CHAPTER 5

FOOD DIVISIBILITY AND INTERFERENCE COMPETITION AMONG CAPTIVE RUDDY TURNSTONES (*ARENARIA INTERPRES*)

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SUBMITTED TO ANIMAL BEHAVIOUR

ABSTRACT

Interference competition among foraging animals arises from agonistic interactions between 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 between 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 (*Arenaria interpres*). 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 the 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 finder's advantage; 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.

INTRODUCTION

Interference competition among foraging animals is the negative effect of forager density on intake rate that results from interactions between foragers (Miller 1967). 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) 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 (for references: 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 how we think about interference competition. By definition, food clumps differ from food items in that they are composed 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 invested 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. Recently, Broom & Ruxton (2003) used a Hawk-Dove game to address the effect of resource divisibility; they compared a model in which resources were consumed throughout the handling process (the 'apple model') with a model in which resources were consumed at the end of the handling process (the 'orange model'). The extent to which resources can be divided differs between these two models; in the apple model each handler gets a proportional part of the resource, whereas in the orange model the whole reward goes to a single (the last) handler. This difference in resource divisibility profoundly affected the extent to which foragers were found to suffer from interference competition: while the relationship between aggressiveness and forager density was positive in the apple model, this relationship was negative in the orange model.

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 (for a review: 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 (*Arenaria interpres*). 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 was 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 inter-pit 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. submitted).

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 to 12 March). Anticipating the experimental design, we selected sixteen of these birds and grouped them in eight pairs of two. To make these sixteen birds individually recognizable, we bleached a small (approximately 25 x 25 mm) area of their back feathers, using commercial hair bleach. After an extensive series of pilot trials (15 March to 19 April), we conducted the experiment from 20 to 29 April, using all eight pairs. As one of the birds died during this experiment, we decided to perform the experiment a second time (3 to 6 May), using a selection of four of the seven remaining pairs. All selections were done with the use of a random number generator. Non-experimental and experimental turnstones were released 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, respectively).

HOUSING

In the experimental facility the turnstones had two roosting aviaries (measuring 4.3 x 1.2 m and 3.0 m high) and an experimental room (7 x 7 m and 3.5 m high) at their disposal. A thin film of running seawater 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 h. A compact disc 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 dominancy 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. 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).

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 seawater, such that the only places remaining dry were two elevated platforms (1 x 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 x 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 in the 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 (Figure 5.1). 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 for mealworm in the layered condition approximately constant; for the same reason we varied the amount of sand between rings (Figure 5.1). 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) was 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; Vahl et al. submitted). 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

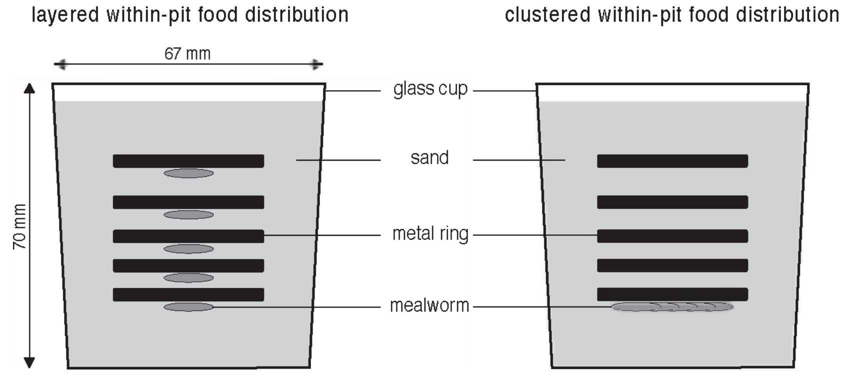

Figure 5.1. Schematic representation of two food pits. Each food pit consisted of a glass cup, buried in the sediment and filled with a constant amount of sand (12 spoons of 12 cm3); the upper 4 mm of each glass cup remained empty. Each cup contained five metal rings (inner and outer diameter: 13 and 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; left drawing), or in a cluster, just below the deepest ring (clustered; right drawing).

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 h and tested them between 0900 and 1300 h on the following day. After all trials had been performed, we weighed all birds and we visually checked their condition. Between 1300 and 1500 h, 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 x 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 tenth 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 h and the other between 1300 and 1500 h. In this run of the experiment birds were deprived of food from 1700 h on the day preceding an experimental day.

VIDEO ANALYSIS AND RECORDED BEHAVIOUR

The same two observers (WKV & SAK) 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), Inter-pit 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 of 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 Inter-pit 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 x 2 x 2), so that we could use an 8 x 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 x 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 Inter-pit distance, we introduced morning and afternoon sessions. Each bird pair performed the same trial twice on a single day, once at each inter-pit distance; the two levels of Inter-pit distance were assigned randomly to either the morning or the afternoon session. Thus, to study effects of Inter-pit distance in the second run of the experiment, we used a split-plot design with Experimental day and Inter-pit distance as whole-plot factors.

We studied treatment effects on trial duration (s), intake (#) and intake rate ($\#s^{-1}$), whereby we defined intake as the number of mealworms swallowed in a trial, and intake rate as the ratio of intake to trial duration. To detect the mechanisms underlying any effects on trial duration, intake and intake rate, 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 8 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 ten 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. In calculating intake rate we did not make this distinction.

DATA TRANSFORMATION AND HYPOTHESIS TESTING

We analysed both runs of the experiment using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL). 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 days and Inter-pit distance as whole plot factors.

We assumed that the treatment factors had a multiplicative effect on trial duration, intake and intake rate. Because general linear models assume treatment effects to interact in an additive way, we log-transformed all observations on these three 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 run 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). For all five 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 randomisation test to study the likelihood of our data (Manly 1997). As randomisation results were almost identical to the GLM results, only the latter are presented.

RESULTS

TRIAL DURATION

Foragers were not able to find all ten mealworms within 600 s in ten 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 ten prey items were all foraging alone; most of them were subordinate individuals (10 out of the 11 cases), foraging at food pits that were far apart (7 out of 11 cases) and in which food items were clustered (8 out of 11 cases).

Trials in which all ten 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 (X ± SD: 151.5 ± 152.3 s, N = 118 versus 109.9 ± 119.3 s, N = 63; Figure 5.2). In both runs of the experiment, birds foraging alone needed more time to find all ten mealworms than birds foraging together with a competitor, and when foraging alone, subordinate birds needed more time than dominant birds. Statistically, this result is indicated by the interaction between Competitor presence and Dominance status (A x D), which was significant in both runs of the experiment (Table 5.1 & 5.2). 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.

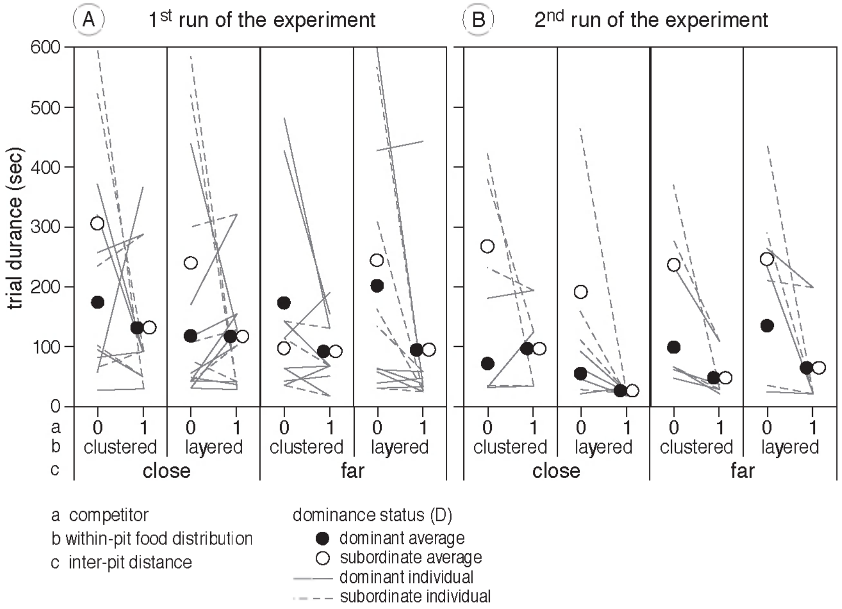

Figure 5.2. The duration of trials in which all ten food items were found in the first (a) and the second (b) run of the experiment. Each graph contains four compartments, one for each combination of the factors Within-pit food distribution and Inter-pit distance, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on the duration of trials; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual, but only within compartments. Note that by definition, trials last as long for subordinate birds as for dominant birds when they forage together (i.e., at the 'Competitor presence 1' condition).

INTAKE

In both runs of the experiment, birds foraging together with a competitor achieved a lower intake than birds that foraged alone (Figure 5.3). 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

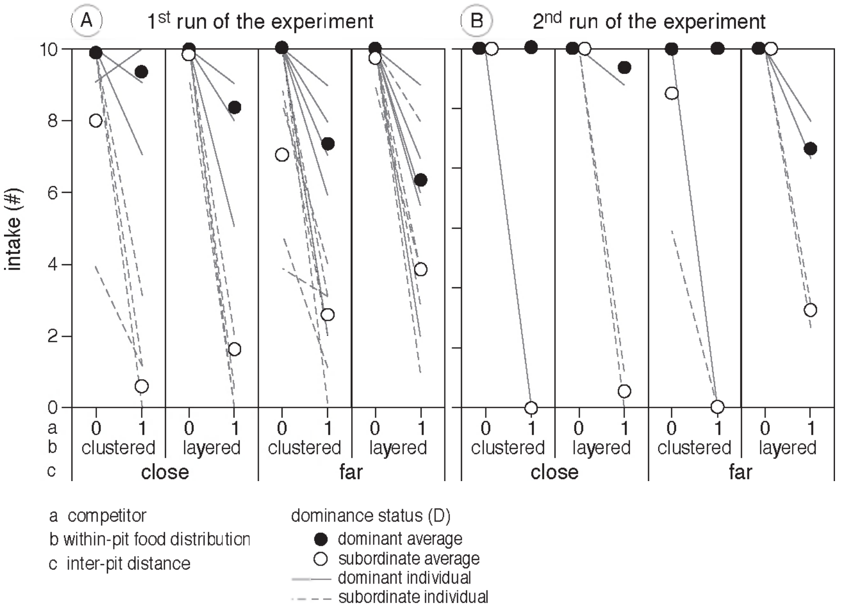

Figure 5.3. The intake of the turnstones in the first (a) and the second (b) run of the experiment. Like in Figure 5.2, each graph contains four compartments, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on intake; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual within each compartment.

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 x D), and between Competitor presence, Inter-pit distance and Dominance status (A x C x D) in the first run of the experiment, and between all four factors (A x B x C x D) in the second run of the experiment (Table 5.1 & 5.2).

INTAKE RATE

Effects on intake rate, the ratio of intake to trial duration, were less straightforward than effects on either intake or trial duration separately (Figure 5.4); treatment effects on intake rate different between the two runs of the experiment and effects varied much between bird pairs. In the first run of the experiment, dominant foragers on average achieved the same intake rate when forag-

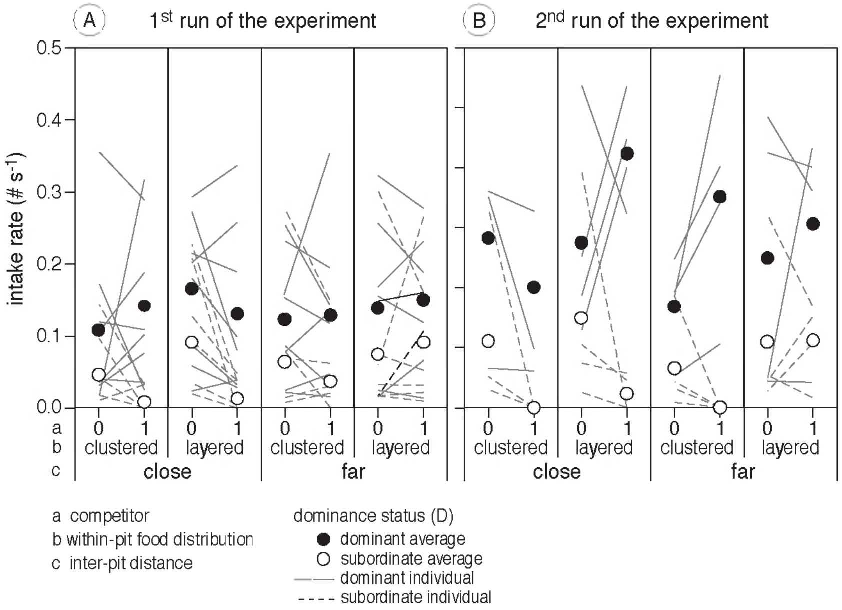

Figure 5.4. The intake rate of the turnstones in the first (a) and the second (b) run of the experiment. Like in Figure 5.2, each graph contains four compartments, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on intake rate; dots represent averages per treatment combination. Thin grey lines connect observations on the same individual within each compartment.

ing alone as when foraging together with a competitor, whereas subordinate birds the presence achieved a lower intake rate when foraging with a competitor, especially when food pits were close to each other. In the second run of the experiment, effects on the intake rate of subordinate birds were comparable to those found in the first run of the experiment, but effects on the intake rate of dominant foragers were quite different: dominant birds generally achieved a higher intake rate when foraging together with a competitor than when foraging alone, but this effect depended much on the inter-pit distance and the within-pit food distribution, and it varied strongly between birds. Statistically, these findings are reflected in a significant interaction between Competitor presence, Inter-pit distance and Dominance status (A x C x D) in the first run of the experiment, and in significant interactions between Competitor presence and Inter-pit distance (A x C), and between Competitor presence, Within-pit food distribution and Dominance status (A x B x D) in the second run of the experiment (Table 5.1 & 5.2).

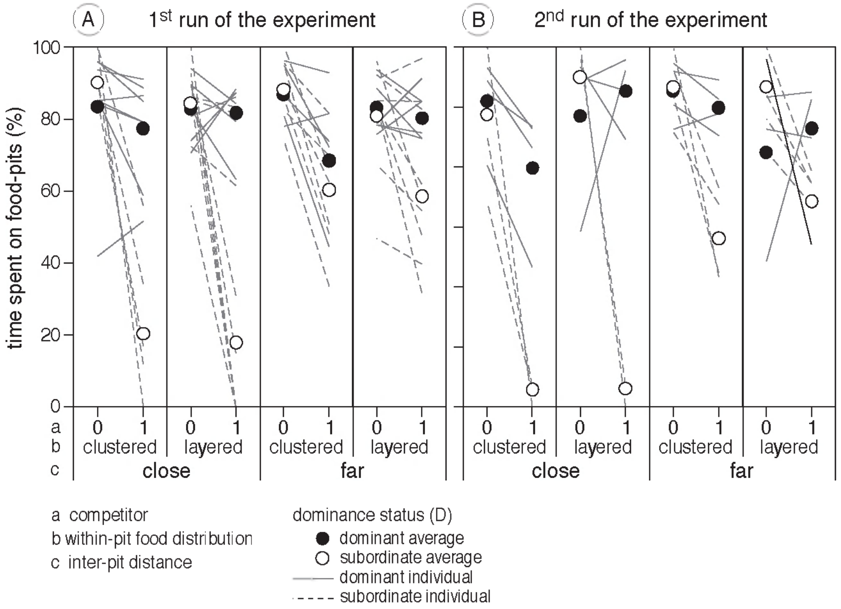

Figure 5.5. The time spent on food pits in the first (a) and the second (b) run of the experiment. Like in Figure 5.2, each graph contains four compartments, as indicated by the labels on the x-axis. Each compartment shows the effect of the absence (0) or presence (1) of a competitor on the time spent on food pits. Dots represent averages per treatment combination, and thin grey lines connect observations on the same individual within each compartment.

TIME ALLOCATION

Foragers differed markedly in the time they spent on the food pits (Figure 5.5). 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, but only so 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 in the interaction term between Competitor presence, Dominance status and Inter-pit distance (A x C x D), which was significant in both runs of the experiment (Table 5.1 & 5.2). 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

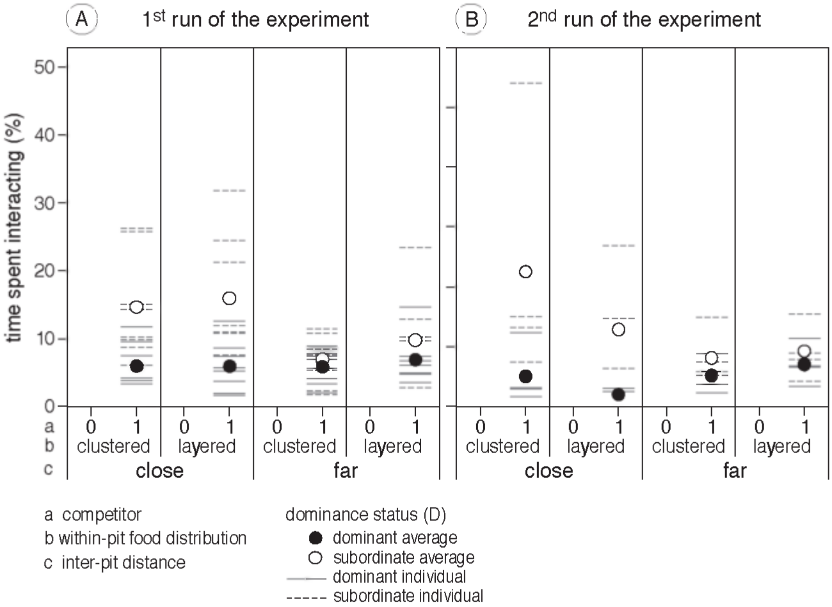

Figure 5.6. The time turnstones spent interacting in the first (a) and the second (b) run of the experiment. Like in figure 5.2, each graph is composed of four compartments as indicated by the labels on the x-axis. Within each compartment, a distinction is made between the absence (0) or presence (1) 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.

found so much more food items than 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 (Figure 5.6). When food pits were far apart, dominant and subordinate 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 subordinate bird could but resume foraging at the food pit that it had left. When the food pits were close to

Table 5.1. Treatment effects on the response variables of the first run of the experiment[a]

	Trial duration (s)			Intake (#)			Intake rate ($\#s^{-1}$)			Time spent on food pits (%)			Time spent interacting (%)		
(dom + sub)	df	SS	F	df	SS	F	df	SS	F	df	SS	F	df	$SS \cdot 10^{-2}$	F
Constant	1	674.3		1	116.7		1	428.0		1	263.0		1	1159.7	
Bird pair	7	12.6		7	5.2		7	13.7		7	1.3		7	28.0	
Day	7	5.0		7	1.1		7	10.4		7	0.3		7	12.7	
A	1	3.4	**30.0**	1	15.8	**90.1**	1	1.7	**5.6**	1	7.3	**148.8**		–	–
B	1	0.1	1.3	1	1.3	**7.6**	1	4.1	**13.5**	1	0.0	0.2	1	1.6	1.0
C	1	0.0	0.2	1	1.1	**6.4**	1	2.5	**8.1**	1	0.8	**17.0**	1	6.7	4.1
A x B	1	0.0	0.4	1	0.0	0.0	1	0.1	0.3	1	0.2	**4.7**		–	–
A x C	1	0.8	**7.1**	1	1.4	**7.7**	1	3.6	**11.7**	1	1.0	**20.3**			
B x C	1	0.0	0.0	1	0.0	0.2	1	0.0	0.0	1	0.0	0.0	1	0.8	0.5
A x B x C	1	0.3	2.3	1	0.0	0.0	1	0.8	2.6	1	0.0	0.2			
Error	28	3.6		38	7.4		38	12.8		38	2.1		13	22.7	
Total	50	25.0		60	33.3		60	49.6		60	13.0		31	67.0	
(dom - sub)															
D	1	0.8	**5.5**	1	17.9	**68.4**	1	30.4	**107.6**	1	2.7	**47.2**	1	25.6	**43.3**
Bird pair x D	7	2.8		7	9.6		7	24.8		7	0.7		7	7.8	
Day x D	7	1.1		7	0.9		7	1.5		7	0.3		7	6.2	
A x D	1	1.2	**7.8**	1	8.7	**33.2**	1	2.1	**7.6**	1	3.8	**68.2**		–	–
B x D	1	0.0	0.1	1	1.9	**7.3**	1	2.2	**7.7**	1	0.1	1.5	1	0.5	0.8
C x D	1	0.0	0.1	1	2.5	**9.7**	1	2.8	**9.8**	1	1.2	**21.4**	1	10.9	**18.4**
A x B x D	1	0.0	0.0	1	0.0	0.1	1	0.1	0.3	1	0.0	0.0		–	–
A x C x D	1	0.0	0.0	1	3.0	**11.3**	1	3.5	**12.4**	1	1.7	**30.1**		–	–
B x C x D	1	0.0	0.0	1	0.0	0.1	1	0.1	0.4	1	0.0	0.3	1	0.0	0.0
A x B x C x D	1	0.0	0.1	1	0.0	0.0	1	0.0	0.0	1	0.0	0.2		–	–
Error	28	4.7		38	11.0		38	11.9		38	2.4		13	8.3	
Total	50	9.2		60	37.7		60	48.9							

[a] Given are GLM results of the treatment factors Competitor presence (A), Within-pit food distribution (B), and Inter-pit distance (C) on the responses of dominant and subordinate pair members, after these were the log-transformed (trial duration, intake and intake rate) 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.

Table 5.2. Treatment effects on the response variables of the second run of the experiment[a]

		Trial duration (s)			Intake (#)			Intake rate ($\#s^{-1}$)			Time spent on food pits (%)			Time spent interacting (%)		
(dom + sub)		df	SS	F	df	SS	F	df	SS	F	df	SS	F	df	$SS \cdot 10^{-2}$	F
wholeplot	Constant	1	405.9		1	59.5		1	168.3		1	126.0		1	513.7	
	Day	3	1.0		3	0.0		3	0.9		3	0.1		3	20.5	
	C	1	0.2	0.3	1	0.1	4.7	1	0.0	0.0	1	0.7	**330.2**	1	0.5	0.5
	Error	3	1.5		3	0.1		3	1.9		3	0.0		3	3.5	
subplot	Bird pair	3	6.1		3	0.1		3	5.4		3	0.1		3	19.8	
	A	1	5.5	**33.0**	1	13.1	**648.1**	1	1.7	**7.5**	1	4.6	**62.7**			
	B	1	1.0	**5.7**	1	0.9	**44.3**	1	3.4	**14.7**	1	0.0	0.3	1	0.6	0.5
	A x B	1	0.1	0.5	1	0.7	**35.2**	1	1.6	**6.8**	1	0.1	1.1	–	–	–
	A x C	1	0.6	3.5	1	0.2	**11.6**	1	1.3	**5.8**	1	0.7	**9.6**	–	–	–
	B x C	1	0.3	1.5	1	0.2	**11.6**	1	0.0	0.1	1	0.1	1.6	1	3.8	3.1
	A x B x C	1	0.5	2.7	1	0.1	**7.2**	1	0.0	0.2	1	0.0	0.0	–	–	–
	Error	14	2.3		15	0.3		15	3.4		15	1.1		3	3.7	
	Total	31	17.4		32	15.9		32	19.7		32	7.4		16	38.2	
(dom - sub)																
wholeplot	D	1	1.5	**229.5**	1	12.2	**294.1**	1	22.8	**638.6**	1	1.7	**49.3**	1	23.5	**15.7**
	Day x D	3	0.5		3	0.0		3	0.7		3	0.3		3	4.2	
	C x D	1	0.0	1.9	1	0.3	7.1	1	0.4	**11.4**	1	0.8	**23.3**	1	10.2	6.8
	Error	3	0.0		3	0.1		3	0.1		3	0.1		3	4.5	
subplot	Bird pair x D	3	1.5		3	0.1		3	2.2		3	0.1		3	9.1	
	A x D	1	1.5	**12.9**	1	11.5	**419.0**	1	4.5	**36.0**	1	3.6	**71.2**	–	–	–
	B x D	1	0.0	0.3	1	1.4	**49.9**	1	1.9	**15.7**	1	0.1	1.0	1	0.6	0.2
	A x B x D	1	0.0	0.3	1	1.1	**41.5**	1	0.7	**5.7**	1	0.1	2.1	–	–	–
	A x C x D	1	0.0	0.1	1	0.4	**15.1**	1	0.3	2.4	1	0.4	**8.1**	–	–	–
	B x C x D	1	0.0	0.0	1	0.4	**15.1**	1	0.4	3.2	1	0.1	2.3	1	0.1	0.0
	A x B x C x D	1	0.0	0.0	1	0.3	**10.7**	1	0.3	2.5	1	0.1	1.1	–	–	–
	Error	14	1.6		15	0.4		15	1.9		15	0.8		3	7.9	
	Total	31	5.1		32	16.1		32	13.3		32	6.5		16	33.9	

[a] Interpretation as Table 5.1.

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 had but to lift their head and threat, but considerably long 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 Inter-pit distance (C x D) was only significant in the first run of the experiment (Table 5.1 & 5.2). Albeit being non-significant 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

Resource divisibility affected the way turnstones divided the food; 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. Instead, subordinate birds achieved a higher intake when food was divisible because they got a finder's advantage under this condition. 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 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.

That the divisibility of resources may affect the division of food over foragers because of a finder's advantage in the case of divisible resources was already assumed by several models of interference competition. What our results additionally show, however, is that the effect of resource divisibility may interact with the distribution of resources. 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 finder's advantage 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) 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 ten 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 the 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 individuals and dominant individuals performed the same number of pilot trials, subordinate birds effectively got less experience in handling the food pits, because there 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.

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 finder's advantage 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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