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Untying the knot

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Chapter 4

Experimental evidence
for cryptic interference among
socially foraging shorebirds

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SUMMARY Foraging rate and the distribution of foragers depend on prey distribution in conjunction with inter-individual interactions. Generalized functional response models predict intake rates and spatial distributions of foragers on the basis of resource distribution and interference competition. The adequacy of these models depends on how well they capture the foragers' essential behavior. In this paper we report on the results of a foraging experiment designed to examine the mechanisms of interference competition using red knots *Calidris canutus* that feed on buried bivalves. Red knots are rarely observed to interfere in the field, but this does not imply absence of interference. Our experimental setup minimized resource depletion which allowed us to quantify interference competition as the decline in intake rate as a function of group size, with prey density and social status as additional treatments. We found that intake rate and searching efficiency decreased with group size and that dominant birds had higher intake rates than subordinates. Additionally, time spent searching for prey increased with group size. The decrease in intake rate was not due to conventional interference mechanisms (such as kleptoparasitism and time spent interacting with conspecifics), but to "cryptic interference", i.e. avoidance of physical encounters with conspecifics. To accurately predict intake rates and foraging distributions, theory and models need to account for the possibility that animals anticipate and try to avoid, at some costs, physical encounters with conspecifics (i.e. conflicts that would make conventional interference behavior visible).

INTRODUCTION

Intake rate and the distribution of foraging animals depend on the distribution of resources and the presence of conspecifics (Krebs 1972). The latter can be both beneficial and detrimental (Stephens et al. 2007, Danchin et al. 2008, Sumpter 2010, Folmer et al. 2012). Conspecific presence can be beneficial because it provides information on food availability (Chapter 5, Krause and Ruxton 2002, Valone 2007, Danchin et al. 2008) and predation risk (Lima and Dill 1990, Krause and Ruxton 2002). In addition, it dilutes the risk of being depredated (Hamilton 1971, Lima and Dill 1990, Quinn and Cresswell 2006). The presence of conspecifics may also lead to interference competition with negative effects on intake rate (Goss-Custard 1980, Sutherland 1983, Tregenza 1995, Johnson et al. 2006, Klaassen et al. 2006b).

If animals behaved ideally and freely (Fretwell and Lucas 1970), intake rates and foraging distributions could be predicted using generalized functional response models (van der Meer and Ens 1997, Smallegange and van der Meer 2009). Such models combine prey density and parameters that capture the negative effect of nearby conspecifics to predict intake rates, which in turn may be used to predict spatial foraging distributions (Beddington 1975, Sutherland 1983, Ruxton et al. 1992, Bautista et al. 1995, Holmgren 1995, Tregenza 1995, Johnson et al. 2006, van Gils et al. 2006b).

There exist two classes of generalized functional response models to describe and predict intake rates in standing stock situations: phenomenological and mechanistic models (van der Meer and Ens 1997). Both have been used to describe and predict intake rates for various species (Bautista et al. 1995, Smallegange and van der Meer 2009, van der Meer and Smallegange 2009, Gyimesi et al. 2010) including shorebirds (Piersma et al. 1995, Stillman et al. 1997, Goss-Custard et al. 2006, van Gils et al. 2006b, Rutten et al. 2010a).

Phenomenological generalized functional response models are based on statistical relationships between intake rate and competitor density and summarize interference into one parameter (Hassell and Varley 1969, Sutherland and Koene 1982). Mechanistic generalized functional response models are derived from basic behavioral processes which are modeled as transitions between mutually exclusive behavioral states (e.g. searching, handling, fighting). Transition rates are assumed to be constant functions of competitor density. These models, however, do not take into account that animals may anticipate events and adjust behavior accordingly. Hence, they assume that animals act as "aimless billiard balls" (van der Meer and Ens 1997). Mechanistic models are considered superior to phenomenological models because they are more generic than case-specific phenomenological models (Stillman et al. 1997, van der Meer and Ens 1997, Smallegange and van der Meer 2009). How well generalized functional response models predict intake rates and spatial distributions depend on how well these models capture essential foraging behavior. Particularly, small differences in the relationship between intake rate and group size (i.e. interference) can have a large influence on the predicted foraging distributions (van der Meer and Ens 1997). Interference has become a central topic in

behavioral ecology, but the current understanding of the behavioral mechanisms of inter-ference competition is still incomplete (van der Meer and Ens 1997, Vahl et al. 2005b). The mechanisms of interference competition are generally assumed to be kleptoparasitism and time lost in aggressive interactions (Tregenza 1995, Stillman et al. 1997, Smallegange and van der Meer 2009).

In the field, the various mechanisms of interference competition are not necessarily observed, because animals may space out to avoid or mitigate interference costs while maintaining the benefits of conspecific presence (Vahl et al. 2007, Folmer et al. 2010, Gyimesi et al. 2010). That is, foragers will trade-off the benefits and costs of social foraging which will lead to "spaced-out gregariousness" (Kennedy and Crawley 1967). The degree of spacing between social foragers will depend on the net benefits of the presence of conspecifics (Folmer et al. 2012). In the field only the net effect of conspecific attraction and interference on the spatial distribution of foraging animals can be observed (Folmer et al. 2010), and the relative strengths of each of the separate mechanisms can only be assessed indirectly (Folmer et al. 2011). Therefore, detailed information on the mecha-nisms of interference competition cannot be obtained from field observations (Vahl et al. 2007, Gyimesi et al. 2010, Rutten et al. 2010a). To gain insight into the various mecha-nisms of interference, experiments are needed.

The objective of this study is to obtain insight into the mechanisms of interference for a gregarious forager to underpin and improve upon generalized functional response models. We used red knots *Calidris canutus* (hereafter called knots), a species that does not show typical interference behavior in the field (van Gils and Piersma 2004). We studied foraging behavior at different competitor densities while ensuring minimal prey depletion to avoid confounding of resource competition and interference competition (Vahl et al. 2005b, Smallegange et al. 2006). Because prey density and social status also influence interference competition, these factors are incorporated as treatments.

METHODS

Birds
Knots are medium-sized shorebirds that outside the breeding season usually feed on mollusks (Zwarts and Blomert 1992, Piersma et al. 1993a, Piersma et al. 1998, van Gils et al. 2003a). Their short prey handling times and the fact that prey items are swallowed in their entirety (Piersma et al. 1995) reduce opportunities for kleptoparasitic acts (Ens et al. 1990, van Gils and Piersma 2004).

The experimental animals, 23 knots of the *islandica* subspecies (Piersma 2007), were captured with mistnets on 7 and 8 February 2005 in the western Dutch Wadden Sea (53°15'N, 5°15'E). The birds were housed in two indoor aviaries at the Royal Netherlands Institute for Sea Research (NIOZ), Texel, The Netherlands. Each aviary, 4.5 m × 1.5 m surface × 2.5 m height, contained a fresh water tray. To keep the aviary floors and the feet of the birds clean, salt water was constantly flowing over the floors. The light was kept at a constant light regime (12:12 h light:dark) and temperatures were kept constant at 12 °C.

To avoid different dominance hierarchies to develop in the two aviaries, every day membership to aviary groups were assigned randomly. A metal identification ring was fitted to the right tibia together with plastic color rings on each tarsus for individual recognition. After the experiment, in June 2005, the birds were returned to the field. The experiment complied with Dutch law regarding animal experiments under permits issued by the DEC-KNAW.

The staple food and experimental prey items were blue mussels *Mytilus edulis*, a mollusk that commonly occurs in the diet of free-living knots (Zwarts and Blomert 1992, Dekinga and Piersma 1993). Every other week fresh mussels were collected from the breakwaters at Den Helder (52°57'N, 4°43'E). After collection, bundles of mussels were disentangled and sorted based on length. Mussels smaller than 20 mm were used as staple food and mussels between 8 and 12 mm were used as experimental prey items.

Experimental setup

Inspired by Smallegange, van der Meer & Kurvers (2006), we kept prey density relatively constant by minimizing prey depletion as follows. In the experimental arena (7 m by 7 m) an elevated lane (6.5 m long, 0.7 m wide and 0.3 m deep) was filled with sand in which the prey items were buried at approximately 3 cm depth (Fig. 4.1). The water in the arena was
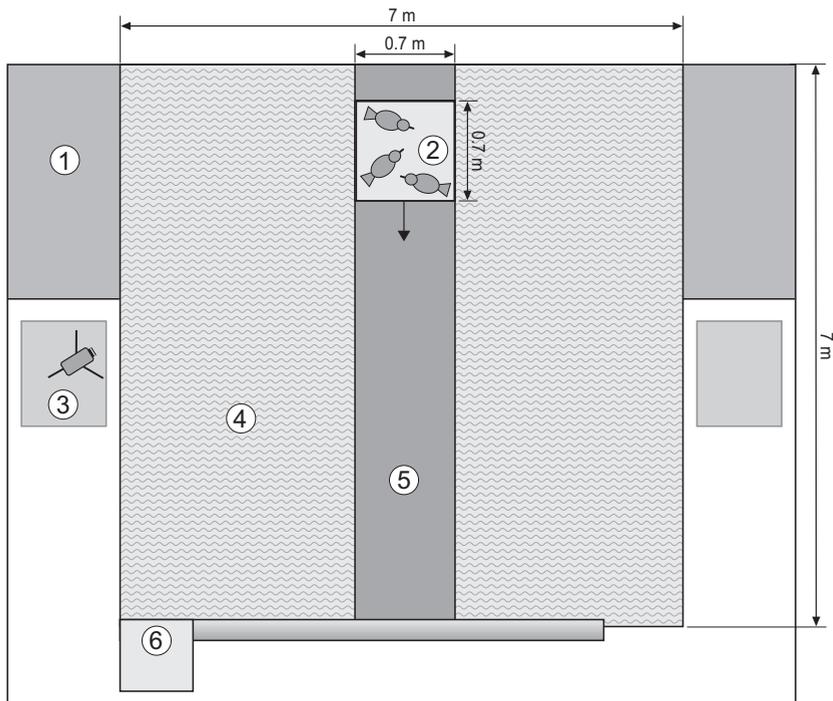

Figure 4.1 The experimental shorebird facility: 1) aviary, 2) food patch, 3) observation hide, 4) water, 5) covered lane and 6) electrical engine with beam to roll the sheet on. 2, 4 and 5 make up the experimental "arena".

kept at such a level that only the lane was above water and accessible for the birds. The lane was covered with a polyester sheet which contained a square hole of 0.7 m × 0.7 m in which the knots were able to forage; this hole is the food patch. During a trial the sheet was rolled onto a beam that was driven by an electrical motor so that it smoothly slid across the lane from one end to the other at an average speed of 1 cm s^{-1}, which mimics the receding water line in the field. As the food patch moved across the lane, new prey became available and the area that had been foraged upon disappeared underneath the sheet (see Online Supplementary Material for an example trial video).

Social status
Prior to the interference trials, we obtained the social status of each experimental animal as follows. We covered the lane with a large quantity of mussels over which the patch moved. After 14 h of fasting, all 23 knots were released in the arena to forage. The number of aggressive interactions between foraging individuals, i.e. threatening, charging (moving towards conspecifics) and receding, was recorded, as were the winners and losers of each interaction. Individuals that retreated were taken as losers. The trial ended when the sheet reached the end of the lane; when one individual had taken control of the patch; or when one individual interacted extremely aggressive towards other birds. The red knot that dominated the group was isolated from the rest and the above procedure was repeated with the reduced group. We repeated the procedure until a group of individuals remained that rarely interacted. The whole procedure was repeated five times per day for four consecutive days.

In a group of 23 birds there are (23 × 22) / 2 = 253 combinations of paired individuals between whom interactions can take place. The 20 repetitions gave a total of 771 interactions between 207 pairs. On the basis of the interactions we calculated a dominance coefficient for each individual as follows. We assumed transitivity, that is, we assumed that if bird A is dominant over B and B is dominant over C, then A is dominant over C, i.e. a linear dominance hierarchy. We estimated dominance coefficients by means of logistic regression, where X_{ij}, which is the number of victories of bird i over j, is binomially distributed
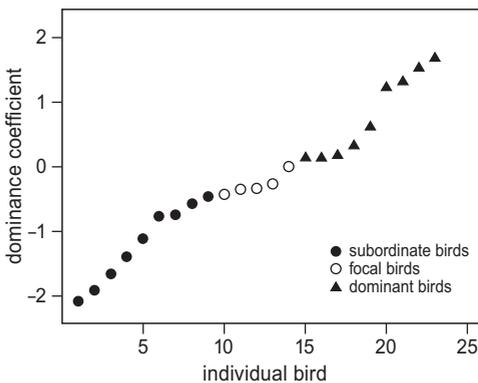

Figure 4.2 Social status of experimental birds ranked by dominance coefficients. The five intermediate birds were selected as focal birds.

with parameters p_{ij}, the probability of bird i winning the pair-wise confrontation, and N_{ij} the total number of disputes between bird i and j. A dominance coefficient d is estimated for each individual and the expected logit p_{ij} equals the difference Δd between the pair's dominance coefficients. In practice it means that the rows of the design matrix are formed by all pair wise combinations of individual birds with the value 1 for the reference bird in the pair, –1 for the partner, and 0 elsewhere (van der Meer 1992, Tufto et al. 1998). Hence, the estimated dominance coefficients represent the social statuses of the birds and allow estimating the probability of winning a pair-wise confrontation as $e^{\Delta d} / (1 + e^{\Delta d})$.

On the basis of their social status, individuals were divided into three groups (Fig. 4.2): nine subordinates, five intermediates (focal bird group) and nine dominants. The average dominance coefficient per group was: subordinates –1.2 (SE 0.2, n = 9), focal birds –0.3 (SE 0.07, n = 5) and dominant individuals 0.8 (SE 0.2, n = 9) (Fig. 4.2).

Interference experiment

From May till June 2005 the foraging behavior of the focal birds was studied under various combinations of bird- and prey densities, and in relative subordinate or dominant social positions. The level of interference competition was set by group size which ranged from two to eight including the focal bird of which there was one per trial. Because we used a fixed patch size (0.5 m^2), competitor density is linearly related to group size.

Two levels of prey density were used: low and high (20 and 30 mussels m^{-2}, respectively). These densities are in line with the densities encountered in the field (Dekker and Beukema 2007) and are sufficiently low to prevent digestive constraints (van Gils et al. 2005b), as indicated by the fact that all birds kept foraging until the end of the trials. The prey items were buried into the lane at predetermined positions with 1 cm^2 accuracy, which allowed retrieving remaining prey items after each trial. To avoid the possibility that birds learned the spatial distribution of prey items, we randomly selected one of the two available configurations of burial positions for each trial.

Social status treatment consisted of composing the group around the focal bird at a trial with birds randomly chosen from either the pool of subordinates or dominants. Accordingly, the same focal bird was either the most dominant or the most subordinate member of the group. Social status is potentially influenced by group size, but we rarely observed subordinate birds attacking dominants, and subordinates suffered more from the presence of dominants than the other way around. We thus conclude that the hierarchy was reflected in the experiments with smaller groups.

The different combinations of treatments consisted of manipulating group size (7 levels, varying from 2–8), prey density (2 levels) and social status (2 levels) resulting in 28 trials per focal bird and 140 trials in total. We ran between 2 and 10 trials per day. We maintained a random order in which the trials were carried out over the 29 days of experimentation.

The knots were fasted for 12 h during the night before each experimental day, and at least 60 min before each trial (i.e. larger than the time needed to digest the consumed prey, van Gils et al. 2005b). The trial lengths were short enough to ensure that all birds

were highly motivated to forage during the trials. Thirty minutes before the trial the birds were released into one of the two randomly chosen aviaries adjacent to the "arena" (Fig. 4.1) to acclimatize. Hereafter, a sliding door between the aviary and the arena was opened so that the birds could enter the arena. The trial started 30 s after the first bird entered the patch. At that moment the electric engine was started to move the food patch. The trial ended when the patch had moved halfway the length of the lane. For efficiency reasons, the lane was split into two sections of equal length and each section was used for one trial. At the end of a trial, the arena, but not the adjacent aviary, was darkened to make the birds fly to the lightened aviary. The polyester sheet was then moved one patch-length so that unexploited mudflat was available for the next trial with new birds. The second trial of a session lasted for the remainder of the lane. The average duration of a trial was 241 s (SD = 12.8). As the beam with the sheet thickened when winding up, the average speed of the moving patch was slightly larger in the second trial which explains the variance in trial duration. This effect is negligible because the standard deviation is less than 13 seconds on a mean of 241 s and we randomly assigned trials to one of the two lane sections. After a session of two trials the remaining prey were dug out and counted per trial to determine prey depletion. New prey items for the following session were then buried according to the method described above.

All trials were recorded on video by an observer who was positioned in a hide near the patch (Fig. 4.1). The videotapes were analyzed using The Observer 5.0 Event recorder (Noldus Information Technology, Wageningen, The Netherlands). The Observer software allowed measurements of time budgets with an accuracy of 0.04 s per behavioral bout.

Following Vahl et al. (2005b), we measured the time spent by the focal birds in a trial on the following, mutually exclusive, behaviors: *searching* (probing the sediment in search of prey, either while moving or standing still), *watching* (watching the surroundings while standing still with the bill at an upward angle of at least 45 degrees with the sediment; note that this may include watching conspecifics), *moving* (taking steps with the bill at an upwards angle of at least 45 degrees with the sediment), *interacting* (both attacking (i.e. moving towards conspecifics aggressively) and evading (i.e. moving away from attacking conspecifics), *handling* (touching prey with bill until swallowed, lost or dropped), and being *off-patch* (not on the food patch). In addition, we scored the number of prey intakes and vigilance acts (head up while tilting the head sideways at least 45 degrees; note that in the wild vigilance behavior is used to detect approaching raptors (Cresswell 1994)). On average, a focal bird showed approximately one vigilance act per trial. Because of the absence of predators the birds may have experienced the experimental area as a safe environment (van den Hout et al. 2010). Vigilance was not included as a fraction in the time budget, because a vigilance act takes less than a second and constitutes a marginal part of the total time budget (Piersma et al. 1995). Instead, we used vigilance rates calculated as the number of vigilance acts divided by trial duration (*vigilance*, # min^{-1}). Handling times are also very short. They were averaged per trial (*handling*, s).

Statistical analyses

One focal bird rarely foraged during trials. Its average intake rate was close to zero, whereas the other four individuals had substantially higher intake rates. The hypothesis of equal average intake rates for the five focal birds was rejected (ANOVA, $F_{4,135}$ = 3.1, P = 0.02), while it was not rejected for the four focal birds without the outlier (ANOVA, $F_{3,108}$ = 0.5, P = 0.69). Therefore the outlier was omitted from further analyses which gave an adjusted sample size of 112.

The average experienced prey density per trial (D, m^{-2}) was calculated by averaging the initial and final prey density. To normalize the distribution of model residuals we *ln*-transformed average experienced resource density. Average intake rate (*IR*, # s^{-1}) per trial was obtained by dividing the number of prey intakes by the duration of the trial. Average searching efficiency (cm^2 s^{-1}) per trial was calculated by 1 / (T_s × D) (i.e. instantaneous rates of discovery, Holling 1959), where T_s is the average searching time per prey item, and D the average experienced resource density.

The following behaviors of the focal bird were analyzed: (1) the time spent off-patch relative to the trial duration. The proportion of time spent off-patch was analyzed using a generalized linear mixed model with binomial errors and focal bird as random intercept. The following on-patch behaviors were analyzed as proportions of time spent on-patch: (2) searching, (3) watching, (4) moving, (5) interacting. The proportions 2 – 5 are "sum constrained", i.e. they sum up to one. The sum constraint was accounted for by ln-ratio-transformation (Aitchison 1986, Kucera and Malmgren 1998). That is, the dependent variables 2 – 5 are

$$y_i' = \ln\left(\frac{y_i}{(\prod_{i=2}^{n=5} y_i)^{\frac{1}{4}}}\right),$$

where y_i is the fraction of time spent on behavior *i*. Zeroes were replaced by δ = 100% × 0.5 × 0.04 / average trial time, which gives half the smallest percentage unit that behavior was recorded in (Aitchison 1986). Note that 0.04 s is the duration of one video frame.

Additionally, (6) handling and (7) vigilance were determined as explained above. Both were *ln*-transformed to normalize the data. To avoid possible zeroes in the *ln*-transformations of vigilance, we increased the argument by one.

The impacts of experimental treatments on intake rate, searching efficiency, time budget, handling time and vigilance rate were analyzed in R v2.11.1 (R Development Core Team 2011) using general linear mixed models with focal bird as random intercept. Because experienced prey density, *IR*, and searching efficiency were negatively and non-linearly related to group size, the latter was *ln*-transformed.

We started the statistical analyses with models including all experimental treatments and their interactions as explanatory variables. The models were simplified by removing non-significant terms (P > 0.05) from the initial model applying a step-wise backward procedure: (i.e. terms were removed one by one in order of decreasing P-values, Quinn and Keough 2002). However, regardless of statistical significance, the main effects of experimental treatments were retained in the final model. Normality of residuals was judged by visual inspection of QQ-plots (Miller 1986).

RESULTS

Experienced resource density

Experienced prey densities slightly declined with ln(group size). The average experienced prey density declined by –0.17 (SE 0.02, $F_{1,108}$ = 70.3, $P < 0.01$) with ln(group size) and at approximately equal rates for both prey densities ($F_{1,108}$ = 2.6, $P = 0.11$) and social status treatments ($F_{1,108}$ = 0.4, $P = 0.53$).

Interference

During the 112 trials we observed only 4 events in which prey items were stolen from conspecifics (i.e. kleptoparasitism). Table 4.1A and Figure 4.3A show that IR was significantly lower in the low prey density treatment than in the high density treatment (–0.008 s^{-1} SE 0.002). In addition, IR declined linearly with ln(group size). The decline was approximately equal for both prey densities (–0.028 SE 0.003; Fig. 4.3A and Table 4.1A). The IR of a focal bird in a dominant position was on average 0.005 s^{-1} (SE 0.002) higher than when it was in a subordinate position. The interactions between ln(group size) and social status, and ln(group size) and prey density were non-significant indicating that the negative impact of ln(group size) on IR did not vary by these treatments. Searching efficiency declined linearly with ln(group size) (–22.47 SE 2.36, Table 4.1B, Fig. 4.3B), but was not affected by either prey density or social status.

Table 4.1 Intake rate (# s^{-1}) and searching efficiency (cm^2 s^{-1}) models. The treatments are: prey density (high and low), social status of focal birds (subordinate and dominant), and ln-transformed group size (number of individuals, including focal). The reference case (intercept at group size = 0) is the high prey density treatment for focal birds in subordinate positions.

	Response variables	Predictors	Coefficient	SE	P
A) Fixed effects	Intake rate (# s^{-1})	Intercept**	0.066	0.005	<0.01
		Group size**	-0.028	0.003	<0.01
		Prey density (low)**	-0.008	0.002	<0.01
		Social status (dominant)*	0.005	0.002	0.04
Random effects		Focal bird	SD = 0.000		
		Residual	SD = 0.013		
B) Fixed effects	Searching efficiency (cm^2 s^{-1})	Intercept**	54.32	4.12	<0.01
		Group size**	-22.47	2.36	<0.01
		Prey density (low)	0.43	2.15	0.84
		Social status (dominant)	1.23	2.15	0.57
Random effects		Focal bird	SD = 1.79		
		Residual	SD = 11.37		

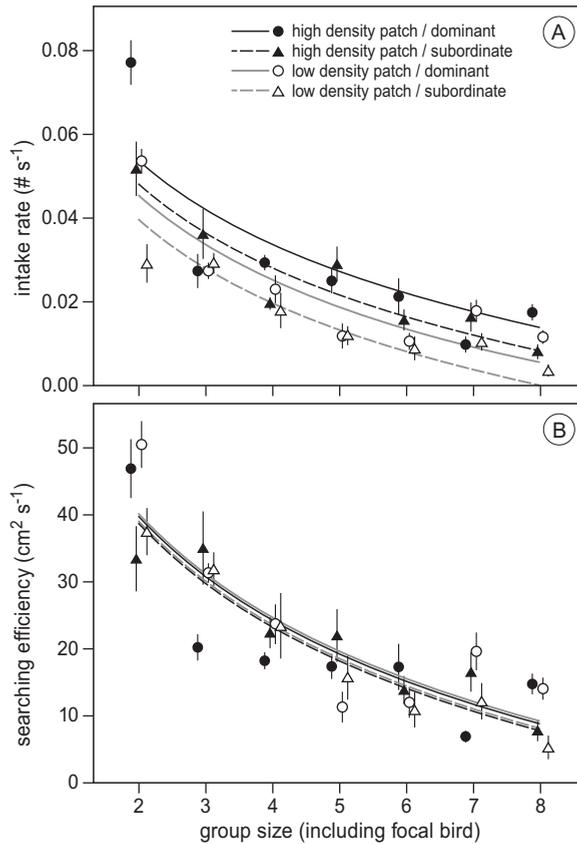* treatment significant at the .05 level
** treatment significant at the .01 level

Figure 4.3 Intake rate (# s^{-1}) (panel A) and searching efficiency (cm^2 s^{-1}) (panel B) as functions of group size. The plotted lines are based on the final regression models (Table 4.2). Vertical bars denote standard errors of the means. The values on the x-axis are adjusted for graphical representation.

Time budgets

Focal birds tended to spend less time off-patch when they were in dominant positions than when they were in subordinate positions (Table 4.2A). However, the fraction of time spent off-patch did not differ by prey density or by group size.

From Table 4.2B and Figure 4.4A it follows that the fraction of time spent searching for prey was larger on the low prey density patch than on the high prey density patch. Moreover, it varied by social status: focal birds in dominant positions spent more time searching than when they were in subordinate positions. An interesting finding is that the proportion of time spent searching for prey increased with group size.

The fraction of time spent watching increased with group size. It was also larger on the low prey density patch than on the high prey density patch (Table 4.2C, Fig. 4.4B). For

Table 4.2 Time budget models. The different behaviors are time spent off the food patch (off-patch), searching for prey (searching), watching with head up (watching), moving (moving), interacting with conspecifics, i.e. attacking or retreating (interacting), handling prey (handling), and vigilance. Treatments and reference case as in Table 4.1. Model estimates refer to transformed data (see Methods).

	Behaviors	Predictors	Coefficient	SE	P
A) Fixed effects	Off-patch	Intercept	-1.53	0.80	0.05
		Prey density (low)	-0.08	0.53	0.88
		Social status (dominant)	-1.11	0.57	0.05
		Group size	0.07	0.13	0.60
Random effects		Focal Bird	SD = 0.00		
		Residual	SD = 0.16		
B) Fixed effects	Searching	Intercept**	1.54	0.21	<0.01
		Prey density (low)*	0.29	0.14	0.04
		Social status (dominant)**	0.83	0.14	<0.01
		Group size*	0.07	0.04	0.04
Random effects		Focal Bird	SD = 0.00		
		Residual	SD = 0.74		
C) Fixed effects	Watching	Intercept*	-0.74	0.29	0.01
		Prey density (low)*	0.30	0.14	0.03
		Social status (dominant)**	1.35	0.37	<0.01
		Group size**	0.18	0.05	<0.01
		Social status (dominant) × Group size*	-0.16	0.07	0.02
Random effects		Focal Bird	SD = 0.21		
		Residual	SD = 0.72		
D) Fixed effects	Moving	Intercept**	-2.42	0.33	<0.01
		Prey density (low)**	1.21	0.38	<0.01
		Social status (dominant)**	0.51	0.14	<0.01
		Group size**	0.32	0.05	<0.01
		Prey density (low) × Group size*	-0.17	0.07	0.02
Random effects		Focal Bird	SD = 0.35		
		Residual	SD = 0.75		
E) Fixed effects	Interacting	Intercept	0.79	0.56	0.16
		Prey density (low)*	-0.93	0.36	0.01
		Social status (dominant)**	-1.90	0.36	<0.01
		Group size**	-0.41	0.09	<0.01
Random effects		Focal Bird	SD = 0.30		
		Residual	SD = 1.88		

Table 4.2 Continued

	Behaviors	Predictors	Coefficient	SE	P
F) Fixed effects	Handling time (s)	Intercept**	-0.64	0.10	<0.01
		Prey density (low)	-0.11	0.06	0.09
		Social status (dominant)*	0.13	0.06	0.04
		Group size	-0.02	0.02	0.11
Random effects		Focal Bird	SD = 0.06		
		Residual	SD = 0.31		
G) Fixed effects	Vigilance (# min^{-1})	Intercept	0.05	0.09	0.62
		Prey density (low)	0.00	0.04	0.94
		Social status (dominant)**	0.47	0.11	< 0.01
		Group size	0.01	0.01	0.73
		Social status (dominant) × Group size**	-0.07	0.02	< 0.01
Random effects		Focal Bird	SD = 0.09		
		Residual	SD = 0.22		

* treatment significant at the .05 level
** treatment significant at the .01 level

subordinates the fraction of time spent watching was smaller than for dominants, but the significant interaction between social status and group size suggests that this difference was mitigated by group size.

The fraction of time spent moving increased with group size (Table 4.2D, Fig. 4.4C). For small group sizes the fraction of time spent moving was higher on the low prey density patch than on the high prey density patch. However, this difference decreased with group size. Additionally, birds in dominant positions spent more time moving than when the birds were in subordinate positions.

The proportion of time spent interacting decreased with group size and was lower on the low prey density patch than on the high prey density patch (Table 4.2E, Fig. 4.4D). In addition, birds in dominant positions spent less time on interactions than in subordinate positions.

Table 4.2F shows that neither prey density nor group size had significant effects on handling times. Birds in a dominant position, however, had larger handling times than when they were in a subordinate position.

Birds in dominant positions tended to be more vigilant than in subordinate positions. However, this effect was mitigated by group size as indicated by the significant negative interaction between group size and social status (Table 4.2G).
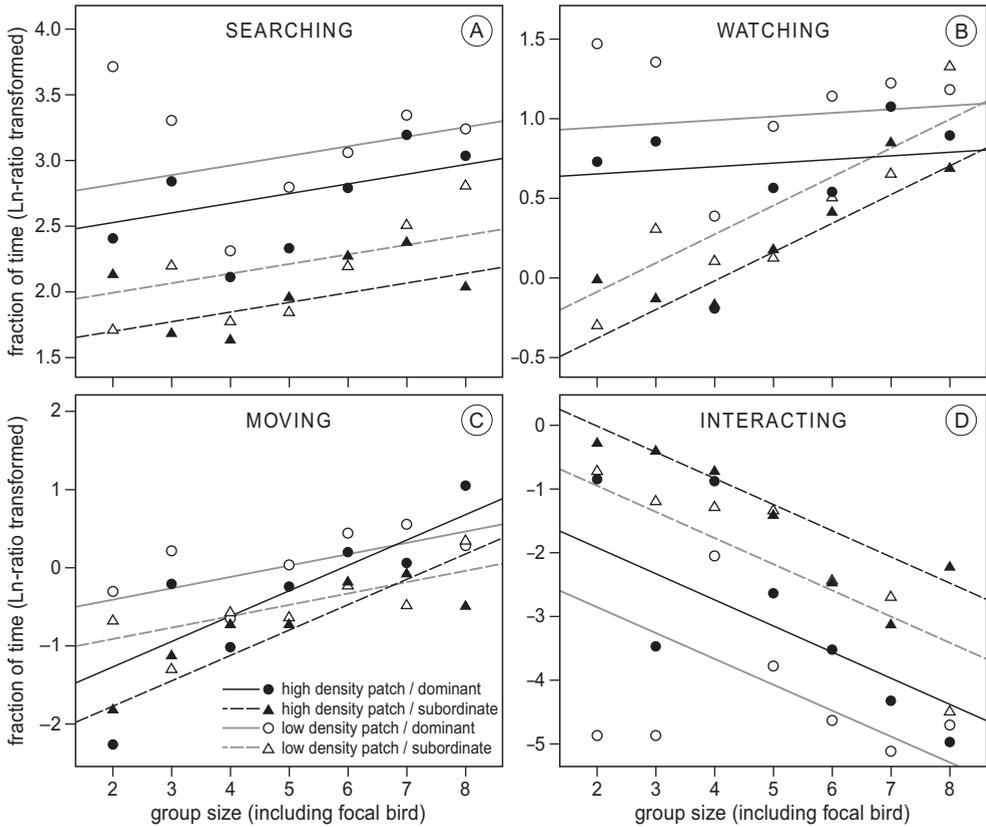
Figure 4.4 Mean transformed fractions of time spent on searching for prey (A), watching (B), moving on the food patch (C) and on interacting with conspecifics (D). The plotted lines are model estimates for prey densities and social status (Table 4.2). Note the differences in range on the vertical axes between panels. Each point in the graph represents the mean value.

DISCUSSION

One main finding of this study is that increasing group size had a negative effect on intake rate. It declined by 93% on the low prey density patch and 78% on the high density patch when group size increased from two to eight. Another important result is that the decline was not due to conventional mechanisms of interference competition. We observed only four cases of kleptoparasitism during the 112 trials and time spent interacting with conspecifics decreased with group size. The reduction in intake rate coincided with a decline in searching efficiency. Furthermore, the time budget models showed that with an increase in group size the time spent searching, watching and moving increased.

To avoid the possibility that decreased intake rate due to resource depletion is incorrectly attributed to interference competition as group sizes increase, resource depletion

needs to be controlled for (Vahl et al. 2005b, Smallegange et al. 2006). Previous experiments accounted for prey depletion by using unnaturally high prey densities or by using very short trial durations (Vahl et al. 2005b, Gyimesi et al. 2010, van Dijk et al. 2012). In experiments with shore crabs *Carcinus maenas* Smallegange et al. (2006), kept prey densities constant by replenishing consumed prey. In our experiment prey density declined 21% when group size increased from 2 to 8 birds. This effect was much smaller than the negative impact of group size on intake rate even though the effects of group size on the other behaviors were smaller than that on intake rate. The methods used here lead to substantially reduced depletion effects compared to comparable interference experiments (Vahl et al. 2005b). Moreover, in our experimental setup we were able to study interference mechanisms in trials of approximately 4 minutes at naturally occurring prey densities (Vahl et al. 2005b, Gyimesi et al. 2010, Rutten et al. 2010a, van Dijk et al. 2012).

As noted in the Introduction, mechanistic functional response models generally assume that the main mechanisms of interference competition are kleptoparasitism and time lost in agonistic interactions. In oystercatchers *Haematopus ostralegus*, for instance, it has indeed been found that kleptoparasitism and time spent interacting with conspecifics increased with forager density while intake rate declined (Sutherland and Koene 1982, Ens and Goss-Custard 1984). For shore crabs *Carcinus maenas* Smallegange et al. (2006) observed that aggressive interactions increased with group size, but that kleptoparasitism rarely occurred. Our results are consistent with the negative effect of group size on intake rate, but the common mechanisms of interference competition were virtually absent or operated in the opposite direction. Kleptoparasitism rarely occurred while time spent interacting declined. However, we found that time spent searching increased with group size, which was also observed in an interference experiment with mallards *Anas platyrhynchos* (van Dijk et al. 2012). Absence of kleptoparasitism was probably due to short handling times (similar results were obtained by van Gils et al. 2003b, van Gils and Piersma 2004, Vahl et al. 2005b). The decrease in time spent interacting, and the increase in time devoted to searching with increasing group size, could be the result of scrambling for prey (Clark and Mangel 1986, Grant 1993, Dubois and Giraldeau 2005). Additionally, a reduction in vigilance with group size could allow more time to be spent searching for prey (Pulliam 1973, Beauchamp 2003, 2009). In our study, the already low vigilance rates (overall one act every 2.4 minutes) indeed decreased with increasing group sizes. However, the amount of time gained from a reduction in vigilance was very small.

Larger group sizes led to more time spent on watching and moving as well as to a decrease in searching efficiency. We hypothesize that these behaviors resulted from birds shunning aggressive interactions. Time spent watching increased with group size, because our knots had to increasingly divert their attention between searching for prey and avoiding interactions with conspecifics which in turn reduced searching efficiency (Goss-Custard 1976, Dukas and Kamil 2001). Time spent moving increased with group size, because our knots increasingly had to avoid collisions with conspecifics. Because this may disturb preferred search paths (e.g. to avoid revisiting the same, depleted locations) it reduced searching efficiency (Cresswell 1997). We follow Gyimesi et al. (2010), in

suggesting to label the decline in intake rate due to *covert* avoidance behavior and associated reduced searching efficiency "cryptic interference": these mechanisms are not the typical overt interference mechanisms.

Dominant birds are less susceptible to interference competition (Ens and Goss-Custard 1984, Stillman et al. 1996), because they may displace subordinates and monopolize food patches (Vahl et al. 2005a, Rutten et al. 2010b). Consequently, subordinates spend time avoiding dominants at the cost of foraging time (Stillman et al. 1997, Smallegange and van der Meer 2009) or at the cost of selecting less preferred foraging locations (Dolman 1995, Rutten et al. 2010b). In line with these results, we found that intake rates were higher when focal birds were dominant than when they were subordinate. Searching efficiencies, however, did not differ between dominance treatments. Dominant birds had higher intake rates because they spent more time on the food patch searching for prey. Subordinate birds on the other hand more often avoided encounters with conspecifics, and were more often excluded from the food patch as indicated by the fact that they spent more time off-patch.

Our experiments have shown that knots incur decreased intake rates from avoiding encounters with conspecifics. In the field this is rarely observed because mechanisms are cryptic (Gyimesi et al. 2010) and because suitable foraging areas are often large enough (van Gils et al. 2006b, Kraan et al. 2009a, Kraan et al. 2009b), such that encounters and physical hindering are minimal while maintaining the benefits of group foraging (Goss-Custard 1976).

Interference models have been used to predict spatial distributions of different species of shorebirds at various spatial scales (e.g., Stillman and Goss-Custard 2010, Quaintenne et al. 2011). For instance, Quaintenne et al. (2011) explain the distribution of knots between wintering areas in NW Europe, including sites in The Netherlands, UK and France, by means of an interference model. Their model is parameterized on the basis of small scale experiments, but applied to explain and predict distributions of knots over large spatial and temporal scales. The explanation of Quaintenne et al. (2011) is therefore (implicitly) based on the notion that interference may operate over large spatial and temporal scales. Our results do not support this hypothesis, since they indicate that knots attempt to avoid direct encounters with conspecifics. In intertidal areas, knots have sufficient opportunities to "space out gregariously" because foraging areas are extensive (Kraan et al. 2009a, Kraan et al. 2009b). Indeed, in the field aggressive interactions and kleptoparasitism between knots are rarely observed.

As explained in the Introduction, a prerequisite for mechanistic generalized functional response models to adequately predict intake rate and spatial distributions is that it adequately captures the foragers' essential behavior. Uncertainty about the mechanisms of interference hampers the validity and generality of predictions from such models. The mechanisms of interference competition that we observed challenge the assumed mechanisms in the existing functional response models (that we know of). For instance, Smallegange and van der Meer (2009), considering a state of conspecifics avoidance, suggest that their model, and in principle any mechanistic model, may be extended to

various situations by expanding the set of behavioral states. However, this requires unambiguous definitions, non-overlapping states and unambiguous observations of behavioral states. In our experiment such unambiguous assignments were perhaps not possible despite detailed behavioral observations. For instance, part of the behavior that we scored as 'searching' could have been a combination of avoiding conspecifics whilst probing. Moreover, since it already is difficult to disentangle behavioral states in an experiment, in the field this will be nearly impossible (Gyimesi et al. 2010).

The phenomenological 'Hassell and Varley model' allows for a decline of searching efficiency with group size (Hassell and Varley 1969), but all behavioral mechanisms are aggregated into one interference parameter. Hence, this model is unable to fully capture the interference mechanisms and lose their generality (van der Meer and Ens 1997, Smallegange and van der Meer 2009).

Our results showed that current generalized functional response models do not adequately capture the interference mechanisms that we have observed. Therefore, the aggregative response functions (i.e. the predicted distributions of foragers across food patches) are imprecise. Perhaps better predictions and understanding of interference may be obtained when current models are elaborated to take into account the fact that animals behave in ways such that agonistic interactions are anticipated and covertly avoided (i.e. cryptic interference).

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