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Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers

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Abstract

We carried out two experiments to quantify effects of human disturbance on foraging and parental care in European oystercatchers (*Haematopus ostralegus*). In experiment 1, pairs incubating a clutch were disturbed on their feeding territory on the mudflat. Disturbance significantly reduced the proportion of time that the clutch was incubated, but also the proportion of time that the pair spent on the mud flat. In experiment 2, foraging oystercatcher pairs with chicks were disturbed by two observers at different distances from the edge of the salt marsh where the chicks resided. Total food collected was independent of disturbance, but a smaller proportion of the food collected was allocated to the chicks with increasing disturbance level. Both experiments demonstrate that human disturbance of foraging in breeding oystercatchers reduced the amount of parental care, and thus presumably reproductive success. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

In many areas, disturbance of foraging is common, by conspecifics and predators, for example but also by humans engaged in recreation or commercial activities. Management regarding the levels of human disturbance that is considered acceptable will have to be based on estimates of the effect of a given level of disturbance on the size and diversity of populations.

The effect and impact of human disturbance on bird populations has been studied at different levels (individuals, populations), on different time scales, and at different stages in the annual cycle (Boyle and Samson, 1985; Götmark, 1989; Davidson and Rothwell, 1993; Keller, 1995; Madsen and Fox, 1995; Carney and Sydeman, 1999). In most studies a correlation approach was used, rather than experiments (e.g. Gutzwiller and Anderson, 1999, and references cited below). Unfortunately, no causal relationship can usually be inferred from such data, leaving room for other interpretations of the data. For example, if density of breeding birds is lower in areas with high levels of recreation, humans could have a direct effect on settlement patterns. Alternatively,

sites that are attractive for humans may be unattractive to particular bird species, even in the absence of humans, but this cannot be decided in the absence of experiments.

From a management perspective, at least on a global scale, the only relevant way to measure effects of human disturbance on bird populations is in terms of effects on population size. In practice this is difficult, but it is possible to measure impacts on reproduction and mortality, which together with immigration/emigration determine population size. Unfortunately, with the exception of specific studies of the effect on nest inspection on the survival of nests and eggs (Götmark, 1992), only a few examples of such studies exist. Åhlund and Götmark (1989a) showed that disturbance of common eider (*Somateria mollissima*) crèche with boats increased predation of ducklings by gulls. Madsen (1995) reported preliminary data from an experiment in which it was shown that increased disturbance of geese in the spring staging areas lowered the probability of successfully breeding the following summer.

Here we report the results of experiments in which we investigated the effects of human disturbance on foraging and parental care in a wading bird, the European oystercatcher (*Haematopus ostralegus*). This species holds feeding territories on the mudflat, and breeding

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territories on land. We carried out short-term experiments, using pairs as their own control. Focal birds were disturbed while foraging on mudflats during incubation and chick-rearing periods. Performances of focal birds were compared between disturbed and control observation sessions. An alternative approach would have been to subject pairs to disturbance throughout the breeding cycle. This would have enabled direct estimates of the fitness consequences of disturbance. However, a power-analysis indicated that owing to the high variability in oystercatcher reproductive output, the required sample size to demonstrate even strong effects was too large to be feasible. With respect to performance, we focussed on time on the eggs for incubating birds, and on chick provisioning rate for birds rearing chicks. Hence we assume that these variables can be used as indicators of the long-term consequences for reproduction (Drent, 1967; Heg, 1999).

2. Methods

Data were collected in 1999 in the oystercatcher population on Schiermonnikoog, an island in the Dutch Waddensea. Oystercatchers breed on the salt marsh, and feed on the mudflat. Two types of pairs are distinguished in this population: 'residents', which have adjoining breeding and feeding territories; and 'leapfrogs', which have a nesting territory that does not border on the mudflat (Ens et al., 1992). For food, leapfrog pairs depend on a separate mudflat feeding territory. Both types of pairs were used in experiments. The largest part of the study area is closed to tourists during the breeding season.

2.1. Experiment 1: incubating birds

These experiments were carried out with oystercatchers with leapfrog territories, so that it was possible to disturb foraging without direct disturbance of incubation behaviour. Feeding territories were mapped using extensive observations from a hide on the mudflat. Observations to delineate feeding territories were started some weeks before the experiments started. The territory boundary was simply drawn by eye around all the observations on a map, giving extra weight to territorial interactions.

The experimental protocol consisted of 3 days of observation. On each day the pair was observed during one low tide period. The first and third day were used as control, and on the second day use of the feeding territory was prevented from 2 h before until 1 h after low tide. This was done by actively pursuing members of the focal pair when they were in the feeding territory until they were outside the territory (where they would then normally continue foraging). Thus, three observation periods were distinguished: Period I: 3 h 15 min — 2 h before low tide, Period II: 2 h before — 1 h after low

tide, Period III: 1 h — 3 h 30 min after low tide. One observer in a hide on the edge of the saltmarsh monitored presence and behaviour (in particular, the time spent on incubation) of the pair on the breeding territory from 3 h 15 min before low tide until 3 h 30 min after low tide. Two other observers quantified intake rate on the mudflat, using a PSION handheld computer with the Observer software package (protocol is described in detail below). These observations were carried out from a 6-m-high hide on the mud flat, 350 m from on the edge of the salt marsh. The duration of these observations depended on accessibility of the hide, but were approximately from 3 h before, until 3 h after low tide. It was not possible to monitor foraging behaviour all the time, mainly because foraging birds spend only part of the time on their feeding territory (Kersten, 1996). The proportion of time (with range in brackets) on the mudflat a foraging bird was observed, Periods I, II and III, was 0.33 (0–0.96), 0.57 (0.04–0.97), and 0.48 (0–0.99), respectively.

2.2. Experiment 2: chick-rearing birds

These experiments were carried out with oystercatchers that had adjoining feeding and breeding territories (residents) because the number of leapfrog pairs available was too small, and because the chicks of resident pairs were easier to observe. Chicks were 2–3 weeks old on the day of the experiment. Control and experimental observations were done within one low tide period, by two observers seated on the mud flat. Each observer followed one pair member. During the observations we noted foraging time of both pair-members, the number of prey captured, and whether or not prey items were fed to the chick. Owing to the fact that these experiments were carried out on resident pairs, observations were practically continuous. Further details of the observation protocol and conversion to food intake are described in detail later. The level of disturbance was varied through variation in the distance between the observers and the edge of the salt marsh where the chicks resided. Decreasing the distance to the edge of the salt marsh effectively reduced the area of the feeding territory available for foraging, and presumably increased predation risk as perceived by the parents. Observations were carried out from 2 h before until 2 h after low tide. Distance between observers and edge of the salt marsh was 100 m (1 h), 200 m (1 h), or 300 m (2 h). There was 1 h at 300 m before and after low tide, and we assumed that this was comparable with the undisturbed situation (observations of completely undisturbed birds were not possible). Whether the first hour was control or disturbed, and whether the first disturbed hour was at 100 m or at 200 m was alternated such that there was no correlation between time relative to low tide and treatment.

2.3. Observation protocol

Exact location of the focal birds (and the human disturbers) was determined using a permanent 50 m grid on the mud flat. During the protocols we recorded place and time allocated to walking, flying, aggression, preening, sleeping, and foraging. Foraging was further divided into searching and handling. Only foraging is of importance in this paper. Feeding success was quantified by noting prey species, and converting number of prey to ash free dry mass (AFDM) collected. Common prey species were sampled in the study area to determine their AFDM, values for less common species were taken from the literature (Table 1).

2.4. Statistical analysis

Data were analysed using general linear models. Since pairs served as their own control, pair was included as a block factor in all analyses. Proportions were arcsine transformed before statistical analysis (Sokal and Rohlf, 1994), although for convenience linear data are presented in the graphs.

3. Results

3.1. Experiment 1: incubating pairs

Complete experiments were carried out on four pairs. In a further three pairs, experiments were aborted after the first control day, because the birds could not be followed in sufficient detail on the mudflat and/or on the breeding territory.

Incubation time (proportion of time bird on eggs) during control observations (Fig. 1A) was comparable with the level observed in an earlier study of this population (86%, N.Verboven and B.J.Ens, pers. comm.). During the hours of disturbance (Period II: 2 h before–1 h after low tide) the incubation time was significantly reduced on the disturbance day, compared with the control days (Fig.1A; $F_{1,7} = 16.9$, $P = 0.01$). There was no significant difference between control and disturbance days in incubation time during Period I (1.25 h before disturbance; $F_{1,7} = 3.4$, $P = 0.1$). The disturbance effect during Period II remained significant ($F_{1,6} = 15.3$, $P = 0.01$) when incubation time in Period I was included as covariate in the model. Incubation time in Period III (following the disturbance period) was not significantly different on disturbance days ($F_{1,7} = 0.66$, $P = 0.4$).

The effect of disturbance on incubation time could be the consequence of foraging interruptions, resulting in longer foraging bouts, and consequently a prolonged stay on the mud flat. However, this was not the case. The proportion of time that one bird was on the mudflat (there was always at least one bird on the breeding territory) was significantly lower during Period II of disturbance days, as compared with control days (Fig.1B; $F_{1,7} = 15.4$, $P = 0.01$). The disturbance effect was equal for males and females, since the share of the male in the time on the mud flats during the disturbance period was not significantly affected by the experiment ($F_{1,7} = 0.10$, $P = 0.8$). Time on the mud flat did not differ between control and experimental days during Period I

Table 1
Diet, by frequency and by ash free dry mass (AFDM, in g) of collected prey, in the two experiments[a]

Species	Experiment 1 (incubation)				Experiment 2 (chick-rearing)		
	AFDM	Number	Prop. by number	Prop. by AFDM	Number	Prop. by number	Prop. by AFDM
Macoma baltica	0.064[b]	0	0	0	0	0	0
Scrobularia plana	0.179	0	0	0	0	0	0
Buried bivalve	0.086[c]	4256	0.795	0.768	98	0.086	0.102
Mya arenaria	2.477[d]	6	0.001	0.031	0	0	0
Syphon *M. arenaria*	1.239[e]	16	0.003	0.041	9	0.008	0.135
Cerastoderma edule	0.226	26	0.005	0.012	42	0.037	0.115
Nereis diversicolor	0.01	330	0.062	0.007	482	0.425	0.058
Arenicola marina	0.088	486	0.091	0.09	416	0.367	0.442
Carsinus menas	0.637[f]	0	0	0	6	0.005	0.046
Unknown	0.102[g]	235	0.044	0.05	82	0.072	0.102

[a] Prey summed over all observations are shown for the two experiments.

[b] AFDM of eaten *Macoma* was calculated assuming prey selection (small *Macoma* are less likely to be eaten) following Zwarts et al. (1996).

[c] 'Buried bivalve' concerns prey where the bird was eating a buried bivalve without us being able to determine whether it was *Macoma baltica* or *Scrobularia plana*. For AFDM the mean of *Macoma baltica* and *Scrobularia plana* was taken, weighed for their frequency in the substrate samples.

[d] From Zwarts (1991).

[e] It was assumed that oystercatchers eating the syphon of *Mya arenaria* take 50% of total prey mass. Fifty percent is an approximation based on Zwarts and Wanink (1984, 1989).

[f] From Zwarts (1988).

[g] For unknown prey species the mean was taken of *Cerastoderma edule*, *Nereis diversicolor*, *Arenicola marina* and 'buried bivalve'.

($F_{1,7}=0.39$, $P=0.4$), and Period III ($F_{1,7}=0.13$, $P=0.7$). The absence of an effect during Period III indicates that the foraging time lost during the disturbance period was not compensated later in the tidal cycle (foraging had always terminated before the end of

Fig. 1. Effect of human disturbance on foraging and incubation, for control ($\bigcirc$), and disturbance days ($\bullet$). Data (untransformed means ±S.E.) for three periods: I, 3 h 15 min–2 h before low tide; II, 2 h before–1 h after low tide (disturbance period on experimental days); III, 1 h–3 h 30 min after low tide. (A) Proportion of time one bird of the pair was sitting on the eggs. (B) Proportion of time one bird of the pair was on the mudflat. (C) Intake rate of birds when on the mud flat (mg AFDM/s), time spent on foraging and other activities combined. Standard errors were corrected for between-nest variation.

Period III). Another form of compensation for lost feeding time would be to increase intake rate when on the mud flat (Swennen et al., 1989; Urfi et al., 1996). However, intake rate of the foraging bird (Fig. 1C; in ash free dry mass) per time observed was not affected by the disturbance experiment in period II or III (Period II: $F_{1,7}=0.06$, $P=0.8$; Period III: $F_{1,5}=0.05$, $P=0.8$). (Repeating the calculations for intake rate per time foraging, instead of per total time on the mud flat, yields the same result.)

3.2. Experiment 2: chick-rearing pairs

Data were collected on six families, and data for the two parents were combined.

The distributions of intake rate for the family, parents and young were skewed to the left, and the natural logarithm of the observations (+1, to accommodate the presence of some zero-values) was taken prior to analysis. The total amount of prey collected by the parents was independent of the distance between the observers and the edge of the salt marsh where the chicks resided (Fig. 2A; $F_{1,17}=0.2$, $P=0.6$, controlling for nest: $F_{5,17}=2.5$, $P=0.07$). However, the proportion of prey items allocated to the chick increased significantly with increasing distance from the edge of the salt marsh (Fig. 2B; $F_{1,17}=35.3$, $P=0.001$, controlling for nest effect: $F_{5,17}=3.7$, $P=0.02$). Hence provisioning rate of the chicks increased significantly with increasing distance ($F_{1,17}=32.7$, $P=0.001$, nest effect: $F_{5,17}=2.7$, $P=0.05$), while the amount of prey consumed by the parents themselves was not related to observer distance ($F_{1,17}=0.3$, $P=0.6$, nest effect: $F_{5,17}=2.0$, $P=0.1$). The depressive effect of disturbance on chick provisioning could be compensated in later parts of the tidal cycle. However, provisioning rate was not related to the level of disturbance in the preceding hour ($P=0.3$), when nest and current level of disturbance were controlled for. Thus, there is no evidence that compensation occurred, at least within the time frame of our experiments.

4. Discussion

In the first experiment, when birds tending a clutch were disturbed, the intake rate of foraging birds was unaffected by disturbance (Fig. 1C), but less time was spent on the mud flat during the disturbance period. From these observations it can be inferred that at low tides birds ended periods of disturbance with reduced total food intake as compared with controls. A reduction in energy stores may reduce the birds' ability to withstand possible adverse conditions (e.g. restricted access to food during very high water) at a later stage (Monaghan et al., 1992). Disturbance of foraging
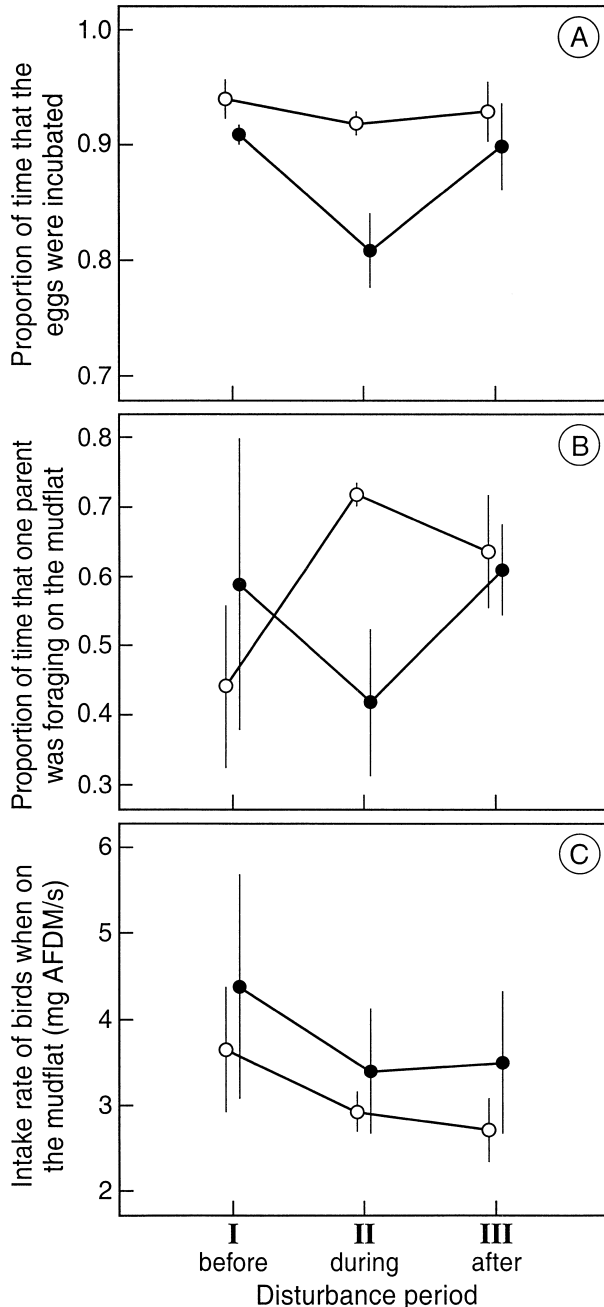
resulted in a reduction in proportion of time that the eggs were incubated (Fig. 1A), which may slow foetal development (Vleck and Vleck, 1996). More importantly, the reduced nest attendance probably increased vulnerability to depredation (Drent, 1967). It is surprising that less time was spent on the eggs during the disturbance period, given that birds spent more time in the breeding territory. Possibly, the disturbance disrupted the co-operation between the pair-members, but detailed data to verify this possibility are lacking. In conclusion, human disturbance of foraging resulted in decreased nest attendance, and presumably a decrease in energy stores at the end of the tidal cycle. Both factors are likely to result in decreased reproductive output, should the experimental level of disturbance be maintained for a long period, but longer-term experiments are required to show this unequivocally.

In the second experiment, pairs with chicks were disturbed while foraging. With decreasing levels of

Fig. 2. Effect of human disturbance on foraging success and prey allocation in oystercatchers feeding young. (A) Total prey collected (mg AFDM/s, ±S.E.) per observation time. The apparent U-shape is due to single very high values at 100 and 300 m and data were ln-transformed before statistical analysis to accommodate this distribution. (B) Proportion of prey fed to the chicks. Data were combined per pair ($n = 6$ pairs), and standard errors were corrected for between-pair variation.

disturbance (increasing distance between observers and the chick), the chicks were fed at a higher rate. This was because a greater proportion of the food could be given to the chick rather than because less food was actually collected by the parent. The effect of disturbance was not compensated at a later stage, at least within the time frame of our experiments, which showed that the disturbance had a permanent impact on the amount of food received by the chick. This is important, because chick survival is related to chick growth (Heg, 1999). Hence it is reasonable to assume that the level of disturbance in the experiment would have an effect on population productivity if all birds were exposed to this disturbance level throughout the breeding season (as would be the case when recreation levels increased). It is interesting that the disturbance affected the allocation of prey to the chick only. This suggests that the parents did not feed the chick when the observers were close to avoid drawing attention to the chick, rather than because of some threat to the parents themselves.

It is important to realise that we performed the disturbance experiments on a population of birds that had already settled in the study area, since we experimented with breeding pairs. Experimental evidence indicates that if the level of disturbance through recreation, for instance, is high for a prolonged period, including the time of year in which initial territory settlement takes place, then the density of breeding birds may be reduced (de Roos and Schaafsma, 1981). Thus, at least on a local scale, the effect of prolonged human disturbance on offspring production in a particular area is probably substantially higher than indicated by our experiments.

When assessing the effect of disturbance on animal populations, the geographic and temporal time scale which is considered cannot be ignored. Time scales are important because some form of habituation to disturbance may occur (Scott et al., 1996), reducing its effect on animal populations. A habituation effect is probably due to a decrease in the perceived predation-risk associated with human disturbance, and will at least in part be contingent on a real change in the threat that humans pose. For example, whether or not a species is hunted can be expected to have a large effect on the extent to which species will habituate to disturbance. Similarly, geographic scales on which human disturbance occurs will affect the scope there is for habituation. When a particular activity is rare on a geographic scale, many individuals of non-sedentary species may be exposed to a source of disturbance, but at low frequency, with little opportunity for habituation as a result. Thus, observed impacts of human disturbance on reproduction and mortality are specific for the level of habituation at the time and place where the study was carried out. In our study, disturbance of the form presented in the experiments was probably rare, and hence the effects that we observed may be stronger
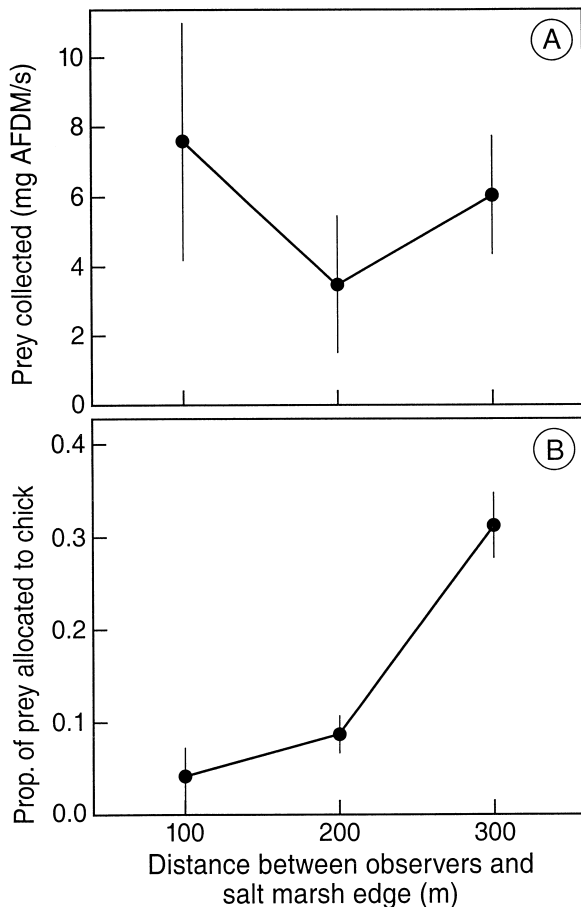
than they would have been if such activities on the mudflat were more common.

In conclusion, we demonstrated that disturbance of foraging results in a reduction in the quality of parental care, which can be expected to reduce population productivity when the disturbance is more frequent. Sample sizes in the two experiments were low due to low availability of suitable breeding pairs, but this conclusion is supported by the fact that both experiments yielded similar results. However, the long-term impact of an increase in disturbance is not clear. On the one hand, it could be stronger, because increased human activity could force birds to settle in less favourable habitat, but on the other hand habituation could mitigate the effects to an unknown extent. We advocate the use of controlled field experiments to further investigate these issues.

Acknowledgements

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