INTRODUCTION

Heavy birds like geese and swans have relatively small maximum flight ranges (Klaassen 1995, Hedenström & Alerstam 1998) and consequently rely on stopover sites to refuel to be able to complete their migratory journeys. In order to understand and predict the use of a stopover site, and in relation to that the speed of migration, we should understand the spatial and temporal distribution of resources and the birds’ foraging behaviour. Foraging behaviour consists of foraging in patches and movement between patches. We see a foraging patch as a discrete spatial entity of the environ-

The influence of social interactions on the foraging path of Bewick’s Swans Cygnus columbianus bewickii

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The efficiency in which high-density food patches are found is determined by the way foragers move between patches. In this study we explore the effect of social interactions on the foraging path, in particular the distance moved between patches. We studied Bewick’s Swans Cygnus columbianus bewickii that foraged on belowground tubers of Fennel Pondweed Potamogeton pectinatus. We accurately mapped the foraging path of individual swans and determined the distances between visited patches. 24% of inter-patch movements are associated with social interactions. When a swan retreats from a patch because it is chased away by another swan, it moves a significantly larger distance to a patch than if the movement is not associated with a social interaction. Such longer movements are thought to reduce the rate at which high-density patches are encountered, and thus the energy gain rate a swan can achieve. We observed a strong social hierarchy in which families are dominant over pairs and singletons, and pairs are dominant over singletons, which represents a producer–scrounger model. Singletons were most frequently observed to retreat from patches and are consequently thought to achieve the lowest gain rates. However singletons might partly compensate for more frequent retreats from patches by moving larger distances to arrive at the front edge of a flock where they encounter unexploited resources.

Key words: animal movement, Cygnus columbianus bewickii, interference, optimal foraging, search path, social dominance

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movement (e.g. a branch for a foraging woodpecker; Olsson et al. 1999) or as a spatial entity that is exploited in the time the forager does not move (e.g. the part of the field that is grazed without moving the legs for a grazing goose, also called ‘foraging station’; Focardi et al. 1996). Foraging patches are depleted over time if prey items are renewed at a lower rate than they are consumed by the forager. A forager that maximises its long-term gain rate is predicted to leave a patch well before all food items are found (Charnov 1976), and consequently to move frequently between patches.

Movement between patches is an important aspect of foraging, because the way animals move through the environment affects the frequency at which high-density food patches are encountered (Benhamou 1992, Nolet & Mooij 2002, Hill et al. 2003). Animals regulate movement between patches in relation to the spatial distribution of food items to enhance their energy gain rate. Grey Plovers Pluvialis squatarola for example successfully concentrate their foraging activities in clumps of high food density by making a short movement from a patch where a large prey was caught (area-restricted search) and making a long movement from a patch where no or a small prey was caught (Pienkowski 1983).

In most natural situations a forager is not alone but interacts with conspecifics. This is especially obvious for geese and swans that typically occur in large and dense groups. In such crowd foragers frequently socially interact about food patches (Giraldeau and Caraco, 2000). Individual members of a group differ in their dominance rank, which has important implications for the foraging opportunities of an individual. Dominant individuals on average occupy the best foraging patches and gain from social interactions with subordinates (Sutherland 1983, Beauchamp et al. 1997). In a group of foragers we can recognize subordinate birds that search for high-density patches (‘producers’) and dominant birds that exploit these high-density patches that they takeover from the subordinates (‘scroungers’) (Barnard & Sibly 1981, Beauchamp & Giraldeau 1996). For swans and geese it has been described that the dominance hierarchy is largely based on family size (Lamprecht 1986, Loonen et al. 1999). For example, Bewick’s Swan Cygnus columbianus bewickii families with young are dominant over pairs without young, and singletons are lowest in rank (van Eerden et al. 1997, Badzinski 2003).

It is not well understood how social interactions affect the movement path of foragers. Possibly, social interactions hamper foragers in their response to spatial pattern in the distribution of food, which would have a negative effect on their energy gain rate. It is consequently interesting to determine the effect of social interactions on the way a forager moves between patches, and also to quantify the proportion of inter-patch movements related to social interactions. Given the social hierarchy we might expect that the influence of social interactions on the foraging path is different for individuals of a different social status (singleton, pair or family).

Here we study the effect of social interactions of the movement pattern of Bewick’s Swans, foraging on belowground tubers of Fennel Pondweed Potamogeton pectinatus. In particular, we study the effect of social interactions on the length of inter-patch movements by comparing the lengths of movements that are and that are not related to social interactions. Furthermore we are interested in how inter-patch movements are affected for individuals that differ in their social ranking.

**METHODS**

**Study system**

Lake Lauwersmeer is situated in the north of The Netherlands. After its embankment in 1969 it has developed from a saline tidal area into a shallow freshwater lake. Fennel Pondweed was recorded for the first time in 1972 (Beekman et al. 1991). Nowadays pondweed occurs in large and dense beds, where it dominates the macrophyte community. Aboveground biomass dies off in late summer and pondweed survives the winter via asexually produced tubers that are buried within the first 30
cm of the sediment (Santamaría & Rodríguez-Gironés 2002). In late autumn the Lauwersmeer is the last stopover site for the migratory Bewick’s Swans before they arrive at their wintering sites in The Netherlands and Great Britain. Swans almost exclusively forage on pondweed tubers during a relatively short exploitation period of about three weeks, before they leave the area or switch to harvest leftovers on nearby farmlands (Dirksen et al. 1991, Nolet et al. 2002). Tuber stocks are not refreshed but strongly depleted. 25–80% of the initial biomass is removed by the swans (Nolet et al. 2001; unpubl. data). Swans cannot know the content of a patch without sampling the patch, i.e. tubers are cryptic to the swans. In order to obtain the deeply buried tubers, swans loosen the sediment by trampling their legs, thus creating craters. Swans retrieve tubers by sieving the loosened sediment with their heads submerged (Brouwer & Tinbergen 1939). A crater is here defined as a foraging patch. A patch is depleted in a series of foraging bouts, consisting of surfacing, trampling and feeding (by head-dipping or up-ending). All observations were carried out in the Babbelaar, which is a small part of the Lauwersmeer that is closed for the public and has a pondweed bed of about 20 ha.

Measurements
A focal swan was haphazardly selected from the flock of foraging swans. We mapped the foraging path of a focal swan by taking a triangular fix of the position of the swan every time it submerged its head, by simultaneously measuring the angle to the swan from the two hides, using two total station range finders (TCR307, Leica Geosystems AG, St. Gallen, Switzerland). Hides were located on shore next to the pondweed bed (40 m apart). Since swans exploit patches in a series of bouts, series of intra-patch movements are alternated with inter-patch movements. We defined that a swan left a patch and started to exploit another patch when a series of measurements was spatially separated from a previous series (a 5% overlap in recorded positions was allowed). The reason why a swan left a patch was determined in the field and classified into ‘free’ (the focal swan moves away from a patch without another swan taking its place and starts to dig a new crater at an empty spot), ‘chase’ (the focal swan moves to another swan which it chases away from the patch) and ‘retreat’ (the focal swan is chased away from its patch and starts to dig a new crater at another location). The behaviour of the focal swan was recorded continuously on a tape and was classified into categories (interacting, surfacing, trampling, feeding, swimming, flying, preening, sleeping, drinking, and other, see Nolet et al. 2001 for details). A focal swan was followed for 30 minutes or until it was out of reach of one of the measuring devices. The social status of each focal swan was determined in the field (singleton, pair or family). Measurements were conducted from 16–31 October 2003, which covers the complete period of exploitation of the pondweed bed by the swans. Peak numbers of Bewick’s Swans (>300 birds) were present during the period 24–30 October. Observations were conducted from dawn to dusk.

Statistics
The effect of ‘social status’ and ‘reason for a movement’ on the length of an inter-patch movement was evaluated in a factorial ANOVA, with ‘movement length’ as the dependent variable and ‘social status’ and ‘reason’ as categorical predictors. Families could not be included in the analysis because the sample size was too small for this group. Distances were log-transformed to meet model assumptions. Analyses were conducted using the STATISTICA package (Statsoft 2004).

RESULTS
We measured the foraging path of 137 swans. Two representative recordings of the foraging paths of swans are presented in Fig. 1. There were no birds in the area marked with neck-collars, thus we could not distinguish between different individuals. Although we could not fully prevent observations on the same individuals we have a strong impression that the vast majority of observations was made on different birds. We based our analy-
ses on observation from 124 birds from which the social status could be determined. 54% of these swans appeared to be paired, 44% were single and only 2% of the swans were observed with one or more young (family). A strong social dominance hierarchy was observed: interactions between families and pairs or singles were always won by families, and interactions between pairs and singles were always won by pairs. The probability that an interaction was won or lost between birds of the same social status was 50%.

24% of all movements were related to social interactions (Fig. 2A). If we only consider these movements related to social interactions, we see a clear difference in the proportion of chases and retreats for individuals that differ in their social rank (Fig. 2B). Most family interactions concerned chases (however this is based on only 4 observations); the majority of pair interactions concerned retreats. For singles this proportion was even higher, as they rarely chase away birds from a patch (Fig. 2B).

Both the social status of the individual ($F_{1,416} = 8.5, P = 0.004$) and the reason for a movement ($F_{2,416} = 34.1, P < 0.001$) had a significant effect on length of an inter-patch movement. The interaction term was not significant ($F_{2,416} = 1.4, P = 0.25$). On average singles moved larger distances between patches than individuals that were paired (Fig. 3). A Tukey post-hoc test for unequal sample sizes revealed that the length of a movement was significantly shorter for free movements than for retreats. The length of movements related to chases did not differ significantly from the length of free movements and retreats (Fig. 3).

**DISCUSSION**

The observations that families of Bewick’s Swans are dominant over singletons and pairs, and that pairs are dominant over singletons, corroborates the existence of a social hierarchy in this species (van Eerden et al. 1997, Badzinski 2003). In this
study system, singletons can be considered as being the ‘producers’ that search for and initiate the exploitation of patches, whereas families and pairs can be considered as being the ‘scroungers’ that profit from the activities of singletons by taking over the patches the singletons initially located.

A retreat is expected to deteriorate the energy gain rate of a forager for three reasons. (i) A retreat implies that a feeding opportunity is lost. This negative effect is amplified by the fact that most of the tuber biomass is found in deeper sediment layers (Santamaría & Rodríguez-Gironés 2002), thus most of the energy is gained during the later stages of exploitation of a patch. (ii) The lengthy movements related to retreats are longer than free movements. Thus, the energetic costs of movements are higher for retreats than for free movements. (iii) The length of a movement related to a retreat is longer than the length of a free movement. In other words, a retreated swan does not necessarily move to the patch it would have moved to in a situation without a retreat. We expect that a retreat has a negative effect on the efficiency in which high-density patches are encountered, and consequently on the energy gain rate.

The frequency of retreats was higher for singletons than for paired swans (Fig. 2A). Families were hardly ever chased away from a patch. Consequently, the negative effects of retreats on the energy gain rate, in part mediated by changes in the foraging path, is expected to be most pronounced for singletons. Singletons are expected to achieve the lowest energy gain rates, which is linked to lower speeds of migration (Hedenström & Alerstam 1998). Using this line of reasoning, it would be expected that especially families achieve...
the highest speeds of migration, also since they mainly profit from social interactions since this mainly concerns chases. However, the speed of migration of families was much lower than birds without young, which was explained by the cygnets being unable to sustain long migratory flights (Ely et al. 1997, Beekman et al. 2002). Whether pairs realize a higher speed of migration than singletons remains to be established.

All in all it seems disadvantageous for a singleton to join a group of swans that (partly) consists of pairs. Nevertheless, singletons could profit from information about the content of patches vicariously shared by others (called public information; Valone 1989), or from a decreased predation risk (Brown 1988). Furthermore, singletons could partly compensate for the negative effects of retreats by remaining at the front end of the flock where unexploited resources are encountered, as had been observed for geese. Typically the highest energy gain rates are achieved at the front edge of the flock (Drent & van Eerden 1980, Prop & Loonen 1989, Rowcliffe et al. 2004). Prop & Loonen (1989) showed that sub-dominant singletons enhanced their walking speed in order to arrive at the front edge of the flock where food stocks were still unexploited. The same could hold for the Bewick’s Swans, for movements of singletons are longer than movements of paired swans, both for movements related to social interactions and free movements. Longer movements would also allow singletons to escape from local high densities of swans, which would decrease the number of social interactions. Singletons have more reasons to escape from social interactions than the dominant pairs, for the simple reason that singles lose a large proportion of interactions they are involved in. In this light, a study in which movements of subordinate and dominant birds are related to the position of other swans would be very valuable.

To conclude, we can state that social interactions have a noticeable effect on the foraging path of swans. A substantial proportion of movements (24%) was related to social interactions, which underlines the impact of social interactions on the movement patterns of swans. Retreats are thought to have a negative effect on the energy gain rate since they are expected to deteriorate the efficiency in which high-density patches are encountered. Singletons face the highest proportions of retreats and consequently are expected to achieve the lowest gain rates. Based on these results we predict that singletons achieve a lower speed of migration than pairs and families.

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REFERENCES


SAMENVATTING

Foeragerende dieren verplaatsen zich geregeld van voedselplek naar voedselplek. De efficiëntie waarmee goede voedselplekken worden gevonden, wordt bepaald door de manier waarop het dier zich door de omgeving voortbeweegt. Bij dit onderzoek kijken we vooral naar het effect van sociale interacties op het foerageerpad van een dier. Hiervoor hebben we heel precies de paden van Kleine Zwanen *Cygnus columbianus bewickii* in kaart gebracht die op ondergrondse knolletjes van het Schedefonteinkruid *Potamogeton pectinatus* foerageerden. Wij konden zo precies de afstanden tussen foerageerplekken bepalen. In 24% van alle gevallen was de verplaatsing naar een andere foerageerplek gerelateerd aan een sociale interactie. Een zwaan die door een andere zwaan van zijn plek werd weggejaagd, zwom een
significant langere afstand voordat hij weer begon met eten dan een zwaan die een vrije beweging maakte (d.i. een beweging niet gerelateerd aan een sociale interactie). We verwachten dat zo’n langere beweging de energieopname van de zwaan negatief beïnvloedt, omdat door de langere beweging goede voedselplekken minder efficiënt worden gevonden. Binnen een groep zwanen bestaat een duidelijke sociale hiërarchie: families zijn dominant over paren en losse vogels, en paren zijn dominant over losse vogels. De laatste worden het vaakst weggejaagd van plekken. We verwachten dus dat zij de laagste energieopnames behalen. Singles kunnen hiervoor mogelijk compenseren door zich meer naar de rand van de groep te verplaatsen, waar ze kunnen profiteren van nog niet geëxploiteerde voedselbronnen.

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