

Kleptoparasitism as an important feeding strategy for migrating Wigeon *Anas penelope*

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Abstract

This study investigated Wigeon *Anas penelope* feeding strategies adopted at two wetlands in response to differing macrophyte communities, water levels and levels of disturbance. Wetland I contained a diverse macrophyte community dominated by Beaked Tasselweed *Ruppia maritima* in shallow areas and stoneworts *Chara* sp. in deeper water. Wigeon did not feed on the *Ruppia maritima* but kleptoparasited Coot *Fulica atra* foraging on *Chara*. In this case, kleptoparasitism was related to food quality, with *Ruppia maritima* having lower nutritional value than *Chara* which contains high quantities of easily digestible non-structural carbohydrates. Thus Wigeon ignored an available but low quality food source in favour of kleptoparasitising Coot to obtain higher quality *Chara*. Wetland II had abundant food resources dominated by Spiral Tasselweed *Ruppia cirrhosa* in both shallow and deeper areas but hunting was permitted, causing shoreline disturbance to feeding Wigeon. Before the hunting season, Wigeon fed primarily in single species flocks in shallow water using pecking and head-dip feeding methods. When the hunting season opened, those Wigeon remaining on the site moved to deeper waters and fed exclusively by kleptoparasitising Mute Swans *Cygnus olor*. Wigeon must feed for most of the day to meet their energy requirement and this study shows that kleptoparasitism is one of the strategies that they use to maintain food intake rates under different foraging constraints.

Key words: *Chara*, feeding ecology, feeding depth, hunting disturbance, *Ruppia*.

Flocks of the strictly herbivorous Wigeon *Anas penelope* use autumn stopover sites in Danish coastal wetlands from September–November, to feed and fulfil their energetic needs, before continuing their migration to wintering areas in western Europe. Wigeon must forage for 10–14 h each day,

depending on food quality, to meet their energy requirements (Owen & Thomas 1979; Mayhew 1988; Madsen 1988) and therefore are reliant on relatively undisturbed wetlands with good feeding opportunities.

Many wetlands are, however, not ideal as feeding areas for Wigeon, because of the

relatively low food availability and quality of the vegetation, and because of human recreation disturbing the birds at these sites. When foraging on submerged vegetation, Wigeon are dependent on very shallow water since they cannot reach food more than 31 cm under water (Pöysä 1983). Shallow areas of Danish coastal wetlands are often dominated by Beaked Tasselweed *Ruppia maritima* and other macrophytes of low nutritious value, whereas high quality food such as Common Stonewort *Chara vulgaris* is primarily found in deeper areas out of reach of Wigeon (Moore 1986; Santamaria *et al.* 1996; Holm 2002; Holm & Clausen 2006; Fogarasi *et al.* 2008). Furthermore, shallow areas with high food availability are most frequently in near-shore areas where the risk of human disturbance, for instance from hunting and wind surfing, is the greatest. Such human recreational activities often have an adverse effect on Wigeon and other waterbirds, because they perceive humans as potential predators and may respond to humans by a reduction in use of optimal feeding and roosting areas (Schulz & Stock 1993; Gill *et al.* 1996; Madsen 1998; Beale & Monaghan 2004; Finney *et al.* 2005).

This study investigated Wigeon feeding strategies adopted at two wetlands in response to differing macrophyte communities, water levels and levels of disturbance, to determine the extent to which Wigeon exhibited the ecological plasticity to adapt to these factors. In particular, the extent to which they used kleptoparasitism (*i.e.* the interspecific theft of procured food, *sensu* Bailey & Batt 1974; Brockmann & Barnard 1979) was assessed.

Methods

Study sites

The study sites were two brackish lagoons, Agger Fjord (Wetland I: 56°45'N 8°14'E, 3.17 km²) and Harboør Fjord (Wetland II: 56°38'N 8°10'E, 1.95 km²) in western Denmark. Both are designated internationally important areas for water birds in accordance with the Ramsar Convention and the EU Bird Protection Directive. At Wetland I, *Ruppia maritima* and Fennel Pondweed *Potamogeton pectinatus* are found in the shallowest water. In deeper areas, out of reach to dabbling ducks, *Chara vulgaris* and Bearded Stonewort *Chara canescens* dominate. Wetland II has shallow-water areas suitable for foraging Wigeon along the shores, but extends down to 110 cm depth in the centre of the lagoon. During the study, the macrophyte community covered the substrate throughout the lagoon and consisted of 98% *Ruppia cirrhosa* and 2% *Potamogeton pectinatus*. To quantify the macrophyte biomass and related water depth in the lagoons, samples were taken along transect lines in early September and late October 1999. The transect lines ran in parallel and were 500 m apart. Sample stations were located at 500 m along the transect lines, where the percentage vegetation cover was estimated to the nearest 5% in a radius of approximately 5 m, and water depth was measured to the nearest cm with a dipstick. The SAS/GRAPH G3GRID procedure with spline smoothing (SAS Institute 1990) was subsequently used to interpolate depth in each grid cell.

Additionally, six vegetation samples were

taken around each sample station to determine biomass. If the plant community was scattered, samples were only taken at sites with leaf cover. Each sample was taken using a 15 cm wide circular core-sampler penetrating 20 cm down into the sediment, then transferred to a sieve (1 mm mesh size) where the sediment was superficially washed out and the resulting material was stored in plastic bags. In the laboratory, samples were sorted into species and into live and dead material, then dried to constant weight at 70° C in an oven and weighed. By knowing the area of the core-sampler, the standing biomass/m² in vegetated areas was finally calculated. These values, however, do not include bare patches in the lagoons. To correct for this, an estimate of the biomass/m² of each plant species at each sample station was calculated by multiplying the average dry weight of the six samples with the percentage of the average leaf cover of each plant species on the same sample station. This estimation method is based on the assumptions that 1) vegetation covered areas had a uniform plant distribution, and 2) proportional coverage has a linear relationship with biomass density (as shown in studies by Percival *et al.* 1996). A more detailed description of the depth profiles and macrophyte communities in the two lagoons, including biomass, distribution and nutritional value, can be found in Holm (2002) and Holm & Clausen (2006). At Wetland I, hunting intensity was negligible because it was a shooting-free reserve (Holm 2002); at Wetland II, hunting on the surrounding salt marshes took place from 1 November to 31 January (Bregnballe *et al.* 2004).

Waterfowl counts and mapping

In autumn 1999, the most abundant herbivorous waterbirds, Wigeon, Mute Swan *Cygnus olor* and Coot *Fulica atra*, were counted five times per month on weekdays between 08:00–16:00 h from the embankments using telescopes. Distributions of the birds were recorded by drawing their precise locations on detailed maps (1:25,000), distributed across a 250 m × 250 m grid superimposed on the maps. Where flocks of birds occurred across more than one grid cell, numbers were apportioned between grid cells, assuming that there was an even distribution of birds within the flocks. The number of bird-days per grid cell was calculated for each species and the proportion of birds in each cell was determined by dividing the bird-days recorded for the cell with the bird-days recorded for the whole lagoon. These numbers were then used to calculate the cumulative number of birds in relation to distance from hunting and the water depth classes. The distance between the centre of each grid cell and the nearest shore with hunting activity was measured on the map. Kolmogorov-Smirnov tests were used to analyse changes in horizontal distribution and changes in depth distribution (Zar 1984). For the horizontal distribution, 41 different measurements were found and used in the analysis, for the depth distribution 31 different measurements were found and used. Niche overlap was calculated using the Simplified Morisita Index (Krebs 1999), to quantify the extent to which the species overlap in their utilisation of space and food resources:

$$C_H = \frac{2 \sum_i^n p_{ij} p_{ik}}{\sum_i^n p_{ij}^2 + \sum_i^n p_{ik}^2}$$

where C_H = the Simplified Morisita index of overlap between species j and species k , P_{ij} = the proportion resource i of the total resources used by species j , P_{ik} = the proportion resource i of the total resources used by species k , and n = the total number of resource states ($i = 1, 2, 3, \dots, n$).

Time budgets

Time budgets were recorded on Wigeon in late September and November 1999. Observations were made using a telescope (20–60 ×) from sunrise to sunset when light and weather conditions permitted. The number of birds of each species engaged in various activities was determined by scanning the flock at 10–15 min intervals (Altmann 1974). The main activities recorded were feeding, roosting, swimming, flying, preening, interacting and walking. Feeding techniques were also recorded, as one of the following: 1) Pecking, where the birds feed by picking food from the surface, 2) Head-dipping, where the birds feed by submerging their head, and 3) Up-ending. Details of whether Wigeon were kleptoparasitising other species, and the species involved, were recorded routinely along with the feeding techniques. Activity budgets were expressed as the proportion of time that birds were engaged in each type of activity.

Nested Generalised Linear Models (GLMs) were used to analyse differences in the birds' time budgets between the two seasonal periods. Data were normalised using arcsine transformation (Zar 1984),

before statistical analysis using SAS/STAT (SAS Institute Inc. 1989).

Results

At Wetland I, the Wigeon arrived in September, and counts peaked at 1 October with 2,600 individuals. Numbers then decreased over a 2-week period in early October, and a flock of 400–600 Wigeon stayed at the site throughout November. During September and October, Wigeon mainly foraged by kleptoparasiting Coot. Wigeon did not forage on the *Ruppia maritima* in shallow waters, but mixed with Coot in deep areas in a ratio of approximately 1 to 1, in flocks of up to 600 individuals. When the Coots foraged by diving, they returned to the surface with a tangled mixture of the two *Chara* species, depositing 20–30 *Chara* plants on the surface. Here they started to feed by pecking and the Wigeon then kleptoparasited them by taking the floating *Chara* species as well. The Simplified Morisita Index showed an overlap between Coot and Wigeon of 0.47 (Table 1). Furthermore, when the Wigeon fed by kleptoparasiting the Coots, the proportion of foraging Wigeon was significantly correlated with that of the Coot ($r_s = 0.379$, $p < 0.05$). Wigeon primarily occurred in *Chara* dominated areas and were not seen in shallow water where *Ruppia* was readily available (Fig. 1).

At Wetland II, Wigeon was the most numerous species with peak numbers up to 2,750 in early October. Thereafter, 1,000–1,400 remained until mid November, decreasing gradually after 1 November when hunting began. When undisturbed,

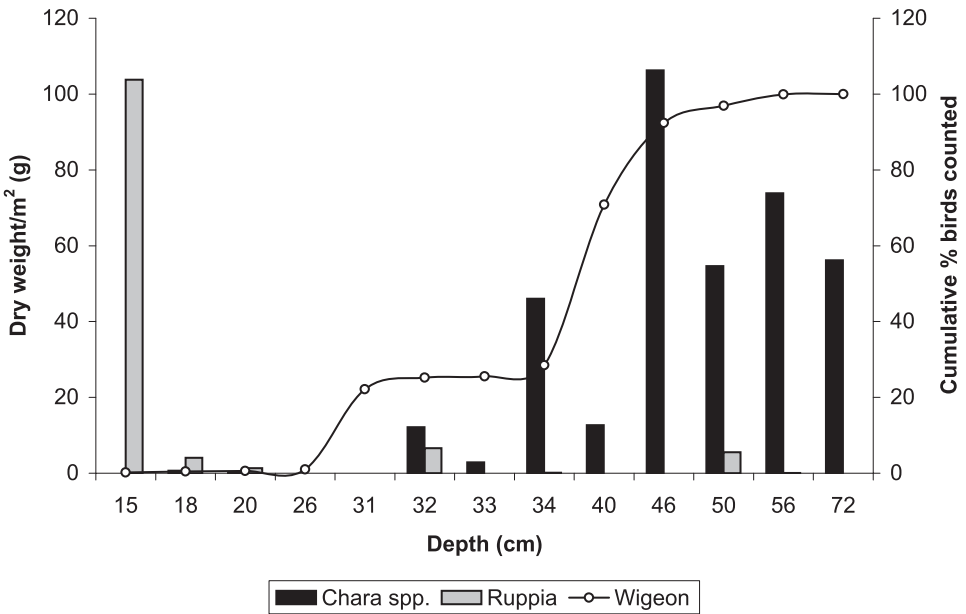


Figure 1. Depth profile for Wetland I. *Chara* dominates the deepest areas, whereas other macrophytes, primarily *Ruppia*, dominate the shallowest water. The majority of the Wigeon are seen where the high quality *Chara* dominates; *i.e.*, in water deeper than the birds' foraging depth of 31 cm.

the number of Wigeon was greatest in the shallowest northern parts of the lagoon (Fig 2), where the macrophytes were within reach of the birds by pecking, head-dipping and upending. In November, the birds redistributed away from the hunting areas near the shore (Kolmogorov-Smirnov tests comparing September–October versus November; $D = 0.4419$; $n = 43$; $P < 0.0001$) and into deeper areas ($D = 0.5484$; $n = 31$; $P < 0.0001$) (Fig. 2; also see Holm 2002 and Holm & Clausen 2006, who give detailed maps of the monthly distribution of Mute Swans, Coot and Wigeon). In the deeper areas the Wigeon started to forage exclusively by kleptoparasitism of Mute Swans. The kleptoparasitism observations

were supported by the Simplified Morisita Index, which showed that the spatial overlap between Wigeon and Mute Swans changed from 0.18 in September–October before the hunting season to 0.71 after hunting commenced in November (Table 1). In spite of the different feeding methods, there was no difference in the proportion of time spent feeding by Wigeon between the two periods ($F_{1,51} = 2.68$, n.s.). The Wigeon fed using the pecking and head-dip feeding methods 90% of the time. There was no significant difference between early October and mid November in the proportion of birds feeding by pecking ($F_{1,38} = 3.35$, n.s.), but foraging by head-dipping increased significantly ($F_{1,38} = 6.81$, $P < 0.05$).

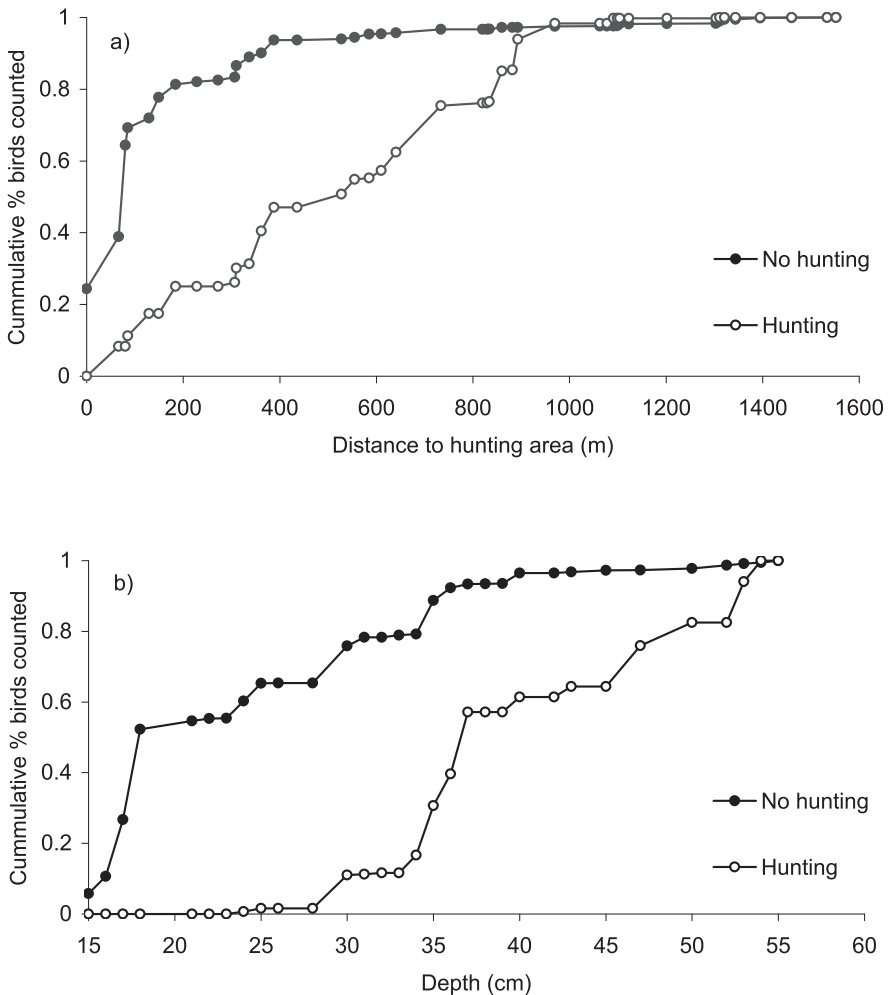


Figure 2. Distribution of Wigeon in relation to a) distance to hunting area, and b) water depth at Wetland II. Wigeon moved away from the hunting area in the open season (upper chart), which means that they redistributed to water deeper than their foraging depth of 31 cm (lower chart).

Discussion

The dominant macrophyte species in Wetland I were stoneworts which contain high quantities of easily digestible non-structural carbohydrates, and hence, represent a high quality food (Holm 2002).

Generally speaking, most of the food supply for Wigeon is both poor in nutrients and difficult to digest (Owen & Thomas 1979), which may be the reason why these birds left the shallowest *Ruppia*-dominated areas in Wetland I (Holm 2002; Holm & Clausen 2006) to kleptoparasite Coots diving for the

Table 1. Niche overlap for the horizontal distribution of Wigeon, Mute Swan and Coot in the two study areas. C_H is the Simplified Morisita Index, where an index of 0 is equivalent to no overlap at all and an index of 1 to a complete 100% overlap between species.

		C_H (Mute Swan, Coot)	C_H (Mute Swan, Wigeon)	C_H (Coot, Wigeon)
Wetland I		0.23	0.29	0.47
Wetland II	No hunting	0.27	0.18	0.18
	Hunting	0.18	0.71	0.15

higher quality *Chara* species. The advantage of adopting kleptoparasitism is that Wigeon can obtain food that would normally be unavailable to them, and this is known to be related to food quality from other studies (Amat & Soriguer 1984). If the Coot under normal conditions are able to ingest all the plant material before it sinks, then kleptoparasitism is energetically costly for the Coot, which must dive more often to compensate for the loss of food (Amat & Soriguer 1984). The Wigeon were successful when kleptoparasiting because the food is not economical for Coots to defend, and for this reason aggressive behaviour might not be effective (Ryan 1981). The result is that through kleptoparasitism Wigeon are able to obtain higher energy plants, and increase their energy intake, than they can by feeding alone. Thus by adopting this strategy, they potentially can leave the area with more fat reserves and/or can forage less during the day, saving energy and potentially exposing them to a lower predation risk.

The shallow areas of Wetland II are the only parts of the lagoon where dabbling

ducks are able to reach their food due to their morphology and feeding behaviour (Pöysä 1983). As a result of hunting disturbance, Wigeon redistributed to deeper areas of the lagoon where water was too deep to permit surface feeding, and hence were forced to forage exclusively by kleptoparasitising swans. When foraging, the swans were uprooting the macrophytes, leaving leaves and stems floating in the water, some of which were available to the Wigeon. The use of the head-dipping method to feed increased significantly during autumn, which indicated that the Wigeon foraged somewhat deeper down in the water when kleptoparasiting Mute Swans to reach the floating plant material, compared to situations where they foraged alone. Other studies have similarly shown that kleptoparasitism may be related to the depth of the food plants (Knapton & Knudsen 1978; Duffy 1980), which is also the case here, where Wigeon kleptoparasite to compensate for lost foraging area due to human disturbances. The gain was probably not as great as stealing highly nutritious *Chara* in Wetland I, but it is

probably better than the alternative, namely to abandon the area (*i.e.* the choice being to kleptoparasitise or leave) or to use the area as a day roost only.

Overall, this study shows that Wigeon can adapt to different conditions regarding macrophyte communities, water depths and human disturbance and show ecological plasticity to cope with these factors. Wigeon must forage most of the day to meet their energy requirement (Madsen 1988, Mayhew 1988) and this study shows that kleptoparasitism is one of the strategies Wigeon can use to maintain food intake rates under different foraging constraints.

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