher level, perhaps restricted by food availability (Fox et al. 1994). Other populations, such as Baltic-breeding long-tailed ducks *Clangula hyemalis* (Pehrsson 1984) show no relationship with winter food supply.

Bell & Owen (1990) extensively reviewed the literature and concluded that there is supportive evidence for the view that "waterfowl populations are limited by the carrying capacity of their wintering and staging areas rather than by resources on the breeding areas" and Meltofte (1993) concluded that there was very little evidence that wader population regulation occurred on breeding areas. Exceptions, however, may be those species of waders and wildfowl that predominantly use artificial habitats, or colonial nesters, like the eider.



## Seasonal changes in body mass

Whether or not waterbirds are limited by non-breeding habitats, they may become more susceptible to the effects of disturbance at certain periods in the annual life cycle. Most waterbird species undergo regular patterns of body mass increase and decline throughout the course of their annual cycle, reflecting the accumulation and use of body stores and reserves (*sensu* van der Meer & Piersma 1994) in response to seasonal changes in the present and future requirements of the individual (e.g. mallard: Owen & Cook 1977, dunlin: Pienkowski et al. 1979, teal: Fox et al. 1992, brent goose: Ebbinge 1989, barnacle goose *Branta leucopsis*: Owen et al. 1992, knot *Calidris canutus*: Piersma 1994). From these patterns, it is possible to determine periods of greatest potential stress (i.e. when reserves are being depleted or stores need to be accumulated rapidly) and hence pin-point periods when enhanced energetic expenditure (through flight from disturbance) or reduced availability (through denial of access to food resource) may prove critical.

## Periods of low body nutrient levels

Waterbirds generally exhibit lowest body mass in late winter and in summer immediately after hatching of young (e.g. Owen 1980), although the latter need not concern the discussion here. Most species of waterbirds are able to maintain a positive energy balance (and hence are able to lay down body stores) until the end of December, taking advantage of the food resource along the flyway to ultimate wintering areas. However, after December, most species show a decline in body weight which in at least two studies has been shown to be the result of a lack of sufficient food availability and was hence a consequence of birds depleting a stored resource accumulated earlier in the season (Owen et al. 1992, Kestenholz 1994). Furthermore, all the descriptive wader studies argue that the mid-winter peak in body mass reflects an accumulation of nutrient stores to overcome subsequent food shortage after this time of the year (Dick & Pienkowski 1979, Davidson 1981, Johnson 1985). The late winter period is particularly critical for waterbirds, since this marks the time when body mass has been depleted during a period of net energy loss, but which may be further exacerbated by factors such as unusually severe weather conditions which has been shown to significantly increase the recovery rates of ringed Anatidae and waders (Baillie et al. 1986, Ridgill & Fox 1990). Since body weights may reach very low levels at this time, and maximal foraging efforts fail to maintain condition during these periods, further reductions in foraging efficiency and/or enhanced energetic costs caused by disturbance are likely to further stress individuals at such times. Body mass may then hit its lowest level before the upturn in spring food avail-

ability enables recouping of lost stores (e.g. Owen et al. 1992).

An alternative explanation is that mid-winter weight loss is adaptive, a hypothesis supported by studies of the weight dynamics of captive birds fed *ad libitum* (Reincke et al. 1982, Perry et al. 1987). However, whatever the cause, the reduction in body stores still inhibits the ability of the individual to meet enhanced energetic demands, as in the case of severe weather or elevated levels of disturbance.

These periods of lowest nutrient reserves may be periods of sensitivity for some species, and whilst mass starvation events are rare, many individuals approach critical levels of reserve depletion in the absence of adequate food supplies. In a very few cases, dramatic mass starvation events have been described for some diving ducks species experiencing severe weather very late in the winter, the result of a combination of food shortage and extra energy demands (e.g. eiders: Wrånes 1988; pochard and tufted ducks: Suter & van Eerden 1992; waders: Piersma 1994). During severe weather in March 1986, more than 20,000 birds starved in two studied areas of Switzerland and The Netherlands as a result of unusually cold weather encountered during the return spring migration when food stocks were low (Suter & van Eerden 1992). Late winter hunting disturbance in wintering areas (German and Swiss lakes) may contribute to exhaustion because birds are denied access to foraging areas and/or because of increased energy expenditure (Meile 1991). Similarly, there are documented cases of widespread starvation of waders, also most frequently as a result of the onset of hard weather late in the winter period when stores are at their lowest (e.g. Davidson & Evans 1982).

## Accumulation of stores

Waterbirds also accumulate body stores to meet anticipated future needs, as for example to obtain enough fuel stores to fly successfully between staging areas of suitable habitat over terrain which may be hostile in terms of high predation risk or poor feeding opportunity. Waterbirds must also store nutrients in spring in preparation for investment in reproductive effort, especially when many long-distance migratory waterbird populations breed in areas where food may be extremely scarce prior to egg-laying (as is the case for most arctic and northern breeding waders and Anatidae). Hence the opportunity for periods of rapid nutrient accumulation (at least in undisturbed situations) also has critical consequences for the fitness of the individual.

Hunting disturbance may affect the acquisition of nutrient stores in two major ways:

- Denial of access to best feeding resources: Birds subject



to hunting pressure may be displaced from areas of highest feeding profitability as a result of the associated disturbance, as has been shown for the wigeon, which respond by movement into improved feeding opportunities after the closure of the season (Mayhew & Houston 1989) or in the absence of hunting disturbance (Madsen 1988). Unless birds can compensate for this loss of feeding opportunity, the reduction in food intake rate below the level in the absence of hunting disturbance must have fitness consequences.

- Loss of feeding opportunity and the extra energetic costs of disturbance: Owens (1977) showed that disturbance to brent geese caused them to fly 1.7% more and feed 3.5% less than in the absence of disruption. These differences may appear small, and may easily be recouped by faster intake rates, sacrificing trivial activity or extending the feeding period (such as feeding at night). However, flying is energetically costly (approximately 12-15 times basal metabolic rate compared with 1.4 times for resting in dabbling ducks, Wooley & Owen 1977) and in situations where tide, daylight, predation risk or other factors limit access to food resources, the effects of these restrictions may be considerable. Indeed, White-Robinson (1982) calculated that disturbance to brent geese increased their net daily energy expenditure by 31%, similar to the results of Bélanger & Bedard (1990) for greater snow geese. Several other authors have also used energy budgets to assess the impacts of disturbance (see Keller 1995).

Evidence for the ultimate impact of these effects on the individual are lacking. In a study of the mallard, Watmough (1983) showed that recreational disturbance increased the daytime energy expenditure by 20%, but since the ducks spent most of the day loafing, this was unlikely to have any overall effect. Indeed, the author argued that the birds would be unlikely to stay within the area if they failed to attain the necessary energy balance at the site. Birds will show a range of responses to compensate for lack of feeding opportunity and the range of responses makes the study of the effects of disturbance difficult to interpret. Waterbirds will often feed at night when disturbance is much reduced, to compensate for feeding in a situation where predation risk may be high during daylight. Owen & Williams (1976), for example, showed that wigeon fed by day on sites which were undisturbed, but in non-refuge areas the same species remained on inaccessible undisturbed refuges and fed only at night. Despite this, increasing the need to feed under cover of darkness may enhance predation risk, so that remaining in an area subject to hunting and maintaining an energy balance may carry a survival cost to the individual. Unfortunately, relatively few studies have adequately addressed the effects of disturbance on a 24-hour basis.

Birds may also increase their feeding rates if the time they are able to spend feeding is reduced in some way. Oystercatchers *Haematopus ostralegus*, for example, can modify their intake rates by reducing search and handling time to accommodate up to 33% reductions in feeding time (Swennen et al. 1989), although these results were obtained from caged birds and may not be directly applicable to natural situations because this experiment obviously did not consider the role of predation risk on the part of the study animals.

## Stores for migration

Flight between wintering and summering areas requires fuel which is usually stored in the form of body fat in waterbirds, accumulated by feeding on appropriate high energy foods and stored within the body in deposits readily available for use en route during migration (e.g. Davidson & Wilson 1992, Evans 1992, Piersma 1994). Birds may use a series of staging areas en route to ultimate breeding areas, and migration strategies of some populations have evolved specifically to exploit such a chain of stopping-off sites for 'refuelling'. Loss of such sites along a migration corridor may then have severe implications for these species (e.g. Evans & Davidson 1990, Evans et al. 1991).

Although there have been few direct studies relating fat storage to migration survival, evidence from studies of birds embarking upon migration show that those in poor body condition are less likely to survive than those in better condition (barnacle geese: Owen & Black 1989, knot: Davidson & Wilson in press). However, there is considerable circumstantial evidence that losses on migration amongst quarry species correlate with population size, and evidence from several studies of non-passerine birds suggests that migration mortality is an important factor in these populations (Owen & Black 1990).

## Impacts on reproduction

Most waterbird species lay eggs which are large and energy-rich relative to body size and have relatively long incubation periods (Alisauskas & Ankney 1992, Krapu & Reinecke 1992). Both traits are considered to have evolved to enable the precocial young to hatch in an advanced state of development where they can rapidly locate their own food and avoid predation without high levels of investment from the parents. Often the female incubates the clutch alone, so as well as obtaining the nutrient stores for egg production, she must store nutrients to sustain her through a prolonged incubation period as well. These life history traits impose severe demands on the females of long-distance migratory waterbirds during the prelude to breeding which may represent bottlenecks



in the annual cycle of waterbird populations (Fox in press).

Studies have shown that larger forms such as swans and geese may accumulate nutrient stores throughout the winter (in particular in the form of fat and protein stores) in preparation for migration and ultimately for breeding (Alisauskas & Ankney 1992, Krapu & Reinecke 1992). However, many smaller forms depend upon a much more rapid accumulation of stores in spring (Ebbinge 1989, Piersma 1994), making them more vulnerable during this period.

Madsen (1995) demonstrated the impacts on subsequent reproductive output in pink-footed geese subjected to disturbance during the spring migration period. These birds failed to accumulate nutrient stores as well as those not disturbed using the same area and subsequently produced less young. Although these impacts were demonstrated on spring staging areas, it is likely that mid-winter depletion of reserves, or the failure to attain critical spring levels of nutrient stores prior to migration to breeding areas may affect reproductive output in waterbird species depending on endogenous stores for successful breeding attempts.

Many dabbling duck species derive much of their protein stores for reproduction from the breeding areas (Krapu & Reinecke 1992), because protein sources are usually abundant in ultimate nesting areas. The same may be true of the *Aythya* and other small diving duck species, but in long-lived species, such as the eider, protein stores are accumulated prior to nesting and transported to the breeding areas for investment in egg formation just as in geese and swans (Krapu & Reinecke 1992). However, most studied duck species accumulate fat stores in areas far from their breeding grounds for investment in reproduction, such that any factors reducing their ability to acquire stores may also affect subsequent nesting success. Unfortunately, there have been no studies of the effects of any form of disturbance on the accumulation of adequate fat stores of ducks and its consequent influence on fitness (in terms of reproductive output or survival). This remains a major research priority for the future.

Such investigations as have taken place also support the hypothesis that shorebirds carry protein stores for reproduction in their flight musculature to the breeding areas (e.g. Davidson & Evans 1988, Piersma 1994).

In conclusion, hunting disturbance is likely to have its greatest impact on survival during the late winter period when body reserves reach their lowest point. Disturbance is most likely to have its greatest impact on breeding output during the subsequent recovery stage, when waterbirds exploit increasingly nutritious feeding resources to restore condition and accumulate stores in preparation for long-distance migration and ultimate breeding.

## Break-up of pair-bonds and social units

Some species of waterbirds show complex social structure, where association with a mate (e.g. gadwall *Anas strepera*: Paulus 1983) or extended family groups (especially amongst long-lived species, e.g. geese: Boyd 1953, Warren 1994) enhances social status and hence access to the best feeding opportunity (Hepp & Hair 1984). Early pairing in mallard confers adaptive advantages on both partners, giving the female protection during pre-breeding nutrient acquisition and ensuring that the male can guard his mate during the prelude to breeding (Rohwer & Anderson 1988). Since the nutritional status of female mallard is known to affect her reproductive success (Krapu 1981), the presence of an associated male has direct consequences for her reproductive output. Similarly, paired gadwall displaced lone birds, giving females access to the best feeding opportunities during the late winter period, well before departure for ultimate breeding areas (Paulus 1983, 1984).

Duck pair-bonds tend to be of relatively short duration, although there is accumulating evidence for some between-year mate fidelity (e.g. mallard: Mjelstad & Sætersdal 1990, gadwall: Köhler et al. 1995 and wigeon: C. Mitchell pers. comm.). Geese and swans tend to pair for life, and annual divorce rates in undisturbed situations are low (e.g. 2% or less in protected barnacle geese, Owen et al. 1988, Black & Owen 1995). There is a cost to separation from an established mate in studied populations, since a bird losing its mate had an 8% probability of successful breeding in the year following the loss, compared with 21% amongst geese remaining with their partners (Owen et al. 1988).

Radio-tracking studies of Canada geese *Branta canadensis* showed that hunting reduced cohesion amongst family units and thereby increased mortality (Bartelt 1987). Snow geese also showed greater rates of family disintegration as a result of hunting disturbance which in turn reduced survival of young (Prevett & MacInnes 1980). Amongst the non-hunted population of barnacle geese, 'orphaned' goslings which had lost parents and siblings suffered harassment from other flock members, were denied access to good feeding opportunity and showed reduced survival compared with young remaining in family units (Black et al. 1992).

These studies suggest that any factor affecting the pair bond or other social groupings may affect the survival or reproductive potential of the members, especially if this disruption continues into spring. Since some studies have shown that disturbance can make it more difficult for pairs or families to remain together, this factor may have an important role to play in reducing survival and reproduction in hunted populations. Indeed, Owen et al. (1988) suggested that disturbance, especially hunting disturbance in autumn, was responsible to a large extent for the



lack of persistent pair and family cohesion in some North American goose populations (e.g. Jones & Jones 1966, Craven & Rusch 1983).

## Conclusions

The review of case studies investigating the effects of hunting disturbance outlined above has shown that the presence of hunters in the vicinity of waterbirds modifies the distribution and abundance of those birds in space (e.g. movement away from heavily hunted feeding areas) and time (e.g. faster turnover at a staging site). The degree to which this modification occurs also varies in time and space, modified by the difference in behavioural trade-offs birds may make between feeding opportunity and predation risk (see review by Lima & Dill 1990). These factors also vary in time and space, as for example during severe winter weather (an example of an unpredictable factor) or during the pre-breeding acquisition of nutrients required for reproduction (a more regular and predictable feature of the life history). Nevertheless, from the review of the available material, the conclusion must be that the net effect of hunting disturbance is to reduce the potential of a site to support numbers of waterbirds to a level below that which would be achieved in the absence of hunting disturbance. Hence hunting disturbance (as is the case with any other form of disruption to natural patterns of waterbird exploitation of a site) reduces the capacity of a site below that which is potentially available.

This review has shown the considerable bias existing in the current literature with regard to coverage of the subject of hunting disturbance (Table 1). Much emphasis has been placed upon the study of quarry geese and dabbling ducks, to the neglect of protected species, waders and diving ducks. The focus has also been placed on studies of the local effects of hunting disturbance, which are relatively easy to demonstrate. However, we still understand little about the direct impact of such disturbance at the population level.

The review does, however, provide evidence to support the hypothesis that many waterbird populations are lim-

ited by conditions prevailing in winter. Because we can demonstrate local and even regional effects from changes in hunting disturbance, we conclude there is reason for concern that hunting disturbance has an impact at the population level.

It can be argued that hunting disturbance cannot be a serious factor impacting on population levels of waterbirds in the Western Palearctic, since many species have recovered in numbers in recent years (e.g. Rose & Scott 1994). The increases, at least in geese, however, have been attributed mainly to improved protection from hunting (Ebbinge 1991). It is known for many species that the overall kill has declined in recent years (Ebbinge 1991, Noer et al. 1995), but there has been no assessment of the apparently secondary impact of the reduction in disturbance associated with this trend.

We still know little about the potential magnitude of the impact of hunting disturbance. Unless we are able to structure complex experimental work, there appears little scope for empirical quantification of its scale. The example of Norwegian-staging pink-footed geese (Madsen 1995) remains one of the few such studies able to demonstrate that any form of disturbance has a direct impact on an individual's reproductive success. However, it still remains to be resolved as to how this impact is expressed at the overall population level. Furthermore, this is a highly specific situation; a small goose population with few stopover sites. Therefore, it is unlikely that this approach can be used as a model for looking at commoner species with wider distributions and more complex interactions.

If we are ever to progress in this field, it is vital that modelling be employed to assess the potential scale of impacts of hunting disturbance, backed by good empirical data to input as model parameters. For instance, what will be the effect of large-scale implementation of reserve networks (such as those described from Denmark) on the overall wintering distribution of birds along the flyway? Using existing data from the experimental reserves, modelling of the effects of changes in turnover is already a possibility. Furthermore, mate loss may appear trivial in the population dynamics of an organism, but data exists

Table 1. Summary table of the number of literature references to demonstrated effects and impacts of hunting disturbance on waterbirds.

Effects/impacts	Cormorants	Swans	Geese	Dabbling ducks	Small diving ducks	Large diving ducks	Waders
Increased escape distance			4	2			1
Modification of behaviour		1	2	8	1		
Local re-distribution	1	3	4	7	2	1	4
Local under-use of habitats		1	4	18	2		2
Regional under-use of sites		4	2			1	
Impacts on reproduction/survival			(2) <sup>1</sup>				

<sup>1</sup> Refers to break-up of pair-bonds.



on the costs (in terms of reproductive output) of mate loss and repairing. It is therefore feasible to explore the consequences of this at the population level, based on simulated and observed levels of occurrence, to assess its impact.

From a management point of view, the wealth of empirical data on the effects of hunting disturbance have proved valuable for site management (e.g. establishing buffer zone widths from escape flight distances). However, with increasing emphasis on international conservation and management planning organised at the population flyway level, international collaboration under legislation and conventions require a more strategic, coordinated approach to management of hunting disturbance. The challenge for the future is to develop population models which identify specific bottlenecks in the annual life cycle of waterbirds. Hunting disturbance can then be set in such a framework, establishing its relative influence and geographical distribution in order to develop international management policies.

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