

University of Groningen

Spatial clumping of food and social dominance affect interference competition among ruddy turnstones

Vahl, WK; Lok, T; van der Meer, J; Piersma, T; Weissing, FJ

Published in:
 Behavioral Ecology

DOI:
[10.1093/beheco/ari067](https://doi.org/10.1093/beheco/ari067)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2005

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Vahl, WK., Lok, T., van der Meer, J., Piersma, T., & Weissing, FJ. (2005). Spatial clumping of food and social dominance affect interference competition among ruddy turnstones. *Behavioral Ecology*, 16(5), 834-844. <https://doi.org/10.1093/beheco/ari067>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Spatial clumping of food and social dominance affect interference competition among ruddy turnstones

Wouter K. Vahl,^{a,b} Tamar Lok,^{a,b} Jaap van der Meer,^a Theunis Piersma,^{a,b} and Franz J. Weissing^b

^aDepartment of Marine Ecology and Evolution, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands, and ^bCentre for Ecological and Evolutionary Studies, University of Groningen, Kercklaan 30, 9751 NN Haren, The Netherlands

In studying the success of foraging animals, studies of interference competition have put emphasis on effects of competitor density, whereas studies of resource defense have focused on the effects of the spatial distribution of food within patches. Very few studies have looked at both factors simultaneously, that is, determined whether the effects of competitor density on foraging success depend on the spatial distribution of food. We studied the behavior and the foraging success of ruddy turnstones (*Arenaria interpres*) using an experiment in which we varied both the presence of a competitor and the food distribution. Because turnstones may differ strongly in their relative dominance status, we also experimentally varied the foragers' relative dominance status. We found that the presence of a competitor only reduced the foraging success of subordinate birds foraging at the clumped food distribution. At this condition, dominant and subordinate birds differed markedly in their foraging success. Contrary to our expectations, we did not observe more agonistic behavior at the clumped food distribution. This indicates that the amount of agonistic behavior observed may be a bad indicator of interference effects. These findings have specific implications for models of interference competition. Most notably they show that the effects of competitor density on agonistic behavior and foraging success may well depend on the spatial distribution of food and the foragers' relative dominance status. Additionally, our results suggest that social dominance will not be fully understood without considering long-term processes such as the formation and maintenance of social dominance hierarchies. *Key words:* agonistic interactions, *Arenaria interpres*, density dependence, foraging behavior, foraging experiment, resource defense. [*Behav Ecol* 16:834–844 (2005)]

Foraging animals often compete with one another for resources (Keddy, 2001). Because the presence of competing individuals may lower the success of foragers, competition may affect the survival and reproduction of foragers. Hence, competition can be important for the dynamics of animal populations (Christian, 1970; Gauthreaux, 1978). Negative effects of other foragers arise through resources, which can either be depressed (*prey depression*: Charnov et al., 1976; Goss-Custard, 1970) or depleted (*exploitative competition*: Grover, 1997; Park, 1954). Negative effects can also arise through behavioral interactions between competitors (*interference competition*: Miller, 1967; Park, 1954), including avoidance behavior (e.g., Baker et al., 1981), the stealing of resources (e.g., Brockmann and Barnard, 1979; Dolman, 1995; Ens et al., 1990), the monitoring of other foragers (Cresswell, 1997), the loss of control over search paths (e.g., Cresswell, 1997), and the loss of concentration (e.g., Dukas, 1998). Both resource competition and interference competition have been of central interest in behavioral ecology (e.g., Huntingford and Turner, 1987) and population dynamics (e.g., Grover, 1997; Keddy, 2001). Nevertheless, our understanding of interference competition in particular is still rudimentary (van der Meer and Ens, 1997).

Mechanistic models of interference competition originally assumed that interference competition results from the loss of time spent on agonistic interactions (e.g., Beddington, 1975;

Ruxton et al., 1992). However, these models did not address the question as to why foragers should interact agonistically with each other (van der Meer and Ens, 1997). This question is of central importance for all mechanistic studies of interference competition (Huntingford and Turner, 1987). Agonistic interactions may be very costly in terms of time and energy, and risk of injury or death (Huntingford and Turner, 1987). Moreover, agonistic interactions may result in a reduced intake rate and in a redistribution of foragers over space, forcing some individuals into suboptimal habitats with, for instance, a high risk of predation and parasitism (Goss-Custard, 1980). From an adaptive point of view, agonistic behavior can only be understood if benefits outweigh the costs for at least some of the participants. More recent models of interference competition, addressing why foragers interact with one another (e.g., Broom and Ruxton, 1998; Giraldeau and Caraco, 2000; Sirot, 2000; Stillman et al., 1997), stipulate that the benefits of agonistic behavior arise from kleptoparasitism (food stealing) and the associated reduction in search time and handling time (Brockmann and Barnard, 1979; Giraldeau and Caraco, 2000). These models assume that individuals fight over single food items.

Interactions over individual food items are only possible when prey-handling time is sufficiently long (Ens et al., 1990). In many systems, such as geese feeding on grass (e.g., Black and Owen, 1989) and sparrows feeding on seeds (e.g., Barnard and Sibly, 1981), prey-handling time is short. Models of interference competition, therefore, do not provide a satisfying answer to the question why foragers interact agonistically in such systems. Alternatively, several studies have suggested that interactions may also concern small food clumps within a foraging patch (e.g., Amat and Obeso, 1991; Bautista et al.,

Address correspondence to W.K. Vahl. E-mail: vahl@nioz.nl.

Received 27 August 2004; revised 28 April 2005; accepted 2 May 2005.

1998; Myers et al., 1979; Stillman et al., 2002). If competition is mainly about access to profitable food clumps, then, obviously, the spatial distribution of food items should strongly influence interference effects (Grant, 1993). Models of interference competition do not account for effects of heterogeneous food distributions, as they assume that food is distributed homogeneously. This assumption is ubiquitous among foraging models, even though it is not often made explicitly. Most models based on Holling's disc equation, for instance, implicitly assume a homogeneous food distribution (Jeschke et al., 2002). If agonistic interactions concern within-patch food clumps, it may be crucial for our understanding of interference competition to study how the effects of competitor density on foraging success depend on the spatial distribution of food.

Although not often acknowledged in the literature on interference competition, the effect of the spatial distribution of food on the foraging process has received ample attention in the resource defense literature (e.g., Brown, 1964; Davies and Houston, 1984; Grant, 1993; Warner, 1980). Several studies of resource defense have experimentally varied the effect of the spatial clumping of food and studied the effects on agonistic behavior and foraging success (Table 1). These studies show that the spatial distribution of food often affects both foraging success and the level of agonistic behavior. Few of such resource defense experiments, however, have studied how the spatial clumping of food may interact with competitor density to effect foraging success (Table 1). Most of the resource defense experiments could not determine the combined effects of spatial clumping and competitor density either because they did not vary competitor density, that is they measured at a single competitor density, or because they did not control competitor density. Competitor density should be controlled experimentally to exclude feedback loops between competitor density, agonistic behavior, and foraging success, which may well counteract the direct effects of competitor density. The potential importance of this can for instance be seen in the ideal-free-distribution theory (Fretwell and Lucas, 1970), which assumes a direct negative effect of competitor density on foraging success but predicts no such relationship between competitor density and foraging success when measured between patches. Only three studies (Benkman, 1988; Rubenstein, 1981; Theimer, 1987) measured the effects of spatial clumping at more than one experimentally controlled competitor density. Together these three studies indicate that interference effects may indeed depend on the spatial distribution of food, even though the conclusions of Benkman (1988) and Rubenstein (1981) should be treated with caution (see footnotes to Table 1). Thus, studies of interference competition have focused on the effect of competitor density on foraging success, and studies of resource defense have concentrated on effects of spatial clumping, but very few studies have determined whether the effect of competitor density on foraging success depends on the spatial distribution of food.

In view of this lack of experimental studies, we examined the behavior and the foraging success of ruddy turnstones (*Arenaria interpres*; henceforth called turnstones) in an experiment in which we varied the spatial food distribution and the density of competitors. Unlike previous studies (Table 1), we studied the effects of competitor density by systematically comparing the behavior and success of individuals foraging alone with that of the same individuals foraging in the presence of one competitor. This approach leaves out potential complicating effects of larger group sizes, which we studied in another experiment (Vahl et al., in press). The use of an indoor experimental facility enabled us to keep most factors of potential importance constant (environmental conditions, energy expenditure, and level of satiation). We chose to study

turnstones because they generally forage in systems where prey-handling time is short and, hence, kleptoparasitism absent (Fuller, 2003; Harris, 1979; Whitfield, 1990). Wintering turnstones forage in relatively small flocks of stable composition (Metcalf, 1986; Metcalfe and Furness, 1985) in which stable dominance hierarchies are generally formed (Metcalf, 1986; Whitfield, 1988). Correspondingly, the turnstones in this experiment differed strongly in their relative dominance status. Similar differences in dominance status among foragers were present in many of the previous studies on the effect of spatial clumping, even though many of these studies did not consider them (Table 1). When present, it may be crucial to consider such differences in the study of foraging behavior (Baker et al., 1981; Daily and Ehrlich, 1994; Piper, 1997; Smith et al., 2001). Therefore, we additionally included the relative dominance status of the subjects as an experimental factor in our design. Previous studies that did take differences in dominance status into account did so a posteriori, when analyzing their data (Table 1). We think this approach is potentially misleading, as dominance in these studies may be the result rather than the cause of observed foraging behavior. Therefore, we determined dominance status independently of our actual experiment.

In summary, we studied whether the effect of the presence of a competitor on the behavior and success of foraging turnstones depended on the spatial clumping of food, while taking into account differences in the foragers' relative dominance status. Based on the assumptions that agonistic interactions are only over food clumps, that interactions reduce intake rate because they cost time, that foragers behave as to maximize their intake rate, and that resources are not notably depleted in the course of our measurements, we expected the following results, in line with resource defense theory (Grant, 1993; Warner, 1980). When food is clumped, it might be beneficial to fight for and defend a profitable food clump. Hence, one should expect high levels of agonistic interactions, resulting in a lower intake rate in the presence of a competitor than in the absence of a competitor. Moreover, intake rates should be skewed, with dominant foragers having a higher intake rate than subordinate ones. When food is dispersed, it may not be economically defendable, and hence domination of food clumps should not be possible. Accordingly, we expected no agonistic interactions and intake rates that are not affected by the presence of a competitor. Because the absolute intake rates at both food distributions depended on experimentally determined characteristics, such as the ease with which individual food items and food clumps were found, we had no a priori expectations on which of both food distributions would yield the highest intake rate.

METHODS

Subjects and housing

We used 17 turnstones (6 females, 11 males; sexed with a standard molecular assay verified for waders by Baker et al., 1999), caught with mist nets on an intertidal mudflat in the eastern Dutch Wadden Sea (53° 29' N, 6° 15' E) on 8 October 2002. We housed the turnstones in the indoor experimental shore-bird facility of NIOZ, Texel. We caught and housed the turnstones according to Dutch legislation (Dutch bird-ringing center license number 351 and DEC protocol 2000.04, respectively). In the experimental facility they had two roosting aviaries (measuring 4.3 × 1.2 m and 3.0 m high) and an experimental room (7 × 7 m and 3.5 m high) at their disposal. A thin film of running 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

Table 1
Experiments on the effect of spatial clumping on agonistic behavior and/or foraging success

	Species	English name	Sample size			Group size	Additional experimental factors	Dominance ^c	Agonistic behavior ^d	Foraging success ^e	Factor ^f	Reference
			<i>n</i> ₁	<i>n</i> ₂	<i>n</i> ₃							
Mammals	<i>Equus burchelli</i>	Plains zebra	1	2	3	9		No	0	No		Ganslosser and Dellert (1997)
	<i>Equus hemionus kulan</i>	Asiatic wild ass	1	2	3	9		No	0	Yes		Ganslosser and Dellert (1997)
	<i>Lepus europaeus</i>	Brown hare	u ^b	2	28	(1–11)		Yes	+	Yes	Dominance	Monaghan and Metcalfe (1985)
	<i>Macaca mulatta</i>	Rhesus monkey	1	2	3	17		Yes	+	Yes	Dominance	Southwick (1967)
	<i>Macaca mulatta</i>	Rhesus monkey	1	2	10	15	Food type	Yes	+, 0, –	Yes	Food type, dominance	Belzung and Andersson (1986)
	<i>Macaca mulatta</i>	Rhesus monkey	1	5	254	74	Food size	Yes	+, 0	Yes	Type of aggression	Mathy and Isbell (2001)
	<i>Macaca radiata</i>	Bonnet macaque	1	2	4	15		Yes	+		Dominance	Boccia et al. (1988)
	<i>Sciurus niger</i>	Fox squirrel	u	3	104	u		No		Yes		Schmidt and Brown (1996)
Birds	<i>Junco hyemalis</i>	Dark-eyed junco	u	2	u	(1–25)		No	+			Ralph (1977)
	<i>Junco hyemalis</i>	Dark-eyed junco	17	2	118	2, 3	Group size	Yes	–, 0	Yes	Group size, dominance	Theimer (1987)
	<i>Lonchura punctulata</i>	Spice finch	3	3	90	5		Yes		Yes		Giraldeau et al. (1990)
	<i>Loxia curvirostra</i>	Red crossbill	5	3	300	1, 4	Group size	Yes	+	Yes, no	Group size	Benkman (1988) ^g
	<i>Motacilla alba alba</i>	White wagtail	u	2	4	(1–30)		No	+			Zahavi (1971)
	<i>Passer domesticus</i>	House sparrow	u	7	35	(1–23)	Sex	No	+	No	Sex	Johnson et al. (2004)
	<i>Spizella arborea</i>	American tree sparrow	2	3	30	8		No	+		Habitat	Prescott (1987)
	<i>Spizella pusilla</i>	Field sparrow	1	3	18	(2–4)		No	0			Pearson (1989)
	<i>Sturnus vulgaris</i>	European starling	1	4	12	11		No	+	No		Feare and Inglis (1979)
	<i>Zenaida aurita</i>	Zenaida dove	u	2	24	(1–15)	Temporal predictability	No	+		Temporal predictability	Goldberg et al. (2001)
	<i>Zonotrichia albicollis</i>	White-throated sparrow	1	3	18	(2–4)		No	+		Group size	Pearson (1989)
<i>Zonotrichia querula</i>	Harris's sparrow	u	2	25	(1–10)		Yes	+		Group size, dominance	Rohwer and Ewald (1981)	

Table 1, continued

	Species	English name	Sample size			Group size	Additional experimental factors	Dominance ^c	Agonistic behavior ^d	Foraging success ^e	Factor ^f	Reference
			n_1	n_2	n_3							
Fish	<i>Cichlasoma nigrofasciatum</i>	Convict cichlid	7	3	21	3	Body size	Yes	+	Yes	Size	Grant and Guha (1993)
	<i>Elassoma evergladei</i>	Everglades pygmy sunfish	12	2	72	1, 4, 8, 16	Group size, food type, sex	Yes		Yes	Dominance	Rubenstein (1981) ^h
	<i>Oncorhynchus keta</i>	Chum salmon	14	2	14	21		No	+			Ryer and Olla (1995)
	<i>Oncorhynchus kisutch</i>	Coho salmon	20	2	20	25	Food ration	No	0			Ryer and Olla (1996) ⁱ
	<i>Oryzias latipes</i>	Japanese medaka	18	6	18	8		No	+, -			Magnuson (1962) (exp IV)
	<i>Oryzias latipes</i>	Japanese medaka	40	2	40	10	Temporal clumping	No	+, -		Temporal clumping	Robb and Grant (1998)
	<i>Salmo salar</i>	Atlantic salmon	6	2	24	>850		No		Yes	Age	Jørgensen et al. (1996)
	<i>Tilapia rendalli</i>	Redbreast tilapia	4	2	8	8		Yes		Yes		McCarthy et al. (1999) ⁱ
Crustaceans	<i>Cherax quadricarinatus</i>	Red-claw crayfish	16	2	54	60	Food ration	No	+			Barki et al. (1997)
Insects	<i>Coccinella septempunctata</i>	Seven-spotted lady beetle	20	2	20	9	Food density	No		Yes, no	Food density	Yasuda and Ishikawa (1999)

^a Three aspects of sample size are given: the number of independent units (n_1), the number of levels of spatial clumping (n_2), and the total number of trials performed (n_3).

^b When group size was uncontrolled (all field experiments), the number of independent units was unknown (u). For these studies, we give (in parentheses) the observed range of group sizes.

^c The column “dominance” indicates whether differences in dominance positions are taken into account in the analysis.

^d The column “agonistic behavior” indicates whether more (+), less (–), or the same amount (0) of agonistic behavior was observed when the level of spatial clumping of food increased. When more than one sign is given, multiple effects were reported.

^e The column “foraging success” indicates whether spatial clumping affected some measure of foraging success. Note that this means that effects on growth rate are not included. When both “yes” and “no” are given, multiple effects were reported.

^f The column “factor” indicates which factors interacted with spatial clumping in their effects on agonistic behavior, foraging success, or both. Note that these factors were not necessarily included in the experimental design.

^g Benkman (1988) blocked treatment combinations within experimental days. The resulting unbalanced design is problematic, especially because the subjects appeared to be learning throughout the experiment. Moreover, results on aggression are only given for two of the three levels of spatial clumping.

^h Rubenstein (1981) does not present the full results of his experiment. Instead, he consistently presents examples of the densities 4, 8, and 16.

ⁱ McCarthy et al. (1999) and Ryer and Olla (1996) simultaneously varied spatial and temporal clumping and therefore could not separate effects of spatial and temporal clumping.

and bathing was always present. 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 constant with respect to air temperature (18°C), water temperature (10°C), and light regime (12:12 h light:dark). Moonlight-mimicking lights illuminated the aviaries between 1900 and 0700 h.

Preexperimental treatment

The experiment took place from 20 November to 5 December 2002. By then, the birds had been accustomed to the aviaries and the experimental procedure for several weeks. To familiarize them with the experimental environment and procedure, the birds participated in pilot trials for 26 days, prior to the experiment.

In the first three pilot days, we determined the social dominance hierarchy. In 24 trials, we observed agonistic interactions among six randomly chosen birds. We recorded the outcome of each interaction ($n = 760$): winners were those individuals that either chased their opponent away or that held ground after being attacked. Assuming a linear dominance hierarchy, we determined cardinal scale rank positions by means of a logit regression analysis (Tufto et al., 1998; van der Meer, 1992). Previously, we used the same technique to study the stability of the dominance hierarchy among a group of 27 captive turnstones (Vahl and van Dullemen, unpublished data). Their dominance hierarchy was rather stable during the 6 months measured. Similarly, dominance hierarchies among turnstones in the field are known to be stable (Metcalf, 1986; Whitfield, 1988), and the results from the current experiment also confirm a stable hierarchy. During winter, no differentiation is apparent among male and female turnstones, and, correspondingly, the position in the dominance hierarchy was independent of sex in this experiment. We designated the three highest-ranking and the two lowest-ranking birds as "nonfocal" individuals and the 12 other birds as "focal" individuals. We collected data on the focal individuals; only we used the nonfocal birds as experimental competitors and to vary the relative dominance status of the focal individuals. To recognize the birds from all angles, we bleached a small area of the back feathers of the focal birds, using commercial hair bleach.

In the remaining 23 pilot days, we trained the birds to recognize food distribution on a foraging platform instantaneously (i.e., prior to landing on the platform; see Appendix). This minimized behavioral changes associated with information gain in the course of a trial, and it excluded the possibility that food distribution had no effect simply because the birds did not know it.

Experimental setup

During the experiments, we flooded the experimental room with seawater to a depth of 20 cm. The only dry area remaining was a foraging platform (1 m²) consisting of four gravel tiles positioned 20 cm above the water level. We recorded the foraging behavior of the subjects using two digital video cameras (Sony dcr-rv900e). One camera was positioned next to the foraging platform at a distance of 1.5 m for a sideways view; the other was mounted directly above the foraging platform at a height of 3.5 m.

In all trials we placed 80 maggots (Diptera larvae) on the foraging platform. To ensure that the birds had to search for their food, we then covered the foraging platform with a 5-cm layer of seaweed (bladder-wrack, *Fucus vesiculosus*). This layer of *Fucus* resembled the natural foraging substrate of turnstones (Fuller, 2003; Whitfield, 1990). Although maggots are

not part of the natural diet of turnstones (Fuller, 2003; Harris, 1979; Whitfield, 1990), they resemble other invertebrates included in the diet (especially the larvae of wrack flies, Coelopa; Fuller, 2003), and the turnstones were keen to eat them. We used 80 maggots per trial to minimize the effects of depletion and because both the density of 80 maggots m⁻² and the local density of 1280 maggots m⁻² (clumped condition) lie within the range of invertebrate densities encountered by foraging turnstones in the field (Fuller, 2003). We placed maggots on the foraging platform in either a dispersed or a clumped way. Turnstones are likely to encounter various levels of clumping of food in the field, though the relative frequency of each level will be hard to assess. To make the food distribution dispersed, we divided the foraging platform into 16 squares of 25 × 25 cm, and we spread out five maggots arbitrarily over each square. We made the food distribution clumped by putting all 80 maggots on one randomly chosen square. We attached white or black plates (1.0 × 0.30 m and 5.0 mm thick) to the sides of the foraging platform to signal a dispersed and a clumped food distribution, respectively (see Appendix).

We varied the relative dominance status of focal birds, defined as the consistent ability of one bird to cause its specific opponent to yield in agonistic encounters (Piper, 1997), through choice of the nonfocal competitor. We assigned focal birds to either be a dominant or a subordinate by the addition of one of the two lowest-ranking or one of the three highest-ranking nonfocal birds, respectively. Hence, dominance was a relative quality rather than an individual attribute (Francis, 1988; Piper, 1997). Thus, rather than studying the determinants of dominance status, we chose to study the consequences of a given dominance status.

Experimental procedure

We deprived the birds of food from 1800 h and tested them between 0930 and 1200 h on the next day. At the start of each experimental day, we placed all birds in fixed groups of two or three in boxes measuring 50 × 35 cm and 25 cm deep, keeping focal and nonfocal birds separated. The birds were very quiet in the dark, and we thus captured and housed them in darkness to minimize stress. Before each trial, we transferred a specific focal bird to one of the roosting aviaries, either on its own or together with a nonfocal bird. After opening the sliding door, we attracted the birds into the experimental room by dimming the lights in the roosting aviary while lighting the experimental room. Subjects readily flew to the experimental platform and started to forage within seconds of the sliding doors being opened. The trials started at the moment the focal bird began to forage and lasted for 120 s.

After each trial we used lights again to entice birds back to the roosting aviary. We transferred the birds to the second roosting aviary and we counted the number of unconsumed maggots left on the foraging platform. We then repeated the procedure. After the trials, we kept all birds together in the experimental room and the two roosting aviaries, with sliding doors open and water level low, and we provided trout food pellets ad libitum till the next food-deprivation period.

Experimental design and statistical analysis

We studied the effects of the fixed factors *food distribution* (clumped or dispersed), *competitor present* (yes or no), and *dominance status* (dominant or subordinate), while accounting for effects of the random block factors *focal bird*, *replicate*, and *experimental day within replicate*. The experiment consisted of six, instead of eight, different treatment combinations, as dominance status was a relative measure and required the

presence of a competitor. We used a 6×6 Latin square design (Fisher and Yates, 1963) to distribute the six treatment combinations over six focal individuals and six experimental days. We replicated the experiment both within and between focal individuals by using two times six experimental days and two times six focal individuals. Thus, the experiment consisted of 12 experimental days on each of which 12 focal birds foraged at one of six different treatment combinations twice.

In principle, each bird took part in one trial per day. However, because three treatment combinations required the participation of a subordinate nonfocal forager, and as we had only two such birds, each day one focal bird had to participate twice, once as a nonfocal. In two of the trials, the focal individual's relative dominance status was not as intended, and in one trial the focal individual was highly inactive. We repeated these three trials at the end of the same experimental day. We thus accumulated 144 successful trials.

Recorded behavior and response variables

We analyzed trials using The Observer 3.0 Event Recorder (Noldus Information Technology, Wageningen, the Netherlands). To limit effects of resource depletion, digestive constraints, and satiation, we measured foraging behavior and success during the first 60 s of each trial. Our omission of the remainder of each trial from the video analysis also served to avoid potential end effects (e.g., birds anticipating the end of a trial). The same two observers examined all trials together. In a first analysis of each trial, we used the side-view recording, which we analyzed at one-fifth of normal speed. In a second analysis, we used the top-view recording to verify the observations from the side-view tape. We distinguished five behavioral categories (*search*, *handle*, *interact*, *vigilant*, and *other*), each consisting of several different behaviors (for a description see Vahl et al., in press).

We studied the effect of treatment on *intake rate*, defined as the number of maggots swallowed per total time (number per min^{-1}). We additionally scored the *time spent on the food clump* (%), we determined their *time allocation* (defined as the total number of seconds allocated to each of the five behavioral categories), and we scored the rate of agonistic interactions (number per min^{-1}). In doing so we distinguished between offensive (*attack* and *threat*) and submissive (*escape* and *avoid*) interactions, and additionally we distinguished between high-intensity (*attack* and *escape*) and low-intensity (*threat* and *avoid*) interactions. We defined high-intensity interactions as those in which the bird that initiated the interaction was actively moving towards its opponent.

Data transformation and hypothesis testing

Data on time allocation is compositional (Aitchison, 1986): the sum of the time allocated to the various behavioral categories is constrained at 100%. We therefore analyzed the ratio of time spent on interactions over time spent on searching, handling, and vigilance behavior. Furthermore, we assumed that the various treatments had a multiplicative effect on all response variables. Because general linear models (GLMs) assume that effects interact in an additive way, we log-transformed all measurements. To avoid taking logarithms of zero, we added the value one to all observations on intake and on the number of interactions. For data on interacting time, zero replacement was achieved by using the procedure for nonessential zeros in compositional data (Aitchison, 1986).

We analyzed the experiment in accordance with the standard Latin square design, using the GLM procedure in SYSTAT 10 (SPSS Inc., Chicago, IL). We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller, 1997).

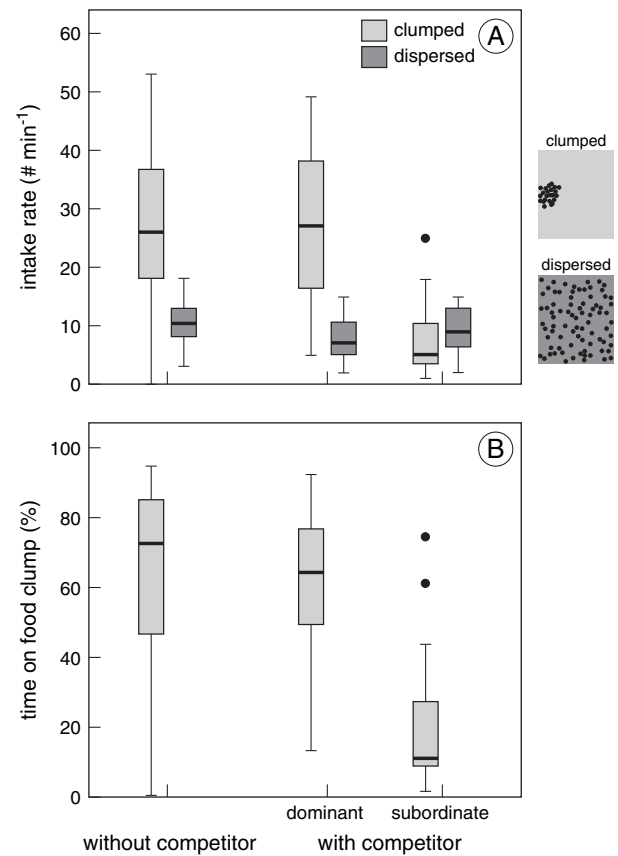


Figure 1

Box plots of foraging success (A) at the clumped and dispersed food condition and, for the clumped food distribution only, the time birds spent on the food clump (B). Horizontal lines mark median values, boxes encompass the central 50% of the data, and whiskers show the range, apart from outliers that are marked as dots.

RESULTS

Foraging success

The presence of a competitor had a strong effect on intake rate, but this effect depended both on the food distribution and on the relative dominance status of the focal bird (Figure 1A; Table 2). The intake rate of birds foraging alone was more than two times higher when food was clumped than when it was dispersed, probably because all birds were able to find the food clump within 60 s and the subsequent discovery of individual maggots was rather easy. When food was dispersed, birds achieved the same intake rate in the presence of a competitor as when foraging alone, regardless of their dominance status. When food was clumped, the presence of a competitor did not affect the intake rate of dominant birds. However, the presence of a competitor reduced the intake rate of subordinate birds more than threefold (Figure 1A). Still, the intake of subordinate birds was not zero because they sometimes found the food clump first and because dominant birds sometimes temporarily left the food clump to search elsewhere on the foraging platform. Intake rates varied considerably between individuals (Table 2).

Time spent on the food clump

Dominant birds spent the same amount of time on the food clump in the absence and the presence of a competitor,

Table 2

Treatment effects on intake rate, time spent on the food clump, interacting time, and on the rate of offensive (*attack, threat*) and submissive (*escape, avoid*) interactions

	Intake rate			Time spent on the food clump			Interacting time ($T_I/(T_S+T_H+T_V)$)			Offensive behavior			Submissive behavior		
	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>	df	<i>F</i>	<i>p</i>
Replication	1	3.2	.08	1	0.0	.84	1	1.2	.28	1	0.4	.53	1	0.0	1.00
Day (replication)	10	0.7	.74	10	0.8	.64	10	0.2	.99	10	1.0	.49	10	1.3	.25
Focal individual	11	3.4	<.01	11	1.5	.17	11	1.1	.37	11	2.0	.05	11	1.2	.28
Treatment	5	26.7	<.01	2	28.9	<.01	3	5.9	<.01	3	77.3	<.01	3	898.9	<.01
Food distribution "A"	1	30.7	<.01	—	—	—	1	4.5	.04	1	1.7	.19	1	0.7	.42
Presence of competitor "B"	1	21.3	<.01	1	13.1	<.01	—	—	—	—	—	—	—	—	—
Dominance status "C"	1	29.9	<.01	1	44.8	<.01	1	2.3	.13	1	206.4	<.01	1	2695.3	<.01
A × B	1	4.3	.04	—	—	—	—	—	—	—	—	—	—	—	—
A × C	1	47.4	<.01	—	—	—	1	10.8	<.01	1	23.9	<.01	1	0.7	.42
Error	116			47			70			70			70		
Total	143			71			95			95			95		

Interacting time is analyzed as the ratio of time spent on interactions (T_I) over time allocated to searching (T_S), handling (T_H), or vigilance (T_V) behavior. GLM test results on log-transformed data are given. Effects significant at the .05 level are indicated by bold *p* values.

whereas subordinate birds spent less than a third of their time on the food clump when a competitor was present rather than absent (Figure 1B; Table 2).

Time allocation

At all conditions, the birds spent most of their time on searching and, to a lesser extent, on vigilance, while only a small amount of time was spent on interactions (Table 3). The amount of time spent vigilant was constant over all treatment combinations, whereas the time allocated to searching, handling, and interacting differed per treatment combination (Tables 2 and 3). Solitary foragers handled more and searched less when food was clumped than when food was dispersed (Table 3). When food was dispersed, the birds spent as much time handling and searching in the presence of a competitor as when foraging alone, regardless of dominance status. When food was clumped, the same was true for dominant birds, but subordinate birds handled less and searched more when a competitor was present. The amount of time spent on interactions depended on both food distribution and relative dominance status (Table 2), as only dominant birds spent

more time interacting when food was dispersed than when food was clumped.

Offensive versus submissive behavior

Dominant birds directed more offensive interactions to their competitors than did subordinate birds and especially so when food was dispersed (Figure 2A; Table 2). Dominant birds did not perform submissive behaviors in response to offensive behavior directed to them by subordinate competitors. Instead, they responded aggressively when attacked by a subordinate competitor (Figure 2B). These results did not change when we took the intensity of agonistic behavior into account (not shown).

Do absolute dominance positions matter?

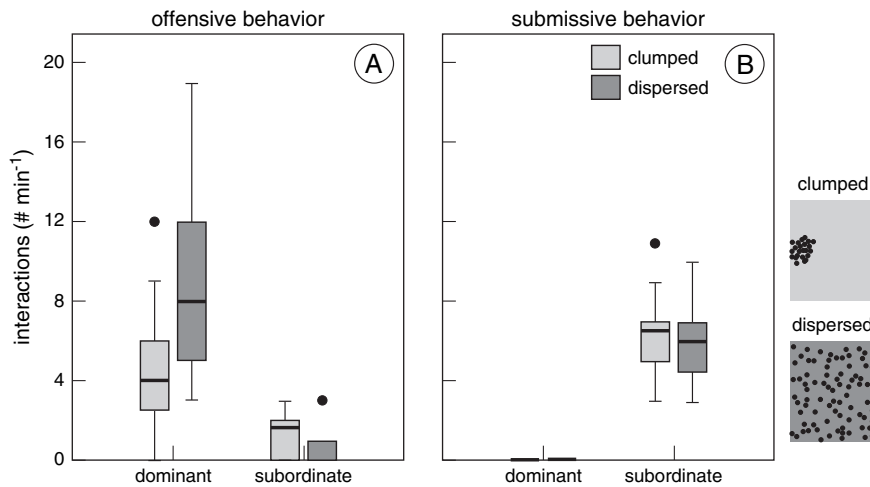
The behavior and success of the turnstones depended strongly on their relative dominance status (Figures 1 and 2; Table 2). When tested on the residuals of the full model (which included relative dominance status), the difference in rank number (i.e., position in the dominance hierarchy)

Table 3

Total amount of time (s) allocated to the behavioral categories searching (T_S), handling (T_H), vigilance (T_V), and interacting (T_I) per treatment combination

Food distribution	Competitor present	Dominance status	T_S	T_H	T_V	T_I
Clumped	No	—	34.6 (3.6)	11.2 (5.0)	14.0 (6.5)	—
	Yes	Dominant	33.8 (5.9)	11.1 (5.3)	12.1 (6.6)	2.7 (1.9)
	Yes	Subordinate	38.9 (4.9)	3.3 (1.6)	13.3 (4.6)	4.1 (1.0)
Dispersed	No	—	43.6 (4.9)	4.0 (0.8)	12.1 (5.1)	—
	Yes	Dominant	38.6 (5.8)	3.0 (1.0)	12.8 (4.4)	5.3 (3.1)
	Yes	Subordinate	39.6 (4.2)	3.7 (1.3)	12.9 (4.1)	3.3 (0.8)

Because data on the behavioral category "other" is not presented, the sum of the time allocated to these four behaviors is only approximately equal to the total trial duration (60 s). Numbers in parentheses represent 1 SD.

**Figure 2**

Box plots of the rate of agonistic interactions for dominant and subordinate birds, at a clumped or dispersed food distribution. We distinguished between offensive interaction behavior directed by focal birds to subordinate competitors (attacks and threats; left panel) and submissive interaction behavior in response to offensive behavior directed by the non-focal bird (escapes and avoidances; right panel). See Figure 1 for an explanation of the composition of box plots.

between focal birds and their nonfocal competitor did not explain any extra variation in intake rate (GLM, $F_1 = 0.08$, $p > .5$) or in the number of agonistic interactions (GLM, $F_1 = 0.01$, $p > .5$). Apparently, knowledge on the relative dominance status of competing individuals sufficed to explain variation in the behavior and success of the turnstones.

DISCUSSION

Treatment effects on foraging success were as expected. Nevertheless, the effects on agonistic behavior deviated from our expectations. To our surprise, dominant and subordinate birds differed strongly in their intake rates when food was clumped, even though they spent the same amount of time on agonistic interactions. This suggests that the amount of agonistic behavior shown by an individual and its intake rate are not directly related. When food is clumped, dominant foragers can apparently monopolize food with few interactions. The most important lesson to be drawn from this is that it may be difficult to predict interference effects from the amount of agonistic behavior observed.

The treatment factors affected agonistic behavior in such a way that two of our expectations were not met. First, the experimental birds did not interact more when food was clumped than when food was dispersed. Instead, dominant birds even spent slightly more time on offensive behavior when food was dispersed. Thus, subordinate birds did not increase their level of agonistic behavior when food was clumped, even though their intake rate was reduced severely at this condition. A similar result was found by some of the other experimental studies (e.g., Belzung and Andersson, 1986; Theimer, 1987). The most extreme example is probably given by Southwick (1967), who found that subordinate rhesus macaques (*Macaca mulatta*) would, in response to diminished food supplies, rather die from starvation than increase their level of agonistic behavior towards dominant individuals. Our results are most likely a consequence of the turnstones being highly familiar with each other. When familiarity is high, relative dominance status of foragers may be so well established that little agonistic behavior is required to maintain ownership of resources (e.g., Balph, 1977). This would imply that aspects related to the formation and maintenance of dominance hierarchies, such as familiarity among the foragers, may well be crucial for a full understanding of interference behavior. Regardless of the proximate explanation, the lack of a behavioral response by subordinate birds to altered food conditions poses the interesting question as to why foragers acquiesce in a subordinate position. Individual differ-

ences in physical characteristics could explain this, but the answer to this question is far from obvious given that dominance hierarchies may also arise from arbitrary conventions alone (Hammerstein, 1981; Maynard Smith and Parker, 1976). Evolutionary biologists have studied this question for a long time (e.g., Landau, 1951), but this problem has certainly not been resolved (e.g., Mesterton-Gibbons and Dugatkin, 1995; van Doorn et al., 2003a,b). Second, contrary to our predictions, turnstones did not cease to interact agonistically when food was dispersed. This can be explained in various ways. Even when the birds were familiar with each other, some agonistic interactions may, for instance, have been needed to serve long-term goals, such as the formation and maintenance of dominance hierarchies (Piper, 1997). Alternatively, the observed agonistic behavior at the dispersed food distribution might reflect the inability of turnstones to adapt to such a distribution. The latter seems a reasonable option because food in the field is often aggregated (Taylor, 1961), and the chance to obtain access to a food clump by displacing another individual may therefore in general be high.

In comparing these results with previous experiments, it is interesting to note that our results correspond well with those of the only other study on spatial clumping that studied competition among two foragers (Theimer, 1987). Dominant dark-eyed juncos (*Junco hyemalis*) also obtained more food than subordinate juncos when food was clumped and the same amount of food when food was dispersed. Moreover, the number of agonistic interactions among the juncos was also less when food was clumped. This suggests that the effects of spatial clumping on agonistic behavior and foraging success may be general among species. However, it should be realized that the possibility to generalize over other experimental conditions may be restricted. This is clearly illustrated by the study of Theimer (1987), who found different effects of spatial food distribution for groups of two and groups of three birds. This might well be the reason that previous experiments (Table 1), which all strongly differed from each other in their design, gave the impression that general effects were absent.

Implications

We found that the strength of interference effects depended strongly on both the spatial food distribution and on the foragers' relative dominance status. The presence of a competitor only strongly reduced intake rate when food was clumped and when the focal bird was subordinate. Together with the fact

that interactions over individual food items were absent in our experiment, this result suggests that interference competition in our experiment arose through agonistic interactions over food clumps. The quantitative relevance of these findings will depend on the relative frequency with which foragers encounter heterogeneously distributed food in the field. Unfortunately, little is known about the frequency with which food distributions occur at specific levels of heterogeneity (Theimer, 1987). Our understanding of the importance of agonistic interactions over food clumps as an interference mechanism would, therefore, clearly benefit from a systematic investigation of food distributions in the field.

Furthermore, we found that knowledge of the foragers' relative dominance status sufficed to explain variation in the behavior and success of the turnstones. One important consequence of this is that for species with a strong dominance structuring any group will consist of dominant and subordinate individuals, even groups composed of the highest or lowest ranked individuals only. In addition, we found that dominant birds cannot always take advantage of their dominance status. Instead, the extent to which they can do so may depend on external conditions, such as the food distribution. Thus, we could have interpreted the effects of the presence of a competitor without acknowledging the foragers' dominance status when food was dispersed but certainly not so when food was clumped. This finding can probably be generalized to all conditions that affect the extent to which resources or space can be monopolized. Another challenge for future research on interference competition may therefore lie in the prediction of such conditions (Grant, 1993; e.g., Cresswell et al., 2001).

Most models of interference competition cannot explain the strong interference effect that we observed because they assume interference competition to arise solely from kleptoparasitism (i.e., interactions over individual food items: e.g., Broom and Ruxton, 1998; Giraldeau and Caraco, 2000; Sirot, 2000). Acknowledging interactions over food clumps as a potential interference mechanism would provide us with an explanation for the fact that many species interact agonistically with each other in systems where prey-handling time is short, that is in the absence of kleptoparasitism. Incorporating these interference mechanisms in models of interference competition may therefore strongly improve our ability to predict interference effects.

To this end, it is an interesting question whether food clumps are different from food items in an essential way. When such differences are absent, food clumps could simply be redefined as the new food items, and the existing models of interference competition could be used to model agonistic interactions over food clumps. This would only require the replacement of model parameters that are characteristics to food items with those that capture clump characteristics, such as clump-handling time. Stillman et al. (2002) took this approach when modeling interference in common cranes (*Grus grus*) foraging on clumps of cereal seeds, thus assuming that agonistic interactions over food clumps are "similar" to those concerning food items. If, on the contrary, agonistic interactions over food clumps and food items are different from each other, the simple redefinition of food items cannot be used to model interactions over food clumps, and models of interference competition should actually be extended to incorporate interactions over food clumps. This may, for instance, be done by relaxing the basic modeling assumption that food is distributed homogeneously. Several studies have already shown how heterogeneous food distributions can be modeled (e.g., Arditi and Dacorogna, 1988; Cosner et al., 1999; Ruxton and Gurney, 1994).

At first glance, it may seem reasonable to assume that interactions over food clumps and interactions over food items are

not essentially different, especially because many of the behaviors constituting both types of interactions are similar. For instance, regardless of what is at stake, foraging animals may try to steal or defend a resource and avoid or monitor other foragers. However, despite this similarity in the underlying behaviors, interactions over individual food items and small food clumps have distinguishing features that may well affect the composition of costs and benefits and hence the strategic choices of individuals. For instance, unlike most food items, food clumps generally can be divided among multiple foragers because they consist of multiple food items. Thus, although foragers that supplant other foragers from food clumps can be considered to "kleptoparasitize" these food clumps (e.g., Smith et al., 2002), this process may differ from kleptoparasitism over food items in that the supplanted foragers may have exploited their food clumps at least partly before being supplanted. Another potential difference is that winning interactions over individual food items provides foragers with concrete resources, whereas winning interactions over food clumps merely results in an increased chance of finding food in the near future. Because uncertainty about rewards is known to affect decision processes (e.g., Kühberger and Perner, 2003), the fact that foragers have less information on the rewards of an interaction over food clumps may also cause kleptoparasitism over food clumps to deviate from that over food items. Future experimental and theoretical investment should be directed at the differences between the various types of interactions and the consequences of these differences for our predictions on interference behavior.

However, regardless of the relation between interactions over food clumps and interactions over food items, there may be more fundamental problems in the way we currently model interference competition. Models of interference competition all assume that interference effects arise through the loss of time to agonistic interactions. We found that there was no such straightforward relationship between the amount of agonistic behavior of an individual and its intake rate and attributed this to the strong establishment of the relative dominance status of the birds. The prime importance of social dominance in this and many other foraging experiments (Piper, 1997; e.g., Baker et al., 1981; Smith et al., 2001) suggests that long-term processes such as acquiring and maintaining dominance status may be connected to the foraging process in such an intimate way that we cannot fully understand the foraging process without them. In the presence of such long-term processes even basic assumptions like the maximization of intake rate may no longer hold.

APPENDIX

Pilot trials

In the first 14 training pilot days we attempted to teach the birds to associate food distribution with a sign of a specific color and shape. Because these attempts were not successful, we trained the birds in the next nine pilot days to recognize the food distribution on the foraging platform instantaneously (i.e., prior to landing on the platform) on the basis of the same black and white plates that we also attached to the sides of the foraging platform in the actual experiment. During these 9 days each bird performed, on its own, 21 trials of about 60 s. The setup in these trials differed from the experimental setup in that two foraging platforms were present. We positioned the additional platform 3 m from the first platform, and this second platform only differed from the first platform in its food distribution, and

hence the color of the plates attached to its sides. We studied the birds' preferences for each food distribution/plate color by recording on which platform each bird landed first in the last four pilot trials. After the experiment, each bird performed another four trials to study potential changes in preference. We tested preference, using a goodness of fit test for binomial distributions with $p = q = .5$.

The frequency distribution of preference for a specific food distribution deviated significantly from binomial, both before ($\chi^2 = 34.45$, $df = 4$, $p < .001$) and after ($\chi^2 = 28.33$, $df = 4$, $p < .001$) the experiment, indicating that most birds were able to distinguish between the two platforms on the basis of the color of the plates attached to the platforms. Before the experiment, an equal number of birds preferred both food distributions, whereas after the experiment the birds only preferred the clumped food distribution. The difference in preference before and after the experiment indicates that learning to instantaneously recognize platform color and/or food distribution continued throughout the experiment and that, at least after the experiment, the birds based their choice on the food distribution rather than on platform color.

We are grateful to Daan Liefhebber, Maarten Brugge, Anne Dekinga, and Bernard Spaans for their practical assistance throughout the experiment and to the Calidris wader ringing group of Schiermonnikoog (especially Kees Oosterbeek, André Duiven, Siemen Deuzeman, and Wim Fokker) for catching the turnstones. We thank Anneke Bol for molecularly sexing the turnstones and Dick Visser for preparing the figures for publication. We also thank Maaik de Heij, Sjouke Kingma, Isabel Smallegange, and Bruno Ens for stimulating discussions and helpful comments on earlier versions of the manuscript and Richard Fuller and Tanya Compton for commenting on the manuscript and correcting the language. In addition, we are grateful to the editor and the two referees for their valuable comments.

REFERENCES

- Aitchison J, 1986. The statistical analysis of compositional data. London: Chapman and Hall.
- Amat JA, Obeso JR, 1991. Black coots (*Fulica atra*; Aves, Rallidae) supplanting conspecifics for foraging sites. *Ethology* 87:1–8.
- Arditi R, Dacorogna B, 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am Nat* 131:837–846.
- Baker AJ, Piersma T, Greenslade AD, 1999. Molecular vs. phenotypic sexing in red knots. *Condor* 101:887–893.
- Baker MC, Belcher CS, Deutsch LC, Sherman GL, Thompson DB, 1981. Foraging success in junco flocks and the effects of social hierarchy. *Anim Behav* 29:137–142.
- Balgh MH, 1977. Winter social behaviour of dark-eyed juncos: communication, social organization and ecological implications. *Anim Behav* 25:859–884.
- Barki A, Levi T, Shrem A, Karplus I, 1997. Ration and spatial distribution of feed affect survival, growth, and competition in juvenile red-claw crayfish, *Cherax quadricarinatus*, reared in the laboratory. *Aquaculture* 148:169–177.
- Barnard CJ, Sibly RM, 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim Behav* 29:543–550.
- Bautista LM, Alonso JC, Alonso JA, 1998. Foraging site displacement in common crane flocks. *Anim Behav* 56:1237–1243.
- Beddington JR, 1975. Mutual interference between parasites or predators and its effects on searching efficiency. *J Anim Ecol* 44:331–340.
- Belzung C, Andersson JR, 1986. Social rank and responses to feeding competition in rhesus monkeys. *Behav Process* 12:307–316.
- Benkman CW, 1988. Flock size, food dispersion and the feeding behavior of crossbills. *Behav Ecol Sociobiol* 23:167–173.
- Black JM, Owen M, 1989. Agonistic behaviour in barnacle goose flocks: assessment, investment and reproductive success. *Anim Behav* 37:199–209.
- Boccia ML, Laudenslager M, Reite M, 1988. Food distribution, dominance, and aggressive behaviors in Bonnet Macaques. *Am J Primatol* 16:123–130.
- Brockmann HJ, Barnard CJ, 1979. Kleptoparasitism in birds. *Anim Behav* 27:487–514.
- Broom M, Ruxton GD, 1998. Evolutionarily stable stealing: game theory applied to kleptoparasitism. *Behav Ecol* 9:397–403.
- Brown JL, 1964. The evolution of diversity in avian territorial systems. *Wilson Bull* 76:160–169.
- Charnov EL, Orians GH, Hyatt K, 1976. Ecological implications of resource depression. *Am Nat* 110:247–259.
- Christian JJ, 1970. Social subordination, population density, and mammalian evolution. *Science* 168:84–90.
- Cosner C, DeAngelis DL, Ault JS, Olson DB, 1999. Effects of spatial grouping on the functional response of predators. *Theor Popul Biol* 56:65–75.
- Cresswell W, 1997. Interference competition at low competitor densities in blackbirds *Turdus merula*. *J Anim Ecol* 66:461–471.
- Cresswell W, Smith RD, Ruxton GD, 2001. Absolute foraging rate and susceptibility to interference competition in blackbirds varies with patch conditions. *J Anim Ecol* 70:228–236.
- Daily GC, Ehrlich PR, 1994. Influence of social status on individual foraging and community structure in a bird guild. *Oecologia* 100:153–165.
- Davies NB, Houston AI, 1984. Territory economics. In: Behavioural ecology: an evolutionary approach, 2nd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 148–169.
- Dolman PM, 1995. The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. *Oecologia* 102:511–514.
- Dukas R, 1998. Constraints on information processing and their effects on behavior. In: Cognitive ecology: the evolutionary ecology of information processing and decision making (Dukas R, ed). Chicago: University of Chicago Press; 89–127.
- Ens BJ, Esselink P, Zwarts L, 1990. Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*. *Anim Behav* 39:219–230.
- Feare CJ, Inglis IR, 1979. The effects of reduction of feeding space on the behaviour of captive starlings *Sturnus vulgaris*. *Ornis Scand* 10:42–47.
- Fisher RA, Yates F, 1963. Latin squares. In: Statistical tables for biological, agricultural, and medical research, 6th ed (Fisher RA, Yates F, eds). New York: Hafner; 86–89.
- Francis RC, 1988. On the relationship between aggression and social dominance. *Ethology* 78:223–237.
- Fretwell SD, Lucas HL, 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor* 19:17–36.
- Fuller RA, 2003. Factors influencing foraging decisions in ruddy turnstones *Arenaria interpres* (L.). Durham: University of Durham.
- Ganslosser U, Dellert B, 1997. Experimental alterations of food distribution in two species of captive equids (*Equus burchelli* and *E. hemionus kulan*). *Ethol Ecol Evol* 9:1–17.
- Gauthreaux SA, 1978. The ecological significance of behavioral dominance. In: Perspectives in ethology (Bateson PPG, Klopfer PH, eds). New York: Plenum; 17–54.
- Giraldeau L-A, Caraco T, 2000. Social foraging theory. Princeton, New Jersey: Princeton University Press.
- Giraldeau L-A, Hogan JA, Clinchy MJ, 1990. The payoffs to producing and scrounging: what happens when patches are divisible? *Ethology* 85:132–146.
- Goldberg JL, Grant JWA, Lefebvre L, 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. *Behav Ecol* 12:490–495.
- Goss-Custard JD, 1970. Feeding dispersion in some overwintering wading birds. In: Social behaviour in birds and mammals (Crook JH, ed). New York: Academic Press; 3–35.
- Goss-Custard JD, 1980. Competition for food and interference amongst waders. *Ardea* 68:31–52.
- Grant JWA, 1993. Whether or not to defend? The influence of resource distribution. *Mar Behav Physiol* 23:137–153.
- Grant JWA, Guha RI, 1993. Spatial clumping of food increases its monopolization and defense by conflict cichlids, *Cichlasoma nigrofasciatum*. *Behav Ecol* 4:293–296.
- Grover JP, 1997 Resource competition. London: Chapman and Hall.
- Hammerstein P, 1981. The role of asymmetries in animal contests. *Anim Behav* 29:193–205.

- Harris PR, 1979. The winter feeding of the turnstone in North Wales. *Bird Study* 26:259–266.
- Huntingford F, Turner A, 1987. *Animal conflict*. London: Chapman and Hall.
- Jeschke JM, Kopp M, Tollrian R, 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecol Monogr* 72:95–112.
- Johnson CA, Grant JWA, Giraldeau L-A, 2004. The effect of patch size and competitor number on aggression among foraging house sparrows. *Behav Ecol* 15:412–418.
- Jørgensen EH, Baardvik BM, Eliassen R, Jobling M, 1996. Food acquisition and growth of juvenile Atlantic salmon (*Salmo salar*) in relation to spatial distribution of food. *Aquaculture* 143:277–289.
- Keddy PA, 2001. *Competition*, 2nd ed. Dordrecht: Kluwer Academic Publishers.
- Kühberger A, Perner J, 2003. The role of competition and knowledge in the Ellsberg task. *J Behav Decis Making* 16:181–191.
- Landau HG, 1951. On dominance relations and the structure of animal societies. I. Effect of inherent characteristics. *Bull Math Biophys* 13:1–19.
- Magnuson JJ, 1962. An analysis of aggressive behaviour, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces: Cyprinodontidae)). *Can J Zool* 68:2688–2691.
- Mathy JW, Isbell LA, 2001. The relative importance of size of food and interfood distance in eliciting aggression in captive rhesus macaques (*Macaca mulatta*). *Folia Primatol* 72:268–277.
- Maynard Smith J, Parker GA, 1976. The logic of asymmetric contests. *Anim Behav* 24:159–175.
- McCarthy ID, Gair DJ, Houlihan DF, 1999. Feeding rank and dominance in *Tilapia rendalli* under defensible and indefensible patterns of food distribution. *J Fish Biol* 55:854–867.
- Mesterton-Gibbons M, Dugatkin LA, 1995. Toward a theory of dominance hierarchies: effects of assessment, group size, and variation in fighting ability. *Behav Ecol* 6:416–423.
- Metcalfe NB, 1986. Variation in winter flocking associations and dispersion patterns in the turnstone *Arenaria interpres*. *J Zool* 209:385–403.
- Metcalfe NB, Furness RW, 1985. Survival, winter population stability and site fidelity in the turnstone *Arenaria interpres*. *Bird Study* 32:207–214.
- Miller RS, 1967. Pattern and process in competition. *Adv Ecol Res* 4:1–74.
- Miller RG, 1997. *Beyond ANOVA: basics of applied statistics*. London: Chapman and Hall.
- Monaghan P, Metcalfe NB, 1985. Group foraging in wild brown hares: effects of resource distribution and social status. *Anim Behav* 33:993–999.
- Myers JP, Connors PG, Pitelka FA, 1979. Territoriality in non-breeding shorebirds. In: *Shorebirds in marine environments* (Pitelka FA, ed). Lawrence, Kansas: Cooper Ornithology Society; 231–246.
- Park T, 1954. Experimental studies of interspecific competition. II. Temperature, humidity and competition in two species of *Tribolium*. *Physiol Zool* 27:177–238.
- Pearson SM, 1989. Food patches and foraging group size in granivorous birds. *Anim Behav* 38:665–674.
- Piper WH, 1997. Social dominance in birds; early findings and new horizons. *Curr Ornithol* 14:125–187.
- Prescott DRC, 1987. The effects of habitat density and the spatial distribution of food on the social behaviour of captive wintering American tree sparrows. *Can J Zool* 65:522–526.
- Robb SE, Grant JWA, 1998. Interactions between the spatial and temporal clumping of food affect the intensity of aggression in Japanese medaka. *Anim Behav* 56:29–34.
- Rohwer S, Ewald PW, 1981. The cost of dominance and advantage of subordination in a badge signalling system. *Evolution* 35:441–454.
- Rubenstein DI, 1981. Population density, resource partitioning and territoriality in Everglade pygmy sunfish. *Anim Behav* 29:155–172.
- Ruxton GD, Gurney WSC, 1994. Deriving the functional response without assuming homogeneity. *Am Nat* 144:537–541.
- Ruxton GD, Gurney WSC, de Roos AM, 1992. Interference and generation cycles. *Theor Popul Biol* 42:235–253.
- Ryer CH, Olla BL, 1995. The influence of food distribution upon the development of aggressive and competitive behavior in juvenile chum salmon, *Oncorhynchus keta*. *J Fish Biol* 46:264–272.
- Ryer CH, Olla BL, 1996. Growth depensation and aggression in laboratory reared coho salmon: the effect of food distribution and ration size. *J Fish Biol* 48:686–694.
- Schmidt KA, Brown JS, 1996. Patch assessment in fox squirrels: the role of resource density, patch size, and patch boundaries. *Am Nat* 147:360–380.
- Siroto E, 2000. An evolutionary stable strategy for aggressiveness in feeding groups. *Behav Ecol* 11:351–356.
- Smith RD, Ruxton GD, Cresswell W, 2001. Dominance and feeding interference in small groups of blackbirds. *Behav Ecol* 12:475–481.
- Smith RD, Ruxton GD, Cresswell W, 2002. Do kleptoparasites reduce their own foraging effort in order to detect kleptoparasitic opportunities? An empirical test of a key assumption of kleptoparasitic models. *Oikos* 97:205–212.
- Southwick CH, 1967. An experimental study of intragroup agonistic behavior in rhesus monkeys (*Macaca mulatta*). *Behaviour* 28:182–209.
- Stillman RA, Bautista LM, Alonso JC, Alonso JA, 2002. Modelling state-dependent interference in common cranes. *J Anim Ecol* 71:874–882.
- Stillman RA, Goss-Custard JD, Caldow RWG, 1997. Modelling interference from basic foraging behaviour. *J Anim Ecol* 66:692–703.
- Taylor LR, 1961. Aggregation, variance and the mean. *Nature* 189:732–735.
- Theimer TC, 1987. The effect of seed dispersion on the foraging success of dominant and subordinate dark-eyed juncos, *Junco hyemalis*. *Anim Behav* 35:1883–1890.
- Tufto J, Solberg EJ, Ringsby T-H, 1998. Statistical models of transitive and intransitive dominance structures. *Anim Behav* 55:1489–1498.
- Vahl WK, van der Meer J, Weissing FJ, van Dullemen D, Piersma T, in press. Experimental evidence for intra-specific interference competition between foraging waders. *Behav Ecol*.
- van der Meer J, 1992. Statistical analysis of the dichotomous preference test. *Anim Behav* 44:1101–1106.
- van der Meer J, Ens BJ, 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. *J Anim Ecol* 66:846–858.
- van Doorn GS, Hengeveld GM, Weissing FJ, 2003a. The evolution of social dominance—I: two-player models. *Behaviour* 140:1305–1332.
- van Doorn GS, Hengeveld GM, Weissing FJ, 2003b. The evolution of social dominance—II: multi-player models. *Behaviour* 140:1333–1358.
- Warner RR, 1980. The coevolution of behavioral and life-history characteristics. In: *Sociobiology: beyond nature/nurture* (Barlow GW, Silverberg J, eds). Boulder: Westview; 151–188.
- Whitfield DP, 1988. The social significance of plumage variability in wintering turnstone *Arenaria interpres*. *Anim Behav* 36:408–415.
- Whitfield DP, 1990. Individual feeding specialisations of wintering turnstones *Arenaria interpres*. *J Anim Ecol* 59:193–211.
- Yasuda H, Ishikawa H, 1999. Effects of prey density and spatial distribution on prey consumption of the adult predatory ladybird beetle. *J Appl Entomol* 123:585–589.
- Zahavi A, 1971. The social behaviour of the White Wagtail *Motacilla alba* wintering in Israel. *Ibis* 113:203–211.