

Carrying capacity of a heterogeneous lake for migrating swans

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Carrying capacity of a heterogeneous lake for migrating swans

Draagkracht van een heterogeen meer voor trekkende zwanen

(met een samenvatting in het Nederlands)

Proefschrift

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Chapter 1

General introduction



Ready for some swans!

As human induced habitat loss and fragmentation are serious threats to biodiversity, studying their effects remains to be a major challenge for scientific research. Depending on the region, human disturbance has various forms: exploitation of natural resources, expansion of agricultural lands, or the desire for recreational activities. Admittedly, the globally growing human population brings about ever increasing pressure on such natural habitats. Often, there are legal obligations to minimize, and in some cases even compensate for the losses in wildlife populations. As a result, policy makers need tools to be able to *predict* the consequences of any proposed change in the management of a natural site. For the development of such a tool, a good understanding of the *relevant factors* shaping the size of an animal population is a requisite.

In the case of migratory animals, conservational measures can not concentrate only on the breeding site, but wintering areas and stop-over sites in between must be adequately protected as well. In order to express the effect of habitat loss at such sites in a simple numerical fashion, managers are interested in predicting the maximum number of animals a habitat can support. This is especially the case, when environmental impact assessment analyses are required prior to the implementation of an area development project. Additionally, the preservation of the current numbers of a certain species is frequently set compulsory. In all these cases, the term *carrying capacity* is commonly used to describe the quality of a habitat for a certain species (Sayre 2008). Often, it is referred to as a property that can be directly measured. However, there is no general definition what carrying capacity practically expresses (Dhondt 1988).

All theories used in ecological studies stem from the notion that there must be an upper limit to the number or density of animals an area can support with food (Newton 1980, Sayre 2008). However, at least two main approaches evolved throughout the past fifty years in defining the way this maximum is reached. A numerical approach describes carrying capacity as the point where population growth stabilizes, i.e. where birth rate equals death rate: the so-called *demographic carrying capacity* (Dasmann 1964). However, stabilizations can occur at different levels, and not necessarily because the habitat under investigation reached a saturation level. First of all, such approach neglects the influence of the surroundings and considers the study site as a closed box (West et al. 2005). For instance, if conditions improve elsewhere and a certain portion of the population decides to switch, this has in fact nothing to do with the carrying capacity of the studied habitat, even though numbers obviously declined. In addition, deterioration in habitat quality may not immediately be mirrored by the size of the population, possibly leading to a misinterpretation of optimal habitats (Goss-Custard et al. 2002).

A more functional approach also considers the constraints of animals to harvest resources. This so-called *energetic carrying capacity* (de Leeuw 1997, van Gils et al. 2004) acknowledges that due to various biological mechanisms not all food is harvestable and accessible to foragers (Zwarts and Wanink 1993). Supporters of this approach argue

that identifying the factors that limit the maximum food intake rate are essential in predicting the number of animals a site can support with food. In this aspect it is also vital to distinguish between animals that are satisfying their needs at a site (Goss-Custard et al. 2002) from those that are maximizing their intake rate (Sutherland and Anderson 1993), although ultimately all behavioural decisions should maximize fitness (i.e. the expected genetic contribution to future generations; McNamara and Houston 1986). This can be achieved by maximizing the chances of survival and reproduction, with the emphasis on survival in unfavourable periods and on reproduction in favourable periods. In situations where predation is absent or is the same everywhere in the habitat, suggested currencies are, for instance, maximizing gross energy intake rate, i.e. the total amount of energy gained per unit of time (Sutherland 1982) or efficiency, i.e. the amount of energy gained per unit of energy spent (Houston 1995). Efficiency, or a modified version of efficiency, proved to be the best currency when energy acquisition or expenditure is limiting (McNamara and Houston 1997). In most cases, however, the net energy intake rate (i.e. intake rate of energy based on accessible food density minus foraging costs) is demonstrated to be the currency to maximize (Schoener 1971, Pyke et al. 1977, Stephens and Krebs 1986).

In the case of migratory birds, estimates of energetic carrying capacity were considered successful in predicting the carrying capacity of stopover sites (e.g. Vickery et al. 1995, Gill et al. 2001b, Goss-Custard et al. 2002). In these studies, exploitative competition, i.e. the depletion of one common food source by a number of organisms (Krebs 2001), was assumed to exclusively determine the distribution of animals. In such cases, it became generally accepted to express the carrying capacity of a stopover site as the cumulative number of birds ('bird-days') that can be accommodated by food for a particular time of the year (Goss-Custard 1985). Note that if this number might also be limited by interference competition, i.e. the decline in intake rate due to the presence of competitors (Goss-Custard 1980), and not only by the available amount of food. Therefore, in such cases 'bird-days' is a less useful unit for carrying capacity, as its derivation requires more than simply summing the number of birds visiting the site (Goss-Custard 1985).

The most basic energetic carrying capacity models (the so-called *daily ration models*; Table 1) assume that the number of bird-days simply depends on the amount of food present and the daily food requirement of an average individual (Alonso et al. 1994, Inger et al. 2006b, Desnouhes et al. 2007). However, the fact that foragers commonly consume only the food above a particular threshold giving-up density (Brown 1988) is also recognized by most of the daily-ration models (Sutherland and Anderson 1993, Gill et al. 2001b). The incorporation of foraging patches of varying quality (MacArthur and Pianka 1966, Charnov 1976) meant a further improvement in carrying capacity models, establishing the so-called spatial depletion models (Sutherland and Allport 1994; Table 1). Patches in these models may differ in available food densities, but also

in foraging costs (Goss-Custard et al. 2002), accessibility, competitor density, predation risk and disturbance levels (Percival et al. 1998), all affecting the initial profitability of patches. Even though in *spatial depletion models* animals can decide which patch is energetically the most valuable, it needed the development of *spatially-explicit models* to recognize the aspects of travelling between patches (Charnov 1976, Bernstein et al. 1988, Goss-Custard et al. 2003).

Table 1: *Carrying capacity models intended to predict the maximum number of birds or bird-days in order of increasing complexity.*

Model name	Considered variables	Examples of study-systems
Daily-ration models	Total amount of food and daily food requirements	Geese and seagrass (Inger et al. 2006b)
	Accessible food and daily food requirements	Cranes and seeds (Alonso et al. 1994)
	Accessible food above giving-up density and daily food requirements	Geese and seagrass (Goss-Custard et al. 2003) Godwits and bivalves (Gill et al. 2001b)
Spatial depletion models	Food supplies comprise patches of differing food density, accessibility and availability Patch co-ordinates, and individual differences not considered	Geese and seagrass (Percival et al. 1998) Geese, wigeons and gras (Sutherland and Allport 1994)
Spatially-explicit individual-based models	Varying patch and individual qualities (e.g. feeding efficiency and dominance)	Oystercatchers and mussels (Goss-Custard et al. 2002) Geese and seagrass (Pettifor et al. 2000)

Both the daily ration and spatial depletion models have in common that they consider a single threshold food density at which animals starve or leave the site (Goss-Custard et al. 2003). This stems from the idea that prey densities below a certain critical level cannot sustain the energy requirements of an individual (Sutherland and Anderson 1993). Unfortunately, this critical prey density is commonly confused with observed giving-up densities, which are consequently assumed to be constant throughout the environment (van Gils et al. 2004). This approach ignores the fact that in heterogeneous environments giving-up densities may spatially vary due to varying initial food densities but also due to spatially varying accessibility and harvestability of the food (Zwarts and Wanink 1993) as well as costs (metabolic, predation and missed opportunity costs) made while foraging (Brown 1988, Nolet et al. 2001b, Goss-Custard et al. 2003, van Gils et al. 2004).

According to Goss-Custard et al. (2003), there are only certain cases when a single, observed giving-up density value representing the food density at which animals leave the area may be used in calculating the carrying capacity of a site, namely when: a) the additional loss of food for reasons others than depletion by the studied consumers is not varying across patches; b) the profitability and availability of patches is not spatially and temporally varying; c) the energy costs of foraging are not different between patches. The importance of acknowledging spatial heterogeneity in ecological processes is gaining evidence (Gross et al. 1995, Englund and Leonardsson 2008, Klaassen and Nolet 2008, Dupuch et al. 2009, Kraan et al. 2009a, van Gils in press). In such spatially heterogeneous environments, the above mentioned differences between patches may all exist, which in turn may affect the individual decisions animals make on where to forage. Therefore, in such cases it might be inevitable to use spatially-explicit models to calculate carrying capacity.

Another problem that both daily ration and spatial depletion models have in common is that they assume all individuals in a population to be identical and interference-free (Goss-Custard et al. 2003). Hence, all individuals are also considered to have the same daily energetic requirements, and as a result to be accommodated at a site just as long as there is enough food, but to die or emigrate as soon as food is depleted (Sutherland and Anderson 1993). However, each animal may be unique in its combination of foraging efficiency, dominance and experience level, affecting the spatial distribution of the whole population (Goss-Custard et al. 1995). Using individual-based models is a potential solution to these problems (Goss-Custard et al. 1995, Pettifor et al. 2000).

In conclusion, defining the necessary level of complexity of carrying capacity models remains a relevant question. Whether a population may be considered as a group of identical animals free of interference seems to be a basic dilemma. The problem of spatial heterogeneity may be solved by using net energy intake rate as a proxy for how animals perceive the quality of a site (Charnov 1976, Pyke et al. 1977). Obviously, the ease of relying on simple measurements, such as total biomass values and single giving-up densities is attractive compared with the use of net energy intake rate, which involves the additional estimation of locally accessible food biomass, harvest rates and foraging costs. Moreover, when predation (or disturbance) costs also vary among patches, these also influence the profitability of a patch (Brown 1988). In such cases, the simple maximization of net energy intake rate is not applicable any more, as animals trade off energy intake with safety (McNamara and Houston 1987), depending on their energy state and marginal value of energy (see review in Brown and Kotler 2004).

This thesis aimed to investigate which of the above mentioned carrying capacity models incorporate enough aspects to describe the number of migratory waterbirds making use of a stopover site. The work focuses on the Bewick's swans (*Cygnus bewickii*) (Fig. 1), which breed at the Pechora Delta in the Russian tundra. Every autumn

they cover roughly 3500 kilometres to their wintering grounds in Northwest Europe (Fig. 2). During this journey they refuel at several stop over sites (Nolet et al. 2001a) on tubers of fennel pondweed (*Potamogeton pectinatus*), such as at the Lauwersmeer (Fig. 3), their last stop over site (Beekman et al. 1991, Nolet et al. 2001b).



Fig. 1: Bewick's swan (*Cygnus bewickii*). Photo by Bart van Lith.



Fig. 2: *Breeding and wintering grounds of Bewick's swans with the line depicting the flyway range.*
Figure from Robinson et al. (2004).



Fig. 3: *A group of Bewick's swans busy with harvesting pondweed tubers in the Lauwersmeer. Careful observers can detect the diving ducks following the foraging swans. Photo by Marycha Franken.*

The Lauwersmeer, with a surface area of approximately 2300 ha found in the northern part of the Netherlands (Fig. 4), was created in 1969 when the Lauwers Sea was closed off from the Wadden Sea. Within a period of two years the water became fresh but the bottom retained the estuarine geomorphology and contained salt for a period of about 20 years (Pot 1984). The northern parts of the lake are predominantly sandy, whereas the southern parts are more clayey. Secchi-depth ranges from 10-45 cm, chlorophyll content varies between 10-250 $\mu\text{g L}^{-1}$ (A. Gyimesi and B. Arevalo, unpubl. data). Water level is regulated by the authorities but it still may rise one meter during periods of strong north-westerly winds when excess water can not be sluiced into the Wadden Sea. The first fennel pondweed beds were observed in the lake already three years after the embankment (van Eerden et al. 1997). During the summer months, a considerable number of mute swans, coots, mallards and gadwalls forage on the aboveground parts of the plant (Pot 1981, van Wijk 1988, Beekman et al. 1991). At the end of the summer these aboveground parts die off, and only the tubers in the sediment remain (Fig. 5). These tuber banks have annually been exploited by Bewick's swans since 1973, with peak numbers and cumulative number of swan days showing strong interannual va-

riation (Fig. 6). In the months October and November a prominent proportion of the whole flyway population (Dirksen et al. 1991), may remain here for a few weeks. After this short exploitation period of tuber banks the swans switch to forage on arable lands (Beekman et al. 1991).

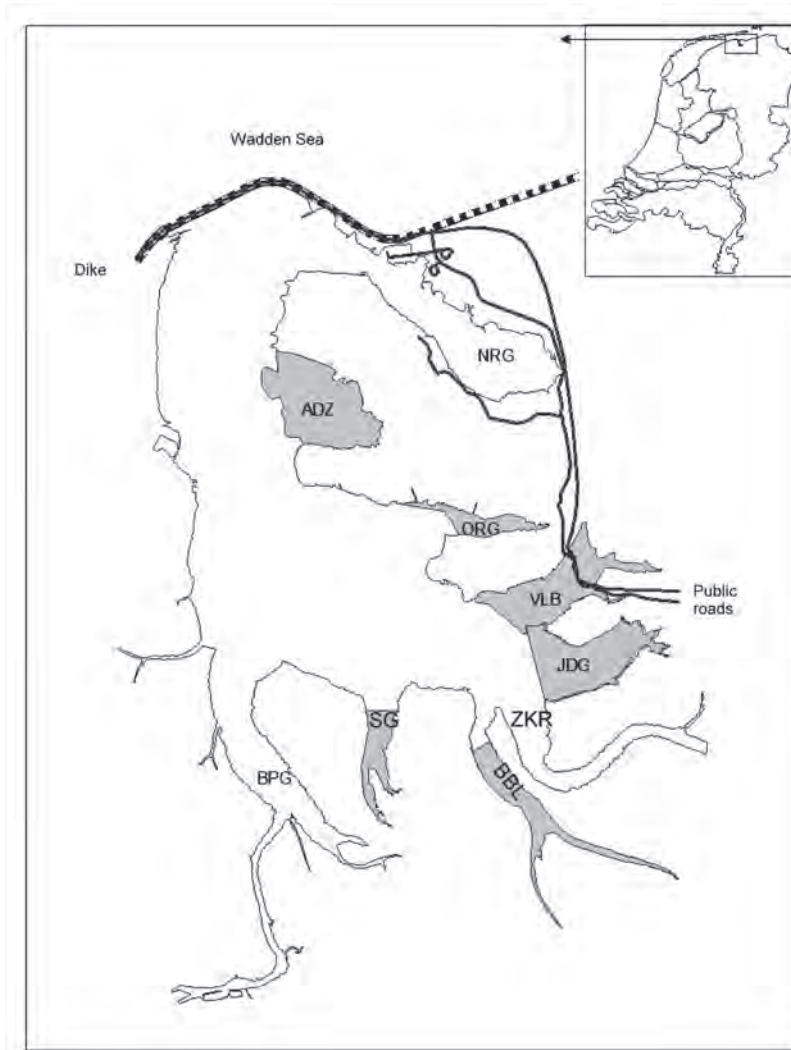


Fig. 4: The Lauwersmeer area (position in The Netherlands in the inset), with public roads passing by on the East, and the Wadden Sea and the sea dike on the North. The creeks are indicated by abbreviations: ADZ: Achter de Zwarten, BBL: Babbelaar, BPG: Blikplaatgat, JDG: Jaap Deensgat, NRG: Nieuwe Robbengat, ORG: Oude Robbengat, SG: Simonsgat, VLB: Vlinderbalg, ZKR: Zoutkamperril. Shaded creeks are closed for boat traffic.

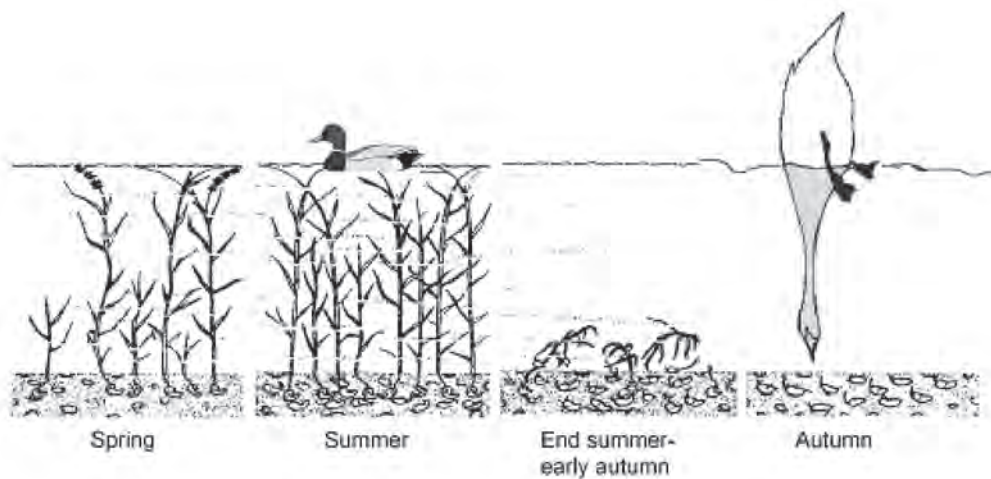


Fig. 5: Life cycle of fennel pondweed with its seasonally typical herbivores in the Lauwersmeer.
Figure adapted from van Wijk (1988).

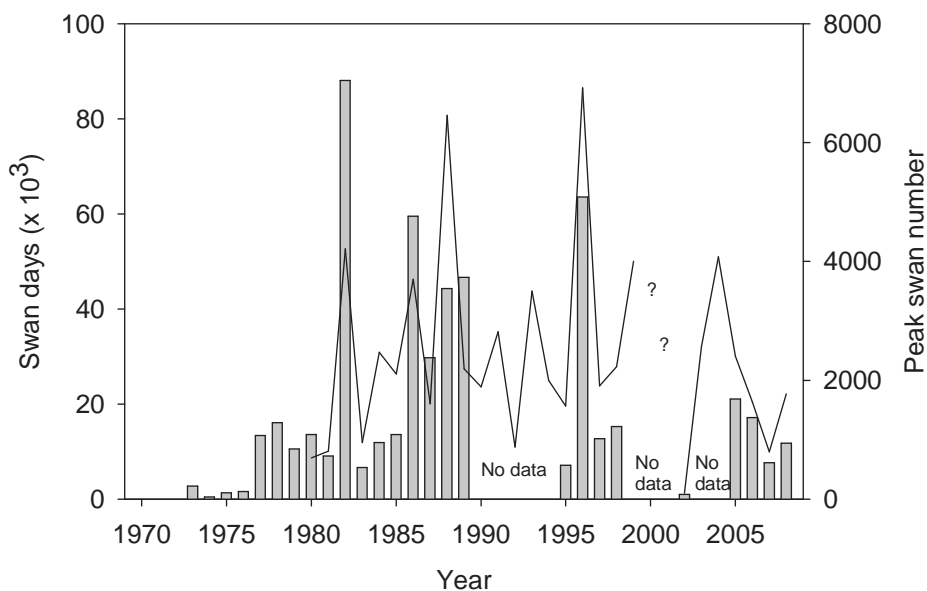


Fig. 6: Cumulative number of swan days (bars; left axis) and peak swan numbers (line; right axis) in the Lauwersmeer in the period 1969-2008. Note that in the case of swan days no data is available for 1990-1994, 1999-2001 and 2003-2004, neither for 2000-2001 in the case of peak numbers.
Data from Prop & Van Eerden (1981), Beekman et al. (1991) and NIOO-KNAW.

The Lauwersmeer provides a perfect study system to investigate questions of carrying capacity. The lake comprises nine creeks, each with different combinations of food density, water depth and sediment texture. Due to the fact that the energy investments in harvesting the tubers depend both on water depth and sediment type (Nolet et al. 2001b, Nolet et al. 2006a), the system provides excellent conditions to investigate the energetic decisions swans rely upon in their foraging site selection. In addition, some creeks experience frequent human disturbance, in the form of boat or road traffic (Fig. 4), limiting the availability of these sites.

Relying on this particular study system, I intended to gain a good understanding of the *relevant factors* shaping the carrying capacity of the Lauwersmeer for Bewick's swans (Fig. 7). The project consisted of a combination of field work, experiments and modelling. In order to get replicates, field work was carried out in four years (2005, 2006, 2007 and 2008). Every autumn, in October and November, Bewick's swans were counted and behavioural observations carried out. In order to estimate food density, just before the arrival of the swans, as well as just after they had left, tuber density was sampled. Estimations of tuber densities were further supported by satellite images in 2005, 2006 and 2007. These images of aboveground plant material in summer were used as clues about the belowground biomass in autumn. Additionally, in two years, counts on summer waterfowl herbivores were also conducted. Finally, a complete sediment and bathymetry map was created by GIS techniques of the shallow zones of the Lauwersmeer. Experiments were carried out with captive swans in individual trials to study feeding efficiencies, effect of food burial depth and interspecific competition with diving ducks. Due to their body size, swans require a large individual space to be able to avoid conspecifics. Hence experiments to reveal details of intraspecific competition were carried out with mallards (*Anas platyrhynchos*), and insight in the importance of intraspecific competition among Bewick's swans was obtained using a modelling approach.

The first two chapters look at how interspecific competition affects the available food biomass of Bewick's swans. **Chapter 2** concentrates on a form of time-staggered interspecific competition observed in the field: does herbivory on the aboveground vegetation of fennel pondweed in the summer (by for instance mute swans) cause reduced tuber densities in the autumn available for Bewick's swans? **Chapter 3** focuses on the species associations observed between various duck species and Bewick's swans. An experimental approach was used to tackle the question whether pochards, the species observed to follow Bewick's swans most closely in the field (Fig. 3), are kleptoparasitizing on Bewick's swans or that the relationship can be described as commensalistic, in which one species profits from the other without imposing costs to that other species. In **chapter 4** the intraspecific competition among Bewick's swans is investigated by an interference model, describing how intake rates changes with increasing competitor densities of conspecifics. Intake rate results are highlighted at densities observed in the

field in 1995 and 1996. How the outcome of interference competition may generally be affected by the spatial distribution of food is examined through experimental results in **chapter 5**. Continuing on this idea, another experiment (**chapter 6**) depicts how individuals change their patch use and total feeding time in the presence of competitors. **Chapter 7** discusses the importance of recognizing individual differences in an animal population. Here, we present an experiment comparing the feeding efficiency of cygnets and adult swans, and discuss how this may affect their spatial distribution in the field. In **chapter 8** we investigate whether in a heterogeneous system such as the Lauwersmeer, food supply alone (eventually corrected for spatially varying accessibility and/or giving-up density), is an adequate predictor of the number of bird-days. Alternatively, we test whether considering foraging costs too, by using net energy intake rate as a currency, improves predictions on swan numbers. For the same reasons of spatial heterogeneity, in **chapter 9** we wonder whether the commonly used practice of describing the effects of human disturbance through measuring giving-up densities is also applicable in our system or inferences from measurements of giving-up net energy intake rates is a better proxy. Besides summarizing these issues, the general discussion in chapter 10 provides further aspects of spatial heterogeneity and future perspectives of food availability.

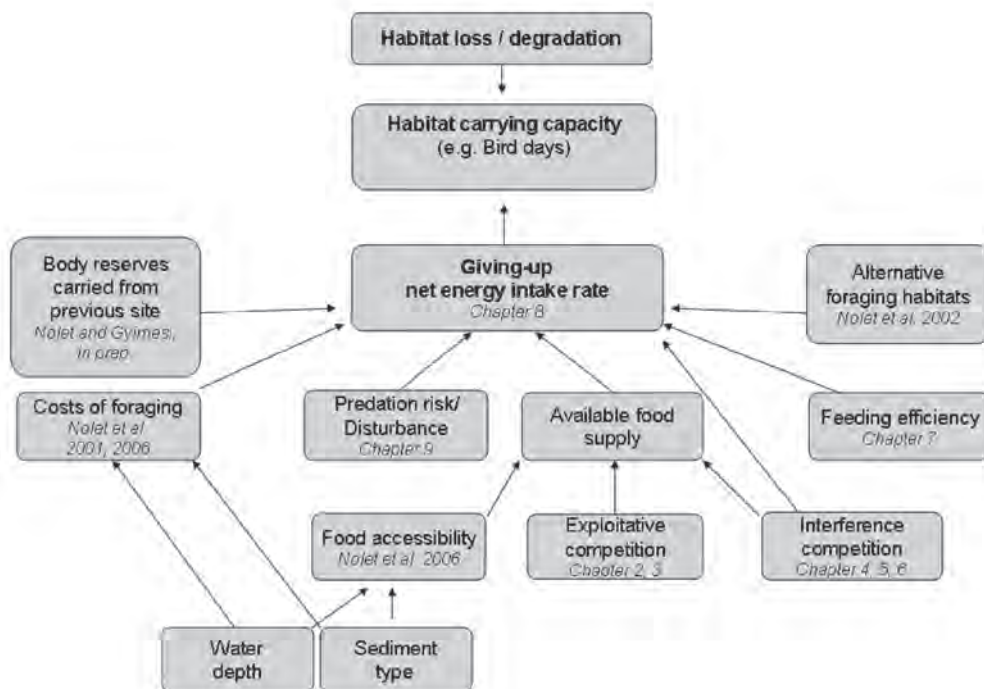


Fig. 7: Factors affecting the carrying capacity (expressed e.g. as the number of bird days) of the Lauwersmeer for Bewick's swans.

Chapter 2

Empty treasury: impoverished propagule banks of fennel pondweed due to summer herbivory

ABEL GYIMESI, PETER P. DE VRIES, THIJS DE BOER and BART A. NOLET



Bewick's swans are not the only ones troubled by the increasing number of mute swans.

Abstract

It is increasingly recognized that herbivory on aquatic macrophytes plays a crucial role in the functioning of freshwater habitats. Most studies, however, are restricted to the direct effect of consumption on vegetation. Carry-over effects of grazing on the next vegetative phase have received little attention. In this paper we investigated to what extent summer herbivory on aboveground biomass of fennel pondweed affects the formation of belowground propagules (i.e. tubers). Cumulative grazing pressure was predicted based on timing of grazing and body mass of the grazers. Cumulative grazing pressures were expected to negatively correlate with mean autumn tuber biomass densities. The importance of cumulative grazing pressure on tuber production was compared to the importance of sediment type and water depth. Predictions on the cumulative grazing pressure gave a significant negative correlation with tuber densities in three of the four years of study. Moreover, in the same three years, cumulative grazing pressure showed a larger effect on tuber production than water depth, sediment type or their interactions. We propose that herbivory early in the summer has the most substantial impact on the fitness of macrophytes. Mute swans (*Cygnus olor*), due to their high consumption rate and their early congregation for moulting, seem to be the key waterfowl species in diminishing propagule production, and hence create a form of time-staggered competition to consumers of the belowground biomass.

Introduction

Submerged vegetation often plays a key role in aquatic ecosystems (Carpenter and Lodge 1986), among others as food source for many organisms of coastal, estuarine and inland wetlands (Lodge 1991, Hakanson and Boulion 2002). Fennel pondweed (*Potamogeton pectinatus* L.) is one of the most common and widespread of submerged aquatic species (van Wijk 1988). Both aboveground green parts of the plant (van Wijk 1988, Søndergaard et al. 1996, Weisner et al. 1997, Hidding et al. 2009b), and belowground reproductive organs (i.e. tubers: Anderson and Low 1976, Nolet et al. 2001a, Badzinski et al. 2006) are preferred food of waterfowl. Quantifying the reduction of biomass caused by direct consumption is already a challenging task (e.g. Kiorboe 1980, Lodge 1991, Lauridsen et al. 1993, Hilt 2006, Hartke et al. 2009), and efforts to study the carry-over effects of grazing on the next vegetative phase have not received much attention. The few studies on such effects mostly concentrated on the grazing of belowground (i.e. tuber) biomass in the autumn and its effect on the abundance of aboveground vegetation the following spring/summer. It has been found that moderate tuber consumption is compensated by density-dependent growth in the following spring (LaMontagne et al. 2003, Nolet 2004, Klaassen and Nolet 2008). Similar effects were found with the closely related water celery (*Vallisneria spiralis* L.) (Sponberg and Lodge 2005). However, indications of how the grazing of aboveground biomass influences the development of the belowground biomass are scarcer (but see

Hidding et al. 2009b).

In theory, summer grazing of waterfowl on aboveground plant material can have a serious impact on tuber production. Peak aboveground biomass and belowground biomass in the autumn are highly correlated (van Dijk et al. 1992, Hangelbroek et al. 2002). Considering that exclosure experiments showed that summer herbivores can remove a considerable proportion of the green matter (van Wijk 1988, Søndergaard et al. 1996), one would predict low tuber abundance at sites grazed in the summer. The importance of interspecific competition for the same food source has long been recognized in evaluating a habitat (Coe et al. 1976, Newton 1980). Similarly, species consuming the vegetative parts of a plant may generate time-staggered competition as they indirectly affect the food abundance of species relying on the generative parts of the same plant. In this paper, we hypothesize that the grazing of summer waterfowl negatively affects the local tuber density in the following autumn. To examine this hypothesis, we create a common currency for grazing pressure of the most common waterfowl species of the Lauwersmeer (The Netherlands) observed in four different years. Hereby, we first correct bird counts for body mass-related food intake (Bruinzeel et al. 1997). Thereafter, based on results of a previous mowing experiment of aboveground vegetation (Klaassen et al. 2006c), we correct bird counts for the time of grazing. We correlate the created cumulative grazing pressures with mean autumn tuber biomass densities. Finally, we test the importance of summer grazing pressure compared to sediment type, water depth and their interaction.

Methods and materials

Study site

The Lauwersmeer is a eutrophic shallow freshwater lake (1970 ha) in the northern part of the Netherlands (53° 22'N, 06° 13'E). The lake is part of a national park and hunting is not allowed. The surface area is about 1970 ha with an average depth of 2.1m. In the nine creeks (approximately 750 ha) of the lake the water depth is less than 1 m, where fennel pondweed forms nearly monospecific stands (Pot 1984, van Wijk 1988, Hidding in press). Grazing of waterfowl on aboveground plant material in the summer can reach high levels (Santamaría 2002, Hidding et al. 2009b). The most common bird species in the Lauwersmeer, which are also thought to largely rely on macrophyte consumption, are mute swan (*Cygnus olor* Gmelin), gadwall (*Anas strepera* L.), mallard (*Anas platyrhynchos* L.) and coot (*Fulica atra* L.). Besides summer grazing, every year in October thousands of Bewick's swans (*Cygnus bewickii* Yarrell), often followed by Pochards (*Aythya ferina* L.), choose this site to feed on the tubers of fennel pondweed (Beekman et al. 1991, Gyimesi, van Lith and Nolet, unpubl. data, Nolet et al. 2001b).

Field data

Staatsbosbeheer Lauwersmeer, the administrative body managing the national park, organizes counts of the birds on the lake in the middle of every month. Our analysis on summer bird numbers relied on their count data of the four most abundant waterfowl species from June, July and August 2005 and 2006. In 2007 and 2008, we supplemented these with own counts at the end of the month, resulting in a dataset of fortnightly counts. One of the count zones of Staatsbosbeheer covers two creeks instead of one. Hence, data analysis relied on seven individual creek counts and one count adding up two creeks.

Tuber biomass densities were measured just before the arrival of Bewick's swans, in the first week of October. In 2005, 2006, 2007 and 2008 ten randomly placed points per creek were sampled. Twelve cores (10 cm in diameter) were taken from the upper 0.35 m of the sediment (cf. Nolet et al. 2006c). In 2005 and 2006 this happened around 1m² plots (as aboveground biomass was removed there for another purpose; Gyimesi, Varghese, de Leeuw and Nolet, unpubl. data), whereas in the other two years within 1m² plots. The extracted cores were washed through a metal sieve of 3 mm mesh size to separate the tubers from the sediment. The tubers were stored in labelled plastic bags at 4 °C until they were dried in the laboratory for ≥ 48 hours at 70 °C.

At each sampling point, a sediment sample was taken for particle-size distribution analysis (Malvern analyzer: Mastersizer 2000). Six sediment particle size categories were submitted to a principle component analysis (PCA). Extracted first component values were used as a proxy for sediment type (cf. Nolet et al. 2001b), and averaged per creek. In addition, water depth measurements were carried out at 5315 points (minimally 10 m apart) spread over the shallow (0-1.3 m) regions of the lake. The obtained depth values were standardized according to the actual water level of the lake monitored by the water managers (Waterschap Noorderzijlvest) measured four times per hour). Subsequently, an inverse distance weighting (IDW) interpolation technique, with a weight of 1.5, was used to generate a bathymetry map with a pixel-size of 5 m using ArcGIS 9.2 (ESRI, Redlands, USA). We obtained average water depth values per creek by applying the statistics function of ArcGIS on the bathymetry map.

Statistical analysis

Based on an experiment (2006c), in which the aboveground vegetation of fennel pondweed was removed either in June, July or August, resulted in a reduction of below-ground biomass of a respectively, 72%, 51% and 27%, compared to control plots. To calculate the cumulative summer grazing pressure per creek (G_c) of the most common waterfowl species we used the following equation:

$$G_c = (\sum t k t^*(N_{stc} * W_{sB})) / A_c.$$

In this equation, N_{stc} is the number of herbivores of a species s in month t in creek c , W_s is the body mass (kg) of species s (cf. Cramp and Simmons 1977), B is the scaling exponent of metabolizable energy intake in waterfowl, which was set to 0.78 according to Bruinzeel et al. (1997), and A_c is surface area (ha) of fennel pondweed vegetation in creek c (Gyimesi, Varghese, de Leeuw and Nolet, unpubl. data). Finally, k is the effect size of grazing in month t (i.e. 0.72, 0.51 and 0.27 in June, July and August, respectively; (Klaassen et al. 2006c)). The values of G_c were ln-transformed to reach normality. Subsequently, yearly cumulative grazing pressure values were correlated with mean autumn tuber densities per creek. As we specifically predicted a negative relationship between cumulative grazing pressure and tuber density, we applied a significance level appropriate for one-tailed analyses.

A best subset regression of generalized linear models was used with Akaike's information criterion, corrected for small sample size (AICc; Burnham and Anderson 2002), to test the importance of cumulative summer grazing pressure (G) compared to sediment type (s), water depth (d) and all their interactions. All statistical analyses were performed with Statistica 8.0 (Statsoft, Inc. 1984-2008, Tulsa, USA).

Results

Except for 2008, Mute swans were usually present in high numbers already in June (Fig. 1). On the contrary, the other species commonly showed increasing numbers throughout the summer. Especially coots tended to gather in large numbers only in August, often reaching a fivefold increase compared to June, except for 2007 when numbers remained relatively stable (Fig. 1).

Tuber densities were similar in 2005 and 2006 (mean for the whole lake $12.1 \text{ g m}^{-2} \pm 2.4 \text{ SE}$ and $11.1 \text{ g m}^{-2} \pm 1.8 \text{ SE}$, respectively). In 2007, tuber production was lower than in the two previous years (i.e. $7.6 \text{ g m}^{-2} \pm 1.3 \text{ SE}$), whereas 2008 was a richer year (i.e. $20.4 \text{ g m}^{-2} \pm 5.9 \text{ SE}$).

Due to the small differences in body mass among gadwall, mallard and coot, their metabolizable foliage intake is similar. However, the metabolizable foliage intake of the large bodied mute swans is at least six times higher than of the other waterfowl species. The regression analysis revealed that cumulative grazing pressure had a significant effect on tuber densities all four years of the study, when applying a one-tailed analysis (Figure 2, Table 1).

Due to their tremendous metabolizable foliage intake, mute swans seem to have the largest impact on tuber densities of the four studied species. In order to gain further insight in the foraging site selection of this important species, mean mute swan numbers of the four study years in the different creeks were correlated with average water depth. This analysis revealed that mute swans prefer shallow areas ($r^2 = 0.94$, $p < 0.0001$; Fig. 3).

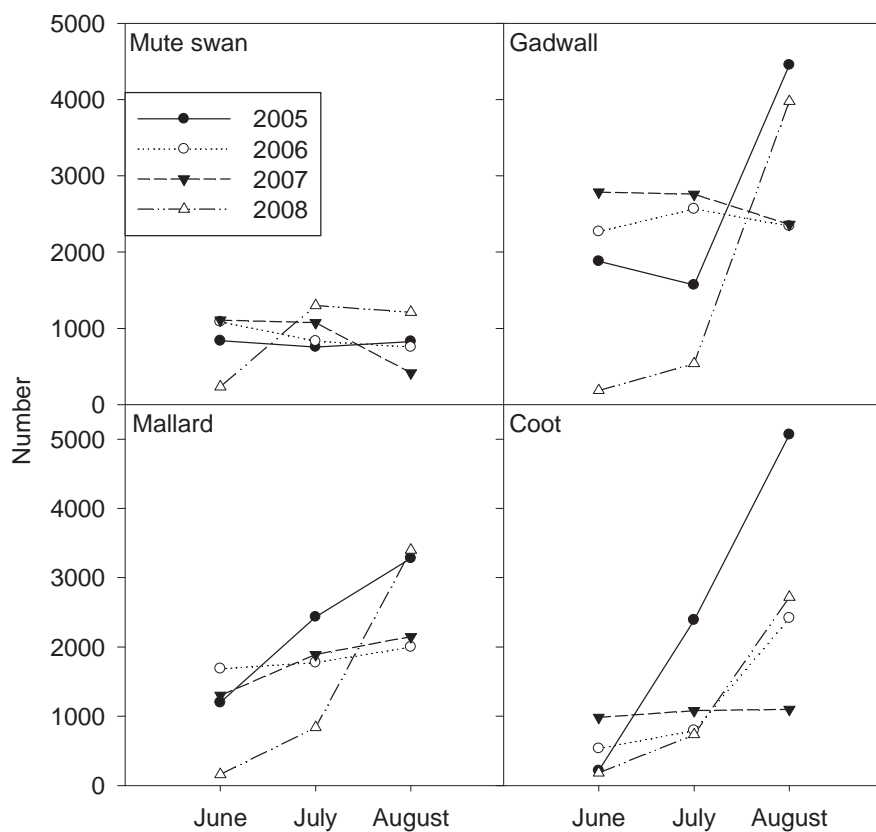


Fig. 1: Changes in the numbers of mute swan, gadwall, mallard and coot in the summer months 2005-2008 in the Lauwersmeer.

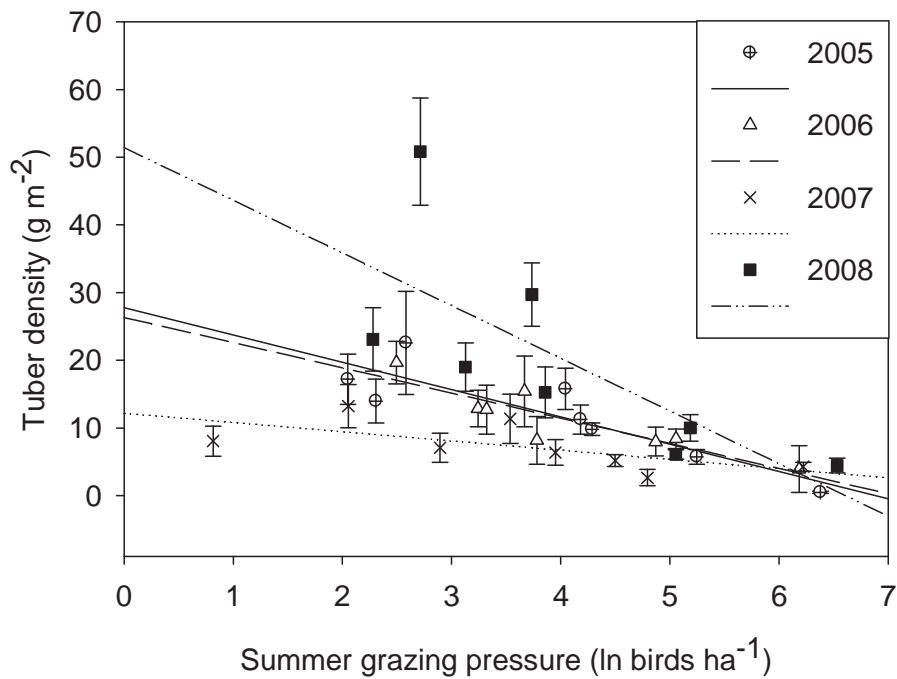


Fig. 2: Regressions between autumn tuber densities and cumulative summer grazing pressure (expressed as \ln -transformed bird density) per creek in 2005-2008. Symbols indicate means, bars standard errors. For statistics, see Table 2.

Table 1: Regression statistics between cumulative summer grazing pressure and autumn tuber densities per creek in 2005-2008.

	r²	p	intercept	slope
2005	0.78	< 0.01	27.8	-4
2006	0.8	< 0.01	26.3	-3.7
2007	0.42	0.08	12.2	-1.4
2008	0.54	< 0.05	51.4	-7.8

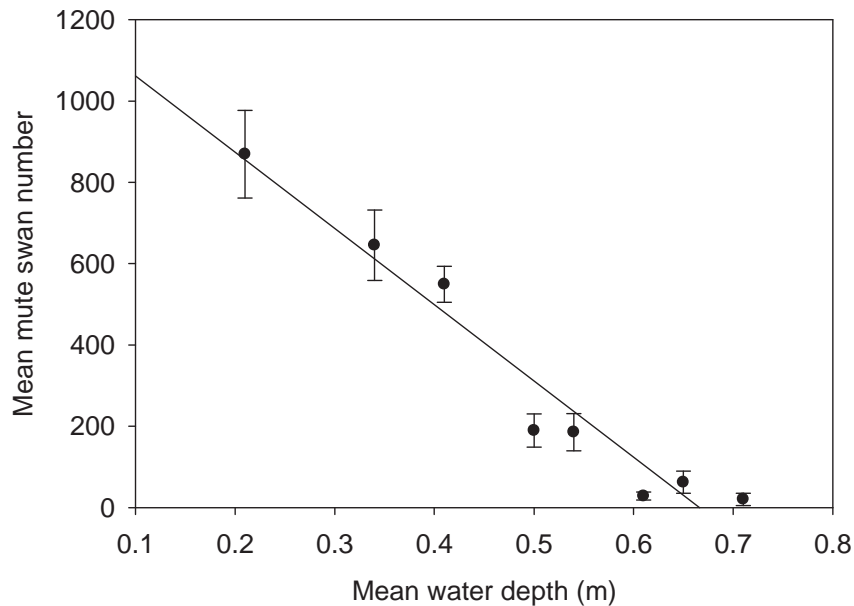


Fig. 3: Relationship between mean water depth per creek (x) and mean observed mute swan numbers per creek ($y = 1249 - 1874x$) in the summers of 2005-2008.

Based on the results of the generalized linear model analysis, cumulative grazing pressure seems to be the most important factor in forming autumn tuber densities at the Lauwersmeer. Except for 2007, cumulative grazing pressure had the lowest AICc value and interactions with water depth and/or sediment type generally ranked lower (Table 2).

Table 2: Order of models according to Akaike's information criterion, corrected for small sample size (AICc) testing the dependence of tuber biomass density in the autumn on cumulative summer grazing pressure (G), water depth (d), sediment type (s) and all their interactions.

	2005		2006		2007		2008	
	Model	$\Delta AICc$	Model	$\Delta AICc$	Model	$\Delta AICc$	Model	$\Delta AICc$
1	G	0	G	0	d	0	G	0
2	d	2.3	s	3.3	s	1.9	d	1.9
3	G*s	9.2	G*s	9.2	G	2.3	G*s	9.6
4	G*d	9.3	G*d	9.3	d*s	9.3	d*s	10.6
5	d*s	11.2	d*s	9.6	G*d	11.3	G*d	11.2
6	s	11.3	d	11.3	G*s	18.6	s	11.3
7	G*d*s	27.3	G*d*s	27.9	G*d*s	27.3	G*d*s	26.0

Discussion

In this study we show how herbivory in summer negatively affects tuber biomass production of fennel pondweed. Our predictions on the cumulative grazing pressure of the four studied waterfowl species suggest that body mass-related metabolizable intake of macrophyte foliage is a good proxy for species-specific effects of macrophyte consumption. In addition, we point out that the time of herbivory is of essential importance. Our findings revealed that, on the level of creeks, summer grazing can have relatively larger effect on tuber biomass densities than water depth and sediment type.

As the aquatic herbivores of the Lauwersmeer mainly rely on fennel pondweed as food source (Pot 1984, Santamaría 2002, Hidding et al. 2009b), their consumption may reach high levels when gathering in large numbers. Likely, summer grazing does not determine autumn tuber biomasses, only influences it, as weather conditions, wind fetch, local water depth and local sediment type can all affect plant growth as well as (e.g. Carr et al. 1997, van den Berg et al. 2003, Wersal et al. 2006). On the scale of a creek, summer herbivory did have a larger effect than water depth and sediment type (Table 2), and hence, creeks experiencing more intense summer herbivory showed lower tuber densities in the autumn (Fig. 2). However, future research should clarify the importance of storm events early in the summer, which can also cause great destruction in the aboveground vegetation (own observation).

A major impact on aboveground vegetation could be caused by the large-bodied mute swans: their metabolizable foliage intake is at least six times higher than of the other studied waterfowl species. Moreover, they reach peak numbers the earliest (i.e. June; Fig. 1), and hence can consume a considerable proportion of the biomass before the other species gather in large numbers (Kiorboe 1980, Hidding et al. 2009b). The long-necked swans are expected to utilize deeper water niches than the other species (Tatu et al. 2007). However, our results revealed that mute swans prefer the shallow sites at the Lauwersmeer (Fig. 3).

Water depth generally plays a key role in the foraging site selection of waterfowl (Schmieder et al. 2006, Bolduc and Afton 2008). As dabbling ducks can only reach the plants close to the water surface, down to approximately 0.3 m (Cramp and Simmons 1977, Guillemain et al. 2000), their foraging is limited to the shallow areas. Due to this large cumulative foraging pressure on these shallow sites locally nearly no aboveground vegetation is left intact (own observation). Often, water depth is applied to indicate the available foraging area to waterfowl, by taking the maximum foraging depth reached (Mitchell and Perrow 1998, Noordhuis et al. 2002). If food is abundant enough, however, herbivory will limit itself to the shallow areas (Noordhuis et al. 2002), and show a smaller effect in deeper parts. This, in turn, can cause a shift in the spatial distribution of the macrophytes preferred by waterfowl. Fennel pondweed, for instance, hardly occurs in water depths below 0.3 m (Kiorboe 1980, van Eerden et al. 1997, Sandsten and Klaassen 2002, Nolet et al. 2006b). As we show in this study, this phenomenon could at

least partly be explained (not to forget other factors, e.g. wind fetch, UV radiance: Scheffer et al. 1992, van Vierssen et al. 1994, van Nes et al. 2003) by the high grazing pressure in the summer occurring in this depth zone. Especially, if we consider that in such shallow waters even tubers can be consumed by ducks and mute swans (Anderson and Low 1976, Scheffer et al. 1992, Idestam-Almquist 1998, Badzinski et al. 2006).

It has been shown earlier that aboveground herbivory early in the summer has the largest effect on tuber production (Søndergaard et al. 1996, Klaassen et al. 2006c). The actual effect sizes of the timing of grazing found by Klaassen et al. (2006c) might of course be different in another system or even in the Lauwersmeer in another year. For instance, the vegetative growth cycle of the plants may largely influence the impact of grazing. In warm and early springs pondweed plants grow faster and start tuber formation earlier (van Wijk 1988). Therefore, by the time waterfowl species complete breeding and gather at large water bodies for moulting, a part of the tuber bank could be formed (Perrow et al. 1997), lowering the impact of vegetation herbivory. In contrast, under common spring conditions herbivores (especially mute swans) can consume already the emerging plants, leading to nearly no local tuber formation (Kiorboe 1980, Søndergaard et al. 1996). Another local characteristic of the Lauwersmeer is that certain creeks experience human disturbance whereas others do not. As human disturbance can have substantial influence on the spatial distribution of animals (e.g. Gill et al. 1996a, Klaassen et al. 2006a, Cresswell 2008), birds might avoid such areas and hence leave there more plant biomass (and consequently more tubers) than in undisturbed creeks (Gyimesi, Franken, Feige and Nolet, unpubl. manuscript).

Our study reveals that summer herbivory on the submerged macrophyte fennel pondweed has further implications than green matter reduction in particular. As plants in certain areas are systematically depleted year after year, the vegetation has no chance to recover (Anderson and Low 1976), which can eventually lead to the disappearance of the species. We believe that the largest effects are to be expected in shallow areas. This not only affects the spatial distribution of aboveground herbivores, but also creates a form of time-staggered competition with tuber consumers in the autumn. For instance, a prominent proportion of the Northwest-European flyway population of Bewick's swans uses the Lauwersmeer as a stop-over site during their autumn migration (Beekman et al. 1991). On the lake level, the extent of herbivory in the preceding summer does not directly seem to affect the number of Bewick's swans (Gyimesi, de Vries, de Boer and Nolet, unpubl. data), likely because the site selection of Bewick's swans is not only influenced by the available tuber density but also by the local costs to harvest them (Nolet and Klaassen 2009, Gyimesi, Varghese, de Leeuw and Nolet, unpubl. data). However, on the scale of a creek, Bewick's swans are shown to select foraging patches with the highest tuber density (Klaassen et al. 2006c, Nolet et al. 2006b). Therefore, by indirectly reducing tuber densities in the shallow zones, summer herbivory influences the spatial distribution of this species too. Therefore, Bewick's swans

are forced to forage in deeper water, which is energetically more costly, making the site generally less attractive. This time-staggered competition is especially intriguing in the sight of the significant increasing trend of mute swan numbers in Northwest-Europe (Kirby et al. 1994, Scott and Rose 1996).

It is worthwhile to pay attention to how alterations in the vegetative growth cycle of macrophytes under recent climate change scenarios influence the level of summer herbivory. It is expected that the start of spring will gradually advance in time. Whether or not the breeding cycle of waterfowl follows this trend, will have an effect on the timing of massive macrophyte herbivory. Besides the logical consequence of the large-bodied mute swans having the largest consumption of aboveground vegetation, we may conclude that herbivory early in the summer reduces the propagule banks (i.e. the treasury of future plants) of aquatic macrophytes the most.

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Chapter 3

Associated waterbird species consuming a single food resource: kleptoparasitism on the provider or true commensalism?

ABEL GYIMESI, BART VAN LITH and BART A. NOLET



One of the enthusiastic volunteers in the foraging experiment.

Abstract

Species associations are common in the animal world. However, it is often difficult to quantify whether the relationship can be described as kleptoparasitic (i.e. one species stealing food from another), mutualistic (i.e. both individuals derive a benefit from the association) or as commensalistic (i.e. one species benefits from the association while the other is unaffected by it). Here we report how groups of tundra swans foraging on water are often accompanied by ducks. Field observations confirmed that there is a strong correlation between the number of foraging swans and the number of foraging pochards, tufted ducks and pintails, with on average one diving duck per swan. We experimentally tested whether the species association of tundra swans and pochards can be described as kleptoparasitic or commensalistic. Food consumption of pochards and tundra swans was compared while foraging alone or in association with the other species, on food items buried in sediment in an experimental basin. The results revealed that pochards, in the company of a feeding swan, can reach up to seven times higher food intake rates than foraging alone. We show that this is mainly due to gleaning food items that float away from the swans and not due to stealing: food intake rates of swans were not affected by the presence of a pochard. Our study provides an example how a relationship previously described as kleptoparasitic based on field observations proves to be commensalistic, with one species facilitating another, and shows how stable species associations can exist in nature.

Introduction

Ecologists have long recognized the importance of interspecific relationships between animals (Pielou 1974). However, most attention has been given to the negative aspects of such relationships (i.e. predation and competition, see Keddy 1989). Although positive effects of one species on another (i.e. mutualism and commensalism) can be just as important, these have received considerably less attention. For instance, in foraging ecology, the co-occurrence of different species consuming the same food source is generally described as kleptoparasitism, where one species is stealing food from another (e.g. Ens and Goss-Custard 1984, Percival and Evans 1997, Dubois and Giraldeau 2005). As the food loss caused by a competing species can be considerable, it is commonly thought that such species should show spatial segregation or behavioral adaptations to reduce the effects of interspecific competition (Kotler and Brown 1990, Rodriguez 1995, de Leeuw 1999, Avgar et al. 2008). However, costs and benefits of associative foraging under controlled conditions have hardly been evaluated (but for field experiments see e.g. Hino 1998, Stienen and Brenninkmeijer 1999). In fact, in some cases it cannot be excluded that such species associations could be described as commensalistic, where one species benefits from the relationship while the other remains unaffected (e.g. Hino 1998, Dijkzen and Ouweneel 2005, Kallander 2005).

The relevance of this distinction goes beyond the calculation of actual food intake

rates. Kleptoparasitism negatively affects one of the species, which logically should lead to an adaptation to reduce the food loss. This adaptation can be a change in foraging technique (i.e. behavioral), in food preference, or in foraging habitats. Commensalistic species, on the other hand, can form a stable relationship, as neither of the species has an advantage in altering it. Moreover, within a certain population, individuals forming a commensalistic relationship enjoy an advantage due to their higher intake rates over individuals that do not engage in such a relationship. This in turn can lead to higher survival rates, increased breeding success, and elevated dominance status.

Our study is based on tundra swans (*Cygnus columbianus bewickii*) visiting the Lauwersmeer, a shallow lake in the northern part of the Netherlands. Here they feed on the tubers of sago pondweed (*Stuckenia pectinata*) for a few weeks before switching to forage on agricultural lands (Beekman et al. 1991, Nolet et al. 2001b). Sago pondweed forms nearly monospecific stands in the shallower (> 1 m) parts of the lake (Pot 1984, van Wijk 1988, Hidding et al. 2009b). Tubers, the asexual reproduction organs of this plant, are buried in the sediment up to 0.35 m (Santamaría and Rodríguez-Gironés 2002, Hidding et al. 2009c). Tundra swans have a special foraging technique to harvest the tubers. By trampling in the water, tundra swans create approximately 1 m² pits in the sediment (van Eerden et al. 1997, Klaassen et al. 2006c). The trampling whirled up the sediment, together with the tubers within. The heavier sediment particles settle quicker in the pit than the tubers, hence these latter get accumulated on the top.

Groups of foraging swans are commonly followed by a large number of foraging waterfowl (Sherwood 1960, Bailey and Batt 1974, Oksanen et al. 1979, Rees 1990). These latter can belong to various species but in the Lauwersmeer most often to pochards (*Aythya ferina*) and tufted ducks (*Aythya fuligula*) (Nolet et al. 2002). It has been suggested earlier that these accompanying birds may steal tubers whirled up by foraging swans (Beekman et al. 1991). Even though they have a much smaller size than swans, they can be present in great numbers. In a preliminary calculation, Nolet et al. (2002) estimated that the consumption of pochards and tufted ducks can cause up to 30% of the total depletion of pondweed tubers in the Lauwersmeer.

However, whether the relationship between tundra swans and other waterfowl can be described as kleptoparasitic has never been challenged experimentally, and a commensalistic relationship remains a valid alternative. The true type of relationship could play an important role, for instance, in site selection and in the timing of habitat switching (Rees 1990). If ducks kleptoparasitize tundra swans, it could reduce the value of the site for this latter group, lead to an earlier habitat switch and swans would be expected to show aggressive behavior towards ducks. On the other hand, if the relationship is commensalistic, ducks could profit undisturbed from the foraging activities of swans and would be expected to closely follow feeding groups of swans.

In this paper we first focus on observed numbers of tundra swans and accompanying duck species, in order to find evidence for species associations. Further we report

on the results of a controlled foraging experiment with tundra swans and pochards that intended to reveal the casual relationship between the two animal species. Based on the results, we discuss the ecological importance of this species' association in the field.

Methods and materials

Field data

Field observations were carried out in the shallow lake Lauwersmeer (1970 ha; 53° 22'N, 06° 13'E). Autumn foraging tundra swan and foraging duck numbers were registered hourly ($n = 92$) throughout the exploitation period of 1995 in one creek (Bab-belaar) of the Lauwersmeer. In 2005, 2006 and 2007 daily counts on foraging tundra swans and accompanying pochards and tufted ducks were carried out in four different creeks of the Lauwersmeer.

Experiment

The experiment took place between the end of February and the beginning of April 2008. It was carried out in a basin of 39 m² surface area. A metal tray (measuring 1 × 1 m with 0.1 m high sides) was placed in the middle of the basin. The tray was completely filled with sand, with wheat grains homogeneously spread at 0.05 m depth. Water saturated wheat grains are similar to pondweed tubers in nutrient composition and size, and have successfully been used in earlier foraging experiments to replace tubers (Nolet et al. 2001b, Nolet et al. 2006a). Finally, the sand was tamped down for higher compaction. Trials were carried out with one of four food densities (i.e. 16 g, 30 g, 52 g, and 74 g m⁻² fresh weight). Water depth was set at 0.45 m above the sediment.

Four pochards (two males and two females) and four tundra swans (two males and two females) took part in the experiment (all > one year old). One tundra swan was caught in the wild and had been in captivity for at least 5 years prior to the experiment, whereas all the other birds were born in captivity. Birds were fitted with leg rings for individual recognition. The immediate surroundings of the basin formed their standard housing for at least a year prior to the experiment. Outside the trials, the birds could make use of the whole basin. During the trials, a 3 × 3 m area was set off for the animals not involved in the current measurements.

In order to familiarize them with the experimental facilities and procedure, the birds were trained for five weeks prior to the experiment. At the end of the training period the animals behaved naturally during the trials and mostly started foraging as soon as they got access to the tray. During the training and the experiment, food was offered only during the morning trials and in the afternoons (between 13:00 and 17:00 hours). All individuals were involved in a combined trial (a swan and a pochard together), and a trial without the other species (a swan or a pochard alone) in each of the four

food densities. This resulted in altogether 48 experimental trials (4 individuals x 4 food densities x 3 forager combination). In order to reduce the effect of different levels of food depletion in the treatments, preliminary estimations on the intake rates of tundra swans based on training results were used to determine trial lengths. For the swan trials, the length was set to 120 seconds cumulative feeding time (i.e. time spent under water), 360 seconds for the pochard trials and 90 seconds swan feeding time for the combined trials.

All trials took place in the morning hours between 8:30 and 13:00. Per day two to four trials were carried out. The order of the trials was randomized, with the restriction that birds entered only one trial per day. The trials were filmed above water (Panasonic NV-GS15) and under water (Pinnacle studio v70205). Cumulative feeding times (see above) of pochards in the combined trials and trampling times were measured from the videos.

After each trial, the sediment of the tray was pumped through a sieve with 3 mm mesh size to collect the wheat grains left behind by the animals. Besides, seeds lying at the bottom of the basin outside the tray were collected separately. Finally, the collected seeds were dried for 48 hours at 60 °C to obtain dry weight (all further weights refer to dry weights). Parallel to a trial, the same amount of seeds as offered in the trial received an identical treatment as a control (put in water and later dried). The amount of consumed seeds was determined by subtracting the weight of the collected seeds from the weight of the control seeds. Intake rates in the individual trials were calculated by dividing the amount of consumed seeds by underwater feeding time. In the obtained dataset, all measured seed weights needed ln-transformation for normality. A GLM (Type III decomposition) with food density, trampling time and their interaction term was used to investigate what affected the amount of seeds found outside the tray after a swan trial.

Results

Field data

During the hourly counts carried out in a single creek in 1995, foraging pochards, tufted ducks, pintails (*Anas acuta*), mallards (*Anas platyrhynchos*), shovelers (*Anas clypeata*), wigeons (*Anas penelope*) and shelducks (*Tadorna tadorna*) were observed in the vicinity of foraging tundra swans. For normality of the dataset, both tundra swan and duck numbers were ln-transformed and subsequently analyzed using ordinary linear regressions with swan numbers as independent and duck numbers as dependent variables. The analyses revealed that the numbers of foraging pochards, tufted ducks, mallards, pintails and wigeons were positively correlated with the number of foraging tundra swans (Table 1). However, the coefficients of determination by mallards and wigeons were low (i.e. $r^2 < 0.12$). The sum of the numbers of the two best correlated diving duck

species (i.e. pochards and tufted ducks) closely followed the number of tundra swans (Fig. 1). The ratio of diving ducks per foraging swan gave a median of 0.75.

Table 1: Regression matrix of observed foraging tundra swan numbers versus observed foraging duck numbers (both ln-transformed) in one creek of the Lauwersmeer. Intercept and slope are given for the significant relationships.

Species	Mean nr /foraging swan	r2	p	intercept	slope
Pochard	2.54	0.78	< 0.00001	0.38	0.76
Tufted duck	0.19	0.55	< 0.00001	-0.19	0.59
Pintail	2.96	0.45	< 0.00001	0.57	0.45
Mallard	0.01	0.11	< 0.01	0.02	0.2
Shoveler	0.14	0.001	> 0.7		
Wigeon	0.01	0.05	< 0.05	-0.04	0.05
Shelduck	0.06	< 0.00001	> 0.9		
Diving ducks	2.73	0.81	< 0.00001	0.52	0.81

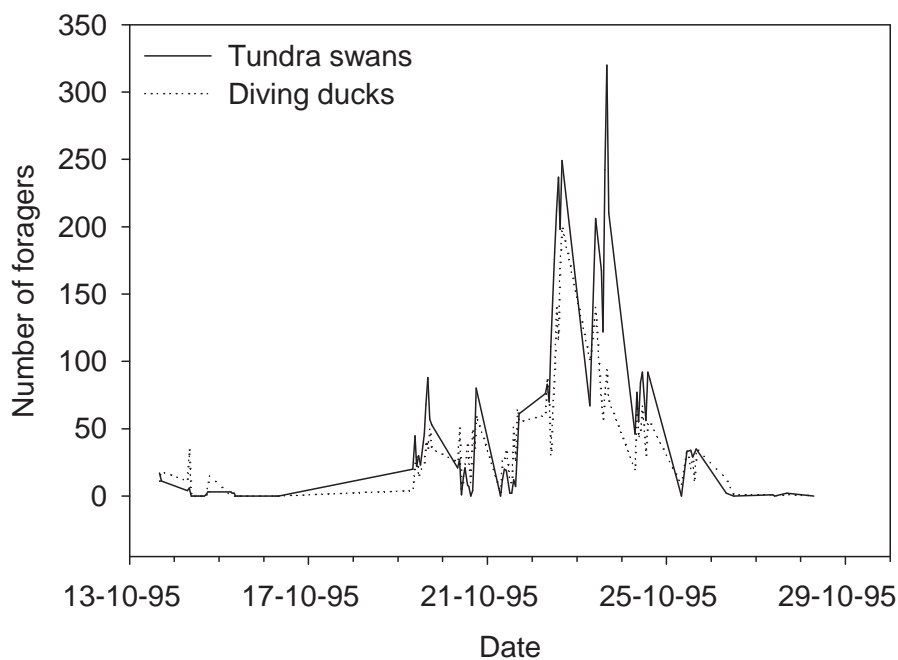


Fig. 1: Number of foraging tundra swans and diving ducks (pochards + tufted ducks) counted hourly in a single creek in autumn 1995.

In the period 2005-2007, daily tundra swan and diving duck counts were averaged per creek per year and square root transformed. Foraging swan flocks and accompanying ducks were observed on average $7.4 (\pm 3.9\text{SD})$, $12.5 (\pm 4.7\text{SD})$ and $5 (\pm 5\text{SD})$ days per creek, respectively. In a GLM analysis (type III decomposition), the effect of observation year alone or in interaction with swan numbers on diving duck numbers proved to be not significant ($F_{2, 6} = 0.26$, and $F_{2, 6} = 0.28$, respectively; both $p > 0.7$). Therefore, data of the three years was pooled together and the relationship between foraging tundra swans and foraging diving ducks was tested with a simple linear regression. The analysis revealed a close positive association ($p < 0.001$, $r^2 = 0.72$; Fig. 2). In this case, the ratio of diving ducks per foraging swan gave a median of 0.97, indicating that on average approximately one diving duck is following one foraging swan. Shapiro-Wilk tests proved that the residuals of all the regressions were normally distributed.

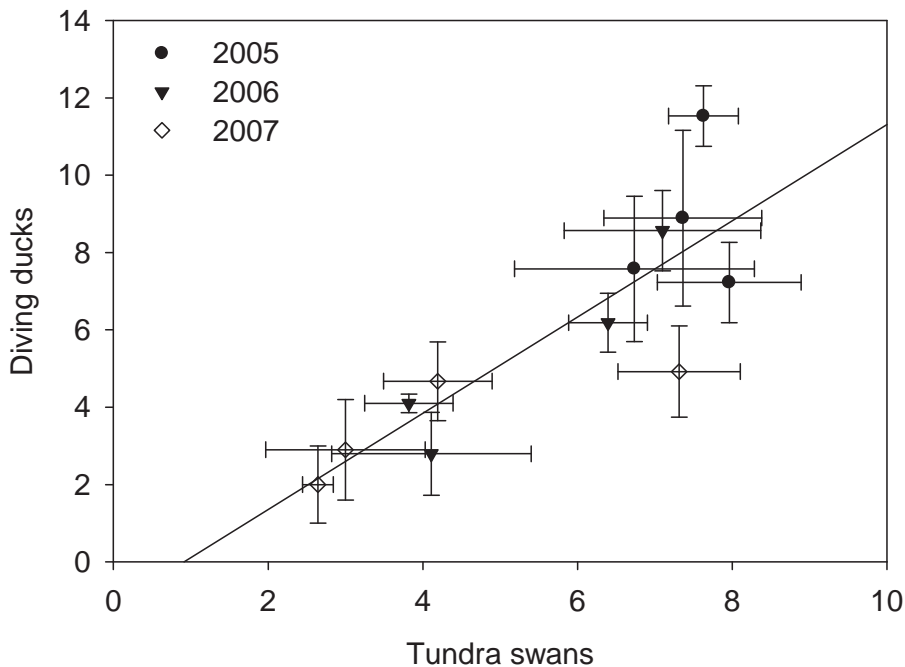


Fig. 2: Linear regression between number of foraging tundra swans and foraging diving ducks (both square root transformed) in four creeks of the Lauwersmeer in autumn 2005-2007. Symbols represent means, bars standard errors.

Experiment

In individual trials, both swans and pochards spent all their feeding time on the tray. The underwater video recordings revealed that pochards are applying filter-feeding from the sediment, while tundra swans are collecting the seeds accumulated in their foraging pit. In the combined trials, the swans were again feeding from the tray but the pochards kept distance from the foraging swan and collected the seeds spread out at the bottom of the basin. Based on the underwater video recordings, only one occasion was documented in which a pochard was searching in the tray while the swan was also feeding there.

Considering only the swan trials, the amount of seeds found outside the tray was only affected by total trampling time ($T_{\text{trampling}}$; Table 2), increasing with time spent trampling ($\ln \text{seeds outside} = 1.09 + 0.04 * T_{\text{trampling}}$). Total trampling time did not differ significantly between the swan trials and the combined trials (t-test: $t_{1, 30} = -0.67$, $p > 0.5$). Therefore, based on trampling time alone, the same amount of seeds was expected outside the tray. However, the amount of seeds found *outside the tray* was lower in the combined trials than in the swan trials (t-test: $t_{1, 30} = -2.93$, $p < 0.01$; Fig. 3), indicating food consumption outside the tray by the pochards. The amount of seeds *in the tray* showed no difference between swan trials and combined trials (t-test: $t_{1, 30} = 0.4$, $p > 0.6$).

Considering both swan and combined trials, total trampling time and initial food density affected the amount of seeds left in the tray, whereas total feeding time (i.e. trial length) did not (Table 3). After correcting for food density, the seeds left outside the tray differed between the swan trials and the combined trials (factorial ANOVA, effect of treatment: $F_{1, 24} = 31.88$, $p < 0.00001$; Fig. 4), whereas the amount of seeds left inside the tray did not (factorial ANOVA, treatment effect: $F_{1, 24} = 0.81$, $p > 0.3$; Fig. 4).

Table 2: ANOVA table (Type III decomposition) of the independent variables food density and total trampling time ($T_{\text{trampling}}$) on the amount of seeds found outside the tray. Lines in *italics* refer to statistical significance.

	SS	Df	MS	F	p
Intercept	2.405072	1	2.405072	30.01113	0.000589
Food density	0.293442	3	0.097814	1.22055	0.363500
<i>Ttrampling</i>	0.635509	1	0.635509	7.93005	0.022632
Food density* <i>Ttrampling</i>	0.273008	3	0.091003	1.13556	0.391386
Error	0.641115	8	0.080139		

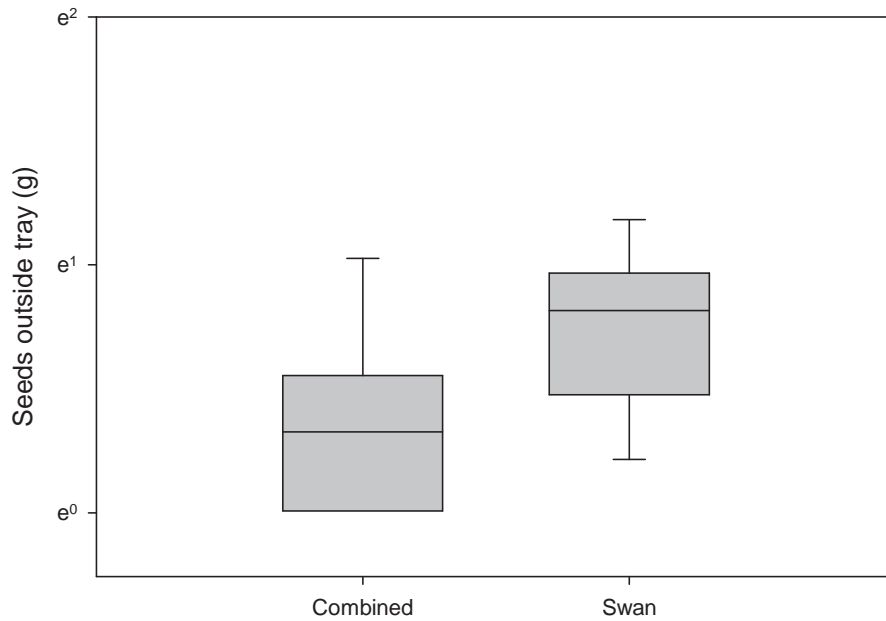


Fig. 3: Amount of seeds found back outside the tray after a trial of either a combined (i.e. swan + duck) or a swan trial. Note natural log scale used for the y-axis. Lines represent medians, bars 5th/95th percentiles.

Table 3: ANOVA table (Type III decomposition) of the independent variables total feeding time (*Tfeeding*), total trampling time (*Ttrampling*) and initial food density on the amount of seeds found inside the tray. Lines in *italics* refer to statistical significance.

	SS	Df	MS	F	p
Intercept	6.853884	1	6.853884	207.1011	0.000000
<i>Tfeeding</i>	0.027133	1	0.027133	0.8199	0.375487
<i>Ttrampling</i>	0.537582	1	0.537582	16.2439	0.000604
Food density	9.099031	3	3.033010	91.6472	0.000000
Error	0.694982	21	0.033094		

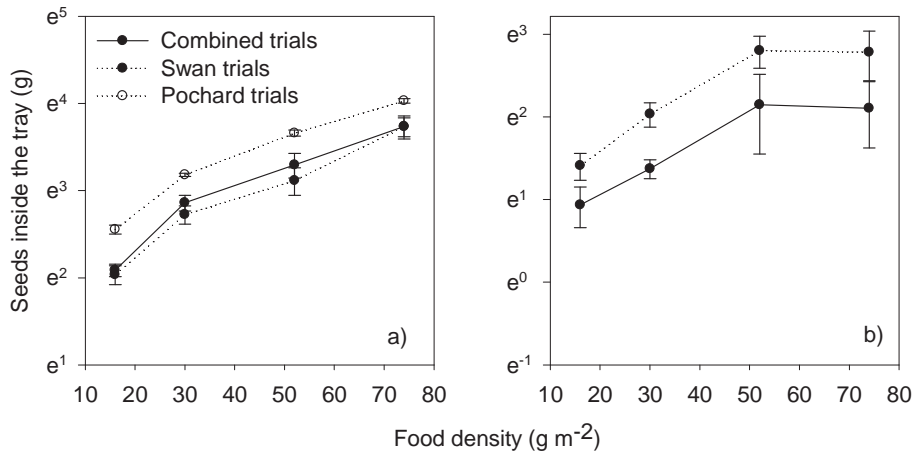


Fig. 4: Amount of seeds found after a trial inside (a; left) or outside (b; right) the tray of either a combined (i.e. swan + pochard; solid line, closed symbols) or a swan trial (dotted line, closed symbols) in four food density treatments. For comparison, pochard trials are presented with open symbols (no seeds found outside the tray in these trials). Note natural log scale used for the y-axis and different ranges for the two panels. Dots represent means, bars standard errors.

Intake rates of both tundra swans and pochards were calculated. In case of the combined trials, the calculations relied on the assumption that pochards were only foraging outside the tray, and swans only inside the tray. Hereby, the amount of seeds outside the tray was predicted based on the regression with trampling time. Pochard intake rates were calculated by subtracting the actually measured amount of seeds outside the tray from the prediction and subsequently dividing by the underwater feeding times. Swan intake rates were calculated by subtracting the seed consumption by pochards from the total amount of missing seeds and subsequently dividing by the underwater feeding times. After correcting for food density, the functional responses revealed that pochards on average could reach up to seven times higher intake rates by foraging on the food that drifted away from the foraging pit of a swan than foraging by themselves (factorial ANOVA, treatment effect: $F_{1, 24} = 13.94$, $p < 0.01$; Fig. 5). The functional response of swans, on the contrary, remained unaffected by the treatment (factorial ANOVA, treatment effect: $F_{1, 24} = 0.002$, $p > 0.9$; Fig. 5).

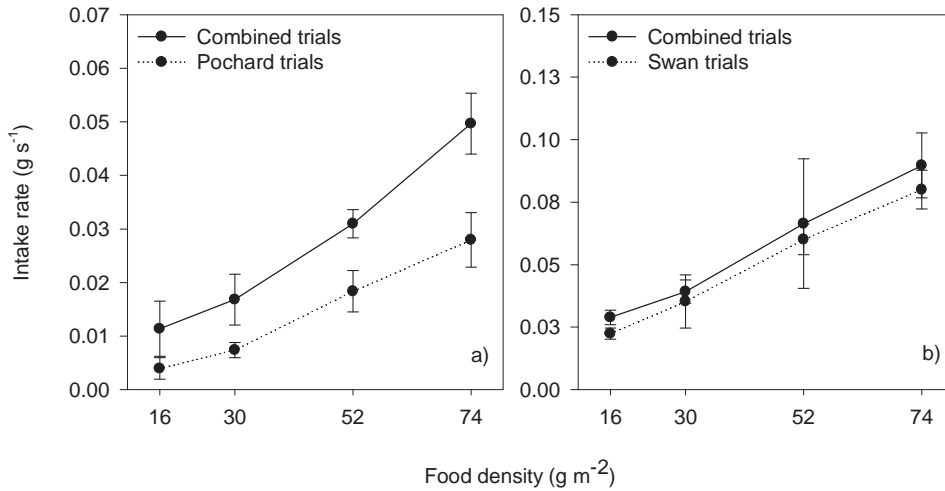


Fig. 5: Predicted functional responses of pochards (a; left) and swans (b; right) in combined (i.e. swan + pochard; solid line) and single trials (dotted lines). Dots represent means, bars standard errors. Note the different scale ranges on the y-axes.

Discussion

In this study we show how different waterbird species form species associations in the field. From a large number of tested duck species, pochards followed most strongly the distribution of foraging tundra swans. The relationship was further improved when the two diving duck species (i.e. pochards and tufted ducks) were summed. This close match proposes an energetic benefit for these diving ducks to stay in the vicinity of swans. Our experiment reveals that the relationship between tundra swans and pochards is commensalistic rather than kleptoparasitic: the foraging behavior of the swans facilitates diving ducks, while the former are unaffected by the presence of ducks.

The detailed hourly scans in one creek of the Lauwersmeer show that tundra swans arriving from migration are not simply joining a group of ducks already present at the site. In this latter case, the duck numbers would remain constant with fluctuating swan numbers (Fig. 1). The hourly scans may have been affected by temporal autocorrelation, but observations carried out in other creeks of the lake in three other years confirm that the relationship between tundra swans and diving ducks is a common phenomenon (Fig. 2).

While exploiting their foraging pits, swans make only short movements (i.e. <1 m) (Klaassen et al. 2006c). Only after reaching a certain quitting harvest rate (Nolet and Klaassen 2009), they move a longer distance, away from the patch (Klaassen et al. 2006c). This was also confirmed in our experiment, where swans also kept their position above their foraging pit in all cases. Since the consumed amount of food from

the tray (i.e. the foraging pit in our case) was not different between swan trials and combined trials (Fig. 4), we can conclude that swans did not suffer from food depletion by pochards.

Thanks to their special foraging technique, tundra swans can accumulate a large food density in their pit. As a result, they can reach much higher intake rates than by simple filter-feeding (Gyimesi and van Lith unpublished data). Moreover, the food that drifts away from the foraging pit is spread out over a large area and forms a much lower density than in the foraging pit. Therefore, we are confident that swans do not attempt to invest time in finding these food items. Diving ducks (including pochards) are also known to consume tubers of sago pondweed (Olney 1968, Bartonek and Hickey 1969, Anderson and Low 1976). However, their natural giving up density (i.e. the amount of food left behind) is much lower than of tundra swans (Lovvorn and Gillingham 1996). Therefore, they do target to collect the food items drifted away from the swans, and by doing so they can considerably increase their intake rate compared to when food items are buried in the sediment (Fig. 5). Interestingly, we observed some pochards in the individual trials to take up the habit of trampling. Even though it had no effect on their intake rate ($F_{1,9} = 0.31$, $p > 0.5$), it might be a useful technique in certain cases (e.g. when food is buried shallower or the water is less deep), as wild pochards are also known to apply trampling (Simmons 1968).

Pochards and tufted ducks as diving ducks have a similar foraging technique. The fact that the sum of these two species gave the best correlation with tundra swan numbers, and that the ratio of diving duck per foraging swan was close to one, suggests an energetic optimum of one duck joining a swan. Likely, this raises interspecific competition among duck species. Our results revealed that tundra swans are also followed by dabbling duck species (Table 1). These birds search for prey on, or close to, the water surface, and hence cannot be considered competitors to bottom-foraging tundra swans. Still, the foraging activities of tundra swans seem to create profitable circumstances for dabbling ducks as well, probably by whirling up invertebrates from the sediment. All in all, our study system gives a good example of how one species (tundra swans in our case) can facilitate a whole community.

Species associations have often been described (see review in Seppanen et al. 2007). However, these studies usually regard animals that consume different prey. On the other hand, heterospecific competition for the same prey is also a key aspect in ecology as it can largely affect the habitat selection of species (Pimm et al. 1985). The presence of one species, for instance, can be attractive to another species (Seppanen et al. 2007, Forsman et al. 2008), especially in the case of direct facilitation of food consumption (van der Wal et al. 2000). Often, however, a close match in observed numbers between different species is thought to be a case of kleptoparasitism (see review in Brockmann and Barnard 1979). Based exclusively on field observations, diving ducks could easily be interpreted as kleptoparasitizing tundra swans (Beekman et al. 1991). The experi-

mental results, however, show that pochards do not negatively affect tundra swans. On the other hand, ducks are not expected to have a positive influence either, e.g. in the form of sentinels for danger, as swans do not have real natural predators in North-western Europe and can detect threat earlier than the small diving ducks (Blumstein et al. 2005). Therefore, the two species most likely form a commensalistic relationship instead.

Albeit our experimentally created conditions not closely match field conditions, and hence the derived functional responses of pochards or tundra swans (for that see Nolet et al. 2001b, Nolet et al. 2002) are not generally applicable, we have no reason to doubt that the behavior observed in the experiment also applies to the field. Likely, diving ducks always keep a safe distance from the much larger swans and do not risk stealing from them. On the other hand, the predicted functional responses suggest that they can reach up to seven times higher intake rates by foraging on the food lost by the swans than by foraging on their own. Even if the actual intake rates in the field are different from those observed in our experiment, the differences were so large that the benefit of following the swans seems undeniable.

We have no evidence that diving ducks follow tundra swans on their migration, as that would result in an influx of diving ducks to the study area at the same time as tundra swans arrive, which is not observed (J. Willems, unpublished data). On the other hand, our observations clearly reveal how the local population accumulates around the groups of foraging swans (Fig. 1). Nowadays, tundra swans spend most of the winter on agricultural land (Dirksen et al. 1991). Historically, however, tundra swans spent the whole winter on freshwater habitats (Brouwer and Tinbergen 1939). It is an intriguing idea that earlier diving ducks could profit from swans throughout the winter. Considering the increase in intake rate pochards can reach, such association with swans could certainly help in surviving winters when food is scarcer.

Most of the described species associations are based on field observations. Unfortunately, quantitative descriptions of the eventual costs and benefits are largely lacking. The strength of our study is that we experimentally tested what the general reasons are for the association between tundra swans and pochards. However, future research could clarify further details of such relationships between two species. For instance, how the profitability of associating changes with food density and with availability or visibility of the food. Besides, whether accompanying animals have a preference to follow individuals that lose more food items (i.e. animals of lower foraging efficiency). Nowadays, when most of the European diving duck populations are showing a decline in numbers (Scott and Rose 1996), insights from such studies might have a great relevance.

Acknowledgements

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Chapter 4

Cryptic interference competition in swans foraging on cryptic prey

ABEL GYIMESI, RICHARD STILLMAN and BART A. NOLET



A Bewick's swan being angry.

Abstract

Interference (i.e. the reduction of intake rate caused by behavioural interactions) can be a key component of food competition and an important density-dependent feedback mechanism limiting the carrying capacity of a site. However, measuring the strength of interference is often difficult in free-living animal populations. In particular, separating the effects of interference and exploitative (depletion) competition can be problematic. We use an individual-based interference model to investigate how the intake rates of free-living Bewick's swans (*Cygnus columbianus bewickii*) foraging on cryptic tubers of fennel pondweed (*Potamogeton pectinatus*) change with increasing competitor density. The model does not incorporate depletion of the prey, and so any predicted reduction in intake rate at higher forager densities is due to interference competition. The model predicts that intake rate declines with increasing swan density, and that the rate of decline is much greater in lower dominance birds than in higher dominance birds. Subdominant birds suffer a large reduction in intake rate at high competitor densities because they spend a large proportion of the time avoiding more dominant individuals, and hence not searching for food. The major decline in the intake rate of sub-dominants occurs close to the maximum competitor densities that were observed in two different years in the field. Therefore, we expect that subordinates leave high density groups and look for another foraging location. Thereby, swans seem to regulate their group density in order to minimize the effects of interference. Hence, the mean population intake rate at field-observed competitor densities is only slightly lower than achieved in the absence of interference. As the effects of interference were mainly due to avoidance behaviour, which is difficult to observe in the field and commonly remains cryptic for the observer, interference may be easily underestimated. Our results can help to explain other field studies in which no relationship was found between competitor densities and intake rates.

Introduction

It is generally accepted that there must be an upper limit to the number of animals a site can support, defined as the carrying capacity of the area (Pielou 1974). Nowadays, it is a commonly used criterion for evaluating the quality of a site (Goss-Custard 1985, Sutherland and Allport 1994, van Gils et al. 2004). Calculations of carrying capacity often rely on the assumptions that all animals are identical and interference-free (Goss-Custard et al. 2003). The ideal free distribution (Fretwell and Lucas 1970) predicts that, in the absence of interference and given perfect knowledge and negligible travel costs, all individuals should forage in the best quality foraging site in order to maximize their intake rate (Sutherland 1983). However, as noted by Fretwell and Lucas (1970), the suitability of a site will often decrease as the number of competitors increases. Commonly, animals living in groups can not be considered interference-free. Their distribution is in fact a trade-off between the benefits of feeding in sites with more resources

but also with more competitors, or in sites with fewer resources and fewer competitors. Therefore, the maximum number of individuals a site can support depends both on the amount of resources present and the number of competitors that are exploiting these resources (Goss-Custard 1980, Rowcliffe et al. 2004, Vahl et al. 2005b). Following this reasoning, the observed maximum number of individuals can not be defined as the carrying capacity of a site (Moser 1988, Schekkerman et al. 1994, van Gils et al. 2004).

Depletion of food by other animals (i.e. exploitative competition, see e.g. Krebs 2001) creates lower resource densities, and hence can cause a reduction in an individual's intake rate. Through interference competition, on the other hand, the presence and behavioural interactions with a competitor causes a decline in intake rate. This can be due to, for instance, creating a barrier to the resource (Cresswell 1997), losing time through interactions (Stillman et al. 1997, Smallegange and van der Meer 2007) and stealing prey items (i.e. kleptoparasitism, see Goss-Custard et al. 1982) or foraging patches (Vahl and Kingma 2007). When interference competition occurs, intake rates are not only determined by the available food biomass and the individual's foraging efficiency, but also by the density of the competitors and the susceptibility of individual animals to interference (e.g. due to their dominance). Goss-Custard (1985) introduced the use of carrying capacity of a stopover site for migratory birds as the cumulative number of animals ('bird-days') that can be accommodated by food for a certain period of time. However, this method assumes no reduction in intake rate at higher forager densities. When interference competition does occur and reduces intake rates, neglecting this process could lead to a large overestimation of the site's carrying capacity (Goss-Custard et al. 2002).

Despite numerous efforts to quantify the effect of interference competition on the intake rate of animals, it remains a difficult task. First of all, it is troublesome to disentangle interference competition from exploitative competition (Smallegange et al. 2006; Bijlveld et al. unpublished data), especially when food items are cryptic (Stillman et al. 2002a). Moreover, due to the complexity of natural animal behaviour, it is often difficult to identify the pure effects of interference competition on intake rate merely by field measurements (Sutherland and Koene 1982, Rowcliffe et al. 1999b, Nolet et al. 2002, Badzinski 2003, Vahl et al. 2007). Particularly, if the main outcome of interference competition is animals subtly avoiding each other (Cresswell 1997, Moody et al. 1997), which may not be easy to separate from interference-free movements.

In order to exclude exploitative competition (by making e.g. food items non-depletable) and just identify the effects of interference competition on intake rate, a modelling approach is a good alternative (Moody and Houston 1995). Hereby, a clear connection can be made between natural forager densities and the development of individual intake rate, without the confounding effect of exploitative competition (Stillman et al. 2002a). Such results can give insight into the importance of distinct interference parameters in a free-living animal population. By this means, it becomes also possible to va-

validate the general significance of interference competition in determining the carrying capacity of a real-life system. Despite its advantages, such approach has been applied for quantitative predictions only in a limited number of studies and only for a few systems (Stillman et al. 1997, Stillman et al. 2002a, Stillman et al. 2002b).

In this study, we test the hypothesis that interference competition has a marginal effect in a freshwater system where consumers forage on cryptic resources, namely Bewick's swans (*Cygnus columbianus bewickii*) foraging on the belowground tubers of the aquatic macrophyte, fennel pondweed (*Potamogeton pectinatus*), in the Lauwersmeer, The Netherlands. On the other hand, we expect interference competition to affect the carrying capacity of this system by limiting the maximum number of animals that can forage together. Based on field observations, it was shown earlier that exploitative competition plays a large role in our particular study system (Nolet et al. 2006b). However, no relationship was found between forager densities and the proportion of birds involved in a social interaction (i.e. a correlate of interference) (Nolet et al. 2002). In order to attain the direct effects of interference competition on individual intake rates, disentangled from exploitative competition, here we present a modification of an existing interference model (Stillman et al. 2002a) parameterized for Bewick's swans, show how individual intake rates change with competitor density and highlight the effect at naturally observed densities.

Methods and materials

The model is individual-based, and follows in a spatially explicit manner the behaviour of individuals foraging in a two-dimensional square arena. Food items / patches are homogeneously distributed. The model progresses in discrete, fixed length time steps. During each time step, each animal can occupy one of four behavioural states, *searching* for food, *handling* food, *fighting* with a competitor or *avoiding* a competitor. At the start of simulations all individuals are given a random location and movement direction within the environment and are set to the searching state. In subsequent time steps, the model predicts changes in the location and behavioural state of animals as they move and encounter food and competitors. The model is described in detail in earlier studies (Stillman et al. 1997, Stillman et al. 2000, Stillman et al. 2002a), and so we only describe the parameterization for Bewick's swans.

We used a modification of the model used to predict the strength of interference competition in common cranes (*Grus grus*) foraging on buried cereal seeds (Stillman et al. 2002a). A key factor in our study system is that Bewick's swans are maximizing their net energy intake rate, instead of satisfying their needs (Nolet et al. 2006b). The model assumes that swans search for and compete over discrete food patches, instead of individual food items as assumed in other models (Stillman et al. 1997, Stillman et al. 2000, Stillman et al. 2002b). Each patch contains an initial amount of food, which swans are able to consume when they occupy a patch. We assume that food resources

within a patch are gradually depleted while a patch is occupied by a swan. However, for simplicity, we assume that food density within a patch is reset to its initial value as soon as the swan leaves the patch. Hence, the effects of exploitative competition (i.e. depletion) are excluded: swans never encounter partially depleted patches. Therefore, any reduction in intake rate with increasing competitor density provides the mere effect of interference competition.

Individual model swans are randomly attributed a dominance position in a linear hierarchy. We assume that swans have perfect knowledge of their own dominance rank and that of others. Searching swans swim with a constant speed (v) in a straight line. During each time step they have a constant probability of finding a patch (i.e. the reciprocal of mean searching time to find the next patch; p). When an individual finds a patch, it consumes food at a constant rate from the patch over a fixed time period (i.e. patch handling time; T_f), consuming up to a maximum amount of food (C). The assumption that food is consumed constantly during handling time differs from other versions of the model that assumed all food was consumed at the end of handling time (Stillman et al. 1997, Stillman et al. 2000, Stillman et al. 2002b). The foraging efficiency of the swans was assumed to be normally distributed with a mean of 1 and a coefficient of variation of 0.48 (based on between-individual variation of interference-free intake rates in experimental measurements; Gyimesi, van Lith and Nolet, unpublished data). After the elapsed patch handling time, swans resume searching.

If a searching individual approaches another searching swan to within the avoidance distance (i.e. the mean minimum distance foraging swans approach each other; D_o), the less dominant individual will start avoiding by swimming directly away from the competitor in a straight line, with constant swimming speed, for a certain period of time (i.e. avoidance time; T_o) before resuming searching. During avoidance, swans cannot engage in any other activities. If a searching individual approaches a swan that is consuming food from a patch (i.e. handling a patch) to within the attack distance (i.e. the observed distance swans moved to displace another individual from a patch; D_A), it may attack the other individual in an attempt to steal the patch. Whether the individual initiates an attack, depends on the profitability of alternative behaviours (measured in terms of intake rate maximisation). We assume that the victim of an attack always responds by initiating a fight in an attempt to keep its patch. A fight lasts for a certain period of time (T_v). We also assume that the more dominant animal always wins the dispute, and then consumes the food remaining in the patch. The loser moves directly away from the victor in a straight line, with constant swimming speed (v), until it is farther than the attack distance.

The data used to parameterise our model were derived from field measurements in the Lauwersmeer, The Netherlands (summarized in Table 1). The encounter rate with patches was derived from the mean searching time between patches (Nolet and Mooij 2002). The width of a patch was based on the observed mean amount of consumed

food from patches (Nolet et al. 2006c). Using the functional response of Bewick's swans (Nolet et al. 2002), we calculated the amount of time it takes to consume this amount of food if the patch was 1 m². Relating this to the observed mean foraging time (Nolet et al. 2006c) allowed us to estimate the size of a patch in the field. Finally, the mean amount of food consumed per patch was calculated by the functional response using the observed initial and final tuber densities, observed patch residence times and calculated patch sizes (Nolet et al. 2006c).

The intake rate per swan over the whole simulation was based on the total number of consumed patches, multiplied by the amount of consumed food (C) from each patch. No data were available for the avoidance time of Bewick's swans (i.e. the time before resuming searching after avoidance). However, it is known that after being displaced from a patch, swans resume foraging from another patch after 4.5 s (Klaassen et al. 2006b). Therefore, we found it reasonable to set avoidance time to 2 s, as was used by earlier studies (Stillman et al. 1997, Stillman et al. 2000).

Table 1: *Parameter values used in the model*

Parameter	Mean \pm SE	Reference	Year of data collection
Swimming speed v (m s ⁻¹)	0.7	(Nolet and Mooij 2002)	1995, 1996
Patch encounter rate p (patches s ⁻¹)	0.0714	(Nolet and Mooij 2002)	1995, 1996
Patch width (m)	0.71	(Nolet et al. 2006c)	2001
Foraging time per patch T_f (s)	273 \pm 36.75	(Nolet et al. 2006c)	2001
Consumed food per patch C (g)	4.68 \pm 0.016	(Nolet et al. 2002, Nolet et al. 2006c)	2001
Attack distance D_a (m)	10.43 \pm 1.75	(Klaassen et al. 2006b)	2003
Avoidance distance D_o (m)	7.01 \pm 0.5	Nolet et al. unpublished data	1995, 1996
Fighting time T_v (s)	4.98 \pm 0.7	Nolet et al. unpublished data	1995, 1996
Avoidance time T_o (s)	2	(Stillman et al. 1997, Stillman et al. 2000)	

All simulations were run with 100 competing individuals. Ten densities were tested (i.e. 1, 16, 32, 64, 96, 128, 194, 256, 384, 512 birds ha⁻¹) by adjusting the size of the arena in which the birds foraged. For each density, 200 simulations were run, each lasting

11 000 time steps. In order to allow the system to stabilize, only the last 10 000 were included in the analysis. For each simulation, variable values were randomly taken from a normal distribution based on the mean and standard error measured in the field (Table 1).

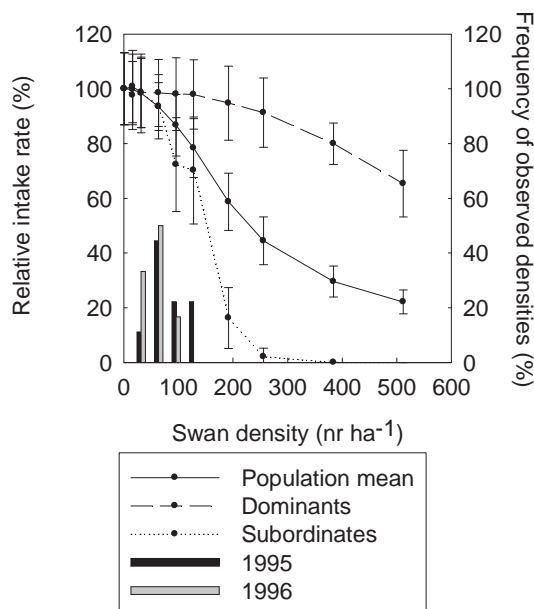
Individual intake rates were averaged per simulation. The predicted intake rate at 1 bird ha⁻¹ was considered to be an interference-free situation, and hence intake rates at all other densities were expressed relative to that at 1 bird ha⁻¹. The intake rates of dominant and subordinate groups were also calculated separately. Individual intake rates of the 33 most dominant birds and for the 33 least dominant birds were averaged, respectively. In addition to intake rate, the total time spent in different behavioural states during the last 10 000 time steps was also calculated for each forager density. Finally, a multiple regression analysis was run to identify the effect of the different parameters on model predictions of intake rate.

Naturally occurring foraging swan densities were determined in 1995 (between 16 and 30 October) and 1996 (between 19 and 28 October) in the Lauwersmeer, in a creek measuring c. 16 hectares. Individual swan positions were measured, using a laser range finder (Geovid 7 × 42 BDA, Leica, Solms, Germany), by taking the distance (± 1 m) and azimuth ($\pm 1^\circ$) to the observer (Nolet and Mooij 2002). After plotting the individual positions, average group densities (swan ha⁻¹) were calculated for every observation day (i.e. $n = 10$ and $n = 13$, in 1995 and 1996 respectively). These were finally categorized according to the ten densities used in the model. A corrected mean field intake rate was calculated based on the simulated mean intake rates per density and the relative frequency of the density categories in the field. These were compared with an interference-free situation, in order to define the consequences of neglecting interference in carrying capacity calculations.

Results

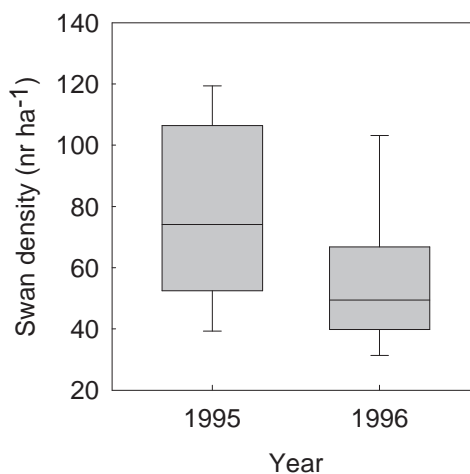
The interference-free simulations (i.e. those based on a swan density of 1 bird ha⁻¹) predicted the mean intake rate per individual to be 0.0168 g s⁻¹. The higher density simulations predicted that relative intake rate (intake rate as a percentage of interference-free intake rate) declined with increasing swan density, but that the rate of decline was much greater in lower dominance birds than in higher dominance birds (Fig. 1). At bird densities below 64 swans ha⁻¹ interference competition had a minor effect on intake rate; relative mean intake rate was above 90% in both dominant and sub-dominant birds. The intake rate of dominant birds remained relatively high (relative intake rate greater than 60%) across the full range of competitor densities simulated. In contrast, the relative intake rate of sub-dominant birds dropped from approximately 70% at 128 birds ha⁻¹ to just above 15% at 192 birds ha⁻¹, and finally to 0 above 384 birds ha⁻¹.

Fig. 1: Relationship between the density of competing swans and the mean (\pm SE) predicted relative intake rate (i.e. intake rate as a percentage of interference-free intake rate (at 1 bird ha⁻¹)). Solid line represents population mean, dashed line dominant individuals (dominance rank > 67%) and dotted line subordinate individuals (dominance rank < 33%). Bars indicate the relative frequencies of swan densities observed in the field in 1995 (in black) and 1996 (in gray).



Interestingly, the swan densities observed in the field always remained below 128 birds ha⁻¹ (Fig. 1). In 1995 the birds tended to form denser flocks, although the swan densities in the two study years did not significantly differ from each other ($t_{20} = 1.8$; $p = 0.08$; Fig. 2). Similarly, the corrected field intake rates in the two years did not significantly differ ($t_{20} = 1.74$; $p = 0.1$). Combining the two years resulted in a corrected mean intake rate of 0.0151 g s⁻¹, i.e. 90% of the predicted interference-free intake rate.

Fig. 2: Swan densities observed in the field in 1995 (left) and 1996 (right). Line represents median, whiskers the 5th and 95th percentiles.

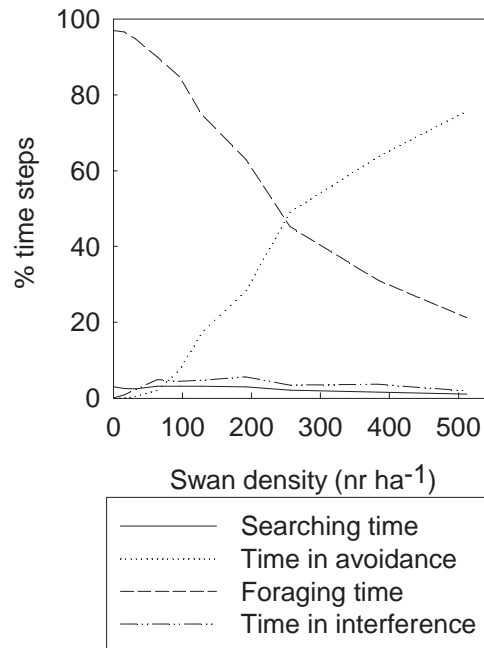


The multiple regression analysis revealed that foraging time per patch alone could explain 92% of the variation in intake rates. It was the only variable that had a significant influence on intake rate (Table 2). However, its importance decreased with competitor density. At lower competitor densities (below 96 birds ha^{-1}) swans spent nearly all their time handling food patches (Fig. 3). At higher densities, avoidance behaviour occurred more frequently. Finally, above 256 birds ha^{-1} , birds spent more time avoiding each other than in other activities. The time spent fighting over and searching for food patches remained low over all competitor densities simulated (Fig. 3).

Table 2: Summary of the multiple regression analysis of the effect of different variables on intake rate. The table also displays the standardized (Beta) and non-standardized (B) regression coefficients, together with their standard errors (SE).

	Beta	SE of Beta	B	SE of B	t194	p
Consumed tubers	0.024	0.02	18.33	12.71	1.44	0.15
Foraging time per patch	-0.97	0.02	-0.36	0.006	-59.36	<0.00001
Avoidance distance	0.015	0.02	-0.4	0.43	-0.93	0.35
Attack distance	0.01	0.02	0.07	0.12	0.62	0.54
Fighting time	-0.001	0.02	-0.02	0.32	-0.06	0.95

Fig. 3: Relationship between swan density (nr ha^{-1}) and the percentage of time steps spent in different behavioural states. Solid line represents searching time for food patches, dotted line time spent avoiding competitors, dash-dot line time spent fighting with competitors and dashed line time handling patches.



Discussion

In this study we show, using an individual-based model, that the average intake rate of a group of Bewick's swans decreases with group density. However, the reduction is only extensive in subdominant birds and for those mainly at competitor densities that are above the ones measured over two years in nature. This suggests that swans are adjusting their density in order to minimize the effects of interference. Therefore, we argue with van Gils et al. (2004) that the maximum observed numbers cannot be used to indicate the carrying capacity of a site. Instead, it is likely that, at densities where interference competition starts to have a large impact on intake rate, individuals leave the group and look for a foraging location elsewhere. Therefore, Bewick's swans seem to follow an ideal free distribution for unequal competitors (Milinski 1982, Korona 1989).

As the functional response of Bewick's swans is nearly linear over observed food densities (Nolet et al. 2001b), intake rate could increase virtually continuously with food density. Without interference competition, all individuals would gather in the best foraging location. However, larger group densities lead to higher levels of interference, which can consequently result in the reduction of intake rates (Goss-Custard 1980, Dolman 1995, Ruxton and Moody 1997). Hence, alternative lower quality foraging locations within a habitat might become just as profitable, leading to the distribution of individuals among foraging locations. If there are enough foraging sites to accommodate the whole population at low competitor densities and the exploitation period is only limited by the amount of food available, interference competition hardly limits the carrying capacity of the habitat.

A number of studies have reported the lack of a relationship between the density of competitors and the number of interactions (e.g. Rowcliffe et al. 1999a, Nolet et al. 2002, Badzinski 2003). Our results could provide a reasonable explanation for this phenomenon. If there are an adequate number of available foraging locations, animals do not need to accumulate at such a density that interference competition would greatly reduce their intake rate. In addition, our results show that lost time due to avoidance behaviour, instead of lost time due to fighting, might be responsible for the reduction in intake rates. In the field, aggressive interactions are much easier to identify, and hence "time spent in interactions" is often used to quantify the amount of interference (e.g. Cresswell 1998, Vahl et al. 2005a, Taillon and Cote 2007). However, our results support the idea that the time lost on actual interactions can be negligible compared to time lost on avoidance behaviour (Cresswell 1997, Moody et al. 1997). This latter behaviour is unfortunately much more subtle, thus more difficult to measure. Interference competition in such cases is cryptic to the observer.

The high level of avoidance implies that animals can recognize the relative dominance rank of competitors (Ens and Goss-Custard 1986, Badzinski 2003, Taillon and Cote 2006). As a result, subdominant animals do not need to risk actual conflicts, which

they would be likely to lose anyway. However, our results show that at higher densities subordinates would reach considerably lower intake rates than dominants. This is mainly caused by subordinates losing more time to avoidance (Smallegange and van der Meer 2007). Therefore, presumably subdominant individuals are the first to leave a group as competitor density increases (Alonso et al. 1997).

Using the estimated avoidance distance of 7.01 m as a radius, an *individual area* (c. 0.015 ha) can be calculated that a Bewick's swan needs to avoid interference. Thus, even if swans occur in a regular pattern, above 65 birds ha⁻¹ avoidance behaviour will occur. Below this density, foraging efficiency is the main determinant of individual intake rate. In our system, foraging efficiency is most closely related to variation of foraging time: a less efficient forager needs more time to consume the same amount of food. Above this density, dominance, acting through avoidance behaviour, starts to play an increasingly important role. Interestingly, in case of Bewick's swans, foraging efficiency and dominance might both be related to body size (Gyimesi, van Lith, and Nolet unpublished data). Therefore, a large bodied swan is expected to be more dominant and a better forager. Dominant birds generally have a higher breeding success (Parker and Sutherland 1986). In addition, they may more easily compensate for the costs of extended parental care due to their higher foraging efficiency (Goss-Custard and Durell 1987a, Catterall et al. 1989).

The strength of interference competition can vary with prey density (Cresswell 1998). Forager densities may increase with food density causing intensified competition (Bautista et al. 1995, Moody and Ruxton 1996). In our system, tuber densities show large inter-annual variation (Nolet et al. 2006b) and during the study years food density varied twofold (Nolet et al. 2001b). Forager densities also seemed to vary, although not significantly (Fig. 2). It would be worthwhile to follow forager densities on a long term to certify its relationship with food density (Beauchamp 2008).

Admittedly, the input parameters of the model were measured under naturally occurring densities. The model makes it clear that at such densities interference competition plays a limited role. The advantage of a modelling approach is that intake rates can be predicted also outside the circumstances the parameters were obtained. However, it cannot be excluded that interference parameters would also be different under such conditions. On the other hand, our model relies on parameters measured in several years (Table 1) with varying environmental conditions.

In addition to food density, its distribution can also have a large effect on the outcome of interference competition (Monaghan and Metcalfe 1985, Theimer 1987). The model assumes a homogeneous food distribution, in which every patch is of equal quality. In such a case, the strength of interference may be lower than in situations in which patch quality varies (Gyimesi, van Rooij and Nolet, unpublished data, Theimer 1987, Vahl et al. 2005a). In our model, patch departure was most often a result of reaching the predetermined patch handling time than a fighting event. On the other

hand, the model also assumes that animals always fight back when they are attacked, which might lead to more interactions than in reality. Bewick's swans can most likely recognize the dominance status of their opponent (Badzinski 2003) and do not enter a fight that would presumably be lost (Badzinski 2003, Klaassen et al. 2006b). Therefore, the underestimation of interference effects due to the assumption of a homogeneous food distribution might be compensated by the overestimation of fights. Nevertheless, it should be tested in the future how the strength of interference varies when food is more heterogeneously distributed.

Our study is the first step in evaluating the importance of interference competition among large freshwater herbivores. We describe a situation in which interference is mainly a cryptic process, due to the difficulty of measuring avoidance behaviour and the natural ability of animal populations to adjust their foraging density, in order to minimize the effects of interference competition. As avoidance behaviour has generally received minor attention in interference studies, it may easily be that it has a substantial relevance in many other systems, which would place the importance of interference competition into a new context.

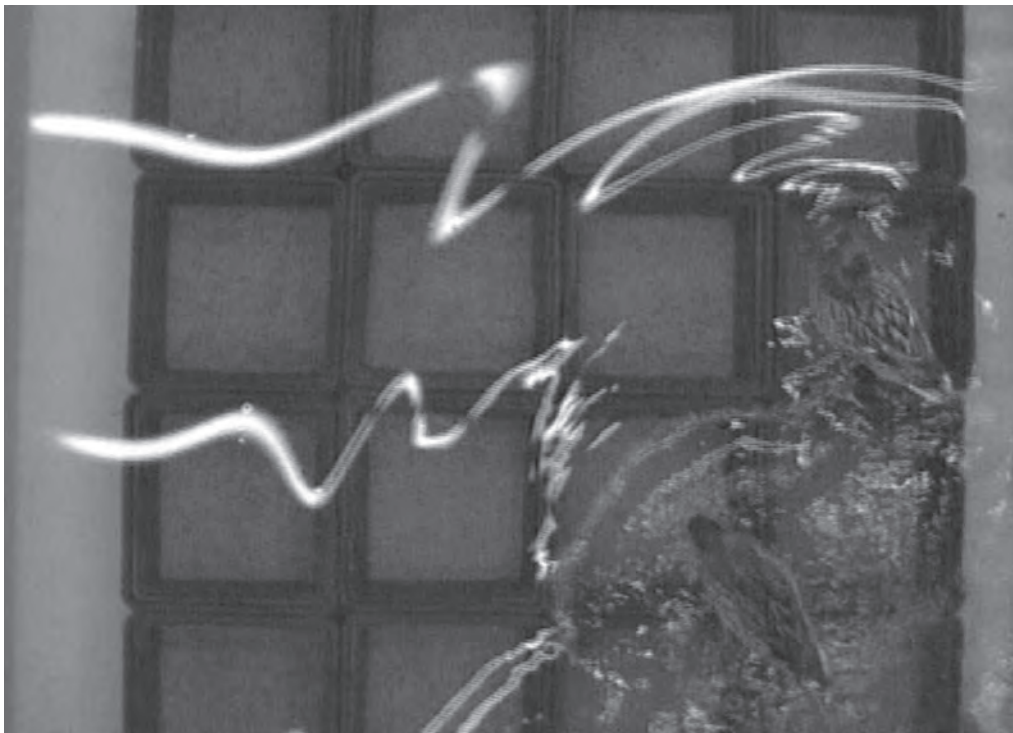
Acknowledgements

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Chapter 5

Nonlinear effects of food aggregation on interference competition

ABEL GYIMESI, ERICA P. VAN ROOIJ and BART A. NOLET



Two ducks searching for food in the experimental setup.

Abstract

Previous research has shown an asymmetric effect of interference competition on intake rate of foragers on clumped resources, with only subordinate individuals suffering. The food distributions in these studies were highly clumped, but in many field situations food is aggregated to a lesser extent. Here, we investigated whether the applied distribution (i.e. uniform, slightly clumped and highly clumped) affects the behavioral response of mallards foraging alone or with a competitor. Even though the amount of food was the same in all food distributions, the mallards reached higher intake rates, visited fewer patches and showed longer average feeding times in the highly clumped distribution. Paired mallards had lower intake rates on the slightly clumped than on the uniform or highly clumped food distributions. Though not reaching significantly higher intake rates than subordinates, dominants showed a higher number of visited patches and shorter feeding times per patch. Therefore, we propose that subordinates do not necessarily suffer from interference competition in terms of intake rate, but of higher search costs. In addition, dominants had significantly higher average feeding times on the best quality patches of the highly clumped food distribution, an effect not found in the slightly clumped distribution. These findings indicate that in an environment where food is aggregated to a lesser extent, dominants cannot monopolize the best foraging spots. Based on these results, we argue that in interference experiments food distributions should be used that resemble the situation the studied animals are faced with in the field.

Introduction

During its life, an animal continuously has to make decisions on what, where and how much to eat. The optimal decisions about these issues might be affected by the presence of other individuals with similar preferences, leading to competition for the limited food resources. When a number of organisms utilize (and deplete) such common resource, exploitative competition occurs (Krebs 2001). However, organisms might also hinder each other, regardless of the resource depletion, through interference competition. This latter form of competition was defined as the decline in intake rate due to the mere presence of competitors (Goss-Custard 1980).

Interference competition can be active, arising from aggression. Competitors may also try to avoid each other to reduce the number of aggressive encounters (Cresswell 1997), hence spend less time with foraging. Eventually, when interference becomes too intense, some might end up in suboptimal habitats (Goss-Custard 1980). Another form of active interference competition is kleptoparasitism, where one individual steals food or takes over good foraging spots from another (e.g. Ens and Goss-Custard 1984, Monaghan and Metcalfe 1985, Triplet et al. 1999). Interference competition can also be passive, when foragers keep an eye on their competitors and consequently lose the control over search paths or face a reduced foraging time (Goss-Custard et al. 1982,

Ens and Goss-Custard 1984, Stillman et al. 1997). An important aspect of interference competition is also that it is “immediately reversible” (Goss-Custard 1980): when the density of competitors decreases, the negative effects of interference follow suit almost immediately.

It has been common practice to study interference competition under various forager densities (e.g. Sutherland 1983, Ruxton and Moody 1997, van Gils and Piersma 2004, Vahl et al. 2005b). In addition, numerous authors have shown that individuals differing in their dominance status are differentially affected by interference competition (Hupp et al. 1996, Alonso et al. 1997, Stahl et al. 2001, Stillman et al. 2002a, Rowcliffe et al. 2004, Klaassen et al. 2006b, Lendvai et al. 2006). Dominants tended to suffer little, if at all, from interference competition and in several cases even increased their intake rate. This latter might arise from a group of animals (notably often the subordinates within the group) more rapidly detecting the most profitable patches than an individual forager (Stahl et al. 2001), after which dominants can easily monopolize these patches (Monaghan and Metcalfe 1985, Bautista et al. 1995, Taillon and Cote 2007). In these cases, subordinates are either displaced or simply avoid the dominants. Therefore, they have to cope with longer searching times (Alonso et al. 1997, Stahl et al. 2001, Rowcliffe et al. 2004, Klaassen et al. 2006b) and a reduced intake rate due to foraging in lower quality patches (Dolman 1995).

When interference is due to birds chasing each other away from good feeding spots, food distribution was also proven to have a detrimental effect on the level of interference competition. Vahl et al. (2005a) emphasized that the effects of interference competition are largely determined by the spatial distribution of the prey. They also pointed out that models of interference competition commonly ignore the fact that in most natural systems food items occur in aggregations (Turchin and Kareiva 1989, Benhamou 1992, Li and Reynolds 1995, Sparrow 1999, Fryxell et al. 2005, Kraan et al. 2009a) and make use of simple homogenous food distributions. Of course, in terms of food intake, there is not much to win through interference in an environment where food is homogeneously distributed: a certain spot in space is just as profitable as any other (Theimer 1987, Vahl et al. 2005a).

In contrast, if food is clumped, interference competition can strongly affect individual intake rate because dominant individuals can monopolize the food patch (e.g. Monaghan and Metcalfe 1985, Theimer 1987, Vahl et al. 2005a). Studies on the effect of spatial clumping on interference competition used concentrated food (basically a single clump; (Theimer 1987, Vahl et al. 2005a)). However, many naturally occurring food items are neither completely spread out nor fully concentrated; their distribution is characterized by positive spatial autocorrelation: high-density patches will tend to be next to high-density patches and low-density patches next to low-density patches (Kotliar and Wiens 1990, Kolasa and Rollo 1991, Li and Reynolds 1995, Klaassen and Nolet 2008, Kraan et al. 2009a).

Therefore, we aimed to experimentally compare the effects of interference competition in a setup with an intermediate food aggregation (henceforth called slightly clumped) with setups where food is distributed homogeneously or concentrated (henceforth called uniform and highly clumped, respectively). We measured the variables food intake, mean feeding time per patch and number of visited patches of female mallards (*Anas platyrhynchos*) in trials where they were foraging alone or with a competitor of either a relatively lower or higher dominance status.

We generally expected clear differences in the measured variables between the applied food distributions. In addition, we hypothesized that the dominant bird would take control over the best quality patches and consequently reach a higher intake rate than the subordinate. However, we expected that the strength of this effect would be stronger in the highly- compared to the slightly clumped food distribution, since in the latter case dominants might be less effective in monopolizing the best foraging spots.

Methods and materials

The trials were carried out in the waterfowl experimental facility of the NIOO-KNAW in Nieuwersluis. Sixteen trays (measuring $30 \times 30 \times 30$ cm), forming a continuous foraging area of 1.44 m², were placed at the bottom of a basin of 2×2 m, with water depth set at 30 cm above the sediment. As food, wheat grains were used, covered with a layer of sand to avoid visual detection. Three food distributions were used by manipulating the food densities in the individual trays. All food distributions contained the same total amount of seeds (1200 seeds; 61.7 ± 3.5 g). For the uniform (UN) food distribution (Fig. 1.), a homogeneous environment was created by filling all 16 trays with an intermediate amount of seeds (75 seeds/tray). The slightly clumped (SC) food distribution (Fig. 1.) consisted of a pattern with five different food densities ranging from 25 seeds per tray ($n = 2$), through 50 ($n = 4$), 75 ($n = 4$) and 100 ($n = 4$) seeds per tray to 125 seeds per tray ($n = 2$) with a positive spatial autocorrelation between food densities. For the degree of clumping, the spatial distribution of fennel pondweed (*Potamogeton pectinatus*) tubers was used as a template (Nolet and Mooij 2002, Nolet et al. 2006c). The highly clumped (HC) distribution (Fig1.) contained a clump of four trays with a very high food density (225 seeds/tray) and 12 with a low food density (25 seeds/tray). Special care was taken that birds could not learn the position of the best patches in the clumped distributions. For each trial in the SC distribution, a different spatial configuration was taken from the field measurements (Nolet et al. 2006c). The position of the food clump in the HC distribution was rotated daily in a random order of 90°, 180° or 270°.

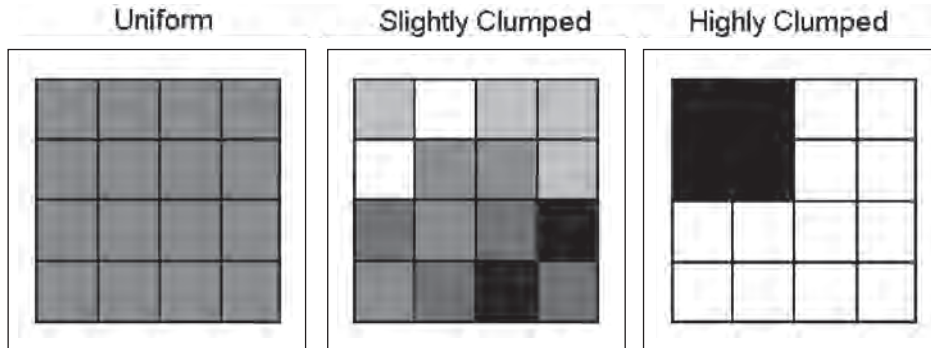


Fig. 1: The uniform (left; 75 seeds/tray) food distribution and configurations for the slightly clumped (middle; 25, 50, 75, 100 and 125 seeds/tray) and highly clumped (right; 25 or 225 seeds/tray) food distributions. Color shades represent different food densities.

We used mallards (>1 year old) for the experiment. Because the focus was on the effects of interference competition and dominance on foraging decisions, we chose to use only females to rule out mate competition. Nine birds were purchased from a breeder (Kooij and Sons Waterfowl Breeding Farm, 't Zand, The Netherlands), but all of them were kept at our waterfowl facility for at least a year prior to the experiment. The animals were housed in an aviary measuring 10×6 m with access to a large pond and were only moved to the experimental room right before a trial.

In order to familiarize them with the experimental facilities and procedure, the birds were trained for four weeks prior to the experiment and for one week during the experiment before switching to a new food distribution (see below). Three of the birds regularly displayed stereotype behavior during the training trials, and hence were left out from the experiment. The six remaining birds were fitted with different color leg bands to allow individual recognition. During the training and the experiment, the birds had access to food only during the trials in the morning hours and for one hour in the afternoon in the aviary.

Prior to the experiment, dominance relations were determined while observing priority of access to the feeding tray after at least eight hours of starvation (cf. Syme 1974, Wagner and Gauthreaux 1990), verifying a linear dominance hierarchy in mallards (Poisbleau et al. 2006). The scoring of dominance was repeated four times throughout the experimental period, confirming that the rank order of the birds remained stable during the experiment.

Experimental trials were carried out in February and March 2006. Trials were done in one bird set-ups (single) with each mallard being used once and in two bird set-ups (pair), where each combination of individuals was tested. In order to minimize potential effects of food depletion, a foraging trial lasted only 120 seconds from the moment

(one of) the mallard(s) started foraging. All the trials took place in the morning hours. The trial sequence of bird densities and the selection of individual ducks for the trials were randomized, with the restriction that individuals were used in only one trial per day. The experiment consisted of 21 trials (i.e. 6 single trials and 15 combinations of pairs) for each food distribution (i.e. 63 trials in total). However, mallards in two single trials and in five paired trials refused to eat, reducing the sample size to 56.

Mallards are highly capable of learning the food distribution they are foraging in (Klaassen et al. 2007). As we aimed to study the effects of interference competition while foraging in a certain food distribution and whilst learning a food distribution, we applied the three distributions separately and not randomly. First the UN, then the HC and finally the SC distribution was tested, with one week of training trials in between to allow the learning of the new food distribution. The trials were filmed with a video camera (Panasonic NV-GS15) positioned above the basin. Videos were analyzed using Observer 5.0 (Noldus Information Technology bv.).

After a trial, all trays were removed from the basin and the sediment was sieved to collect the wheat grains left behind by the mallards. Wheat grains were then counted to define the consumed number of seeds per patch. The number of seeds eaten per individual during the trial was divided by 120s to calculate intake rates per second over the whole trial. Functional responses measured in individual training trials on the slightly clumped distribution revealed that the instantaneous intake rates per food density did not significantly differ among individuals ($F_{17,18} = 0.59$, $p = 0.86$). Therefore, when both individuals ate from the same tray (29% of the cases), the total number of seeds eaten from a tray was divided in proportion to the feeding time of each individual on that tray. The final intake rate results (seeds s⁻¹) were subjected to a square root transformation to obtain normality. The number of patches visited and the mean feeding time (i.e. time with head under water; s) per patch were analyzed from the videos. These results were subjected to ln-transformations to reach normality.

Two full-factorial GLMs were carried out to test the effect of the interaction of food distribution (i.e. UN, SC, and HC) with number of foragers (i.e. single or pair trials; GLM1) and with dominance status (i.e. single, subordinate, dominant; GLM2) on intake rate, mean feeding time per patch and number of visited patches. Type III sums of squares of the software Statistica 8.0 (Statsoft, Inc. 1984-2008) were applied, which compares least square means, correcting for unequal sample sizes. Post-hoc tests were conducted using Unequal N HSD.

Results

Intake Rate

The interaction term food distribution with number of foragers was significant (GLM1: $F_{2,96} = 8.4$, $p = 0.0004$). The post-hoc test revealed that this was mainly caused by mallards in single trials on the highly clumped distribution reaching higher intake rates than in any other trial types (all $p = 0.001$; Fig. 2.). In addition, the paired trials of the slightly clumped distribution showed lower intake rates than the paired trials of the other two distributions (both $p < 0.05$; Fig. 2.). Looking at dominance differences did not add new information: singles in the highly clumped food distribution reached higher intake rates than in any other case (GLM2: $F_{4,93} = 4.9$, $p = 0.001$; post-hoc test: all $p < 0.05$; Fig. 2.), but there was no difference found between dominants and subordinates in any of the comparisons.

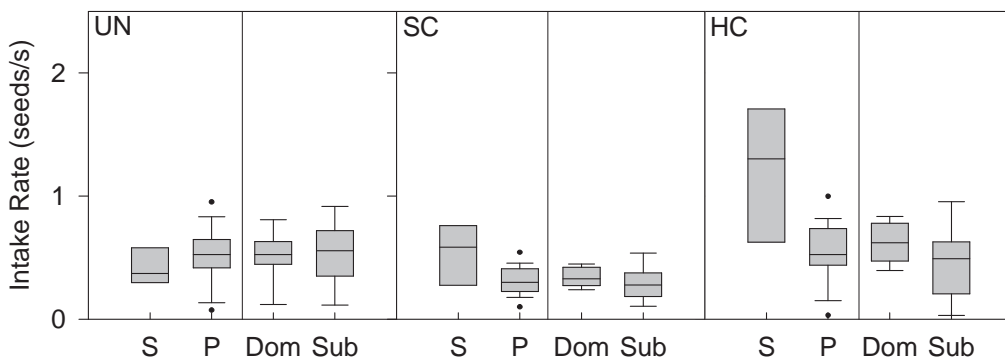


Fig. 2: Intake rate (seeds s⁻¹) for all food distributions (uniform = UN, slightly clumped = SC and highly clumped = HC). Mallards were foraging alone (S = single trials) or together with a competitor (P = paired trials). These latter results are also subdivided into dominants (Dom) and subordinates (Sub). Box plot shows median (line in box), interquartile range (box), 10th and 90th percentile (bars) and outliers (dots; data points outside the 10th and 90th percentiles).

Number of visited patches

The interaction of food distribution with number of foragers showed no significant effect on the number of patches visited by mallards (GLM1: $F_{2,96} = 1.97$, $p = 0.1$; Fig. 3.). However, the main effect of food distribution did give a significant result (GLM1: $F_{2,96} = 3.33$, $p = 0.04$). Namely, birds in the highly clumped distribution visited significantly fewer patches (post-hoc test: both $p < 0.05$; Fig. 3.).

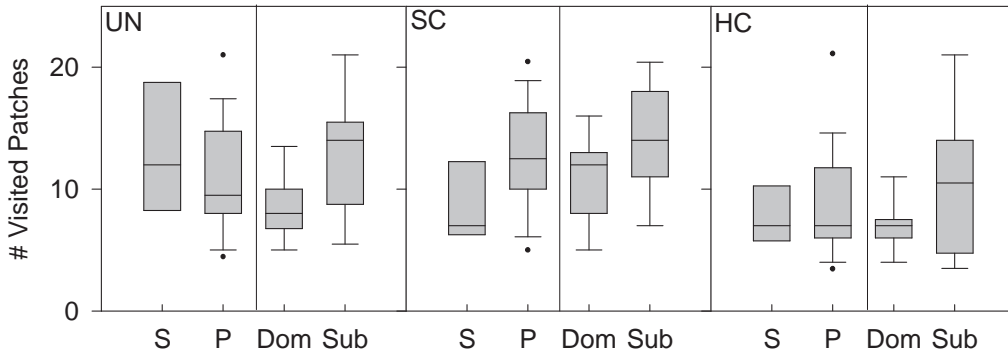


Fig. 3: Number of visited patches for all food distributions (uniform = UN, slightly clumped = SC and highly clumped = HC). Mallards were foraging alone (S = single trials) or together with a competitor (P = paired trials). These latter results are also subdivided into dominants (Dom) and subordinates (Sub). Box plot shows median (line in box), interquartile range (box), 10th and 90th percentile (bars) and outliers (dots; data points outside the 10th and 90th percentiles).

The interaction of food distribution with dominance was not significant either (GLM2: $F_{4,93} = 1.14$, $p = 0.3$; Fig. 3.). However, the main effect of dominance was significant (GLM2: $F_{2,93} = 5.95$, $p = 0.004$): subordinates generally moved around more (i.e. visited more patches) than dominants (post-hoc test: $p = 0.003$; Fig. 3.).

Feeding time

The interaction of food distribution with the number of competitors had no significant effect on the average feeding time per patch (GLM1: $F_{2,96} = 1.15$, $p = 0.3$). However, the main effect of food distribution was significant (GLM1: $F_{2,96} = 6.04$, $p = 0.003$), with mallards showing longer average feeding times per patch in the highly clumped distribution (Fig. 4.).

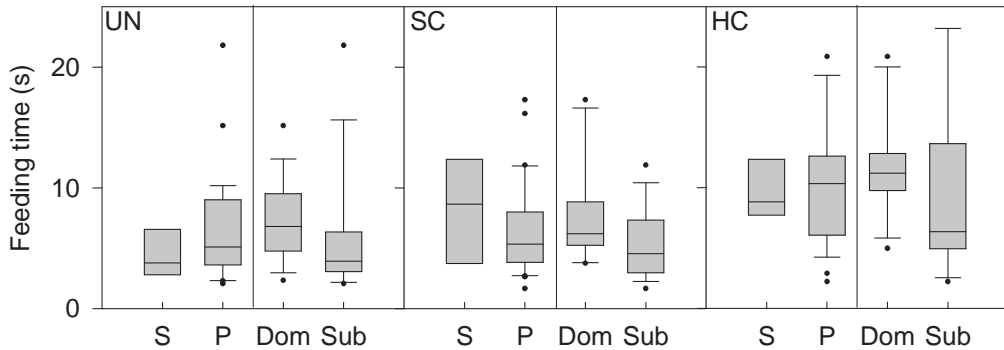


Fig. 4: Average feeding times (s) per patch for all food distributions (uniform = UN, slightly clumped = SC and highly clumped = HC). Mallards were foraging alone (S = single trials) or together with a competitor (P = paired trials). These latter results are also subdivided into dominants (Dom) and subordinates (Sub). Box plot shows median (line in box), interquartile range (box), 10th and 90th percentile (bars) and outliers (dots; data points outside the 10th and 9th percentiles).

The interaction of food distribution with dominance level was not significant either (GLM2: $F_{4,93} = 0.64$, $p = 0.6$; Fig. 4.) but the main effect of dominance was (GLM2: $F_{2,93} = 6.09$, $p = 0.003$; Fig. 4.), due to subordinates showing significantly shorter average feeding times per patch compared to dominants (post-hoc tests, both $p < 0.01$; Fig. 4.). An additional analysis revealed that in the highly clumped distribution dominance had a significant effect on the average feeding time spent on the high quality patches (one-way ANOVA: $F_{2,31} = 3.53$, $p = 0.04$). Namely, dominant individuals spent more time on these patches than subordinates (post-hoc test: $p = 0.04$; Fig. 5.). However, the same effect was not found in the slightly clumped food distribution (one-way ANOVA: $F_{2,23} = 2.4$, $p = 0.1$; Fig. 5.).

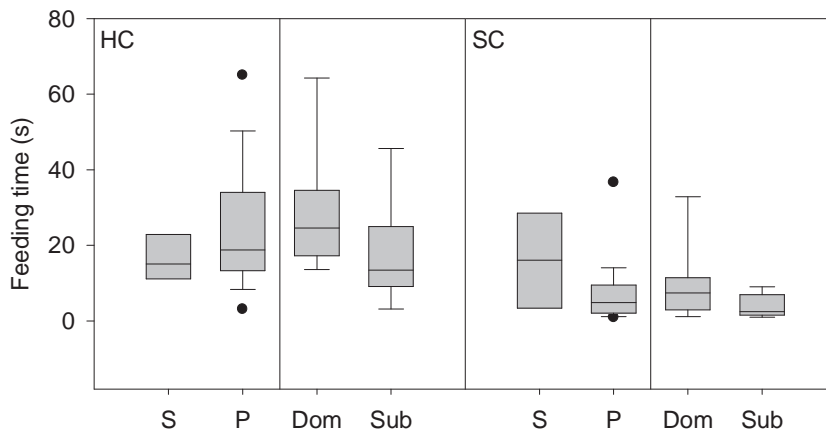


Fig. 5: Average feeding times (s) on the best quality patches for the highly clumped (HC) and slightly clumped (SC) food distributions. Mallards were foraging alone (S) or in pairs, subdivided into dominants (Dom) and subordinates (Sub). Symbols represent means with SE bars.

Discussion

In this study we show that the degree of food aggregation used in interference competition studies has a significant effect on the behavior of foraging animals. Despite of the amount of food being the same in the three applied food distributions, mallards reached higher intake rates, visited fewer patches and showed longer average feeding times in the highly clumped distribution than in the other two. Pairs had lower intake rates on the slightly clumped distribution than on the other two distributions. Even though we did not observe the expected higher intake rates for dominants compared with subordinates, we did see subordinates visiting more patches and showing shorter feeding times. Therefore, we propose that the disadvantage for subordinates to forage with dominants is not necessarily manifested in lower income but in higher costs. In addition, dominants had significantly higher average feeding times on the best quality patches of the highly clumped food distribution, which effect was not found in the slightly clumped distribution. This indicates that subordinates are easier excluded from better foraging circumstances when the degree of food aggregation is high.

Our results for the uniform food distribution, where all patches are equal in quality, match the expectations based on previous studies. In this distribution, no apparent effect of interference competition was found. In such an environment, spending time to compete with other individuals for food patches brings about only costs, as the achievable intake rates are the same everywhere. Therefore, dominants cannot profit from their higher status in the hierarchy through kleptoparasitism of patches (Theimer 1987, Vahl et al. 2005a).

The similar individual intake rates measured in single and paired trials on homogeneously distributed food provide a proof for the absence of a food depletion effect in our two minute long trials. Otherwise, also in the absence of interference competition, the longer cumulative foraging time in the paired trials (i.e. 240 s due to two birds foraging) would lead to lower individual intake rates compared to the 120 s in the single trials, simply due to food exploitation through exploitative competition.

The foraging scale (i.e. the scale above which foragers respond to spatial heterogeneity, also called "grain") was defined for mallards as 2 x 2 cm (Klaassen et al. 2006d). Therefore, we are confident that the mallards could distinguish between the three food distributions we applied in our experiment. Consequently, we expected dominant birds taking control over the better quality patches in the two clumped food distributions and therefore spend relatively more time on these patches than subordinate foragers (e.g. Hupp et al. 1996, Klaassen et al. 2006b, Lendvai et al. 2006). Even though we did not find dominant individuals reaching higher intake rates than subordinates in either of the clumped distributions (Fig2.), subordinates generally did have a larger number of visited patches (Fig3.) and shorter feeding times (Fig4.) than dominants. This might have been the result of subordinates either avoiding dominants or being displaced from their foraging spot (Smith et al. 2001, Stahl et al. 2001). Such effects can

subsequently result in longer searching times for a suitable patch, leaving less time for feeding (Belanger and Bedard 1992, Vahl et al. 2005b, Klaassen et al. 2006b). In this experiment we focused on the effects of interference competition; hence the trials were kept very short to avoid food depletion. Looking at a longer time frame, and assuming that in the experiment individuals were foraging at their maximum instantaneous intake rate after food deprivation, the constantly shorter feeding times of subordinates would likely hamper them to reach comparable long-term intake rates to dominants. This is especially likely for the highly clumped food distribution, where, even in our short trials, dominants spent more feeding time on the high quality patches than subordinates (Fig5.). Animals can effectively learn the distribution of the patches that they are foraging on (Kotliar and Wiens 1990, Benhamou 1992), and this is proven for mallards as well (Klaassen et al. 2006d). Hence, in a highly clumped food distribution they are expected to quickly discover that there are only two patch qualities: a good one and a bad one. Subsequently, they will most likely be able to accurately assess the quality of a patch. Once the good patch is found in such a highly clumped distribution, there is no need to continue searching or to fight for the other patches, as they are logically of lower quality (Vahl et al. 2005a). This results in animals showing a nearly omniscient behavior with shorter search times (i.e. lower number of visited patches; Fig3.), longer average feeding times (Fig4.) and highly increased intake rates (Fig2.) compared to other food distributions.

In contrast, in a food distribution with food items showing a lower degree of aggregation, dominants were not occupying the best quality patches longer than subordinates (Fig5.). In such a situation, differences between patches are less pronounced (Li and Reynolds 1995, Nolet and Mooij 2002, Nachman 2006, Nolet et al. 2006c). Hence, even if subordinates are displaced from the best quality patches, they are not left without any food, as could be the case in a highly clumped food distribution. Moreover, spatial heterogeneity in the distribution of food has also implications for the foraging strategy individuals choose in competition (van Dijk, Duijns, Gyimesi, de Boer and Nolet, *subm.*). If a dominant is certain about occupying the best patch, it should not leave it until depleting it to its final quitting intake rate (Charnov 1976, Nolet et al. 2006c). However, in a slightly clumped food distribution, it becomes more difficult for individuals to instantaneously assess the relative patch quality. This can obviously have a large impact on the decision of dominants whether to stay and monopolize the current patch, to continue searching or to steal a patch from a subordinate. This uncertainty of competing individuals about the best foraging position could lead to lower intake rates in a slightly clumped food distribution compared to highly clumped or homogeneous food distributions in both the subordinate and dominant (Fig2.).

The necessity of investigating the effects of interference competition in different food distributions has been pointed out earlier (e.g. Monaghan and Metcalfe 1985, Theimer 1987, Vahl et al. 2007) but in previous experiments most commonly uniform (homoge-

neous) and/or highly clumped food distributions were used (for review, see Vahl et al. 2005a). Many environments, however, contain intermediate distributions (Benhamou 1992, Gross et al. 1995, Li and Reynolds 1995, Sparrow 1999, Kraan et al. 2009a). The strength of this study is that we add a clumped distribution with a lower degree of food aggregation as well, which was based on the belowground distribution of fennel pondweed tubers (Nolet and Mooij 2002, Nolet et al. 2006c), a common food source of many herbivorous waterfowl species (Anderson and Low 1976, Nolet and Drent 1998, Santamaría 2002, Hilt 2006).

Our results show that the food distribution used in interference studies highly influences the outcome of the experiment. In less aggregated environments, uncertainty about where the best patches are may hamper the dominant's monopolization of the food, and in fact the intake of both dominants and subordinates. Therefore, building upon the results coming forth from a long history of interference studies, we recommend to use food distributions that resemble the situation the studied animals are faced with in the field.

Acknowledgements

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Chapter 6

Patch use of mallards under exploitative competition on a heterogeneous food distribution

JACINTHA G.B. VAN DIJK, SJOERD DUIJNS, ABEL GYIMESI,
WILLEM F. DE BOER and BART A. NOLET



Jacintha busy with creating a new experimental setup in “Building D”.

Abstract

Although animals foraging in groups may benefit from a faster detection of food and predators, competition by group members may also reduce their intake rate. Competition may alter patch exploitation, which can be influenced by dominance, affecting foraging behaviour and energy intake. Mainly theoretical studies focused on these subjects, therefore we conducted an experimental study to investigate patch exploitation of solitary and group foragers with different dominance status foraging on a natural (slightly clumped) food distribution. Under exploitative competition on depletable resources, we studied the effects of forager density on the foraging behaviour of focal mallards, *Anas platyrhynchos*, in which the same individual participated in single and group trials, varying their dominance status. As predicted, individuals in a group had a shorter patch residence time and visited more foraging patches. However, they were feeding a larger proportion of the trial time, and probably because of that achieved a similar intake rate as solitary foragers. Dominance status had no effect on the foraging behaviour of individuals in a group, which we attribute to the inability of dominants to monopolize resources in this slightly clumped food distribution. Apparently competition alters the way patches are exploited by group foragers, in which they might be able to compensate for the effects of competition.

Introduction

Animals forage alone or in groups. Group foraging has the advantage of predator detection, due to the many eyes effect (Pulliam 1973, Clark and Mangel 1986). Additionally, food patches may be located faster when foraging in a group (Clark and Mangel 1984, 1986), in which resources can be shared, reducing variances in food encounter rate (Giraldeau and Beauchamp 1999). With the use of public information, individuals can assess the quality of resource patches by observing the foraging success of others (Valone 1989, Templeton and Giraldeau 1995). A negative impact arises when this information is misused by so called scroungers, which are solely joining and exploiting the food patches discovered by other companions (Barnard and Sibly 1981, Smith et al. 1999), hereby decreasing the rate of finding food by the group. Food availability determines whether group foragers may benefit from each other. When food is limited, the number of foragers present can affect an individual's feeding rate (Hake and Ekman 1988, Triplet et al. 1999). This might be caused through depletion of available prey (exploitative competition; Krebs 1978) or through behavioural interactions (interference competition; Goss-Custard 1980; Stillman et al. 1997), such as aggression and kleptoparasitism (Brockmann and Barnard 1979, Kotrschal et al. 1993).

While patch use has been extensively studied for solitary foragers, little is known about how competition may alter patch exploitation. A much used classical model predicting patch use of solitary foragers is the Marginal Value Theorem (MVT), developed by Charnov (1976). This model predicts that an animal should leave a patch and

move to another patch when the net energy intake rate of the used patch falls below the expected value of the average of the habitat, in which little or no patch revisitation occurs. This can be measured using the giving up density (GUD), which is the density of resources within a patch at which a forager leaves the patch. Only few studies, mainly theoretical, have focused on differences in patch exploitation between solitary and group foragers (Mitchell 1990, Visser 1991, Ranta et al. 1993, Sjerps and Haccou 1994, Rita and Ranta 1998). Nolet et al. (2006) suggested that group foragers should forage each patch to their current estimate of the critical energy gain, re-adjusting (i.e. lowering) their patch leaving threshold (PLT) during depletion of the habitat (flexible PLT strategy). Solitary foragers, on the other hand, were expected to deplete each part of the habitat until their energy gain would drop to the ultimate critical level (fixed PLT strategy).

A complicating factor is that patch use under competition can be influenced by dominance, affecting foraging behaviour and energy intake (Desrochers 1989, Henderson and Hart 1995, Donazar et al. 1999, Smith et al. 2001). Dominant birds may monopolize the high quality patches (Theimer 1987; Vahl et al. 2005), forcing subordinates to positions where they experience a higher predation risk (Schneider 1984, Koivula et al. 1994). In a field study with oystercatchers, *Haematopus ostralegus*, it was shown that an increase in the feeding density of conspecifics had a strong negative effect on the intake rate of subordinates, but dominant birds were hardly affected, and could even benefit (Ens & Goss-Custard 1984). The way food is dispersed in the environment can have an effect on whether or not dominants realize a foraging advantage over subordinates. In a homogeneous environment, dominance may have little effect on the foraging success of individual flock members, whereas in a highly clumped food distribution the presence of a competitor reduces the foraging success of subordinate birds (Vahl et al. 2005).

The aim of this study was to investigate patch exploitation of solitary and group foragers with different dominance status foraging on a natural food distribution. In reality different prey densities are usually not uniform or randomly distributed throughout the area, but the resource distribution is often clustered (Li & Reynolds 1995). In an experimental set-up, we studied the effects of forager density on the foraging behaviour of focal mallards, *Anas platyrhynchos*, under exploitative competition minimizing depletion differences, in which the same individual participated in single and group trials, varying their dominance status. In group trials focal mallards were foraging with two competitors of different dominance status. We generally expected a lower intake rate and feeding time of individuals foraging in a group, due to the increased number of foragers present. Group foragers were expected to search for the high quality patches first, hereby spending a small amount of time per patch on a high number of patches, as a result leaving the patch with a high GUD. Patches were expected to be revisited more often with group foraging individuals as they were only partly

exploited the first time. Regarding the dominance status, we expected that dominant individuals foraging in groups could compensate for competitor effects and achieve a similar or even higher intake rate than when foraging solitary. Subordinate individuals were expected to suffer from the exploitative competition and achieve a lower intake rate than when foraging alone.

Methods and materials

The design used for the experiment was a 4×4 Latin square. The effect of four treatments was studied using four focal individuals, with each treatment and focal bird occurring once a day (to correct for day effects respectively to assure motivation), resulting in four consecutive experimental days. The four treatments consisted of a focal bird (1) foraging solitary, or foraging in a group of three being either (2) subordinate, (3) intermediate, or (4) dominant. Three non-focal subordinates and three non-focal dominants were used to vary the dominance status of focal individuals in group trials. Non-focal individuals also participated once a day to assure motivation. The same 4×4 Latin square design was replicated immediately after finishing the first experiment, using the same focal and non-focal individuals. Hence 31 trials were conducted in total, as one focal bird did not actively participate in a dominance trial. Reason for this is unknown, as all the other trials with this focal bird went smoothly.

An essential part of a Latin square design is that the same individuals participate in the experiment as single, subordinate, intermediate, and dominant individual; facilitating the detection of the treatment effects, without being blurred by individual variation. Due to the four treatment levels, a 4×4 Latin square design was chosen, starting with 20 birds of which, after determining the dominance hierarchy, 13 birds could participate in the experiment. An 8×8 Latin square design, which means doubling the number of birds needed for the experiment, was practically unfeasible as four trials already covered a full day. Besides, each individual had to be equally motivated to participate in each trial and with eight trials a day this was not achievable.

Subjects and Housing

We used mallards, as previous experiments with this species in a similar setting have shown that they are easy to handle and perform well in foraging trials (Klaassen et al. 2007). Only females were used, as the focus was competition for food and not for mates. All birds were captive-bred: 14 birds originated from a waterfowl breeder (P. Kooy & Sons, 't Zand, The Netherlands) and six birds were bred at the Netherlands Institute of Ecology. The birds were individually marked with colour rings to allow visual recognition, and the primary feathers of one wing were clipped to prevent the birds from flying. The mallards were housed in an outdoor aviary of $10 \times 5 \times 2$ m height, with access to a large freshwater pond (18.5 m^2) and shelter in the form of tall vegetation surrounding the aviary. Food consisted of a mixture of commercial food pellets (Natu-

ral Free Range Layer Pellets, HAVENS Graanhandel NV, Maashees, The Netherlands) and seed-based mixed grains (Van Havens Green-Line and Natural Scratching Grains, HAVENS Graanhandel NV), which was provided in two food dispensers. Drinking water was always available. Experimental trials were carried out in an indoor water-fowl experimental facility, containing a water filled basin of 2 x 2 m. All trials took place in April and May 2008. After the study, the birds were set on a normal feeding regime in the outdoor aviary. The experiment received ethical approval by the KNAW Animal Experiment Commission (DEC protocol CL0801).

Pre-experimental treatment

On the first 17 days, we determined the dominance hierarchy of the birds by observing them for 0.5 h in the morning and 0.5 h during feeding in the afternoon in the outdoor aviary. Between 1600-1700 hours the birds were allowed to feed ad libitum from the food dispensers. Each agonistic interaction ($N = 746$) between the individuals was scored in a dominance matrix, which is the most efficient way to classify individuals (de Vries et al. 1993; Poisbleau et al. 2006). Winners were those individuals that either chased their opponent away or that held ground after being attacked (Vahl et al. 2005). A linear dominance hierarchy for mallards was found, confirming results of other studies (Poisbleau et al. 2005, Poisbleau et al. 2006). By ranking the birds from a low to a high dominance status, we were able to determine which birds to choose for the experiment. Four birds were chosen from both the highest and the lowest-ranking group of individuals, and assigned as respectively dominant non-focals and subordinate non-focals. Of the intermediate-ranking group five birds were chosen and assigned as focal individuals. One individual of each group acted as a reserve (i.e. one focal, one non-focal subordinate, one non-focal dominant), having in total six non-focal individuals and four focal individuals participating in the experiment. We have only chosen those birds which were consistently dominant, intermediate or subordinate.

A focal individual was assigned as being dominant or subordinate, depending on the dominance status of the non-focal birds. When placed together with two dominant non-focal birds, the focal became subordinate, and when placed together with two subordinate non-focal birds, the focal became dominant. Together with this relative dominance status we were able to vary the position of the focal birds in group trials, as either being dominant, intermediate or subordinate. During these dominance trials, no physical injuries occurred and subordinates could always escape from their aggressors.

After determining the dominance hierarchy, the birds were familiarized with the experimental environment, procedures and experimentators. In 13 pilot days, each bird participated only once a day, either alone in a single trial or together with two competitors, in group trials.

The experiment

A spatially heterogeneous food distribution of four wheat grain densities was offered in 64 plastic trays (15 x 15 x 8 cm each), representing patches. The four food densities of 5, 10, 20 and 40 seeds per tray (respectively 11, 23, 46 and 91 g/m²) were grouped to resemble a slightly clumped food distribution that mallards would encounter in a natural environment (Fig. 1). Mallards are sensitive to a spatial pattern in the distribution of food densities, and use pre-harvest information in their assessment of the content of patches (Klaassen et al. 2007). Pondweed tuber densities (g/m²) and spatial variation in density, measured in 2001 in the Lauwersmeer area (Nolet et al. 2006), were used as a template. Mallards are known to forage on tubers (Cramp and Simmons 1977, Combs and Fredrickson 1996). Of the 64 trays, six trays were filled with 5 seeds, 15 with 10 seeds, 35 with 20 seeds, and eight with 40 seeds (1200 seeds, 61.7 ± 3.5 g), and covered with sand to avoid visual detection of seeds. The trays were placed next to each other at the bottom of the water filled basin forming a total of 1.44 m² foraging area. The water level above these trays was kept at 32 cm above the sediment, which is a manageable depth for mallards to forage up-ending (i.e. feeding with the posterior part of the body pointing upward and the anterior part of the body submerged; Cramp and Simmons 1977, Thomas 1982). Considering the good learning capabilities of the birds, the original set-up was rotated daily in a random order of 90°, 180° or 270° in order to change the absolute positions of the food patches each day, while the same food distribution was used.

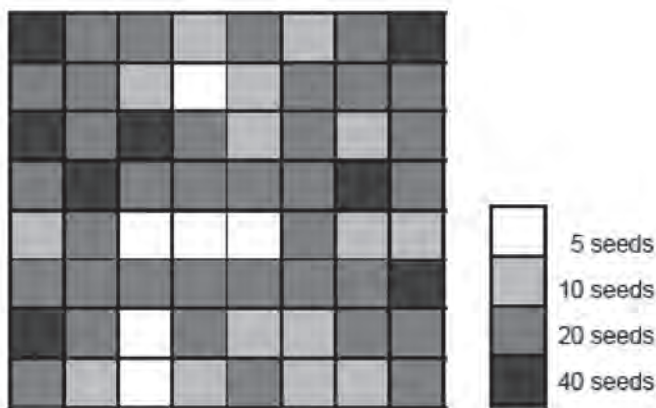


Fig. 1: Slightly clumped food distribution offered to the focal mallards in both single and group trials.

Single trials lasted 180 s and group trials 60 s, starting when the first individual started to forage. Different census times for single and group trials were desirable to avoid dissimilarity in depletion effects among single and group trials, as intake rate is a function of depletion. In this way, exploitative completion could be disentangled. By lowering the trial duration of the group trials to 60 s, depletion differences were minimized, as 3 individuals forage in total for 180 s, similar to the trial duration of the singles (180 s). Hence, the total foraging time was equal between the two trials (180 s). Results show that differences in depletion effects were successfully avoided (Table 1).

Table 1: *Percentage of seeds left in the trays at the end of the trial (mean \pm SE) for single and group trials, with group trials divided in subordinate, intermediate and dominant regarding the dominance status of the focal mallard. The number of seeds left in the trays after foraging is given between brackets. Each trial started with a total number of 1200 seeds.*

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Mean \pm SE
Single	91 (1094)	87 (1046)	87 (1045)	88 (1057)	84 (1010)	89 (1064)	86 (1026)	91 (1091)	87.8 \pm 0.9
Group subordinate	88 (1058)	88 (1061)	89 (1068)	91 (1090)	89 (1070)	81 (972)	88 (1056)	81 (977)	87.0 \pm 1.3
Group intermediate	88 (1054)	88 (1053)	91 (1089)	85 (1025)	84 (1008)	90 (1084)	88 (1053)	88 (1061)	87.8 \pm 0.8
Group dominant	89 (1062)	91 (1096)	86 (1036)	87 (1045)	91 (1091)	83 (990)	89 (1063)	85 (1023)	87.6 \pm 1.0

The experimental trials were carried out between 0700 and 1600 hours. Birds participating in trials were caught in animal transport cages with the help of a sluice system in the outdoor aviary and transported to the experimental room, enabling us to catch and transport the mallards without being held in hand. Before the start of each trial, the birds were weighed to monitor their condition. Observations were carried out from an adjacent room through a one-way window. The foraging behaviour of the mallards was recorded with a digital video camera (Panasonic NV-GS15; 0.8 Megapixels), positioned approximately 2.5 m above the basin. During the experiment, the birds were given an additional amount of food (400 g) in the afternoon in the outdoor aviary.

Data analyses

After each trial, the content of all trays was sieved over a 2 mm sieve, and the number of seeds was counted to determine the consumed number of seeds per tray. The sieving error, estimated as the number of seeds miscounted from trays where the birds had not fed, was marginal (average 0.2 % range, $N = 23$ trays).

The recorded trials were analysed with Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) at one-fifth of the normal speed. For each focal individual, the proportion of time feeding (i.e. head under water) per trial, feeding time per tray per visit (PRT), number of different visited trays, and the number of revisited trays (i.e. return to a tray with at least one other visited tray in between) per trial was analysed. A focal bird was considered to visit a patch when the head was under water and clearly visible in the tray. The GUD, defined as the number of seeds left at the moment of leaving the tray, was calculated per trial for each of the four seed densities separately, only for those trays visited by the focal birds. To assess the intake rate (seeds/s) over the trial per focal bird, the number of consumed seeds was divided by the total trial length, i.e. the time spent feeding, plus swimming and head-up processing time.

In some cases, a non-focal bird foraged from the same tray before or after the focal bird, complicating the assessment of the number of consumed seeds. In order to account for this, the instantaneous intake rate (seeds/s feeding) was measured for each bird participating in the experiment (excluding one individual that initially did not participate). The instantaneous intake rate was based on the four seed densities used in the experiment. The feeding time lasted exactly 30 s, and in total 36 trials were conducted (i.e. nine birds and four seed densities). We did not find any difference in instantaneous intake rate on the four seed densities between the individuals (GLM: $F_{8,24} = 0.121$, $P = 0.296$). In addition, data of the experiment showed a significant linear relationship between foraging time and number of seeds consumed (Linear Regression: $F_{1,18} = 172.117$, $R^2 = 0.49$, $P < 0.001$), based on only those trays which had been visited once by the focal bird in group trials. Therefore the number of consumed seeds was divided between individuals according to the proportion of time each individual foraged per tray.

Generalized linear models (GLMs) were performed with trial type (i.e. single, group subordinate, group intermediate, and group dominant) as the main factor of interest, and focal bird as random factor. Tukey post hoc analysis were used to identify differences between the four trial types and contrast tests to assess the effect sizes of the significant differences found between the trial types (Field 2005). Model assumptions were checked. All data was normally distributed, which was confirmed by Kolmogorov-Smirnov tests. Only feeding time was arcsine transformed as it contained a proportion. The reported mean values and SE of the proportion of time feeding were back-transformed. The variances in each experimental condition were similar, which was tested with a Levene's test. Observations were independent, and sample sizes fairly balanced.

For each trial the mean PRT was calculated, and the mean GUD per seed density. Sample sizes of the GUD differed per seed density as the focal birds did not visit every seed density each trial. The number of different visited and revisited trays of single trials was recalculated in 60 s to be comparable with group trials. All other foraging variables of single trials were based on 180 s.

All statistical analysis were conducted using SPSS 15.0 (SPSS Inc., Chicago, IL, U.S.A.). Results are expressed as (least square) means \pm SE and the significance threshold was set at 0.05.

Results

The intake rate did not differ between solitary, subordinate, intermediate and dominant group foragers (Table 2 and Fig. 2). However, the proportion of feeding per trial time differed between the four groups (Table 2). Intermediate and dominant group foragers were feeding a larger proportion of the time than solitary foragers (effect sizes respectively 0.87 and 0.85) (Fig. 3). Dominance status appeared to have no effect on the proportion of time feeding in group foraging mallards. PRT and the number of different visited trays differed significantly between solitary and group foragers (Table 2). Solitary foragers were spending more time per tray compared to subordinate, intermediate and dominant group foragers (effect sizes respectively 0.27, 0.33 and 0.31) (Fig. 4). Group foragers however, were visiting more different trays compared to solitary foragers, having effect sizes of 0.59 (subordinate), 0.67 (intermediate) and 0.58 (dominant) (Fig. 5). Both PRT and number of different trays were similar for birds with a different dominance status (Table 2). The GUD did not differ on the 5, 10 and 40 seed density between solitary, subordinate, intermediate and dominant group foragers (Table 3 and Fig. 6). However, even though the overall analysis on the 20 seed density did not differ between the four groups (Table 3), there was a difference in GUD between solitary and intermediate group foragers ($P = 0.044$) for this seed density, with an effect size of 0.42. The number of trays revisited did not differ between the four groups (Table 2 and Fig. 7).

Table 2: Foraging behaviour (least square mean \pm SE) of focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status. Proportion of time feeding shows upper and lower limit of the SE due to back transformation.

	Single	Group subordinate	Group intermediate	Group dominant	df	F ratio	P
Intake rate (seeds/s)	0.8 \pm 0.1	1.0 \pm 0.1	0.9 \pm 0.1	0.9 \pm 0.1	3,24	0.737	0.540
Proportion of time feeding (%)	69.0 \pm (2.4-2.4)	76.5 \pm (2.2-2.3)	79.3 \pm (2.2-2.2)	78.8 \pm (2.3-2.4)	3,24	4,250	0.015
Patch residence time (s)	5.0 \pm 0.3	3.6 \pm 0.3	3.3 \pm 0.3	3.4 \pm 0.3	3,24	6,046	0.003
Number of different trays visited	7.2 \pm 0.6	10.8 \pm 0.6	11.6 \pm 0.6	10.7 \pm 0.7	3,24	9,880	<0.001
Number of revisited trays	0.5 \pm 0.3	0.5 \pm 0.3	0.6 \pm 0.3	1.1 \pm 0.3	3,24	0.865	0.473

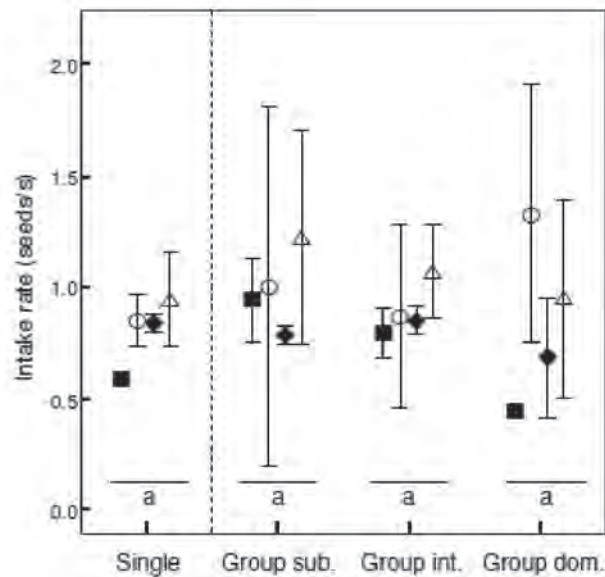


Fig. 2: Intake rate of focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status. The results of each of the four focal birds are shown for all trial types. Error bars with different letters are significant different ($P < 0.05$).

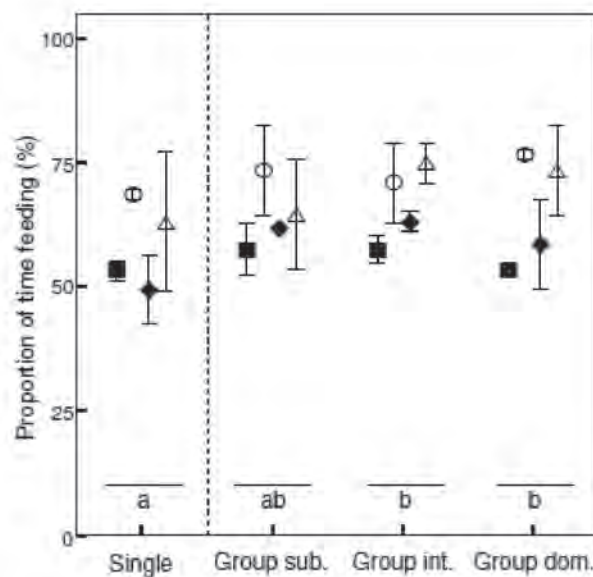


Fig. 3: Proportion of feeding per trial time of focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status. The results of each of the four focal birds are shown for all trial types. Error bars with different letters are significant different ($P < 0.05$).

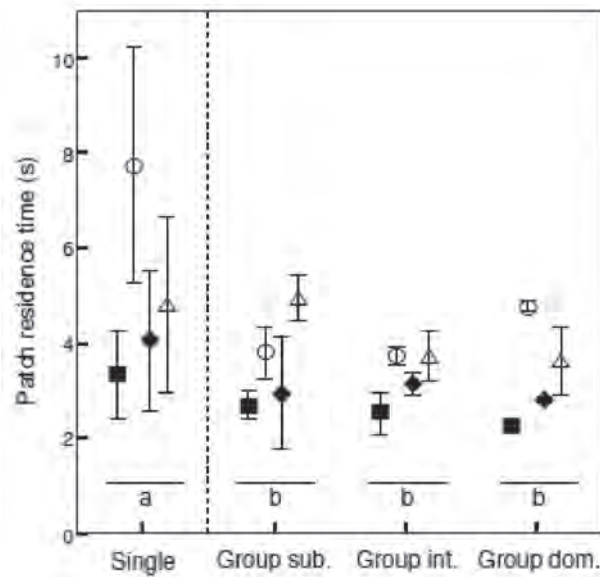


Fig. 4: Patch residence time (PRT) of focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status. The results of each of the four focal birds are shown for all trial types. Error bars with different letters are significant different ($P < 0.05$).

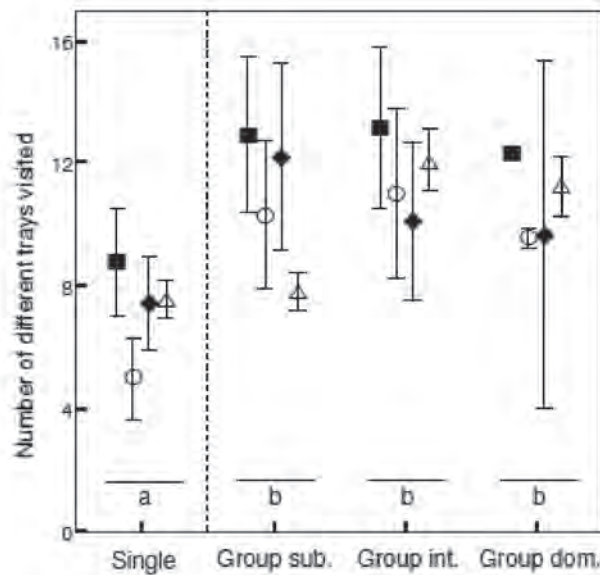


Fig. 5: Number of different trays visited by focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status. The results of each of the four focal birds are shown for all trial types. Error bars with different letters are significant different ($P < 0.05$).

Table 3: Giving up density (GUD) per seed density (least square mean \pm SE) of focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status.

Seed density	Single	Group subordinate	Group intermediate	Group dominant	df	F ratio	P
5	4.0 \pm 0.3a	4.0 \pm 0.3a	3.8 \pm 0.3a	4.2 \pm 0.3a	3,15	0.303	0.823
10	7.3 \pm 0.4a	7.3 \pm 0.5a	7.5 \pm 0.4a	7.8 \pm 0.5a	3,23	0.270	0.846
20	13.4 \pm 0.6a	14.9 \pm 0.6ab	15.7 \pm 0.6b	14.3 \pm 0.6ab	3,24	2,809	0.061
40	22.4 \pm 2.5a	26.0 \pm 2.7a	28.4 \pm 2.7a	32.95 \pm 3.7a	3,19	2,057	0.140

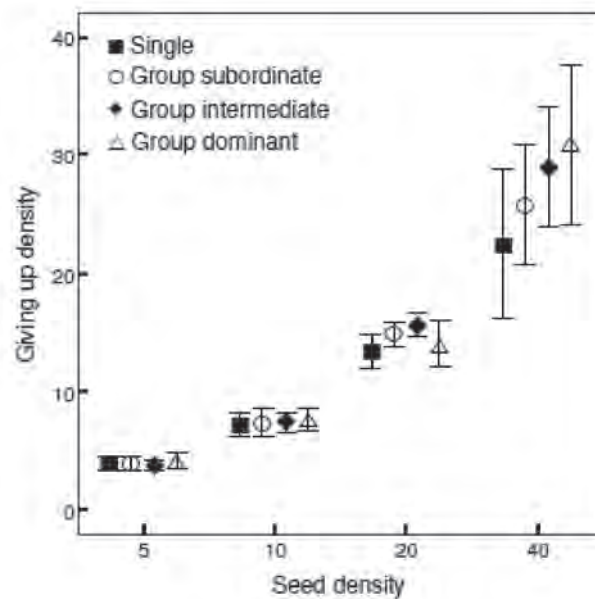


Fig. 6: Giving up density (GUD) of focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status on each of the four seed densities.

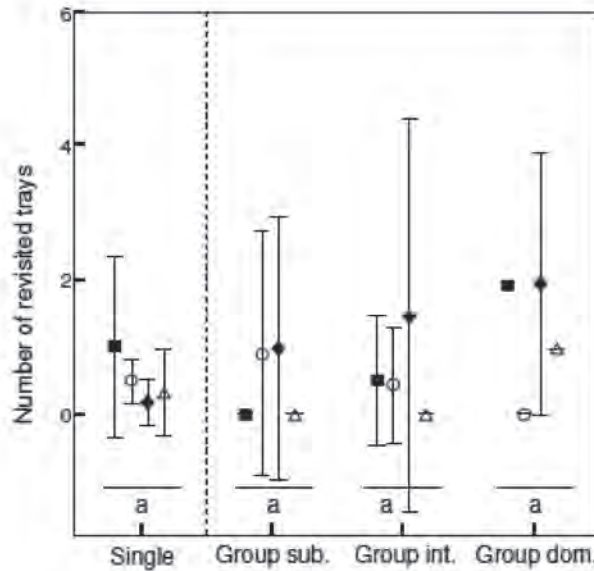


Fig. 7: Number of revisited trays visited by focal mallards foraging solitarily or in a group of three, either a subordinate, intermediate or dominant dominance status. The results of each of the four focal birds are shown for all trial types. Error bars with different letters are significant different ($P < 0.05$).

Discussion

As predicted, individuals foraging in a group had a shorter PRT and visited more trays than when foraging alone. The GUD and the number of revisited trays however, were similar between solitary and group foragers. Unexpectedly, the proportion of time feeding of intermediate and dominant group foragers was higher than when the same individuals were foraging alone. In the end, both solitary as group foragers achieved a similar intake rate. This suggests that individuals foraging in a group did not suffer from exploitative competition through a reduction in intake rate or feeding time, as they managed to increase their total intake rate to a similar level as solitary foragers by increasing their proportion of feeding per trial time, significantly so for intermediate and dominant group foragers. Surprisingly, dominance status appeared to have no effect on the intake rate, proportion of time feeding, PRT, GUD, and the number of trays visited and revisited.

These results suggest that individuals foraging in a group, regardless of their dominance status, exploit patches differently than when foraging alone on a slightly clumped food distribution. Part of the results was not as expected; as we predicted a lower intake rate and shorter feeding time for group foragers. It seems that group foraging individuals were able to compensate for exploitative competition by increasing their proportion of time feeding, hereby increasing their intake rate to a similar level as solitary

foragers. It has been suggested that effects of competition can be compensated by the benefits of group foraging. For example, a reduction in predator vigilance could lead to an increase in food intake, as more time is then allocated to foraging (Beauchamp 1998). The extra time spent foraging may also be used to maintain the intake under increased competition, as the increase in intake from the increased time available to forage is balanced by a decrease in intake from competition. In this way, effects of competition could be compensated by the benefits of reduced individual vigilance (Sansom et al. 2008). Cresswell (1997) showed that individual blackbirds, *Turdus merula*, could compensate for their reduced feeding rate in a patch, which was caused by monitoring conspecifics, by reducing their time spent scanning for predators. In this study we did not observe vigilant behaviour, most likely due to the training period in which the mallards were familiarized with the safe indoor environment. Besides predation, the increase in foraging rates might also be a consequence of increased scramble competition for resources (i.e. increased feeding speed) when the number of competitors increases (Clark and Mangel 1986, Beauchamp 2003). Rieucau and Giraldeau (2009) stated that the increase in feeding rate in nutmeg mannikins, *Lonchura punctulata*, can be the result of competitive pressure rather than release from predation pressure. This could well be applicable in our study, even though the exploitation speed is difficult to measure, it seemed that individuals foraging in a group were attempting to out-eat the others. Nevertheless, individuals foraging in a group increased their proportion of time feeding, thereby compensating for the effects of exploitative competition in such a way that they managed an equal intake rate as when foraging alone.

Nolet et al. (2006) predicted that solitary foragers should follow a fixed PLT and group foragers a flexible PLT. When comparing the results of our experiment with this study, it seems that solitary individuals have the tactic to follow a fixed PLT and group foragers a flexible PLT, however the results are not unambiguous. The PRT is predicted to be longer in solitary individuals following a fixed PLT (Nolet et al. 2006), which is in agreement with our experiment. Even though we did not find any significant differences in GUD on the four seed densities between solitary and group foragers, our results suggest that both on the 20 and the 40 seed density group foragers had a higher GUD.

We did not find any evidence that dominance status had an effect on the foraging behaviour of individuals in a group. This is in contradiction with findings from other studies (e.g. Leopold et al. 1989, Bautista et al. 1995). In dark-eyed juncos, *Junco hyemalis*, dominant individuals increase their intake rate by stealing the food found by subordinates, whereas subordinates gain no advantage of group foraging in comparison to foraging alone (Baker et al. 1981). A similar result was found in a study on barnacle geese, *Branta leucopsis*, in which subordinate individuals found quality patches but were displaced by dominant individuals, who were able to monopolize these patches. Apparently subordinates tried to compensate for a lower energy intake by exploring and by lengthening the foraging bout (Stahl et al. 2001). In our study the intake rate

between dominant, intermediate and subordinate individuals did not differ, suggesting that on a slightly clumped food distribution with more competitors, dominant birds are less capable of excluding subordinates from the richer patches.

To conduct this experiment we have deliberately chosen for the balanced design of a Latin square. We do realise the small sample size used in this experiment, however by using the same individual both in single and group foraging trials we believe we have investigated patch exploitation by solitary and group foragers in the best possible way. Our findings demonstrate that on a slightly clumped food distribution solitary and group foraging individuals exploit patches differently. Group foragers increase the proportion of time feeding, by which they manage to achieve a similar intake rate then when foraging alone. Dominance status of group foraging individuals had no effect on patch exploitation under our experimental set-up.

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Chapter 7

Tough childhood? Difficulties with feeding efficiency and foraging site selection faced by Bewick's swan cygnets

ABEL GYIMESI, BART VAN LITH and BART A. NOLET



A few days old swans following Bart van Lith, their thought-to-be father.

Abstract

In order to estimate the food requirements of a certain animal population (e.g. in carrying capacity calculations), the resource harvesting efficiency of the foragers must be known. Many calculations use an 'average' animal, consuming food at one certain rate. However, it is well-established that remarkable differences may exist in feeding efficiency between adults and young animals, with the latter group reaching significantly lower instantaneous intake rates. In animal species with extended parental care (i.e. families staying longer together), this phenomenon might also affect the parents, as they adjust their behaviour to their offspring. On the one hand, families might try to monopolize the best feeding places in the environment to compensate for the lower efficiency of the young. On the other hand, families might give up foraging at food densities that are still profitable for adults but not for youngsters. Therefore, the intake rate of young animals might play a more important role in the spatial distribution of an animal population than hitherto proposed. We measured the instantaneous intake rate of first-year and adult Bewick's swans (*Cygnus columbianus bewickii*) in an experiment. Subsequently, we investigated in the field whether there is an age-related difference in the spatial distribution of Bewick's swans. We found that first-year Bewick's swans reach a lower instantaneous intake rate than adults under the same experimental circumstances. However, no behavioural aspect could clarify the difference. The first factor coordinates of a principal component analysis on morphological measurements (explaining 52.9% of the variation) showed a significant correlation with instantaneous intake rates in the deep treatment. These coordinates correlated the strongest with body mass, width of the foot-web and body length. In the field, first-winter young birds were observed more often in smaller groups of foraging conspecifics, which more frequently occurred at sites experiencing human disturbance but also higher food densities. We propose that young animals may try to compensate for their lower feeding rate by following a risk-prone behaviour, and hence select foraging sites that are largely unexploited due to human disturbance and in the same time show lower intraspecific competition.

Introduction

The amount of food a foraging site can provide in a given time frame to maintain a number of foragers has been widely used to express the carrying capacity of the area (Goss-Custard 1985). However, even this very basic approach requires knowledge on the food intake rate of the species in question (van Gils et al. 2004). Most of the methods used nowadays to calculate carrying capacity use a single value for food intake rate of consumers (e.g. Sutherland and Anderson 1993, Fryxell et al. 2005, Desnouhes et al. 2007). However, it is acknowledged that large differences between individuals (due to for example age and/or sex classes) likely influence intake rates (Coe et al. 1976, Bautista et al. 1995).

In a wide range of species, young animals show remarkably lower feeding efficiency

compared with adults, which is assumed to be the consequence of lower experience level (Draulans and Van Vesseem 1985, Gibbons et al. 2005), minor foraging skills of young animals (Goss-Custard and Durell 1987c, Catterall et al. 1989, Bystrom et al. 2006, Munn and Barboza 2008) and/or lower dominance position (Goss-Custard and Durell 1987a, Catterall et al. 1989). This may force them to forage at lower quality sites (Draulans and Van Vesseem 1985, Breitwisch et al. 1987, Bildstein et al. 1991) and can generally lead to a reduction of fitness (Goss-Custard et al. 1998, Schmutz and Laing 2002, Nevoux et al. 2007). However, in case of extended parental care in the early life-stages of the young ones, parents may try to adjust their behaviour to compensate for the lower feeding efficiency of the juveniles (Rees and Bowler 1991, Alonso and Alonso 1993, Thiel 1998, Wilkinson et al. 2008). For instance, families might monopolize better quality foraging patches (Earnst and Bart 1991, Stahl et al. 2001, Tinkler et al. 2007). Parents might also help their offspring directly with foraging (Earnst, 2002, Earnst and Bart, 1991, Badzinski, 2005). In other cases indirectly, by increasing their own vigilance time or by supporting them in aggressive encounters (Evans 1979, Belanger and Bedard 1992, Alonso and Alonso 1993, Aviles and Bednekoff 2007), thereby providing the young ones relatively longer undisturbed feeding times (Alonso and Alonso 1993, Badzinski 2005).

Despite parental assistance, juvenile feeding efficiency might still be relatively low (Draulans 1987, Goss-Custard and Durell 1987c), forcing families to give-up foraging at resource densities that would still be profitable for adults in isolation (Bildstein et al. 1991, van Eerden et al. 1997). This may cause differential distributions of families versus adults without dependents (Black et al. 1991). Therefore, in determining the carrying capacity of a site for an animal population, accounting for differences in feeding efficiency with age might be very relevant. The problem is not negligible considering that young animals themselves, but especially together with their parents, might comprise a considerable proportion of animal populations.

Young animals often occupy a lower rank in the dominance hierarchy than adults (Goss-Custard and Durell 1987b, Catterall et al. 1989, Korhonen and Alasuutari 1995, Hirsch 2007). Hence, they are often forced to feed in environments of lower food quality compared to adults (Draulans and Van Vesseem 1985, Catterall et al. 1989, Milinski et al. 1995). Field observations alone are therefore often insufficient to determine whether a lower feeding efficiency of young animals is an inherent difference or is solely caused by being subordinate to adults. A proper approach would be to investigate feeding efficiency experimentally, before evaluating field observations.

The main goals of this study were to experimentally test whether the instantaneous intake rate of first-year Bewick's swans (*Cygnus columbianus bewickii*) is different from that of adults under the same circumstances, and to investigate whether the results can directly be linked to differences in morphology or to foraging techniques. We expected that young birds have greater difficulties in harvesting resources when these are hard

to reach. Finally, based on field observations in three different years, we investigate whether the spatial distribution of first-year birds (i.e. families) on a staging site during autumn migration differs from that of adult singles and pairs. We discuss in how far such divergence can be explained by knowledge on feeding efficiency and dominance differences.

Methods and materials

Foraging behaviour

Especially during their autumn migration, Bewick's swans show a strong preference for fennel pondweed (*Potamogeton pectinatus*) tubers, despite the availability of other food sources (Beekman et al. 1991, Dirksen et al. 1991, Nolet et al. 2002). These tubers, the asexual reproduction organs of this macrophyte, are buried in the sediment up to 0.35 m (Santamaría 2002, Hidding et al. 2009c). Tuber density is gradually increasing with burial depth until intermediate depths and thereafter is again lower (Santamaría and Rodríguez-Gironés 2002, Hidding et al. 2009c). Bewick's swans trample with their feet in water to whirl up the sediment and tubers within. First, the denser sediment particles settle in the created pits, leaving a layer of concentrated tubers on the top of the sediment, which are subsequently harvested (Gyimesi, A., van Lith, B. & Nolet, B.A., unpublished data).

Experiment

The experimental trials were conducted between 9 May and 16 June 2006. At the bottom of a concrete basin of 27m², four 2m² foraging plots (1.40m x 1.43m) were created, consisting of a sand layer of 0.25 m thick. Water depth was set at 0.50 m above the sediment. Four first-year (two males and two females) and four adult Bewick's swans (two males and two females) were used in the experiment.

Prior to the experimental trials, the swans were trained for three weeks. The aim of the training trials was to accustom the birds to the surroundings of the basin and to the experimental procedure. Experimental trials were carried out with a single individual, which was offered 67.5 g m⁻² of wheat grains as food items, either buried at 0.05 m (shallow treatment) or at 0.10 m (deep treatment). Water saturated wheat grains are similar to pondweed tubers in nutrient composition and size and have successfully been used in earlier foraging experiments to replace tubers (Nolet et al. 2001b, Nolet et al. 2006a). A trial lasted four minutes of cumulative feeding (head under water) time.

All trial combinations had four replicates, resulting in 64 trials (4 trials per individual per burial depth). The chosen bird and burial depth followed a randomized design, with the restriction that individuals were used in only one trial per day. The birds not involved in the trial stayed always in the surroundings of the basin allowing visual and audible contact between all birds. In order to reach maximization of intake rates

during the trials, the birds were deprived of food the night before an experimental day. All trials were carried out in the morning, after which all birds were allowed to feed ad libitum in the afternoon (12:00 – 17:00).

All trials were recorded on video (Panasonic NV-GS15) and were analysed using Observer 5.0 software (Noldus Information Technology bv.) to define the mean length of a feeding bout, the total time of trampling and the mean length of a trampling bout. After a trial, the remaining wheat grains were collected to define the amount of food consumed. Total food consumption divided by the feeding time provided the intake rate of the focal bird.

The mean experimental body mass of the birds (to the nearest g) was defined by measurements a day before the start, halfway and on the last day of the experiment. In addition, beak length, width of the beak at the inception, tarsus length and web width were measured to the nearest mm, and neck length and body length to the nearest 0.5 cm on the last day of the experiment.

Fieldwork

Immature swans are easy to identify in the field due to their greyish plumage. As adult Bewick's swans provide extended parental care (Scott 1980, Earnst and Bart 1991), young swans practically indicate the presence of families. Field counts were carried out at the Lauwersmeer, a shallow freshwater lake in the northern part of The Netherlands. The lake (ca. 1970 ha) is the last stopover site on the autumn migration route of Bewick's swans (Beekman et al. 1991, Nolet et al. 2006b). It is part of a nature reserve, but three of the nine discrete creeks are accessible to boat traffic. The total number of foraging adult Bewick's swans was counted per creek per day in the years 2005, 2006 and 2007. In addition, the number of foraging first-year birds within the same group was also registered. The dataset of foraging adults with first-year birds comprised of 90, 76 and 37 observations (days x creeks), respectively for the three years.

In the same years, belowground tuber densities were measured in the first week of October (i.e. presampling before swan arrival). In all years, ten randomly placed points per creek were sampled. In 2005 and 2006 twelve and in 2007 sixteen cores (10 cm in diameter) per point were taken from the upper 0.35 m of the sediment. In 2007, this happened within 1 m² plots, whereas in the other two years directly around 1m² plots (as aboveground biomass was removed in the summer for another purpose; Gyimesi, A., Varghese, S., de Leeuw, J. & Nolet, B.A., unpublished data). The extracted cores were washed through a metal sieve of 3 mm mesh size to separate the tubers from the sediment. The tubers were stored in labelled plastic bags at 4 °C until they were dried in the laboratory for ≥ 48 hours at 70 °C.

Statistical analysis

The experimental results were analysed with GLM repeated measures ANOVA, with burial depth, sex and age class as categorical predictors. The amount of seeds eaten in the trials was ln-transformed to obtain normality. The morphological measurements were subjected to a PCA analysis. The first and second factor coordinates were correlated as independent variables with the mean intake rate per individual as dependent variable.

The number of foraging swans per creek was ln-transformed and the percentage of first-year birds within a flock was arcsine transformed, and were analysed with GLM with year and access by boats (Fig. 1) as categorical predictors. In all GLMs type III decomposition was used.



Fig. 1: The Lauwersmeer area, with location in The Netherlands in the inset. Creeks with white lettering are accessible to boat traffic. The creeks are indicated by abbreviations: ADZ: Achter de Zwarten, BBL: Babbelaar, BPG: Blikplaatgat, JDG: Jaap Deensgat, NRG: Nieuwe Robbengat, ORG: Oude Robbengat, SG: Simonsgat, VLB: Vlinderbalg, ZKR: Zoutkamperril.

Results

Experiment

Sex did not show any significant effects in the repeated measures GLM, and hence was omitted from all further analyses. Both first-year and adult Bewick's swans reached significantly lower intake rates when food was buried at 0.10 m than when buried at 0.05 m ($F_{1,12} = 6.5$, $p < 0.05$; Fig. 2). First-year Bewick's swans had lower intake rates compared with adults at both burial depths ($F_{1,10} = 7.9$, $p < 0.05$; Fig. 2). The reduction of intake rates (approximately 25%) between the two burial depth treatments was similar in the age groups with a tendency for a larger difference with deeper burial (interaction term age*burial depth: $F_{1,10} = 0.1$, $p = 0.07$; Fig. 2).

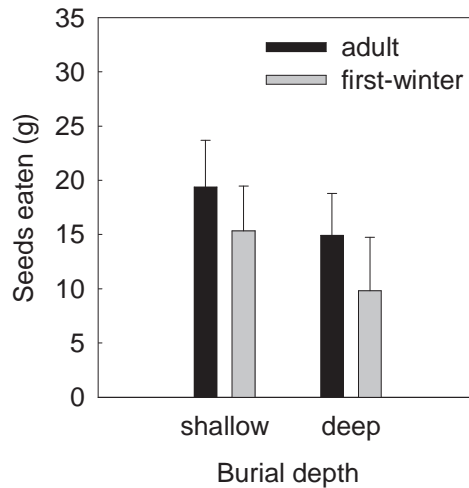


Fig. 2: Amount (mean \pm SD) of consumed seeds (g) by adult and first-year Bewick's swans after 4 minutes of underwater feeding. Food was buried at 0.05 m (shallow) or at 0.10 m (deep).

The lower intake rates of first-year birds could not be related to lower investments in the length of trampling or head-dipping. Rather, both total trampling time in a trial ($F_{1,12} = 4.10$, $p = 0.07$) and the mean length of a trampling bout in a trial ($F_{1,12} = 4.13$, $p = 0.07$) showed a tendency to be longer in first-year than in adult birds, the mean lengths of head-dipping bouts being similar ($F_{1,12} = 0.68$, $p > 0.4$).

The first factor coordinates of the principal component analysis on morphological measurements (explaining 52.9% of the variation) tended to correlate negatively with the mean intake rate of individuals ($p = 0.07$; $r^2 = 0.44$). The correlation was significant when only intake rates of the deep treatment were considered (i.e. 0.1 m food burial depth; $p < 0.05$; $r^2 = 0.52$). The loadings of the different morphological variables re-

led that body mass, width of the web and body length had the strongest negative correlations with the first principal component coordinates (-0.95, -0.89, -0.86, respectively). At the moment of the experiment, the web-width of young birds was on average only 1 cm (6.9%) less than of adult birds ($13.5 \text{ cm} \pm 0.4\text{SD}$ and $14.5 \text{ cm} \pm 0.6\text{SD}$, respectively; one-way ANOVA: $F_{1,6} = 8.0$, $p < 0.05$) and their body length was less than 3 cm (6.5%) shorter ($40.4 \text{ cm} \pm 2.2\text{SD}$ and $43.2 \text{ cm} \pm 2.2\text{SD}$, respectively; one-way ANOVA: $F_{1,6} = 3.4$, $p = 0.1$). The body mass of young swans, however, was on average 19% less than of the adults (i.e. $5628 \text{ g} \pm 569 \text{ SD}$ and $6942 \text{ g} \pm 772 \text{ SD}$; one-way ANOVA $F_{1,6} = 9.97$, $p < 0.05$). A year later the body mass difference between the same individuals was reduced to 10% (one-way ANOVA $F_{1,6} = 1.76$, $p = 0.23$) and two years later to 3% (one-way ANOVA $F_{1,6} = 0.13$, $p = 0.73$).

Field observations

In the years 2005, 2006 and 2007, respectively 982, 498 and 176 bird-days of first-year Bewick's swans were counted. In the same period, 20323, 15705 and 7428 bird-days of adult swans were registered, resulting in an average first-year swan percentage of 4.8, 3.2 and 2.4 over the entire Lauwersmeer. In all three years, these percentages remained below the countrywide average of the Netherlands (Fig. 3). Generally, more first-year swans were observed in a larger group of foraging adult swans (2005: $r^2 = 0.15$, $p < 0.05$; 2006: $r^2 = 0.1$, $p < 0.01$; 2007: $r^2 = 0.09$, $p < 0.1$). However, the confidence intervals of the slopes did not include "1" in any of the cases: the number of first-year swans did not proportionally follow the number of adult swans. In fact, the percentage of first-year swans in a foraging group decreased with the size of the group (Fig. 4; $r^2 = 0.55$, $p < 0.00001$; $r^2 = 0.5$, $p < 0.00001$; $r^2 = 0.61$, $p < 0.000001$, respectively).

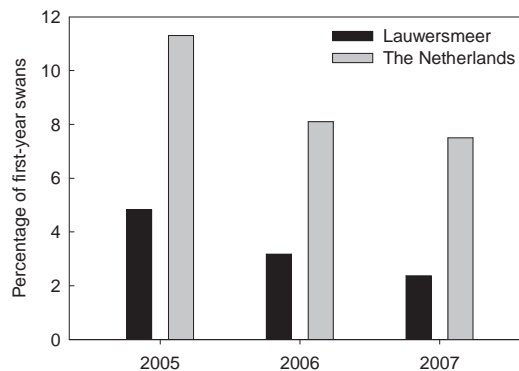


Fig. 3: Three years' data on the percentage of first-year Bewick's swans at the Lauwersmeer and generally in the Netherlands (Tijssen, W., unpublished data).

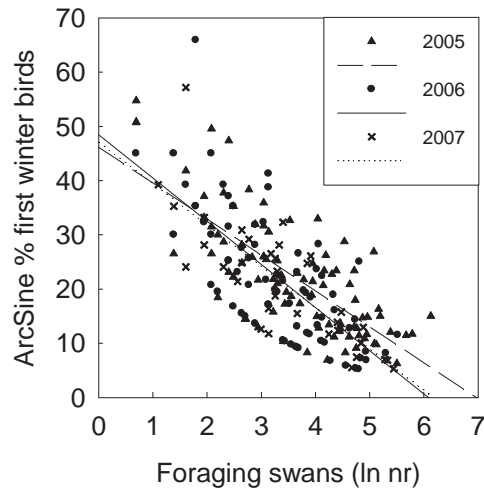


Fig. 4: Proportion of first-year Bewick's swans (arcsine transformed) in foraging flocks observed in three years.

After leaving out the insignificant interaction term year*access by boats, foraging adult swans turned out to form larger flocks in creeks not accessible to boats (GLM: $F_{1,200} = 11.1$, $p < 0.01$). In the case of first-year birds, however, there was no significant difference in creeks that were or were not accessible to boats, with even a small tendency for first-winter birds to be present in higher numbers in accessible creeks (GLM: $F_{1,200} = 2.3$, $p = 0.13$). This resulted in a higher percentage of first-year birds in swan groups foraging in creeks where boat traffic was permitted (Fig. 5; GLM: $F_{1,200} = 16.2$, $p < 0.0001$).

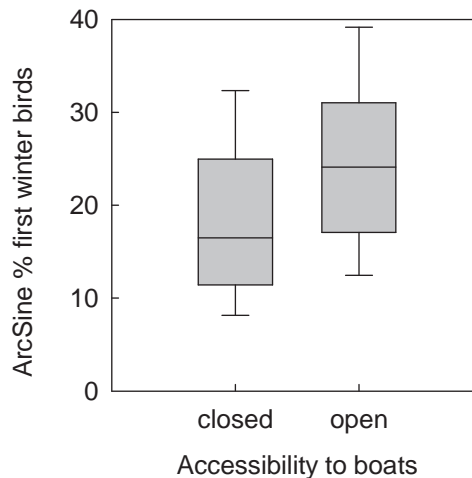


Fig. 5: Proportion of first-year Bewick's swans (arcsine transformed) in foraging flocks in creeks accessible and inaccessible by boats observed in three different years. Box plot shows median (line in box), interquartile range (box), 5th and 95th percentile (bars).

The effect of year and of accessibility to boats on initial tuber densities was tested with a full-factorial ANOVA. The main effects of year ($F_{2,264} = 5.1$; $p < 0.01$) and accessibility ($F_{1,264} = 13.4$; $p < 0.001$; with higher densities in creeks accessible to boat traffic) turned out to be significant, but there interaction term was not ($F_{2,264} = 2.3$; $p > 0.1$).

Discussion

In this study, we experimentally show that first-year Bewick's swans have a significantly lower intake rate compared to adults when foraging under identical circumstances. The difference remained similar in the two burial depth treatments, but young swans tended to have more difficulties with harvesting deeper buried food. Dissimilarities in foraging techniques could not explain the results, intake rate differences were not resulting from first-year birds investing less energy in foraging. On the contrary, they seemed to compensate for their lower efficiency by more and longer trampling bouts. Individual intake rates, however, correlated with web width, body length and body mass. Moreover, one large young male reached comparable intake rates to light adult females. Therefore, we suspect that age-related perception of the right foraging technique is not the primary reason for reaching lower intake rates. Based on our experimental results a more mechanistic explanation is likely: being in some aspects smaller or lighter is more important. Finally, our field observations suggest that families, despite their high dominance status, try to compensate for the lower feeding efficiency of cygnets by selecting sites with lower bird numbers, thus with lower levels of intraspecific competition and lower levels of food exploitation.

We propose that the trampling technique of larger or heavier birds is more efficient. A larger web could, for instance, displace more water during trampling and create a stronger water current to stir up the sediment. Web widths and body lengths of adult and first-year Bewick's swans, however, only slightly differed. Differences in body mass were more pronounced. Being heavier and possibly having stronger leg muscles, might help to put more power in a trampling movement. The fact that principal component factor coordinates showed a significant correlation (i.e. $p < 0.05$) with intake rates only in the deep burial depth treatment might point towards greater advantages of being heavier when food is buried deeper. Following the body mass of the individuals for two more years after the experiment proved that young Bewick's swans are still developing after their first-year (Evans and Kear 1978). However, already a year later, the body mass of adult and young birds was not significantly different anymore. Although we did not measure feeding efficiency, our data suggest that 2nd and 3rd year birds therefore have similar foraging efficiencies than adult birds.

Van Eerden et al. (1997) observed Bewick's swan families staying shorter at the Lauwersmeer and leaving the lake earlier than pairs and singles. Our results suggest that first-year swans have a lower success rate in harvesting food, thus reach critical intake rates at a higher giving-up food density, which forces them to leave (together with their

parents) the habitat earlier (Green 1984, Olsson and Holmgren 1998). Interestingly, as our observations also confirmed (Fig. 3), overall families' attendance of freshwater habitats was low in comparison to that of terrestrial (mainly agricultural) habitats (Dirksen et al. 1991). This could also indicate that the feeding efficiency of young animals (relative to that of adults) is lower when foraging on cryptic food items buried in the sediment than when feeding on apparent sources. This might cause families preferring to forage on terrestrial habitats (Inger et al. 2006c).

Our field observations revealed that young swans (i.e. families) occur proportionally less often in large groups of adult foraging birds (Fig. 4), similar to the findings of Earnst (1994). The number of first-year birds expressed as the percentage of a foraging group showed high similarity among the three different years, indicating the robustness of our observations. These smaller groups were found more often at disturbed sites, as these are commonly less preferred by animals (Gill et al. 1996a, Cresswell 2008). Analogously, in our study system, creeks accessible to boat traffic are less frequently used compared to other creeks (Gyimesi, A. Franken, M. S., Feige, N. & Nolet, B.A., unpublished data). This despite families being the most dominant social class, a general trend in species with extended parental care (i.e. young animals remaining for a longer period with their parents) (Scott 1980, Alonso and Alonso 1993, Stahl et al. 2001, Badzinski 2003, Klaassen et al. 2006b, Tinkler et al. 2007), which could allow them to keep away pairs and singles from the preferred foraging sites. Alonso et al. (1997) found that also common crane (*Grus grus*) families were found in relatively smaller flocks on relatively poor patches, despite being the most dominant in the hierarchy.

Even if families as a unit are the most dominant, young animals themselves are the least dominant in the hierarchy, and hence need the protection of their parents (Scott 1980, Alonso and Alonso 1993). This might also be a reason why families were observed to be involved in 33% more interactions than non-family units (Badzinski 2003). However, parents could also assure higher undisturbed feeding times for their young, as a compensation for their lower feeding efficiency, by foraging in small flocks with lower exploitative and interference competition. In addition, summer herbivores might also avoid creeks with human disturbance, leading to less damage in the aboveground vegetation of fennel pondweed, and hence higher tuber production (Gyimesi, A., de Vries, P.P., de Boer, T. & Nolet, B.A., unpublished data). In order to benefit from these advantages, parents apparently accept a risk-prone behavior, which is not common for adult animals with a high fitness (Olsson et al. 2002, Heithaus et al. 2007, Olsson and Molokwu 2007). This highlights that, next to behavioral observations, the spatial distributions of families should also be accounted for when evaluating parental investments.

As young animals form the future of populations, conservation measures should specifically target the satisfaction of their habitat requirements. This holds especially for long distance migrants, such as most arctic breeding species. Bewick's swans, for in-

stance, have a very short summer period to prepare for migration (Beekman et al. 2002, Rees 2006). Juveniles have merely a few weeks to develop between fledging and taking off for a 3500 km journey. It is of international importance to improve the survival chances of such migrating species by protection of their natural stop over sites (Fiedler and Jain 1992). We propose that sustaining an adequate size of foraging areas on these sites is a necessity to ensure low competitor densities required by young animals, which on its turn could also lead to the relative increase of the site's carrying capacity.

The strength of our study is that we go beyond merely presenting individual differences in intake rates. The findings of our experiment help us elucidating dissimilar spatial distributions of young and adult animals. They also provide an explanation for the apparent contradiction that dominant families avoid larger aggregations of conspecifics by accepting sites that are generally considered suboptimal.

Acknowledgements

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Chapter 8

Net energy gain as a common currency to explain the distribution of swans over a heterogeneous lake

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Captain Sam searching for swans with the speedboat.

Abstract

Food biomass is commonly used as the sole predictor of carrying capacity, which has proved to work in several study systems. The general applicability of this practice is challenged by the view that animal distribution follows the locally achievable net energy intake rate. This latter is determined by the density of accessible food biomass and the costs related to harvesting these resources, both of which may occasionally show large spatial variation. This study reports on a detailed, satellite image-based mapping of the belowground tuber density of sago pondweed during two years in a 2300 ha shallow lake in the Netherlands. We also predicted, in a spatially-explicit way, the costs tundra swans have to make to harvest these tubers, and we created corresponding net energy gain maps. In order to select the best predictor of bird numbers, we correlated observed cumulative bird numbers per creek with (1) total food biomass per creek, (2) total food biomass per creek above the giving-up density, (3) total accessible food biomass per creek above the giving-up density, and (4) total achievable net energy gain per creek above the quitting threshold level. In addition, we also compared observed bird numbers under the four examined candidate predictions with estimations based on a set of functional-aggregative responses. These were derived from earlier experimental measurements and calculated foraging times as a function of resource densities. In both years, observed bird numbers showed a significant match with the estimated total net energy gain, but not with any of the other predictions. Among the functional-aggregative response models, the one based on net energy gain was the only one to fit the observed relationships. Therefore we argue that in systems showing large spatial heterogeneity, predictions about consumer numbers (e.g. in calculations of carrying capacity) cannot rely exclusively on the amount of consumable food resources.

Introduction

Human pressure on natural habitats is ever-increasing. As a logical consequence, the ability to predict the number of animals visiting a site, as well as the period a site can provide animals with food, has become of crucial importance (Harper 1992). Carrying capacity, a concept presupposing a maximum to the number of animals an area can support, was introduced as early as the 1870s to qualify natural habitats (Sayre 2008). The term carrying capacity became widely used in the twentieth century, without a clear definition (Dhondt 1988, McLeod 1997, Price 1999). In the case of migratory birds, however, it became generally accepted to express the carrying capacity of a stopover site as the cumulative number of birds ('bird-days') that can be accommodated by its available food (Goss-Custard 1985). These stopover sites provide resting and refueling opportunities during migration and are often essential for birds to successfully complete their journey (Hedenström and Ålerstam 1998). Hence, a proper assessment of their carrying capacity is of essential value.

It is commonly assumed that carrying capacity largely depends on the amount of

food present (Newton 1980, Percival and Evans 1997, Nolet et al. 2006b, Salewski and Schaub 2007). Consequently, numerous authors relied on a straightforward approach in their carrying capacity estimations: dividing a site's total food supply by the amount of food an average individual daily consumes (e.g. Anderson and Low 1976, Goss-Custard and Durell 1990, Alonso et al. 1994, Desnouhes et al. 2007). Some authors considered that foragers only deplete food sources until a certain giving-up density and corrected for this in their food supply estimations (e.g. Sutherland and Anderson 1993, Gill et al. 2001b, Goss-Custard et al. 2003). Others also warned that part of the food might not be accessible to the foragers, due to e.g. tidal cycles and human disturbance (Zwarts and Wanink 1993, Percival et al. 1998, Gill et al. 2001a, Nolet et al. 2006a).

In conventional foraging models, food intake is corrected for foraging costs and animals are assumed to maximize the net rate of energy intake (i.e. intake rate based on accessible food density minus foraging costs) while foraging (Stephens and Krebs 1986). However, both accessible food density and the energetic costs of foraging can show considerable spatial variation at both relatively large (van Gils et al. 2006, Kraan et al. 2009b) and small scales (Brown 1988). Examples of such costs vary from diving costs for ducks depending on water depth (Houston and Carbone 1992, de Leeuw et al. 1999) to digging in snow by ungulates depending on snow density (Fancy and White 1985).

The ease of relying on simple measurements, such as total biomass values, is attractive compared to the use of net energy intake, which involves the additional estimation of foraging costs. However, due to the spatial and/or temporal fluctuation of net energy intake rates, calculations that simply rely on food density may overestimate or underestimate a site's actual carrying capacity (van Gils et al. 2004). Thus, the question remains relevant whether the food supply itself can accurately predict the number of animals a site can support. More specifically, we can ask whether more complicated models including accessibility of resources and costs of foraging are needed.

This paper reports on the distribution of tundra swans (*Cygnus columbianus bewickii*) in relation to their possible energy gains and costs, as documented in a shallow lake in The Netherlands, based on satellite imagery, as well as field and laboratory measurements. During their last stop-over on the autumn migratory journey, the swans forage here for a few weeks exclusively on tubers of sago pondweed (*Stuckenia pectinata*) (Beekman et al. 1991, Nolet et al. 2002). The lake comprises nine creeks, each with different combinations of food density, water depth and sediment texture. Due to the fact that the energy investments in harvesting the tubers depend both on water depth and sediment type (Nolet et al. 2001b, Nolet et al. 2006a), the system provides excellent conditions to investigate the energetic decisions swans rely upon in their foraging site selection.

In order to select the best predictor of bird numbers in carrying capacity calculations, we correlate observed cumulative bird numbers per creek with (1) total food biomass

per creek, (2) total food biomass per creek above the giving-up density, (3) total accessible food biomass per creek above the giving-up density, and (4) total achievable net energy gain per creek above the quitting threshold level. Earlier, Nolet and Klaassen (2009) showed that functional-aggregative response models can be adequately used to predict bird numbers in the field, at least in a small scale setup (four 250 x 250 m sections). Here, we compare the observed bird-days under the four examined predictions with bird-days calculated by a set of functional-aggregative response models on the scale of the whole stop-over site.

Study system

The Lauwersmeer is a freshwater lake situated in the northern part of The Netherlands (06° 13'E and 53° 22'N). Water level is regulated by a sluice. The surface area is close to 2300 ha, with approximately 850 ha shallow regions (water depth less than 1 m). In these latter areas the macrophyte stands are heavily dominated by sago pondweed (Pot 1984, van Wijk 1988, Santamaría 2002). In October, when tundra swans arrive to the area, the aboveground parts of these plants have already decayed and been washed away. Only tubers, the asexual reproduction organs, are left behind, buried in the sediment (van Wijk 1988). Hence, at that time of the year, no visual cues reveal the whereabouts and the density of the tuber stands. Tundra swans have a special technique to harvest the tubers from the sediment. A foraging bout always begins with trampling in water to loosen the sediment. Subsequently, the tubers whirled up from the sediment are reached by head-dipping in shallow water or, in a more costly way, by up-ending in deep water (Nolet et al. 2006a). After tuber exploitation, the swans switch to foraging on crop wastes of sugar beets on the agricultural fields surrounding the lake or spread out to their wintering sites (Beekman et al. 1991).

Methods and materials

Plant biomass sampling and bird counts

Large-scale sampling of belowground biomass with an adequate sample size brings about huge practical difficulties (Spencer et al. 1994). Therefore, a remote sensing technique was applied to estimate tuber density in the Lauwersmeer. Our approach relied on the positive linear relationship between the aboveground (green matter) biomass in summer and the belowground (tuber) biomass in autumn (Hangelsbroek and Santamaría 2004). 15 m spatial resolution ASTER satellite images (for technical details see Yamaguchi et al. 1999) were acquired from the Lauwersmeer in two years, at the time of peak aboveground biomass occurrence (25 July in 2006 and 2 June in 2007).

In order to test whether summer aboveground biomass density correlates with the autumn belowground biomass in our study area too, a summer sampling campaign was conducted in 2006, between 26 July and 30 July. At 77 sites, randomly chosen in

seven creeks of the lake, all aboveground biomass was collected from a 1 m² area. The sites were at least 100 m apart, so as to avoid spatial autocorrelation of the biomass (Nolet and Mooij 2002). The location of the sampling points (as of all further points) was recorded with a LEICA differential GPS (<0.2 m accuracy). The measurements were georeferenced using Dutch Rijksdriehoekstelsel control points. The collected samples were dried for ≥ 48 hours on 60 °C to obtain dry weight in g/m² (all further biomass values mentioned refer to dry weight).

Belowground biomass sampling campaigns were conducted in both study years. In the first week of October, just before the arrival of the swans, sediment cores (0.1 m in diameter) were taken from the upper 0.35 m of the sediment (Nolet et al. 2006c), and washed through a metal sieve of 3 mm mesh size to extract the tubers. The tubers were stored in labeled plastic bags at 4 °C until they were dried in the laboratory on 70 °C for ≥ 48 hours.

In 2006, tuber sampling occurred around the 1 m² plots where aboveground biomass had been removed (collected) during the summer and not within. Per point 12 cores were taken (cf. Nolet et al. 2006c), three on each side within 0.3 m of the square meter. Additionally, twenty randomly placed new points were also sampled for tubers in the two remaining creeks not sampled for aboveground biomass. These points were used during a validation of the belowground biomass prediction.

In 2007, 90 new plots were randomly generated for tuber sampling. When small sampling plots are overlaid with larger resolution (15 m in our case) spectral reflectance data (Dogan et al. 2009), mixed pixels might occur. On the other hand, a larger sampling area might cover several pixels of the satellite image. Therefore, in order to improve the interpretation of the satellite image, an area of 12x12 m was sampled in 2007, instead of 1 m². Within this area, four quadrates of 4x4 m were set out, measured from the corner points. One sampling core was taken at the corners of each quadrate, providing a total of 16 cores per plot but collected as four subsamples. During the interpretation process, the subsamples could be weighted according to the extent the sampling quadrate fell within the satellite image pixel.

Throughout the whole period that the swans were present at the Lauwersmeer (from mid-October until mid-November), bird counts and behavioral observations were carried out daily per creek, using binoculars and telescopes.

Sediment and bathymetry mapping

In order to create a sediment texture map, sediment cores of 0.07 m in diameter were taken at 350 points from the upper 35 cm of the lake bed. The core layers 0.05 - 0.1 m and 0.2 - 0.25 m were subjected to a particle-size distribution analysis using a Malvern analyzer (Mastersizer 2000). Following Nolet et al. (2001b) a principle component analysis (PCA) was conducted on six particle size categories. The first component values were extracted to serve as a sediment texture index. In order to create the sediment

map, 70% of these indices were randomly selected for interpolation, the rest served for validating the final map.

Spread uniformly over the shallow (0-1.3 m) regions of the lake, water depth was measured at 5315 points, minimally 10 m apart. The measurements were corrected to the fixed Amsterdam Ordnance Datum (NAP) level using actual quart hourly water level measurements of the lake conducted by the water managers (Waterschap Noorderzijlvest). Again, 70% of the points were randomly selected for interpolation, the rest served for validating the final map.

In order to select the best performing interpolation technique, the methods of kriging and of inverse distance weighting (IDW) with five different weight values (1, 1.5, 2, 2.5 and 3) were compared using ArcGIS 9.2 (ESRI, Redlands, USA). Based on the calculated mean error and the root mean square error (RMSE) values, the interpolation techniques were ranked (Burrough and McDonnell 1998). In case of the sediment mapping, the IDW method with weight 2.5, whereas for bathymetry the IDW with a weight of 1.5 was selected to generate pixel-specific values.

Plant biomass prediction

All biomass predictions were carried out for areas with water depth above 0.31 m. According to Nolet et al. (2006b) (and verified by the biomass sampling of this study), the occurrence of sago pondweed at lower depths is negligible at the Lauwersmeer. Moreover, the prediction accuracy of remote sensing is limited in very shallow water, due to e.g. variations in bottom color shades and sediment composition (Armstrong 1993, Valta-Hulkkonen et al. 2003, Silva et al. 2008).

In 2006, spectral information was extracted (using Erdas Imagine 9.1; Erdas Inc., Norcross, USA) from the pixels of the satellite image where aboveground biomass sampling sites were located. In order to improve the classification of the satellite image, in both years 20 locations without vegetation were also added. The digital numbers of the pixels were used to calculate NDVI values (Normalized Difference Vegetation Index) and several wavelength band ratios (green/infrared, green/red, infrared/red and red/infrared). These variables, together with water depth and sediment texture, were used to find the best description of aboveground biomass. This was carried out by a backward selection procedure based on a Gaussian logit curve described by Huisman et al. (1993):

$$B = M \frac{1}{1 + e^{(a + b(X_1) + c(X_1)^2 + d(X_2) + e(X_2)^2 + f X_1 X_2)}}$$

where B is the predicted aboveground biomass density; M is the maximum sampled aboveground biomass density; X_1 , X_2 are the biomass explanatory variables; and a, b, c, d, e and f are the parameters of the variables. The most significant description incor-

porated NDVI (X_1) and water depth (X_2) as explanatory variables (including sediment resulted in no improvement). Estimates for the parameters were calculated iteratively (Table 1), using SPSS 15.0 (SPSS Inc., Chicago, USA).

Table 1: *Explanatory variable estimates for the aboveground (2006) and belowground (2007) sago pondweed predictions.*

Parameter	2006	2007
a	5.77	2.00
b	0.00	-14.06
c	2.47	37.49
d	-0.18	-10.11
e	0.01	10.92
f	-0.19	18.56

Finally, predicted aboveground biomass density B was used to estimate tuber biomass density D. Hereby, the 77 corresponding above- and belowground biomass samples were ln-transformed and subjected to a geometric mean regression (Ricker 1984). Based on the resulting regression equation, tuber density was predicted per pixel for 2006 using ArcGIS 9.2.

In 2007, no aboveground biomass was collected. The logit-curve described by Huisman et al. (1993), parameterized on the 2006 data (Table 1), was directly applied to predict the belowground biomass density from the spectral image. The validation of the prediction was carried out on the dataset of the 90 belowground biomass field samples.

Prediction of net energy gain

The spatial-explicit prediction of the achievable net energy gain was carried out using ArcGIS 9.2. The procedure was based on a modified version of the functional response model reported by Nolet and Klaassen (2009), considering the metabolizable energy intake rate and energy expenditure of tundra swans while foraging on sago pondweed tuber biomass:

$$nei(d, s) = \varphi(s) \cdot q \cdot e \frac{a(s)D(d)}{(1 + a(s)t_h \cdot D(d))} - c(d, s);$$

where nei is the net energy intake rate while foraging (J/s or W) as a function of water depth d and sediment type s ; q is the assimilation efficiency of sago pondweed tubers by tundra swans; e is the energy density (J/g) of tubers; t_h is the handling time (s/g)

(i.e., the time required for a forager to extract the food item from the substrate and consume it); Φ is the proportion of foraging time spent feeding (s) (i.e., with head under water), as a function of sediment type s ; a is the attack rate (m^2/s), as a function of sediment type s ; D is the accessible tuber biomass density (g/m^2), as a function of water depth d ; and c is the energetic costs related to foraging (W), as a function of both water depth d and sediment type s .

The parameter values in the equation remained the same as provided by Nolet and Klaassen (2009) (Table 2). However, instead of using two sediment categories (i.e. sandy and clayey) as Nolet and Klaassen (2009), sediment type was adjusted to be a continuous variable with pixel-specific values. Hereby, the sediment particle size distributions of the earlier two sediment categories were added to the PCA analysis of the 350 sediment samples of the current study. The generated first component values for the two sediment categories were used (as explanatory variables) in simple linear regressions with the corresponding proportion of foraging time spent feeding Φ , attack rate a and burial depth b values (for exact data see Nolet and Klaassen 2009) to produce regression equations (Table 3). Subsequently, these were used to generate pixel-specific values for the sediment type-dependent variables. Considering the foraging costs and giving-up densities, the regression equations were corrected (Table 3) for the switch in foraging modes from head-dipping in shallow water ($\leq 0.51\text{m}$) to the more costly up-ending in deep water (Nolet et al. 2006a). Hereby, water depth was standardized to the average water level of the period the swans were present at the Lauwersmeer, but excluding the days when no swans were foraging due to high water levels.

Table 2: Parameter values derived by Nolet et al. (2002) used in the functional response calculations.

Parameter	Value (mean \pm SE)
Tuber assimilation efficiency q	0.90 ± 0.02
Energy density of a tuber e	$16866 \pm 296 \text{ J g}^{-1}$
Handling time th	$1.82 \pm 0.48 \text{ s g}^{-1}$

Model comparison

Tuber biomass and net energy gain values were calculated per pixel according to the criteria of the four candidate predictions. Bird numbers are expected to increase proportional to the natural logarithm of tuber biomass density and net energy gain (Nolet and Klaassen 2009). In order to account for this, both pixel-specific tuber biomass density and net energy gain values were subjected to \ln -transformation and summed per creek. Nolet and Klaassen (2009) estimated the quitting net energy intake rate of tundra swans at $56 W$, hence only pixels above this value were taken into account for

Table 3: Regression equations applied to compute the sediment texture (s) dependent variables for the functional response calculations.

Variables	Regression equation
proportion of foraging time spent feeding $\varphi(s)$	$-0.0096s + 0.744$
attack rate $a(s)$	$-0.000098s + 0.000857$
foraging cost in shallow water ($\leq 0.51\text{m}$) $c(s)$	$(0.0721s + 1.1198) \cdot 45.1$
foraging cost in deep water ($> 0.51\text{m}$) $c(s)$	$(0.0721s + 1.1198) \cdot 56.7$
tuber burial depth profile $b(s)$	$0.0000312s + 0.0008219$
giving-up density in shallow water ($\leq 0.51\text{m}$) $D_{\text{GUD}}(s)$	$1.3453s + 11.186$
giving-up density in deep water ($> 0.51\text{m}$) $D_{\text{GUD}}(s)$	$3.3632s + 18.891$

the net energy gain calculations. Subsequently, the sum of the tuber biomass and net energy gain values per creek were used in simple linear correlations on the sum of the observed swan numbers.

Finally, bird numbers were also estimated per creek based on functional-aggregative response models. The input variables of these corresponded to the four examined candidate predictions.

Model 1 was based on initial belowground biomass density D (g/m^2):

$$t = \frac{1}{(3600\varphi(s))} \cdot \left(-\frac{1}{a(s)} \cdot \ln D + t_h D \right);$$

where t (h/m^2) is the foraging time per area.

Model 2 was based on biomass density above a threshold density D_f (g/m^2):

$$t = \frac{1}{(3600\varphi(s))} \cdot \left\{ \frac{1}{a(s)} \cdot \ln \frac{D}{D_f} + t_h (D - D_f) \right\};$$

Model 3 was based on accessible biomass density $D(d)$ (g/m^2) above the threshold density:

$$t = \frac{1}{(3600\varphi(s))} \cdot \left\{ \frac{1}{a(s)} \cdot \ln \frac{D(d)}{D_f} + t_h (D(d) - D_f) \right\};$$

Model 4 was based on potential net energy gain nei (W) above the threshold level of 56 W , based on empirical relationships derived from Fig. 4c in Nolet and Klaassen (2009):

for sandy creeks: $t = 0.3050 \cdot \ln nei - 1.2703$;

and clayey creeks: $t = 0.4735 \cdot \ln nei - 1.9435$;

Finally, foraging time per area was transformed into bird-days S (per creek) through the equation:

$$S = \frac{A}{T},$$

where A is the available foraging area in a creek (m^2) and T is the total feeding time per day (10 h; (Nolet et al. 2006b)).

Results

Based on the 77 samples of 2006, a positive correlation between summer aboveground biomass density B and autumn belowground biomass density D was confirmed also in our case ($D = 0.5434B + 0.3423$; $r = 0.65$; $p < 0.0001$). Taking the entire Lauwersmeer into account, the predicted belowground biomass density in 2006 was 15.6 g/m^2 (± 7.2 SD) (Fig. 1a). The final validation carried out on the 20 additional sampling points collected in the autumn of 2006 resulted in a root mean square error (RMSE) of 7.5 g/m^2 . In 2007 the predicted mean tuber biomass density was 7.1 g/m^2 (± 5.0 SD) (Fig. 1b) with a RMSE value of 8.3 g/m^2 for the validation. Except for the creek Vlinderbalg (VLB; Fig. 1), all the others showed tuber biomass levels 22-90% less in 2007 than in 2006.

The Malvern analysis of the sediment samples (Table 4) revealed that there is a north-south gradient in the Lauwersmeer with sandy sediments (i.e. particles $> 63 \mu$) in the northern creeks and clayey areas in the southern creeks. The interpolation of the sediment texture (Fig. 2) achieved a RMSE value of 1.7, while the RMSE of the bathymetry map (Fig. 2) had a value of 0.1 m. Total available foraging area A in the studied creeks varied largely with year and with the applied prediction criteria. In 2006, considering all biomass present or the biomass above threshold level resulted in approximately 30% more available foraging area than the area with accessible food biomass only, and five times as much area than where the net energy gain was above the threshold level. In 2007, the area of total biomass and biomass above threshold level was more or less the same as in 2006. However, the area of accessible biomass and of suitable net energy gain was less than 60% of that in 2006. This latter partly resulted from the water level being on average 0.05 m higher during the exploitation period in 2007.

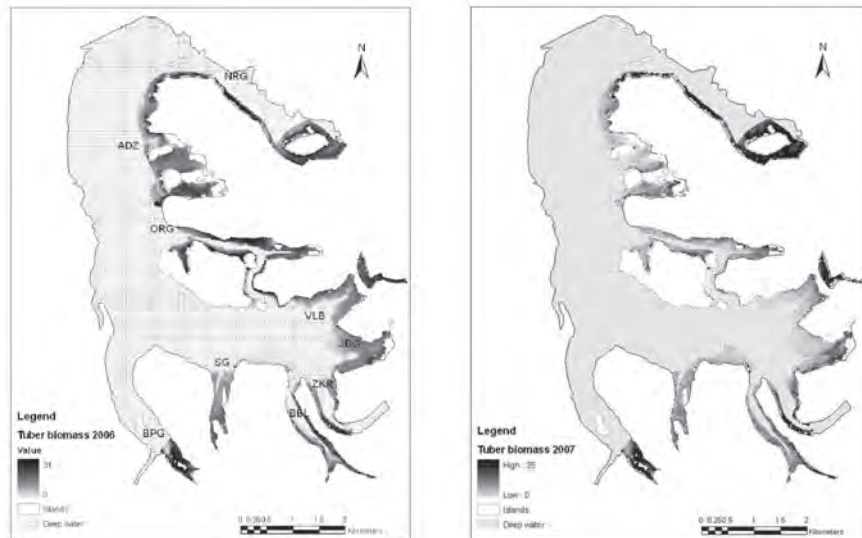


Fig. 1: Prediction map of sago pondweed belowground biomass in the Lauwersmeer in 2006 (left) and 2007 (right). The darker the coloring, the more biomass. The values in the legend are given in g/m², dry weight. The deep parts of the lake (> 1.5 m; excluded from the analyses) are dotted. The creeks are indicated by abbreviations: ADZ: Achter de Zwarten, BBL: Babbelaar, BPG: Blikplaatgat, JDG: Jaap Deensgat, NRG: Nieuwe Robbengat, ORG: Oude Robbengat, SG: Simonsgat, VLB: Vlinderbalg, ZKR: Zoutkamperril.

Table 4: Table 4: Mean (\pm SE) granulometric composition in percentages of the sediment samples collected in the Lauwersmeer ($n = 350$).

<16 μ m	16-< 50 μ m	50-< 63 μ m	63-< 125 μ m	125-< 250 μ m	250-< 500 μ m
2.23 \pm 0.15	2.78 \pm 0.22	3.5 \pm 0.18	42.74 \pm 0.56	46.18 \pm 0.82	2.51 \pm 0.12

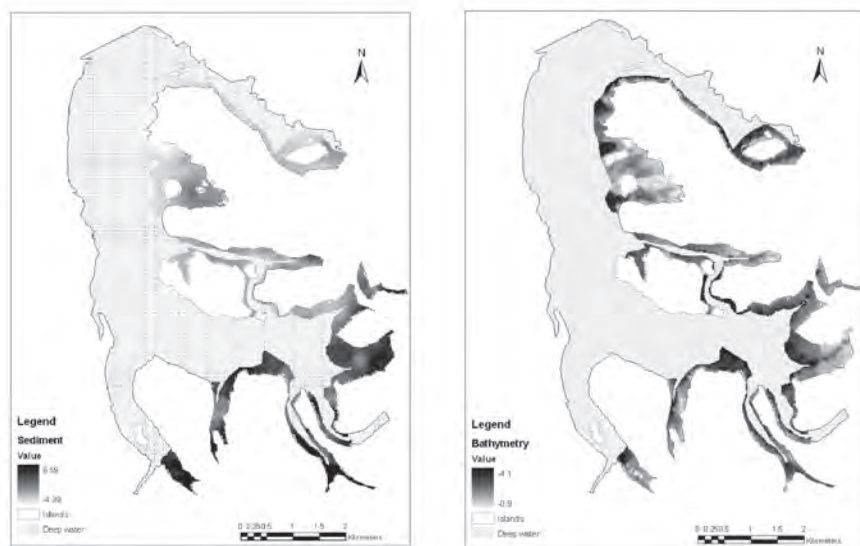
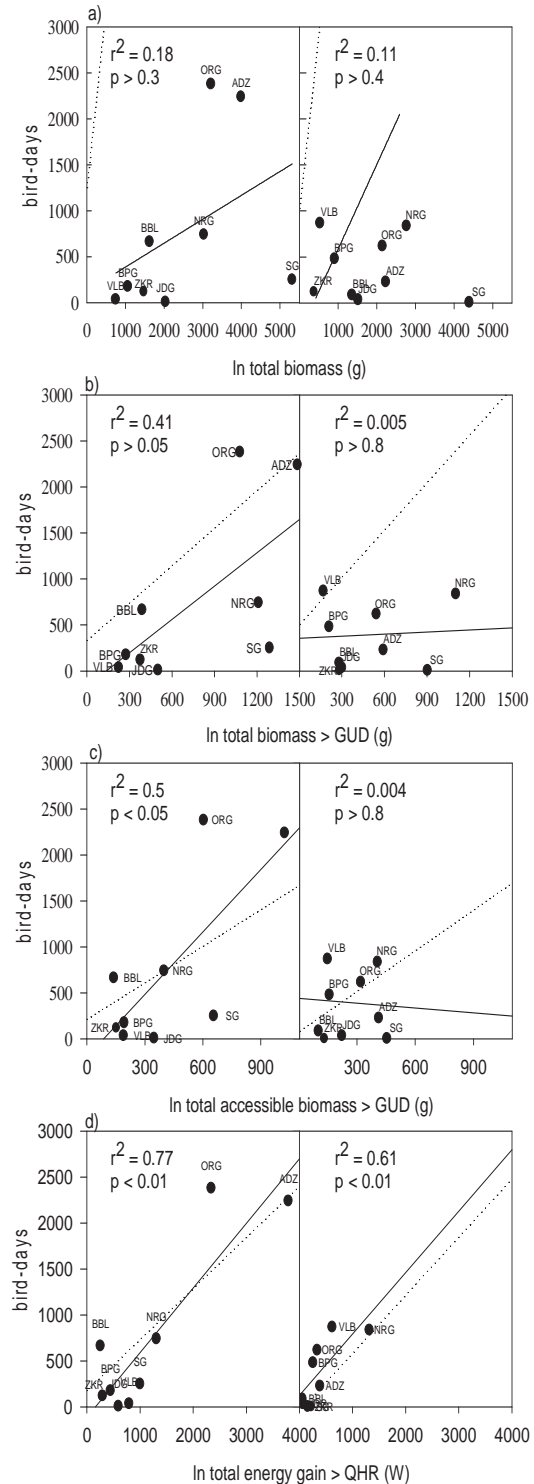


Fig. 2: Sediment texture (left) and bathymetry map (right) of the shallow regions (< 1.5 m) of the Lauwersmeer, based on IDW interpolation. The darker the color, the higher the clay content of the sediment (left) and lower the lake bottom elevation (right). The values in the sediment map legend are texture indices, increasing with clay content. The bathymetry legend values are expressed relative to the Amsterdam Ordnance Datum.

In 2006, tundra swans were present at the lake from 11 October until 10 November. The total number of foraging bird-days (i.e. the cumulative number of foraging swans per day) was 6607 for the whole Lauwersmeer, with a mean of 734 (± 310 SE) foraging bird-days per creek. Similarly to 2006, the exploitation period lasted in 2007 from 12 October until 16 November. However, the mean foraging bird-days per creek was only 322 (± 119 SE), adding up to a total of 2898 foraging bird-days, less than half in 2006. Considering all the creeks, the percentage of birds foraging was 47.5 % (± 8.15 SE) in 2006 and 49.63 % (± 9.32 SE) in 2007, being not significantly different from each other ($t_{36} = 2.03$, $P > 0.9$). However, the spatial distribution of the birds considerably changed between the two years. In 2006, more than 75% of the foraging birds were observed in two of the nine creeks (Oude Robbengat – ORG and Achter de Zwartten – ADZ; Fig. 1). In 2007, these two creeks accounted for only a third of all the bird-days: the swans were more equally spread among the creeks.

The prediction on the total biomass above the local giving-up density showed a reasonable relationship with the observed bird-days per creek in 2006 (Fig. 3b). However, only the total net energy gain above a threshold value of 56 W provided a significant correlation in both years (Fig. 3e). Especially in 2006, the explanatory power of the predictions largely improved from taking simply the total biomass towards considering the total achievable net energy gain (Fig. 3).

Fig. 3: The sum of observed bird-numbers per creek against four biomass and energy gain predictions (solid line shows simple linear regression): a) the sum of the (ln-transformed) food biomass per creek, b) the sum of the (ln-transformed) food biomass per creek above the local giving-up density, c) the sum of the accessible (ln-transformed) food biomass per creek, d) the sum of the accessible (ln-transformed) food biomass per creek above the giving-up density and e) the sum of the (ln-transformed) net energy gain per creek above the quitting threshold level (56 W). In the left column data from 2006 and in the right from 2007. For comparison, the data points are labeled with the abbreviations of the creeks (Fig. 1). Dotted lines provide predictions based on functional response calculations.



Comparing these predictions with the estimations derived from the functional-aggregative response models resulted in a similar picture. In 2006, model 2 (i.e. based on the biomass above giving-up density) had a comparable slope to the regression of the observational data. However, the intercept was still considerably different (Fig. 3b). Model 3 (i.e. based on the accessible biomass) fitted the observational data better (Fig. 3c), but again only in 2006. Considering both years, only model 4 (i.e. based on achievable net energy gain) gave a real good match (Fig. 3d).

Discussion

Estimation of food resources

Satellite imagery has recently become a useful alternative to labor-intensive and time consuming field measurements (Canfield et al. 1990, Spencer et al. 1994, Sabol et al. 2002, Vis et al. 2003). Even though remote sensing has its limitations in aquatic environments (Mumby and Edwards 2002), the validation of the plant biomass prediction showed that the results are sound. Therefore, we believe that satellite imagery can also be a valuable tool in estimating belowground food resources of a large area. It is also worth mentioning that the accuracy of our tuber biomass estimates of 2007, attained directly from the satellite image, was close to that of 2006, when the interpretation of the image was based on the actually observed aboveground biomass values. Thereby, it seems that the prediction of Huisman et al. (1993) is applicable to directly predict belowground biomasses from satellite images without additionally sampling aboveground biomass. Still, a potential problem remains in predicting tuber biomass based on the aboveground biomass. After assessing the biomass, herbivory still might take place later in the summer, which is known to affect tuber production (Klaassen et al. 2006c, Hidding et al. 2009b).

Besides the prediction of tuber biomass, our spatially-explicit net energy gain calculation mainly relies on interpolations of water depth and sediment texture. The former was based on a much larger number of measurements, hence expected to be more reliable. On the other hand, sediment changes occur on larger spatial scales than water depth changes. Therefore, we expect also our sample size of sediment measurements to give a good base for the interpolation. The predicted general trend of increasing clay content from north to south also corresponds to earlier descriptions of the area (Beekman et al. 1991). The final sediment map was used to derive spatially explicit values for foraging costs. Hereby, we applied linear regressions between sandy and clayey sediments, which is also a common practice in specifically oriented agricultural studies to calculate the power requirements of loosening soils of different compaction levels (Oztas et al. 1999, Alimardani et al. 2007).

When defining foraging costs and giving-up densities, we took the average water level that occurred in the period the swans were present at the lake, whereas the actual

water level varied. The accessible biomass stock is mainly dependent on the bathymetry, hence changing water levels have different effects in the creeks. Moreover, the moment of within year water level changes is also of importance. High water levels occurring at the end of the exploitation period might force the last large groups to leave the area, even if the amount of food is otherwise still acceptable. Although there are indications that the spatial and temporal variation in the vertical distribution of tuber biomass (i.e. the other factor determining the amount of accessible biomass) is negligible (Nolet and Gyimesi, unpublished data), this needs in the future more attention, as such differences could change the outcome of the regression equations.

Estimation of carrying capacity

In this study we report that the observed cumulative number of foraging tundra swans is correlated with the total achievable net energy gain (above the quitting harvest rate) from sago pondweed tuber biomass. Among the four compared candidate predictions, this is the only one that produced a significant relationship in both years (Fig. 3). Also, bird-days estimations by the functional-aggregative response calculations also matched with the net energy gain predictions only. This implies that food biomass alone, even if corrected for accessibility and/or a threshold giving-up density, does not adequately predict bird numbers in a system with a high heterogeneity: the spatial variation in gross intake rate and in foraging costs have to be accounted for too (van Gils et al. 2004). Moreover, net energy gain unifies a number of separately measured parameters (Goss-Custard et al. 1992, Mayor et al. 2009) and therefore can be a useful currency in carrying capacity calculations.

Foraging costs might have a larger influence on feeding site selection in times of resource scarcity. In 2007, when the amount of food was less than half of 2006, predictions based exclusively on food biomass showed much weaker correlations with bird numbers than in 2006 (Fig. 3). This was further underlined by the functional response models: in 2007, except for the net energy gain model, all the others largely deviated from the expectations. However, the smaller range of values in 2007 compared to 2006 may have blurred these latter relationships.

Earlier, Gill et al. (2001b) argued that depletion models, relying on non-spatial functional responses, can effectively predict the abundance of consumers. In addition to the concerns raised by van Gils et al. (2004), Goss-Custard et al. (2003) suggested that depletion models might not be applicable if the characteristics of foraging sites within a habitat largely differ. In our system, not only foraging costs are characterized by a great spatial variability, but also several components of the functional response model (Table 3), most importantly the accessibility of the food items (Nolet and Klaassen 2009). Moreover, the effects of wind fetch (Scheffer et al. 1992, Wersal et al. 2006) and summer grazing (Hidding et al. 2009b) on the development of the aboveground biomass might differ per creek and per year. This might be a reason why interannual changes

in food density do not have the same direction in all the creeks. Therefore, it can occur that the total biomass in the lake remains the same, just distributed in a different way. Net energy gain is a single currency that comprises all spatial variations in costs and benefits and can be used alone as a proxy for animal distribution, instead of relying on a number of separate parameters (e.g. Goss-Custard et al. 1992, Hoyer and Canfield 1994, Micol et al. 1994, Mayor et al. 2009).

Relying only on the number of foraging instead of the total number of birds per creek was an essential step in the data analysis. Swans use some areas almost exclusively as resting sites while foraging elsewhere. Therefore, total bird numbers do not provide a proper representation of the carrying capacity of a site. We also have to highlight the impact human disturbance can have on the bird distribution (see e.g. Hockin et al. 1992, Gill et al. 1996a, Gill et al. 2001a). All the tested models rely on the main assumption that birds are free to choose their foraging site. However, our study area is exposed to varying levels of recreational activities. Animals might trade-off safety with energetic returns, resulting in relatively shorter exploitation times at sites that are perceived to be more risky (Bowers et al. 1993, Brown et al. 1994, Gill et al. 1996b, van Gils and Tijssen 2007, Gyimesi, Franken, Feige and Nolet, unpublished manuscript). The magnitude of this effect might change with the level of recreational activities but also with the amount of food present. In years of low resource abundance, animals might be more willing to forage in higher-risk habitats (Inger et al. 2006a, Godvik et al. 2009). Especially, as birds grazing on the aboveground vegetation in the summer might also avoid sites open to the public, which might result in higher tuber production in these sites (Nolet 2004, Hidding et al. 2009b, Gyimesi, de Vries, de Boer and Nolet, unpublished manuscript).

Conclusions

Our findings have essential implications for carrying capacity assessments. First of all, in systems with a high heterogeneity, relying only on biomass estimations without considering a threshold can lead to large overestimations. Large areas with too low biomass levels can be worthless for animals. On the other hand, sites with high biomass levels but with relatively high foraging costs are also avoided. In such cases, applying the net energy gain as a currency for animal distribution can also help managers of nature reserves to assign areas within the reserve that are of high value for a certain species, hence need extra protection.

In resource management, carrying capacity calculations are primarily carried out deductively. In such cases, the number of individuals an area can sustain is calculated based on the available food supply and the known food demand of an individual (e.g. Alonso et al. 1994, McLeod 1997, Desnouhes et al. 2007, Hetherington and Gorman 2007). We are convinced that carrying capacity calculations should also be tested inductively, i.e. whether the number of foragers relates to the food supply. To our know-

ledge, this is the first case that an inductive approach is used for investigating the carrying capacity of a large-scale system with high heterogeneity.

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Chapter 9

Giving-up net energy intake rate exposes the effect of human disturbance on Bewick's swan habitat use

ABEL GYIMESI, MARYCHA S. FRANKEN, NICOLE FEIGE AND BART A. NOLET



Nicole on the mobile watchtower on a beautiful Dutch autumn day.

Abstract

Outdoor recreational activities are on the increase, as is the need for tools to evaluate their impact on wildlife. In mammal studies, an accepted technique for assessing disturbance is to measure the reduction in resource utilization (through the so-called *giving-up densities* - GUD). However, when the accessibility of the food items and the costs to harvest them spatially vary, these factors also shape giving-up densities. In this study, we account for this by estimating *giving-up net energy intake rates* (GUNEI). We determined initial and giving-up densities of tubers of fennel pondweed (*Potamogeton pectinatus* L.), which forms the exclusive food source of Bewick's swans (*Cygnus bewickii* Yarrell) during their migratory visit at a shallow lake in The Netherlands. By correcting for biomass accessibility and foraging costs we also calculated net energy intake rates. Subsequently, we investigated whether access of creeks by boats caused differences in giving-up densities and/or giving-up net energy intake rates. GUDs showed no difference in creeks open or closed to boat traffic. However, GUNEI was generally higher, after correcting for initial energy intake rates, in creeks open to boat traffic. Distance to boat channel did not linearly affect GUNEI. Furthermore, we measured higher tuber consumption than expected based on daytime bird counts in creeks open to boat traffic. This suggests that swans (at least partly) compensate for disturbance by switching from closed to disturbed creeks at night. The use of GUNEI is a useful proxy to quantify the cumulative effect of disturbance on an animal population as a whole, even when giving-up densities fail due to the heterogeneity of the environment. It allows direct quantification of how changes in disturbance regimes affect animal habitat use, and consequently the carrying capacity of a specific site.

Introduction

The growing popularity of outdoor recreational activities has brought about a conservation interest in determining the influence of human disturbance on the behaviour and distribution of animal populations (Boyle and Samson 1985). Hunting and fishing may kill animals, but many recreational activities have no direct lethal effects on animals. However, it is becoming increasingly clear that non-lethal consequences of disturbance play a major role in determining population and community dynamics (Cresswell 2008). In some cases, human disturbance directly affects the survival and/or the reproductive success of individual animals (West et al. 2002). However, the effects are often less obvious, as in the case of reduced access to resources, such as food supplies or breeding sites (Hockin et al. 1992, Gill et al. 2001a, Rode et al. 2006).

For migrating birds, the access to food at stop-over sites is of great importance for completing migration and for subsequent breeding success (Hedenström and Alerstam 1998, Drent et al. 2007). Effective conservation of stop-over sites requires the quantification of habitat quality deterioration related to human activities (Klaassen et al. 2006a, Kraan et al. 2009b). Animals often respond to humans in the same way as to potential

predators, and hence human disturbance can be studied in a similar fashion as natural predation (Gill et al. 1996a).

Expressing the risk of predation from the animal's point of view is considered to be a major challenge in studying habitat selection (Sinclair et al. 2006). Reduction in resource utilization is an accepted indicator of the perceived risk of predation. Animals trade off safety with food intake: the amount of food left behind by a forager, the so-called giving-up density (GUD) is higher in food patches with a higher predation risk (e.g. Brown 1988, Thorson et al. 1998, Hochman and Kotler 2007). Therefore, quantifying food consumption in patches with varying levels of predation risk is known to be a useful method to investigate the effects of human disturbance, especially in the case of animals exercising a cryptic or nocturnal life-style (Gill et al. 1996a, Brown and Kotler 2004). However, even this approach has most often been applied in studies on mammalian foragers, and less on birds (see review in Brown and Kotler 2004). In this latter group, due to their distinct alert position and flight response, alert- and flight distances became the most widespread method to quantify the effects of human disturbance (Blumstein et al. 2005, Laursen et al. 2005, Rees et al. 2005, Moller 2008). Yet, when all individuals avoid regularly disturbed areas no direct behavioural responses can be measured, and hence alert- and flight distances are not helpful. A rare disturbance event, on the other hand, might provoke a spectacular flight response, and hence be interpreted as a serious impact, whereas birds are capable of quickly returning, resulting in a smaller disturbance effect than expected from the flight response (Gill et al. 1996a, Cardoni et al. 2008). Using GUD measurements in disturbance studies provides a solution to these problems since the actual changes in the habitat use of animals are measured (Cresswell 2008).

However, GUD is obviously not solely influenced by the presence or absence of predators. The gross intake rate and the energetic costs of foraging are important aspects in shaping the GUD (Brown 1988, Nolet et al. 2001b). Therefore, when the accessibility of the food items and the costs to harvest them spatially vary, giving-up density differences cannot be directly linked to human disturbance. The net rate of energy intake incorporates in one currency all the differences in food density, intake rate, energetic costs, predation risk and missed opportunity costs of foraging (i.e. the value of alternative activities; Brown 1988). According to the marginal value theory, the giving-up net energy intake rate (i.e. the net energy intake rate at the moment the animal leaves the patch) is expected to be the same over the entire habitat in the absence of predation (Charnov 1976, Brown 1988, Nolet and Klaassen 2009). Therefore, giving-up net energy intake rate differences between patches with or without predation risk may be used to quantify the effect of predation risk even in a heterogeneous habitat.

Here we present a study where we examined the habitat use of Bewick's swans *Cygnus bewickii* Yarrell at the Lauwersmeer. This shallow lake in the northern part of the Netherlands is the last stopover site of Bewick's swans on their autumn migration.

Here they feed in the shallow parts on belowground tubers of fennel pondweed *Potamogeton pectinatus* L. for several weeks (Beekman et al. 1991). The swans accumulate these tubers in sediment pits, created by trampling movements with their feet. After depletion of the tuber banks, Bewick's swans switch to beet feeding on surrounding agricultural fields or spread out to their wintering grounds further west and southwest (Nolet et al. 2002).

The Lauwersmeer comprises nine creeks differing in food density, water depth and sediment type, which all influence energetic decisions swans make when choosing a foraging site (Nolet et al. 2001b, Nolet et al. 2006a). In an earlier study, Nolet and Klaassen (2009) found that the giving-up net energy intake rate of Bewick's swans in an undisturbed creek of the Lauwersmeer was equal for different sediment type - water depth combinations. Even though hunting is prohibited, the lake is a popular recreational destination, with several creeks open to boat traffic (Fig. 1). This introduces varying levels of perceived predation, bearing energy and time costs to the swans in addition to the energetic costs of foraging.

In this study we look at giving-up densities and giving-up net energy intake rates at the scale of the whole lake. We determined initial and giving-up densities in all nine creeks and, by correcting for biomass accessibility and foraging costs, we calculated giving-up net energy intake rates, based on patch-type specific functional responses (Nolet and Klaassen 2009). We compared measured giving-up densities and giving-up net energy intake rates in creeks open and closed to boat traffic, expecting generally higher values in the former. In addition, we investigated whether decreasing distance from boat channels affected Bewick's swan habitat use. In order to see whether swans compensated for human disturbance by foraging at night (Lourenço et al. 2008), we predicted the duration needed to accomplish the measured level of food consumption, and compared it with the duration the swans were observed feeding at the lake during daytime. We hypothesized lower observed than predicted feeding durations in creeks open to boat traffic: swans would avoid disturbed creeks during daytime when the observations were carried out, but visit these sites during the night hours. If so, this could lead to the opposite in creeks closed to boats: swans foraging here during daytime would switch to disturbed creeks during the night, resulting in higher observed than predicted feeding durations.

Methods and materials

Field measurements

During the whole period Bewick's swans were present at the Lauwersmeer (October -November), the number of foraging Bewick's swans was daily recorded per creek in four different years (2005-2008) using a 20-60x telescope (Swarovski ATS-80 HD).

In the same four years, belowground tuber densities were measured in the first week of

October (i.e. presampling before swan arrival: initial tuber density (D_i)) and at the end of November - early December (i.e. after the swans had left: giving-up or final tuber density (D_f)). By October, tuber production has stopped and natural tuber mortality can be neglected over the short period Bewick's swans visit the Lauwersmeer (winter mortality over the period November – March amounts to only $0.07\% \pm 0.06$ SE; B.A. Nolet, unpublished data). In all years, ten randomly placed points per creek were sampled. In 2005, 2006 and 2008 twelve and in 2007 sixteen cores (0.1 m in diameter) per point were taken from the upper 0.35 m of the sediment. In 2007 and 2008, this happened within 1 m² plots, whereas in the other two years directly around 1 m² plots (as aboveground biomass was removed in the summer for another purpose; A. Gyimesi, S. Varghese, J. de Leeuw, B.A. Nolet, unpublished data). The extracted cores were washed through a metal sieve of 0.03 m mesh size to separate the tubers from the sediment. The tubers were stored in labelled plastic bags at 4 °C until they were dried in the laboratory for ≥ 48 hours at 70 °C.

At each sampling point, water depth was measured and a sediment sample was taken for particle-size distribution analysis (Malvern analyzer: Mastersizer 2000). Water depths were standardized to the water level pursued by the water manager Waterschap Noorderzijlvest (0.92 m below Amsterdam Ordnance Datum (NAP)). Six sediment particle size categories were submitted to a principle component analysis (PCA). Extracted negative first component values were defined as sandy sediment, whereas positive ones as clayey (cf. Nolet et al. 2001b).

The number of boats was scored for 15 minutes in 2007 and for one hour in 2008, on multiple days and at various periods during the day in the three creeks open to boat traffic (Fig. 1).

Fig. 1: The Lauwersmeer area, with position in The Netherlands in the inset. The creeks are indicated by abbreviations: ADZ: Achter de Zwarten, BBL: Babbelaar, BPG: Blikplaatgat, JDG: Jaap Deensgat, NRG: Nieuwe Robbengat, ORG: Oude Robbengat, SG: Simonsgat, VLB: Vlinderbalg, ZKR: Zoutkamperril. Creeks with white lettering are open to boat traffic.



Data analysis

Giving-up net energy intake rates (GUNEI) were calculated by applying the patch-type specific functional response of Bewick's swans foraging on fennel pondweed tubers (Nolet and Klaassen 2009):

$$GUNEI(d,s) = \varphi(s) \cdot q \cdot e \cdot (a(s) \cdot Df(d) / (1 + a(s) \cdot th \cdot Df(d))) - c(d,s)$$

where *GUNEI* is the giving-up net energy intake rate ($J s^{-1}$ or W) as a function of water depth *d* and sediment type *s*, $\varphi(s)$ is the proportion of foraging time spent feeding (with head under water) as a function of sediment type *s*, *q* is the assimilation efficiency of fennel pondweed tubers by Bewick's swans and *e* is the energy density of the tubers ($J g^{-1}$). The model further includes the variables *a(s)*, the attack rate ($m^2 s^{-1}$) as a function of sediment type *s*; *th*, the handling time ($s g^{-1}$) (i.e. the time required for a forager to extract the food item from the substrate and consume it); *Df(d)*, the giving-up tuber density, considering only the accessible part of the biomass, which is a function of water depth *d*; and *c(d,s)*, the energetic costs of foraging as a function of water depth (i.e., head-dipping in shallow water or up-ending in deep water) and sediment type. The values of the parameters and the calculation of the accessible tuber biomass are described by Nolet and Klaassen (2009).

In order to reduce the effect of data points where no tuber consumption took place, the assumption was made that animals would not invest in foraging at locations where their energy balance is negative. Therefore, only samples were included in the analyses with positive initial energy intake rates ($n = 193$). To reach normality, all initial- and giving-up tuber densities were square-root transformed, whereas initial- and giving-up net energy intake rate values were increased by hundred (due to some negative giving-up net energy intake rate values) and ln-transformed.

Differences in giving-up densities and giving-up net energy intake rates between creeks open and closed to boat traffic were tested using GLMs (type III sum of squares), with year and initial net energy intake rate as covariates. Distance between a sampling point and the nearest boat channel was measured using ArcMap 9.1 (1999-2005 ESRI Inc.) for points ($n = 141$) where passing boats could be in the sight of swans. In a subsequent GLM analysis (type III sum of squares), again with initial net energy intake rate and year as covariates, we tested the effect of distance to the boat channel on giving-up net energy intake rates. Year showed no significant effect in any of the analyses, and hence final full-factorial tests were carried out without year.

Due to the large number of tubers per time unit that swans encounter in their foraging pits, even at relatively low food densities, they can probably estimate patch quality well, allowing them to approach prescient foraging behaviour (i.e. a forager that has an accurate knowledge of the patch quality immediately upon arrival; Valone and Brown 1989, Klaassen et al. 2006c). Therefore, we assumed that they immedia-

tely abandon patches with energy intake rates below the threshold (k) that maximizes long-term average intake rate, whereas patches of better quality are harvested until this threshold (Olsson and Brown 2006). We estimated the threshold giving-up energy intake rate of open and closed creeks by a least-squares fit of the data to the following set of equations:

$$\begin{aligned} \text{if } inei \leq k, \text{ then } GUNEI &= inei, \\ \text{if } inei > k, \text{ then } GUNEI &= k, \end{aligned}$$

where $inei$ is the initial net energy intake rate.

After correcting for the 10.6% tuber biomass that was removed during presampling (i.e. before the swans arrived), tuber consumption by swans was calculated by subtracting the giving-up density from the initial tuber density. Based on the realized tuber consumption and the patch-type specific functional response of Bewick's swans on sandy and clayey soils (Fig. 4. in Nolet and Klaassen 2009), the expected feeding time (h m^{-2}) was predicted (t_{pred}):

$$\begin{aligned} \text{If } inei > 56 \text{ J s}^{-1}: \quad t_{pred} &= 0.3050 \cdot \ln inei - 1.2703 \text{ (sandy sediment)} \\ t_{pred} &= 0.4735 \cdot \ln inei - 1.9435 \text{ (clayey sediment)}. \end{aligned}$$

$$\text{If } inei \leq 56 \text{ J s}^{-1}: \quad t_{pred} = 0.$$

Based on satellite images of pondweed vegetation and interpolations of sediment type and water depth, net energy intake rate maps were created for 2006 and 2007 (Gyimesi, Varghese, de Leeuw and Nolet, in prep.). Using the observed tuber consumption, this provided the possibility to predict the cumulative feeding time per creek (T_{pred}). Conversion to swan-days was reached by multiplying by 10, i.e. the hours Bewick's swans are assumed to spend feeding per day (Nolet et al. 2006b). The daily swan counts per creek provided the total observed feeding time in swan-days (T_{obs}). After \ln -transformation for normality, the predicted total feeding time was compared with the total observed feeding time using one-tailed paired t-tests, for creeks open and closed to boat traffic separately. Since year showed no effect on giving-up net energy intake rates (see above), we pooled data from 2006 and 2007.

Results

The field observations in the three creeks open to boat traffic revealed that disturbance by boats is effectively present. Yet, there was a great variance between years, but also within years among creeks and within creeks (Table 1). Motorized and sailing boat types were both observed in the creeks providing suitable foraging area to Bewick's swans (i.e. water depth below 0.86; Nolet et al. 2006a), but no other sources of disturbance

(such as surfers and kite-surfers, which do occur elsewhere in the Lauwersmeer.

Table 1: Number of boats passing per hour in the three creeks open to boat traffic. For the location of the creeks, see Fig. 1.

Creek	2007	2008
BPG	8.21 ± 11.8 (n = 14)	3.25 ± 3.62 (n = 8)
NRG	1.1 ± 2.81 (n = 29)	1.21 ± 1.37 (n = 14)
ZKR	11.4 ± 13.2 (n = 14)	2.19 ± 2.51 (n = 16)

Initial tuber densities turned out to be higher in creeks open to boat traffic compared to closed creeks (one-way ANOVA: $F_{(1,191)} = 4.5$; $P < 0.05$). Giving-up densities were not significantly different, however, nor was the effect of the interaction term initial tuber density \times access of creeks by boats. Initial net energy intake rates were not generally different in creeks open and closed to boat traffic (one-way ANOVA: $F_{(1,191)} = 1.1$; $P > 0.2$). Giving-up net energy intake rates, on the other hand, were significantly higher in open creeks than in creeks closed to boat traffic (95%-CI: $69.9 \text{ J s}^{-1} - 109.5 \text{ J s}^{-1}$ and $50.4 \text{ J s}^{-1} - 71.0 \text{ J s}^{-1}$, respectively; $F_{(1,190)} = 36.7$; $P < 0.001$). However, this was also the case for the interaction term with initial net energy intake rate ($F_{(1,190)} = 40.4$; $P < 0.001$): giving-up net energy intake rates increased with initial energy intake rates but more steeply in creeks open to boat traffic (Fig. 2a). Sampling points were on average 351 (± 337 SD) meters away from the nearest boat channel. The measured distance had no effect on giving-up net energy intake rates, neither alone nor in interactions with initial net energy intake rate and year.

Estimations for the threshold giving-up energy intake rate (i.e. intake rate that maximizes long-term average intake rate; k) also resulted in marked differences between open (194.6 J s^{-1}) and closed creeks (95.7 J s^{-1} ; Fig. 2b).

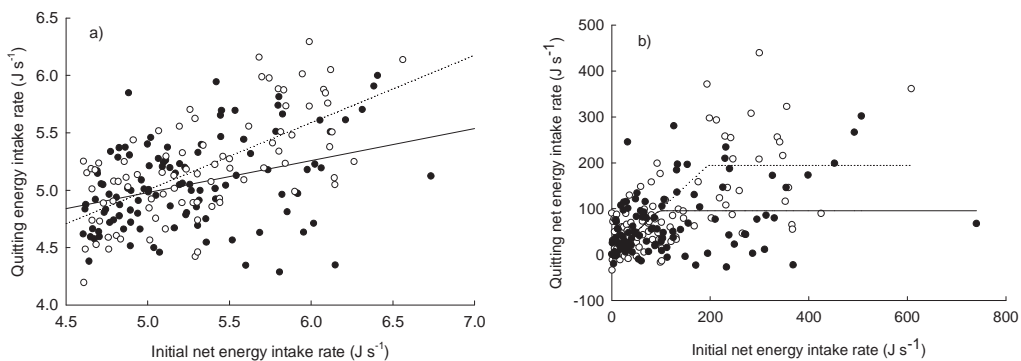


Fig. 2: a) Relationship between initial and giving-up net energy intake rate (both \ln -transformed) in creeks closed (filled symbols, solid line) and open (open symbols, dotted line) to boat traffic. b) Estimations of the threshold giving-up energy intake rates (plateau of the lines) based on initial net energy intake rates for creeks closed (filled symbols, solid line) and open (open symbols, dotted line) to boat traffic.

The predicted total feeding time in 2006 and 2007 tended to be higher in the creeks open to boat traffic than the observed total feeding time ($t_5 = -1.6$, $P = 0.08$; Fig. 3). However, in closed creeks the predicted time and the observed time were similar ($t_{11} = -0.3$, $P > 0.7$; Fig. 3).

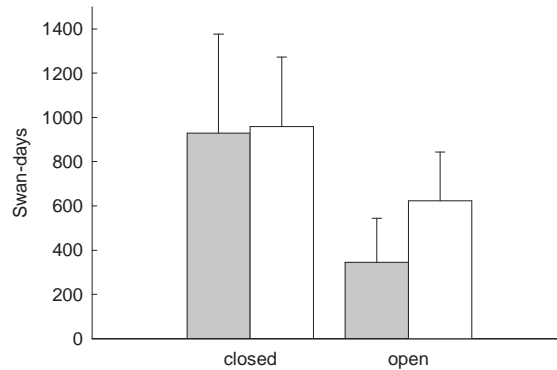


Fig. 3: The observed cumulative feeding time (filled bars) compared to the predicted (based on food consumption) (open bars; both expressed as bird-days) for creeks closed and open to boat traffic.

Discussion

Considering giving-up densities, no difference was discovered between creeks that were open and closed to boat traffic. However, giving-up net energy intake rates, for a given initial net energy intake rate, revealed that Bewick's swans were foraging less at patches where boat traffic was present. At a more detailed level, distance to the boat channel did not linearly affect giving-up net energy intake rates of swans. Our predictions, based on measured tuber consumption, compared to observed total feeding times suggest that Bewick's swans partly compensated for lost feeding time due to disturbance by switching from foraging in undisturbed creeks during daytime to creeks open to boat traffic during the night.

While GUD measurements have successfully been used earlier to investigate the effects of human disturbance (see review in Brown and Kotler 2004), its applicability might be more limited when the environment shows large spatial heterogeneity (A. Gyimesi, S. Varghese, J. de Leeuw, & B.A. Nolet unpublished data). Applying net energy intake rates accounts for spatial differences in food availability and foraging costs. Consequently, differences in giving-up net energy intake rates between disturbed and undisturbed sites can directly be used to represent effects of human disturbance.

Nolet and Klaassen (2009) showed that the giving-up net energy intake rate of Bewick's swans was equal (i.e. 56 J s^{-1}) among patches of different sediment type - water depth combinations in an undisturbed creek of the Lauwersmeer. In this study we looked at the scale of the entire lake and included both disturbed and undisturbed creeks. The confidence intervals of our measured giving-up net energy intake rates

included 56 J s^{-1} only in the creeks closed to boat traffic, and not in open creeks. The influence of the initial net energy intake rate on the giving-up net energy intake rate in our GLM analysis could be explained by the presence of sampling points where the initial net energy intake rate is lower than the threshold giving-up energy intake rate (Olsson and Brown 2006). Especially in clumped food distributions, as is the case in pondweed tubers (Nolet and Mooij 2002, Klaassen and Nolet 2008), foragers may distinguish between patch qualities and concentrate their effort on areas energetically profitable (Benhamou 1992, Klaassen et al. 2006c, Klaassen et al. 2007). Consequently, in patches below threshold giving-up energy intake rate grazing pressure is low or absent (Olsson and Brown 2006).

Disturbance causing animals to flush certainly comes with high costs (Goss-Custard et al. 2006). However, already alert behaviour brings about elevated heart rates, and hence extra energy consumption (Riddington et al. 1996, Ackerman et al. 2004). In addition to these direct energetic costs, the fear of eventual risks (i.e. predators and humans) may be even more substantial in rendering disturbed sites less attractive for animals (Gill et al. 2001a, Brown and Kotler 2004). However, animals that rely partly on nocturnal foraging, such as Bewick's swans (Nolet and Klaassen 2005), can compensate for disturbance during daytime by foraging at night (Hockin et al. 1992, Riddington et al. 1996). Switching from creeks closed to boat traffic to disturbed areas during the night could have caused the higher measured food consumption in open creeks compared to the observed (daytime) number of foraging swans (Fig. 3). As the opposite trend was not observed in the closed creeks, swans might adopt such a switching behaviour only when a disturbed creek is in the immediate vicinity of an undisturbed one, making flight costs negligible. Besides, switching might not occur extensively because it could increase the level of intraspecific competition, which in its turn could lead to reduced intake rates (West et al. 2002, Inger et al. 2006a; A. Gyimesi, R. Stillman, & B.A. Nolet unpublished data). All in all, this proposed night time foraging did not fully compensate for the lost daylight hours: the giving-up energy intake rates were still higher in the creeks open to boat traffic. Observations in disturbed areas at night may provide valuable information on the exact compensation mechanism taking place.

In a previous study, Bewick's swans were found to have higher giving-up densities on beet fields closer to a road (van Gils and Tijssen 2007). However, we did not find a negative relationship between giving-up net energy intake rates and distance to boat channels. Besides boat traffic, disturbance by cars, pedestrians (occasionally with dogs) and bikers may also occur in the three open creeks of the Lauwersmeer. Moreover, all these disturbances fluctuate in frequency; both within and between creeks and years (see Table 1 for boat traffic). Therefore, animals foraging at different sampling points likely experience varying levels of disturbance, which might overshadow the single effect of distance to, for instance a boat channel (Taylor and Knight 2003, Rees et al. 2005, Preisler et al. 2006). Moreover, a certain disturbance source could cause total avoidance

until a certain safe distance (Mori et al. 2001), instead of an effect linearly decreasing further away. In addition, the effect of disturbance also depends on the size, composition and condition of the group being disturbed (Rode et al. 2006, Sirot 2006, Stankowich 2008). For instance, it would be interesting to study the effect of boat traffic on waterfowl foraging on the aboveground vegetation of fennel pondweed in the summer. In case these herbivores also avoid disturbed sites, this could lead to lower consumption of aboveground vegetation, which could consequently lead to higher tuber biomass levels locally (A. Gyimesi, P.P. de Vries, T. de Boer, & B.A. Nolet unpublished data).

Decisions about where to forage are often influenced by the position of other individuals as well (Valone and Giraldeau 1993, Kennedy and Gray 1994, Seppanen et al. 2007). Especially, when food items are cryptic, and even heterogeneously distributed, the location of the best foraging sites is uncertain. In such cases, social information derived from the mere presence or absence of conspecifics can provide valuable information about the quality of the local environment (Holt 2007). Using other animals as cues can considerably reduce search costs, improve the chances of foraging success and increase the accuracy of foraging decisions (Hancock and Milner-Gulland 2006). In a similar fashion, the emptiness of a site might indirectly communicate the message to newcomers to avoid the area, even without effectively experiencing any risk themselves (Taylor and Knight 2003, Holt 2007).

Besides human disturbance, animals of course perceive the presence of natural predators at a site as risky, leading to different giving-up energy intake rates (Brown et al. 1994). The only potential predators of Bewick's swans at the Lauwersmeer that in rare cases may prey upon a swan are red foxes (*Vulpus vulpus*) and white-tailed eagles (*Haliaeetus albicilla*), but there are no local records of such killings. In systems where natural predators do play a role, giving-up energy intake rates as a proxy for human disturbance must be applied with care.

Animals of different species, but even of the same species but at another site or in another life-phase, might have different goals in terms of energy gain (Brown et al. 1994, Brown and Kotler 2004, Heithaus et al. 2007, van Gils in press). Bewick's swans are migrating birds, which maximize energy intake during their stop-over at the Lauwersmeer (Nolet et al. 2006b). The perception of fear might be different for animals that are satisfying their energy needs instead of maximizing and/or that permanently stay at a site (Stankowich 2008). Especially in the case of this latter group, habituation to disturbance must also be accounted for (Hockin et al. 1992, Taylor and Knight 2003). Migrating animals often visit a staging site only for a few days to weeks, and hence barely have time to habituate to local diverse disturbance factors (Hockin et al. 1992, Rees et al. 2005). Applying giving-up energy intake rates partly solves the problem of habituation, as it measures avoidance behaviour at a population level and not only direct flight or alert behaviour of certain individuals. Still, giving-up energy intake rate can also be biased towards the choices of the individuals that are the most tolerant or

have the lowest fitness value (Olsson et al. 2002, van Gils et al. 2004, van Gils and Tijssen 2007).

The value of food increases when it is less abundant (e.g. Krebs 1980, Bowers et al. 1993, Olsson et al. 2002, Persson and Stenberg 2006, Olsson and Molokwu 2007). Consequently, the effect of predation risk on habitat use can be more pronounced in years when food is abundant than in scarce years. We found no effect of year, but food densities at the Lauwersmeer can be higher than in our study period (Nolet et al. 2006b). Therefore, the abundance of available food should not be neglected in future studies on the impact of human recreational activities.

Nowadays, when the pressure on natural areas is ever increasing, it is of essential importance to adequately measure the effect of disturbance on wildlife. We believe that the use of giving-up energy intake rate provides a better proxy than giving-up densities for expressing the cumulative long-term effect of disturbance on an animal population living in a heterogeneous environment. In addition, as net energy intake rates are translatable to foraging durations of animals (Nolet and Klaassen 2009; A. Gyimesi, S. Varghese, J. de Leeuw, & Nolet unpublished data), increased levels of giving-up net energy intake rates can be used to directly quantify the influence of human disturbance on the carrying capacity of a specific site.

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Chapter 10

General discussion and summary



Thijs resting at the end of a heavy fieldwork day.

General discussion

Predicting carrying capacity

Earlier studies tried to define the carrying capacity of a habitat by finding the maximum number of animals that ever occurred (Moser 1988, Schekkerman et al. 1994), or the maximum density that was ever observed at a given surface area (Ebbinge 1992, Kraan et al. 2009b). Such historical data may help to define when carrying capacity is reached, but it may be less constructive when it comes to *predicting carrying capacity* due to, for instance, a habitat change. Relying exclusively on field observations may also give way to overestimations of the carrying capacity in cases of short, temporal aggregations of a large number of animals not dependent on the local food sources. Therefore, understanding the underlying behavioural processes, the choices individuals make in foraging site selection and in the length to stay at one site, may be inevitable to properly estimate carrying capacity. Basically, we need to have a quantification, a *common currency*, that can approximate the decision criteria of animals (McNamara and Houston 1986). In the case of carrying capacity calculations, such currency should give a representation of the habitat quality as perceived by animals, i.e. integrating the advantages and disadvantages of one site compared to another.

It is of course also necessary to specify the *factors* that shape this currency. As *food* is always a necessity for every living animal, it is a basic determinant of the carrying capacity of natural habitats (Newton 1980). It has been assumed that, besides food density, there are at least three processes of behavioural ecology that also play a particularly important role in the distribution of animals, namely: *information*, *interference* and *exploitative competition* (Sutherland and Anderson 1993, Rowcliffe et al. 1999a). Moreover, it is becoming increasingly clear that the decisions of animals, and hence the factors shaping the carrying capacity of their habitat, not only depend on the amount of food but also its spatial distribution (Iwasa et al. 1981, Bernstein et al. 1988, Klaassen et al. 2006c, Nachman 2006). Therefore, it is not surprising that animals try to detect the spatial pattern of their food and disperse accordingly (Klaassen et al. 2006e, Scharf et al. 2009, van Gils in press). In most natural environments, we have to account for *spatial heterogeneity* (Sparrow 1999). This heterogeneity not only holds for the distribution (Kraan et al. 2009a) but also for the availability (Zwarts and Wanink 1993, Amano et al. 2004), and harvesting costs of food (Brown 1988, Carbone and Houston 1994).

Aspects of behavioural and spatial ecology may both be of particular importance for my study system, where Bewick's swans (*Cygnus columbianus bewickii*) forage on belowground tubers of fennel pondweed (*Potamogeton pectinatus*) during their stop over at the Lauwersmeer, in The Netherlands. As the strength of interference did not seem to correlate with swan density (Nolet et al. 2002), foraging site selection was assumed to be driven mainly by exploitative competition (Nolet et al. 2006b) under imperfect knowledge (Nolet and Mooij 2002, Klaassen et al. 2006c, Klaassen et al. 2006e).

Examples of spatial heterogeneity in this system have also been pointed out at the level of foraging patches; aspects of accessibility (Nolet et al. 2006a, Nolet and Klaassen 2009) and costs of harvesting (Nolet et al. 2001b, Nolet et al. 2006a) have been described in detail.

Food and its consumers

Building on this knowledge accumulated in the previous 25 years, I used this system to perform a field test of what factors should be taken into account in predicting the number of birds a stop over site can accommodate. Regarding the basic determinant, food, this thesis discusses several aspects that likely influence the *interannual variation in tuber density*. Fennel pondweed is one of the most common and widespread species of submerged aquatic vegetation (van Wijk 1988). Both aboveground green parts of the plant (van Wijk 1988, Søndergaard et al. 1996, Weisner et al. 1997, Hidding et al. 2009b), and belowground reproductive organs (i.e. tubers: Anderson and Low 1976, Nolet et al. 2001a, Badzinski et al. 2006) are preferred food of waterfowl. **Chapter 2** argues that among the factors shaping local densities of belowground propagules, *time-staggered indirect competition* resulting from foraging on the aboveground vegetation during summer must also be taken into account. Considering that a single mute swan may consume roughly 3.8 kg fresh weight of aquatic vegetation per day (Bailey et al. 2008), 1000 of these swans can obviously remove considerable amounts of aboveground vegetation in a few weeks. Fennel pondweed is the most dominant species in the Lauwersmeer (Pot 1984, van Wijk 1988, Hidding et al. 2009a) and also suffers the most from herbivory (Hidding et al. 2009a). This is especially the case for shallow areas (water depth below 30 cm), where ducks can reach down to the lake bottom (Noordhuis et al. 2002). This is probably also the case in the shallowest creek of the Lauwersmeer, the Jaap Deensgat, causing local tuber densities at the end of the growing season to be already well below the energetically profitable density for Bewick's swans (Nolet et al. 2006b) in all four study years. Bearing in mind that populations of mute swans and gadwalls have been significantly increasing in most parts of Europe over the past 30 years (Scott and Rose 1996, Delany and Scott 2006), one could wonder whether this can account for the total avoidance of the Jaap Deensgat by Bewick's swans nowadays, compared to the early 1980s when van Eerden et al. (1997) reported foraging Bewick's swans in this creek. If so, and assuming a further population increase of summer herbivores, other creeks of the Lauwersmeer, as well as other freshwater habitats, might experience diminishing tuber banks to accommodate Bewick's swans as well as other tuber feeding organisms in autumn.

Chapter 3 investigates the underlying mechanisms behind the observed species associations between Bewick's swans and diving ducks (Fig. 1), earlier described as kleptoparasitism (Beekman et al. 1991). The experiment we conducted exposed that pochards do not steal from Bewick's swans, just profit from the tubers floating away,

suggesting that the two species form a *commensalistic relationship*. It is an intriguing but open question whether pochards are capable of selecting swans that are less efficient foragers and leave more food unconsumed, such as for instance first-winter swans (Chapter 7). All in all, it became obvious that it is highly profitable for pochards to join Bewick's swans while these forage on pondweed tubers. These results, however, also reveal that Bewick's swans, and with their help pochards and other waterfowl, may considerably reduce the total amount of fennel pondweed tubers in autumn. Hidding et al. (2009b) showed that a reduced level of tuber biomass does not limit aboveground biomass in the following summer. However, they did show that it caused a delay in peak biomass. This may have a subtle but important effect: the delayed vegetative growth may coincide with the mass influx of herbivores (due to aggregations for moulting after breeding in spring), allowing consumption of emerging instead of developed plants. Hypothetically, this phase-shift in herbivory may nearly prevent tuber formation locally (Kiorboe 1980, Sondergaard et al. 1996, Perrow et al. 1997, Klaassen et al. 2006c).

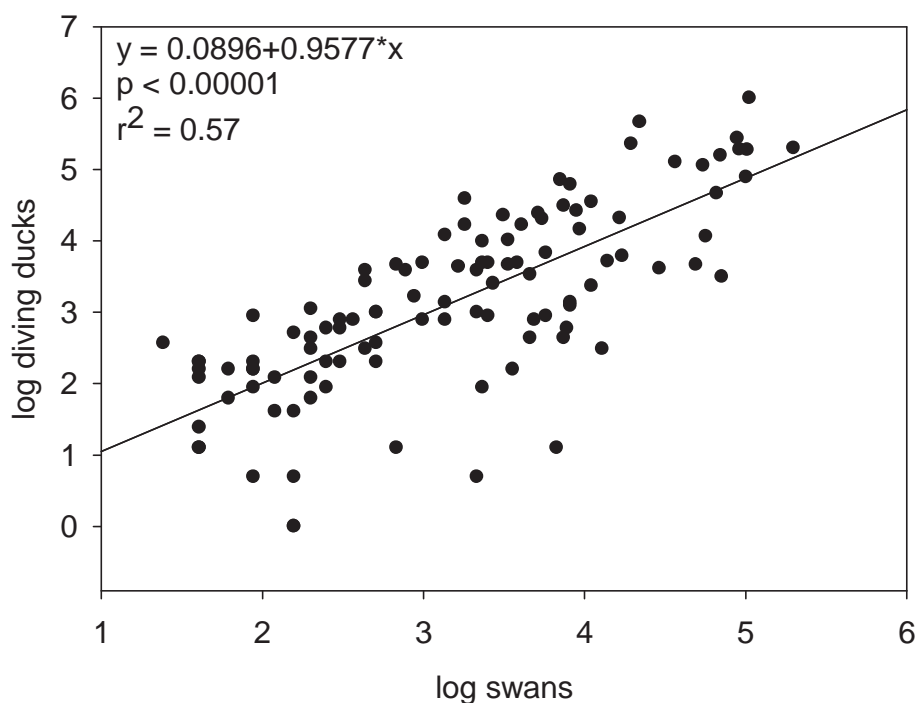


Fig. 1: Number of diving ducks in relation to the number of Bewick's swans observed in foraging flocks in the Lauwersmeer in the period 2005-2008.

Besides exploitative competition, intraspecific interference competition is considered to be the main determinant of animal distribution (Sutherland 1983). Goss-Custard (Goss-Custard 1985) argued that the carrying capacity of a habitat can only be expressed as bird-days, if interference competition is not affecting intake rates. Nolet et al. (2006b) showed that the total number of swan-days in a given year increases proportionally with the accessible tuber density in one creek of the Lauwersmeer (Fig. 2), suggesting a low level of interference competition. The model and the related field observations described in **chapter 4** revealed that this is due to the self-regulating capacity of swans to aggregate in densities which ensure intake rates close to interference-free levels. However, such a capacity might only be valid as long as animals have enough possibilities to spread out within a certain site, or have *alternative foraging habitats*.

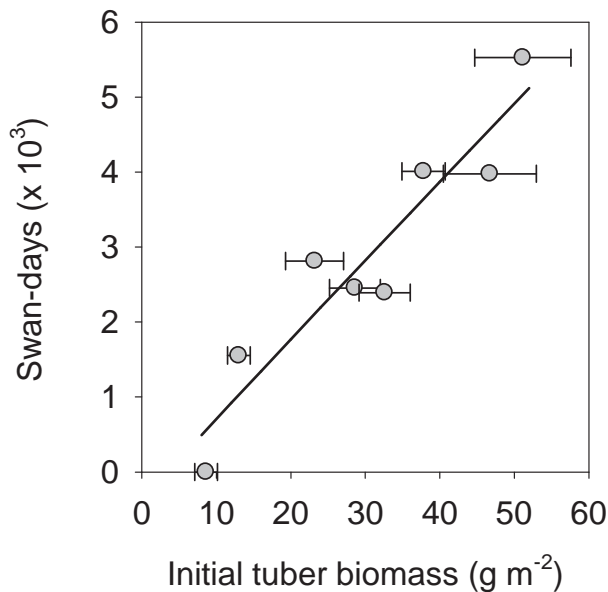


Fig. 2: Observed relationship between yearly average tuber biomass density before the arrival of Bewick's swans and the total number of swan days in the Babbelaar. Solid line is second-order polynomial regression, $r^2 = 0.88$, $p < 0.01$.

Spatial distribution of resources

According to the model described in **Chapter 4**, interference competition among Bewick's swans occurs mainly through avoidance behaviour. Two experiments conducted with mallards (**Chapter 5 and 6**) revealed that also on *slightly clumped food distributions* (such as is the case for fennel pondweed tubers) avoidance (hence more travelling and higher search costs) might be the main disadvantage to subordinates when foraging with competitors and not so much a reduction in intake rate. Furthermore, the experiment discussed in **chapter 5** points out the importance of recognizing

spatial clumping of food items. Animals foraging in a heterogeneous world mostly have to cope with *imperfect knowledge* on the whereabouts of resources. This is especially true for Bewick's swans searching for their cryptic food, pondweed tubers buried in the sediment. Spatially autocorrelated food distributions, however, may help foragers to find the better quality food patches, and hence reach a higher long-term intake rate (Klaassen et al. 2006c, van Gils in press). Even though solitary Bewick's swans, which are subordinate to pairs and families (Scott 1980, Badzinski 2003), were shown to move longer distances when foraging in a flock (Klaassen et al. 2006c, b), spatial autocorrelation of food items may help such individuals to keep search costs limited by moving at the front of a flock, trying to quickly find unexploited high-density patches, such as described for barnacle geese (Stahl et al. 2001). Whether this holds for Bewick's swans as well, still needs verification.

Besides quantity, the *quality of the food* may also show spatial heterogeneity. The findings regarding spatial variance in tuber quality presented in **Box I** give an extra aspect to the site preference of the consumers. It was long known that Bewick's swans start the exploitation of the tuber banks in the northern creeks, known to be sandier (Beekman et al. 1991). By showing that these tubers are qualitatively not better, this supports the hypothesis that site preference is related to foraging costs and harvest rates (being respectively higher and lower in clayey sediments; Nolet et al. 2001b, Nolet et al. 2002, Nolet et al. 2006a). As small tubers seemed to contain more protein, the preference for larger food items (van Eerden et al. 1997, Hangelbroek 2004), appears not to be due to a qualitative difference either. Moreover, the energy content and metabolisability of tubers is generally high, and hence qualitative differences in tubers might not play an important role in the foraging site selection of Bewick's swans.

Box I

Out of the 90 sites visited during the sampling in October 2008, we selected 16 to represent a balanced design to study the effect of tuber size, sediment type (sandy or clayey), water depth (above or below 51 cm, i.e. the switching point in foraging methods) and north-south position within the Lauwersmeer on the C:N ratio of tubers, with assuming a higher protein content indicating a better quality (Bakker et al. 2009). From these sites we took the largest and the smallest tuber. After drying and grinding the percentage of carbon and nitrogen was measured of 1 mg samples. Water depth and position in the lake seemed to have no effect on the C:N ratio of tubers. Large tubers, however, seemed to have a higher C:N ratio ($F_{1,27} = 5.6$, $p = 0.03$), as well as tubers of sandy sediments ($F_{1,27} = 7.4$, $p = 0.01$; Fig. I.1; Gyimesi, Korthals, van Lith and Nolet, unpublished data).

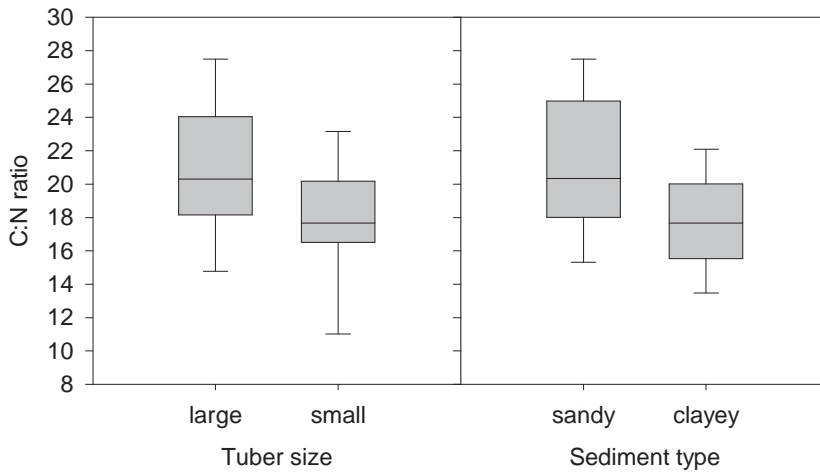


Fig. I.1: C:N ratios of tubers in relation to size and sediment type ($n = 16$ in each category). Boxes represent interquartile range, lines within medians, bars 5th/95th percentiles.

Furthermore, the spatial heterogeneity of food densities is commonly only described in two dimensions. Food buried in the soil in the sediment, however, may show heterogeneity also in a third dimension, resulting in a *depth profile*. In case of pondweed tubers, depth profile of tubers varies among stop over sites (Hidding et al. 2009c) as well as within a site among sediment types (i.e. tubers are being buried slightly deeper at sandy sites; Santamaría and Rodríguez-Gironés 2002, Nolet and Klaassen 2009). Deeper buried food items may be simply out of reach for their consumers, but also harvesting the accessible part might require higher foraging costs (Owen and Cadbury 1975, Zwarts and Wanink 1993, Nolet et al. 2006a). In case of swans this translates to more trampling, the most costly part of a foraging bout (Nolet et al. 2002), used to excavate the tubers from the sediment. Box II shows that the Jaap Deensgat is the only creek where most of the tuber biomass is found close to the sediment surface. As the sediment of this creek can principally be described as nutrient-rich clay (see Fig. 2 in **chapter 8**), resource deficiency is likely not a reason for this shallow burial. An alternative explanation may stem from the above discussed intense summer herbivory. Due to this, total tuber biomass is low in this creek, making the site uninteresting for Bewick's swans: for the entire four years of fieldwork the total number of swan-days reached 480, compared with, for instance, more than 3550 days for the Nieuwe Robbengat, a creek with frequent human disturbance. It is exciting to consider whether the absence of Bewick's swan foraging in the Jaap Densgat has lead to shallower tuber burial, which would support the ideas put forward by Hidding et al. (2009b, 2009c).

Box II

We conducted a burial depth sampling in October 2008, just before the arrival of the swans, in all nine creeks of the Lauwersmeer (Gyimesi, de Boer, de Vries and Nolet, unpubl. data). At ten points per creek a sediment core (7 cm in diameter) of 35 cm depth was taken and all the tubers were collected per 5 cm segments. Fig. II.1. depicts the results, summarized as proportions (arcsine transferred) of the total tuber biomass per 10 cm (for clarity). The burial depth profile of most of the creeks seems to show a conservative variation, but it catches the eye that in the Jaap Deensgat, the shallowest creek of the Lauwersmeer, an exceptionally high percentage (i.e. 69.7%) of the total biomass is in the top 10 cm of the sediment.

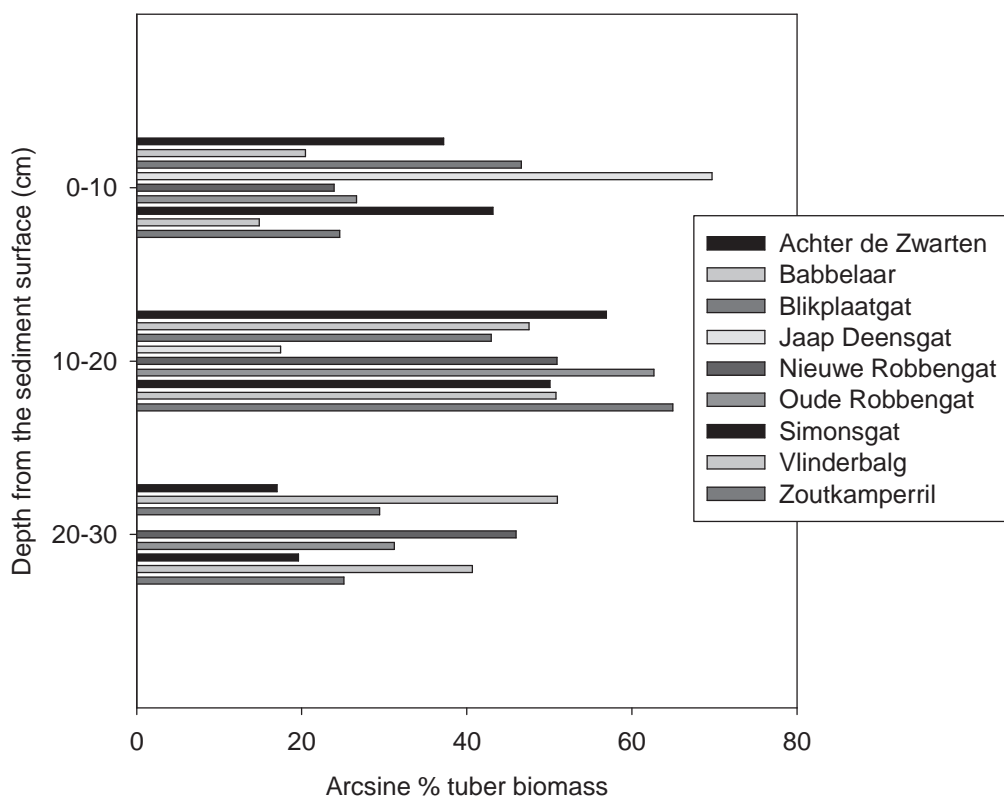


Fig. II.1: Arcsine transformed proportions of the total tuber biomass per 10 cm depth segments in the nine creeks of the Lauwersmeer. Bars show means.

Fennel pondweed is shown to be phenotypically plastic, avoiding predation by deeper burial of its tubers (Hidding 2009). Bewick's swans, however, may directly shape the burial depth distribution of tubers while foraging. It is predicted that animals under exploitative competition should deplete patches to the current average intake rate of the environment, and only reach the final quitting intake rate through revisiting the same patch in succession (Nolet et al. 2006c). This theory also seemed to be supported by our experimental results discussed in **chapter 6**. Moreover, field observations also suggest that the utilisation of tuber banks by Bewick's swans occurs in several waves (van Eerden et al. 1997). Considering this phenomenon, it is imaginable that during their first visit to a patch, swans only excavate tubers from the upper sediment layer. Sedimentation has a high rate in the Lauwersmeer even outside the swan exploitation period (i.e. approximately 2 cm month⁻¹; P. Bodelier, pers. comm.), which is likely much higher when hundreds of swans are simultaneously whirling up the sediment. Therefore, a partly depleted foraging patch of swans may be covered by a new sediment layer by the next visit. All in all, deeper buried food biomass seemed to indeed increase the foraging costs of Bewick's swans, as it is shown in Box III.

Box III

An experiment was conducted with four adult swans in the spring of 2007 (Gyimesi, van Lith and Nolet, unpubl. data) to investigate the effect of food burial on patch use of Bewick's swans. We offered wheat grains (in a density of 19.5, 58, 96.5 or 135 g m⁻²) buried either at 5 cm or at 10 cm to swans in individual trials. Food was offered simultaneously in two different patches of 2 m² and a trial lasted until the swan gave up foraging in the second patch too (further details of the experimental setup were equivalent to the one described in **chapter 7**). Concentrating the analysis on the foraging behaviour performed at the first patch visited (focal patch), we found that swans managed to reach similar intake rates in both burial depth treatments (interaction term burial depth and food density in full-factorial ANOVA: $F_{3,22} = 3.2$, $p > 0.7$), but had to count with higher foraging costs for that. Namely, they had significantly longer head-dipping times with deeper buried food and higher food density (interaction term full-factorial ANOVA: $F_{3,22} = 3.2$, $p < 0.05$; Fig. III.1.), and a tendency for longer trampling times when food was buried deeper (main effect burial depth full-factorial ANOVA: $F_{3,22} = 3.2$, $p = 0.08$; Fig. III. 1.).

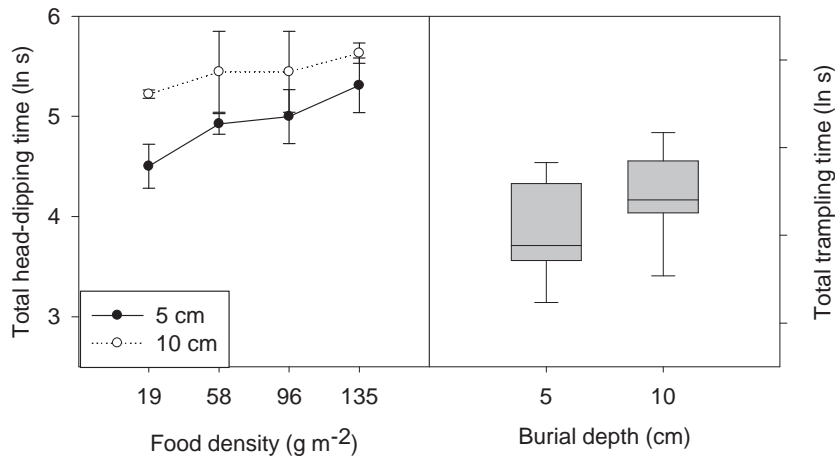


Fig. III.1: Left: Mean total head-dipping time per food density for food buried at 5 cm (solid line, filled symbols) or 10 cm depth (dotted line, open symbols). Bars show standard errors. Right: Mean total trampling time per burial depth. Boxes represent interquartile range, lines within medians, bars 5th/95th percentiles.

Individual differences in foraging strategies affected by humans

These above-discussed findings are in accordance with the suggestion raised in **chapter 6** that, whenever possible, animals experiencing foraging constraints may increase their efforts to keep intake rates unaffected. It remains a question, however, to what extent increasing feeding time is a compensation option to animals maximizing their energy intake rate. Bewick's swans, for instance, are thought to maximise the time spent foraging while at the Lauwersmeer (Nolet et al. 2006b). Calculated and observed feeding times suggested this *maximum daily feeding* time to be just above 12 h (12.4 h day⁻¹ and 12.2 h day⁻¹, respectively) and an interspecific comparison of daily submerison times resulted in 10 h day⁻¹ (Nolet and Klaassen 2005, Nolet et al. 2006b). What the explicit reasons are (e.g. cooling down in cold water, limiting competition, avoiding predators) for Bewick's swans to restrict their maximum foraging time to such a relatively low level still need further attention.

Increasing daily feeding time, hence seems not to be that simple. Nonetheless, **chapter 7** discusses how individuals (swan families in our case) may try to win undisturbed feeding time by following a risk-prone behaviour and selecting sites that experience human disturbance but also a lower level of intraspecific competition. Future investigations might clarify whether there are further dissimilarities in the habitat selection of individuals from different dominance classes, probably by tracking individually marked birds of a known social status. Due to their lower competence level, habitat loss may first affect the more subordinate birds, and hence such studies could contribute to more accurate risk assessment. **Chapter 7** also proposes that the lower

feeding efficiency of cygnets may be caused by their smaller size, probably not being heavy enough to create a strong water current to excavate the tubers from the sediment. As dominance is likely also related to body size (Scott 1978), it is an interesting idea that feeding efficiency might also correlate with dominance. However, the details of the unique foraging technique of Bewick's swans are not yet fully understood and it requires a more mechanistic study to unravel what exactly makes one animal an efficient forager. Nevertheless, **chapter 7** is a testimony to how individuals of *different social classes* make different foraging decisions, and hence raises the problem how far animal populations may be treated as a group of identical individuals. Furthermore, the habitat selection of families with cygnets, favouring human-disturbed sites, may also be the first indication of interference competition limiting the carrying capacity of the Lauwersmeer for Bewick's swans. **Chapter 8** shows that presently swan-days on the population level are correlated to a resource-based currency (i.e. net energy intake rate), which suggests that merely exploitative competition determines the distribution of Bewick's swans at the Lauwersmeer. Conceivably, this is due to the possibility for individuals to still spread to other creeks or to an alternative foraging habitat (in our case sugar beet fields in the area surrounding the Lauwersmeer).

Future perspectives of food availability

Chapter 9 examines how *human disturbance* limits the availability of certain creeks in the lake nowadays. Table 1 provides an overview of the increasing human disturbance in the Lauwersmeer over the past few years. Of course, recreational activities may have intensified due to favourable weather conditions in these years, but according to Statistics Netherlands (Centraal Bureau voor de Statistiek) the number of overnight stays in tourism in the period 2005-2007 was on average 34% higher compared with the situation ten years before. Moreover, the provinces of Groningen and Friesland anticipate an increase of sleeping accommodations from the current 3000 to 8800 in the near future (Poelman and Beemster 2008). These trends lead to increasing demands to open up more areas to human recreational activities, which may cause a limited availability of foraging habitats to animals (Goss-Custard et al. 2006, Olsson and Molokwu 2007, Cardoni et al. 2008).

Table 1: *Total number of visitors to holiday park Suyderoogh, total number of vehicles travelling on road N-388 at Lauwersoog and total number of recreational boats passing by the sluices of Dokkummer Nieuwe Zijlen in the months October and November in the years around our study period.*

	2003	2004	2005	2006	2007	Source
Nr of visitors	no data	no data	2432	2934	3878	Landal Greenparks
Nr. of vehicles			71028	72648	75387	Province of Groningen
Nr of boats	503	497	540	641	Closed	Province of Friesland

Animals may compensate by visiting alternative foraging habitats (van Gils et al. 2004). In case of Bewick's swans at the Lauwersmeer, such possibility is provided in the form of sugar beet harvest leftovers on agricultural fields in the immediate vicinity. However, in 2006, the European Union decided to gradually cut down on subsidies for sugar beet production. Probably as a result hereof, the total area of sugar beet fields in the four municipalities around the Lauwersmeer has been reduced by 20% within the last four years (Fig. 3). This forecasts that by 2015, when European subsidies on sugar beet production may be totally lost, only a fragment of this alternative food source will be available to Bewick's swans (likely applicable to all European Union countries).

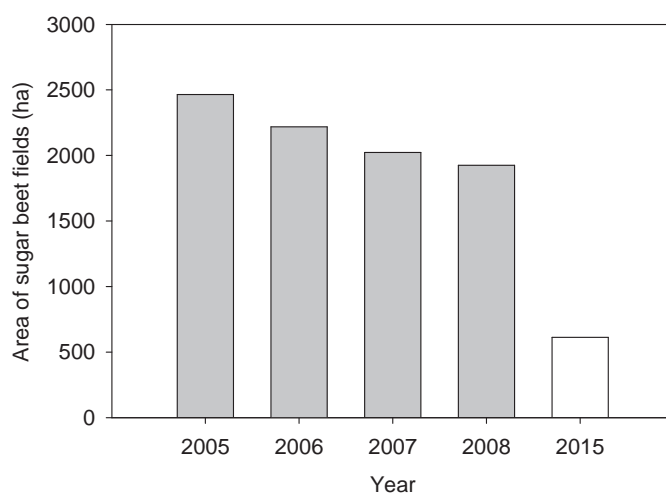


Fig. 3: Development of total area of sugar beet fields in the four municipalities surrounding the Lauwersmeer. Data from CBS Statline. White bar is predicted area in 2015, based on the observed decreasing trend in the period 2005-2008.

Assuming an increase of human recreational activities in the Lauwersmeer and a parallel reduction in available sugar beet fields in the surroundings, interference competition for pondweed tubers may increase and further limit the carrying capacity of the Lauwersmeer in the future. Due to lower feeding efficiency and/or susceptibility to interference, cygnets and subordinates are likely to be the first groups to be affected. In contrast, if more foraging areas were made available by, for instance, stricter protection or lower water levels, forager densities could become lower and these social classes could also attend the safe freshwater habitats in larger numbers, instead of choosing the more risky terrestrial foraging.

Propagule densities are obviously determined by a number of biotic and abiotic factors (Scheffer et al. 1992, van Nes et al. 2003). Herbivory and storm events in the summer may lead to destruction of aboveground macrophyte vegetation, and potentially to such a reduction in the photosynthetic capacity of plants that hardly any tuber production is possible. In addition to the above-discussed increasing number of sum-

mer herbivores, summer storms are also expected to occur more regularly in the future due to human-induced climate change (Mooij et al. 2005). These storms may raise the frequency of wave damage on submerged vegetation. Another often studied effect of climate change scenarios is the rising of water levels (e.g. Mooij et al. 2005, Durell et al. 2006, Traill et al. 2009), which may reduce the accessibility of food buried in the sediment (Nolet and Gyimesi, in prep.), generally affecting the quality of the site for consumers (de Leeuw et al. 1998, Noordhuis et al. 2002). Even though the water level of most freshwaters are strictly regulated in the Netherlands, in the Lauwersmeer target water level is not being met in approximately 80% of the time in autumn (Waterschap-Noorderzijlvest 2003). As rising water levels may become a global problem, this case could be a warning sign to managers in general. This phenomenon might especially be threatening for migrating waterbirds, which rely on a chain of freshwaters to successfully reach their destination. Effects of deterioration of one site may be compensated by increased use of preceding and following sites (Klaassen et al. 2006a) but the loss of a whole stop over site due to inaccessible food may be detrimental to migrating birds (Hedenström and Alerstam 1998), notably if such losses occur suddenly (Klaassen et al. 2006a).

Conclusions

Chapter 8 argues that in heterogeneous systems, where the accessibility of food, the harvesting costs and the level of predation risk may all vary, single measures of food biomass and giving-up densities are not appropriate to predict the number of consumers. Thereby, my findings validate the proposition of Goss-Custard et al. (2003) that when differences are too large between foraging patches, daily ration models are not applicable, and spatial models are needed. Using net energy intake rates may incorporate all the factors affecting the profitability of patches. At the moment, this currency seems to be a good predictor of swan-days at the Lauwersmeer. However, my results also revealed that interference competition and individual differences among Bewick's swans are also present, yet only marginally affecting the carrying capacity of the site. A reduction in intake rate through interference competition seems to be limited by the redistribution of birds, with subordinate birds and families avoiding interference and selecting alternative foraging sites or habitats. Thereby, it seems that in the current situation the Lauwersmeer and its surroundings can still provide enough possibilities for individuals to compensate for their lower intake rates, which may occur due to occupying lower quality patches or having a lower feeding efficiency. The coming years should reveal whether the foraging possibilities will deteriorate as a result of increasing levels of human disturbance and vanishing sugar beet fields, and whether that would lead to increased interference competition (with individual differences of substantial importance). Alternatively, a larger number of Bewick's swans may skip this site and try to put up with areas that are presently viewed as suboptimal.



Summary

Due to climate change, human disturbance, habitat degradation and fragmentation, natural areas are under increasing pressure and there is growing need to set conservation priorities. One way to express the value of a site is its capacity to harbour a particular target species. In the case of migratory birds, it became accepted to use as a currency for this *carrying capacity* the cumulative number of birds ('bird-days') that can be accommodated at a site for a given period of time. However, there is no general consensus on the factors determining the number of bird-days, and whether bird-days is a correct unit for expressing carrying-capacity.

The most basic models assume that the number of bird-days simply depends on the amount of food present. More advanced models consider that not all the food might be accessible and harvestable to the foragers, while further extensions suppose that foragers only deplete food sources until a certain giving-up density (i.e. the food density at the moment the animals leave the patch). The giving-up density is often assumed to be the same everywhere on the site, and equivalent to the critical food density (i.e. the density that provides an intake rate just sufficient to keep the energy budget in balance). In heterogeneous environments, however, both the spatially varying accessible food density and the costs of foraging (metabolic, predation and the missed opportunity costs) shape giving-up densities. Therefore, calculations that rely on a single fixed giving-up density may overestimate or underestimate a site's actual carrying capacity.

In this project, my aim was to accomplish a good understanding of the *relevant factors* shaping the number of migratory waterbirds making use of a stopover site. By focusing on Bewick's swans (*Cygnus bewickii*) foraging on tubers of fennel pondweed (*Potamogeton pectinatus*) in the Lauwersmeer, the Netherlands, we tested which of the above factors should be taken into account to predict the number of birds the site can support.

First of all, I show that in a heterogeneous environment, such as my study system, predictions about consumer numbers cannot rely exclusively on the amount of available food: accessibility, harvest rates and foraging costs cannot be ignored. These factors can be combined together with food supply in a single measure, the locally achievable net energy intake rate, which proved to be a good proxy for explaining the distribution of animals. This currency also provided evidence that swans exploit human-disturbed

parts to a lower extent. On the other hand, the resulting lower competitor densities at these parts seemed to offer first-winter swans the chance to compensate for their lower feeding efficiency, by following a risk-prone behaviour and selecting these disturbed foraging patches that are largely unexploited.

Our results revealed that the outcome of interference competition is largely dependent on how food is distributed in the environment and that in spatially autocorrelated, slightly clumped food distributions, differences between dominants and subordinates are less prominent due to difficulties with monopolizing the resources. Interference competition seemed to generally regulate the maximum group density of Bewick's swans in the field: in order to minimize the effects of interference swans avoid high competitor density. Hence, the mean population intake rate at field-observed competitor densities is only slightly lower than achieved in the absence of interference. Therefore, using bird-days, which assumes that the effects of interference competition on individual intake rates is negligible (i.e. the food consumption of ten birds in one day is equal to that of one bird in ten days), may be an appropriate unit for expressing the carrying capacity of the Lauwersmeer for Bewick's swans.

Furthermore, I discuss how the available tuber density to Bewick's swans is shaped by competition with other species. Based on field observations, it was hypothesized that pochards (*Aythya ferina*) kleptoparasitize the swans. However, through a controlled experiment I show that pochards are only gleaning food items that float away from the swans and are not stealing: the two species form a commensalistic relationship. On the other hand, we demonstrate that through time-staggered interspecific competition, avian herbivores, such as mute swans (*Cygnus olor*), consuming aboveground vegetation of fennel pondweed in the summer, do reduce tuber density in the autumn available for Bewick's swans.

I realize that for describing complex ecological processes certain simplifications are inevitable. In heterogeneous environments, however, oversimplification lures. Based on my results, I am convinced that the spatial variation in biotic and abiotic factors and the foraging behaviour of the studied species have to be taken into account when forecasting the numbers a site can contain.

Nederlandse lekensamenvatting

Het onderzoek heeft aangetoond dat voor het verklaren van de aantallen zwanen die in de herfst gebruik maken van de pleisterplaats er rekening moet worden gehouden met de ruimtelijke heterogeniteit. Het is niet voldoende om de voedsel dichtheid te weten. Er is ook informatie nodig over andere omgevingsfactoren zoals waterdiepte en (onderwater)bodemtype. Deze factoren bepalen namelijk mede hoeveel voedsel (knolletjes in de onderwaterbodem) er bereikbaar is, hoe snel het kan worden opgegeten en hoeveel het kost om het te bemachtigen.

Het gedrag van de zwanen speelt ook een rol. De zwanen concurreren met elkaar, maar toch kan de draagkracht van de pleisterplaats worden uitgedrukt in “vogeldagen” (waarbij 10 vogels op 1 dag evenveel eten als 1 vogel in 10 dagen). Dit komt doordat competitie door interferentie (een afname in voedselopnamesnelheid met het aantal concurrenten) vrij zwak is in het systeem en bovendien grotendeels wordt voorkomen door herverdeling van de zwanen als interferentie dreigt.

Een verrassende uitkomst is dat de plekken waar zwanen in de herfst door recreanten worden verstoord te herkennen zijn na vertrek van de zwanen van de pleisterplaats. De berekende netto energieopname op het achtergelaten voedsel is tweemaal zo hoog op verstoorde plekken als op ontoegankelijke plekken. Het verschil is een maat voor in hoeverre de zwanen verstoring ervaren op toegankelijke plekken.

Een andere verrassende uitkomst is dat begrazing van groene delen door knobbelzwanen in de zomer een grote invloed heeft op de beschikbaarheid van knolletjes voor kleine zwanen in de herfst. Dit roept nieuwe vragen op met betrekking tot de rol die verstoring in het zomerhalfjaar speelt in dit systeem.

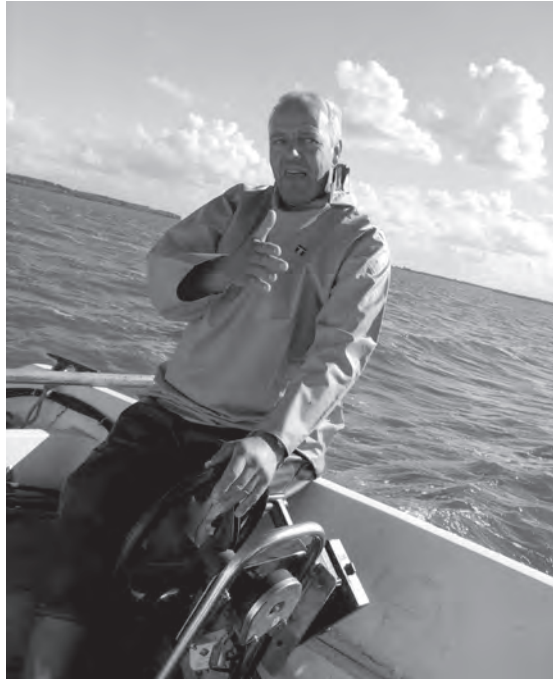
Acknowledgements

I would like to start with an apology to many of you that I write also this part in English. You were in the last couple of years, unknowingly and maybe unwillingly, my Dutch teachers, and owing to that I should be able to thank you all in your mother tongue. However, there are also some who then wouldn't understand a word of it, so out of simplicity I keep it like this.

First of all, I would like to thank Bart, and surely not only for being the most keen on teaching me (with varying success) Dutch expressions and proverbs. In official terms, he was my daily supervisor, which quite often also meant that we had daily discussions. But on the other hand, I don't find supervisor really descriptive for his role in helping me through all the difficulties. He wasn't just looking after my work but was really involved in it, more like a real tutor. And if I consider that he trusted me with carrying out his project, which was honoured by NWO with quite a reasonable amount of money, then I should probably call him my mentor. Anyhow, thanks for all your time, for having your door was always open for me, for your involvement and concerns. I've always hoped that I could fulfil your expectations and that you are now finally pleased with the product.

I'm grateful to Marcel for being so supportive from the moment on that I entered the workgroup as a volunteer. Without him arranging that possibility for me, my life could have taken a totally different turn and I would never be writing the acknowledgements of this thesis. Also during this project, a pat on the back from him meant a lot for me. Thanks also for struggling yourself through my manuscripts and coming up with new ideas. Here I would also like to thank Theunis, who also spent a lot of his time with making my work readable and understandable.

I could thank almost all former colleagues of the Plant-Animal Interactions group for helping out during fieldwork. But I would like to emphasize how important Thijs, Peter and Koos were in completing four years of sampling and counting. They took surely more than half of the altogether 9360 tuber cores, and practically all the 350 sediment cores. Not to mention all the water depth measurements and bird counts! But above all this quantitative input, the importance of their qualitative input was just as



Koos showing the way.

important. And then I don't only mean their help in planning and preparing the field trips, but how they can keep the spirit up during the days in the field. Even with a body hurting all over and with a heavy head waking up every day at six in the morning to spend like eight-nine hours working in the water, you cannot avoid getting a good mood when you hear Peter and Thijs singing "Begin de dag met een lachje". And I don't know how others felt about it, but the simple presence of Koos always gave me a relaxed feeling that it would all work out fine. Thanks for your trust in me and for your friendship throughout these years!

Bart van Lith formed a one-person PDI department in Heteren, which I happily joined on a regular basis. From the beginning on, he taught me a lot about the swans, how to handle them and how to carry out experiments with them. I also greatly appreciate that he year after year participated in my crazy shovelling exercises, replacing several cubic meters of wet sand every day. Bart, thanks for your company and interest! Here I should not forget the other PDI members of Heteren: the swans. For some mysterious reasons they trusted me with their cooperation, making a series of experiments possible that not that much people believed in.

Here I would like to mention that I was blessed to have quite some enthusiastic students helping me out throughout the years. Marit and Helena were the first ones, with whom we were basically discovering the world of swan experiments together, not to forget that they were sort of the foster parents of the first Bewick's swans born in Heteren. With Delphine we welcomed the first of some international guests dispatched from the ITC in Enschede. The black lady out Cameroon, in the middle of the Lauwersmeer - probably she was the happiest that she survived my first fieldwork... In the years after, with the help of ITC, we could significantly broaden the list of nationalities visiting the Babbelaar, finally checking off nearly all other continents. Boris from Bolivia, walking around with bamboo-sticks in Heerenveen, or Sam from India wearing pink rubber gloves during field work to keep his hands warm. I had a great time with you, and I'm extremely glad that we could work together! Nicole from Germany joined the department as a volunteer, and I'm really happy for you that you didn't get engaged only in our work! Enrique and Lucia expanded our map database of the Lauwersmeer, and meanwhile gave some nice time to many of us by presenting the Spanish virtue of life. Students of the Aquatic Ecology course, Marloes and Simone, Sven and Andre, unfortunately did not have the chance to work with real Bewick's swans, but still did their best to deliver a nice piece of work. Mariska and Susan provided a representation of the ideal fieldworkers. I wanted to protect them from spending too much time in the tough autumn days at the Lauwersmeer but probably it says enough that three years later they still contact me that they would like to sample tubers or count swans in wind and rain. Erica and Marcelle grew above me as experts in experiments with ducks, working quite some time in a basin filled with water of ten degrees. My compliments that you carried on! Probably I shouldn't even mention Jacintha and Sjoerd among the

students, because meanwhile they are busy with carrying out undoubtedly much nicer work than I could ever imagine. I'm honoured that we could have a common chapter in this book. Good luck with your projects! Finally, Marycha and Stefan proved that my presence during the swan counts is absolutely not necessary; I hope you keep some valuable memories from your time at the NIOO. Many thanks to all of you, without you this thesis surely wouldn't exist!

I could have started my acknowledgements with Jan van Gils, who was my first supervisor during the grass experiment with the swans, then later became my roommate and finally accepted to be my paranimf. Thanks for entering me to the PDI, for all your support, inspiring ideas and company! Here I would like to express my gratefulness also to Jan de Leeuw, who became a sort of external supervisor for me. I greatly appreciate all the time he set apart for me for discussions and sharing ideas. He not only introduced me to the world of remote sensing but also widened my ecological knowledge. Also many thanks for helping to improve my writing skills. All the best to you in Kenya! I would like to thank Jan Willems for all his technical help during the fieldworks, to find my way at the Lauwersmeer and especially for the (unfortunately) regular rescue operations when we got stuck somewhere with the car.

Of course, I couldn't have made it without all the other former PDI members. Raymond provided an excellent start-off to this work and helped me out several times later on. I was happy to have Bert just working parallel with me; he gave me a lot of inspiration. Together with Casper, Bert also regularly helped out during the tuber sampling campaigns. Thanks a lot for your help and company! Of course they also made my days in Nieuwersluis enjoyable, but here I should mention other PDIs too: Liesbeth, Olivier, Silke, Steffen, Harry, Geerten, Naomi and last but not least Bethany who was my roommate after Jan. Thanks for the nice time! I would also like to thank all the footballers in Heteren, especially organizer Gregor, for all the fun together! That I could carry out my work was of course largely dependent on the excellent management teams, as well as the technical experts Ab and Gilles in Heteren, and Hennie (Koszonom!) and Dick in Nieuwersluis.

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Curriculum vitae

Abel Gyimesi was born on the 30th of March 1978 in Budapest, the beautiful capital of Hungary. He studied environmental management in Gödöllő, Hungary and completed an MSc in environmental sciences in Wageningen, the Netherlands. All the MSc projects focused on the different aspects of the interaction between birds and a freshwater fishery in Hungary, first under the supervision of Dr. Gabor Bakonyi in Hungary, later of Dr. Rudi Roijackers in Wageningen. In March 2004, he joined the Plant-Animal Interactions group of the Netherlands Institute of Ecology as a volunteer, working under leading of Jan van Gils on an experiment with Bewick's swans foraging on grass. From 2005 onwards Abel continued on as a PhD student under the supervision of Dr. Bart Nolet. The project investigated whether aspects of spatial- and behavioural ecology should be acknowledged in calculating the carrying capacity of stop-over sites of migrating birds, using the study system of Bewick's swans foraging on fennel pondweed tubers in the Lauwersmeer, the Netherlands. From November 2009, Abel is working at the department of Bird Ecology of Bureau Waardenburg in Culemborg.

Publications

Nolet, B. A., A. Gyimesi, and R. H. G. Klaassen. 2006. Prediction of bird-day carrying capacity on a staging site: a test of depletion models. *Journal of Animal Ecology* 75:1285-1292.

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Gyimesi, A., Franken, M., Feige, N. & Nolet, B.A. Giving-up net energy intake rate exposes the effect of human disturbance on Bewick's swan habitat use. (submitted)

Gyimesi, A., van Lith, B. & Nolet, B.A. Associated waterbird species consuming a single food resource: kleptoparasitism on the provider or true commensalism? (submitted)

Gyimesi, A., van Lith, B. & Nolet, B.A. Tough childhood? Swan cygnets face difficulties with feeding efficiency and foraging site selection. (submitted)

Gyimesi, A., Stillman, R.A. & Nolet, B.A. Cryptic interference competition in swans foraging on cryptic prey. (submitted)

Gyimesi, A., Varghese, S., De Leeuw, J. & Nolet, B.A. Net energy gain as a common currency to explain the distribution of swans over a heterogeneous lake. (submitted)

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