

INTERFERENCE COMPETITION, THE SPATIAL DISTRIBUTION OF FOOD AND FREE-LIVING FORAGERS

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ABSTRACT

Studies of interference competition among foraging animals generally assume that variation in the spatial distribution of food can be neglected. This assumption may be problematic as resource defence experiments suggest that such variation is of the essence in some interference mechanisms. Interpretation of the results of field experiments on this topic, however, is hard because of the way these experiments have been analysed: variation in the abundance of foraging animals has consistently been treated as nuisance or as a predictor variable, whereas it usually is one of the prime responses. We performed a field experiment in which we provided wild ruddy turnstones (*Arenaria interpres*) with experimental plots that varied in the distance between a fixed number of so-called food pits, and, using multivariate statistics, we studied effects on the combination of the turnstones' behaviour and abundance. We found that when food pits were more spaced out, turnstones were present in higher numbers, while interacting less with each other, but that they spent about the same time digging for food, our measure of intake rate, at each inter-pit distance. These findings imply that to reliably predict the combination of the number, intake rate and amount of aggression of turnstones, the spatial distribution of food has to be known. We would not have reached this conclusion if we had used univariate statistics or if we had treated variation in forager abundance as mere nuisance. Moreover, treating forager abundance as a response variable led to the insight that while experiments on captive foragers usually exclude patch choice decisions, experiments on free-living foragers necessarily involve patch choice decisions.

INTRODUCTION

The intake rate of foraging animals is often negatively related to the density of foragers because of competition. Competition is generally thought to arise in either of two ways (Keddy 2001). *Exploitative competition* is the negative effect of others through the removal of resources. As the exploitation of resources is a straightforward process, this type of competition is (presumably) relatively easy to understand. Interference competition is the negative effect of others through direct interactions between individuals. Behaviours underlying *interference competition* are various and complex (e.g., Huntingford & Turner 1987; Ens & Cayford 1996; Hassell 2000) and our understanding of this type of competition is still rudimentary (van der Meer & Ens 1997; Vahl et al. 2005a, b).

Students of interference competition among foraging animals usually study the effects of forager density concurrently with effects of food density (van der Meer & Ens 1997). In this approach it is implicitly assumed that variation in the spatial abundance of resources ('spatial clumping') does not affect the interference process. This may well be problematic. According to literature on resource defence, the 'economically defendability' (Brown 1964) of a given amount of food should decrease with the surface area over which the food is spread (Warner 1980; Grant 1993), as both the movement costs involved with defending a food clump and the number of intruding competitors are expected to be higher when the food is spread over a larger area (Davies & Houston 1984). With defendability decreasing, the use of aggressive behaviour to acquire resources and the extent to which resources will be monopolized should also be reduced when food is more spread out (Grant 1993). Numerous empirical studies have determined the effects of spatial clumping on the amount of aggression and resource monopolization; generally (though not unanimously) these studies confirm the resource defence expectations (for a review, see Vahl et al. 2005a).

The effect of spatial clumping on resource defence suggests that the spatial distribution of food has to be considered explicitly in order to arrive at a better understanding of interference competition; variation in the spatial distribution of food may well be of the essence in at least one mechanism underlying interference competition – resource monopolisation. Acknowledging variation in the spatial distribution of food may therefore be crucial, especially since natural food distributions generally are not homogeneous (Taylor 1961; Wiens 1976). Unfortunately, neither the literature on interference competition, nor the literature on resource defence provides clear-cut expectations on how the spatial clumping of food should affect the relationship between forager density and intake rate. Some empirical studies, however, shed light on this question. At least four studies (Rubenstein 1981; Theimer 1987; Benkman 1988; Vahl et al. 2005a) have manipulated both the spatial distribution of food and the abundance (i.e., either the number or the density) of foragers to determine effects

on the amount of aggression and intake rate. These studies found that the spatial clumping of food strongly affected the interference process, but that effects could not be understood without considering variation in the relative social dominance status of the foragers. Theimer (1987) and Vahl et al. (2005a), for instance, found that dominant foragers can better monopolize food that is spatially clumped than food that is dispersed, and that as a consequence, subordinate foragers suffer more from interference competition when food is clumped than when food is dispersed.

The extent to which these findings are important to understand the behaviour of free-living animals foraging under natural conditions is still an open question, because the four studies mentioned above were all conducted in the laboratory, using captive foragers. The most direct approach to study whether interference effects among free-living foragers depend on the spatial distribution of food would involve manipulation of both the spatial distribution of food and the density of wild foragers (Vahl et al. 2005b). Manipulating the density of free-living foragers, however, is very difficult and we are not aware of any study that has attempted to do so. Therefore, the most relevant data to date comes from studies that have manipulated the spatial distribution of food in the field, but not the density of foraging animals. Several such experiments have been performed (Table 4.1). Quite consistently, these studies found that with increasing plot size (1) the number of foragers increased, whereas forager density decreased and (2) the amount of aggression decreased (see Table 4.1). With regard to the correlations between forager abundance and intake rate or the amount of aggression, and with regard to effects of plot size on intake rate and the amount of aggression after correction for variation in forager abundance, the studies were less consistent (Table 4.1).

Unfortunately, interpretation of these results is not straightforward. The way these field experiments have been analysed complicates their interpretation in two ways. The first complication regards the way these studies dealt with variation in forager abundance. As mentioned above, forager abundance was an uncontrolled response variable in all field experiments, and, indeed, most of the studies reported a change in forager abundance in response to variation in the spatial distribution of food (Table 4.1). Nevertheless, when analysing the correlations between forager abundance, intake rate and the amount of aggression, some of the studies treated forager abundance as a predictor variable, either by including forager abundance as a covariate in an ANCOVA (Johnson et al. 2004) or by defining abundance categories (Balph 1977). Similarly, when studying treatments effects on intake rate and the amount of aggression, several of the studies treated variation in forager abundance as nuisance which had to be corrected for statistically, either by treating forager abundance as a covariate in ANCOVAs (Elgar 1987; Johnson et al. 2004, 2006), by treating forager abundance as a predictor variable in regression analyses (Goldberg et al. 2001), or

Table 4.1. Field experiments on the effect of the plot size (X) on the abundance (Y_1), the foraging success (Y_2) and the frequency of (per-capita) agonistic behaviour (Y_3) of free-living foragers†

species	English name	size of experiment		food	surface area	main effects			correlations			corrected effects		ref.	
		n_1	n_2			XY_1	XY_2	XY_3	Y_1Y_2	Y_1Y_3	$XY_2 Y_1$	$XY_3 Y_1$	$Y_{1,n}$		$Y_{1,d}$
birds															
<i>Junco hyemalis</i>	dark-eyed junco	2	u	amount	variable	(+)	(-)	(-)			+0		-		1
<i>Passer domesticus</i>	house sparrow	2	u	neither	variable		(+)	-	0,-		+				2
<i>Passer domesticus</i>	house sparrow	7	35	density	variable	+	-	-	+		+0	+	0	-	3
<i>Passer domesticus</i>	house sparrow	2	26	density	variable	(+)	0	0			+0,-				4
<i>Turdus merula</i>	European blackbird	2	498	density	variable			-			-		(0)	(-)	5
<i>Zenaidura macroura</i>	Zenaida dove	2	24	amount	constant		+	0,-					+0,d,c		6
-	several passerines‡	2	24	amount	constant	+									7
mammals															
<i>Lepus europaeus</i>	European hare	2	28	amount	constant			(-)			+0,-				8

† The column 'size of experiment' indicates the number of levels of plot size (n_1), and the total number of trials performed (n_2). For some studies the latter aspect is unknown (u). The column 'food' indicates whether the amount or the density of food was kept constant, or neither of them. The column surface area indicates whether the surface area over which forager abundance was expressed was constant or not; in the former case, effects on the number and the density cannot be distinguished (Y_1), whereas in the latter case, the number ($Y_{1,n}$) and the density ($Y_{1,d}$) of foragers are uncoupled. In the 'main effects' column, the 'correlations' column and in the 'corrected effects' column, it is indicated whether the relationship or the correlation between two variables was negative (-), positive (+), absent (0), dome-shaped (d) or cubic (c). Signs within brackets are not given by the original author(s), but are deduced by us. The correlation between forager abundance and amount of aggression in the study of Goldberg et al. (2001) depended on the temporal predictability of food patches; the correlations between forager abundance and intake rate and amount of aggression in the study of Monaghan & Metcalfe (1985) depended strongly on the dominance status of foragers. All other multiple effects depended on plot size.

‡ Included in the analyses were northern red cardinals (*Cardinalis carolinensis*), field sparrows (*Spizella pusilla*) & white-throated sparrows (*Zonotrichia albicollis*). references: (1) Balph 1977, (2) Elgar 1987, (3) Johnson et al. 2004, (4) Johnson et al. 2006, (5) Cresswell 1997, (6) Goldberg et al. 2001, (7) Pearson 1989, (8) Monaghan & Metcalfe 1985

by excluding observations on higher abundances from the analyses (Cresswell 1997). Several of these approaches violate statistical assumptions (e.g., the independence of predictor variables, the absence of measurement error on predictor variables, and the absence of feedback effects of response variables on predictor variables). All of them are unwanted, because they distract attention from what may be the most important effect of the spatial distribution of food – a change in the abundance of foragers. The second complication lies in the fact that none of the studies acknowledged the multivariate nature of their data; to study treatment effect on forager abundance, intake rate and the amount of aggression, all investigators used univariate statistics. Such an approach precludes the detection of effects on combinations of response variables, and it invokes the risk of an inflated type I error (Harris, 1975).

To solve these interpretational problems, the field experiments could be reanalyzed. Rather than doing so, we performed a new field experiment to describe effects of the spatial distribution of food on free-living foragers, and we took care to avoid the above-mentioned shortcomings in the statistical analyses. In this experiment, we provided wild birds with experimental plots in their usual foraging area, and we manipulated the distribution of food by varying the distance between a fixed number of regularly distributed food pits. We recorded the responses of visiting ruddy turnstones (*Arenaria interpres*; henceforth called turnstones), a species that we previously used to address the same question in laboratory experiments on captive foragers (Vahl et al. 2005a,b). In analysing our experiment, we used multivariate statistics and we tried to be consistent in acknowledging forager abundance as a response variable; rather than treating variation in forager abundance as nuisance, we treated it as one of the prime response variables. In the discussion, we examine whether the use of univariate statistics and the use of ANCOVAs (which treat forager abundance as nuisance) would have affected our results, and we reflect on the way in which multivariate analysis helps to clarify the research question.

METHODS

We designed our experiment according to a randomized block design: we studied the effect of one treatment factor – the distance between food pits – with three levels (10, 20 and 30 cm) and we blocked our observations in groups of three trials (we refer to these blocks as ‘triplets’) to minimize variation due to measurements at different moments in time. The experiment consisted of 10 triplets, each containing all three inter-pit distances once (in random order). There was one missing value and hence we had 29 data points.

We studied treatment effects on three response variables: the number, intake rate and the amount of aggressive behaviour of turnstones. As plot size varied

between treatments, the density of turnstones did not have a one-to-one relationship with the number of turnstones. Moreover, the experimental plots did not only attract turnstones, but also sanderlings (*Calidris alba*), red knots (*Calidris canutus*), laughing gulls (*Larus atricilla*), herring gulls (*Larus argentatus*), ring-billed gulls (*Larus delawarensis*) and starlings (*Sturnus vulgaris*). To see whether conclusions would be different if measures of abundance other than the number of turnstones were used, we repeated all analyses using (1) the density of turnstones ($\#m^{-2}$), (2) the biomass (kg), or (3) the biomass density (kgm^{-2}) of all species present on the experimental plot as the measure of abundance.

STUDY SYSTEM AND SUBJECTS

The experiment was conducted at one of the beaches of Delaware Bay, U.S.A., on five days between 24 and 30 May 2003. Delaware Bay is one of the most important spring stopover sites for shorebirds along the east coast of North America (Clark et al. 1993). Turnstones are among the most abundant species in the bay, with peak counts of over 100,000 individuals (Clark et al. 1993). The main food source for turnstones foraging in this bay are the eggs of horseshoe crabs (*Limulus polyphemus*; Tsipoura & Burger 1999). Turnstones forage on loose eggs that are brought to the beach surface by the re-working of waves, tides, and bioturbation of horseshoe crabs and other fauna (Kraeuter & Fegley 1994; Sherman et al. 1994) but they are also able to dig up clusters of eggs buried in the sand (Sullivan 1986; Tsipoura & Burger 1999). In doing so, they attract individuals of several other species (Myers et al. 1979) that cannot reach buried eggs themselves. In 2003 the amount of food on the beaches was relatively low (Smith & Bennett 2004) and turnstones got crab eggs mainly by digging for them in the sediment.

STUDY SITE AND EXPERIMENTAL SET-UP

The experiment was performed at one beach in the village Reed's Beach, Cape May County, New Jersey. This beach is quite small (depth x width: 10 x 90 m). It is unique in that it is enclosed by 2 m high walls on all but the bay-side. Hence, the beach has a basin-like appearance. Since this beach was completely flooded at high tide, and since at low tide the birds would be far out on the mudflats, we conducted all trials at incoming or outgoing tides ($X \pm SD = 2.32 \pm 0.33$ h before and 1.34 ± 0.46 h after high tide). Triplets took 45 min at most ($X \pm SD = 34.6 \pm 5.3$ min).

In each trial we created one experimental plot at approximately 3 m from the water line. To mark experimental plots for the observers, we placed black stones, which were abundant on the beach, on their corners. Each plot contained 25 food pits, positioned in a regular 5 x 5 grid. Food pits were holes of approximately fixed size and cylindrical shape; we created them by pressing a film canister in the sand (diameter: 31 mm; depth: 51 mm). In each pit, we

placed a spoonful of crab eggs ($X \pm SD = 4.2 \pm 0.7$ g, $N = 50$), corresponding to approximately 750 eggs (1 gram of eggs = 183.1 ± 16.3 eggs [based on 9 egg counts]), and a thin layer of sand (5.7 ± 0.2 ml, $N = 10$) to cover the eggs. The upper 4 cm of each pit was left empty so that foragers could easily see the food pits. Eggs used in the experimental trials were isolated from sediment samples by elutriation, and had been stored at 4 °C for at most one day. The experimental food pits resembled the pits turnstones dug themselves to reach buried egg clusters, both in size (depth: 51.3 ± 7.4 mm, $N = 16$) and shape, and turnstones were eager to forage in them. Importantly, food at the experimental plot was abundant and easy to gather relative to food in the direct neighbourhood of the experimental plot (as was also clear from the strong preference of foragers for the experimental plots).

Between trials we experimentally varied the distance between food pits. The smaller two experimental inter-pit distances (10 cm and 20 cm) fell below the size range of turnstones (length: 210 – 255 mm; Hayman et al., 1986). Nevertheless, monopolization of multiple food pits required the turnstones to move actively between food pits at each of the three inter-pit distances. While varying the distance between food pits, we kept constant the number of food pits per plot and the number of eggs per food pit. Consequently, the size of the experimental plot (0.25, 1.00 or 2.25 m²) and the density of food pits (100, 25 or 11 #m⁻²) varied concurrently with inter-pit distance. We think that the simultaneous variation of several aspects of the distribution of food is inevitable in experiments on the effect of the spatial distribution of food.

During each trial we recorded the behaviour of birds on the experimental plot with a video-camera (Sony dcr-trv 900e), positioned on the veranda of one of the elevated houses bordering the beach. Experimental plots were only 20-30 m away from the camera. Although birds that foraged on the experimental plot could see the observer and the camera, this did not seem to affect them, probably because they were used to people, and because the observers were not actually on the beach.

EXPERIMENTAL PROCEDURE

The same two observers (WKV & KM) conducted all trials together. To create an experimental plot, one observer set foot on the beach from the site opposite to that of the camera. In doing so, he necessarily disturbed the birds foraging on the beach, which readily took off for another beach. However, new birds would arrive even before the observer had left the beach, and the first birds generally started to feed on the experimental plot within the first minute after preparation. Video-recording started when the first turnstone entered the experimental plot and lasted for five minutes. Trials in which (at any moment) more than three laughing gulls, and/or more than one herring gull or ring-billed gull were present were excluded from the experiment.

VIDEO ANALYSIS AND RECORDED BEHAVIOUR

We analysed our video-recordings at one-fifth of normal speed, using The Observer 4.1 Event Recorder (Noldus Information Technology 2002). To minimize start-effects, such as a gradual rise in the number of foragers, we discarded the first 60 s of each record. To limit effects of resource depletion, digestive constraints and satiation, we additionally discarded the last 60 s of each record. Thus, we restricted all analyses to a 180 s time span. Because of an external disturbance one trial only lasted for about 220 s. After exclusion of the first 60 s, we therefore had only a 160 s interval for analysis. We extrapolated response variables for this trial by multiplying all events with a factor $180 / 160$.

We calculated the abundance (either the number or the density) of foragers as the average of 5 s interval counts of the number of individuals per species on the experimental plot. Collective biomass was estimated by summing for all species the product of the average number of individuals (Table 4.2) and the median body mass of an individual (sanderling: 71.5 g; turnstone: 137.0 g; red knot: 152.5 g; laughing gull: 320.0 g; big gull: 802.5 g; mass values from del Hoyo et al. 1996, and starling: 82.5 g; Feare 1984). Note that, we grouped herring gulls and ring-billed gulls in the category 'big gulls', because our subjective observations suggest that the two species had the same effect on turnstones.

To determine intake rate and the amount of aggression, we recorded the behaviour of focal turnstones. As focal individual we chose the turnstone closest to the centre of the experimental plot. When a focal turnstone left the experimental plot, we continued the analysis by recording the behaviour of a new focal bird. We approximated intake rate by measuring the time spent digging in the food pits (%); when 'digging', turnstones were actively routing with their bill through the sand. We could not measure intake rate directly, because plot size restricted the extent to which we could zoom in on the turnstones. However, digging time and intake rate (the number of swallowing movements)

Table 4.2. The number of individuals per species observed on the experimental plot. Given are the averages per treatment with the associated standard deviations and maxima in brackets

species	inter-pit distance (cm)		
	10	20	30
turnstone	2.9 (1.3; 4.9)	9.4 (1.6; 11.5)	12.1 (4.5; 20.9)
sanderling	2.0 (1.9; 4.9)	3.8 (2.8; 7.6)	8.3 (8.2; 21.1)
red knot	0.1 (0.1; 0.3)	0.1 (0.4; 1.2)	0.2 (0.4; 1.4)
laughing gull	0.4 (0.4; 0.9)	0.5 (0.5; 1.4)	0.6 (0.9; 2.2)
'big gulls'	0.1 (0.1; 0.3)	0.0 (0.1; 0.2)	0.0 (0.1; 0.3)
starling	0.1 (0.1; 0.3)	0.1 (0.1; 0.4)	0.2 (0.3; 0.7)

were strongly correlated ($R^2 = 0.91$, $F_{1,67} = 641.7$, $P < 0.01$) in an observational dataset gathered on nearby beaches by systematically recording the behaviour of foraging turnstones for 60 s ($N = 68$). We measured the amount of aggression as the number of intra-specific agonistic interactions that focal turnstones performed per trial ($\#/180$ s). Interactions comprised ‘fighting’, ‘attacking’, ‘threatening’, ‘avoiding’ or ‘escaping’ (for a detailed description of the latter four interaction behaviours: see Vahl et al. 2005b). In analyses based on all species, the amount of aggression was measured as the rate of all (intra- and inter-specific) interactions performed by focal turnstones.

DATA TRANSFORMATION AND HYPOTHESIS TESTING

We analyzed our data using the GLM procedure in SYSTAT 10 (SPSS Inc. 2000), treating both ‘triplet’ and ‘inter-pit distance’ as categorical factors. This procedure is able to handle missing values. In all graphs that include information on triplets, we replaced the missing value with the associated treatment average. We log-transformed all response variables (Vahl et al. 2005a, b). In the analyses, we did not replace the missing value; to study the effects of our treatment factor, we ran a MANOVA on the combination of the three response variables – the number of turnstones, the time spent digging and the rate of intra-specific interactions. We repeated this analysis three times, using either the density of turnstones, the biomass of all species or the biomass density of all species as measure of abundance. In each of the four MANOVAs, we used a 0.01 significance level. This implies that the overall experimentwise error rate did not exceed 0.04. We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller 1997).

RESULTS

The distance between food pits had a significant effect on the combination of the number of turnstones on the experimental plots, their intake rate, and the amount of their aggression (Table 4.3). There was almost no overlap between the combination of the three response variables at the three inter-pit distances, as is clear from both the multivariate representation – the three clouds of points were clearly separated (Figure 4.1A) – and from the strong correlation between the inter-pit distance and the first canonical variate (Table 4.3). The most pronounced effect was on the combination of the number of turnstones and the amount of their aggression (Figure 4.1D), and on the combination of the number of turnstones and their intake rate (Figure 4.1B); the combination of the amount of aggression and intake rate was not so much affected (Figure 4.1C). The combination of response variables at the smallest inter-pit distance differed mainly from that at the two larger inter-pit distances in that fewer turn-

Table 4.3. The effect of inter-pit distance (X) on the number of foragers (Y_1), the percentage of time turnstones spent digging (Y_2) and the rate of agonistic interactions (Y_3). Given are MANOVA results, the canonical correlations regarding inter-pit distance (X), and the associated canonical loadings. on log-transformed data Effects significant at the 0.01 level are indicated by bold P-values†

	multivariate ANOVA				canonical correlation analysis		
	Y ₁ Y ₂ Y ₃			P	loadings		
	df	value†	F		Y ₁	Y ₂	Y ₃
triplet	27, 44	0.19	1.2	0.25			
inter-pit distance (X)	6, 30	0.05	18.0	<0.01			

X	correlations				loadings		
	r	χ^2	df	P	Y ₁	Y ₂	Y ₃
variate 1	0.97	76.3	6	<0.01	-0.70	-0.17	0.08
variate 2	0.46	5.9	2	>0.05			

† The MANOVA results indicate that the combination of the three (log-transformed) response variables differs significantly between the three inter-pit distances, but not between the ten triplets. The canonical correlation analysis gives the correlation (r) between inter-pit distance (X) and two canonical variates, which are compound variables formed by the linear combination of response variables that results in the greatest amount of among-group to within-group variation. Inter-pit distance is strongly and significantly correlated with the first canonical variate, but not with the second. The canonical loadings indicate the correlation between the first canonical variate and each of the three response variables; as it turns out, it is the number of turnstones (Y_1) that is most closely aligned with the first canonical variate.

‡ Value given is Wilks' lambda; other multivariate statistics led to identical conclusions.

stones were present at the smallest inter-pit distance (Figs 1A, D and G). The combination of response variables, however, also differed between the two larger inter-pit distances; when food pits were 20 cm apart, the turnstones, which were present in slightly lower numbers than when food pits were 30 cm apart, interacted more with each other (Figs 1A, D and F).

The effect of inter-pit distance on the combination of response variables is furthermore apparent from the correlations among the responses variables (Table 4.4); inter-pit distance affects the correlation between the number of turnstones and both the time spent digging (Figure 4.1B) and the rate of agonistic interactions (Figure 4.1D). Especially the latter correlation depends much on whether or not variation in inter-pit distance is acknowledged. Overall, that is, when variation in inter-pit distance is neglected, the number of turnstones is uncorrelated with the rate of agonistic interactions, while when variation in inter-pit distance is acknowledged, the number of turnstones and the amount of aggression are clearly positively correlated (Figure 4.1D).

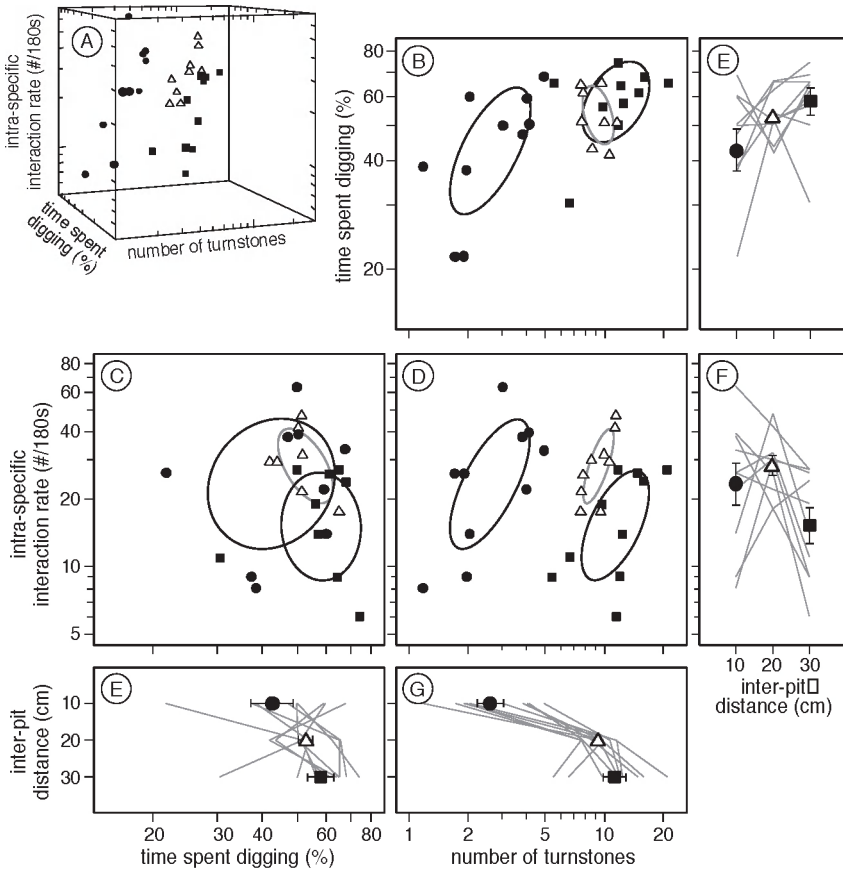


Figure 4.1. Effects of the distance between food pits on the three response variables – the number of turnstones, the time spent digging (our measure of intake rate) and aggression. In all panels, symbols (circles, triangles and squares) indicate inter-pit distance (10, 20 and 30 cm, respectively). Panel A gives the three-dimensional relationship between the three response variables. The panels B–D and the panels E–G give the two- and one-dimensional projections of this three-dimensional relationship, respectively. Note that panel E features twice. In panels A–D symbols represent averages per trial. In panels B–D ellipses indicate the 95% confidence intervals of the mean for each inter-pit distance (confidence intervals for the intermediate treatment level are dashed). In panels E–G symbols represent averages per treatment level, and error bars indicate one standard error of the treatment averages. The thin grey lines connect observations within triplets; they represent the ten blocks of our randomized block design.

Table 4.4. Correlations among the three (log-transformed) response variables – the number of turnstones (Y_1), the time spent digging (Y_2), and the intra-specific interaction rate (Y_3). For each pair of response variables, the simple (unconditioned) correlation coefficients are given, as well as the 1st, and 2nd order correlation coefficients conditioned on either the block factor triplet, the distance between food pits (X), or both (as indicated by the set of variables given within braces)[†]

pair	simple		(partial) correlation coefficients					
			1 st order				2 nd order	
	set	r_s	set	r_s	set	r_s	set	r_s
Y1Y2	{-}	0.59	{X}	0.50	{triplet}	0.61	{triplet, X}	0.36
Y1Y3	{-}	0.13	{X}	0.65	{triplet}	-0.04	{triplet, X}	0.61
Y2Y3	{-}	-0.09	{X}	0.01	{triplet}	-0.19	{triplet, X}	-0.03

[†] The effect of the distance between food pits on the correlations between the response variables can be studied in two ways: (1) simple correlations can be compared with first order partial correlations conditioned on the distance between food pits, and (2) first order partial correlations conditioned on the block factor triplet can be compared with the second order partial correlations conditioned on both the block factor triplet and the distance between food pits.

TURNSTONE DENSITY

Even though turnstones were present in higher numbers when the distance between food pits was larger, their density was lower at this condition. Effects on the number and the density of turnstones could be different because the distance between food pits also affected the size of experimental plots; the surface area of experimental plots was nine times larger when food pits were far apart than when food pits were close together. Analyses based on the density of turnstones yielded qualitatively the same results as analyses based on the number of turnstones: inter-pit distance had a strong ($r = 0.89$) and significant effect on the combination of the three response variables (Wilks' lambda = 0.17, $F_{6,30} = 7.1$, $P < 0.01$). The main difference between the three inter-pit distances was in the combination of turnstone density and intake rate and in the combination of turnstone density and the amount of aggression: when food pits were 30 cm apart, turnstone density was about half of that at the two smaller inter-pit distances (Figure 4.2B), whereas intake rate was somewhat higher and the amount of aggression lower than at the two smaller inter-pit distances. That turnstone density did not differ significantly between the 10 cm and the 20 cm treatment suggests that the increase in the number of turnstones between these two treatment levels was proportional to the corresponding increase in plot size.

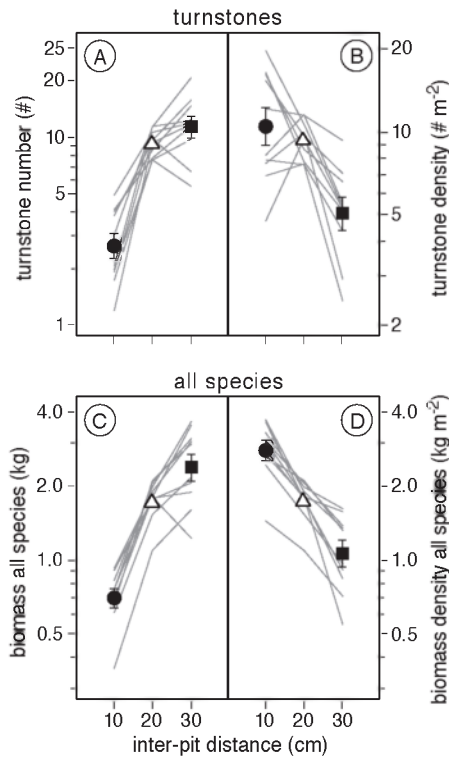


Figure 4.2. The effect of the distance between food pits on (A) the number and (B) the density of turnstones, and on (C) the biomass and (D) the biomass density of individuals of all species on the experimental plot. Symbols represent averages per inter-pit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the ten blocks. Note that panel A corresponds to Fig. 2.1G.

ALL SPECIES

Effects of inter-pit distance on the biomass and the biomass density of the individuals of all species together were similar to effects on the number and density of turnstones (Figure 4.2). With increasing distance between the food pits, the biomass of all species together increased (Figure 4.2C), but not so much as to be proportional to the increase in plot size; therefore, the biomass density of all species together decreased with inter-pit distance (Figure 4.2D). Effects on the rate of intra- and inter-specific interactions together were also similar to those on the rate of intra-specific interactions alone (Figure 4.3). Even though the number of individuals of species other than turnstones was substantial, most interactions of focal turnstones were directed at conspecifics; at all three inter-pit distances, the rate of inter-specific interactions (Figure 4.3B) was much

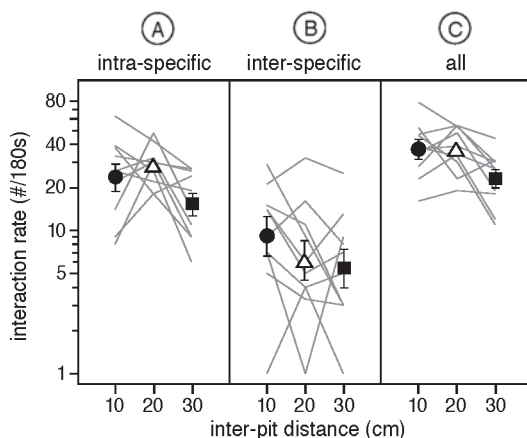


Figure 4.3. The effect of the distance between food pits on (A) the rate of intra-specific interactions, (B) the rate of inter-specific interactions, and (C) the rate of all (intra- and inter-specific) interactions. Symbols represent averages per inter-pit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the ten blocks. Note that panel A corresponds to Figure 4.1F, but that the ordinate has a different range.

lower than the rate of intra-specific interactions (Figure 4.3A). Most inter-specific interactions comprised of attacks and threats towards the many sanderlings that tried to share the food pit owned by the focal forager, and escapes and avoidances from the occasional gull that was attracted by the experimental plot. Statistically, treatments effects on biomass and biomass density were also highly comparable to those on the number and the density of turnstones, respectively.

DISCUSSION

The spatial distribution of food strongly affected the behaviour and success of the free-living foragers participating in our experiment. Multivariate analysis showed that it was the combination of, especially, the number of turnstones and the amount of their aggressive behaviour that depended on the spatial distribution of food. Inspection of the correlation coefficients also revealed that the correlation between the number of turnstones and both their intake rate and their aggressive behaviour depended on the distance between food pits. The immediate lesson that can be drawn from this finding is that there was not a one-to-one relationship between the amount of food and the combination of the three response variables; the same amount of food yielded a different combination of the three response variables, depending on the spatial distribution of the food.

This implies that to reliably predict the number, intake rate and amount of aggressive behaviour of turnstones, the spatial distribution of food has to be known. Additionally, these findings imply that the pressure exerted by turnstones on their prey varied with the distance between food pits; when food was spaced out, the product of intake rate and the number of foragers (the ‘foraging pressure’) was higher (Figure 4.4). This illustrates the idea that reduced predation pressure as a result of increased predator interference may be an important advantage of clumping to prey, as was pointed out by Taylor (1977). Although clearly outside the scope of this study, this suggests that the small-scale distribution of food may ultimately affect the dynamics of both predators and their prey.

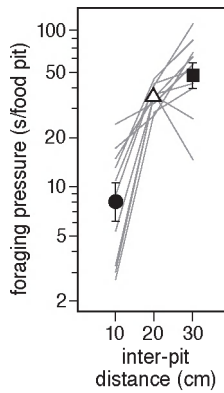


Figure 4.4. The estimated foraging pressure per inter-pit distance. Foraging pressure was calculated as the product of the average number of turnstones and the time spent digging per trial. Symbols represent averages per inter-pit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the ten blocks.

While the number of turnstones increased with inter-pit distance, the density of turnstones decreased. This shows that the relationship between the number of foragers and surface area is not one-to-one; just as the relationship between the number of foragers and the amount of food, this relationship depends on the spatial distribution of food. Effects on the biomass and the biomass density of all species on the experimental plot strongly resembled these effects on the number and the density of turnstones, suggesting that effects of the spatial distribution of food are general over species, conform the findings of Pearson (1989). The general conclusion that can be drawn from tests that use either turnstone density, all species biomass or all species biomass density as measure of abundance, is the same as that from tests that use the number of turnstones:

the spatial distribution of food affects the combination of the abundance, intake rate and amount of aggression of free-living foragers.

As plot size, food density and inter-pit distance varied concurrently, we cannot determine to which of these three aspects of the food distribution the foragers responded. Although this may seem as a flaw to the experimental design, we think that simultaneous variation of various aspects of the distribution of food is inevitable. Indeed, in all field experiments on the effect of the spatial distribution of food, several aspects of the distribution of food varied concurrently. We think that effects of the various aspects of food distribution can only be disentangled by performing a sequence of experiments that vary in the aspects of food distribution that are simultaneously manipulated. Meanwhile, we need to be careful in attribution treatment effects to specific aspects of the food distribution, and we need to take in account the subtle differences between experiments when comparing experiments.

COMPARISON WITH PREVIOUS WORK

Our results deviated from those of previous field experiments in that none of the previous experiments detected effects on the combination of response variables. To see whether we would have reported different main effects of the spatial distribution of food on each of the three response variables if we had not analysed our data using multivariate statistics, we performed ANOVAs on each of the three response variables (see APPENDIX A). Similarly, to study whether we would have drawn different conclusions regarding the correlations of the number of foragers with intake rate and amount of aggression and regarding the treatment effects after correction for variation in the number of foragers, we performed ANCOVAs on intake rate and amount of aggression, with the number of turnstones as a covariate (see APPENDIX B).

Based on the ANOVA test results we would have concluded that the distance between food pits had a significant main effect only on the number of turnstones on the experimental plot, and not on their intake rate, nor on the amount of their aggression. These findings would have corresponded to the results of Balph (1977) and Johnson et al. (2004, 2006), who also found the number of foragers to increase with plot size, and to the results of Johnson et al. (2006), who also reported plot size not to affect intake rate (Table 4.1). However, these results would have contradicted the general finding that amount of aggression decreases when food is spaced out. Based on the ANCOVA test results, we would have concluded that neither the distance between food pits nor the number of turnstones affected the intake rate of turnstones, and that both the distance between food pits and the number of turnstones affected the rate of intra-specific interactions. These results would have corresponded to those of Balph (1977), Johnson et al. (2004) and Cresswell (1997) in the treatment effects found after correction for variation in the number of

foragers, but they would have differed from the results found by most other field experiments with regard to the correlations between the number of foragers with intake rate and amount of aggression (Table 4.1).

ADDED VALUE OF THE MULTIVARIATE ANALYSIS

The most obvious virtue of our multivariate analysis is that we were able to detect an effect of the distance between food clumps on the combination of the number of foragers and the amount of their aggression. This would not have been possible if we would have use univariate statistics, whether we had corrected for variation in the number of turnstones (ANCOVA) or not (ANOVA). The use of statistical tests, however, should not be made dependent on the experimental results only. Rather, tests should be selected on the basis of their match with the experimental design. The use of ANCOVAs to detect treatment effects in experiments in which forager abundance is a response variable, for instance, can not be justified because it violates several statistical assumptions (Sokal & Rohlf 1995). For instance, analysis of covariance assumes independence of the covariate and the response variable. That forager abundance would be independent of either intake rate or amount of aggression is not at all obvious. Feedback effects of the rate of intra-specific interactions on the number of turnstones, are, for instance, quite likely, given that the prime reason of aggression may be to lower the number of competitors. Similarly, analysis of covariance assumes that the covariate itself is not affected by the treatment. In most field experiments, the number of foragers was affected by the spatial distribution of food. In our experiment, the number of turnstones was even the response variable that was affected most strongly by the distance between food pits. Also, analysis of covariance assumes that the covariate is measured without error and that it is under control of the investigators. Such was clearly not the case for the number of turnstones and therefore the ANCOVA results may be biased.

Perhaps more importantly, however, the correct identification of the relationship between the various variables involved in the experiment helps to clarify the way in which the experimental results are to be interpreted. In experiments in which the number of foragers is an uncontrolled response variable, feedback effects of aggression and intake rate on the number of foragers are possible; in response to changes in amount of aggression and intake rate, foragers may adjust their distribution over food patches. Interpretation of the results of such experiments therefore requires considerations on patch choice decisions of the foragers. In experiments in which the number of foragers is experimentally controlled and thus a predictor variable, on the contrary, feedback effects of aggression and intake rate on the number of foragers are deliberately excluded and experimental results can be interpreted without considerations on patch choice. This implies that whether or not the number of foragers is experimentally controlled actually changes the research question that can be addressed. If the

number of foragers is experimentally controlled, the effects the spatial distribution of food on intake rate and amount of aggression can be studied *per se*; if the number of foragers is not experimentally controlled it is the consequences of these effects on the distribution of foraging animals over patches of food and the resulting relationships between the number of foragers, intake rate and amount of aggression that can be studied. These are different things; even when the same effects of the spatial distribution of food on intake rate and amount of aggression *per se* operate in experiments in which the number of foragers is experimentally controlled as in experiments in which the number of foragers is not experimentally controlled, these two kinds of experiments can yield different results. One implication of this insight is that it can not easily be determined whether captivity affects the relationship between spatial clumping, aggression and intake rate. To just compare results of experiments on free-living foragers with results of experiments on captive foragers does not suffice, because these experiments differ in whether they used captive or free-living foragers *and* in whether or not they excluded patch choice decisions.

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REFERENCES

- Ralph, M. H. 1977. Winter social behaviour of dark-eyed juncos: communication, social organization and ecological implications. *Animal Behaviour*, 25, 859-884.
- Benkman, C.W. 1988. Flock size, food dispersion and the feeding behavior of crossbills. *Behavioral Ecology and Sociobiology*, 23, 167-173.
- Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bulletin*, 76, 160-169.
- Clark, K. E., Niles, L. J. & Burger, J. 1993. Abundance and distribution of migrant shorebirds in Delaware Bay. *Condor*, 95, 694-705.
- Cresswell, W. 1997. Interference competition at low competitor densities in blackbirds *Turdus merula*. *Journal of Animal Ecology*, 66, 461-471.
- Davies, N. B. & Houston, A. I. 1984. Territory economics. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 148-169. 2nd edn. Oxford: Blackwell Scientific Publications.

- del Hoyo, J., Elliott, A. & Sargatal, J. 1996. Handbook of the Birds of the World. Barcelona: Lynx Edicions.
- Elgar, M. A. 1987. Food intake rate and resource availability: flocking decisions in house sparrows. *Animal Behaviour*, 35, 1168-1176.
- Ens, B. J. & Cayford, J.T. 1996. Feeding with other Oystercatchers. In: The Oystercatcher: from Individuals to Populations (Ed. by J. D. Goss-Custard), pp. 77-104. Oxford: Oxford University Press.
- Feare, C.J. 1984. The Starling. Oxford: Oxford University Press.
- Goldberg, J. L., Grant, J. W. A. & Lefebvre, L. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behavioral Ecology*, 12, 490-495.
- Goss-Custard, J. D. 1980. Competition for food and interference amongst waders. *Ardea*, 68, 31-52.
- Grant, J. W. A. 1993. Whether or not to defend? The influence of resource distribution. *Marine Behaviour and Physiology*, 23, 137-153.
- Harris, R. J. 1975. A Primer of Multivariate Statistics. 1st ed. New York: Academic Press, Inc.
- Hassel, M. P. 2000. The Spatial and Temporal Dynamics of Host-Parasitoid Interactions. Oxford: Oxford University Press.
- Hayman, P., Marchant, J. & Prater, T. 1986. Shorebirds: an Identification Guide. Boston: Houghton Mifflin Company.
- Huntingford, F. & Turner, A. 1987. Animal Conflict. London: Chapman & Hall.
- Johnson, C. A., Grant, J. W. A. & Giraldeau, L-A. 2004. The effect of patch size and competitor number on aggression among foraging house sparrows. *Behavioral Ecology*, 15, 412-418. doi: 10.1093/beheco/arh026.
- Johnson, C. A., Giraldeau, L-A. & Grant, J. W. A. 2006. Intensity of interference affects the distribution of house sparrows, *Passer domesticus*, at food patches. *Animal Behaviour*, 71, 965-970. doi: 10.1016/j.anbehav.2005.10.003.
- Keddy, P. A. 2001. Competition. 2nd ed. Dordrecht: Kluwer Academic Publishers.
- Kraeuter, J. N. & Fegley, S. R. 1994. Vertical distribution of sediments by horseshoe crabs (*Limulus polyphemus*) during their spawning season. *Estuaries*, 17, 288-294.
- Miller, R. G. 1997. Beyond ANOVA: Basics of Applied Statistics. London: Chapman & Hall.
- Monaghan, P. & Metcalfe, N. B. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. *Animal Behaviour*, 33, 993-999.
- Myers, J. P., Conners, P. G. & Pitelka, F. A. 1979. Territoriality in non-breeding shorebirds. In: Shorebirds in Marine Environments (Ed. by F. A. Pitelka), pp. 231-246. Los Angeles: Cooper Ornithological Society.
- Pearson, S. M. 1989. Food patches and foraging group size in granivorous birds. *Animal Behaviour*, 38, 665-674.
- Rubenstein, D. I. 1981. Population density, resource partitioning and territoriality in Everglade pygmy sunfish. *Animal Behaviour*, 29, 155-172.
- Sherman, D. J., Nordstrom, K. F., Jackson, N. L. & Allen, J. R. 1994. Sediment mixing depths on a low-energy reflective beach. *Journal of Coastal Research*, 10, 297-372.
- Smith, D. & Bennet, S. 2004. Horseshoe crab spawning activity in Delaware Bay: 5 years of a standardized and statistically-robust survey. Report to ASMFC horseshoe crab management board.
- Sokal, R. R. & Rohlf, F. J. 1995. Biometry: the Principles and Practice of Statistics in Biological Research. 3rd edn. New York: W.H. Freeman and Company.
- Sullivan, K. A. 1986. Influence of prey distribution on aggression in ruddy turnstones. *Condor*, 88, 376-378.
- Taylor, L. R. 1961. Aggregation, variance and the mean. *Nature*, 189, 732-735.
- Taylor, R. J. 1977. The value of clumping to prey. *Oecologia*, 30, 285-294.

- Theimer, T. C. 1987. The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos, *Junco hyemalis*. *Animal Behaviour*, 35, 1883-1890.
- Tsipoura, N. & Burger, J. 1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor*, 101, 635-644.
- Vahl, W. K., Lok, T., van der Meer, J., Piersma, T. & Weissing, F. J. 2005a. Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology*, 16, 834-844. doi:10.1093/beheco/ari067.
- Vahl, W. K., van der Meer, J., Weissing, F. J., van Dullemen, D. & Piersma, T. 2005b. The mechanisms of interference competition: two experiments on foraging waders. *Behavioral Ecology*, 16, 845-855. doi:10.1093/beheco/ari067.
- van der Meer, J., Ens, B. J. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology*, 66, 846-858.
- Warner, R. R. 1980. The coevolution of behavioral and life-history characteristics. In: *Sociobiology: Beyond Nature / Nurture* (Ed. by G. W. Barlow & J. Silverberg), pp. 151-188. Boulder: Westview.
- Wiens, J. A. 1976. Population Responses to Patchy Environments. *Annual Review of Ecology and Systematics*, 7, 81-120.

APPENDIX 4A: UNIVARIATE ANALYSES

To study whether univariate analysis of each of the three response variables would have led to different conclusions than the multivariate analysis, we reanalyzed our data using ANOVAs on intake rate, on the rate of intra-specific interactions and on the number of turnstones, after log-transforming each of these three response variables. In these ANOVAs, inter-pit distance (X) was included as a (categorical) treatment factor, and triplet as a (categorical) block factor. To facilitate comparison of conclusions with conclusions drawn in the main text, we used a 0.01 significance level in all tests in both appendices.

We found that the distance between food pits had a significant effect on the number of turnstones on the experimental plots ($F_{2,17} = 66.5$, $P < 0.01$), but not on the intake rate of these turnstones ($F_{2,17} = 3.8$, $P = 0.04$), nor on the amount of their aggressive behaviour ($F_{2,17} = 3.2$, $P = 0.07$). The largest main effect on the number of turnstones was between the two smallest inter-pit distances; when food pits were 20 cm apart, more than three times as many turnstones were attracted by the same number of food pits and the same amount of food than when food pits were 10 cm apart (Figure 4.1G). The intake rate of turnstones, measured as the percentage of time that focal turnstones spent digging, increased with the distances between food pits, but treatment averages did not differ significantly (Figure 4.1E). Similarly, the rate of intra-specific interactions was lower when food pits were 30 cm apart than when they were 10 or 20 cm apart, but the overlap between treatments was substantial, and this effect was not statistically significant (Figure 4.1F). The block factor triplet did not explain variation in any of these three responses (statistics not shown; Figs 1E, F and G).

APPENDIX 4B: ANALYSES OF COVARIANCE

To study whether a univariate analysis that treats the number of foragers as a predictor variable would have led to different conclusions than the multivariate analysis presented in this paper, we reanalyzed our data using ANCOVAs on log-transformed intake rate and log-transformed rate of intra-specific interactions. In these ANCOVAs, inter-pit distance (X) was included as a (categorical) treatment factor, triplet as a (categorical) block factor, and the number of turnstones as a covariate (C). Additionally, the interaction between the treatment factor and the covariate (X·C) was included.

With regard to intake rate, we found the slope of the regression line of intake rate on the number of turnstones to be the same for all three inter-pit distances (as indicated by the non-significance of the interaction term (X·C): $F_{2,14} = 1.7$, $P = 0.22$). After removing the interaction term from the model, we found that intake rate actually did not depend on the number of turnstones (as indicated by the non-significance of the covariate (C): $F_{1,16} = 2.3$, $P = 0.15$). After removing the covariate from the model (which reduced the model to a simple ANOVA) we found that the distance between food pits did not significantly affect intake rate either (X: $F_{2,17} = 3.8$, $P = 0.04$). Based on this analysis, we would conclude that intake rate was about the same at each inter-pit distance and that variation in intake rate was independent of variation in the number of turnstones.

Performing the same analysis on the rate of intra-specific interactions, we found the slope of the regression line of amount of aggression on the number of turnstones to be the same for all three inter-pit distances (X·C: $F_{2,14} = 0.8$, $P = 0.48$). After removing the interaction term from the model, we found that the rate of intra-specific interactions was significantly affected by both the distance between food pits (X: $F_{2,16} = 9.3$, $P < 0.01$) and the number of turnstones (C: $F_{1,16} = 9.3$, $P < 0.01$). Post hoc comparisons (Bonferroni method) revealed that it was the largest inter-pit distance that differed significantly from the two smaller ones (1 vs 2: -0.49 , $P = 0.08$; 1 vs 3: -0.85 , $P < 0.01$; 2 vs 3: -0.36 , $P < 0.01$). Based on this analysis we would conclude that inter-pit distance significantly affected the turnstones' amount of aggressive behaviour, as did the number of turnstones.

AFTERTHOUGHTS ON CHAPTER 4

When forager density is not under experimental control, foragers may adjust their distribution over food patches. We argued therefore that in such studies the density of foragers should be treated as an uncontrolled response variable, just as intake rate and the amount of aggression are. Only in experiments in which forager density is experimentally controlled, effects of forager density on intake rate can be studied *per se*. Here, I present three ideas that follow on this insight. First, I discuss how the experiment presented in chapter 4 can be interpreted as a patch choice experiment. Second, I discuss the relationship between the generalized functional response and the aggregative response. Third, I discuss the extent to which the generalized functional response can be determined through observations on foraging animals that are free to choice among food patches.

A SEQUENTIAL PATCH CHOICE EXPERIMENT

The general approach to study patch choice decisions is to provide several patches to one or more foraging animals simultaneously (for a review: see Tregenza, 1995). Our experiment was not set up in such a way. Instead, in each trial, we provided free-living birds with a single experimental food patch. This set-up can be interpreted as a ‘simultaneous’ patch choice experiment in which foragers could choose between the experimental patch and ‘the environment’. Interpreted in this way, our experiment would make a rather weak patch choice experiment, because we have little quantitative information about the quality of the environment. However, there may be another, more fruitful way of looking at our experiment.

To minimize variation due to measurements at different moments in time, we performed trials in groups of three (‘triplets’), whereby each treatment level of the factor inter-pit distance featured once in each triplet. Under the assumption that the environment was constant throughout triplets, the within-triplet response of the free-living birds to the three treatment levels can be interpreted in terms of patch choice. Such an interpretation would render our experiment as a *sequential* patch choice experiment. Let me make this clear by comparing predictions of the ideal-free-distribution model with our experimental results.

In its original form (Fretwell and Lucas 1970), the ideal-free-distribution model predicts patch quality to affect the number of foragers, but not their intake rate; more foragers should gather in the better patches, but as a consequence the intake rate of all foragers should be the same (no predictions are made regarding the amount of aggression). If the intrinsic quality of patches is assumed to increase with the extent to which food is spaced out, these predictions of the ideal-free-distribution model would imply that the number of turnstones on the experimental plots should be higher when food is more spaced

out, whereas the time spent digging (our measure of intake rate) should be the same at each of the three inter-pit distances. Thus, interpreted as a sequential patch choice experiment, our data would actually match the predictions of the ideal-free-distribution model. Although this match should be treated with caution¹, I think the example nicely shows how our experiment can be interpreted as a sequential patch choice experiment.

Although we never designed our experiment for this reason, our design may have one advantage over simultaneous patch choice experiments. For foragers it may be easier to distinguish between one experimental patch and the environment than between two (or more) experimental patches, because foragers are presumably more familiar with their environment than with experimental patches, and because experimental food patches usually differ less from each other than from the environment. The downside of this is that a difference in knowledge of the environment and of experimental patches introduces the question of how animals cope with risk.

RELATING RESPONSES

The notion that the interpretation of experiments as studying the direct causal effects of forager density or as studying the consequences of such effects depends on whether or not forager density is experimentally controlled, made me reconsider the relationship between the generalized functional response and the aggregative response. First, I thought about these two responses as quite distinct. Now I have come to think of them as intimately related. In the absence of patch choice, that is, when animals are forced to forage on a specific patch, there is but one relationship; the generalized functional response. As I said in the General introduction, this response describes the relationship between food density, forager density and intake rate. To emphasize the fact that it captures the functional response and what has been referred to as the interference response, I think it may be illuminating to visualize this relationship in three dimensions, together with its two-dimensional projections (Figure 4.5): the functional response and the interference response can be found by projecting the 3-d relationship (Figure 4.5A) on the food density – intake rate plane (Figure 4.5B) and the forager density – intake rate plane (Figure 4.5C), respectively.

The aggregative response cannot be derived from the generalized functional response directly. To do so requires the use of a model that specifies how animals distribute themselves over food patches (a ‘distribution model’). What this model does, is to specify what combinations of food density, forager density and intake rate will be realized. The ideal-free-distribution model, for instance, predicts that at any moment in time, animals will achieve the same intake rate at different combinations of food density and forager density, that is, all observations will lie on lines of equal intake rate (‘isoclines’; Figure 4.6A-C). Once the way foraging animals distribute themselves over food patches has been speci-

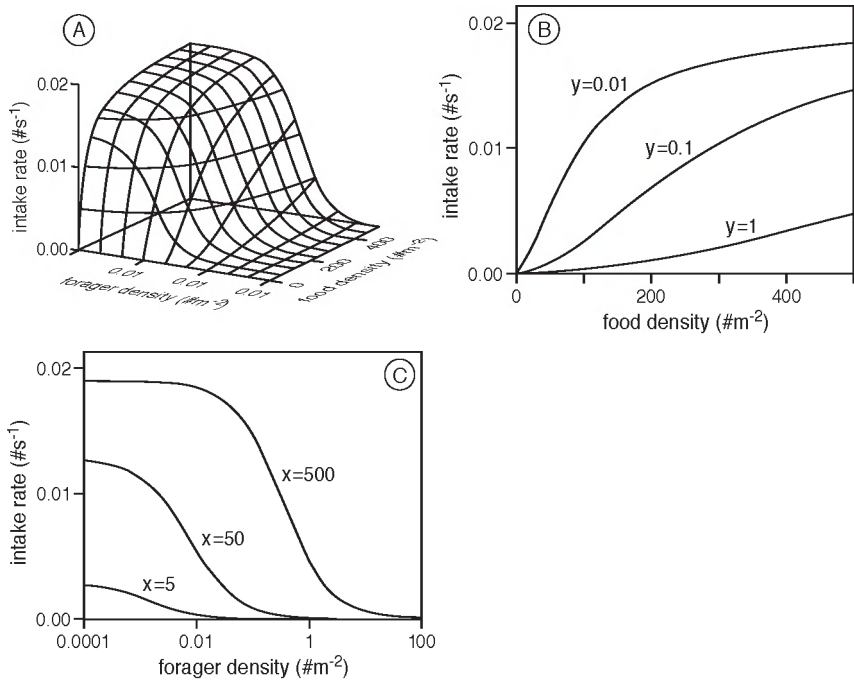


Figure 4.5. Example of a generalized functional response curve, that is, the relationship between food density, forager density and intake rate (A). This response extends the well-known relationship between food density and intake rate – the functional response (B) – by accounting for a negative effect of forager density on intake rate (C). The latter two relationships can visually be derived from the generalized functional response by projecting lines of constant forager density y and food density x on the food density - intake rate and the forager density - intake rate plane, respectively. Note that forager density is plotted on a logarithmic scale.

fied, the aggregative response can be found visually by projecting the generalized functional response on the food density – forager density plane (Figure 4.6D). How the aggregative response can be derived from the generalized functional response analytically was explained by van der Meer and Ens (1997).

DETERMINING THE GENERALIZED FUNCTIONAL RESPONSE

One implication of the above line of thinking is that the generalized functional response can be determined both in the absence and in the presence of patch choice. To see that this is the case, it should be realized that all observations on food density, forager density and intake rate in multi-patch situations (i.e., in the presence of patch choice) lie on the generalized functional response (Figure 4.6). This implies that by collecting enough data of animals foraging in multi-patch situations, it should be possible to determine the generalized functional

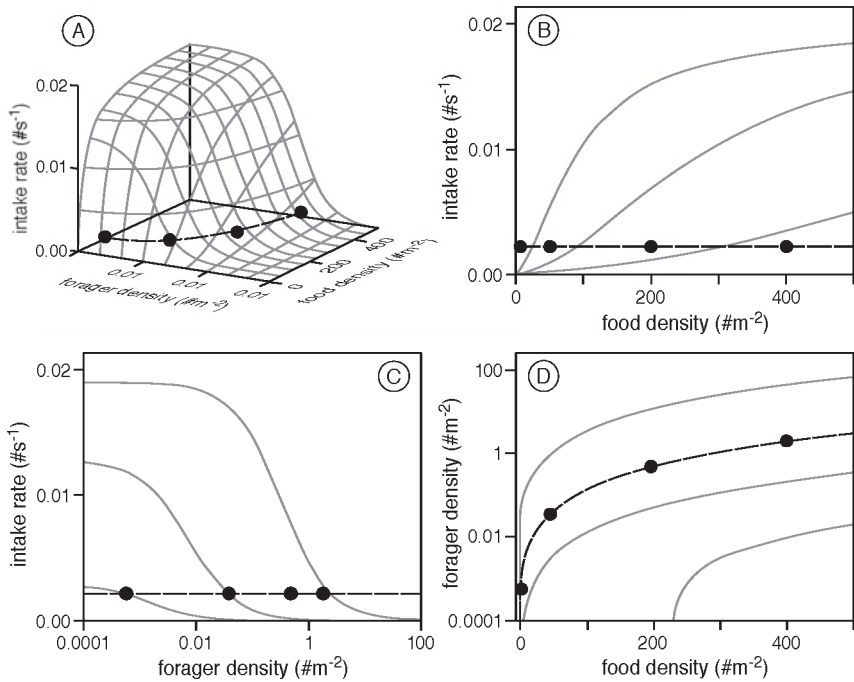


Figure 4.6. Predictions (black dots) of the realized combinations of food density, forager density and intake rate in a four-patch system. These predictions are generated from the combination of a generalized functional response (thin grey lines) and the ideal-free-distribution model. At any moment in time, only a very limited part of the underlying generalized functional response is realized; all observations on intake rate lie on a straight line. Panels A-C as in Figure 4.6. Panel D give the aggregative response, i.e. the realized combinations of food density and forager density. The aggregative response can be derived from the realized generalized functional response (A) by projecting isoclines of intake rate on the food density - forager density plane (D). Note that forager density is plotted on a logarithmic scale.

response. Hence, whether observations are gathered in the absence or presence of patch choice does not determine whether or not the generalized functional response can be determined; that can be done either way. What differs between the two types of observations is the ease with which they allow for determination of this relationship.

Observations on foraging animals that cannot choose between food patches provide the most straightforward way to determine the generalized functional response, because such observations are not affected by feedback effects of aggression and/or intake rate on forager density. This implies that intake rate can be measured at any experimentally determined combination of food density and forager density, and thus that the generalized functional response can easi-

ly be determined for the whole range of relevant food densities and forager densities. In a multi-patch situation, on the contrary, foraging animals can choose between food patches, and hence feedback effects may come into play; foragers may adjust their distribution in response to, or even in anticipation of, interference effects. As a consequence, combinations of food density and forager density realized in a multi-patch system will not be random; instead, they will be inter-correlated (i.e., there will be collinearity). Certain combinations of food density and foragers density will feature less often than other combinations, and some combinations may not be encountered at all. For instance, of high forager densities on patches with a low food density, or observations of low forager densities on patches with high food density will not often be realized. This implies that observations gathered from a multi-patch system may not easily reveal the entire generalized functional response. In fact, they may reveal only a very small part of it. Figure 4.6 illustrates the potential severity of this idea: according to the ideal-free-distribution model, at any moment in time, all observations on food density, forager density and intake rate will lie on an isocline of intake rate. This isocline lies on the generalized functional response, but it reveals only a very limited part of it. Of course, a larger part of the generalized functional response may be revealed by collecting observations over a longer period of time. However, doing so may increase the risk of confounding effects of uncontrolled factors. Thus, the generalized functional response can be determined from observation of animals foraging in a multi-patch situation, but this involves two risks. Observations may reveal only a small part of the generalized functional response, so that interference effects are likely to be underestimated, and they may be confounded by effects of uncontrolled factors.

NOTE

- ¹ We never designed the experiment to study patch choice decisions, and therefore too much emphasis on a match between experimental results and the predictions of the ideal-free-distribution model would be opportunistic. Moreover, the assumption that patch quality increases with inter-pit distance is not obvious. As is clear from chapters 3 and 5, the relationship between the distribution of food and the intrinsic quality of patches may well differ for birds of different dominance status. Also, the failure to detect an effect on the time spent digging (our measure of intake rate) may indeed be actual (as predicted by the ideal-free-distribution model), but it may also have been due to a lack of statistical power.

REFERENCES

- Tregenza T, 1995. Building on the ideal free distributions. *Advances in Ecological Research* 26:253-307.
- van der Meer J, Ens BJ, 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology* 66:846-858.

