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# Responses of Incubating Hooded Plovers (*Thinornis rubricollis*) to Disturbance

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## ABSTRACT



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Hooded Plovers (*Thinornis rubricollis*) and recreationists co-occur on the ocean beaches of southern Australia, and it has been suggested that disturbance of the breeding birds by humans constitutes a conservation problem. This study examines whether humans disturb incubating Hooded Plovers and places that disturbance in context with naturally occurring disturbances. Incubating Hooded Plovers encountered and responded to a variety of human and natural stimuli. The most common response involved leaving the nest for a period of time (an “absence”), and humans were responsible for 33.1% of time spent off nests. The response rates of incubating birds varied with the type of stimulus, with higher than expected response rates to two species of potentially predatory birds. About 17% of encounters with potential causes of disturbance occurred while birds were already responding to other disturbance, and this prolonged the return to the nest. Absences from the nest that were not apparently caused by disturbance were shorter and less frequent than those caused by external disturbance stimuli. Nest habitat influenced the response to encounters with humans, and on average foredune nests suffered the greatest decrease in attendance per encounter. This study has confirmed that human disturbance is more frequent than natural disturbances, and that humans decrease nest attendance substantially and more than any other source of disturbance.

**ADDITIONAL INDEX WORDS:** Shorebirds, coastal birds, coastal nesting species, threatened species, conservation, management.

## INTRODUCTION

Humans have a long history of exploiting coastal areas for food, transport, and settlement (RAFFAELLI and HAWKINS, 1996). The growth in public recreation associated with greater mobility, affluence, and leisure time during the 20th century (BODEN and OVINGTON, 1973) has resulted in even more people using coastal habitats. Recreationists can potentially affect birds directly, through predation or disturbance (e.g., BURGER, 1994; MADSEN, 1993), or indirectly, through processes such as habitat modification (e.g., BOWLES and MAUN, 1982; MCDONNELL, 1981).

Although the potential for conflict between humans and birds is already high, it is likely to intensify in the foreseeable future. Projections of participation rates in outdoor recreational activities and of population growth, indicate that non-consumptive recreational activities will become increasingly common, and their frequency will increase into this century (BODEN and OVINGTON, 1973). In addition to increased rates of recreation, coastal developments and rising sea levels are likely to intensify the spatial overlap between coastal birds and humans (DAVIDSON and ROTHWELL, 1993). Advances in transport technology and new sports or activities (e.g., wind-surfing) can rapidly emerge and become popular, causing dis-

turbance in hitherto undisturbed areas or increasing the frequency of disturbance in areas already subject to some disturbance (BURGER, 1998; SMIT, LAMBECK, and WOLFF, 1987; STOKES *et al.*, 1996). Knowledge of the effects of disturbance lags far behind the growing problem, yet such knowledge is essential to mitigate possible long-term effects (SKAGEN, KNIGHT, and ORIAN, 1991; YALDEN and YALDEN, 1988; YORIO and BOERSMA, 1992).

Human disturbance is recognized as a threatening process for some plovers (e.g., MELVIN, GRIFFIN, and MACIVOR, 1991). Disturbance can decrease the reproductive success of plovers, causing shifts in their distribution and declines in their numbers (FLEMMING *et al.*, 1988; NICHOLLS and BALDASSARRE, 1990; PRATER, 1989; SCHULZ and STOCK, 1993; WARRINER *et al.*, 1986). Ocean beaches in southeastern Australia, the habitat of Hooded Plovers *Thinornis rubricollis* (after CHRISTIDIS and BOLES, 1994), are used extensively by humans, particularly recreationists (BUICK and PATON, 1989; DOWLING and WESTON, 1999). Limited breeding along coasts extensively used for human recreation makes Hooded Plover populations vulnerable to any negative effects of disturbance (PATON, CARPENTER, and SINCLAIR, 1994).

Disturbance from humans may be a process threatening the species, which is thought to be declining in areas where human disturbance is high. It is thought that the species' habit of leaving the nest when people are nearby is an important influence on Hooded Plover breeding success. The absence of the incubator may lead to higher rates of predation

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and egg chilling or overheating (SCHULZ, 1992; SCHULZ and BAMFORD, 1987). Under minimal disturbance conditions, incubation in Hooded Plovers is uniformly high (averaging over 90% of daylight time) across the incubation period. Although there is a relationship between incubation rates and ambient air temperature, it is slight, and incubation rates are high throughout the day and at all air temperatures (WESTON, 2000).

Disturbance is likely to occur throughout more of the distribution of Hooded Plover than any other threatening process except perhaps for introduced predators. However, disturbance to Hooded Plovers has not yet been rigorously investigated. This article examines the response of incubating Hooded Plovers to disturbance and places recreational disturbance in context with natural disturbances.

## METHODS

The study area consisted of ocean beaches from Johanna Beach, west of Cape Otway (38°45' S, 143°23' E), to Oberon Bay, Wilson's Promontory (39°04' S, 146°20' E), Victoria, Australia. Data were collected over three breeding seasons, 1995–1998.

### Operational Definitions

In this study a "stimulus" was any natural or human agent that had the potential to cause a response among breeding Hooded Plovers. An "encounter" was any event in which a stimulus passed within 100 m of a nest. An "absence" was a period of time when the nest was not incubated. The term "multiple disturbance" describes prolonged absences from the nest caused by repeated disturbances. "Discrete disturbance" describes circumstances where a bird returned to its nest, and there were no intervening encounters. "Return time" was the interval between departure from the nest and return to it.

### Field Procedures

Nests were observed from a hide (88.6%), a hidden position amongst rocks (2.9%), a car (2.9%), or on the beach hidden behind a tarpaulin (5.7%). Hides were always erected the day before observations began and were positioned at least 30 m from the nest. The approach to the observation posts sometimes resulted in a response from the attendant adults. Under these circumstances, the data collected before the birds resumed incubation were excluded. The observer (the senior author) did not leave his hidden position during observations.

Nests came from a variety of popular and remote beaches and from three habitats. Nests were on the beach (below the foredune), in the foredune, or in the dunes (the landward side of the foredune). The lower boundary of the foredune zone was defined as the point of lowest vegetation or greatest change in slope (whichever was lower). The upper boundary was delimited by a platform or, if there was no platform, the top of the primary dune.

Nests were observed under different weather conditions, which were generally fine and mild (daily average temperatures, 12.0–30.3°C;  $\bar{x}$  = 19.9°C) and typical of Hooded Plover

breeding areas during the breeding season. Most studies of bird disturbance do not account for weather (see, for example, DAVIDSON and ROTHWELL, 1993). The effect of weather on the response to disturbance is not analyzed here, because temperature had only a slight influence on incubation behaviour (WESTON, 2000), there was a relatively narrow range of weather conditions sampled, and few stimuli occurred frequently enough across different conditions to allow meaningful analysis. Natural and human stimuli, evoking all possible responses from incubating birds, were recorded in all weather conditions.

Attempts were made to observe nests from as many pairs as possible, regardless of their disturbance levels. Because nests were few in number and not long-lived, data from nests were collected in an opportunistic fashion (WESTON, 2000).

Activity scans were made every 5 min to record the behaviour and identity of each bird. Birds were classified as incubating, foraging, roosting, preening, or engaging in "other" activities. Nests were considered "attended" when an adult was incubating.

Continuous observations determined the response of incubating birds to passing stimuli. Encounters, and the level of habitat occupied by the stimulus, were recorded. The habitat was classified into five levels: (1) rock platforms, (2) lower beach (constant wave wash), (3) midbeach (the flat and wet section covered by the previous nocturnal tide), (4) upper beach (above the previous nocturnal high-tide mark), and (5) foredunes and dunes. The response of the incubating bird to encounters was recorded as: "Nest Absence," "Crouching over the Nest," or "No Response." These observations also allowed the identification of "incubator-initiated" absences from the nest, where nest departures were made in the absence of potentially disturbing external stimuli. Incubator-initiated absences, therefore, include voluntary absences and absences during changeovers of the incubators. These absences were characterized by slower departures by the bird from the nest and were associated with less vigilance (*i.e.*, watching) during and immediately after the departure, in comparison with departures from the nest associated with a response to a stimulus. It is possible that a small number of absences classified as incubator-initiated absences were made in response to an undetected stimulus; however, the observation post always afforded excellent views in all directions, and care was taken to minimize such a bias. If it occurred, this bias would effectively underestimate the occurrence and effect of disturbance. In order to maximize available data, the response of incubators to encounters was examined using 35 nests observed for at least 3 h. Return times were determined using a stopwatch.

In order to determine whether disturbance affected nest attendance, we examined data from 32 nests in which the adults were incubating and where observations lasted at least 10 h. "Observation days" refer to observations where pairs were observed at their nests for 10–12 h in a day ( $\bar{x}$  = 11 h). At some nests several days of observation occurred (an overall total of 49 observation days occurred at these 32 nests), but only the most disturbed day from each nest was selected for this analysis. Nest attendance was measured from the proportion of activity scans that involved incubation,

Table 1. The relative frequency of encounters with stimuli at nests ( $n = 1821$  encounters regardless of whether an incubator was on the nest).

Stimulus	Percentage Occurrence
Walker with no dog	49.5
Walker with dog	16.1
Raven*	10.8
Jogger with no dog	6.3
Bird of prey	6.0
Australian Magpie†	4.9
Bicycle	2.0
Jogger with dog	1.4
Dog‡	0.9
Silver Gull§	0.8
Intruding Hooded Plover	0.5
Other**	0.4
Vehicle	0.3
Horse	0.1

\* *Corvus coronoides*, *C. tasmanicus*, and *C. mellori*.

† *Gymnorhina tibicen*.

‡ These dogs had roamed so far from their owners that they passed the nest without humans.

§ *Larus novaehollandiae*.

\*\* These stimuli encountered nests only once.

and disturbance rates were measured as the total number of encounters with natural and human stimuli per observation day, regardless of whether an absence from the nest occurred.

### Statistical Analysis

When analyzing the incubating bird's response to disturbance, we assumed that each disturbance event was an independent data point. Other statistical procedures follow those outlined in ZAR (1996). Summary statistics are presented as mean  $\pm$  one standard deviation (untransformed). Dashes in tables indicate that data were unavailable.

## RESULTS

### Sources of Encounters

Overall, nests encountered  $3.0 \pm 4.2$  stimuli per hour ( $n = 49$  observation days; 555 observation hours). The hourly rate of encounters with human stimuli was  $2.4 \pm 4.0$  per hour (maximum 24.2); the rate of encounters with natural stimuli was  $0.7 \pm 0.9$  per hour (maximum 3.5). Of 49 observation days, only 16.3% were without an encounter with a human stimulus, and 22.4% were without an encounter with a natural stimulus. Only one observation day involved no encounters with natural or human stimuli (2.0% of observation days).

The relative occurrence of different types of stimuli at nests is shown in Table 1. Overall, 75.7% of all stimuli were due to humans or their companion animals, and 24.3% involved natural stimuli ( $n = 1821$ ). Of all encounters, 73.3% involved humans on foot. Within this category, walkers without dogs were the most frequently encountered stimulus at nests, and they accounted for about half of all encounters.

### Response to Disturbance

The typical response of incubating birds to nearby human and natural stimuli was to leave the nest and return at a

later time. Absences were by far the most common response to an encounter; 90.9% of encounters that caused a response ( $n = 580$ ) resulted in an absence from the nest. Other responses involved the incubator crouching over the nest (9.1%). Absences were not only made in response to encounters with external stimuli. For 36.0% of all nest absences ( $n = 753$ ), we could detect no external stimulus at the time of departure from the nest (*i.e.*, these absences appeared to be initiated by the incubator). Disturbance-initiated absences were significantly more frequent ( $1.1 \pm 1.1$  per hour) than incubator-initiated absences ( $0.5 \pm 0.5$  per hour) (paired *t* test on logged data,  $t = 3.895$ , degrees of freedom [DF] = 48,  $p < 0.001$ ;  $n = 49$ ).

## Factors Influencing Nest Absences

### Type of Stimulus

Human stimuli were responsible for 57.5% of disturbance-induced absences, with natural stimuli responsible for the remainder. Details of the absence from the nest in response to different stimuli are provided in Table 2.

In order to test whether incubating birds were responding at different rates to different stimuli, the observed frequency of nest absences was compared with the frequency that would be expected if the birds did not discriminate between stimuli. Expected values were based on the number of encounters with different stimuli multiplied by the overall rate of nest absences per encounter. Thus, in calculating expected values, it was assumed that each encounter had an equal probability of eliciting an absence (Table 3). Overall, observed frequencies of nest absences differed from expected frequencies (where expected values exceeded five,  $\chi^2 = 109.044$ , DF = 9,  $p < 0.001$ ). Observed frequencies of nest absences differed substantially from expected frequencies for three types of stimulus. There was a lower than expected frequency of nest absences in response to walkers without dogs and higher than expected absence frequencies in response to magpies and ravens. Combined, these accounted for 86.4% of the overall  $\chi^2$  value.

Of 620 absences where there were no intervening encounters between departure from the nest and return to it, incubator-initiated absences ( $3.4 \pm 11.4$  min) were on average of shorter duration than those caused by disturbance ( $4.6 \pm 6.9$  min) (*t* test on logged data,  $t = 10.902$ , DF = 362.5,  $p < 0.001$ ).

### Multiple Disturbance

Often a number of successive stimuli were encountered before a bird returned to its nest; 24.3% of stimuli encountered at nests ( $n = 1821$ ) were part of multiple disturbance, where at least one encounter occurred between departure from the nest and return to it. In other words, 16.9% of all encounters occurred while the attendant was absent from the nest because of a previous disturbance.

In order to examine the influence of multiple disturbance on return time, we examined multiple disturbances initiated by encounters with walkers without dogs, because these were the most common source of encounters. Higher numbers of



Table 2. The response of incubating birds to a variety of stimuli encountered during nest observations (pooled across pairs). The frequency data are from disturbance events where the attendant was on the nest when it encountered the stimulus ( $n = 1491$ , excluding 22 cases where the response was not adequately determined). The duration data (mins) are from discrete disturbances ( $n = 349$ ).

Stimulus	<i>n</i>	Percentage of Encounters That Caused an Absence	Average Duration of Absence	Standard Deviation of Duration of Absence	Maximum Duration of Absence
<b>Human</b>					
Jogger(s) with dog	18	44.4	1.5	2.9	2.6
Walker(s) with dog off leash	224	38.4	3.9	4.5	30.5
Jogger(s) without dog	92	25.0	4.3	5.0	19.3
Walker(s) without dog	717	21.5	3.9	4.3	24.5
Walker(s) with dog on leash	19	21.1	2.5	—	2.5
Bicycle	30	3.3	3.0	—	3.0
Vehicle	6	0.0	—	—	—
<b>Nonhuman</b>					
Australian Magpie	82	74.4	4.8	6.6	39.0
Intruding Hooded Plover	10	70.0	8.3	7.8	19.0
Raven	162	53.7	5.1	7.2	49.7
Horse	2	50.0	—	—	69.1
Dog	16	43.8	2.9	2.5	5.8
Bird of prey	94	37.2	6.6	8.3	42.0
Silver Gull	12	33.3	7.3	8.1	18.0
Other	7	42.9	3.5	8.1	20.0

encounters ( $N_{\text{dist.}}$ ) in multiple disturbances were associated with longer return times to the nest ( $\text{Time}_{\text{return}}$  min) (linear regression,  $\log \text{Time}_{\text{return}} = 0.712N_{\text{dist.}} + 1.735$ ,  $F_{1,43} = 12.274$ ,  $p < 0.001$ ,  $R^2 = 0.222$ ;  $n = 46$  multiple disturbances).

Some studies report increasing responses with increasing exposure to disturbance (see SMIT and VISSER, 1993). Thus, multiple disturbance could cause a delayed return once the disturbance passed, apart from the additive effects of multiple disturbance on return time. The time taken to return to the nest after a walker without a dog had caused a discrete

absence from the nest ( $3.9 \pm 4.3$  min) was not significantly different from the time between the last encounter (again involving a walker without a dog) during a multiple disturbance, and the eventual return to the nest ( $4.3 \pm 5.2$  min) (t test on logged data,  $t = 0.573$ ,  $DF = 88.1$ ,  $p = 0.568$ ).

### Habitat

Humans, the most frequent cause of disturbance, did not occur in all levels of the habitat to the same degree. Humans occurred predominantly in the midbeach: 71.7% of 2361 people who passed nests were in the midbeach. This means that nests in different habitats (beach, foredune, dunes) may be differentially affected by human disturbance. To examine this in more detail, we used data from encounters with walkers ( $n = 946$  encounters where the occurrence of a nest absence was established). The proportion of encounters that caused a nest absence differed significantly between habitats ( $\chi^2 = 59.676$ ,  $DF = 2$ ,  $p < 0.001$ , Figure 1), as did the duration of absences (one-way analysis of variance on logged data,  $F_{2,191} = 5.272$ ,  $p = 0.006$ , Figure 1), although the  $R^2$  value was low (0.052), suggesting that factors other than nest habitat affected return time. Post hoc Tukey pairwise comparisons revealed that the duration of absences at foredunes was longer than for dune ( $p = 0.040$ ) or beach nests ( $p = 0.012$ ). We calculated the average time off nests for 100 encounters with humans by multiplying the frequency of absences expected for 100 encounters with the back-transformed average duration of absences. On average, the time off nests per 100 encounters with humans was 12.7 min for dune nests, 72.8 min for foredune nests, and 63.6 min for beach nests.

### The Effect of Disturbance on Overall Nest Attendance

Generally, the proportion of time spent incubating remained high across all nests regardless of the frequency of

Table 3. Observed and expected frequency of nest absences in response to encounters with different stimuli. Expected frequencies are derived from the observed frequencies with which each stimulus category occurred, assuming an equal probability of eliciting an absence. The "Other" category has been excluded. Percentage values refer to the percentage of absences. The  $\chi^2$  value is shown where expected frequencies exceeded five.

Stimulus	Observed		Expected		Partial $\chi^2$
	<i>n</i>	%	<i>n</i>	%	
Human					
Walker(s) without dog	154	32.2	230.9	48.3	25.637
Walker(s) with dog off leash	86	18.0	72.2	15.1	2.658
Jogger(s) without dog	23	4.8	29.6	6.2	1.485
Jogger(s) with dog	8	1.7	5.8	1.2	0.836
Walker(s) with dog on leash	4	0.8	6.1	1.3	0.734
Bicycle	1	0.2	9.7	2.0	7.767
Vehicle	0	0.0	1.9	0.4	
Nonhuman					
Raven	87	18.2	52.2	10.9	23.235
Australian Magpie	61	12.8	26.4	5.5	45.293
Bird of prey	35	7.3	30.3	6.3	0.737
Intruding Hooded Plover	7	1.5	3.2	0.7	
Dog	7	1.5	5.2	1.1	0.661
Silver Gull	4	0.8	3.9	0.8	
Horse	1	0.2	0.6	0.1	

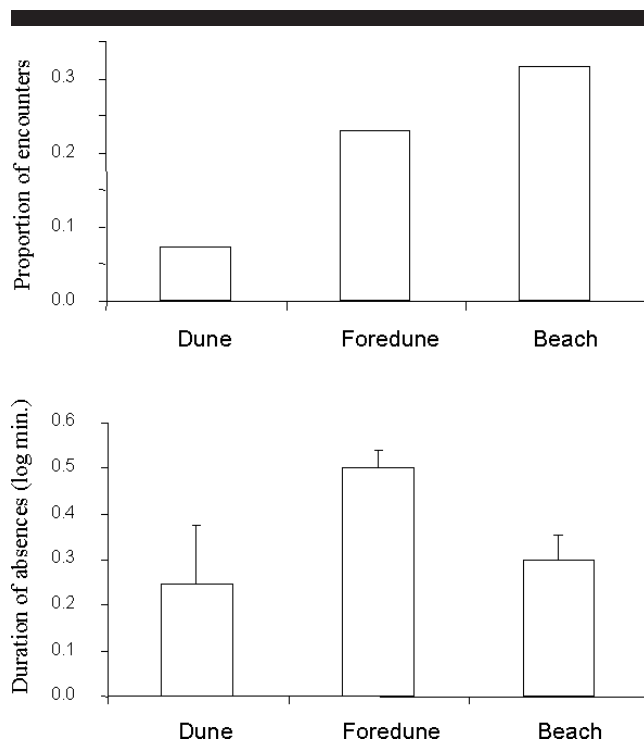


Figure 1. The effect of nest habitat on the response of incubating Hooded Plovers to encounters with humans. The proportion of encounters that caused an absence from the nest (top) and the average plus standard error duration of absences (bottom) are shown.

encounters ( $86.0 \pm 0.1\%$  of scans;  $57.8\text{--}98.9\%$  of scans;  $n = 31$  nests). However, at one nest attendance was considerably lower ( $36.2\%$ ).

Decreased rates of nest attendance ( $P_{\text{inc.}}$ ) were associated with higher numbers of encounters ( $N_{\text{dist.}}$ ) (linear regression, arcsine  $P_{\text{inc.}} = -0.085 \log N_{\text{dist.}} + 1.437$ ,  $F_{1,30} = 15.735$ ,  $p < 0.001$ ,  $R^2 = 0.344$ ).

In total, multiple disturbance resulted in  $49.1\%$  of time off nests. It was impossible to assign a single cause for the absence during multiple disturbance, so only discrete disturbances are considered here. Table 4 presents the agents responsible for "time off the nest." Humans were responsible for more time off the nest ( $33.1\%$ ) than any other source, and  $68.0\%$  of time off nests was caused by external stimuli.

## DISCUSSION

Disturbance frequently and substantially disrupted incubation in Hooded Plovers. The overwhelming response of Hooded Plovers to disturbance is to leave the nest and return at a later time (for reports of similar behaviour in other plovers, see BYRKJEDAL, 1989; PAGE *et al.*, 1983; YALDEN and YALDEN, 1990). Nest absences due to disturbance are more frequent and longer than those initiated by the incubator (see also HENSON and GRANT, 1991). In this study, absences from the nest commonly occur when both potential predators and humans encounter incubating adults, but humans are the most frequently encountered stimulus at nests and are the

Table 4. The factors responsible for time off the nest (discrete disturbances only).

Cause	Percentage of Time off the Nest (total 43.1 h)
Human	33.1
Voluntary	17.0
Changeover of incubator	15.0
Raven	14.2
Australian Magpie	11.2
Bird of prey	7.7
Silver Gull	1.2
Intruding Hooded Plover	0.7

single greatest cause of time off nests. Although many studies of disturbance document nest absences in response to disturbance (e.g., HENSON and GRANT, 1991; YALDEN and YALDEN, 1990), few examine the effect of those absences on overall nest attendance. For Hooded Plovers, disturbance decreases overall diurnal nest attendance, suggesting an inability to compensate for incubation time lost to disturbance during the course of a day.

## Factors Influencing Nest Absences

### Type of Stimulus

Many birds vary their response, or the distances or frequencies at which they respond, according to different stimuli (e.g., GRUBB and KING, 1991; HENSON and GRANT, 1991; MADSEN, 1993). Humans often evoke different responses or levels of response compared with other stimuli (BRUNTON, 1990; BUNNI, 1983; ROBERTS and EVANS, 1993). The highest nest absence rates in this study are in response to natural and not human stimuli (see also WARD, STEHN, and DERKSEN, 1994). This suggests that for Hooded Plovers, some natural disturbances are particularly threatening. The two sources of natural disturbance, where nest absence rates are high, involve ravens and magpies. Ravens are predators of Hooded Plover nests, and although magpies did not prey on nests, avoidance of predation required nest absences coupled with aggressive and distracting behaviour (WESTON, 2000).

Hooded Plovers leave their nests less frequently than expected in response to walkers without dogs. This could be due to a number of factors. Shorebirds and other birds are generally less responsive to slowly moving humans (e.g., walkers), compared with rapidly moving humans (e.g., joggers) (BURGER, 1981; BURGER and GOCHFELD, 1991; YORIO and BOERSMA, 1992). Habituation is promoted by stimuli that do not represent any real threat to the birds (KNIGHT, GROUT, and TEMPLE, 1987; PLATTEEUW and HENKENS, 1997). In this study, the only direct persecution of Hooded Plovers was from natural predators and unleashed dogs (personal observation). Habituation may be promoted by a constant stream of similar stimuli (SMIT and VISSER, 1993) that behave in a predictable fashion (PLATTEEUW and HENKENS, 1997). Walkers without dogs may be less threatening than other stimuli because they are slow moving, do not persecute the birds, and occur frequently. All of these factors may facilitate habituation.

Dogs are particularly disturbing to shorebirds (e.g., BUR-

GER, 1986; YALDEN and YALDEN, 1988, 1990). For the Hooded Plover, the types of human stimuli that cause the highest frequencies of nest absences involve dogs. The observed percentage of nest absences in response to encounters with leashed dogs is lower than expected, but the observed percentage of nest absences in response to encounters with unleashed dogs is higher than expected. The percentage of encounters with leashed dogs that caused an absence from the nest was similar to the percentage of encounters with walkers without dogs that caused an absence (*ca.* 21%). This suggests that it is the behaviour of dogs rather than their presence that influences whether nest absences occur. The particularly disturbing nature of unleashed dogs is probably explained by their tendency to move up and down the beach perpendicular to the water's edge (see BURGER, 1986). Additionally, unleashed dogs directly pursued Hooded Plovers at times (pers. obs.).

### Multiple Disturbance

Encounters often prolong nest absences, such that an individual may experience at least one further encounter before it returns to the nest. For Hooded Plovers, the cost of multiple disturbance in terms of lost incubation time seems considerable; less than 25% of all encounters in this study were part of a multiple disturbance, yet these accounted for almost 50% of time off the nest. Delayed return to the nest while a number of disturbances pass by results in one long nest absence instead of many short absences. There are possible benefits of not moving to and from the nest following each disturbance, and these may include reduced energy expenditure by the adults and reduced foot traffic to and from the nest (BUICK and PATON, 1989; PIENKOWSKI, 1984).

Why do Hooded Plovers often delay their return to the nest until a number of encounters have occurred? Our data suggest multiple disturbance does not shorten or prolong the time taken to return to the nest once the disturbance finally passes. Rather, the temporal separation of stimuli probably does not allow enough time for a return to the nest between encounters. It is also possible that the birds do not return to their nest when human or natural stimuli are approaching, so that the location of the nest is not advertised to the approaching stimulus (see PAGE *et al.*, 1983; YALDEN and YALDEN, 1989).

### Distance and Habitat

Nests in different habitats are at different distances from passing humans. In this study, the frequency of nest absences in response to walkers is higher among beach than among foredune nests. Foredune and beach nests have good vision of nearby humans, but foredune nests are farther from passing humans than beach nests. Perhaps the most common finding of observational studies of disturbance is that the degree of disturbance is proportional to the proximity of the stimulus (*e.g.*, BURGER, 1998; PLATTEEUW and HENKENS, 1997), and this may explain the observed frequency of Hooded Plover nest absences at foredune and beach nests.

Dune nests are even farther from passing humans compared with foredune and beach nests, but other factors, such

as vision and cover, probably mediate the response of incubating Hooded Plovers. Not all dune nests afford good vision of the beach. At the approximate height of an incubating bird, a person walking along the base of the dunes was visible from 57.9% of dune nests ( $n = 19$ , unpublished data). For some birds, habitat and vision influences the rate and intensity of responses to disturbance (BURGER and GOCHFELD, 1991; SCHULZ and STOCK, 1993). For Hooded Plovers, humans infrequently cause absences from dune nests, probably as a result of increased distance and cover.

Nesting birds subject to disturbance may alter their nest sites or habitat in subsequent nesting attempts (*e.g.*, DATTA and PAL, 1993; ERWIN, 1980; KNIGHT and FITZNER, 1985). If habitat mediates the frequency and duration of disturbance-induced absences from Hooded Plover nests, and given that pairs are able to shift between nesting habitats (see WESTON, 2000), then why don't all Hooded Plovers nest in the least disturbed dune habitat? There could be disadvantages to nesting in dunes that outweigh any potential reduction in disturbance. These might involve different predation rates and increased energy expenditure and risk of detection involved in commuting to and from the nest, and perhaps there are problems with navigating a brood from the dune to the beach, where most foraging occurs (WESTON, 2000). Additionally, suitable dunes are not available on every territory (unpublished data).

### Disturbance as a Conservation Problem and a Management Issue

The impact of disturbance to populations is of central interest to conservation biologists (HOCKIN *et al.*, 1992). For some species, even small effects of disturbance may be biologically significant and might warrant a management response (GIESE, 1996). The Hooded Plover is threatened (GARNETT and CROWLEY, 2000), and populations appear limited by poor reproductive success, so the reproductive performance of pairs could be critical to the survival of whole populations (WESTON, 2000).

Although we have been unable to establish a direct link between disturbance and reduced reproductive success, we have demonstrated that disturbance, predominantly by humans, causes the incubator to leave the nest frequently and for longer periods than would otherwise occur. The proportion of time spent incubating decreased with increasing disturbance. This potentially increased exposure of the eggs to temperature extremes and predation (SCHULZ, 1992; SCHULZ and BAMFORD, 1987). For the Hooded Plover, some extreme egg temperatures have been recorded during absences from the nest caused by disturbance, although predators did not prey upon eggs during these absences (WESTON, 2000). The demonstration of a potential mechanism through which disturbance could reduce reproductive success suggests that disturbance to incubating Hooded Plovers may constitute a conservation problem worthy of management.

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