

Experimental evidence for interference competition in oystercatchers, *Haematopus ostralegus*. I. Captive birds

Anne L. Rutten,^a Kees Oosterbeek,^{a,b} Jaap van der Meer,^c Simon Verhulst,^d and Bruno J. Ens^{b,e}

^aAnimal Ecology Group, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands,

^bSOVON Dutch Centre for Field Ornithology, SOVON-Texel, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands, ^cRoyal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, The Netherlands, ^dBehavioural Biology Group, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands, and ^eWageningen IMARES (formerly Alterra- Texel), PO Box 167, 1790 AD Den Burg, The Netherlands

Interference competition, the immediately reversible decrease in per capita foraging success with increasing forager density, has important implications for the distribution of foragers. Theoretical models predict the strength of interference at different prey densities for birds differing in dominance. Observational studies have been used to validate the theoretical predictions, but there is reason to believe that these nonexperimental studies suffer from confounding factors. We therefore manipulated forager density of oystercatchers *Haematopus ostralegus* foraging on live cockles *Cerastoderma edule* (low density: 1 bird per 50 m² and high density: 2 birds per 50 m²) in a unique experimental facility closely mimicking natural feeding conditions. In the high-density situation, the intake rate was on average reduced by 36% compared with the interference-free intake rate. However, this effect depended on status with intake rate of subordinates being more strongly reduced than intake rate of dominants (−45% vs. −25%). We could not investigate all possible mechanisms, but we observed that birds actively avoided each other, possibly to avoid kleptoparasitism. Our experiment shows that the decline in intake rate with increasing density of conspecifics is at least partly due to direct interactions between birds and possibly also to indirect interactions via prey depression but not to an unidentified confounding factor that covaries with intake rate and bird density, as may have been the case in nonexperimental field studies. **Key words:** *Cerastoderma edule*, cockle, density dependence, dominance, experiment, *Haematopus ostralegus*, interference, intraspecific competition, oystercatcher. [*Behav Ecol* 21:1251–1260 (2010)]

A major aim of animal ecology is to understand and predict the distribution of animals, and resource competition is an important process determining animal distributions (Fretwell and Lucas Jr 1969). Competition can take place via resource exploitation or via interference, which in the case of foraging animals has often been defined as a more or less immediately reversible decline in per capita foraging success with increasing forager density (Goss-Custard 1980; Sutherland 1983; Ens and Goss-Custard 1984). Some authors stress that interference competition requires direct behavioral interactions between foragers, for example, Vahl, van der Meer, et al. (2005). Others explicitly include prey depression, where prey make themselves temporarily unavailable in response to the presence of foraging predators (Charnov et al. 1976), as a mechanism of interference (Selman and Goss-Custard 1988; Stillman et al. 2000). In this paper, we take the view that interference can arise directly through behavioral interactions and indirectly through prey depression.

A comparison of models predicting the distribution of foraging animals indicated that the shape of the interference function describing the relationship between foraging suc-

cess and forager density profoundly affected the predicted distribution (van der Meer and Ens 1997). Hence, reliable predictions of optimal forager distribution and effects of forager density on intake rate require detailed knowledge on the mechanism of interference because these will determine the shape of the interference function. An increasing number of theoretical studies has taken up this challenge and derived the strength of interference from basic behavioral elements assumed to remain relatively constant with respect to the densities of both prey and predators, like attack distance (Ruxton et al. 1992; Holmgren 1995; Moody and Houston 1995; Stillman et al. 1997, 2002; van der Meer and Smallegange 2009). The next step consists of models that specifically consider the adaptive value of the decision to attack or avoid a conspecific. In a thought-provoking chapter in the thesis of Vahl (2007), Vahl, van Doorn, and Weissing concluded that the available game theory models of interference behavior did not provide a comprehensive understanding of interference competition. They developed a systematic approach for studying the evolution of interference behavior and show that seemingly minor differences in the assumptions on the structure of interactions, the presence of asymmetries, and their payoff function may strongly affect predictions regarding the evolutionary stability of interference strategies, explaining why apparently similar models yield strikingly different predictions. Reviewing the literature, Vahl (2007) concluded that our understanding of the interference process is still rudimentary, both from a theoretical and from an empirical perspective.

Address correspondence to: B.J. Ens. E-mail: bruno.ens@sovon.nl.
A.L. Rutten is now at Prinzenweg 22A, 82319 Starnberg, Germany.

Received 8 November 2009; revised 21 July 2010; accepted 29 July 2010.

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Shorebirds foraging on intertidal mudflats proved an ideal system for empirical studies on interference and the distribution of foraging animals in the wild (Drinnan 1957; Goss-Custard 1970; Bryant 1979; Zwarts and Drent 1981; Sutherland and Koene 1982; Ens and Goss-Custard 1984; Vahl 2007). Shorebirds feed in an open habitat on easily identifiable prey. As a result, the distribution behavior of the birds, their intake rate, and the distribution of prey can be quantified with great accuracy. These advantages apply in particular to the oystercatcher *Haematopus ostralegus*, and this species has become an empirical “model” species (Blomert et al. 1996; Goss-Custard 1996) that figures prominently in studies linking the behavior of individuals to population processes (Goss-Custard 1996; Sutherland 1996). However, with a few exceptions reviewed by Vahl (2007), shorebird studies have relied on nonexperimental field data to quantify interference. Hence, reported negative correlations between intake rate and forager density may not reflect interference but instead result from an unidentified third factor that covaried with intake rate and bird density. For instance, in the studies on oystercatchers, variation in predator density is often obtained through the influence of the tidal cycle; with higher bird densities occurring at higher water levels, see Ens and Cayford (1996) for a review. Shellfish prey living in areas with a long exposure time generally grow poorly because they can only feed themselves when immersed (Wanink and Zwarts 1993). These slow-growing shellfish are less profitable to oystercatchers and this leads to lower intake rates for oystercatchers at the stages in the exposure period that bird densities are highest. Moreover, in birds feeding on intertidal benthic prey, the stage of the tidal cycle also influences prey behavior, for example, Esselink and Zwarts (1989), prey choice, for example, de Vlas et al. (1996), and success in opening prey (Hulscher 1996). Furthermore, feeding motivation may vary through the exposure period due to circatidal rhythms (Daan and Koene 1981; Swennen et al. 1989) or digestive bottlenecks (Zwarts and Dirksen 1990; Kersten and Visser 1996). The presence of a negative correlation between intake rate and competitor density obtained via natural variation could be due to any of these factors. Similarly, the absence of a negative relationship between intake rate and competitor density does not necessarily demonstrate absence of interference, for example, because individuals succeed in distributing themselves in a way that equalizes interference competition across space and time. Thus, it is not clear what we should infer from the finding that 4 of 5 observational field studies on cockle-eating oystercatchers failed to find evidence for interference (Goss-Custard 1977; Sutherland and Koene 1982; Ens et al. 1996; Norris and Johnstone 1998); the exception being Triplet et al. (1999).

One potential solution is to employ statistical models to control for confounding factors, for example, Goss-Custard et al. 1984 and Goss-Custard and Durell (1987). However, this approach is necessarily constrained to the factors that are known to influence intake rate. Unidentified factors determining intake rate may well be important, given that the level of unexplained variation in intake rate in such models is usually substantial. We therefore believe a more reliable solution consists of experimental manipulation of forager density to demonstrate and quantify interference. The added benefit of experiments is that they can also shed light on the mechanisms underlying interference, for example, Vahl, van der Meer, et al. (2005).

Forager density can be manipulated either by changing the number of foragers or by the size of the foraging area. We applied the latter approach to free-living oystercatchers and report the results in a companion paper (Rutten et al. 2010). In the present study, we manipulated the number of foragers using captive oystercatchers foraging in large (50 m²) outdoor cages with running seawater and mudflats

and studied the effect on intake rate and possible interference mechanisms.

Goss-Custard and coworkers developed a sophisticated behavior-based distribution model (Goss-Custard, Caldow, Clarke, Durell, et al. 1995; Stillman et al. 1997). The model was initially developed for oystercatchers foraging on shellfish beds and later generalized to other species of shorebirds feeding on benthic prey, Brent geese *Branta bernicla* feeding on plants, and common scoter *Melanitta nigra* diving for shellfish; see Stillman (2008) for references. Because of its history, interference in the model results from precisely those mechanisms that are believed to be important in oystercatchers: kleptoparasitism and avoidance behavior (Ens and Cayford 1996). In kleptoparasitic disputes birds directly steal prey from a conspecific, which implies that dominant birds may actually increase their intake rate with increasing bird density. The cost of kleptoparasitism consists of lost prey items, at least to the victim, and of lost time through interactions. When birds are actively avoiding each other—to prevent attacks or prey depression—the cost mainly consists of lost time. Especially, subdominant birds are expected to show avoidance behavior, so as not to lose prey to more dominant birds. The model was repeatedly validated using observational field data (Goss-Custard, Caldow, Clarke, Durell, West 1995; Stillman et al. 1997, 2000). The general picture is that of qualitative but not quantitative agreement between predictions and observations. For instance, Stillman et al. (1997) accurately predicted the occurrence of interference in 11 of 13 combinations of shorebird and prey species. Yet, observed feeding densities of oystercatchers differed significantly from predicted feeding densities (Goss-Custard, Caldow, Clarke, Durell, West 1995; Stillman et al. 2000). The quantitative disagreement may be due to errors in parameter estimates, but a not mutually exclusive possibility is that the behavioral processes were not correctly modeled, for example, because they are not sufficiently identified and/or understood. Resolving this issue is scientifically interesting and also of applied importance because behavior-based models are increasingly used to address applied problems, like shellfish fishery (Stillman et al. 2001), habitat loss (Stillman et al. 2005), and the efficacy of proposed mitigation measures (Durell et al. 2005).

The Goss-Custard–Stillman behavior-based distribution model is the only model that has a well-developed methodology to estimate parameters and whose predictions have been extensively tested with field data. In the most recent version of the model (Stillman et al. 2002), a strict dominance hierarchy is assumed and individuals only initiate attacks when the expected benefits exceed the costs. Subdominant individuals continue to show avoidance behavior until there are no dominant neighbors within the attack distance. As a result, the model predicts that the intake rate of subdominant birds declines more steeply with an increase in the density of conspecifics than the intake rate of more dominant birds. We tested this prediction and further examined the results for evidence of kleptoparasitism and avoidance behavior. Finally, we compared the decline in intake rate of each individual to model predictions kindly provided by Stillman.

MATERIALS AND METHODS

Housing

The experiments were conducted at the artificial mudflat facilities of the Royal Netherlands Institute for Sea Research (NIOZ), Texel, the Netherlands. The ground plan of these facilities is depicted in Figure 1 and in the legend to this

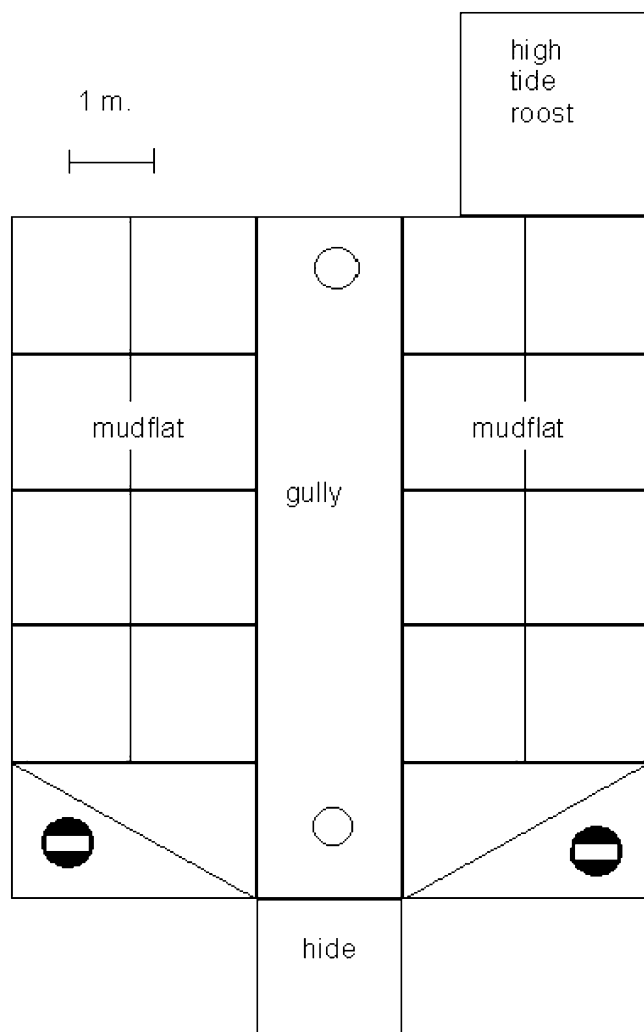


Figure 1

Map of the tidal cage. It consists of a 2.5-m high aviary with a ground surface of 50 m², with a layer of approximately 30 cm of sandy substrate as flooring to resemble a natural mudflat. Adjacent to the mudflat is an observation hide, and a second cage with a floor area (well above the high-tide level) of approximately 8 m², which the birds can use as a high-tide roost. The parts of the mudflat to the left and right of the hide that are out of view are covered with netting to prevent the birds from using it. Seawater can be pumped in and out from a nearby reservoir through a 1-m wide and about 50-cm deep gully in the middle of the mudflat. Birds typically hop over it (with one wing beat) or cross it at the edge of the cage. The tidal regime is regulated by a series of computer-driven pumps and valves and was set in our experiment to provide two 4-h low-water periods each 24 h. At high tide, the water level is 25 cm above the mudflats. The birds can forage from or up to a depth of 15 cm, which corresponds to a foraging period of little over 5 h around and including each low-water period under this regime. Freshwater is continuously available in the high-tide cage.

figure we provide details on the possibilities for tidal manipulation; see also Swennen et al. (1989). The mudflats can be stocked with live shellfish, closely mimicking the foraging conditions of oystercatchers in the wild. Given the size of the artificial mudflat (50 m²), 2 oystercatchers feeding jointly represents a feeding density of 400 birds per hectare. This is high, but within the range found in free-living birds (Ens and Cayford 1996; Triplet et al. 1999). Between experiments, birds were housed in holding cages (ca. 1 × 1 × 2 m) with a con-

tinuous supply of freshwater and an ad libitum supply of freshly thawed cockles and mussels.

Birds

Eight oystercatchers divided over 4 pairs were used because this was the minimum number required for the experiment for statistical reasons. We decided against a larger number of test pairs because 1) oystercatchers are difficult to keep in captivity, 2) the experiments were very labor intensive, 3) the ethical and legal need to minimize discomfort to experimental birds. Six wild-caught birds had previously been in captivity at the University of Groningen for several years. Two birds were caught shortly before the experiment on a high-tide roost with a canon net. Three pairs of birds were tested between April and November 1996, and the fourth pair was tested in February and March 2000. The reason that we did not collect data on the fourth pair in 1996, or shortly thereafter, is related to the severe winter of 1996/1997. The outdoor facility could not be operated during freezing conditions and all the cockles in the cage died. As most of the cockles on the natural beds in the Wadden Sea and Delta area also died, it was impossible to obtain sufficient numbers of cockles after the severe winter had ended. We had to wait for a new spatfall of cockles, and this spatfall had to grow to a sufficient size.

It took the birds up to a few weeks to become accustomed to the tidal cage. After the experiments on a pair of birds were finished, the birds were returned to the Zoological Laboratory and new birds were collected to replace them. The 2 wild-caught birds were released after the experiment. Birds were held captive on Texel for on average 6 weeks after which they were returned to the University of Groningen. To transport the birds between Groningen and Texel or between the site of capture and Texel, we used small transporting cages, measuring approximately 60 × 40 × 40 cm, designed in such a way that the birds could not damage themselves.

We took several measures to minimize stress of the captive birds. First, we blocked the vision from ground level to 1 m above ground, so people walking at some distance no longer disturbed the birds. Second, we observed the birds from a hide during experiments. Third, we minimized our visits to the cage. However, a minimum of 1 visit per day was necessary to remove empty shells, to replenish the stock of live cockles, to weigh the birds and check the status of their bills. If birds weighed less than 400 g, they were removed from the tidal cage and given the opportunity to recover in a holding cage with an ad libitum supply of freshly thawed cockles. When feeding on large cockles, the birds could damage the tip of their bills (Rutten et al. 2006). Usually, 1 or 2 mm of the top of the lower or upper bill tip had broken off. Such damage is also regularly observed in wild birds and impairs the feeding efficiency of the affected birds (Rutten et al. 2006). When the birds with damaged bills were allowed to feed on freshly thawed cockles, which are already open, the original shape of the bill tip (i.e., without a difference in length between the upper and the lower bills) was restored in less than 2 weeks.

Dominance could be assigned unambiguously in all pairs. During experiments, the bird that initiated most (usually all) of the observed fights also won practically all conflicts and was therefore considered to be dominant. Fights consisted of one bird (the winner) chasing or pecking the other (the loser), which would quickly retreat. On rare occasions, one bird grabbed the other by the wing and held on for a few seconds. We did not observe escalated fights and we did not expect them either on the basis of previous studies using the same setup (Leopold et al. 1989; Swennen et al. 1989).

Hierarchies were well established before the onset of experimental observations and never changed in the course of the experiment. All birds used the “stabbing” technique to open shells in which the bird stabs its bill between both valves of the shell and tries to cut the adductor muscles (Hulscher 1996).

Prey

The birds in the tidal cage were fed with live cockles that were within the size range that oystercatchers usually select in the wild. Fresh cockles were collected from either the Dutch Wadden Sea (2000) or the Oosterschelde estuary (1996) prior to each experimental period. The cockles were divided over the artificial mudflat in a density that would lead to a biomass density close to 44 g of ash-free dry mass (AFDM) per square meter. This is well within the range of cockle densities that oystercatchers are known to exploit in the field (Zwarts et al. 1996). The bivalves dug themselves into the substrate within one high-water period. Eaten cockles (numbers derived from empty shell counts) were regularly replaced by live ones from the same stock that had been kept in gullies with running seawater. Densities, mean sizes, and mean biomass density of the cockles used in the experiment can be found in Table 1. Cockle size and density varied between experimental pairs but not within pairs, so this variation will not have affected the pairwise comparisons that form the core of our experiment.

During experiments, the combined consumption of 2 birds never exceeded 30 g AFDM (see below). Depending on size and condition of the cockles (Table 1), this amount of biomass corresponded to between 40 and 200 cockles, representing less than 2% of the total stock in the cage.

Experimental procedure

Prior to the experiment, the birds were subjected to a training period in the experimental cages during which birds were allowed to feed individually (in most cases) in the tidal cage for one tidal cycle. The training period lasted until the birds were able to sustain body weight, which typically took about a week. Birds were subsequently observed while foraging alone or in pairs during one 5-h low water period. The order in which birds underwent the different treatments was randomly assigned. If possible, multiple trials were conducted for each bird for each treatment. However, birds sometimes damaged their bill during foraging (Rutten et al. 2006). If this happened, we stopped using the bird in experiments on interference. To study how bill tip damage affects feeding behavior, we continued observations on 4 birds weighing more than 400 g (Rutten et al. 2006). During the trials when both birds were foraging together, observations were made of one bird only to obtain independent data.

Table 1
Mean size, density, and biomass density of cockles in the experimental cage for each experimental period

Experimental pair (year of experiment)	Cockle size (mm)	Cockles/m ²	g AFDM/m ²
1 (1996)	31.0	133.3	34.7
2 (1996)	30.9	133.3	44.7
3 (1996), total ^a	23.9	297.3	43.8
Small	22.9	267.3	31.9
Large	33.0	30.1	11.9
4 (2000)	36.8	64.5	44.1

^a For pair 3, a mixture of smaller 2-year-old and larger 3-year-old cockles was used.

The following behavioral elements were distinguished: foraging behavior (searching, handling, and eating prey), aggressive behavior (attacking or being attacked, including occurrence and outcome of kleptoparasitic disputes), other behavior (walking while not foraging, flying, preening, resting), and unknown behavior (a small part of the high-tide roost cage could not be seen from the observation hide). We noted the exact timing of each change in behavior, so the duration of a behavior could be calculated as the difference between the moment the behavior started to the moment a new behavior was initiated. Along with the protocols, the position of the bird(s) in the cage was recorded every 2 min by means of a grid of 16 squares of about 2 m² each that was laid out on the mudflat (Figure 1).

For the first 3 pairs of birds, in 1996, data were directly entered using a handheld computer (PSION LZ 64 organizer) and The Observer software (Noldus). Trials of the fourth pair were recorded with a video camera, and behavioral data were later transcribed.

Data analysis

Occurrence of interference was tested for by comparing intake rates of birds foraging alone and the same birds foraging in pairs. The intake rate was calculated as the amount of food in milligram AFDM ingested (the number of cockles consumed × the average AFDM of these cockles), divided by the time spent on foraging behavior over an entire low-water period. Intake rate was ln transformed to obtain a normal error distribution.

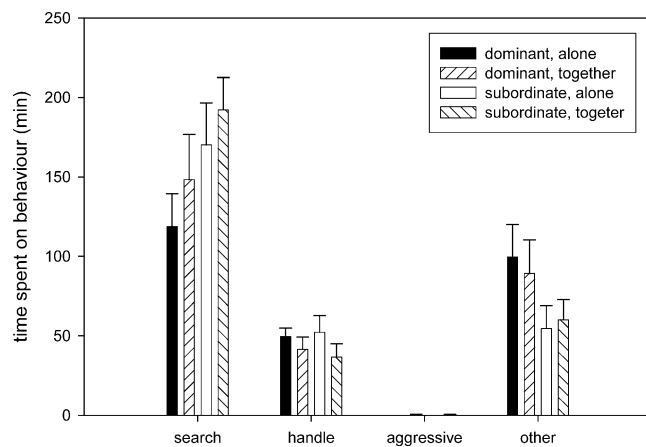
If birds are able to compensate for a loss in foraging efficiency by extending the time spent foraging, their total intake will remain relatively constant across treatments. We therefore compared the total time spent feeding as well as the total intake, the total amount of food in milligram AFDM ingested during one low-water period for birds foraging in both situations.

In 2 pairs, we only collected 1 data point for each bird (dominant or subdominant) under each condition (feeding singly or with the other bird); in the 2 other pairs, we had 2 or 3 data points for each bird under each condition. To avoid pseudoreplication, all measures were averaged per bird per treatment. The experimental results were analyzed by a multi-factor analysis of variance (ANOVA), with 2 fixed factors (density and dominance) and 1 random factor (pair). The design of such an experiment is sometimes called a factorial randomized block design. See, for example, Quinn and Keough (2002) for further explanation.

Using the model of Stillman et al. (2002), the intake rate in the high-density treatment for our 2 birds was predicted to be 89.9% of the interference-free intake rate (IFIR) for the subdominant and 101.2% of the IFIR for the dominant bird for our parameter values (see Table 2). The predicted increase in the intake rate of the dominant bird with increasing forager

Table 2
Parameter values used to predict relative intake with the model of Stillman et al. (2002)

Parameter	Symbol (units)	Value
Handling time	T_H (s)	120.8
Prey encounter rate	λ (/s)	0.101
Search speed	S_S (m/s)	0.22
Attack distance	D_A (m)	2.63
Probability of stealing prey	P_S	0.24
Kleptoparasitic dispute time	T_K (s)	3.14

**Figure 2**

Time budget of dominant and subordinate birds in different feeding situations. Indicated are mean values \pm SE (min). Dominant alone, black bars; dominant with subordinate, right-hatched bars; subordinate alone, white bar; subordinate with dominant, left-hatched bar. "Other" behavior consists mainly of resting and preening and for a small part of locomotor activity that is not related to foraging or aggression. Time budgets did not change significantly with changing density. SE, standard error.

density is due to kleptoparasitism. We used a one-sample *t*-test to test observed intake rates against these model predictions.

We tested whether foraging birds avoided each other by comparing interbird distance when they were feeding together with the expected distance under the null hypothesis that birds selected their foraging location independent of the other bird. The position data of the birds when feeding alone were used to determine the probability that a bird would feed on a particular position in the cage. We then calculated the average distance between both positions over an observation period that we expected if the birds did not avoid each other from the joint probability function of the birds being at a particular position. Only cases in which both birds were foraging were considered for the calculation of the observed distance.

RESULTS

We analyzed the time spent on searching for prey, handling prey, aggressive behavior, or other behavior with a multifactor ANOVA and found no significant effect of dominance or density (Figure 2). The data suggested that subdominant birds spent more time feeding (searching plus handling) per tide than dominant birds (219 min on average for the subdominants vs. 176 min for the dominant birds) and the multifactorial ANOVA indicated that this difference bordered significance ($P = 0.07$; Table 3).

Intake rate in the high-density situation was 64% of their IFIR (i.e., their intake rate when foraging alone) (Figure 3), and this decline was statistically significant (Table 4). Dominant individuals achieved 75% of their IFIR at the high-density situation, and subordinates only 55% (Figure 3), a difference that was significant (see dominance \times density interaction in Table 4). For subordinates, but not for dominants, the decrease is significantly different from the prediction derived from the model of Stillman et al. (one-sample *t*-test: dominant: $t_3 = -2.215$, $P = 0.114$ and subordinate: $t_3 = -4.464$, $P = 0.021$).

When feeding together with the dominant individual, the total food intake of subordinates was significantly reduced to 50% of their intake when feeding alone (Figure 4). When

Table 3

Results of a multifactor ANOVA with total time spent foraging (searching plus handling) per tide (min) as the dependent variable, density, and dominance as fixed factors and pair as a random variable

Source	df	SS	MS	F	P
Pair	3	42 933.832	14 311.277		
Dominance	1	6406.780	6406.780	7.615	0.070
Dominance \times pair	3	2523.903	841.301		
Density	1	13.726	13.726	0.009	0.931
Density \times pair	3	4634.362	1544.787		
Dominance \times density	1	0.022	0.022	0.000	0.992
Dominance \times density \times pair	3	561.016	187.005		

df, degrees of freedom; SS, sum of squares; MS, mean square.

feeding together with the subdominant individual, the total food intake of dominant birds was 78% of the total food intake when feeding alone (Figure 4). Multifactorial ANOVA showed a significant effect of density and of status, but the interaction between density and status was not significant, though the results bordered significance ($P = 0.075$; Table 5).

Two possible mechanisms underlying the observed interference, not mutually exclusive, are kleptoparasitism and avoidance behavior. We observed between a minimum of 4 and a maximum of 14 kleptoparasitic interactions per tide during tides where the 2 birds fed together and each interaction generally lasted less than 10 s. Thus, the time loss was negligible and the amount of food involved was too small to explain the decrease in intake for either the 2-bird situation or the difference in response between the dominant and the subordinate birds (Table 6). The observed distance between 2 foraging birds was larger than the distance expected under the null hypothesis of independent space use, indicating that at least one of the birds avoided the other (Figure 5; Paired *t*-test: $t_3 = 8.177$, $P = 0.004$).

DISCUSSION

The decrease in intake rate we observed in the high-density situation provides the first experimental evidence for interference between cockle-feeding oystercatchers. We also found evidence for interference in our experimental field study; see companion paper (Rutten et al. 2010). These results contrast with 4 of 5 nonexperimental field studies that failed to detect interference in free-ranging cockle-feeding oystercatchers (Triplet et al. 1999). These contrasting results underline the importance of experimentally studying interference.

Mechanisms of interference

A variety of mechanisms can cause interference among searching predators. Identifying the mechanisms causing the interference effect would provide more insight in the interference process, which is not only interesting but also useful for the individual-based models that build on such effects. Our experimental design excluded some possibilities beforehand. There were no interspecific kleptoparasites such as gulls in the cages, so this cannot play a role in our experiment. Also, there was no spatial variation in prey density, so birds could not chase each other from good feeding spots, a major cause of interference in turnstones *Arenaria interpres* (Vahl, Lok, et al. 2005; Vahl and Kingma 2007; Vahl et al. 2007). Below, we investigate the interference mechanisms that could have operated in our study: prey depression, kleptoparasitism, and avoidance behavior. However, before turning to the interference mechanisms, we

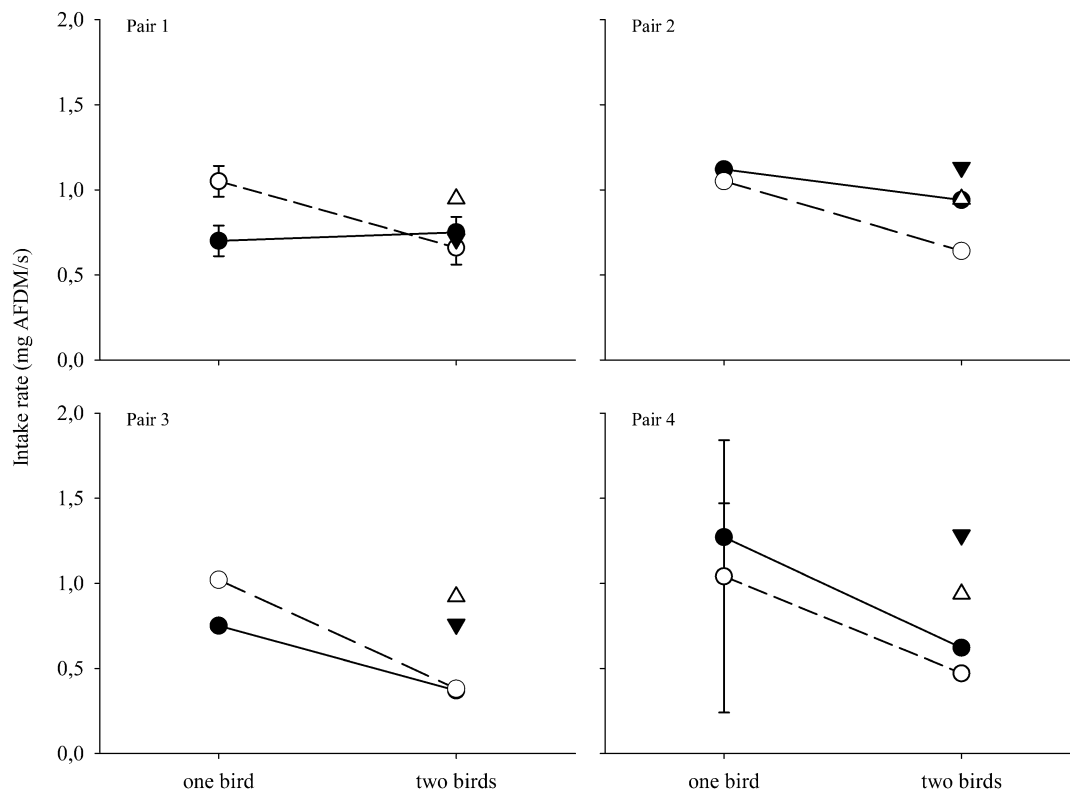


Figure 3

Intake rate \pm SE (mg AFDM/s) for all 8 birds under different feeding densities. Solid line, solid markers: dominants; dashed line, open markers: subordinates; triangles: predictions by the model described in Stillman et al. (2002); dots, actual data. Pair number above each graph. No error bars are provided when $N = 1$. SE, standard error.

must examine the possibility that intake rate declined due to depletion.

During the experimental sessions, some prey were removed by the birds, but the fraction of prey removed per tide was sufficiently small ($<2\%$ when the birds were feeding together) that this cannot explain the decline in intake rate. However, this argument does not necessarily hold if at any one tide, only a small fraction of the cockles is actually available. The cockles were buried very shallow in the cage, as they do in the wild, so they were always within reach of the birds. It remains possible, however, that at any one tide, only some cockles were visible or gaping such that they could be successfully attacked (oystercatchers can hunt by touch, but the birds in our experiment hunted by sight). If so, this small attackable fraction might become depleted during the course of the

experiment. In that case, a consistent and quite dramatic decline in intake rate during each experimental session would occur, especially in experiments with 2 birds, but we did not observe such a decline (Oosterbeek K, Ens BJ, unpublished data). The argument assumes that the cockle's vulnerability to predation changes very little within a tide. If continuous renewal of attackable cockles occurs within a tide, this might lead to temporary local depletion of this attackable fraction due to the foraging birds, without a concomitant decline in intake rate in the course of the tide. One might consider this a form of prey depression.

Oystercatchers foraging on shellfish use different techniques to open the shells, but in this study, all birds used the stabbing technique to open cockles, where the bill is inserted quickly between the gaping valves to cut the adductor muscle, preventing the cockle from closing itself. If the birds depend on gaping cockles, and if their feeding activity caused the cockles to close temporarily, this prey depression could also explain interference (Stillman et al. 2000). However, because prey depression is expected to affect both dominant and subordinate, it cannot explain why dominants suffered less from interference.

Kleptoparasitism played only a minor role in our study because on average, only 0.42% of the dominant bird's total intake consisted of prey stolen from the subordinate. This gain is too small to explain the differential response of both birds to the increased density. However, the risk of kleptoparasitism may induce avoidance behavior, which may impair foraging efficiency (Ens and Cayford 1996). Kleptoparasitism would thus influence intake rate indirectly.

The distance between both birds was larger than expected by chance, indicating avoidance behavior. Whether birds avoided

Table 4

Results of a multifactor ANOVA with \ln -transformed intake rate (mg AFDM/s) as the dependent variable, density, and dominance as fixed factors and pair as a random variable

Source	df	SS	MS	F	P
Pair	3	0.46148	0.15383		
Dominance	1	0.00619	0.00619	0.129606	0.7428
Dominance \times pair	3	0.14327	0.04776		
Density	1	1.14423	1.14423	11.61891	0.0422
Density \times pair	3	0.29543	0.09848		
Dominance \times density	1	0.09593	0.09593	11.27262	0.0439
Dominance \times density \times pair	3	0.02554	0.00851		

df, degrees of freedom; SS, sum of squares; MS, mean square.

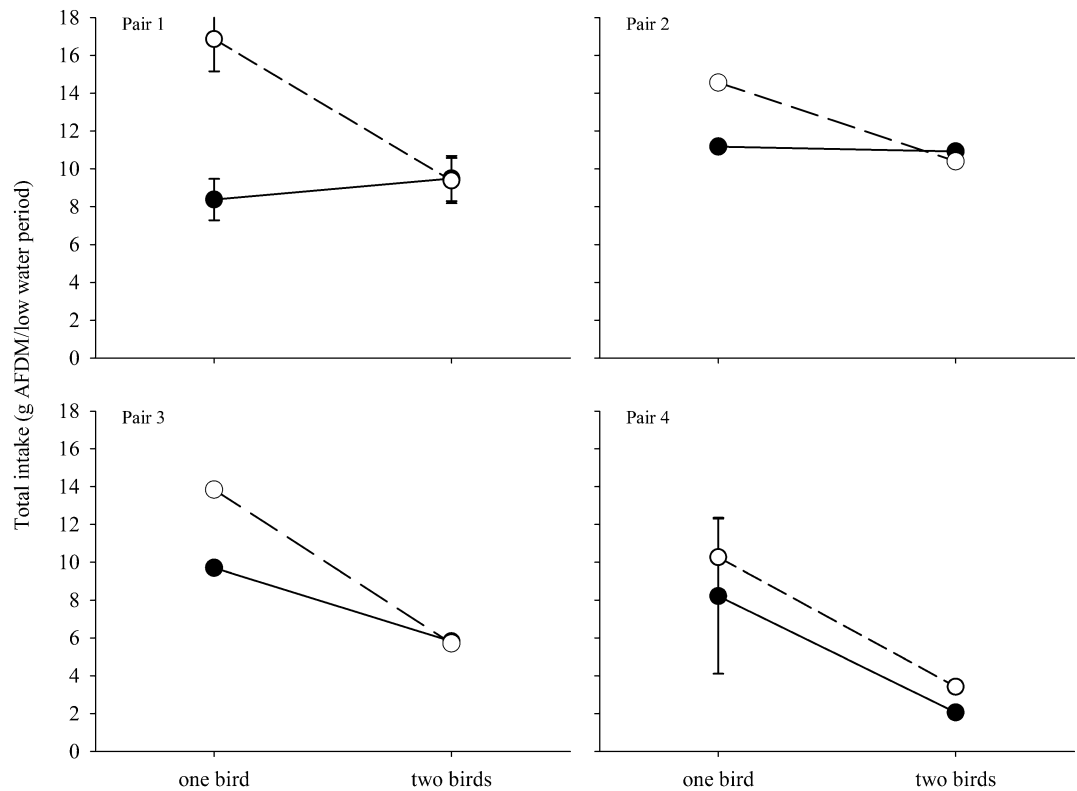


Figure 4
Total intake \pm SE (g AFDM) for all 8 birds under different feeding densities. Solid line, solid markers: dominants; dashed line, open markers: subordinates. Pair numbers above each graph. No error bars are provided when $N = 1$. SE, standard error.

each other to reduce prey depression, aggressive interactions, or kleptoparasitism cannot be derived from our observations. However, avoidance of the dominant by the subdominant is the most likely explanation for the observation that the intake rate of subdominant birds was more affected by the presence of a competitor than the intake rate of the dominant birds.

Summarizing, we conclude that prey depression, affecting both dominant and subdominant, and avoidance, affecting only the subdominant, are the most likely interference mechanisms explaining decreased intake rate at higher density.

Comparison to model predictions

Comparing our findings on interference among cockle-feeding oystercatchers to the predictions of the Goss-

Custard–Stillman model, we found that the average decrease in intake rate was larger than predicted. Moreover, the difference in response between dominant and subordinate birds was larger than predicted and the intake rate of the dominant decreased instead of increased.

A possible explanation for the discrepancy between theory and data is that interference among cockle-feeding oystercatchers is not only due to kleptoparasitism and avoidance behavior, as assumed in the version of the Goss-Custard–Stillman model from which we derived predicted intake rates, but also due to prey depression. As explained above, prey

Table 5
Results of a multifactor ANOVA with total intake per tide (mg AFDM) as the dependent variable, density, and dominance as fixed factors and pair as a random variable

Source	df	SS	MS	F	P
Pair	3	81.226	27.075		
Dominance	1	21.788	21.788	13.766	0.034
Dominance \times pair	3	4.748	1.583		
Density	1	80.161	80.161	18.125	0.024
Density \times pair	3	13.268	4.423		
Dominance \times density	1	18.980	18.980	7.184	0.075
Dominance \times density \times pair	3	7.925	2.642		

df, degrees of freedom; SS, sum of squares; MS, mean square.

Table 6
The effect of kleptoparasitism on total food intake (g AFDM) per tide and feeding time (min) per tide comparing dominants and subdominants

	Dominant		Subdominant	
	Mean	SD	Mean	SD
Total intake (g AFDM)				
Feeding singly	10.34	1.32	13.92	3.55
Feeding together	8.25	3.90	7.39	4.10
Feeding together exclusively kleptoparasitism	8.22	3.89	7.82	4.57
Total feeding time (min)				
Feeding singly	179	47	219	49
Feeding together	181	88	221	67
Feeding together exclusively kleptoparasitism	180	88	220	67

SD, standard deviation.

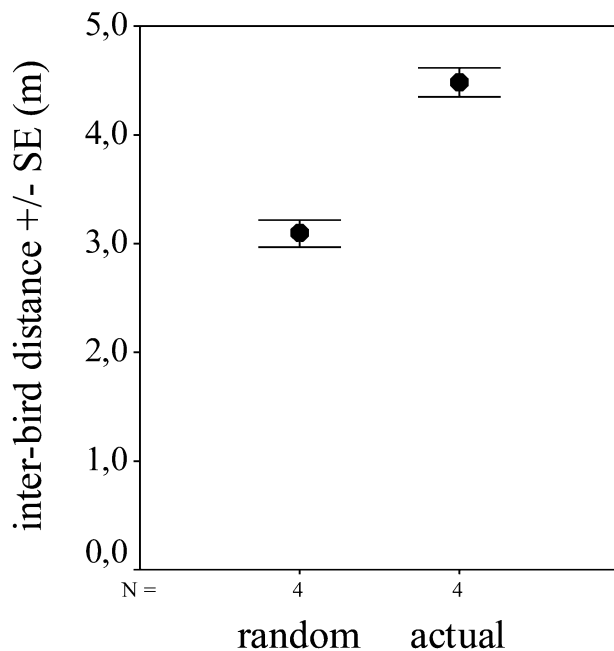


Figure 5

The difference between the mean actual distance (m) between the birds, and the expected mean distance (m) between both birds had they ignored each other. See text for the explanation on how the distances under the random expectation were obtained. Only cases in which both birds displayed foraging-related behavior were considered.

depression or a very similar process may have occurred in our experiment (and may occur in the field) and would explain why the intake rate of the dominant declined, whereas it should have increased according to the predictions of the model.

The discrepancy between predicted and actual observations may also be due to our experimental conditions, where the subordinate could only escape the dominant by moving to the resting cage where no food was available, whereas in the wild subordinate birds will presumably have the option to move to areas where at least some foraging is possible, which would decrease the difference in intake rate.

The rate of kleptoparasitic attacks in our study was substantially lower than observed in the field (Triplet et al. 1999). These authors observed an equivalent of 26 attacks per tidal feeding period of 200 min compared with 4–14 attacks per tide observed by us, whereas our feeding density (corresponding to 500 birds per hectare) was much higher than the average of 164 birds per hectare observed by Triplet et al. (1999). Thus, in our experiment, the dominant may not have gained as much profit from feeding close to more subordinate individuals compared with natural conditions perhaps because it was probably easy for the subordinate to keep track of the dominant and evade this bird. In addition, the dominant could not benefit from chasing the subordinate from good feeding spots because we did not offer a clumped food distribution. Thus, the advantage of experimentally controlling food density, available feeding time, and competitor density to demonstrate interference may have been bought at the expense of confronting the oystercatchers with unnatural feeding conditions. We therefore followed up the present study with an experimental manipulation of competitor density in the field, the results of which are reported in a companion paper (Rutten et al. 2010).

A final possibility to consider is that the Goss-Custard–Stillman model assumes large numbers of foragers and hence performs less well when only a few birds are involved. A stochastic version of the Beddington–DeAngelis functional response model was recently developed to model interference among a finite number of predators (van der Meer and Smallegange 2009). Intake rates predicted by the stochastic model clearly differed from predictions by the deterministic model for forager numbers below 6. The model proved successful when tested in the laboratory on shore crabs (Smallegange and van der Meer 2010). In that experiment, the crabs were carefully matched for size because the model does not distinguish among foragers differing in competitive ability. Hence, the current version of the model cannot be tested on oystercatchers, which always develop a clear dominance hierarchy.

Compensation

Judging from the decrease in total intake for both birds, which was very similar to their decrease in intake rate, it can be concluded that the birds did not compensate for the loss in foraging efficiency. That we found no significant changes in time allocation confirms this finding, although the lack of any significant changes in this regard can also be due to lack of statistical power. In the low-density treatment, the total food intake of the subordinate birds was consistently higher than that of the dominant birds. Field observations suggest considerable differences in foraging efficiency among individuals (Goss-Custard and dit Durell 1987; Goss-Custard and dit Durell 1988), but there is no evidence in our data that subordinate birds were more efficient foragers compared with dominants. Perhaps the subordinate birds needed more food. If so, the somewhat surprising finding that total food intake of subordinate birds equaled the total food intake of the dominants at high forager densities would actually indicate that the subdominants fulfilled their food needs to a lesser extent than the dominants at these high forager densities.

The absence of unequivocal evidence for compensation contrasts with the results of Swennen et al. (1989) who showed that, under some circumstances, captive oystercatchers are able to increase their intake rate to compensate for a loss in foraging time. It is, however, in line with a field study by Meire (1996) who showed that oystercatchers do not increase their intake rate above normally observed levels after a period of insufficient foraging and a field study by Urfi et al. (1996) who showed that oystercatchers do not increase their intake rate to compensate for lost foraging time. Our study indicates that prolonged periods of increased densities may lead to starvation in oystercatchers, considering their apparent inability to compensate for the losses in foraging efficiency that arise through interference as previously reported by Goss-Custard et al. (2001). In a companion paper, we show that oystercatchers chased from their preferred feeding area may not only suffer from a reduction in intake rate resulting from interference but also experience a reduced intake from being forced to feed in an unfamiliar area (Rutten et al. 2010).

FUNDING

The Technology Foundation STW (code GBI 4804), applied science division of NWO; technology programme of the Ministry of Economic Affairs supported the research.

We are grateful to Jort Verhulst and Edward Klun for their help in collecting cockles, to the Royal Netherlands Institute for Sea Research

(NIOZ) for allowing us to use their facilities, to Richard Stillman for providing his model predictions, and to Niels Dingemanse for helpful comments on the manuscript. Birds were captured and kept in captivity under license of the Dutch Ministry for Agriculture, Nature Conservation, and Food Quality.

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