

INTERFERENCE AMONG OYSTERCATCHERS,
HAEMATOPUS OSTRALEGUS, FEEDING ON MUSSELS,
MYTILUS EDULIS, ON THE EXE ESTUARY

BY B. J. ENS* AND J. D. GOSS-CUSTARD†

*Zoological Laboratory, State University of Groningen, Kerklaan 30, Haren (Gr.),
The Netherlands and †The Institute of Terrestrial Ecology, Furzebrook Research Station,
Wareham, Dorset BH20 5AS England*

SUMMARY

(1) Oystercatchers *Haematopus ostralegus* eating mussels *Mytilus edulis* on the Exe Estuary were aggressive and often stole mussels from each other. A stable and linear dominance hierarchy existed amongst ten birds studied in detail. The intake rates (biomass consumed per 10 min foraging) of six out of eight birds on which adequate data were obtained, decreased with increasing densities of oystercatchers. However, this did not happen in the two top-dominant individuals, which therefore did not seem to suffer from interference.

(2) Interference in the subdominants was due to increased intraspecific kleptoparasitism, to decreased capture rates probably caused by avoidance, and, perhaps, to increased time spent in aggression. Subdominants avoided high densities of conspecifics, but they did not stop feeding when high densities occurred.

(3) It is possible to account for our data in terms of the increased opportunities for dominants to steal food from subdominants at high bird densities. Competition for small-scale feeding sites may have been important too. It is suggested that the dispersion of oystercatchers over the mussel bed can be described by a modification of the 'ideal despotic distribution' proposed by Fretwell (1972).

INTRODUCTION

Studies of interference between predators have shown its possible importance in the interaction between populations of predator and prey (Hassell 1978) and in determining the dispersion of predators while foraging (Goss-Custard 1970). Hassell (1978) classifies the effect of encounters between searching predators under the general heading of 'mutual interference'. Because encounters may be very subtle and because individuals may suffer from each others presence in other ways, for instance, via prey depression (Charnov Orians & Hyatt 1976), we define interference operationally as a reversible and more-or-less immediate decrease in intake rate due to an increase in the density of conspecifics (Goss-Custard 1980).

Few field studies have been done, partly because intake rate is often difficult to measure. However, several field studies on wading birds (*Charadrii*) have shown that intake rate may decrease as bird density increases (Goss-Custard 1976; Koene 1978; Sutherland & Koene 1982; Zwarts 1978; Zwarts & Drent 1981). This is due to interference rather than to depletion of the food because a change in bird density has an immediate effect and the intake rate recovers as soon as the density of birds decreases. A number of mechanisms

* Present address: Research Institute for Nature Management, P.O. Box 59, 1790 AB Den Burg (Texel), The Netherlands.

has been postulated (Goss-Custard 1980) but little has been done to distinguish between the alternatives available.

Interference occurs in oystercatchers *Haematopus ostralegus* L. eating mussels *Mytilus edulis* L. (Koene 1978; Zwarts & Drent 1981; Sutherland & Koene 1982) and may be the direct or indirect result of aggressive encounters over food which are common in oystercatchers and increase in frequency as bird density rises (Vines 1980). However, both the aggressiveness of oystercatchers and their success varies enormously between individuals (Goss-Custard, Durell & Ens 1982a). Birds that attack others most frequently are more successful in stealing mussels from other birds and in retaining their own mussels when they themselves are attacked. Therefore, birds may vary in their susceptibility to interference, a possibility which may have important consequences for the population dynamics of waders (Goss-Custard 1980).

This study tests whether interference was distributed unequally among oystercatchers wintering on the Exe Estuary in South Devon, England. Our observations allow some components of interference to be identified. We then go on to examine the consequences of our findings for the way oystercatchers disperse over the musselbeds.

STUDY AREA AND METHODS

The Exe Estuary and its mussel beds are described by Goss-Custard *et al* (1982b). The work was done from September to November 1980, on bed 4, which attracted high densities of birds throughout autumn and winter. The detailed study area on this bed is described in Goss-Custard *et al* (1982a). The study area was subdivided into 25 × 25 m squares marked out with stakes. A hide was placed on a 3 m high tower in the middle of the area. The observer entered the hide on the receding tide before the mussels were exposed and the birds had arrived.

The food supply in each square was measured by taking five (25 × 25 cm) quadrats at random. Since oystercatchers on the Exe mainly eat the larger mussels (Goss-Custard *et al*. 1980), only mussels longer than 20 mm were counted and measured. A selection of mussels was taken from each square to determine ash-free dry weights, but the results were so similar that the data were combined to estimate the flesh-content for each size class within the whole study area.

Ten colour marked individuals feeding near to the hide (usually within 75 m) were studied. When possible, one bird was followed throughout the tidal cycle. Otherwise birds were observed for shorter periods, usually of 1 or 2 hours. Data for individuals were spread over a minimum of five and a maximum of fifteen tidal cycles and 140 hours of observations were collected in total.

The exact moment of changes in the behaviour of the focal animal and the sites where it was feeding were recorded on a tape recorder. Non-aggressive behaviours lasting less than 2 s were ignored. Behaviour was classified as sleeping, preening, looking around, flying, being aggressive, fleeing, searching and handling prey. The following details were recorded whenever aggression occurred: (i) whether the opponent was a carrion crow or oystercatcher; (ii) whether the focal animal was the attacker or victim, the outcome of the encounter and whether a mussel was involved; (iii) the postures used by both focal animal and opponent. An encounter was defined as lost when the bird retreated from the opponent, even though it retained its mussel. This was justified because in all nine cases where a marked bird attacked another marked bird of superior rank, the dominant retaliated immediately instead of running away.

The size of mussels eaten was estimated by comparing their length with the size of the colour ring on the bird's leg, a method which provided valid results (Ens 1982). This was sometimes difficult when the birds were too far away for the mussels to be seen clearly. In these cases, mussel size was estimated indirectly from the mean length of those present in the square where the bird was feeding, using a relationship based on all the mussels that could be measured.

Sometimes a bird stole a mussel that had already been partly consumed by the finder. Field observations suggested that the tissue most likely to be left in the shell on these occasions was the posterior adductor muscle and some of the mantle. The muscle alone accounted for 14% of the total biomass, and we guessed that the mantle tissue added an additional few per cent. Therefore, we used 20% as an estimate of the percentage of flesh remaining in mussels that had already been partly consumed by the finder.

The density of oystercatchers in the vicinity of the focal animal was measured by counting the number of oystercatchers in the square every 10 min, making allowance by eye for the proportion of the square that was under water and therefore unavailable for feeding. Because the frequency distribution was highly skewed towards occasions when bird density was low, we used the log transformation of bird densities in the analysis.

With the aid of a computer program in Algol 60 the continuous record of behaviour was cut into 10-min periods, with the measure of oystercatcher density in the middle. The term 'intake rate' refers to the ingestion rate made over the whole time the bird was active, including time spent in aggressive interactions, i.e. searching, handling prey, attacking or fleeing. The 'capture rate', on the other hand, was measured only over the times when the bird was actually feeding, i.e. while searching and handling. Occasions when severe disturbance occurred or when the focal animal spent less than 3 min active or feeding were omitted from the analysis. Statistical analyses were performed with the procedures of SPSS (Nie *et al.* 1975).

RESULTS

Dominance ranking

Dominance score was calculated as the percentage of interactions with any other bird, whether colour-marked or not, which the focal animal won. Individual scores varied between 96 and 16%, and were based on a sample of between 42 and 357 encounters (Table 1). Since only 10% of the individuals on the bed were colour-marked, encounters between known individuals formed only a small fraction of the total. Nonetheless, the dominance score predicted the outcome of encounters between colour-marked individuals (Fig. 1): birds with high dominance scores almost invariably beat birds with a lower score. Many cells of the matrix contain no data because many individuals never met, which was due to the strong site fidelity of some individuals (Goss-Custard *et al.* 1982a).

Dominance and interference

The intake rates of six of the birds were significantly reduced at high bird densities (Fig. 2; Table 1). Partialling out any possible effect of the biomass density or size of the mussels where the bird was feeding hardly changed the correlation coefficients (Table 1). This suggests that six of the ten birds were subject to interference.

Sample size was low in the two subdominant birds whose correlation coefficients were very small and statistically non-significant (birds 8 and 10). This is partly because subdominant birds occurred irregularly on bed 4 (Goss-Custard *et al.* 1982a) so data on

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TABLE 1. The correlation coefficients between intake rate and log oystercatcher density in ten oystercatchers of different dominance. The mean size and biomass density of the mussels were held constant in the partial correlation analysis. Values in brackets show the number of encounters from which dominance score was calculated

Dominance rank	Dominance score	<i>N</i>	Correlation coefficient	
			simple	partial
1	96 (131)	41	+0.10	+0.21
2	84 (357)	91	+0.05	+0.08
3	82 (121)	44	-0.27*	-0.25
4	78 (234)	70	-0.31†	-0.26*
5	75 (203)	81	-0.32†	-0.30†
6	51 (161)	69	-0.23*	-0.20
7	41 (69)	26	-0.39*	-0.36*
8	38 (62)	22	-0.06	-0.08
9	27 (199)	89	-0.36‡	-0.35‡
10	16 (42)	22	+0.03	+0.15

* $P < 0.05$; † $P < 0.01$; ‡ $P < 0.001$ are one-tailed levels of significance.

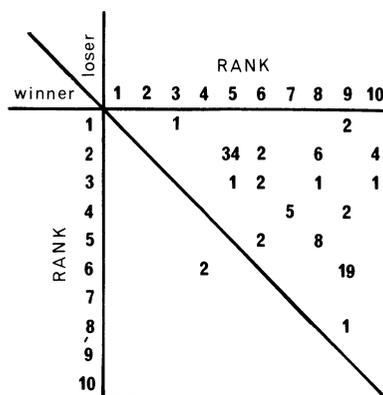


FIG. 1. Matrix showing the outcome of encounters with a clear outcome involving birds of known rank.

them were particularly hard to obtain. Furthermore, few data were obtained at high bird densities (Fig. 2). We think this is because subdominant birds actually avoided bed 4 when bird density was high. They arrived much later than the dominants on Neap tides (Fig. 3) when less of the bed was exposed and bird densities were highest. The paucity of data and the restricted range of bird densities over which they were collected means that we were unable, convincingly, to test for interference in these two birds.

This was not the case with the two top dominant birds whose intake rates also did not significantly decrease with increasing bird density. Both were often observed at high densities and sample size, particularly in bird 2, was adequate. Indeed, combining the data from each, so that sample size was 132 and their combined dominance score 90%, still provided no evidence for interference (partial correlation coefficient = +0.11, $P = 0.887$, one-tailed).

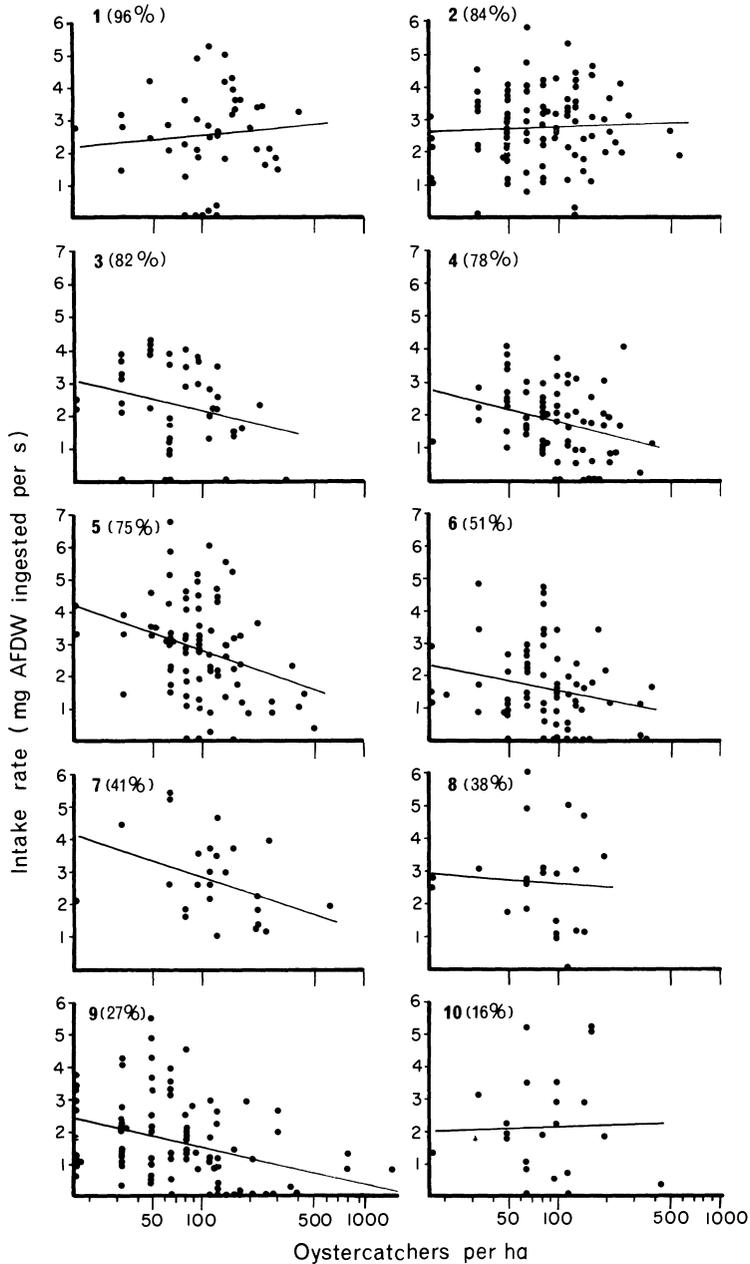


FIG. 2. The intake rate of the ten intensely studied oystercatchers in relation to the density of oystercatchers. Birds are identified according to rank (1–10), the figures in brackets showing the proportion of encounters won.

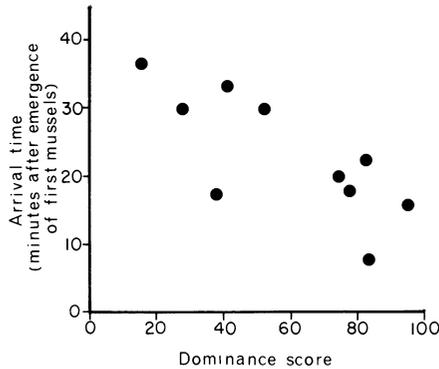
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FIG. 3. The mean time of arrival, expressed in minutes after emergence of the first mussels, in relation to dominance rank. Data for five Neap tides are shown. $r_s = -0.73$, $P < 0.05$ two-tailed.

We conclude, then, that interference did not affect the two most dominant individuals, but did occur in at least six of the remaining birds. Amongst these birds, susceptibility to interference did not vary consistently with their social status (Table 1, Fig. 2). It seems that the subdominants were equally prone to interference, even though their dominance scores varied considerably, while a small change in the dominance score at the top of the hierarchy was associated with a big change in susceptibility to interference.

Foraging behaviour and the components of interference

An increase in the density of oystercatchers was not accompanied by an increase in the amount of kleptoparasitism by carrion crows *Corvus corone* (Table 2). Furthermore, there were only forty-five encounters between carrion crows and oystercatchers, compared to 2209 intraspecific encounters. A total of eighteen mussels was lost partly or completely to crows, compared to eighty-nine successful intraspecific robberies. Nor were the differences between individuals in their susceptibility to interference due to crows: nearly half of all mussels lost to carrion crows (eight) were lost by the two top-dominant birds! In contrast to Koene's (1978) study, interspecific kleptoparasitism was not a major cause of interference among oystercatchers on the Exe.

The time lost in aggression is another possible cause of interference. Fighting over mussels and feeding sites, and the incidence of piping, increased with oystercatcher density (Fig. 4, Table 3). However, most encounters were of short duration (Table 4) so that the amount of time lost was small (Fig. 5). More importantly, the time spent in aggression by

TABLE 2. Rate at which carrion crows attacked oystercatchers for mussels, and the rate at which mussels were lost to carrion crows at three densities of oystercatchers. Data are lumped for all individuals, because there were so few encounters with crows

Density of oystercatchers	Crow attacks per 10 min	Mussels lost to crows per 10 min
Low: less than 72 birds ha ⁻¹	0.11	0.04
Intermediate: 72–104 birds ha ⁻¹	0.06	0.03
High: more than 104 birds ha ⁻¹	0.06	0.02

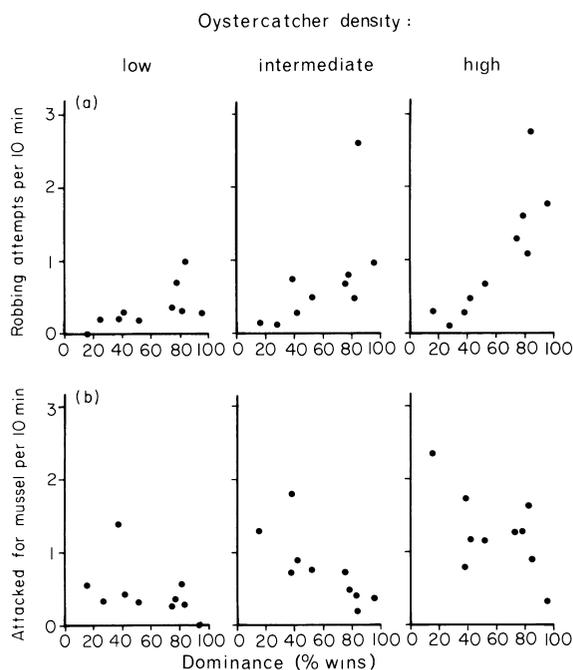


FIG. 4. The rate at which birds (a) attempted to rob others, and (b) were attacked themselves, in relation to their dominance score at three levels of bird density: (i) low means less than 72 birds ha^{-1} , (ii) intermediate indicates between 72 and 104 birds ha^{-1} and (iii) high means more than 104 birds ha^{-1} . Boundaries were chosen such that an equal number of observations pertained to each class of bird density.

TABLE 3. Rates of various types of aggression in relation to dominance and log density of oystercatchers. $n = 571$. Piping is a characteristic display which seems to occur when birds are disputing dominance (Ens & Goss-Custard, 1983): solitary piping is where one bird does it alone, apparently in response to the activities of a distant bird, while piping ceremonies involve several, typically three, birds

Behaviour	Correlation coefficient with			
	density of oystercatchers		dominance	
	simple	partial	simple	partial
Focal animal attacked opponent for mussel	0.24‡	0.23‡	0.32‡	0.32‡
Opponent attacked focal animal for mussel	0.29‡	0.30‡	-0.10*	-0.13‡
Focal animal displaced opponent	0.31‡	0.30‡	0.16‡	0.14‡
Opponent displaced focal animal	0.19‡	0.21‡	-0.22†	-0.24‡
Solitary piping	0.13†	0.11†	0.39‡	0.38‡
Piping ceremony	0.06	0.05	0.18‡	0.18‡

* $P \leq 0.05$; † $P \leq 0.001$; ‡ $P \leq 0.001$ represent two-tailed levels of significance.

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TABLE 4. Average duration in seconds and absolute frequency of all aggressive interactions observed. Focal animals more often won than lost encounters with a clear outcome

	Mean duration (s)	N
Encounters over mussels		
Focal animal lost mussel	11.8	99
Focal animal fled with mussel	12.1	167
Focal animal rebuffed robbing opponent	7.8	160
Focal animal failed to locate stolen mussel	13.3	88
Focal animal consumed stolen mussel	12.5	86
Opponent fled with mussel	8.0	303
Opponent rebuffed focal animal	13.4	35
Encounters not over mussels		
Focal animal displaced opponent	12.1	406
Opponent displaced focal animal	13.7	219
Outcome unclear to observer	6.4	110
Dominance behaviour		
'Solitary piping'	12.1	476
'Piping ceremonies'	89.8	60

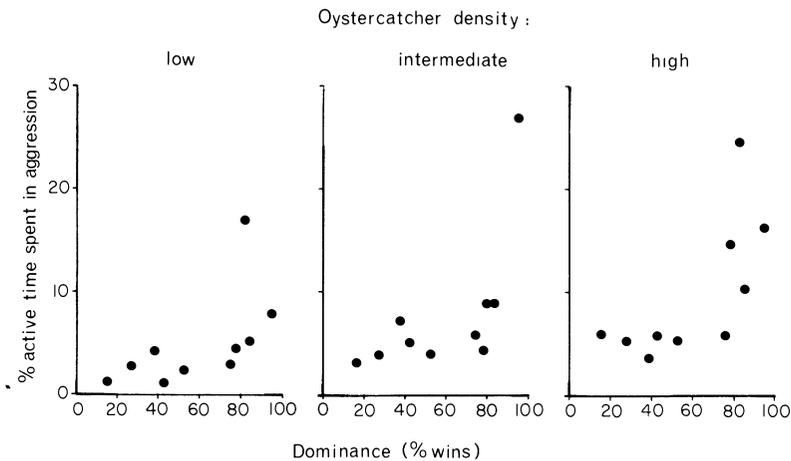


FIG. 5. The proportion of active time spent in aggressive encounters by the ten oystercatchers in relation to their dominance. The definition of low, intermediate and high bird densities is the same as in Fig. 4.

each individual increased only slightly as bird density increased. Indeed, the dominants lost more time in aggression because they performed most piping, both in solitary displays and in the time-consuming piping ceremonies (Tables 3 & 4). Though time lost in aggression must have contributed to interference because it cost birds more searching time at high bird densities, its influence was clearly small.

Interference may have been due more to mussels being stolen than to foraging time being lost. The number of stealing attempts did increase with dominance, especially at high bird densities (Fig. 4, Table 3). At the same time the frequency with which an individual

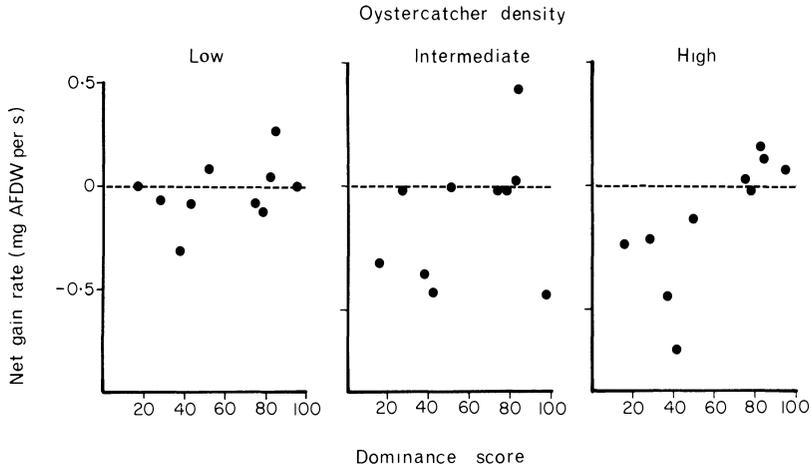


FIG. 6. Net rate of gain expressed in mg AFDW consumed per second active, in relation to dominance score at three levels of bird density. Net gain rate was calculated as biomass stolen (and consumed) from other oystercatchers, minus biomass lost to other oystercatchers and, occasionally, carrion crows. The big loss of the most dominant bird at intermediate densities was exclusively due to carrion crows.

was attacked decreased with dominance, though all animals were attacked more often at high bird densities. The result of this was indeed a net gain for the dominants and net loss for the subdominants, particularly at the higher bird densities (Fig. 6). But since the effect of density only applied to the five lowest ranking individuals, it is hard to see why only the two top-dominant birds were unaffected by interference, if robbing provided a complete explanation.

Another possibility is that bird density *per se* was in some way a major cause of interference. If so, the change in intake rate with bird density should have been primarily determined by the way capture rate, i.e. amount of food captured during foraging excluding time spent on any other activity, also changed with density. As expected, there was a strong positive correlation, when for each bird, the slope based on capture rate was plotted against the slope based on intake rate (Fig. 7). However, the slope for intake rate was more negative than the slope for capture rate in nine of the ten birds. This discrepancy must have been due to the increased loss of mussels and increased aggression at high densities of oystercatchers. But we cannot decide whether the decreased capture rate or the increased loss of time and mussels at high bird densities contributed most to the observed interference. This is because our estimates of the interference slopes were so imprecise, as the large standard errors in Fig. 7 show. This is due to the inescapably large variance in intake rates: birds find mussels at variable, perhaps random, intervals, yet each prey adds a great deal to intake rate. Birds may find between zero and three mussels per 5 min foraging, giving an enormous range in intake rates.

The avoidance by subdominants of the dominants seems the most likely explanation for decreased capture rates at high bird densities. If so, the subdominants would be expected to range more widely over the mussel beds as they make repeated attempts to avoid the dominants. Since the total area visited by an individual increased with observation time,

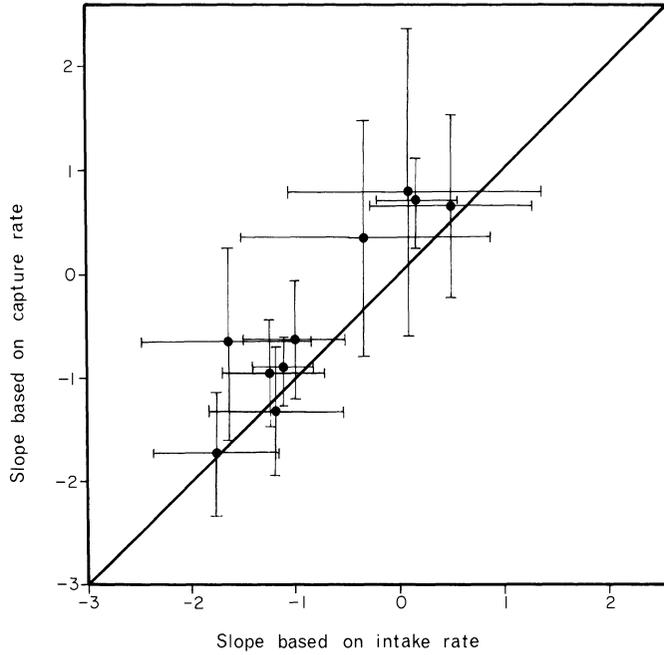
Interference among oystercatchers

FIG. 7. Relationship between interference slopes of the ten birds calculated in two ways: x , based on intake rates in which all foraging activities, including encounters over mussels, were included, and Y , based on capture rates in which only time spent in searching for and handling mussels was included.

the sizes of feeding ranges were compared after 3.5 hours of foraging time had been accumulated, the period for which the least studied individual was observed. As expected, the subdominants wandered widely over the mussel bed whereas dominants restricted their activities to small, unchanging areas (Fig. 8).

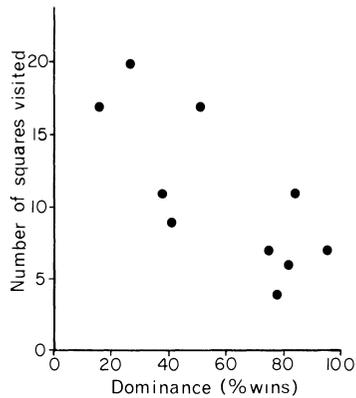


FIG. 8. The numbers of 25×25 m squares visited after 3.5 hours of foraging in relation to the dominance score. Spearman $r_s = -0.67$, $P < 0.05$ two-tailed.

Dominance and intake rate

Dominant birds had the highest intake rates even when the effects of bird density were partialled out (Table 5). This was not only because the dominant birds simply stole more and lost fewer mussels than the subdominants as capture rate also increased with dominance, even when the effects of bird density were partialled out. Goss-Custard *et al.* (1981, 1982b) showed that dominant birds fed where mussels were large and numerous and, in this study, dominance was also related to mussel size, though not to mussel density expressed as biomass (Table 5). However, the higher intake rates of the dominant birds may not have been related simply to the food supply because controlling for these two parameters of food supply did not affect the correlation between dominance and capture rate. Either some unmeasured feature of the mussels where the dominants fed improved their intake rate or dominance is itself correlated with another attribute of the bird, such as its experience in feeding, which increased intake rate (Goss-Custard, Clarke & Durell 1984).

TABLE 5. Correlates of dominance. In the first order partial correlation coefficient log density of oystercatchers was held constant. In the third order partial correlation coefficient density of oystercatchers, mean size and biomass density of mussels were controlled for

	<i>n</i>	Correlation coefficient with dominance		
		simple	first order partial	third order partial
Intake rate	555	0.17***	0.19***	0.18***
Capture rate	527	0.18***	0.19***	0.17***
Mussel size	527	0.25***		
Mussel density	527	-0.01NS		

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$ represent two-tailed levels of significance.

DISCUSSION

As was shown by Koene (1978) and Zwarts & Drent (1981) in Holland, interference occurred amongst the oystercatchers eating mussels on the Exe. Amongst the eight well-studied birds, intake rate did decrease at high bird densities in all but the most dominant individuals. Interference occurred because more mussels were stolen by other oystercatchers, capture rates were reduced and, perhaps, an increasing amount of time was spent in aggression, at high bird densities. In contrast to the study of Koene (1978), kleptoparasitism by other species contributed little to interference on bed 4. In Koene's study (l.c.), 75% of all the successful food-stealing attempts were made by herring gulls, *Larus argentatus*, compared with the 14% made by the carrion crows in this study.

It proved impossible to decide which factor contributed most to interference, because of the enormous variability in intake rates. However, we propose that it is possible to attribute interference to a basic cause, i.e. the increased opportunities for stealing at high bird densities amongst birds in a well-established dominance hierarchy. It seems best simply to treat robbing as a problem of prey choice (Dunbrack 1979). The percentage of the diet stolen by a bird increased with dominance, (Fig. 9), in this and another study on the Exe (Goss-Custard *et al.* 1984). Searching and robbing were not mutually exclusive activities in the sense of Barnard & Sibly (1981): focal animals just interrupted their own searching activity every now and then to rush at a nearby oystercatcher handling a mussel.

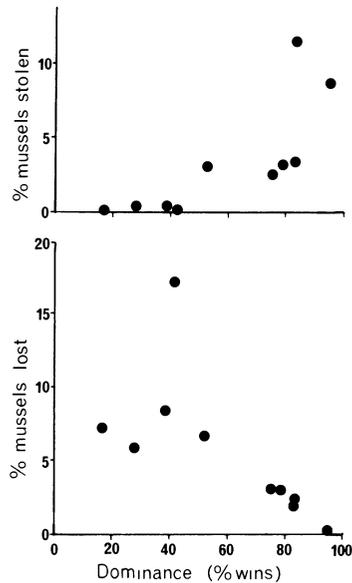
Interference among oystercatchers

FIG. 9. The relationship between the dominance of ten oystercatchers and (a) percentage of the diet that was obtained by stealing from other oystercatchers. $r_s = 0.91$, $P < 0.001$ two-tailed. (b) percentage of the diet that was lost to other oystercatchers. $r_s = -0.75$, $P < 0.05$ two-tailed.

Since the chances of making a successful attack decrease with the initial distance between attacker and victim (Vines 1980) the dominant should only rob when a victim is close enough for the expected benefit from the attack to exceed or equal its average intake rate. The observed increase in food stealing as bird density increased is expected on this hypothesis and, because in these conditions the dominant birds have more opportunities to make profitable attacks, their intake rate should not be reduced at high bird densities. Indeed, it might even increase. In contrast, a subdominant has to strike a balance at high bird densities between losing more of its mussels to robbing dominants and finding fewer because of increased avoidance. With an increasing density of oystercatchers, the probability of losing mussels increases and hence it pays to show more avoidance behaviour, even though this means intake rate will still go down.

There are a number of possible ways in which avoidance might lead to reduced capture rates. By taking evasive actions, the subdominants may have lost searching time or have been simply distracted from locating mussels by the need to avoid, and so to watch, the nearby dominant birds. Alternatively, they may have fed more often in poorer areas, or in places already depleted of catchable items.

Encounters which did not involve mussels usually involved only a short period of threat, with the victim fleeing more or less immediately. The aggressor usually took up the position previously occupied by the victim, suggesting these were fights over small-scale feeding sites. If this interpretation is correct, the capture rates of subdominant birds may also have decreased at high bird densities because they were more often displaced from good feeding positions.

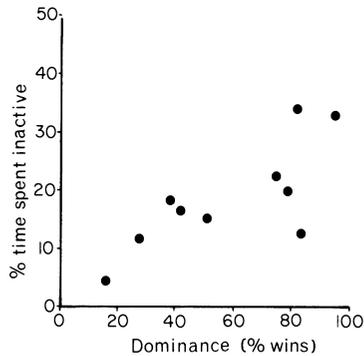


FIG. 10. Relationship between dominance and the amount of time spent inactive at high bird densities (more than 104 birds ha^{-1}). Spearman $r_s = 0.66$, $P < 0.05$ two-tailed.

Local avoidance is not the only option open to the subdominants at high bird densities. Subdominants apparently refrained from landing on the mussel bed when bird densities were very high and likely to remain so for some time. They probably continued feeding on less preferred areas of the estuary, as do immatures in winter (Goss-Custard *et al.* 1981, 1982b). Alternatively, some may have stopped feeding altogether. Koene (1978) showed that the mean proportion of birds feeding decreased with rising bird densities and Zwarts & Drent (1981) suggested that feeding was inhibited in some individuals. However, our data do not support this interpretation because it was the dominants that were most inactive at high densities (Fig. 10). It is unlikely that they were inhibited by the high densities of subdominants!

There is evidence that oystercatchers on the Exe compete for preferred mussel beds (Goss-Custard *et al.* 1981, 1982b; 1984), and the findings in this paper suggest a hypothesis for the mechanism involved. It is derived from Fretwell's (1972) 'ideal despotic distribution' model for habitat distribution: clearly, the 'ideal free distribution' (Fretwell 1972) does not apply on the Exe because of the considerable differences between individuals. As bird density rises on the most preferred beds, the intake rate of the subdominants will decrease so that it eventually becomes more profitable for them to feed on less preferred beds where, though the food supply is less suitable, interference is lower because fewer birds feed there. If all individuals behave so as to maximize their intake rate, the lowest ranking birds on all beds would be expected to have similar intake rates once the distribution has stabilized (Fig. 11). Feeding density should be higher on a rich mussel bed than on a poor one and the intake rate of the top-dominant on the rich bed should exceed the intake rate of the top-dominant on the poor bed. The hypothesis therefore predicts a positive correlation between average feeding density and mean intake among mussel beds. The same prediction was derived *mutatis mutandis* by Fretwell (1972) for the despotic distribution. However, in his model there is a dichotomy between settled and unsettled individuals, whereas we propose smooth changes in dominance. The fact that adults tend to dominate immatures (Goss-Custard *et al.* 1982b) allows a more interesting prediction. We expect that among the adults the lowest-ranking individuals are free to move, so that their intake rate is expected to be the same for all musselbeds. Hence we predict, as before, a positive correlation between average feeding density and mean intake

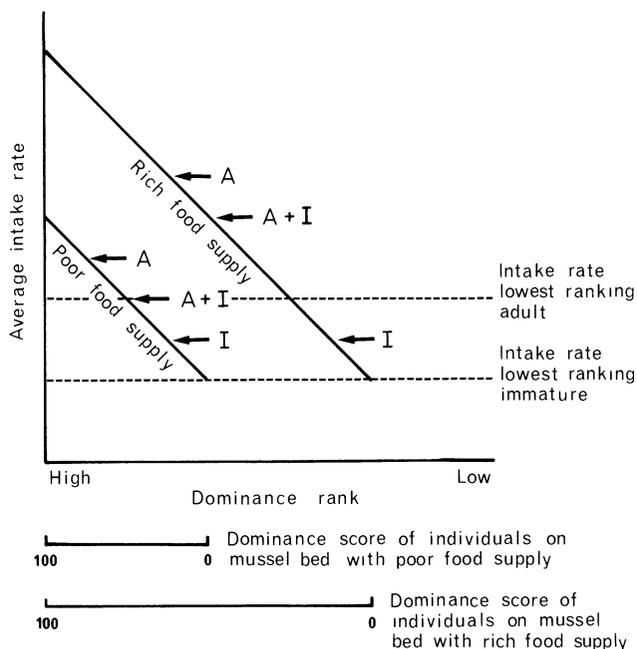
Interference among oystercatchers

FIG. 11. Graphical illustration of the modified ideal despotic distribution. We compare a hypothetical musselbed with a rich food supply and one with a poor food supply, which are assumed to be of equal size for convenience. (If the two musselbeds are not of equal size we need to define a quantity we might call the effective rank of an individual, which would describe the density of oystercatchers dominating the individual, instead of the number of oystercatchers dominating the individual as does dominance rank.) We assume that each individual attempts to maximize its intake rate and that intake rate decreases with dominance rank. The graph depicts the situation once the distribution has stabilized. Since the beds are of equal size the density of oystercatchers is clearly higher on the musselbed with the rich food supply. Arrows indicate average intake rates for (A) adult, (I) immatures and (A + I) adults and immatures combined. The predictions derived in the text are dependent on the shape of the curves relating intake rate with dominance rank, but the predictions will hold for a wide variety of curves as long as these curves decrease monotonically and do not cross each other.

rate among musselbeds for the adults. The situation is different for the immatures. Since the highest-ranking immature always resides under the lowest-ranking adult (in the ideal case), intake rates for the highest-ranking immatures should be equal among musselbeds with at least some adult residents. Hence, we expect no significant differences in the average intake of immatures among the musselbeds. However, it may prove difficult to test these predictions on the Exe, because probably different rates of energy expenditure on different beds (Goss-Custard *et al* 1981; 1984) render simple comparisons of gross intake rate inappropriate.

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