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The mechanisms of interference competition: two experiments on foraging waders

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Models of population dynamics that include interference competition have often been applied to foraging waders and less so to other foragers, even though these models are, in principle, generally applicable. At present, however, it is still unclear whether interference competition is of importance for foraging waders. To support this idea experimental evidence and knowledge of the mechanisms underlying interference effects are required. We experimentally determined the relationship between forager density and foraging success in two wader species: the red knot (*Calidris canutus*) and the ruddy turnstone (*Arenaria interpres*). With each of the two species, we conducted an experiment consisting of 300 one-min trials. In these trials we scored the behavior and the foraging success of focal individuals at specific combinations of bird and prey density. Irrespective of prey density, individuals of both species discovered fewer prey items at higher bird densities. Despite this, only in turnstones did intake rates decline with increasing bird density. Knots compensated for a lower prey-discovery rate by rejecting fewer prey items at higher bird densities. In knots, bird density had a complex, nonmonotonic effect on the time spent vigilant and searching. In turnstones the main effect of increased bird density was a reduction in the prey-encounter rate, that is, the reward per unit search time. Effects on the time spent vigilant and the time spent searching were less pronounced than in knots. Thus, the mechanistic basis of the effects of bird density was complex for each of the two species and differed between them. *Key words: Arenaria interpres*, behavioral mechanisms, *Calidris canutus*, density dependence, exploitation competition, social dominance. *[Behav Ecol 16:845–855 (2005)]*

Competition among foraging animals is generally divided into two types (Keddy, 2001). *Exploitative competition* is the negative effect of others through the removal of resources (Grover, 1997; Park, 1954). *Interference competition* is the negative effect of others through behavioral interactions (Miller, 1967; Park, 1954). Because the presence of competing individuals may lower the survival and reproduction of foragers, competition can be important for the dynamics of animal populations (Christian, 1970; Gauthreaux, 1978). Most models of population dynamics consider only the effects of exploitative competition (Grover, 1997; Huisman and Weissing, 2001; Keddy, 2001). Interference competition, however, can be just as relevant (Goss-Custard, 1980) because behavioral interactions can be very costly (either directly, through injury or loss of energy or time, or indirectly, through a reduction in intake rate).

Models of population dynamics that include interference competition have often been applied to foraging waders (also known as shorebirds), and less so to other foragers, even though these models are, in principle, generally applicable (e.g., Stillman et al., 1997; Sutherland, 1983). Foraging success in these models is assumed to decrease with increasing forager density. This reduction in foraging success is generally assumed to result from agonistic interactions between the foragers, whereby interactions are thought to be over individual food items (e.g., kleptoparasitism). When more time is spent interacting, less time can be spent on searching for food, and therefore foraging success should decrease (e.g., Ruxton et al., 1992; Sirot, 2000; Stillman et al., 1997). At present, however, it is an open question whether interference competition is especially prevalent among foraging waders. The importance of interference competition among foraging waders may differ from that among other birds because of characteristics typical to the habitats used by foraging waders; the openness of their habitat, for example, may affect predator detection, and the distribution of their prey may also be unlike the distribution of prey of other species. Knowledge of the relationship between the density and the success of foragers and of the mechanisms responsible for this relationship, however, is still surprisingly rudimentary (van der Meer and Ens, 1997).

One reason why our knowledge is still limited is that experimental control of forager density is essential; natural changes in the distribution of foragers over resource patches may result in any relationship between forager density and foraging success between patches (van der Meer and Ens, 1997). Ideal-free-distribution theory (Fretwell and Lucas, 1970), for instance, assumes a direct negative effect of forager density on foraging success, but predicts no relationship between forager density and foraging success when measured between patches. However, it is no trivial task to manipulate the density of foraging birds. In his review on the relationship between density and success of birds, Beauchamp (1998) reported only 12 studies where the researchers had been able to manipulate forager density while studying foraging success. None of these studies was on waders. The relationship between the density and the success of foragers was negative in only three of these studies. In contrast, the sole study in which the density of a foraging wader was varied experimentally (van Gils and Piersma, 2004), reported the expected decline in foraging success with forager density. This study did not address the behavioral mechanisms causing the decline in intake rate. Clearly, more manipulative studies are required for a satisfactory comparison between the effect of forager density on foraging success of waders and that of other birds. To understand potential differences between groups of birds, special attention should additionally be paid to the mechanisms underlying any effects of forager density on

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foraging success, as it is only through understanding such mechanisms that we can link effects of forager density with characteristics of the environment.

We conducted two experiments on the effect of forager density on foraging behavior and foraging success, using either red knots (*Calidris canutus*; henceforth called knots) or ruddy turnstones (*Arenaria interpres*; henceforth called turnstones). Knots and turnstones are both medium-sized waders that inhabit intertidal coastal areas outside the breeding season (Branson et al., 1978; Piersma and Davidson, 1992). Yet, the two species differ strongly in their feeding styles and dominance structure. It has been suggested that interference competition is of limited importance for knots (Stinson, 1980; van Gils and Piersma, 2004) but of major importance for turnstones (Metcalfe and Furness, 1986). Knots generally forage in large flocks of apparently varying individual membership in which no dominance structure is apparent (Metcalfe and Furness, 1986; Vahl and Piersma, personal observation). They eat mainly bivalves buried in soft sediments (Piersma et al., 1993a, 1994), detecting their prey by probing the mud with their bill (Piersma et al., 1995; Zwarts and Blomert, 1992). Bivalves are swallowed whole and digested internally (Piersma et al., 1993b; van Gils et al., 2003). In contrast, turnstones forage in relatively small flocks of stable composition (Metcalfe, 1986; Metcalfe and Furness, 1985; Whitfield, 1988) in which a stable dominance hierarchy is generally formed (Metcalfe, 1986). They feed mainly on barnacles, mollusks, and small crustaceans (Harris, 1979; Whitfield, 1990), for which they search by rooting through a layer of seaweed that usually covers these prey items (Fuller, 2003; Whitfield, 1990; Vahl and Piersma, personal observation). In each of these two waders, we experimentally determined the effect of forager density on foraging success by quantifying time allocation and prey-encounter rate under controlled conditions. The use of an indoor experimental shorebird facility enabled us to keep most factors of potential importance either constant (environmental conditions, energy expenditure, and level of satiation) or fixed at different levels (prey density). In particular, it allowed us to vary forager density experimentally and unambiguously.

Thus, through an experimental manipulation of forager density, we hoped to determine the presence, nature, and strength of interference effects. The use of two contrasting species of waders and two different prey densities should shed some light on the generality of interference effects and the behavioral mechanisms involved.

MATERIALS AND METHODS

The two experiments each consisted of 300 trials of 60 s. Both experiments had a multifactorial design and their general setup was comparable: in all trials, the foraging behavior of one bird was studied under a specific combination of bird and prey density. The experiment with turnstones included two additional factors: (1) the dominance position of the birds and (2) a refuge site that was either present or absent.

Subjects

In the first experiment, from 13 to 28 May 2001, we used 25 knots (Table 1). In the second experiment, from 11 September to 8 October 2001, we used 27 turnstones. All birds were caught with mistnets at night on intertidal flats in the Wadden Sea (under Dutch bird ringing center license numbers 851 and 351 for knots and turnstones, respectively). Data were collected on 10 "focal" knots and 15 "focal" turnstones; nonfocal birds were used only to manipulate bird density. Assignment of focal status was random (knots) or based on dominance position (turnstones). Assuming a linear dominance hierarchy, cardinal-scale dominance positions were determined by means of a logit regression analysis (Tufto et al., 1998; van der Meer, 1992). To account for variation in dominance position, we designated as focal individuals the five lowest-, the five middle- and the five highest-ranking turnstones (called, respectively, *subordinate*, *intermediate*, and *dominant*). To allow us to recognize focal birds from all angles, they received a unique mark. Focal knots were marked with a section of bright yellow or orange rubberized cloth (kapron), glued (with cyano-acrylate) to the back or scapular feathers.

Table 1
Numbers and characteristics of the subjects used

				Juvenile		Adult	
Species	Catch date	Status	Dominance position	♂	♀	♂	♀
Red knot	9 February 1997	Nonfocal	—	—	—	—	1[a]
	31 August 2000	Nonfocal		—	—	1[a,b]	—
	26–30 March 2001	Nonfocal		—	2	1	—
		Focal		—	—	—	1
	24 April 2001	Focal		—	—	5[c]	4[c]
		Nonfocal		—	—	5[c]	5[c]
Ruddy turnstone	23–25 September 2001	Focal	Dominant	—	—	3	2
		Nonfocal	Dominant	2	—	2	2
		Focal	Intermediate	1	2	1	1
		Nonfocal	Subordinate	2	3	—	1
		Focal	Subordinate	—	5	—	—

Status indicates whether behavior was recorded (focal birds) or not (nonfocal birds). Dominance position could only be determined for turnstones. Juvenile indicates first-year individuals. Sex was determined from DNA using standard methodology verified for these wader species by Baker et al. (1999).

[a] Individual had been used in previous experiments.

[b] Catching date, molt pattern, and weight curves indicated this knot to be of the subspecies *canutus*, whereas all others were of the subspecies *islandica*.

[c] Prior to the current experiment, 14 of these individuals had participated in an experiment on prey choice for 5–10 days. Conditions in both experiments were comparable except for the prey species used (*Macoma balthica* in the earlier experiment and *Mytilus edulis* in the current experiment).

Focal turnstones had a small area of their back feathers bleached, using commercial hair bleach.

Housing and pre- and postexperimental treatment

All subjects were housed in two roosting aviaries measuring 4.3 × 1.2 m and 3.0 m high, in the indoor experimental shorebird facility of NIOZ (according to protocol 2000.04 of the DEC, the Dutch committee for animal experiments). The floor of these aviaries was continuously covered with a thin film of running seawater to keep the feet of the birds salty and wet, and a tray of running freshwater for drinking and bathing was always present. The indoor environment had a constant air temperature (18°C) and photoperiodic regime (15:9 h light:dark). The aviaries were illuminated by moonlight-mimicking lights between 2200 and 0700 h.

Outside the experimental trials, knots were fed blue mussels (*Mytilus edulis*), a common prey species in their natural environment (Piersma et al., 1993a; Zwarts and Blomert, 1992). We collected these mussels from nearby dykes. The mussels were rinsed, spread out over wire trays, and stored in running, unfiltered seawater for up to 5 days. Before serving them to the knots, we put the mussels through a mesh to break the byssus threads that held them together and to sort them by size. Lengths used in the experiment ranged from 13 to 17 mm. Turnstones were fed ad libitum with trout food pellets on days without trials, as well as between the end of an experimental day and the beginning of the next fasting period. Knots were denied food from 0800 h on an experimental day and tested between 1000 and 1800 h; turnstones were denied food from 2200 h and tested between 0930 and 1430 h on the next day.

To familiarize them with the experimental environment and procedure, all knots and turnstones participated in pilot trials for 3 and 8 days, respectively, prior to the experiments. During the pilot trials, we observed agonistic interactions ($n = 321$) among the turnstones and recorded the outcome of each interaction: winners were those individuals that either chased their opponent away or held their ground after being attacked. To study their consistency, we recorded agonistic interactions once more, soon after the turnstone experiment was finished ($n = 548$). Both knots and turnstones were released on intertidal mudflats in the Wadden Sea shortly after each experiment had ended.

Experimental setup

Both roosting aviaries were separated from an experimental room (7 × 7 m and 3.5 m high) by a sliding door. During the experiments, we flooded the experimental room with seawater to a depth of 20 cm. The only dry areas remaining were one ("refuge absent"; knots and turnstones) or two ("refuge present"; turnstones) platforms (1 × 1 m and 15 cm deep) filled with sand and positioned slightly above the water level. Because these platforms were the only available places for the birds to stand on, bird density remained effectively constant within a trial. In the knot experiment, we inserted mussels into the sediment of the foraging platform to resemble a situation with buried prey. The mussels were inserted to a fixed depth (1.5 cm) and at arbitrary positions (cf. Piersma et al., 1995). In the turnstone experiment, we spread out mealworms (*Tenebrio molitor*) arbitrarily over the foraging platform and then covered them with a 5-cm layer of seaweed (bladderwrack *Fucus vesiculosus*). The refuge platform differed from the foraging platform only in that it did not contain prey items and was not covered by bladder-wrack.

We recorded foraging behavior of the subjects using two digital video cameras (Sony dcr-trv900e). One was positioned next to the foraging platform at a distance of 1.5 m for a sideways view, while the other was mounted 3.5 m directly above the foraging platform.

Experimental procedure

At the start of each experimental day, all birds were placed in groups of four in boxes measuring 50 × 35 cm and 25 cm deep. To minimize stress, we captured and housed the birds in darkness, as they were very quiet in the dark. Before each trial, a specific focal bird and the required number of nonfocal birds were transferred to one of the roosting aviaries. After opening the sliding door, the birds were attracted into the experimental room by dimming the lights in the roosting aviary while lighting the experimental room. Subjects readily flew to the experimental platforms and started to forage within seconds of the sliding doors being opened. The trials started the moment the focal bird began to forage and lasted for 150 s (knots) or 120 s (turnstones).

After each trial, lights were used again to entice birds back to the roosting aviary. If birds had to participate in another trial, they were returned to the boxes. Otherwise, they were transferred to the second roosting aviary, where they stayed until the last trial of the day had been performed. Focal knots and turnstones took part in on average 2.9 and 1.1 trials per day, respectively. Necessarily, the number of trials that nonfocal birds took part in exceeded this (averages of 8.8 and 6.5 for knots and turnstones, respectively).

In the knot experiment, depletion was estimated from observations on the number of mussels consumed or rejected during the previous trial. Initial prey densities were restored before the next trial through the addition of fresh mussels. In addition, the sandy sediment on the foraging platform and all prey items were renewed after 5 (bird densities 4, 8, or 16) or 10 (bird density 1 or 2) trials. In the turnstone experiment, the mealworm supply was renewed and the seaweed cover was replaced after each trial.

Experimental design and statistical analysis

In the knot experiment, we studied the effects of the fixed factors *bird density* (A: 1, 2, 4, 8, and 16 birds) and *prey density* (B: 50 and 200 mussels). Although we refer to factor A as *bird density*, it could also be interpreted as *group size* because we manipulated the number of birds on a 1 m^2 platform (see Arenz, 2003; Fernandez-Juricic et al., 2004; Lima, 1990). We controlled for variability among individual birds by using a random factor *focal bird* (γ: 10 different birds). In the turnstone experiment, we also studied the effects of the fixed factors *bird density* (A: 1, 3, 5, 9, and 13 birds) and *prey density* (B: 50 and 200 mealworms), but in addition we studied the effect of the fixed factors *refuge present* (C: yes or no) and *dominance position* (D: dominant, intermediate, and subordinate). The random factor *focal bird* was nested within the dominance position ($\gamma[D]$: five different turnstones per dominance position). Both experiments followed a split-plot design (Appendix).

Treatment levels

The range of bird densities we used in the experiments encompasses and exceeds densities usually seen in the field (which, for both species, will usually not exceed 1 m^{-2}; Fuller, 2003; Vahl and Piersma, personal observation). Still, the densities are well below the physical maximum and the maximum observed in systems where food is extremely abundant. For instance, in Delaware Bay, USA, where knots and turnstones feed on the eggs of horseshoe crabs (*Limulus polyphemus*; Tsipoura and

Burger, 1999), bird densities can be about three times the maximum density used in this experiment (Vahl and Piersma, personal observation). Using bird densities that exceed the natural levels at comparable resource densities may help us to understand why natural bird densities are generally lower.

We used prey items that resembled the natural prey and that were easy to get. Mussels are among the favorite prey species of knots (Zwarts and Blomert, 1992), and although mealworms are not part of the natural diet of turnstones, they resemble other invertebrates included in the diet (especially the larvae of wrack flies [Coelopidae], Fuller, 2003) and are strongly favored by turnstones (Whitfield, 1990). The low (50) and high (200) experimental prey densities used lie within the range of densities observed in the field for bivalves (Piersma et al., 1993a) and other invertebrates (Fuller, 2003). We buried the mussels in the soft sediment of the foraging tray (as sometimes occurs on intertidal flats; Piersma T, personal observation) in order to impose some search time on the knots.

The presence of a refuge may well affect opportunities for resource monopolization and the outcome of competition experiments (Łomnicki, 1988). We therefore included this factor in the turnstone experiment.

Wintering turnstones are known to form dominance hierarchies (Metcalfe, 1986); the high familiarity among turnstones in our experimental facility probably enhanced this process. Because dominance status was assigned on basis of the position in the dominance hierarchy, dominance was treated as an absolute attribute rather than as a relative quality (Francis, 1988).

Recorded behavior and response variables

We analyzed trials using The Observer 3.0 Event Recorder (Noldus Information Technology, Wageningen, the Netherlands). To limit effects of resource depletion, digestive constraints and satiation, foraging behavior, and success was measured during the first 60 s of each trial. Our omission of the remainder of each trial from the video analysis also served to avoid potential end-effects (e.g., birds anticipating the end of a trial). Each trial was analyzed by two observers together, and all trials were examined twice. The first analysis was performed at one-fifth of normal speed using the side-view recording. The second analysis, performed in real time using the top-view recording, was used to verify the observations from the side-view tape. In both experiments, five behavioral categories were distinguished, each consisting of several behaviors (Figure 1).

In both species we studied the effect of treatment on *intake rate*, defined as the number of prey items swallowed per unit of total time (# s^{-1}). Because not all prey items found were consumed, we also studied the effect on *prey-discovery rate*, defined as the number of prey items found per unit of total time (# s^{-1}). To investigate the causes of interference effects, we calculated *time allocation*, defined as the total number of seconds allocated to each of the five behavioral categories (s), and *prey-encounter rate*, defined as the number of prey items found per unit of search time (# s^{-1}). As differences in prey-encounter rate may reflect both differences in prey density and changes in foraging behavior, we also calculated the *searching efficiency*, defined as the proportion of available prey found per unit search time (m^2 s^{-1}; i.e., we divided the prey-encounter rate by the initial prey density [either 50 or 200 m^{-2}]; this measure approximates the instantaneous area of discovery [see Holling, 1959, Piersma et al., 1995] but deviates from it as prey density was not constant throughout a trial). In the calculation of these response variables we excluded prey items that had been rejected before the focal bird found them.

Behavioral category	Description
Search 	Focal bird searches for food using either vision or touch. Tactile search refers to probing the mud with the tip of the bill (knots) or rooting through seaweed (turnstones).
Handle 	Focal bird is in physical contact with a prey item. A distinction is made between prey previously undiscovered, prey previously rejected (knots) and prey stolen from others.
Interact 	Focal bird either initiates an interaction by taking up a threatening position or by moving quickly towards the opponent, or responds to a threatening or attacking non-focal bird by moving away from this opponent.
Vigilant 	Focal bird is looking around (head up): vigilance encompasses alertness directed at other birds (actually a form of interaction) and that towards some other aspect of the environment, as no distinction could reliably be made.
Other 	Focal bird is preening its feathers or pecking its identification mark.

Figure 1
Ethogram of foraging and interacting turnstones, with sketches of the behavioral categories recorded in the video analysis. The same ethogram was used for the knots.

Missing values and their treatment

Not all trials were successful. In the knot experiment, the focal bird failed to forage normally in a number of trials. Instead, it spent its time pecking at the plumage mark, preening, or being highly inactive. Some of these trials were successfully repeated in the 2 days after the initial experimental period. However, as foraging was again not normal in nine of these repeated trials, a second repeat was performed on the third day after the experimental period. In total, this resulted in 283 successful trials and hence 17 missing data points. In the turnstone experiment, foraging behavior was interrupted in 11 trials, either due to disturbance by a bird that landed in the water or because the focal bird was preening. Each of these trials was repeated at the end of the same experimental day. This resulted in 300 successful trials.

Data transformation

For the statistical analysis we assumed that the various treatments had a multiplicative effect on the response variables. We therefore log-transformed all measurements, as general linear models assume that effects interact in an additive way. Data on time allocation is compositional (Aitchison, 1986);

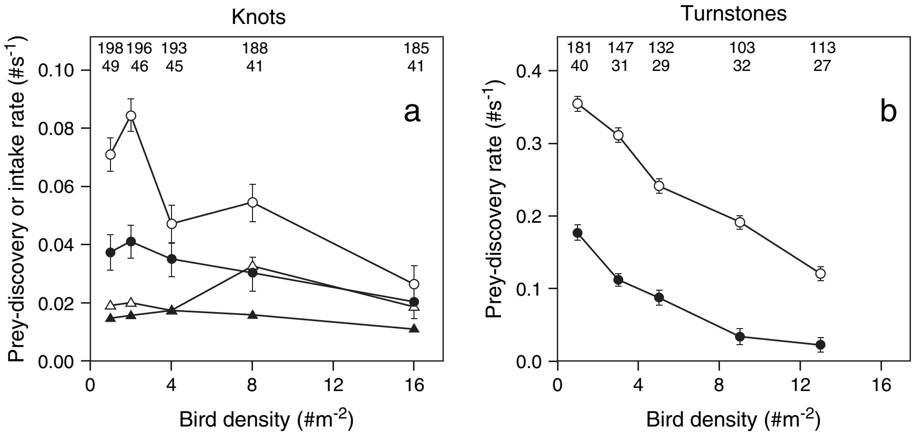


Figure 2
Foraging success of knots (a) and turnstones (b) at initial prey densities 50 (black) and 200 (white). For both species, foraging success is given as prey-discovery rate (circles). Intake rate was identical to prey-discovery rate in turnstones but not in knots, as only knots did not consume all prey items discovered. Therefore intake rate (squares) is given only for knots. Values above the graph indicate the estimated average number of prey items remaining after 60 s at prey density 50 (bottom row) and prey density 200 (top row). Symbols represent the means in accordance with the ANOVA model, that is, the least square means, and error bars represent one standard deviation of these means.

the sum of the time allocated to the various behavioral categories is constrained at 100%. We therefore used ratios of time allocation for analysis.

For all response variables based on the number of prey items swallowed or discovered, we added the value one to avoid taking logarithms of zero. For data on time allocation, zero replacement was achieved by using the procedure for nonessential zeros in compositional data (Aitchison, 1986). As the time spent interacting necessarily took a value of zero when there was only one forager, the analysis of interacting time (univariate, excluding bird density 1) was performed separately from the analysis of time allocation involving other behavioral categories (multivariate, including bird density 1). We do not present any information on the behavioral category "other," as very little time was allocated to this category (for knots and turnstones, the average per trial was 1.1 and 0.8 s, respectively) and as it was not affected by any of the experimental factors. We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller, 1997).

Hypothesis testing

Data were analyzed using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL). The knot experiment was analyzed in accordance with the standard split-plot design. We grouped interaction terms between the block factor and the whole plot factors in the whole plot error term and those between the block factor and the subplot factor in the subplot error term. Replacement of the 17 missing values using the harmonic mean method (Miller, 1997) hardly affected test outcomes. Therefore, tests based on the 283 successful trials are presented.

The design of the turnstone experiment was not perfectly balanced with respect to the distribution of bird density over plots. Although this causes no problems for the GLM procedure, the estimated sums-of-squares are no longer independent, and some caution must be exercised with their interpretation. In the GLM model, we grouped four-way interactions in the error term, against which we tested all terms that included the random factor focal bird. Effects of the factor refuge present were tested against the plots; all other terms were tested against their interaction with the random factor focal bird.

RESULTS

Intake rate and prey-discovery rate

Individuals of both species discovered fewer prey items at higher bird densities and low prey density (Figure 2; Table 2a). From the lowest to the highest bird density studied, prey-discovery rate more than halved (Figure 2). The four-fold increase in prey density resulted in approximately a doubling of prey-discovery rate. Turnstones consumed almost all prey they discovered, and therefore their intake rate was affected by bird density ($F_{4,48} = 104.6, p < .01$) and prey density ($F_{1,12} = 204.2$, $p < .01$) in the same way as their prey-discovery rate. Knots, however, rejected some of the prey items they had found. Because fewer prey items were rejected at higher bird densities and at the low prey density, there was no straightforward effect of bird density ($F_{4,18} = 3.5, p = .03$) and prey density ($F_{1,18} = 17.1$, $p < .01$) on intake rate (Figure 2a), despite changes in prey-discovery rate. Apparently, knots compensated for a reduced prey-discovery rate by becoming less critical in their acceptance of prey items.

Turnstones occupying different dominance positions discovered (Table 2a) and consumed ($F_{2,12} = 1.0$, $p = .39$) an equal number of prey items. In addition, an equal number was discovered (Table 2a) and consumed ($F_{1,8} = 3.7$, $p = .09$) in the absence and presence of a refuge. In fact, the main effect of the presence of a refuge was a small increase in the number of times a bird flew off the foraging platform during an experimental trial (average 0.12 versus 0.05). As movement caused disturbance, this resulted in a small increase in the number of interactions. As intake rate and prey-discovery rate of turnstones did not depend on either dominance position or the absence or presence of a refuge, we do not further discuss the effects of these factors on time allocation and prey-encounter rate.

Time allocation and prey-encounter rate

The reduction in prey-discovery rate with increasing bird density is generally assumed to be caused by an increase in time spent interacting, which, in turn, results in a reduction in time spent searching. Indeed, time spent on interactions increased monotonically with bird density in both species (Figure 3; Table 2b). However, interacting time seemed to have a marginal effect on searching time because both species

Table 2

GLM test results for knots and turnstones on prey-discovery rate (a), time allocation (b and c) and prey-encounter rate (d)

	a				b				c				d			
	Prey-discovery rate				$T_I/(T_S+T_H+T_V)$				T_V/T_S, T_H/T_S				Prey-encounter rate			
Factor	df	SS	*F*	*p*	df	SS	*F*	*p*	df	λ^a	*F*	*p*	df	SS	*F*	*p*
Knots																
Between plots																
Block "τ"	2	2.5			2	3.0			4,324	0.9			2	0.6		
Bird density "A"	4	14.9	9.6	<**.01**	3	244.1	18.3	<**.01**	8,14	0.1	10.3	<**.01**	4	9.5	7.4	<**.01**
Prey density "B"	1	8.7	22.4	<**.01**	1	2.2	0.5	.49	2,1	0.5	10.4	<**.01**	1	10.4	32.5	<**.01**
A × B	4	1.6	1.1	.41	3	6.7	0.5	.69	8,14	0.8	0.5	.86	4	1.8	1.7	.24
Whole plot error	18	7.0			14	62.2			36,324	0.7			18	5.8		
Within plots																
Focal bird "γ"	9	29.5	13.0	<**.01**	9	70.4	2.4	**.01**	18,324	0.4	9.5	<**.01**	9	12.4	5.2	<**.01**
A × γ	36	8.8	1.0	.53	27	118.5	1.3	.14	72,324	0.6	1.4	**.03**	36	10.2	1.1	.36
B × γ	9	3.3	1.5	.17	9	37.3	1.3	.26	18,324	0.9	1.2	.24	9	2.2	0.9	.49
A × B × γ	36	6.6	0.7	.87	27	76.9	0.9	.64	72,324	0.7	0.9	.64	36	8.8	0.9	.58
Subplot error	163	41.1			129	419.7							163	42.8		
Total	283				225								283			
Turnstones																
Between plots																
Refuge "C"	1	1.0	4.1	.08	1	30.3	14.5	**.01**	2,7	0.3	7.0	**.02**	1	0.7	2.4	.16
Plot "η(C)"	8	1.9			8	16.8			16,74	0.8			8	2.5		
Within plots																
Subplot "ξ(η[C])"	10	3.2			10	9.2			20,74	0.7			10	3.8		
Bird density "A"	4	46.1	100.9	<**.01**	3	134.9	31.5	<**.01**	8,94	0.2	18.6	<**.01**	4	50.8	59.8	<**.01**
Prey density "B"	1	48.3	212.6	<**.01**	1	1.1	0.7	.43	2,11	0.1	81.0	<**.01**	1	68.3	215.1	<**.01**
Dominance "D"	2	1.4	0.9	.42	2	25.9	1.9	.20	4,22	0.6	1.3	.29	2	2.2	1.7	.22
Focal bird "γ(D)"	12	9.0	4.7	<**.01**	12	83.7	5.8	<**.01**	24,74	0.1	6.8	<**.01**	12	7.6	3.2	<**.01**
A × B	4	2.6	4.6	<**.01**	3	6.2	1.7	.18	8,94	0.6	3.1	<**.01**	4	0.6	0.8	.50
A × C	4	0.8	1.1	.38	3	12.5	3.0	**.04**	8,94	0.8	1.0	.44	4	0.4	0.4	.78
Interaction terms	215	31.6			172	230.6							215	42.9		
Error	38	6.1			24	28.7							38	7.5		
Total	300				240								300			

Time could be allocated either to searching (T_S), handling (T_H), vigilance (T_V), or interacting agonistically with other birds (T_I). Treatment effects on time allocation were tested separately for effects on interacting time at bird densities higher than 1 (b) and time spent on other behaviors at all bird densities (multivariate; c). All tests were performed on log-transformed data after zero values had been treated as described in the text. To simplify representation, nonsignificant higher-order interaction terms in the turnstone experiment are grouped ("interaction terms"). Effects significant at the .05 level are indicated by bold *p* values.

[a] Multivariate test statistic used is Wilks' λ.

spent less than 10% of their time on interactions. Other aspects of the birds' time allocation appeared to be at least as important.

Bird density had a strong effect on the time allocation of knots (Figure 3a,b; Table 2c), most obviously in the nonlinear effect on the time spent vigilant and searching. Vigilance time in knots was highest at a very low or very high bird density and searching time neatly mirrored this pattern (Figure 3a,b). Bird density also reduced prey-encounter rate, that is, the number of prey items encountered per second spent searching (Figure 4a; Table 2d). However, although knots found fewer prey items, total handling time did not decrease markedly with increasing bird density (Figure 3a,b), as the percentage of prey items rejected was lower at the higher bird densities. Time allocation of knots depended slightly on prey density (Figure 3a,b; Table 2c), probably because they encountered more prey per second spent searching when prey density was high (Figure 4a; Table 2d). The searching efficiency, that is, the proportion of available prey found per unit search time, was also different at the two prey densities ($F_{1,18} = 202.5$, $p < .01$; Figure 4b).

For turnstones, the main effect of bird density was a strong reduction in prey-encounter rate (Figure 4c; Table 2d). As a consequence, the birds spent less time handling at higher densities (Figure 3c,d). Although patterns in vigilance and searching time qualitatively resembled those observed in knots, the effects in turnstones were less pronounced (Figure 3c,d). Turnstones encountered about three times more prey when prey density was high than when it was low (Figure 4c; Table 2d), and therefore, they also spent more time handling and less time searching (Figure 3c,d). Prey density did not, however, affect vigilance or interacting time (Figure 3c,d; Table 2b). The searching efficiency did not depend on prey density ($F_{1,12} = 1.3$, $p = .27$; Figure 4d).

Thus, bird density induced a lower prey-discovery rate in knots through effects on both vigilance and searching time and through changes in prey-encounter rate, whereas the prey-discovery rate in turnstones was lowered mainly through a reduced prey-encounter rate.

DISCUSSION

Exploitative and interference competition

In both knots and turnstones, prey-discovery rate decreased with increasing bird density (Figure 2). This indicates that for

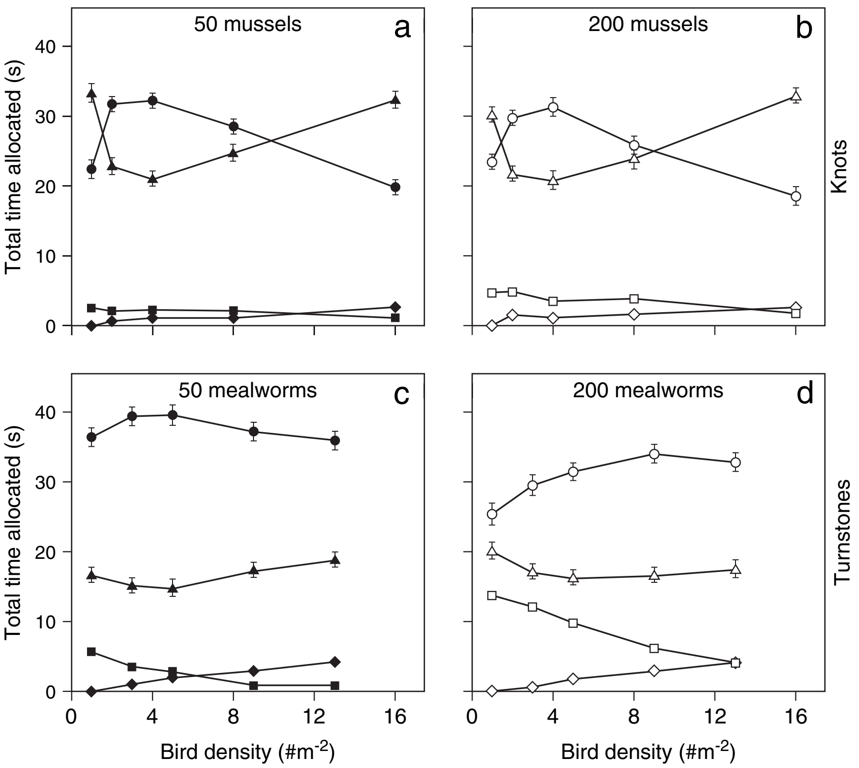


Figure 3
Total amount of time allocated to searching (filled circles, open circles), being vigilant (filled triangles, open triangles), handling (filled squares, open squares), and interacting with other birds (filled diamonds, open diamonds) by knots (a and b) and turnstones (c and d) at prey densities 50 (a and c) and 200 (b and d). Symbols represent least square means, and error bars represent one standard deviation of these means.

both species the main effect of the presence of conspecifics was negative. The decrease in prey-discovery rate was brought about by both forms of competition (exploitation and interference), as both resource depletion (Figure 2) and time spent interacting (Figure 3) were positively related to bird density. Although it is not possible to quantify the relative importance of exploitation and interference in these experiments, a closer look at the prey-discovery rates shows that resource depletion alone cannot account for the observed negative effect. After the 60-s observation period, the amount of remaining food (185 [knots] or 113 [turnstones]; Figure 2) at the highest bird density and the high initial prey density was still at least twice as high as the initial amount of food for solitary foragers at the low prey density. However, despite this difference in food density, prey-discovery rate in the latter condition was slightly higher than that in the former condition. This suggests that part of the observed effect was also due to interference, without ruling out other explanations, such as removal of the most detectable prey (Wanink and Zwarts, 1985). Clearly, a proper distinction of the two forms of competition requires an experiment in which food is not depleted.

Mechanisms of interference competition

Most mechanistic models of interference competition assume that animals interact over individual food items (e.g., Giraldeau and Caraco, 2000; Sirot, 2000; Stillman et al., 1997). In our experiments, kleptoparasitic events were absent and prey density had no significant effect on interacting time. Therefore, it is very unlikely that interactions took place over individual food items. Many of the aggressive interactions we observed were directed to searching animals, suggesting that interactions concerned small food patches rather than individual food items. It seems that our current understanding of the adaptive value of the behavioral mechanisms of interference competition is still rudimentary, despite its central importance to all mechanistic approaches to the study of interference competition.

Increases in bird density reduced the prey-discovery rate through changes in both prey-encounter rate (Figure 4) and time allocation (Figure 3). Effects on time allocation were more complex than the monotonic effects on interacting and searching time assumed by models of interference competition. Several distinct processes may jointly account for this complex effect.

At low bird densities, searching time increased with bird density, while vigilance time decreased. Vigilance was especially reduced in knots, where the presence of a second bird resulted in the reduction of vigilance time by approximately one third. Such a reduction has often been observed (Beauchamp, 1998) and may have been a response to an increase in vigilance at the group level (e.g., Lima, 1995) or other beneficial effects of foraging in the presence of others, such as the dilution of predation risk (e.g., Lima, 1990). Assuming that this "group-size effect" increases with the extent to which species naturally form groups, the observed difference between the two species in the reduction in vigilance time is in line with the observation that knots generally occur in bigger groups in the field than turnstones (Myers, 1984).

At high bird densities searching time decreased with bird density, while interacting time and vigilance time increased. Such effects on searching and interacting time have been assumed in models of interference competition, but we found the size of the increase in interacting time to be very small. However, it is well known that vigilance behavior can serve several functions (Beauchamp, 2001; Desportes et al., 1991; Robinette and Ha, 2001), some of which could be interpreted as interacting. Vigilance may, for instance, serve to prevent others from mounting sudden attacks or serve to spot opportunities for kleptoparasitism on resources discovered by others (Smith et al., 2001). Therefore, acknowledging that some interactions may well have been subtle (scored as vigilance) rather than obviously agonistic (scored as interactions), part of the expected increase in interactions may have been reflected by the increase in vigilance time.

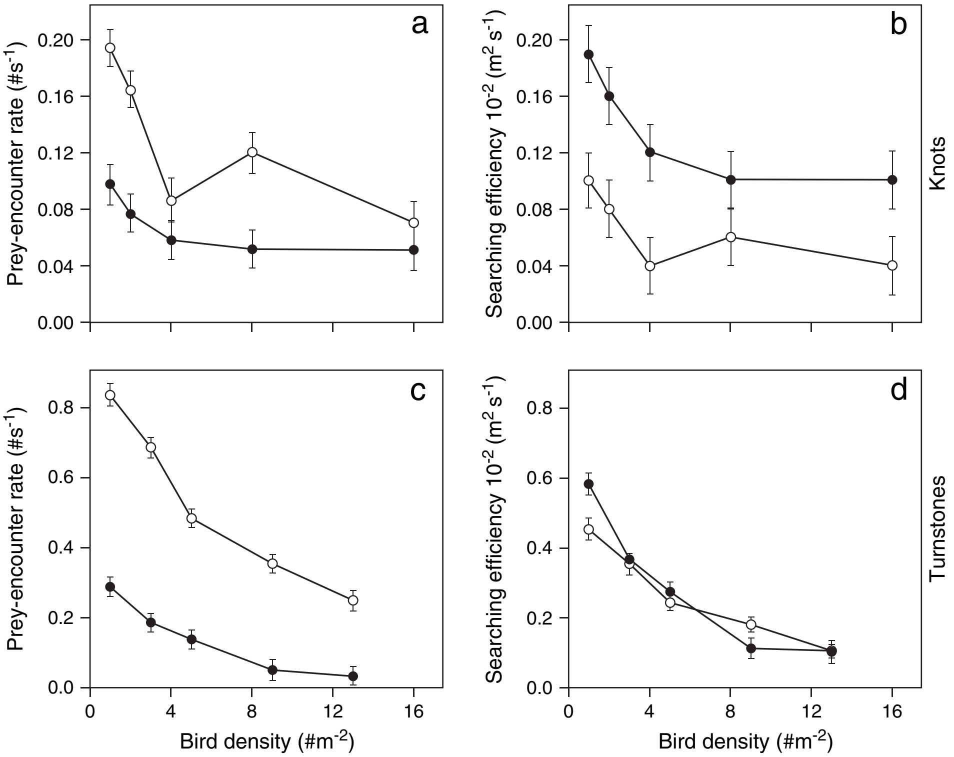


Figure 4
Prey-encounter rate (a and c) and searching efficiency (b and d) of knots (a and b) and turnstones (c and d) at prey densities 50 (black) and 200 (white). Symbols represent least square means, and error bars represent one standard deviation of these means.

The increase from the lowest to the highest bird density led to a decrease in prey-encounter rate. This was especially apparent in turnstones, where handling time also decreased with increasing bird density. The decline in prey-encounter rate will partly have resulted from increased resource depletion at higher bird densities. Most likely, interference additionally lowered prey-encounter rate, especially so in knots where resource depletion was low. High bird density may, for instance, have resulted in a loss of concentration due to multiple tasking (Dukas, 1998) or a loss of control over the search path (Cresswell, 1997).

For both species more prey items were encountered when the initial prey density was high than when it was low (Figure 4a and c). For turnstones, the searching efficiency, that is, the proportion of available prey found per unit search time was the same at both prey densities, indicating that changes in prey-encounter rate were only due to the higher number of prey items. For knots, on the contrary, the searching efficiency was lower when the food density was high. This indicates that changes in the prey-encounter rate of knots were due not only to the higher number of prey items but also to differences in the birds' behavior at the two prey densities. Such behavioral differences could be caused by a reduction in the efficiency of the prey-detection system (Piersma et al., 1998) or in motivation or by a difference in the frequency with which buried prey items were rejected.

Generality of interference effects

Interference effects were similar in knots and turnstones in terms of interacting time, but may have differed in terms of vigilance time. Effects of forager density, however, were certainly not general because forager density affected other aspects of the foraging behavior of the two species differently. The reduction in vigilance time at low bird densities, for instance, was more pronounced in knots, whereas turnstones suffered most from a reduction in prey-encounter rate. This may have been due to intrinsic differences between the two species (e.g., search mode or performance of digestive organs; see Battley and Piersma, 2005) or to differences in the environment because prey species and substrate type differed as well. In view of this complex interplay of interference, depletion, and vigilance effects, we think it is wrong to assume a general effect of forager density when modeling interference competition. Future research should attempt to understand how each of the behavioral mechanisms involved is affected by forager density, in order to predict how their combined effect depends on characteristics of the species and its environment.

Relevance to field situations

Conditions in the experimental facility obviously differed from those encountered in the field and birds in our study may well have altered their behavior accordingly. In particular, three aspects of our experiments may hamper direct interpretation of the conclusions for a natural setting.

The high rate of prey rejection by knots in the present experiment is uncommon in free-living individuals (Vahl and Piersma, personal observation). This change in behavior may be explained by various artificial aspects of our experimental setup, such as the relaxed climatic conditions, the abundance of food on offer, the high predictability of food, and the relatively short fasting period. As a consequence, the relevance of the observed effects of forager density on intake rate (but not prey-discovery rate) is probably quite limited. Instead, the conditional rejection of prey items hints at flexibility of behavior and shows that social interactions may affect foraging success even in the absence of noticeable effects on intake rate. Similar behavioral flexibility has been observed in oystercatchers (*Haematopus ostralegus*) in response to experimental variation in tide length (Swennen et al., 1989).

Contrary to our expectations, dominance position, included as a factor in the turnstone experiment, did not affect any of the response variables. It is unlikely that we assigned dominance positions incorrectly, as our assessments of dominance before and after the experiment were strongly correlated (Spearman rank correlation coefficient $r_{s,25} = .88$, $p < .001$). An alternative explanation is that in the experimental setup, birds could not actually benefit from their social dominance because they were not able to monopolize resources (Myers, 1984). Interestingly, the presence or absence of a refuge did not interact statistically with dominance position to explain foraging parameters. This indicates that this refuge was not enough to allow for monopolization of resources. Apparently, the turnstones preferred to endure social harassment on the foraging platform over staying on a platform with no food at all.

In this study we investigated the effects of treatments on instantaneous intake rate to allow a direct comparison with model assumptions. When interpreting these results for field situations, it should be realized that what foragers are striving to maximize is fitness rather than instantaneous intake rate and that processes minimized or excluded from our experiments may also play a role. Resource depletion and digestive constraints, for instance, have been shown to be of importance for the long-term intake rate of knots, together with social interference (van Gils and Piersma, 2004).

Implications

In our experiments, increased forager density led to reductions in the foraging success of the two species through both resource depletion and social interference. Thus, our results support the idea that interference competition is an important factor in determining the foraging success of waders, as is assumed when population dynamic models that include interference competition are applied to waders. However, interference competition may well occur for reasons other than those considered in these models, and the mechanistic basis of effects of bird density may be more complex than assumed. In our experiments, forager density affected foraging success through an increase in time spent interacting, a decrease in vigilance time, and a decrease in prey-encounter rate. Although similar mechanisms appeared to be at work, their importance differed. This implies that our current knowledge of the behavioral mechanisms causing interference competition is not sufficient to build robust models for the population dynamics of waders.

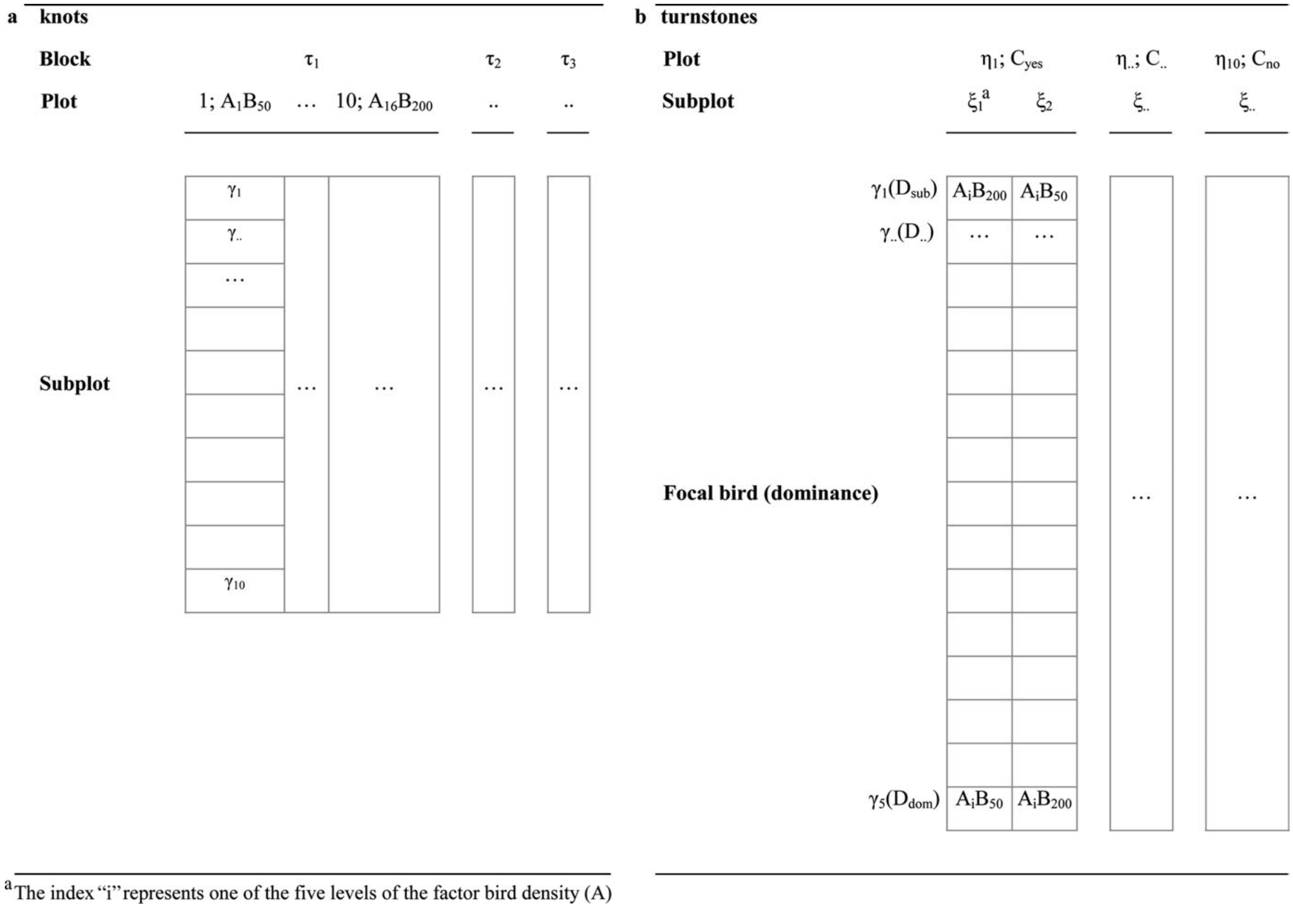
APPENDIX

Design of the experiments

The multifactorial knot experiment (fixed factors *bird density* A with five levels: 1, 2, 4, 8, and 16 birds; and *prey density* B with two levels: 50 and 200 mussels: random factor *focal bird* γ with 10 levels; i.e., 10 different knots) followed a split-plot design (see Table A1a), in which the two fixed factors A and B were among-plot factors. Each of the resulting 10 plots (factor A × factor B combinations) contained 10 subplots, one for each focal bird (factor γ). These 10 plots (i.e., 100 subplots) were replicated in three successive blocks, where block was treated as a random factor (τ with three levels). Both the order of subplots within plots and of plots within blocks was completely

Table A1

Schematic representation of the statistical designs used in the experiment with knots (a) and turnstones (b)



[a] The index "i" represents one of the five levels of the factor bird density (A)

randomized in time. Plots took half a day, blocks took five consecutive days, and the whole experiment took 15 days.

The multifactorial turnstone experiment (fixed factors *bird density* A with five levels: 1, 3, 5, 9, and 13 birds; *prey density* B with two levels: 50 and 200 mealworms; *refuge present* C with two levels: yes and no; *dominance position* D with three levels: dominant, intermediate, and subordinate; random factor *focal bird nested within dominance* $\gamma[D]$ with five different turnstones per dominance position) also followed a split-plot design (see Table A1b), but the fixed factor C was the only among-plot factor. For each of the two levels of C, five replicate plots (random factor η) were laid out. Each plot contained two *subplots* (random factor ξ). Within each subplot 15 trials were performed, one for each of the 15 focal birds ($\gamma[D]$). Moreover, within each plot, each of the 30 combinations of the factors prey density (B) and focal bird (γ), was used once. Both the order of trials within subplots and the order of plots were completely randomized in time. Regardless of the plot-subplot structure, the five levels of the fixed factor bird density (A) were attributed at random over the 300 trials. Each subplot took 1 day, each plot took 2 days, and the whole experiment lasted 20 days.

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