



Food divisibility and interference competition among captive ruddy turnstones, *Arenaria interpres*

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Interference competition among foraging animals arises from agonistic interactions among foragers. Interactions can concern single food items but also clumps of food. Food clumps consist of multiple food items, and are therefore easier to divide among foragers than food items. Theoretical studies indicate that differences in divisibility can be essential to the interference process. Empirically, however, little is known about effects of resource divisibility on interference competition. Therefore, we performed an experiment with captive ruddy turnstones. Turnstones foraged either alone or together with a competitor. We offered food at two so-called food pits and varied the divisibility of food in these pits by burying a fixed number of food items either in several layers (divisible) or in a single layer (indivisible). Additionally, we varied the distance between food pits. We accounted for differences in the social dominance status of foragers by using pairs of foragers as our experimental unit: each pair had both a dominant and a subordinate member. We found a strong asymmetry in the intake of birds of different dominance status. The strength of this asymmetry depended on both the divisibility of food and on the distance between food pits. Only when food was divisible did subordinate foragers get a share of the food; only when food pits were close to each other could dominant foragers monopolize food pits. These findings imply that to understand and predict interference competition we need to consider both the detailed characteristics of resources, and the determinants of dominance status.

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Interference competition among foraging animals is the negative effect of forager density on intake rate that results from interactions among foragers (Vahl et al. 2005a, b). There is a variety of ways in which foraging animals can interact, but most attention has been paid to agonistic interactions over food, probably because such interactions are the most obvious. Mechanistic studies of interference competition have concentrated on agonistic interactions that concern single food items ('kleptoparasitism':

Sutherland 1996; Krause & Ruxton 2002). In some predator–prey systems, however, interactions over food items are not possible, because the handling time of food items is so short that a food item is ingested before it can be stolen. This may, for instance, be the case for geese foraging on grass (e.g. Black & Owen 1989; Stahl et al. 2001) and for passerines foraging on seeds (e.g. Barnard & Sibly 1981). To explain interference competition in such systems, it has repeatedly been suggested that interference competition may also arise from agonistic interactions over clumps of food (see Vahl et al. 2005a).

We are interested in the question as to whether it matters what is at stake in agonistic interactions, that is, whether food items and food clumps differ in a way essential to interference competition. By definition, food clumps differ from food items in that they are composed

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of multiple items. This difference may be essential to the interference process, because it affects the extent to which food can be divided over multiple foragers, that is, the 'divisibility' of food.

Few theoretical studies have investigated the extent to which the divisibility of resources affects the interference process. Most models assume that resources are either all indivisible (e.g. hawk–dove games) or all divisible (e.g. producer–scrounger models), but whether or not resource divisibility affects the interference process is generally not studied. The few theoretical studies that do consider the effect of resource divisibility (e.g. Broom & Ruxton 2003; Stevens & Stephens 2002) generally conclude that the divisibility of resources may profoundly affect the extent to which foragers suffer from interference competition. Broom & Ruxton (2003), for instance, found that depending on whether food was divisible or not, aggressiveness increased (divisible) or decreased (indivisible) with forager density.

Empirically, little is known of the effects of resource divisibility on interference competition. Several studies have shown that the spatial clumping of food (i.e. the distribution of resources) can affect agonistic behaviour and intake rate (see Vahl et al. 2005a); when resources are more clumped in space they can be monopolized more easily, so that there is less division of the resources. Only Elgar (1986) was able to show directly that the divisibility of a resource (and not its distribution) affected the social behaviour of foraging animals: when bread was offered to house sparrows, *Passer domesticus*, the same amount of bread brought about more chirrup calls (and thus more joiners) when it was offered as (divisible) crumbs rather than as (indivisible) slices.

To empirically study how resource divisibility affects the interference process, we performed two runs of the same experiment with captive ruddy turnstones. We varied the divisibility of food in two so-called food pits by burying a fixed number of food items either in several layers (divisible) or in a single layer (indivisible). We composed food pits in such a way that the handling time and the reward were the same for divisible and indivisible food pits; we only varied the relationship between handling time and reward. To study the effect of forager density, we systematically compared the behaviour and the food intake of focal turnstones that foraged alone or with a competitor. We accounted for variation in the social dominance status of foragers by using pairs of birds as the basic unit of our experiment; each pair had both a dominant and a subordinate member. Additionally, we varied the distance between the two food pits, because a previous experiment indicated that interpit distance can be of prime importance; it may determine the extent to which resources can be monopolized, as we found in a field experiment on free-living turnstones (Vahl et al. 2007).

METHODS

Subjects

Thirty turnstones were caught with mist nets on an intertidal mudflat in the eastern Dutch Wadden Sea

(53°29'N, 6°15'E) on 15 October 2003. We housed these birds in the indoor experimental shorebird facility of NIOZ, Texel. Twenty-two individuals were selected to participate in pilot trials in which we determined the dominance hierarchy among the turnstones (8–12 March). Anticipating the experimental design, we selected 16 of these birds and grouped them in eight pairs of two. To make these 16 birds individually recognizable, we bleached a small (approximately 25 × 25 mm) area of their back feathers, using commercial hair bleach. After an extensive series of pilot trials (15 March–19 April), we conducted the first run of the experiment from 20 to 29 April, using all eight pairs. As one of the birds died during this run, we decided to perform the experiment a second time (3–6 May), using a selection of four of the seven remaining pairs. All selections were done with the use of a random number generator.

Nonexperimental and experimental turnstones were released in healthy condition on an intertidal mudflat in the Wadden Sea on 22 April and 12 May, respectively. At this time of the year, weather conditions are mild, food is ample, and there are plenty of turnstones around to join in migration to the breeding areas. Catching, housing and releasing occurred according to Dutch legislation (Dutch bird ringing centre license number 351 and Dutch animal ethics committee protocol 2004.01).

Housing

In the experimental facility the turnstones had two roosting aviaries (measuring 4.3 × 1.2 m and 3.0 m high) and an experimental room (7 × 7 m and 3.5 m high) at their disposal. A thin film of running sea water continuously covered the floors of the roosting aviaries to keep the feet of the birds salty and wet, and a tray of running freshwater for drinking and bathing was always present. On days on which no trials were performed trout feeding pellets were present ad libitum. The floor of the experimental room was covered by a 30-cm layer of sand, to mimic one of the natural habitats of turnstones. The indoor environment was approximately constant with respect to air temperature (range 12.3–19.0°C). Moonlight-mimicking lights illuminated the aviaries between 1900 and 0700 hours. A compact disk containing sea sounds ('Ocean Surf'; Solitudes Ltd., Toronto, Canada) was played continuously to buffer sudden noises from outside the aviaries.

Pre-experimental Treatment

On the first five pilot days, we determined the dominance hierarchy among the turnstones (for methods see Vahl et al. 2005a) on the basis of 930 agonistic interactions, which we collected in 36 trials. Interactions generally encompassed threat or attack behaviour of one individual and avoid or escape behaviour of another individual. Only occasionally these interactions would involve physical contact (one bird pecking the other); in no instance did such contact lead to visual physical harm. Although we would have been prepared to

intervene when either a bird was physically harmed, or when it was being exhausted by its opponent, such intervention was not required in any of the trials.

Knowledge of the dominance hierarchy enabled us to determine the relative rank of pair members independently of the experimental trials. As we paired the birds at random, the difference in absolute dominance position of pair members varied between pairs. Regardless of the difference in absolute dominance position, however, all pairs contained one (dominant) individual that consistently dominated its (subordinate) pair member. A previous experiment (Vahl et al. 2005a) revealed that the relative dominance status of foraging turnstones suffices to explain variation in the behaviour and intake rate of focal individuals. Therefore, we used this relative dominance status of the pair members to account for variation in dominance. Treating dominance status as a relative quality rather than as an (absolute) individual attribute (Francis 1988; Piper 1997) has the advantage that dominance status can be imposed upon the birds experimentally, and, thus, that confounding effects of characteristics that correlate with absolute dominance position can be minimized.

In 24 other pilot days, we familiarized the birds with the experimental set-up. On each of these pilot days, all birds performed one trial, either alone, or together with its pair member.

Experimental Set-up

On experimental days, we flooded the experimental room with sea water, such that the only places remaining dry were two elevated platforms (1 × 1 m each, located at constant positions, 3 m apart from each other). One of these platforms served as foraging patch; here we placed a tray (1 × 1 m and 10 cm deep) filled with sand. The other platform served as refuge: on this platform we only placed two layers of gravel tiles, to give both platforms the same height. Behaviour on the foraging patch was recorded using two digital video cameras (Sony DCR-TRV900E). One camera, positioned 1.75 m from the foraging patch, was set fixed to record the whole patch; the other camera, positioned 6 m from the foraging patch, was used to zoom on the forager(s) as much as possible.

The foraging patch always contained two identical food pits, which were positioned either 5 cm ('close') or 63 cm ('far') from each other. To manipulate the divisibility of the food in the pits while keeping all other aspects constant, the food pits had a very specific, standardized composition (Fig. 1). Food pits contained five defrosted mealworms, *Tenebrio molitor*, of approximately constant length (mean ± SD = 23.5 ± 1.7 mm; estimated on the basis of 50 measurements). Between trials, we varied the distribution of these mealworms within the two food pits; mealworms were positioned either in a clump, just below the deepest ring ('clustered'), or apart from each other, one below each ring ('layered'). We used rings to make the handling time per mealworm in the layered condition approximately constant; for the same reason we varied the amount of sand between rings (Fig. 1). This specific

set-up ensured that both the number of mealworms (the total reward) and the time to find all mealworms (the total handling time) were the same for clustered food pits as for layered food pits. What varied was the relationship between handling time and reward (the reward function); when the within-pit food distribution was layered, reward cumulated throughout the handling process, whereas when it was clustered, all reward was received at the end of the handling process.

In composing the food pits, we were inspired by the foraging situation of turnstones foraging in Delaware Bay, U.S.A., where turnstones regularly have to dig for their main food source (Sullivan 1986). Although we are not aware of any comparable foraging situation along the East Atlantic flyway, the experimental birds learned to dig for their food within days. In doing so, they did not seem to be bothered by the glass cups. Moreover, it took only few days before most of the experimental birds could skilfully remove the metal rings out of the cups by putting their bill in the hole of the metal rings and then tossing them up. The turnstones were keen to eat the mealworms, even though mealworms are not part of their natural diet (e.g. Fuller 2003).

Experimental Procedure

In the first run of the experiment, we deprived the birds of food from 1500 hours and tested them between 0900 and 1300 hours on the following day. After all trials had been performed, we weighted all birds and we visually checked their condition. Between 1300 and 1500 hours, we provided trout feeding pellets ad libitum as well as some extra mealworms. The length of the deprivation period and the amount of extra mealworms were chosen such that the birds were maximally motivated to forage in the experimental trials, maintained good condition and stayed within their natural weight (range 84–190 g; del Hoyo et al. 1996).

On experimental days, members of the same pair together awaited trials in boxes (measuring 50 × 35 cm and 25 cm high) that were placed in a dark room to minimize stress. At the start of each trial, we transferred either one ('competitor absent') or two ('competitor present') specific birds to one of the roosting aviaries. After opening a sliding door, we attracted the birds into the experimental room by dimming the lights in the roosting aviary whilst lighting the experimental room. Subjects readily flew to the experimental platform and started to dig in the food pits within seconds of the sliding doors being opened. The trials started at the moment the first bird began to forage, and then lasted till 30 s after the 10th mealworm had been consumed, or after 600 s had passed, whichever came first. After each of the birds had performed its trial, we put all birds together in the experimental room and the two roosting aviaries, with sliding doors open and water level low (so that birds could also use the sandy spaces between the raised platforms).

In the second run of the experiment the same procedure was followed, but now there were two experimental sessions per day: one between 0900 and 1200 hours and

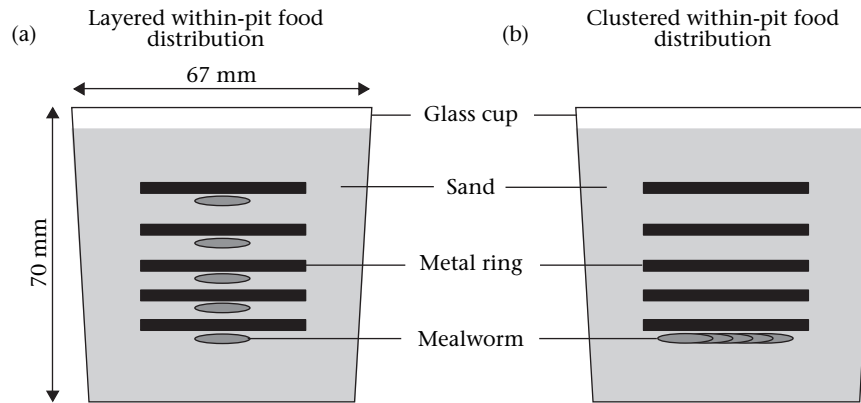


Figure 1. Schematic representation of two food pits. Each food pit consisted of a glass cup, buried in the sediment and filled with a constant amount of sand (12 spoons of 12 cm³); the upper 4 mm of each glass cup remained empty. Each cup contained five metal rings (inner and outer diameter: 13 and 36 mm, respectively), which were positioned at fixed depths, separated from each other by a fixed amount of sand (4, 1, 1, 1, 2, 3 spoons from the bottom upwards; this distribution kept the amount of sand that had to be removed per metal ring effectively constant, given that some sand covering the higher rings fell on the lower rings). Each cup contained five mealworms, which were either positioned apart from each other, one below each ring (layered: a), or in a cluster, just below the deepest ring (clustered: b).

the other between 1300 and 1500 hours. In this run of the experiment birds were deprived of food from 1700 hours on the day preceding an experimental day.

Video Analysis and Recorded Behaviour

The same two observers (W.K.V. & S.A.K.) examined all trials together, using The Observer 4.1 Event Recorder (Noldus Information Technology, Wageningen, The Netherlands). Per trial, we recorded all prey captures within 600 s, noting both food pit and finder. For the first 120 s, we additionally recorded in detail the whereabouts of the foragers (i.e. whether they were on the one food pit, on the other, on the foraging platform or elsewhere), as well as their behaviour. Most importantly, we determined the amount of time the turnstones were 'interacting', that is, either 'fighting' (both foragers behave aggressively), 'threatening' (the aggressor does not approach its opponent), 'attacking' (the aggressor does move towards its opponent), 'avoiding' (in response to a threat) or 'escaping' (in response to being attacked).

Experimental Design and Statistical Analysis

We studied the effect of four fixed factors: competitor presence (absent, 0; or present, 1), within-pit food distribution (both food pits clustered or both food pits layered), interpit distance (close or far) and dominance status (dominant or subordinate). As it is difficult to assign both levels of the factor dominance status to an individual bird, we decided to use pairs of birds, rather than individual birds, as the basic unit of our experiment. We estimated treatment effects that were independent of the factor dominance status by running a test on the sum of the response of pair members (which yields identical results as using the average response), and we estimated treatment effects that were dependent on the factor dominance status by running the same test on the

difference in response of pair members. This approach is identical to that used in a split-plot design with dominance status as a within-plot factor.

In both runs of the experiment, we accounted for effects of the random block factors bird pair, and experimental day by using a Latin square design (Fisher & Yates 1963) to distribute the treatment combinations (of competitor presence, within-pit food distribution and interpit distance) over trials. At the 'competitor absent' treatments, the two members of a pair performed a trial separately, one directly after the other. In the first run of the experiment, we had eight bird pairs and eight treatment combinations ($2 \times 2 \times 2$), so that we could use an 8×8 Latin square design. In the second run of the experiment, we could no longer use eight bird pairs (one of the birds had died). Therefore, we decided to use a 4×4 Latin square design to distribute the four treatment combinations of competitor presence and within-pit food distribution over four bird pairs and four experimental days. To additionally estimate the effect of interpit distance, we introduced morning and afternoon sessions. Each bird pair performed the same trial twice on a single day, once at each interpit distance; the two levels of interpit distance were assigned randomly to either the morning or the afternoon session. Thus, to study effects of interpit distance in the second run of the experiment, we used a split-plot design with experimental day and interpit distance as whole-plot factors.

Much of the foraging literature is phrased in terms of intake rate, that is, the number of prey items ingested per unit time. Because the experimental treatment factors affected both components of this ratio, we studied treatment effects on trial duration (s), and intake (number) separately, whereby we defined intake as the number of mealworms swallowed in a trial. To detect the mechanisms underlying any effects on trial duration and intake, we additionally studied effects on the time spent on food pits (%), and the time spent interacting (%). These latter two responses are expressed as a percentage of the trial

duration (censored at 120 s), whereby time spent on empty food pits is excluded.

Missing values and their treatment

As one of the experimental birds died in the middle of the first run of the experiment, we had four missing values: three at the 'competitor absent' treatment and one at the 'competitor present' treatment. Therefore, we had in total 60 rather than 64 paired observations on the eight bird pairs. Following Yates (1933), we replaced these missing values and we adjusted the degrees of freedom in all tests correspondingly. All 32 paired observations of the second run of the experiment were successful.

Foragers were not able to find all 10 mealworms within 600 s in 11 trials. In presenting treatment effects on trial duration, we first verbally report on the 11 censored trials, and we then present the data and statistics on the uncensored trials.

Data transformation and hypothesis testing

We analysed both runs of the experiment using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL, U.S.A.). The two runs of the experiment were not independent of each other; birds featuring in the second run of the experiment had also featured in the first run. Nevertheless, we analysed the two runs separately, to account for differences in their experimental design. This approach introduces the risk of pseudoreplication. We consider this risk of minor concern because we performed the second run of the experiment to support rather than to generalize findings of the first run. We analysed the first run of the experiment according to the standard Latin square design. The second run of the experiment was analysed according to the standard split-plot design, with experimental day and interpit distance as whole-plot factors.

We assumed that the treatment factors had a multiplicative effect on trial duration and intake. Because general linear models assume treatment effects to interact in an additive way, we log-transformed all observations on these two response variables. To avoid taking logarithms of zero, we added the values of 0.12 and 0.25 to observations on the number of mealworms swallowed in the first and second runs of the experiment, respectively; these specific values were chosen because they minimized the effect of unusual observations (Berry 1987). As time spent on food pits and time spent interacting both comprise percentages, we applied a Freeman and Tukey's arcsine transformation to all observations on these two responses; more specifically, we applied the slightly modified version given by Zar (1996, page 283). For all four response variables, we first performed the transformation, and we then calculated the sum and the difference of observations on dominant and subordinate foragers. Visually inspection of probability plots (Miller 1997) indicated that model residuals of intake, time spent on food pits and time spent interacting were not normally distributed, not even after transformation. Therefore, we repeated the analyses on these three response variables using a randomization test to study the likelihood of our data (Manly 1997). As

randomization results were almost identical to the GLM results, only the latter were presented.

RESULTS

Trial Duration

Foragers were not able to find all 10 mealworms within 600 s in 10 trials (16.7%) of the first run of the experiment and in one trial (3.1%) of the second run of the experiment. The foragers that did not find 10 prey items were all foraging alone; most of them were subordinate individuals (10 out of 11 cases), foraging at food pits that were far apart (seven out of 11 cases) and in which food items were clustered (eight out of 11 cases).

Trials in which all 10 food items were found generally lasted longer for birds in the first run of the experiment than for birds in the second run of the experiment ($\bar{X} \pm SD = 151.5 \pm 152.3$ s, $N = 118$ versus 109.9 ± 119.3 s, $N = 63$). In both runs of the experiment, birds foraging alone needed more time to find all 10 mealworms than birds foraging together with a competitor (186.5 ± 169.6 s, $N = 85$ versus 93.2 ± 95.1 s, $N = 96$), and when foraging alone, subordinate birds needed more time than dominant birds (243.1 ± 179.6 s, $N = 38$ versus 140.8 ± 147.7 s, $N = 47$). Statistically, these effects are indicated by the interaction between competitor presence and dominance status ($A \times D$), which was significant in both runs of the experiment (Tables 1 and 2). These observations suggest that the birds became more skilful throughout the experiment, and that subordinate birds were less skilled in finding the food than dominant individuals, even when foraging alone.

Intake

In both runs of the experiment, birds foraging together with a competitor achieved a lower intake than birds that foraged alone (Fig. 2). The strength of this competition effect differed markedly between dominant and subordinate individuals; under most conditions dominant foragers got almost as many of the food items when foraging in the presence of a competitor as when foraging alone, whereas subordinate birds found only few of the food items when foraging together with a competitor. This effect was especially apparent in the second run of the experiment. How much subordinate birds suffered from competition depended on the distribution of food within food pits and on the distance between food pits. In the first run of the experiment subordinate foragers got more mealworms when the within-pit food distribution was layered than when it was clustered, and also when food pits were placed far apart rather than close to each other. In the second run of the experiment, subordinate birds foraging in the presence of a competitor only got some mealworms when food pits were far apart and when the within-pit food distribution was layered. In line with these observations, there was a significant interaction between the within-pit food distribution and dominance status ($B \times D$), and between competitor presence, interpit distance and dominance status ($A \times C \times D$) in the first run of the

Table 1. Treatment effects on the response variables of the first run of the experiment*

	Trial duration (s)			Intake (no.)			Time spent on food pits (%)			Time spent interacting (%)		
	<i>df</i>	SS	<i>F</i>	<i>df</i>	SS	<i>F</i>	<i>df</i>	SS	<i>F</i>	<i>df</i>	SS×10 ⁻²	<i>F</i>
dom+sub												
Constant	1	674.3		1	116.7		1	263.0		1	1159.7	
Bird pair	7	12.6		7	5.2		7	1.3		7	28.0	
Day	7	5.0		7	1.1		7	0.3		7	12.7	
A	1	3.4	30.0	1	15.8	90.1	1	7.3	148.8	—	—	
B	1	0.1	1.3	1	1.3	7.6	1	0.0	0.2	1	1.6	1.0
C	1	0.0	0.2	1	1.1	6.4	1	0.8	17.0	1	6.7	4.1
A*B	1	0.0	0.4	1	0.0	0.0	1	0.2	4.7	—	—	
A*C	1	0.8	7.1	1	1.4	7.7	1	1.0	20.3	—	—	
B*C	1	0.0	0.0	1	0.0	0.2	1	0.0	0.0	1	0.8	0.5
A*B*C	1	0.3	2.3	1	0.0	0.0	1	0.0	0.2	—	—	
Error	28	3.6		38	7.4		38	2.1		13	22.7	
Total	50	25.0		60	33.3		60	13.0		31	67.0	
dom-sub												
D	1	0.8	5.5	1	17.9	68.4	1	2.7	47.2	1	25.6	43.3
Bird pair*D	7	2.8		7	9.6		7	0.7		7	7.8	
Day*D	7	1.1		7	0.9		7	0.3		7	6.2	
A*D	1	1.2	7.8	1	8.7	33.2	1	3.8	68.2	—	—	
B*D	1	0.0	0.1	1	1.9	7.3	1	0.1	1.5	1	0.5	0.8
C*D	1	0.0	0.1	1	2.5	9.7	1	1.2	21.4	1	10.9	18.4
A*B*D	1	0.0	0.0	1	0.0	0.1	1	0.0	0.0	—	—	
A*C*D	1	0.0	0.0	1	3.0	11.3	1	1.7	30.1	—	—	
B*C*D	1	0.0	0.0	1	0.0	0.1	1	0.0	0.3	1	0.0	0.0
A*B*C*D	1	0.0	0.1	1	0.0	0.0	1	0.0	0.2	—	—	
Error	28	4.7		38	11.0		38	2.4		13	8.3	
Total	50	9.2		60	37.7		60	10.2		31	30.8	

*Given are GLM results of the treatment factors competitor presence (A), within-pit food distribution (B), and interpit distance (C) on the responses of dominant and subordinate pair members, after these were log-transformed (trial duration and intake) or arcsine-transformed (time spent on food pits and time spent interacting). Treatment effects independent of the foragers' dominance status (D) were found by using the sum of the response of both pair members ('dom + sub'; upper half), whereas treatment effects that depended on this factor were found by using the difference in the response of dominant and subordinate pair members ('dom - sub'; lower half). Effects significant at the 0.05 level are indicated by bold *F* values.

experiment, and between all four factors (A*B*C*D) in the second run of the experiment (Tables 1 and 2).

Time Allocation

Foragers differed markedly in the time they spent on the food pits (Fig. 3). Dominant individuals spent about the same amount of time on food pits under all conditions. Subordinate birds also spent about the same amount of time on food pits under all conditions when they were foraging alone. When subordinate birds were foraging in the presence of their dominant pair member, they spent much less time on food pits when these were far from each other than when these were close to each other, regardless of the within-pit food distribution. This effect was especially apparent in the second run of the experiment, in which subordinate individuals hardly spent any time on the food pits at all. Statistically, this effect is reflected on the interaction term among competitor presence, dominance status and interpit distance (A*C*D), which was significant in both runs of the experiment (Tables 1 and 2). As time spent on food pits was highly correlated with the time

spent digging for food (Pearson correlation coefficient: $r = 0.98$, $t_{192} = 68.2$, $P < 0.001$), variation in the time spent on food pits explains at least partly why dominant foragers found many food items compared to subordinate foragers when food pits were close to each other; apparently, dominant birds were able to monopolize the food pits under this condition.

Depending on the distance between the food pits, foragers also differed in the time they spent interacting (Fig. 4). When food pits were far apart, dominant and subordinate foragers spent about the same amount of time on interactions, regardless of the within-pit food distribution; what generally happened under this condition was that both foragers occupied a food pit until the dominant forager decided to supplant its subordinate competitor from the food pit; sometimes this happened because the dominant forager had emptied its own food pit, but this was not always the case. Such supplant interactions took about the same time for dominant and subordinate foragers. Sometimes, however, the subordinate forager was the first to leave its food pit (even though this food pit was not empty yet) in an attempt to join its dominant competitor. Joining, however, was never tolerated so that the

Table 2. Treatment effects on the response variables of the second run of the experiment*

	Trial duration (s)			Intake (no.)			Time spent on food pits (%)			Time spent interacting (%)		
	df	SS	F	df	SS	F	df	SS	F	df	SS×10 ⁻²	F
dom+sub												
Whole plot												
Constant	1	405.9		1	59.5		1	126.0		1	513.7	
Day	3	1.0		3	0.0		3	0.1		3	20.5	
C	1	0.2	0.3	1	0.1	4.7	1	0.7	330.2	1	0.5	0.5
Error	3	1.5		3	0.1		3	0.0		3	3.5	
Subplot												
Bird pair	3	6.1		3	0.1		3	0.1		3	19.8	
A	1	5.5	33.0	1	13.1	648.1	1	4.6	62.7	—	—	—
B	1	1.0	5.7	1	0.9	44.3	1	0.0	0.3	1	0.6	0.5
A*B	1	0.1	0.5	1	0.7	35.2	1	0.1	1.1	—	—	—
A*C	1	0.6	3.5	1	0.2	11.6	1	0.7	9.6	—	—	—
B*C	1	0.3	1.5	1	0.2	11.6	1	0.1	1.6	1	3.8	3.1
A*B*C	1	0.5	2.7	1	0.1	7.2	1	0.0	0.0	—	—	—
Error	14	2.3		15	0.3		15	1.1		3	3.7	
Total	31	17.4		32	15.9		32	7.4		16	38.2	
dom-sub												
Whole plot												
D	1	1.5	229.5	1	12.2	294.1	1	1.7	49.3	1	23.5	15.7
Day*D	3	0.5		3	0.0		3	0.3		3	4.2	
C*D	1	0.0	1.9	1	0.3	7.1	1	0.8	23.3	1	10.2	6.8
Error	3	0.0		3	0.1		3	0.1		3	4.5	
Subplot												
Bird pair*D	3	1.5		3	0.1		3	0.1		3	9.1	
A*D	1	1.5	12.9	1	11.5	419.0	1	3.6	71.2	—	—	—
B*D	1	0.0	0.3	1	1.4	49.9	1	0.1	1.0	1	0.6	0.2
A*B*D	1	0.0	0.3	1	1.1	41.5	1	0.1	2.1	—	—	—
A*C*D	1	0.0	0.1	1	0.4	15.1	1	0.4	8.1	—	—	—
B*C*D	1	0.0	0.0	1	0.4	15.1	1	0.1	2.3	1	0.1	0.0
A*B*C*D	1	0.0	0.0	1	0.3	10.7	1	0.1	1.1	—	—	—
Error	14	1.6		15	0.4		15	0.8		3	7.9	
Total	31	5.1		32	16.1		32	6.5		16	33.9	

*Interpretation as Table 1.

subordinate bird could but resume foraging at the food pit that it had left. When the food pits were close to each other, subordinate individuals spent more time on interactions than did the dominant forager. As when food pits were far apart, this effect was independent of the within-pit food distribution. What generally happened under this condition was that the subordinate forager attempted to reach the food pits, evoking a threatening behaviour of the dominant forager, which occupied one of the food pits, but monopolized both. Such monopolization interactions were short for dominant foragers, which only had to lift their head and threat, whereas they took considerably longer for subordinate birds, which had to run away from their dominant competitor. Although this pattern of time allocation to interactions was comparable between the two runs of the experiment, the interaction term between dominance status and interpit distance ($C*D$) was only significant in the first run of the experiment (Tables 1 and 2). Albeit being nonsignificant in the second run of the experiment, this interaction term explained considerable variation in both runs of the experiment, as indicated by the sum of squares (SS) and the variance ratios (F).

DISCUSSION

The divisibility of food clumps affected the share of the mealworms going to either of the pair members; subordinate birds foraging in the presence of a competitor were more likely to get some mealworms when these were offered in several layers than when these were placed in a single layer at the bottom of food pits. This effect was not due to subordinate birds spending more time on the food pits when food was offered in layers, nor to the loss of time spent interacting under the clustered condition. Rather, it resulted from subordinate birds getting some reward prior to being chased of a food pit by their dominant competitor at the layered within-pit food distribution. Subordinate birds that were supplanted from food pits in which food was clustered got nothing, even though they sometimes spent a considerable amount of time digging. The most extreme illustration of this was found in the second run of the experiment, where subordinate birds, foraging at food pits that are far apart and at food that is clustered within food pits, spent about 50% of their time on food pits but got none of the

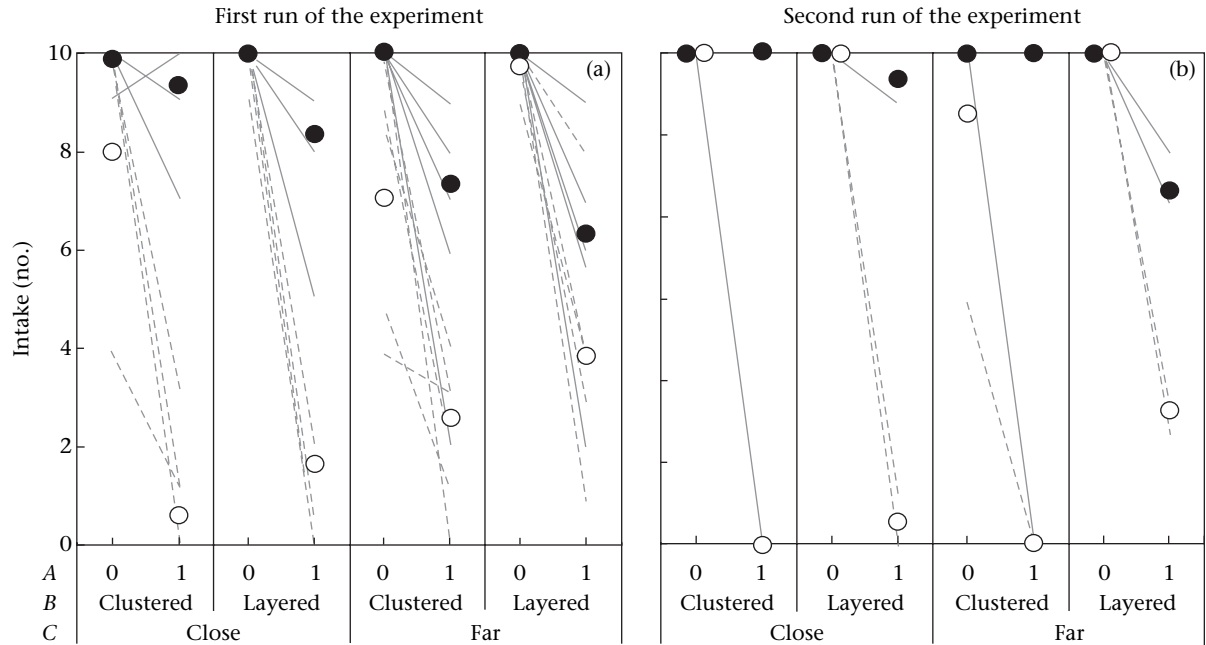


Figure 2. The intake of the turnstones in the first (a) and the second (b) run of the experiment. Each graph contains four compartments, one for each combination of the factors within-pit food distribution and interpit distance (A, competitor; B, within-pit food distribution; C, interpit distance; D, dominance status: ●, dominant average; ○, subordinate average; —, dominant individual; - - - subordinate individual). To give an example, the left-most compartment of both graphs presents the intake of focal turnstones foraging at the 'clustered' within-pit food distribution and the 'close' interpit distance. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on intake; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual, but only within compartments.

mealworms. A similar mismatch between time investment and intake was reported by Di Bitetti & Janson (2001), who observed that subordinate capuchin monkeys, *Cebus apella*, consumed only a small percentage of the

experimentally offered resources, even though they discovered a high percentage of the feeding platforms.

In addition to the within-pit distribution of mealworms, the distance between the food pits also affected the

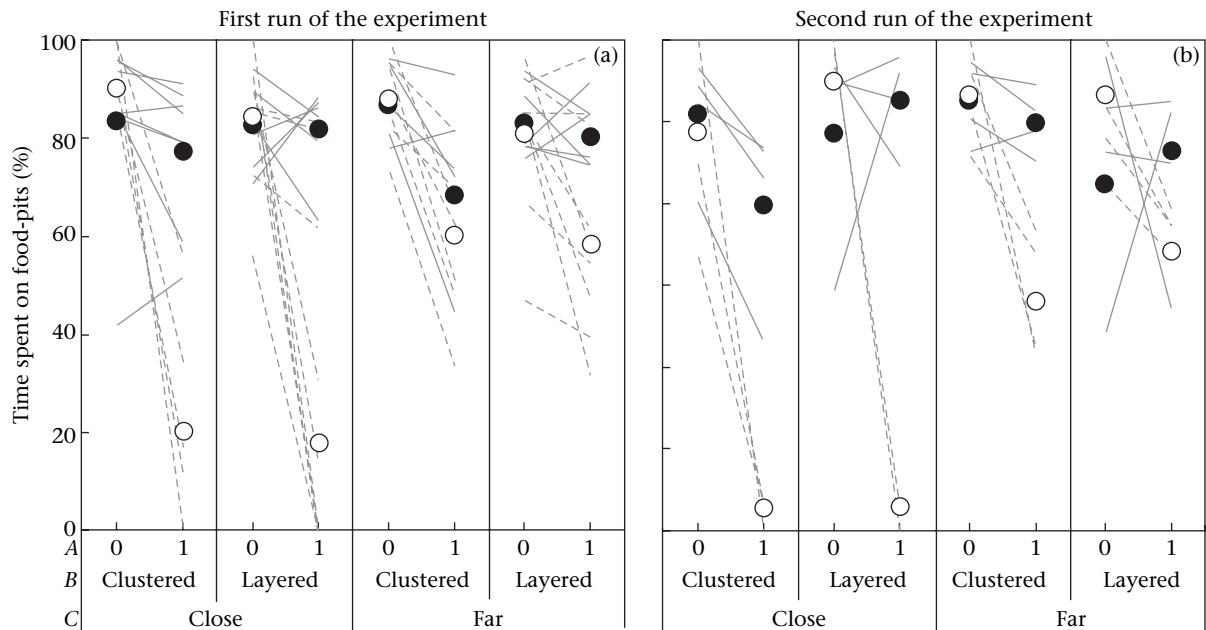


Figure 3. The time spent on food pits in the first (a) and the second (b) run of the experiment. Like in Fig. 2, each graph contains four compartments, as indicated in the legend of Fig. 2. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on the time spent on food pits. Dots represent averages per treatment combination, and thin grey lines connect observations on the same individual within each compartment.

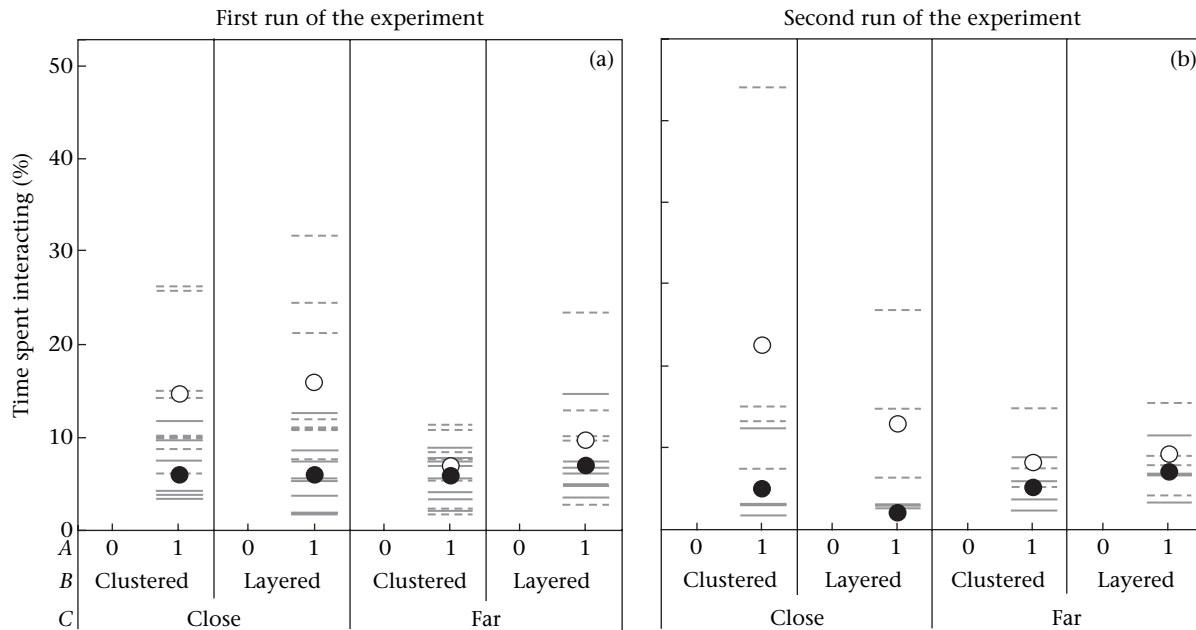


Figure 4. The time turnstones spent interacting in the first (a) and the second (b) run of the experiment. Like in Fig. 2, each graph is composed of four compartments as indicated in the legend of Fig. 2. Within each compartment, a distinction is made between the absence (0) or presence (1) of a competitor (for conformity with other graphs). Note that interactions occur only when a competitor is present. Dots represent averages per treatment combination, whereas thin grey lines indicate observations on individuals.

distribution of mealworms over the members of a pair. Only when the two food pits were close to each other could dominant turnstones monopolize both of them. This finding is in line with most experiments on the effect of the spatial distribution of food (see Vahl et al. 2005a). What our experiment additionally shows, however, is that the effect of the divisibility of the food pits may interact with the spatial distribution of the food pits. Subordinate birds got more mealworms when food pits were divisible than when food pits were indivisible, but especially so when food pits were far apart. When food pits were close to each other, dominant foragers could monopolize them, so that subordinate foragers got even fewer food items. This effect was most pronounced in the second run of the experiment, in which the monopolization of food pits that were close to each other was so strong that subordinate foragers could not even get a share of the food when food pits were divisible.

The most striking result of our experiment, however, was the large and consistent difference in the intake of dominant and subordinate foragers. By no means was the effect of the presence of a competitor general for foragers of different dominance status; under some conditions the presence of a competitor had no effect on the intake of dominant foragers, but a very strong negative effect on the intake of subordinate foragers. This result is striking especially because we assigned the birds a social dominance status at random, so that subordinate members of some pairs had a higher dominance ranking (i.e. they were more dominant in terms of their absolute position in the dominance hierarchy) than the dominant members of other pairs. Apparently, knowledge of the relative dominance status suffices to explain much of the variation in

the behaviour and the intake of interacting birds. We reached the same conclusion in a previous experiment (Vahl et al. 2005a).

Learning

Throughout the experiment, the turnstones improved their foraging skills, as was apparent from the shorter duration of trials in the second run of the experiment. We tried to prevent the birds from changing their behaviour during the experiment by performing a considerable number of pilot trials, but apparently we did not succeed. In principle, a change in foraging skills is unwanted because it adds variation to the data, which may blur effects of the experimental factors. Within the two runs of our experiment, however, the change in foraging skills will probably not have affected our treatment estimates, because the block factor experimental day in the Latin square design controlled for any time-related confounding. Differences between birds at the start of our experiment and differences between the two runs of our experiment, on the contrary, may have been due to changes in the birds' foraging skills. In fact, we think that the change in foraging skills explains at least two of our findings.

First, subordinate birds were less successful in finding all 10 mealworms and they needed more time to find the mealworms than dominant birds, even when foraging alone. This is surprising as we assigned birds a dominance status at random, so that there should be no intrinsic differences between the subordinate and dominant individuals. The most likely explanation for this difference

in foraging skills is that subordinate birds were already excluded from the food pits in pilot trials in which they foraged together with their dominant competitor. This would imply that although subordinate and dominant individuals performed the same number of pilot trials, subordinate birds effectively got less experience in handling the food pits, because these were excluded from the food pits in half of the pilot trials. From this explanation it becomes apparent that dominance status and foraging skills may well be interrelated.

Second, subordinate birds foraging together with a competitor got no food at all from clustered food pits in the second run of the experiment, whereas they got some in the first run. This difference probably arose because dominant birds learned to first empty one food pit before supplanting their subordinate competitor from the other. As dominant birds were quicker to find food than subordinate birds, they could empty one food pit and supplant their subordinate competitor before this competitor had reached the food, so that the dominant bird managed to get all the resources. This explanation illustrates that the foraging skills of dominant birds *relative* to those of subordinate birds may be of prime importance to the interference process.

Links to theory

Few models have considered how divisibility of food affects interference competition among foraging animals. At least two models, however, seemingly resemble our experiment closely.

Stevens & Stephens (2002) study the optimal level of harassment for beggars (i.e. nonfood owners) and the optimal level of sharing (i.e. joint use of a monopolizable food source) tolerated by food owners, and they consider how predicted behaviour depends on the divisibility of the food. Their model predicts that beggars should always harass when there are benefits to harassment even when owners do not share. Owners should only share when beggars harass and when the efficiency of consumption when harassed is low. Food divisibility does not affect the behaviour of beggars, but owners should raise the proportion of the food shared when food is divisible. In our experiment, we found harassment but no sharing, regardless of the within-pit food distribution.

Broom & Ruxton (2003) addressed the effect of food divisibility through a study of the consequences of differences in prey type on kleptoparasitism. They either assumed that food was consumed throughout the handling process (the 'apple model'), or that food could only be consumed at the end of the handling process (the 'orange model'). This difference in prey type profoundly affected the extent to which foragers were found to suffer from interference competition: while an increase in, for instance, forager density, per capita prey handling time, or per capita fighting time resulted in an increase in the number of aggressive encounters in the apple model, an increase in either of the variables resulted in a decrease in the amount of aggressive interactions in the orange model. We did not find such effects of the within-pit food distribution on the amount of aggressive interactions.

Direct comparison of predictions from these two models with our experimental results, however, is not possible for at least two reasons. First, several of the model parameters cannot be determined experimentally (Stevens & Stephens 2002: e.g. the intensity of harassment, and the factor that measures the noncontingent benefits of harassment; Broom & Ruxton 2003: e.g. the encounter rate of competitors, and the probability of attack upon encounter). Second, several of the assumptions of these models are not met by our experimental system. Most notably, turnstones are not all identical; they differ strongly in their relative dominance position.

CONCLUSIONS

Interference competition was expressed mainly as an asymmetry in the distribution of food over foragers of different dominance status. The strength of this asymmetry depended on the distance between food pits, because dominant foragers could monopolize food pits only when these were close to each other, as we also found in a previous experiment (Vahl et al. 2005a). In addition, however, the skew in resource distribution between dominant and subordinate pair members depended on the divisibility of food, because subordinate foragers got a share of the food only when resources were divisible. As the second run of the experiment showed, the effect of the distance between food pits and of resource divisibility can sometimes interact. These results imply that for the interference process it matters whether foragers are interacting over food items or over food clumps, because food clumps can be split over multiple foragers more easily than can food items. The overriding effect of the social dominance status of foragers shows that when interference competition results from the monopolization of resources, differences in dominance status are of crucial importance to understand and predict the interference process.

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