Effects of human approaches to nests of northern New Zealand dotterels

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Abstract

The northern New Zealand dotterel *Charadrius obscurus aquilonius* is an endangered shorebird, and it is thought that human disturbance may decrease its nesting success. We made three types of approach to nests (walking, running or leading a dog). We measured the flush distance, length of time parents spent off the nest and distraction display intensity. Leading a dog caused the greatest disruption of incubation, while responses to walking and running approaches did not differ significantly. Distraction display intensity appeared to be unrelated to approach type. There was evidence of habituation to humans on busy beaches. Our results provide the first experimental evidence that shorebirds perceive dogs as posing more of a threat than humans on foot, and that their subsequent avoidance response is greater. We recommend that human activity, particularly the walking of dogs, should be limited near nesting sites. Further study on causes of nest failure is required. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

According to the IUCN red list, the New Zealand dotterel *Charadrius obscurus* is endangered (Collar et al., 1994). Species accorded this status are faced with a high risk of extinction in the wild in the near future. The species is endemic to New Zealand. Approximately 1500 birds of the northern subspecies *C. o. aquilonius* remain, its range and numbers having declined dramatically during the past 150 years (Dowding, 1994). The decline has been attributed to predation, and humans and their dogs are also thought to have an adverse effect during the breeding season (Dowding, 1989, 1993). Empirical evidence of these suggested causes is sorely lacking, although human disturbance has been shown to decrease the time chicks spend foraging (Lord et al., 1997). To date, no published study has investigated effects of human disturbance on this species during the incubation period.

New Zealand dotterels usually lay their eggs on open sandy beaches (Dowding, 1989; Marchant and Higgins, 1993) and incubate them for approximately 1 month (McKenzie, 1953, 1954). Chicks leave the nest immediately after hatching. Well-developed distraction displays are given (Phillips, 1980; Marchant and Higgins, 1993) by both male and female; both also incubate and defend the nest (Marchant and Higgins,1993).

New Zealand dotterels leave their nests if potential predators (including humans) approach (Dowding and Chamberlin, 1991). This is a common response among ground-nesting birds (Burger and Gochfeld, 1983; Evans and Pienkowski, 1984), and may be a primary cause of low hatching success in birds frequently exposed to human activity (e.g. Piatt et al. 1990; but see Gillet et al., 1975).

It is desirable, although often not practical, to prohibit human access from breeding areas occupied by threatened or endangered species. In areas that are highly valued for recreational use, a compromise may be reached by determining whether certain types of human activity are more disruptive than others, and, once these are identified, to limit such activities.

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We tested the response of nesting dotterels to three types of disturbance that they regularly encounter (walking, running and dog-walking) to compare the relative effects. We measured flush distance, length of time spent off nests, and intensity of distraction displays. Second, we examined whether dotterels habituated to these types of disturbance by comparing responses on busy and quiet beaches.

2. Methods

2.1. Study sites

From September to December 1995 we experimented with a total of 15 dotterel pairs occupying nests at nine different beaches on the east coast of the North Island of New Zealand. Our sample comprised 2–3% of the total world breeding population, and was spread over a range of beaches because of the rarity and sparse distribution of nests and to include both busy and quiet beaches in the sample. The spring and summer nesting period coincides with the holiday season, when people frequently come in contact with the birds. Nests were discovered by observing the behaviour of parents. We waited at least 3 days after discovery before experimenting.

Nesting birds at sites subjected to either high or low levels of human activity were sampled. Sites were rated as receiving high levels of activity if they received between 7–20 visitors per hour, and were on popular beaches with easy access and near housing settlements (seven nests). Sites without these attributes received from 0–3 visitors per hour and were rated as receiving low levels of activity (eight nests). Visitor numbers were counted on each of our visits to the site, which included weekends as well as weekdays. Counts varied depending on the weather, date and time of day, but the final ranking represented average visitation rates, which were probably consistent with those of previous years.

2.2. Procedure

Three types of approach were made towards the incubating bird. These were: (1) a person walking; (2) a person running; and (3) a person walking with a leashed and muzzled dog. The walking approach mimicked the most common human behaviour in the breeding area. The running approach was used because it mimicked joggers on the beach, and because the speed of approach may contribute to an animal's assessment of threat intensity (Gochfeld, 1984; Tyler, 1991; Wilson et al., 1991). The dog approach was included because people commonly exercise dogs on New Zealand beaches, and dogs pose a direct and significant threat to shorebirds (Burger, 1981a). The three approaches were all carried out to the same nest on the same day, and the order changed randomly between nests.

At a given site, all approaches were made from the same direction, which was determined by the ease of access and where the incubating bird was most visible from. The direction usually followed the route typical of beach visitors.

Three behavioural responses of nesting dotterels to the approachers were measured: flush distance, time spent off the nest, and intensity of distraction displays. The flush distance is the distance between the approacher and nest when the incubating bird leaves the nest. It is assumed that a bird will leave its nest earlier in response to a more threatening approach (Barash, 1975; Burger and Gochfeld, 1981, 1983; Keller, 1989). The length of time a bird spends off its eggs in response to an approach may also reflect the degree of threat perceived by the bird. Injury-feigning distraction displays, which are given by many shorebirds in defense of eggs or chicks, may also be a useful measure of disturbance intensity. Gochfeld (1984) stated that "Distraction displays are given to intruders that appear to be hunting... or that might be deluded...". It might therefore be expected that more intense displays are given to intruders that are perceived as posing a relatively greater threat.

All approaches to a given nest were made between 10:00 and 19:00 h (NZDT), and were separated by 2 h 'settling' periods. So that any thermal stress on the eggs caused by the approach would be minimised, tests were not carried out during rainy or very windy weather, and we ensured that the tested bird was undisturbed and incubating for at least 10 min prior to being approached. Approaches began 200 m from the nest and were stopped 5 m from the nest. The 5 m stopping point was adopted to ameliorate the disturbance caused to birds by the experiment. After remaining 5 m from the nest for 1 min, the investigator turned and walked away (even when the initial approach involved running). For each approach, the following measurements were taken: (1) flush distance (the distance between the investigator and the incubating bird when it left the nest); (2) the total time for which incubation was disrupted; and (3) the intensity of every distraction display performed by the bird during the 1 min period following arrival near the nest. Nests were tested either during early incubation (days 1–10; 10 nests), or late incubation (days 21–32; five nests). The onset of incubation was known (with an accuracy of at least 4 days) from weekly monitoring of nesting sites and contact with local residents.

We also recorded the temperature at an unshaded ground position following each approach, as this could conceivably affect a parent's willingness to expose its eggs. The sex of the incubating parent was not routinely recorded, because although some of the study birds had been colour-banded and their sex recorded from previous

mating observations by other researchers, this was not always the case. Visual sexing of New Zealand dotterels can be very unreliable (Dowding, 1989). Both sexes were observed to incubate at different times. When both parents were present at the nest during an approach, only the displays of the bird that had been incubating at its outset were recorded.

A potentially confounding factor was that all nests situated on high use beaches had been roped off by beach residents to prevent human access as a conservation measure. The investigator simply stepped over the rope during approaches, and passed the dog leash under it.

Distraction displays were graded on the basis of their intensity (see Marchant and Higgins, 1993, for a full description and diagrams). Level 1, considered to be the least intense, consisted of a 'rodent-run', where the body was held horizontal as the bird ran. During level 2 displays the tail became spread and the body tilted to one side during the run. Level 3 included a full 'broken-wing display', during which the tail was widely flared, the body tilted to one side and the lower wing spread and dragged on or near the ground as the bird moved along. The upper body was always turned to the investigator. At the fourth (highest) level of intensity, a 'dying display' was performed, during which the bird lay on its belly, beating its extended wings with its tail flared. The displays actually involve a continuum of increasing intensity, and were delineated into levels for the purpose of the study. It was assumed that a more intense display reflected a relatively greater perception of threat by the bird; more intense displays probably entail greater risk to the performer relative to other behaviour (Brunton, 1990).

2.3. Statistical analysis

2.3.1. Model A

The data for both flush distance and time spent off the nest were highly skewed and transformation did not normalise the data. Therefore, the data were analysed using multiple log-linear regression analyses with an appropriate correction for overdispersion (Crawley, 1993). The underlying model for the analyses was:

$$\text{Log (flush distance or time off nest)} =$$
$$\text{ID}_i + \text{AP}_k + \text{TE} + \text{TE}^2$$

where ID_i is the ith of a set of coefficients specific to the 15 pairs of dotterels, AP_k is the kth set of coefficients for the three approach types and TE is temperature recorded on each visit to the nest. TE^2 was included to check for curvilinear relationships. The statistical significance of each predictor in the model was assessed by the change of deviance recorded by removing it and then adding it back to the model. This change in deviance is distributed asymptotically as χ^2. The minimum adequate model was reached when no variable could be added or

deleted from the model without causing a significant change in deviance.

The order in which approaches were made to the nest was excluded from the modelling process because it was random with respect to approach type (Cramer's coefficient $v = 0.19$, $P = 0.53$, following Siegel and Castellan, 1988).

2.3.2. Model B

To compare the responses of birds on beaches with different levels of activity, alternative models were developed. The procedure described above was used, except the underlying model was:

$$\text{Log (flush distance or time off nest) for either}$$
$$\text{(1) walk, (2) run or (3) dog} = U_i + \text{Or}_j + A_k$$

where U_i is the ith of a set of coefficients specific to busy or quiet beaches, Or_j is the jth of a set of coefficients specific to the order in which the nest was approached and A_k is the kth set of coefficients for the age of the nest (either early [within 10 days of start of incubation] or late [21–32 days]). To avoid pseudoreplication, a separate model which used only one data point from each pair was constructed for each approach type.

To correct for overdispersion in the model (Crawley, 1993), standard error values were multiplied by $\sqrt{(\text{residual deviance/residual degrees of freedom})}$ after fitting models A and B. The means and standard errors for approach types were back-transformed from model output by taking the exponential of the parameter estimate. Contrasting was used to further compare grouped approach types where deemed appropriate. This was carried out by grouping factor levels together (i.e. run and walk vs. dog) and re-fitting the new factor. If the new factor accounted for a significant amount of the deviance then it was accepted. Modelling was carried out using GLIM 4.0 (NAG, 1993).

The maximum display intensity was scored from 0 (none) to 4. These data were analysed using a Freidman test in MINITAB version 12.0. This non-parametric test holds constant the effect of pair whilst investigating the effect of approach.

The construction of separate models for each response variable (i.e. flush distance and time off nest) for both modelling approaches (i.e. A & B) therefore increased the probability of a Type I error. In addition, separate models were constructed for each approach type in model B, further increasing the probability of Type I error. To account for these unknown sources of error we adopted a conservative approach to significance testing by using the Bonferonni corrected value for eight repeated tests. Therefore all results with a P-value equal to or greater than 0.0064 were regarded as non-significant.

3. Results

There was a positive correlation between flush distance and the time birds spent off the nest in response to all approaches (r_s = 0.40, d.f. = 37, $P = 0.013$). When model A was fitted to data for flush distance, the variables remaining in the minimum adequate model were individual pair and approach type. Therefore, flush distance was significantly influenced by the type of approach the incubating bird experienced when the variation caused by individual pair, order of approach and temperature was taken into account ($\chi^2 = 9.98$, d.f. = 2, $P = 0.0063$, Fig.1a). When running and walking approaches were grouped into one category [mean flush distance 64.1 m (55.3–74.3, 95% cl)], the flush distance was significantly shorter than in response to the 'walk + dog' approach [mean flush distance 93.7 m (75.0–117.9, 95% cl)] (χ^2 = 7.6, d.f. = 1, $P < 0.006$).

To check for any effect of the nests' stage of incubation on flush distance, this variable was included in the model in place of 'individual pair' (as the two were confounded), and was not found to have an effect ($\chi^2 = 0.17$, d.f. = 1, $P = 0.67$).

The same variables (approach type and individual pair) remained in the minimum adequate model for the length of time the bird spent off its nest. Fitting model A showed that approach type ($\chi^2 = 15.4$, d.f. = 2, $P < 0.001$, Fig. 1b) affected the response, and that when

running and walking approaches were grouped into one category [mean time off nest 204 seconds (185–224, 95% cl)], the time spent off the nest was significantly less than in response to the dog [mean time off nest 288 seconds (249–332, 95% cl)] ($\chi^2 = 14.6$, d.f. = 1, $P < 0.001$). The effect of stage of incubation was again checked as described earlier, and was not significant ($\chi^2 = 4.08$, d.f. = 1, $P = 0.04$).

The results of type B models showed that birds nesting on beaches with high levels of human activity responded with shorter flush distances when approached by a walker ($\chi^2 = 11.3$, d.f. = 2, $P < 0.001$), but beach usage level did not significantly affect responses when nests were approached by a running person ($\chi^2 = 2.69$, d.f. = 1, $P = 0.10$) or a person with a dog ($\chi^2 = 1.66$, d.f. = 1, $P = 0.20$; Fig. 2a). Beach usage level was not significantly related to the amount of time spent off the nest in response to any approach. However, during the approach with a dog, there was a trend for incubation to be disrupted for longer periods at beaches receiving few visitors ($\chi^2 = 6.79$, d.f. = 1, $P = 0.009$; Fig. 2b). This was less obvious when the approacher walked ($\chi^2 = 3.91$, d.f. = 1, $P = 0.05$) or ran to the nest ($\chi^2 = 6.44$, d.f. = 1, $P = 0.12$).

We were unable to examine whether the nests' stage of incubation independently affected response intensity, as it was confounded with beach type (most of the nests tested during late incubation were on remote beaches).
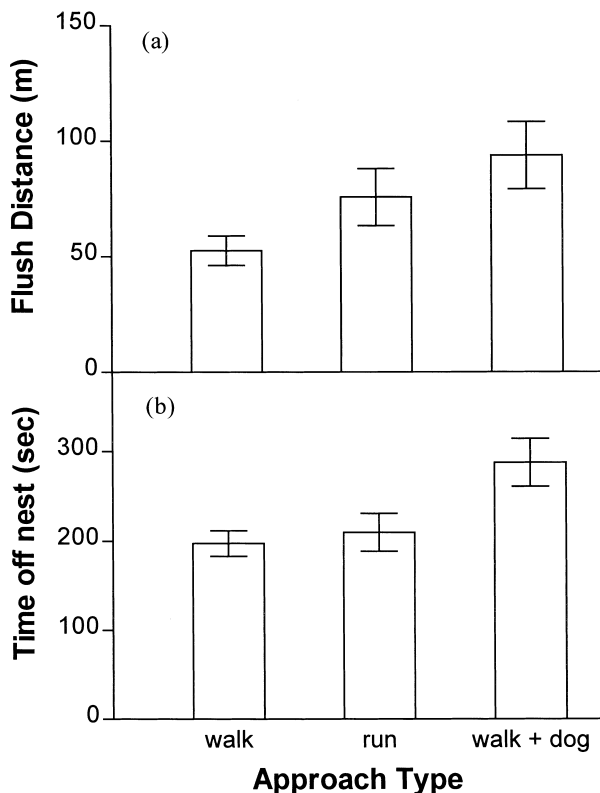

Fig 1. Effect of approach type on (a) flush distances and b) time spent off nest (back transformed means and standard errors).
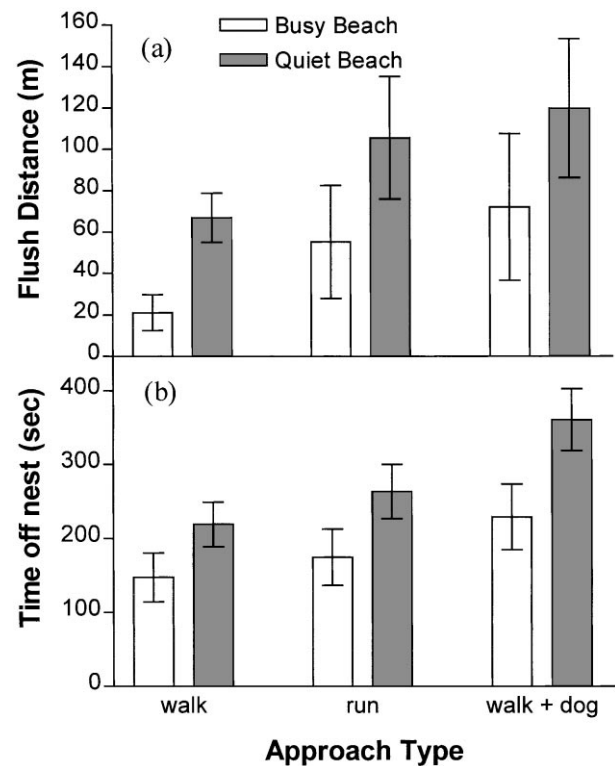

Fig. 2. Effect of beach activity level on (a) flush distance and (b) time spent off nest (back transformed means and standard errors).

However, the stage of incubation was included as a predictor in all models and was not found to significantly affect responses ($P > 0.07$, in all cases).

The most common maximum display performed had an intensity of level 1 (the rat run), and 22% of birds performed no display at all (Table 1). This intensity was unaffected by approach type ($S = 0.81$, d.f. $= 2$, $P = 0.67$) or beach activity level (Mann–Whitney tests for each approach type; $P > 0.24$, in all cases). Other known potential predictors were also checked (inter-pair variation and order of approach) but neither were found to significantly affect display intensity.

4. Discussion

New Zealand dotterels flushed from their nests earlier and stayed off them for longer when approached by a person leading a dog, compared to when the person was walking or running. This suggests that dogs at nesting sites disrupt incubation more seriously than do lone people. This study did not measure hatching success, but other studies suggest that increased thermal stress and predation rates result from such disruption (Pienkowski, 1984; Westmoreland and Best, 1985). The disruption caused by a lone walker or runner was less severe but also notable, and responses were less intense on busy beaches.

Leaving nests upon the approach of a potential predator may be a strategy to reduce the vulnerability of eggs and/or parents to predators (Montgomerie and Weatherhead, 1988). The extremely cryptic and well-camouflaged nature of New Zealand dotterel nests and eggs makes them almost impossible for most people to find or see; a trained observer is able to do so by observing an adult leaving or arriving at a nest (J. Dowding, pers. comm.; pers. obs.) As the flushing behaviour itself entails risk, parents need to discern the threat posed by a predator in order to assess the trade-off. Our results suggest that such discrimination does occur in New Zealand dotterels.

4.1. Relative levels of threat

New Zealand dotterels apparently perceive that an accompanied dog poses a greater threat than does a lone person. Although other authors have stated that dogs pose a significant threat to shorebirds (Burger, 1981a), these results provide the first experimental evidence that shorebirds perceive dogs as posing more of a threat than humans on foot, and that the birds' subsequent avoidance response is such that breeding success may be reduced.

This result supports that of Mainini et al. (1993), who showed that marmots *Marmota marmota* were more disturbed by a hiker with a dog than by a lone hiker. Dogs are likely to be more dangerous than people to dotterels; dogs pose a direct threat to shorebirds as they can catch and kill them (Burger, 1981a). Dogs are probably more likely to discover the location of the dotterels' extremely well-camouflaged eggs because of their keen sense of smell. By flushing at a greater distance and staying off the nest until the threatening animal has had longer to retreat, parents reduce the chance that their own movement and location will reveal the whereabouts of the nest.

As the length of time that eggs are unattended may be positively related to egg mortality (Teal, 1965; Burger, 1981b), the hatching success of New Zealand dotterels may be reduced where dogs are commonly present. Temporary nest abandonment may also give other potential predators easier access to eggs (Pienkowski, 1984; Westmoreland and Best, 1985; Dowding and Chamberlin, 1991).

It should be noted that the dog used in the current experiment was controlled with a leash and muzzle; free roaming dogs could well behave in an exploratory manner more similar to hunting. It is possible that nesting birds may perceive this difference in behaviour and respond even more intensely to an unrestrained dog.

There is a possibility that the increased intensity of response caused by the inclusion of the dog may have been because, during this approach, there were two approachers rather than one. Burger and Gochfeld (1991a, b) reported a positive relationship between the size of approaching groups and birds' flush distance. The inclusion of a fourth approach in which the investigator was accompanied by another person, or led an animal that was unlikely to threaten nesting birds, would have distinguished any such effect. However, flocks of New Zealand dotterels did not react more strongly to groups of people than they did to single person during a companion study (Lord et al., unpublished data).

The speed at which the investigator was travelling had no significant effect on measured responses. Contrasting results are reported by Gochfeld (1984), Tyler (1991) and Wilson et al. (1991). Dotterels may be responding more to the species of the potential predator than to its behaviour. Cresswell (1993) reported that the response of redshanks *Tringa totanus* to a potential predator depended on its species. Further, dotterels may percieve

Table 1
Level of the most intense distraction display recorded during 1 min spent 5 m from nest following each approach

Approach	Level				
	0	1	2	3	4
Walk	1	8	4	1	3
Run	4	9	0	3	2
Walk + dog	6	2	4	1	5

that a running person is no more likely to discover a nest than is a walking person.

We had hypothesised that the most intense distraction display performed by parents to the approacher(s) would vary with approach type, reflecting parents' perceived threat to eggs. This was not shown to be the case, and no other predictors were identified. It is thought that distraction displays are effective in deterring predators (Armstrong, 1956), and are given at risk to the performing bird (Barash, 1975; Andersson et al. 1980; Greig-Smith, 1980; Brunton, 1986). It is possible that a significant effect of approach type may have been observed if the experimenter had approached the nest more closely rather than stopping 5m away.

4.2. Habituation

There were indications that New Zealand dotterels habituate to human activity. Birds nesting on high-use beaches consistently showed a tendency to allow a closer approach before flushing and stay off their nests for a shorter period than birds nesting on remote beaches. A decreased intensity of response is likely to be adaptive for birds exposed to high levels of human activity.

A comparable conclusion was drawn by Keller (1989) in her study of great crested grebes *Podiceps cristatus*, which also displayed reduced flush distances in sites frequently used by humans. She noted that if the flush distances of nesters in frequently used sites were as large as those observed in relatively unused sites, breeding in the recreational areas would be impossible, as the incubating bird would be flushed so often that the chance of the eggs being robbed or cooling down during the parent's absence would be too great.

In spite of the habituation reported in Keller's (1989) study, clutch losses in the frequently disturbed recreational areas were significantly higher than in undisturbed areas. Furthermore, although habituation may be apparent in behavioural responses to human approach, potentially harmful physiological responses such as elevated corticosterone levels may remain in place unless exposure to humans is very high and consistent (Fowler, 1999). Giese (1998) reported that the heart rate of Adelie penguins *Pygoscelis adeliae* became elevated when an approacher came no closer than 15 m from the nest, yet disruption of incubation did not occur until the approacher got much closer.

The ropes preventing human access at high use beaches did not delineate the flush distance, as the birds always flushed well before the approacher reached the rope. The ropes may, however, have facilitated the reduction in the intensity of the behavioural response (Figs. 2a, b), because beachgoers would often examine the site without entering the roped-off area (pers. obs.). Therefore, human attention was never directly associated with harm to eggs or parents. It was not possible

to separate the effects of beach usage and ropes, and if eggs were unharmed by people at unroped, high use sites, a similar decrease in response intensity may result.

New Zealand dotterels are long-lived (Dowding, 1989) and display high breeding-site fidelity (Dowding and Chamberlin, 1991); both these characteristics may give birds the opportunity to learn from encounters with potential predators, including humans (Andersen, 1990).

4.3. Summary

The presence of both people and dogs near nesting areas elicited responses from New Zealand dotterels that potentially decrease hatching success. The larger flush distances and longer time that New Zealand dotterels spent off their nests in response to a dog with a person meant that eggs were uncovered more often and for longer, possibly exposing them to increased predation and thermal stress.

There was evidence that the birds habituated to humans on high-use beaches. Studies of other species that habituate in such a manner record lower levels of breeding success in areas exposed to high levels of human disturbance, in spite of the habituation, and this is also likely to be the case for the New Zealand dotterel.

4.4. Conservation recommendations

Results of the present study suggest that disruption of incubation would be greatly minimised if dogs were banned within a 100 m radius of dotterel nesting sites. Human access should be prevented within a 50 m radius on busy beaches, and 70 m on remote beaches. More generous distances would probably be prudent, as it is likely that energetically costly hormonal and nervous responses to potential predators are elicited at greater distances than are flush responses. Further work, such as measurement of hatch rate, is required to ascertain the impact of human disturbance on the nesting success of the endangered New Zealand dotterel. Information on the contribution of predation to nesting success is also required.

References

Andersen, D.E., 1990. Nest-defense behavior of red-tailed hawks. Condor 92, 991–997.

Andersson, M., Weklund, C.G., Rundgren, H., 1980. Parental defense of offspring: a model and an example. Animal Behaviour 28, 536–542.

Armstrong, E.A., 1956. Distraction display and the human predator. Ibis 98, 641–654.

Barash, D.P., 1975. Evolutionary aspects of parental behavior: distraction behavior of the alpine accentor. Wilson Bulletin 87, 367–373.

Brunton, D.H., 1986. Fatal antipredator behavior of a killdeer. Wilson Bulletin 98, 605–607.

Brunton, D.H., 1990. The effects of nesting stage, sex, and type of predator on parental defense by killdeer (Charadrius vociferus): testing models of avian parental defense. Behavioural Ecology and Sociobiology 26, 181–190.

Burger, J., 1981a. The effect of human activity on birds at a coastal bay. Biological Conservation 21, 231–241.

Burger, J., 1981b. Effects of human disturbance on colonial species, particularly gulls. Colonial Waterbirds 4, 28–36.

Burger, J., Gochfeld, M., 1981. Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. Journal of Comparative and Physiological Psychology 95, 676–684.

Burger, J., Gochfeld, M., 1983. Behavioural responses to human intruders of herring gulls (Larus argentatus) and great black-backed gulls (L. marinus) with varying exposure to human disturbance. Behavioural Processes 8, 327–344.

Burger, J., Gochfeld, M., 1991a. Human activity influence and diurnal and nocturnal foraging of sanderlings (Calidris alba). Condor 93, 259–265.

Burger, J., Gochfeld, M., 1991b. Human disturbance and birds: tolerance and response distances of resident and migrant species in India. Environmental Conservation 18, 158–165.

Collar, N.J., Crosby, M.J., Stattersfield, A.J., 1994. Birds to Watch 2: The World List of Threatened Birds (The official source for birds on the IUCN red list). Birdlife International, Cambridge.

Crawley, M.J., 1993. GLIM for Ecologists. Blackwell Scientific Publications, Oxford.

Cresswell, W., 1993. Escape responses by redshanks, Tringa totanus, on attack by avian predators. Animal Behaviour 46, 609–611.

Dowding, J.E., 1989. An introduction to the New Zealand dotterel. The Stilt 14, 61–63.

Dowding, J.E. 1993. New Zealand dotterel recovery plan (Charadrius obscurus). Threatened species recovery plan series no. 10. Department of Conservation, Wellington.

Dowding, J.E., 1994. Morphometrics and ecology of the New Zealand dotterel Charadrius obscurus, with a description of a new subspecies. Notornis 41, 221–223.

Dowding, J.E., Chamberlin, S.P., 1991. Annual movement patterns and breeding-site fidelity of the New Zealand dotterel (Charadrius obscurus). Notornis 38, 89–102.

Evans, P.R., Pienkowski, M.W., 1984. Population dynamics of shorebirds. In: Burger, J., Olla, B.L. (Eds.), Shorebirds: Breeding Behavior and Populations. Behavior of Marine Animals: Current perspectives in research, volume 5. Plenum Press, New York, pp. 83–123.

Fowler, G.S., 1999. Behavioural and hormonal responses of Magellanic penguins (Spheniscus magellanicus) to tourism and nest site visitation. Biological Conservation 90, 143–149.

Giese, M., 1998. Guidelines for people approaching breeding groups of Adelie penguins (Pygoscelis adeliae). Polar Record 191, 287–292.

Gillett, W.H., Hayward Jr., J.L., Stout, J.F., 1975. Effects of human activity on egg and chick mortality in a glaucous-winged gull colony. Condor 77, 492–495.

Gochfeld, M., 1984. Antipredator behaviour: Aggressive and distraction displays of shorebirds. In: Burger, J., Olla, B.L. (Eds.), Shorebirds: Breeding Behavior and Populations. Behavior of Marine Animals: Current perspectives in research, volume 5. Plenum Press, New York, pp. 289–377.

Greig-Smith, P.W., 1980. Parental investment in nest defence by stonechats (Saxicola torquata). Animal Behaviour 28, 604–619.

Keller, V., 1989. Variations in the response of great crested grebes Podiceps cristatus to human disturbance — a sign of adaptation? Biological Conservation 49, 31–45.

Lord, A., Waas, J.R., Innes, J., 1997. Effects of human activity on the behaviour of northern New Zealand dotterel Charadrius obscurus aquilonius chicks. Biological Conservation 82, 15–20.

Mainini, B., Neuhaus, P., Ingold, P., 1993. Behaviour of marmots Marmota marmota under the influence of different hiking activities. Biological Conservation 64, 161–164.

Marchant, S., Higgins, P.J., 1993. Handbook of Australian, New Zealand and Antarctic Birds: Vol. 2 Raptors to Lapwings. Oxford University Press, Melbourne, pp 818–827.

McKenzie, H.R., 1953. Nesting of New Zealand dotterel. Notornis 5, 121–122.

McKenzie, H.R., 1954. Classified summarised notes – New Zealand dotterel. Notornis 6, 225.

Montgomerie, R.D., Weatherhead, P.J., 1988. Risks and rewards of nest defense by parent birds. The Quarterly Review of Biology 63, 167–187.

NAG (Numerical Algorithms Group Ltd), 1993. Generalised Linear Interactive Modelling. The Numerical Algorithms Group Ltd, Oxford.

Phillips, R.E., 1980. Behaviour and systematics of New Zealand plovers. Emu 80, 177–197.

Piatt, J.F., Roberts, B.D., Lidster, W.W., Wells, J.L., Hatch, S.A., 1990. Effects of human disturbance on breeding least and crested auklets at St. Lawrence Island, Alaska. Auk 107, 342–350.

Pienkowski, M.W., 1984. Breeding biology and population dynamics of ringed plovers Charadrius hiaticula in Britain and Greenland: nest-predation as a possible factor limiting distribution and timing of breeding. Journal of Zoology 202, 83–114.

Siegel, S.C., Castellan, N.J.Jr., 1988. Non-Parametric Statistics for the Behavioural Sciences. McGraw-Hill International Editions, Singapore.

Teal, J.M., 1965. Nesting success of egrets and herons in Georgia. Wilson Bulletin 77, 257–263.

Tyler, N.J.C., 1991. Short-term behavioural responses of Svalbard Reindeer *Rangifer tarandus platyrhynchus* to direct provocation by a snowmobile. Biological Conservation 56, 179–194.

Westmoreland, D., Best, L.B., 1985. The effect of disturbance on mourning dove nesting success. Auk 102, 774–780.

Wilson, R.P., Culik, B., Danfeld, R., Adelung, D., 1991. People in Antarctica — how much do Adelie penguins *Pygoscelis adeliae* care? Polar Biology 11, 363–370.