Managing predation on ground-nesting birds: The effectiveness of nest exclosures

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ABSTRACT

Ground-nesting birds have declined world-wide, probably partly due to high nest predation. A non-lethal method for decreasing predation uses protective cages at nests. Tests have mainly looked at the effect of such nest exclosures on hatching success and adult predation, but several additional aspects need to be explored for a comprehensive evaluation of this conservation technique. Here, we test the effect of nest exclosures in two common European shorebirds: northern lapwing (*Vanellus vanellus*) and redshank (*Tringa totanus*), measuring hatching success, incubation length, hatching synchrony, hatchability, partial clutch loss, chick condition, and adult predation. In both species, protected nests had higher hatching success than unprotected nests. Taking into account incubation time, nest abandonment, hatchability and partial clutch loss, protected nests still hatched more young than unprotected controls. In lapwings, but not in redshanks, protected nests were incubated longer, but this did not impair the condition of lapwing chicks. Protected redshanks suffered increased predation on incubating adults, which often sit on the nest until a predator is close by. Our results emphasize the need for caution in the use of nest exclosures, particularly in redshanks and other species with similar incubation behaviour. Exclosures can, however, be a useful management tool in shorebirds that leave their nest early, when an approaching predator is still far away.

1. Introduction

Many ground-nesting bird species have decreased drastically in recent years (Senner and Howe, 1984; Tucker and Heath, 1994; Pain and Pienkowski, 1997; Chamberlain et al., 2000). Habitat loss and fragmentation are considered the major causes for the decline (Senner and Howe, 1984; Donald et al., 2001; Newton, 2004). Therefore, management of declining species has often focussed on protection and restoration of their habitats, but this is not always enough. High nest predation rate, caused by native or exotic species, may also limit bird populations, and both lethal and non-lethal predator control have been used to decrease predation on ground-nesting birds (Goodrich and Buskirk, 1995; Reynolds and Tapper, 1996; Johnson and Oring, 2002; Jackson et al., 2004).

The effect of lethal predator control on breeding populations of prey is not clear, however. Although hatching success and post-breeding population size seem to increase, the breeding population of the protected species does not always increase (Coté and Sutherland, 1997; Newton, 1998). Moreover, lethal predator control is problematic since it may evoke negative responses among the public, and the predator may itself be threatened (Goodrich and Buskirk, 1995; Conover,

2002; Roemer and Wayne, 2003). Several non-lethal techniques have therefore been proposed and implemented.

It is important that the pros and cons of these techniques are examined closely, since the protected species might be affected in many different ways. Conservation techniques that are not properly evaluated can cause damage (e.g. Ausden et al., 2001; Martínez-Abraín et al., 2004), which is particularly serious for threatened species. Yet, few reports have tested the effect of specific management actions (Fazey et al., 2005), possibly because of publication bias where negative results are seldom reported. Moreover, most results derive from practical management actions rather than research experiments, and are therefore rarely disseminated widely (Fischer and Lindenmayer, 2000; Fazey et al., 2004; Pullin et al., 2004).

One non-lethal technique to reduce nest predation is exclusion of predators from habitat patches or individual nests of e.g. birds or turtles. Fencing of habitat patches has been used to decrease predation from mammalian predators (Jackson, 2001; Conover, 2002; Moseby and Read, 2006). Fencing does not, however, protect nests from aerial predators, and it may delay or hinder the exit of the broods unless carefully constructed.

Protection of individual nests has been applied to ground-nesting birds and turtles (e.g. Rimmer and Deblinger, 1990; Ratnaswamy et al., 1997; Yerli et al., 1997; Johnson and Oring, 2002). These nest exclosures are placed as protective cages around the nests to hinder predators from reaching the eggs. In turtles, cages only need to protect the eggs and allow the hatchlings to exit, whereas in birds the incubating adult must have free access to and from the nest, accept the exclosure, and be able to incubate the eggs properly.

Nest exclosures have been used for more than two decades in threatened plovers (Charadriidae) in North America, and receive increasing interest in Europe and Australia (Jönsson, 1993; Garnett and Crowley, 2000; Johnson and Oring, 2002; Middleton, 2003). Mabeé and Estelle (2000) pointed out that although many studies have reported increased hatching success in protected nests, the primary objective in those studies has often been to protect as many nests as possible, and they have therefore lacked proper experimental design. Testing nest exclosures on three plover species in North America, Mabeé and Estelle (2000) and Johnson and Oring (2002) found conflicting results on hatching success. This was attributed to differences in predator community, and the authors cautioned that increased adult predation can counteract positive effects of increased hatching success.

Protective cages can potentially affect many more aspects. Incubation length, hatching synchrony and hatchability can be affected if incubating parents in protected nests become more wary and incubate unevenly. This could in turn lead to impaired chick condition, which ultimately may reduce the long-term survival of a population. Partial clutch loss may be affected if small mammals, which can enter the exclosure, learn to associate these structures with nests. Partial clutch loss might also increase if eggs in protected nests are more likely to be damaged by uneven incubation or trampling by parents eager to exit a cage when threatened.

Most exclosure studies of birds have dealt with plovers; two studies have dealt with sandpipers (Scolopacidae). Many plovers and sandpipers are threatened regionally and globally (IUCN, 2006) and are potential target species for nest exclosures. It is therefore important to further evaluate this method in species of both families. Here, we examine the effect of exclosures on nesting success of two common and widespread waders in northern Europe; northern lapwing (*Vanellus vanellus*) (Charadriidae) and redshank (*Tringa totanus*) (Scolopacidae).

2. Methods

We studied the effects of exclosures on redshank nests in 2002 and on lapwing nests in 2002 and 2004 at three coastal pastures on the Swedish west coast: Ölmevalla (57°23′N, 12°07′E), Båtafjorden (57°14′N, 12°08′E) and Fyrstrandsfjorden (57°10′N, 12°14′E). All three pastures are grazed by cattle and in addition by sheep at Fyrstrandsfjorden. From late March until early June, lapwing and redshank nests were located by searching the pastures on foot, or by locating incubating adults with binoculars. Nests receiving an exclosure (protected) were assigned randomly among the nests found; nests not receiving an exclosure were used as controls. Eggs in nests found after clutch completion were floated in water to estimate laying date (van Paassen et al., 1984). After positioning the cage, which took less than one minute, we checked if incubation continued either by (1) observing the nest from a distance or (2) by turning the eggs, pointed end outwards, and later returning to check if the arrangement of the eggs had changed. Incubating waders arrange the eggs so that the pointed ends meet (Lack, 1968). All nests were checked about every third day until they hatched or were preyed upon. A nest was considered depredated if the eggs disappeared a week or more before the expected day of hatching. When eggs disappeared within a week of expected hatching, the nest was considered depredated if it did not contain any signs of hatching (such as small eggshell fragments in the nest cup, Green, 2004) and we did not find adult birds tending newly hatched chicks nearby.

As part of a different study 39 adult redshanks were caught and colour-ringed on 24 nests protected by exclosures. Five of these nests were abandoned following the ringing activities and therefore excluded in the analyses of this study.

We measured daily nest survival rate, nest abandonment (proportion of nests abandoned by the parents after incubation began), incubation length (in nests found before incubation started), hatchability (proportion of nests hatching that contained non-hatching eggs), partial clutch loss (proportion of nests hatching that lost one or more eggs before the day of hatching) and hatching synchrony (a nest was considered hatching synchronously if all eggs hatched within 24 h).

2.1. Total hatching success

Arnold (1999) introduced a method for calculating the expected number of eggs hatching (R) for groups of nests:

$$R = \text{clutch size} \times \text{DSR}^I \times \text{PC} \times H,$$

where DSR is daily survival rate, I is incubation length, PC is partial clutch loss (in this case calculated as proportion of eggs that survived in clutches that reached hatching)

and H is hatchability (proportion of eggs that survived until hatching and did hatch). Here, clutch size is set to four since both redshank and lapwing normally lay four-egg clutches. We use this method to illustrate the differences in total hatching success between protected and control nests. In addition, we include data on nest abandonment.

2.2. Predator community

Both avian and mammalian predators were present in the study areas. Many depredated eggs were found at crows' egg shell dumps, indicating that hooded crows (*Corvus corone cornix*) are important predators on wader eggs (see also Wallander et al., 2006). Bite marks on depredated eggs, showed that also mammalian predators prey on wader eggs in the study areas, the most common species being red fox (*Vulpes vulpes*), American mink (*Mustela vison*) and badger (*Meles meles*). Gulls (*Larus* sp.) were also seen eating wader eggs and chicks.

2.3. Exclosure design

The most common design of exclosures used in previous studies is circular or triangular, made of woven mesh wire, with a diameter of 1–3 m and a height of 1 m, with or without a roof (e.g. Rimmer and Deblinger, 1990). Our exclosures were smaller (Fig. 1), similar in size to those of Estelle et al. (1996). In our study areas there are cattle, and some predators (e.g. badgers) that might tilt the exclosure, so we used a firm construction designed by one of us (ML) and constructed from plastic coated steel bars. Before using the construction in the field, we tested and modify it using captive red foxes, badgers and hooded crows.

Fig. 1 – Male lapwing incubating in the nest exclosure, made of a top ring ($\varnothing$ = 60 cm) and a bottom ring ($\varnothing$ = 70 cm) connected by 26 cm welded bars. The spacing between sidebars (6.5–8.5 cm) varied for each species. Four sidebars extend down by further 20 cm to anchor the exclosure. The roof is made of 4 × 4 cm steel bar netting extending 7 cm beyond the sides, pointing slightly downwards, to prevent foxes and badgers from tilting the cage or reaching the nest from the sides. Exclosure weight is 3.3 kg.

2.4. Data analysis

To avoid including the same birds in more than one year, we used different areas in the two years. Data on lapwings in 2002 and 2004 were therefore pooled. As soon as a protected nest hatched or was preyed upon, we randomly assigned the exclosure to a new nest among those available at that time. Daily survival rate (DSR) for protected and unprotected nests was calculated using the method of Mayfield (1975) and Johnson (1979).

In calculating differences in incubation length we controlled for laying date, since there is a seasonal decline in incubation time in some Charadriiformes (e.g. Parsons, 1972; Hotker, 1998). We performed a multiple linear regression analysis, with incubation length as dependent variable, and time of season and proportion of incubation time protected as independent variables. There was no significant interaction between the latter two variables (lapwing: $p = 0.70$, $t = 0.39$, $n = 59$; redshank: $p = 0.93$, $t = 0.09$, $n = 28$). Residuals from linear models revealed no obvious deviations from normality (Shapiro–Wilks test; lapwing: $p = 0.75$, $n = 59$, redshank: $p = 0.10$, $n = 28$).

As a measure of chick condition we used the residuals from the linear regression of log10 weight (g) on log10 body size, measured as length of tarsus + toe (mm) ($r_2 = 0.42$, $p < 0.0001$, $F_{1,38} = 27.8$, $n = 40$). The effect of exclosures on chick condition was tested by correlating the residuals from the linear regression against the proportion time protected.

Differences in adult predation, hatchability, nest abandonment, partial clutch loss and hatching synchrony were tested using Fisher's exact test (Quinn and Keough, 2002). All tests are two-tailed, with $\alpha < 0.05$. Statistics were calculated in SPSS 13.0.1.

3. Results

We found 190 lapwing nests in 2002 and 2004, and 68 redshank nests in 2002. Of these, 37 lapwing nests and 34 redshank nests were protected by exclosures. Most lapwings and all redshanks accepted the exclosure within 30 min. Some lapwings were more reluctant to enter the cage, but all birds finally accepted it and incubated.

3.1. Protected versus unprotected nests

Protected nests had significantly higher daily survival rate than unprotected nests in both lapwing (0.989 versus 0.966; $p < 0.0001$, $Z = 4.1$, $n = 190$ nests) and redshank (0.997 versus 0.964; $p < 0.001$, $Z = 3.67$, $n = 66$ nests) (Fig. 2). Protected nests, however, were not entirely safe: predation occurred at seven protected lapwing and two protected redshank nests. One protected redshank nest was destroyed by a red fox and the other probably by a smaller mammalian predator. Six of the seven destroyed lapwing nests were depredated by unknown predators and one by a fox.

In lapwings, incubation time decreased with time of season ($p < 0.0001$, $t = -4.27$, $n = 59$, multiple regression analysis) while no such effect was found in redshank ($p = 0.63$, $t = -0.48$, $n = 28$). Incubation time increased by one day in protected lapwing nests (mean ± SE: 27.5 ± 0.3 days) compared to
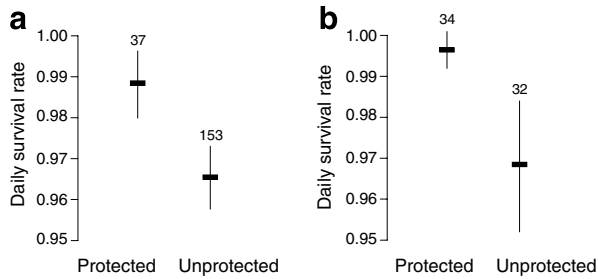
a

b

Fig. 2 – Estimated daily survival rates, with 95% confidence intervals, for protected and unprotected nests of (a) lapwing and (b) redshank. Protected nests of both species had significantly higher nesting success than unprotected nests. Figures above bars denote numbers of nests.

control nests (26.3 ± 0.3 days) ($p = 0.02$, $t = 2.37$). No such effect was found in redshanks ($p = 0.99$, $t = 0.004$, $n = 28$). Despite the increase in incubation time, we found no significant correlation between lapwing chick condition and proportion of time the nest was protected ($p = 0.33$, $r_s = 0.16$, $n = 40$, Spearman rank correlation). We were not able to catch enough redshank chicks from unprotected nests to analyse differences in chick condition.

In lapwings there was no significant difference in hatching synchrony between protected and unprotected nests ($p = 0.21$, Fisher's exact test, $n = 57$ nests), 90% of the clutches hatching all eggs within 24 h. In redshank nests, all eggs hatched within 24 h, showing that cages did not cause asynchronous hatching (data from 14 protected and 1 unprotected nest). There was an almost significant increase in nest abandonment in protected lapwing nests (3 out of 37 nests) compared to controls (2 out of 153 nests) ($p = 0.052$, Fisher's exact test, $n = 190$ nests). No result was calculated for redshanks since some abandonment of protected nests took place after the birds had been caught for ringing.

There was no significant difference in partial clutch loss (lapwing: $p = 0.11$, Fisher's exact test, $n = 102$ nests, redshank: $p = 0.14$, Fisher's exact test, $n = 37$ nests), but 12% of the unprotected nests suffered partial clutch loss whereas none

of the protected nests did so. There is, however, significantly higher partial clutch loss in unprotected nests if the data from the two species are combined ($p = 0.008$, Fisher's exact test, $n = 139$). Hatchability did not differ between protected and control nests (lapwing: $p = 1$, Fisher's exact test, $n = 102$ nests, redshank: $p = 1$, Fisher's exact test, $n = 37$ nests).

Taken together, the expected number of eggs hatching in four-egg clutches of both lapwings and redshanks was higher in protected clutches than in unprotected clutches (Table 1).

3.2. Adult predation

Predation on adult birds was higher in protected than in unprotected redshank nests ($p = 0.03$, Fisher's exact test, $n = 68$ nests). There was no adult predation at the 190 lapwing nests. In all, nine adults were depredated in 8 out of 37 protected redshank nests, whereas only one adult was depredated in 31 unprotected nests. Carcasses were often found next to the exclosures at protected nests.

4. Discussion

Management techniques must be rigorously tested before being applied to threatened species. Nest exclosures have been used for more than 20 years and can sometimes be an important non-lethal management tool in threatened ground-nesting birds. But, the method needs further evaluation since exclosures have been used almost exclusively in one group, plovers (Charadriidae). In this study, we have extended the test, comparing one charadriid and one scolopacid shorebird, and testing several aspects of breeding performance not previously measured in studies using exclosures.

In accordance with other studies, we found positive effects of exclosures on hatching success in both lapwing and redshank. Also when we include the several other variables measured, the net effect of exclosures on hatching success was positive for both redshank and lapwing.

A major drawback was increased predation on adult redshank, which reached such proportions that we decided not to use exclosures on redshanks in the second year. Increased adult mortality at protected nests has also been found in some other exclosure studies (e.g. Johnson and Oring, 2002;

	Clutch size	I^a	DSR	DSR^I	PC^b	H^c	A^d	R^e
Table 1 – The expected number of eggs hatching (R) in protected and unprotected nests of lapwing and redshank								
Lapwing								
Protected	4	27.5	0.989	0.739	1	0.953	0.918	2.58
Unprotected	4	26.3	0.966	0.399	0.955	0.945	0.986	1.42
Redshank								
Protected	4	24.6	0.997	0.924	1	0.978	–	3.61
Unprotected	4	24.4	0.964	0.413	0.946	1	–	1.56

Modified from Arnold (1999).
a Incubation length (days).
b Partial clutch loss.
c Hatchability.
d One-nest abandonment.
e $R = \text{Clutch size} \times DSR^I \times PC \times H \times A$.

Murphy et al., 2003). Since both plovers and sandpipers are long-lived, markedly increased rates of adult mortality are unacceptable in a management program.

Increased predation on adult redshanks is probably related to the incubation behaviour of redshanks and many other sandpipers. Redshanks usually sit tight on their well-concealed nests, and flush only at close distance when approached by a predator (Cramp and Simmons, 1983). When flushed from a protected nest they tend to fly into the top of the cage, and may not get out of the cage fast enough to escape the predator. Although we did not observe predation on redshanks directly, we suspect that hooded crows learned how to catch redshanks when trying to leave the exclosures. Therefore, the incubation behaviour of the protected species must be examined before applying nest exclosures. They should be used only with extreme caution, or not at all in species with incubation behaviour similar to that of the redshank. Niehaus et al. (2004) found that long-tailed skuas (*Stercorarius longicaudus*) learned to associate exclosures with nests of western sandpiper (*Calidris mauri*). Such learning has also been observed in corvids (M. Marriot cited in Liebezeit and George, 2001) and needs to be carefully controlled in the use of nest exclosures.

Protected lapwing nests took one day longer to hatch compared to controls. The increase in incubation time could be due to several causes. Lapwings nest in short vegetation in open areas and rely on early visual detection of predators (Cramp and Simmons, 1983). An exclosure may reduce visibility and induce more vigilant behaviour. This could result in adults leaving the nest more often or for longer periods, leading to later hatching. Exclosures could also affect incubation behaviour differently in males and females. If one sex is more reluctant to incubate in exclosures and the other sex cannot fully compensate, incubation time may increase. Moreover, predators and domestic livestock might be attracted to cages and increase disturbance to the incubating adult (Picozzi, 1975; Beintema and Müskens, 1987), leading to less efficient incubation. We cannot separate between these possibilities. There was no clear effect of nest exclosures on incubation time in redshanks which, in contrast to lapwings, lay their eggs in well-concealed nests and rely on crypsis while incubating. They may therefore be less disturbed by the exclosure.

We found no effect of increased time to hatching on lapwing chick condition. Larsen et al. (2003) found that lapwing chicks from experimentally enlarged five-egg clutches on average hatched one day later than normal four-egg clutches. These chicks were lighter than chicks from control nests, indicating that prolonged incubation might have reduced chick body mass. It is not clear why there was no such effect in lapwing chicks in our study. One possibility is that chicks in five-egg clutches suffer less from prolonged incubation per se than from uneven warming of the eggs, which might raise metabolic demands. It is important to monitor chick condition since in both lapwing and some Scolopacidae, heavier chicks survive better than smaller chicks (e.g. Grant, 1991; Blomqvist et al., 1997).

Although all adults accepted the exclosure initially, they led to increased nest abandonment in lapwings later on. Vaske et al. (1994) analysed the impact of several types of predator exclosure on nest abandonment in piping plover (*Charadrius melodus*), concluding that exclosures with a roof might increase abandonment. Omitting the roof is not a realistic option when avian predators are present or when exclosures are small, as in this study, since mammals might be able to enter the cage from above. Nest abandonment in protected lapwings might also be related to disturbance, since increased disturbance at protected nests might cause an increase in nest abandonment. Although nest abandonment in this study increased in protected lapwing nests, on average they still hatched more chicks than unprotected nests.

The higher partial clutch loss in unprotected nests suggests that predation, and not removal of damaged eggs by the parents, was the likely cause. Partial nest predation was probably caused by a predator large enough to be excluded from the protected nests.

The positive result of increased hatching success can possibly be turned negative by an increase in predation on chicks. If there is a sudden increase in one type of prey (e.g. chicks), it might trigger predators to switch from other prey and form a search image for that newly abundant prey (e.g. Crozé, 1970). Such density-dependent predation occurs in some bird species (Newton, 1998 and references therein), and chick survival needs to be estimated in future studies using nest exclosures.

Lapwing and some other Charadriiformes have aggressive antipredator behaviour that offers some protection from nest predators, also for prey species nesting nearby (Göransson et al., 1975; Eriksson and Götmark, 1982; Cramp and Simmons, 1983; Elliot, 1985). We suggest that further research should be conducted to see if nest exclosures could be used at nests of these aggressively nest-defending species. In such a scheme, threatened species might benefit from the protective umbrella formed by the aggressive species (e.g. Dyrcz et al., 1981), at the same time avoiding the potential negative side effects from exclosures. However, during such a scheme one must beware of the opposite possibility; that predators are attracted to the exclosures and destroy unprotected nests nearby.

4.1.   *Management recommendations*

Caution needs to be exercised in the use of nest exclosures for redshanks and other species with similar incubation behaviour, because there is a risk of increased predation on adults. However, since protected nests hatch more chicks than unprotected nests, nest exclosures can be an important tool in achieving increased hatching success in ground-nesting birds that leave their nest early when approached by a predator.

REFERENCES

Arnold, T.W., 1999. What limits clutch size in waders? Journal of Avian Biology 30, 216–220.

Ausden, M., Sutherland, W.J., James, R., 2001. The effects of flooding lowland wet grassland on soil macroinvertebrate prey of breeding wading birds. Journal of Applied Ecology 38, 320–338.

Beintema, A.J., Müskens, G.J.D.M., 1987. Nesting success of birds breeding in Dutch agricultural grasslands. Journal of Applied Ecology 24, 743–758.

Blomqvist, D., Johansson, O.C., Götmark, F., 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. Oecologia 110, 18–24.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C., Shrubb, M., 2000. Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. Journal of Applied Ecology 37, 771–788.

Conover, M., 2002. Resolving Human–Wildlife Conflicts: The Science of Wildlife Damage Management. Lewis, Florida.

Coté, I.M., Sutherland, W.J., 1997. The effectiveness of removing predators to protect bird populations. Conservation Biology 11, 395–405.

Cramp, S., Simmons, K.E.L., 1983The Birds of the Western Palearctic, vol. 3. Oxford University Press, Oxford.

Crozé, H., 1970. Searching image in carrion crows. Zeitschrift für Tierpsychologie 5, 1–86.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proceedings of the Royal Society of London Series B 268, 25–29.

Dyrcz, A., Witkowski, J., Okulewicz, J., 1981. Nesting of "timid" waders in the vicinity of "bold" ones as an antipredator adaptation. Ibis 123, 542–545.

Elliot, R.D., 1985. The exclusion of avian predators from aggregations of nesting lapwings (*Vanellus vanellus*). Animal Behaviour 33, 308–314.

Eriksson, M.O.G., Götmark, F., 1982. Habitat selection: do passerines nest in association with lapwings *Vanellus vanellus* as defence against predators? Ornis Scandinavia 13, 189–192.

Estelle, V.B., Mabee, T.J., Farmer, A.H., 1996. Effectiveness of predator exclosures for pectoral sandpiper nests in Alaska. Journal of Field Ornithology 67, 447–452.

Fazey, I., Salisbury, J.G., Lindenmayer, D.B., Maindonald, J., Douglas, R., 2004. Can methods applied in medicine be used to summarize and disseminate conservation research? Environmental Conservation 31, 190–198.

Fazey, I., Fischer, J., Lindenmayer, D.B., 2005. What do conservation biologists publish? Biological Conservation 124, 63–73.

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. Biological Conservation 96, 1–11.

Garnett, S.T., Crowley, G.M., 2000. The Action Plan for Australian Birds 2000. Environment Australia, Canberra.

Goodrich, J.M., Buskirk, S.W., 1995. Control of abundant native vertebrates for conservation of endangered species. Conservation Biology 9, 1357–1364.

Göransson, G., Karlsson, J., Nilsson, S.G., Ulfstrand, S., 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26, 117–120.

Grant, M.C., 1991. Relationships between egg size, chick size at hatching, and chick survival in the whimbrel *Numenius phaeopus*. Ibis 133, 127–133.

Green, R.E., 2004. Breeding biology. In: Sutherland, W.J., Newton, I., Green, R.E. (Eds.), Bird Ecology and Conservation, A Handbook of Techniques. Oxford University Press, Oxford, pp. 57–83.

Hotker, H., 1998. Intraspecific variation in length of incubation period in Avocets (*Recurvirostra avosetta*). Ardea 86, 33–41.

IUCN, 2006. 2006 IUCN Red List of Threatened Species. http://www.iucnredlist.org (accessed 10.10.06).

Jackson, D.B., 2001. Experimental removal of introduced hedgehogs improves wader nest success in the Western Isles, Scotland. Journal of Applied Ecology 38, 802–812.

Jackson, D.B., Fuller, R.J., Campbell, S.T., 2004. Long-termed population changes among breeding shorebirds in the Outer Hebrides, Scotland, in relation to introduced hedgehogs (*Erinaceus europaeus*). Biological Conservation 117, 151–166.

Johnson, D.H., 1979. Estimating nest success: The Mayfield method and an alternative. Auk 96, 651–661.

Johnson, M., Oring, L.W., 2002. Are nest exclosures an effective tool in plover conservation? Waterbirds 25, 184–190.

Jönsson, P.E., 1993. The Kentish plover project – report for 1992. Anser 32, pp. 29–34 (in Swedish with English summary).

Lack, D., 1968. Ecological Adaptation for Breeding in Birds. Methuen, London.

Larsen, V.A., Lislevand, T., Byrkjedal, I., 2003. Is clutch size limited by incubation ability in northern lapwings? Journal of Animal Ecology 72, 784–792.

Liebezeit, J.R., George, T.L., 2001. A summary of predation by corvids on threatened and endangered species in California and management recommendations to reduce corvid predation. Species conservation and recovery program report 2002-02, California Department of Fish and Game, Sacramento, California.

Mabeé, T.J., Estelle, V.B., 2000. Assessing the effectiveness of predator exclosures for plovers. Wilson Bulletin 112, 14–20.

Martínez-Abraín, A., Sarzo, B., Villuendas, E., Bartolmé, M.A., Mínguez, E., Oro, D., 2004. Unforeseen effects of ecosystem restoration on yellow-legged gulls in a small western Mediterranean island. Environmental Conservation 31, 219–224.

Mayfield, H., 1975. Suggestions for calculating nesting success. Wilson Bulletin 87, 456–466.

Middleton, P., 2003. Population ecology, conservation and management of little ringed plovers in South Yorkshire. British Birds 96, 344–346.

Moseby, K.E., Read, J.L., 2006. The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. Biological Conservation 127, 429–437.

Murphy, R.K., Michaud, I.M.G., Prescott, D.R.C., Ivan, J.S., Anderson, B.J., French-Pombier, M.L., 2003. Predation on adult piping plovers at predator exclosure cages. Waterbirds 26, 150–155.

Newton, I., 1998. Population Limitation in Birds. Academic Press, London.

Newton, I., 2004. The recent decline of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146, 579–600.

Niehaus, A.C., Ruthrauff, D.R., McCaffery, B.J., 2004. Response of predators to western sandpiper nest exclosures. Waterbirds 27, 79–82.

Pain, D.J., Pienkowski, M.W., 1997. Farming and Birds in Europe. The Common Agricultural Policy and its Implications for Bird Conservation. Academic Press, London.

Parsons, J., 1972. Egg size, laying date and incubation period in the Herring Gull. Ibis 114, 536–541.

Picozzi, N., 1975. Crow predation on marked nests. Journal of Wildlife Management 39, 151–155.

Pullin, A.S., Knight, T.M., Stone, D.A., Charman, K., 2004. Do conservation managers use scientific evidence to support their decision-making? Biological Conservation 119, 245–252.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge, UK.

Ratnaswamy, M.J., Warren, R.J., Kramer, M.T., Adam, M.D., 1997. Comparisons of lethal and non-lethal techniques to reduce raccoon depredation of sea turtles nests. Journal of Wildlife Management 61, 368–376.

Reynolds, J.C., Tapper, S.C., 1996. Control of mammalian predators in game management and conservation. Mammal Review 26, 127–155.

Rimmer, D.W., Deblinger, R.D., 1990. Use of predator exclosures to protect piping plover nests. Journal of Field Ornithology 61, 217–233.

Roemer, G.W., Wayne, R.K., 2003. Conservation in conflict: the tale of two endangered species. Conservation Biology 17, 1251–1260.

Senner, S.E., Howe, M.A., 1984. Conservation of Nearctic shorebirds. In: Burger, J., Olla, B.L. (Eds.), Shorebirds Breeding Behaviour and Populations. Plenum Press, New York, pp. 379–421.

Tucker, G.M., Heath, M.F., 1994. Birds in Europe: Their Conservation Status. BirdLife International, Cambridge, UK.

van Paassen, A.G., Veldman, D.H., Beintema, A.J., 1984. A simple device for determination of incubation stages in eggs. Wildfowl 35, 173–178.

Vaske, J.J., Rimmer, D.W., Deblinger, R.D., 1994. The impact of different predator exclosures on piping plover nest abandonment. Journal of Field Ornithology 65, 201–209.

Wallander, J., Isaksson, D., Lenberg, T., 2006. Wader nest distribution and predation in relation to man-made structures on coastal pastures. Biological Conservation 132, 343–350.

Yerli, S., Canbolat, A.F., Brown, L.J., Macdonald, D.W., 1997. Mesh grids protect loggerhead turtle *Caretta caretta* nests from red fox *Vulpes vulpes* predation. Biological Conservation 82, 109–111.