The Effectiveness of Removing Predators to Protect Bird Populations

ISABELLE M. CÔTÉ AND WILLIAM J. SUTHERLAND
School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, U.K.

Abstract: The control of predators for nature conservation purposes is becoming an increasingly important issue. The growing populations of predator species in some areas and the introduction of predators in other areas have led to concerns about their impact on vulnerable bird species and to the implementation of predator control in some cases. This is set against a background of increasingly fragmented semi-natural habitats and declining populations for many species. To assess the efficiency of predator removal as a conservation measure, the results of 20 published studies of predator removal programs were meta-analyzed. Removing predators had a large, positive effect on batching success of the target bird species, with removal areas showing higher batching success, on average, than 75% of the control areas. Similarly, predator removal increased significantly post-breeding population sizes (i.e. autumn densities) of the target bird species. The effect of predator removal on breeding population sizes was not significant, however, with studies differing widely in their reported effects. We conclude that predator removal often fulfills the goal of game management, which is to enhance harvestable post-breeding populations, but that it is much less consistent in achieving the usual aim of conservation managers, which is to maintain and, where appropriate, increase bird breeding population sizes. This may be due to inherent characteristics of avian population regulation, but also to ineffective predator removal and inadequate subsequent monitoring of the prey populations.

Efectividad de la Remoción de Depredadores para Proteger Poblaciones de Aves

Resumen: El control de depredadores con propósitos de conservación de la naturaleza se está convirtiendo en un aspecto importante. Las poblaciones crecientes de especies depredadoras en algunas áreas y la introducción de depredadores en otras, ha originado preocupaciones sobre su impacto en poblaciones vulnerables de especies de aves y a la implementación de control de depredadores en algunos casos. Esto se establece en base a un cúmulo de información sobre el incremento de hábitats seminaturales fragmentados y el declive de poblaciones de muchas especies. Para evaluar la eficiencia de la remoción de depredadores como una medida de conservación, los resultados de 20 estudios publicados sobre programas de remoción fueron meta-analizados. La remoción de depredadores tuvo un efecto positivo elevado en el éxito de eclosión de las especies de aves blanco. Con áreas de remoción mostrando un éxito de eclosión mayor en promedio, que un 75% de las áreas control. Sin embargo, la remoción de depredadores incrementó significativamente el tamaño poblacional post-reproducción (i.e. densidades de Otoño) de las poblaciones de aves blanco. De cualquier manera, el efecto de la remoción de depredadores en la población reproductora no fue significativo, con estudios difiriendo ampliamente en los efectos reportados. Concluimos que la remoción de depredadores usualmente alcanza la meta de manejo deportivo, que implica obtener poblaciones cosechables post-reproducción, pero que es mucho menos consistente con la meta usual de manejadores conservacionistas de mantener y cuando es posible incrementar el tamaño poblacional de aves reproductoras. Esto puede deberse a las características inherentes a la regulación poblacional de aves, pero también a una remoción ineficiente de depredadores y a un monitoreo subsecuente inadecuado de las poblaciones de presas.

Address correspondence to: I. M. Côté, e-mail i.cote@uea.ac.uk
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Introduction

Predation is widely believed to have shaped nearly every aspect of the life histories and behavior of birds. Mortality due to predation can be high, particularly in early avian life stages. For example, O’Connor (1991) reviewed 74 studies of nesting success of various bird species and found that one in three nests failed due to predation. Similar estimates were also found by Martin (1993; 41.4% of nests lost to predation in 55 species) and Côté and Sutherland (1995; 38.4% of nests lost to predation in 98 species). Such rates of mortality can generate strong selection on reproductive behavior and may affect population sizes.

The most extreme examples of the potentially damaging impact of predation on prey populations are seen in the extinction of several species of oceanic island birds following the introduction of non-native predators. Of 110 species of birds that have become extinct since c.1600, the loss of at least 34 (31%) has been ascribed to introduced predators, such as cats, rats, mustelids, mongooses, snails, and monkeys (Groombridge 1992). Most of these island birds evolved in predator-free environments and lacked defensive behaviors (e.g., Bunin & Jamieson 1995). Many became flightless and nested in accessible areas. It is revealing that the impact of introduced predators was more marked on temperate than on tropical islands. On the latter, birds co-occur with native rodents and land crabs, and the behaviors evolved to defend nests and self against native predators may have also given some protection against alien species (Atkinson 1985).

The impact of non-introduced predators on bird populations is far less clear. Many avian populations seem able to withstand high rates of egg predation without apparent effects on population size, and there are few declines in bird populations that have been ascribed unequivocally to the sole action of native predators (see Paine et al. 1990; Fitzner et al. 1994 for exceptions). The more common explanation for declines in many bird populations is habitat change, in the form of degradation, fragmentation or destruction (e.g., Robbins et al. 1989; Terborgh 1989), with predation acting as a secondary, exacerbating factor. Human intervention may also affect avian population declines by changing predator community structure. In the northern Great Plains of North America, for example, persecution has led to a change in canid composition from a multi-species, wolf (Canis lupus)-dominated predator community to a single-species red fox (Vulpes vulpes) population. This in turn has been related to increased predation rates on Mallard (Anas platyrhynchos) nests (Johnson & Sargeant 1977). Finally, landscape alterations influence predator distribution, which may ultimately increase predation rates on birds in some habitats (e.g., Greenwood et al. 1995).

Declining bird populations are only one manifestation of the potential impact of predators on their prey. Predation may also result in stable prey populations which persist at lower densities than they would in the absence of predation. In some cases these small populations, reduced by predation, then face inherent risks of extinction because of chance demographic or environmental events (Pimm et al. 1988; Rosenzweig & Clark 1994).

Of all the potential sources of avian mortality (e.g., climatic factors, food availability, diseases and parasites, human exploitation, accidents), predation is often perceived as the most important and one which can be reduced if necessary. Several countries, such as Great Britain and the United States, have a long history of controlling native predators to increase populations of game birds and waterfowl for hunting purposes (Potts 1986). This artificial lowering of predator populations may have been beneficial to many birds other than game species. Circumstantial evidence for this is provided by the fact that in some areas where nature reserves were established and predators were no longer removed, increased predation rates on ground-nesting birds were observed (Suarez et al. 1993). The control of both native and non-native predators has thus been advocated, and in some cases implemented, for conservation purposes (Beggs & Wilson 1991; Moors et al. 1992; Harold 1994).

Our goal is to review published studies documenting the impact of predator removal on bird populations. Predator removal is by no means the only method of predator control. Alternative, non-lethal methods have also been used widely for bird conservation (Côté & Sutherland 1995). Nevertheless, because predator removal studies generally lasted longer, assessed more prey population parameters, and killing predators is generally more contentious than other methods of control, we limited our review to such studies.

The effectiveness of predator removal programs may be measured in a number of ways. We assessed the effect of predator removal on each of three population parameters using meta-analyses. These population parameters include one short-term measure, namely hatching success, and two longer-term measures, breeding and post-breeding (autumn) population sizes. The ethics of predator control are beyond the scope of this review.

Methods

Literature Survey

The studies in the meta-analyses were obtained from a thorough survey of the primary literature. We used a literature review by Newton (1993) as the beginning of our search, complementing it with a computerized search (Bath Information and Data Services) for post-1980 literature and tracking older references from the
Meta-analysis offers at least three important advantages over more traditional methods of “vote counting.” In vote counting, studies are divided into categories according to whether they are statistically significant and whether they support the hypothesis under test. The proportions of studies “voting” for or against the hypothesis are then counted, and the relationship is considered real if a significant proportion of studies support the hypothesis. Because it considers only significant results, vote counting can be overly conservative, particularly in ecological studies where sample sizes, and hence statistical power, are low. Meta-analysis overcomes this problem by weighing each correlation coefficient by the size of the sample from which it is computed. Larger studies are therefore given more weight. A second advantage of meta-analysis is that it provides a quantitative estimate of the overall magnitude of the effect under study. It also determines whether the relationship varies among contrasting groups of studies and can reveal how much variation exists among and within groups of studies. Finally, meta-analysis reduces the likelihood of Type II errors (failing to reject the null hypothesis when it is false), which can be a great advantage for conservation research where committing a Type II error can be more harmful than committing a Type I error (rejecting the null hypothesis when it is true) (Fernandez-Duque & Valeggia 1994). In the present situation, a Type II error would lead one to believe wrongly that predator removal has no effect on bird populations, which could have serious consequences for vulnerable bird species.

A detailed discussion of the statistics of meta-analysis is provided in Hedges and Olkin (1985). The method used in this review is identical to that used by Fernandez-Duque and Valeggia (1994). This method involves the following calculation of an effect size (di) for each study:

\[ d_i = \frac{[1 - (3/((4m - 1)))](\bar{x}_R - \bar{x}_C)}{S_p} \]

where \( m \) is \( N_R + N_C - 2 \), \( N_R \) and \( N_C \) are the number of sites or years that contributed to calculating the mean population parameters \( \bar{x}_R \) and \( \bar{x}_C \) for removal and control areas respectively. \( S_p \) is the pooled standard deviation of the removal and control areas.

In addition to the calculation, as given in Fernandez-Duque and Valeggia (1994), of an overall effect size (\( d_{+++} \)), variance in effect size (\( s^2(d_{+++}) \)), and upper and lower limits for the 95% confidence interval for \( d_{+++} \), we tested statistically for the homogeneity of effect sizes (Hedges & Olkin 1985). The Q statistic tests the null hypothesis that all individual effect sizes are equal and is calculated as

\[ Q = \sum_{i=1}^{k} (d_i - \bar{d})^2 / \bar{d}_i - 1 \]

where \( k \) is the number of studies, \( d_i \) is the effect size of the ith study, and \( \bar{d} \) is the mean effect size. A significant \( Q \) value indicates heterogeneity among the effect sizes, while a non-significant \( Q \) value suggests homogeneity.
A different pattern emerges for breeding population sizes between categories was also calculated as

\[ Q_B = \sum_{i=1}^{p} \sum_{j=1}^{m} \frac{(d_{i+j} - d_{i+j})^2}{s^2(d_{i+j})}, \]

where \( m \) is the number of studies within each category and \( p \) is the number of categories. The significance of \( Q_B \) is similar to a \( \chi^2 \) of similar value with \( p - 1 \) degrees of freedom.

There are some potential problems associated with meta-analysis that deserve attention. Meta-analysis assumes that the studies being synthesized are independent. Although several studies in our review contributed more than one population parameter, each population parameter was analyzed in a separate meta-analysis. A small number of studies measured the responses of more than one bird species. We considered these results to be independent because the biology of the prey species studied differed widely. In addition, a single species may have been the focus of several studies, widely separated in time and geography. We also considered these results to be independent of each other.

A bias in the results of a meta-analysis may exist when studies with non-significant results are under-represented in the literature. This may increase the probability of Type I errors. It is possible to calculate a “fail-safe” number, \( N_n \), of unpublished, non-significant studies required to reduce the probability of a Type I error using the following formula:

\[ N_n = \frac{N(d/d_c - 1)}, \]

where \( N \) is the number of studies in the meta-analysis, \( d \) is the calculated mean effect size, and \( d_c \) is the minimum meaningful value of the effect size (Hunter & Schmidt 1990). Cohen (1977) suggested that effect sizes of a magnitude of 0.2 or less could be considered small. Hence, \( d_c \) was set at 0.2 in our calculations of fail-safe sample sizes.

Finally, several study design artifacts, such as measurement error or range variation in the measured variables (Hunter & Schmidt 1990), can influence meta-analysis statistics. We could not correct for these artifacts because data to do so are seldom provided in the literature. Hence, some of the observed heterogeneity among studies may be attributable to these uncontrolled factors.

**Results**

The literature survey yielded 20 studies that reported one or more of the three required prey population parameters for 22 species or groups of species (Table 1). An additional 9 studies (on 14 species or groups of species) reported effects on hatching success that could not result in calculations of means or standard deviations (Table 2).

The results of the meta-analyses are summarized in Fig. 1. Predator removal had a large, positive effect on hatching success of the target bird species, with an overall effect size of 0.676 and a 95% confidence interval (CI) of 0.300–1.050. This effect size can be interpreted as an average increase of 0.676 standard deviations, or 75%, in the hatching success of birds in predator removal areas compared to control areas. This means that the average site where predators were removed had more birds than 75% of the control sites. The studies in Table 2 reflect this general trend, with 12 out of 14 species showing higher hatching success in removal areas. There was no significant heterogeneity among studies (\( Q = 18.39, \text{df} = 13, p = 0.12 \)), suggesting that all studies share a common effect size, regardless of experimental design, status, or migration behavior of the prey population, type of predator removal, study site location, or whether the species was hunted or not.

The removal of predators also had a large effect on post-breeding population size (Fig. 1). The overall effect size, \( d_{i+j} \), was 0.953 standard deviations and the 95% CI (0.547–1.359) again did not encompass zero, which indicates an effect size significantly different from zero. Post-breeding population sizes of birds in predator removal areas were thus, on average, larger than on 83% of the control areas. Studies reporting post-population breeding sizes were also homogeneous in their results (\( Q = 16.91, \text{df} = 11, p = 0.09 \)).
### Table 1. Studies of predator removal included in the meta-analyses.

<table>
<thead>
<tr>
<th>Target</th>
<th>Predator removed</th>
<th>Hatching success</th>
<th>Post-breeding population size</th>
<th>Breeding population size</th>
<th>Type</th>
<th>Pop. trend</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Various ducks</td>
<td>striped skunk</td>
<td>2.8 ± 2.2 (5)</td>
<td>15.2 ± 14.4 (5)</td>
<td>1.08</td>
<td>SEC</td>
<td></td>
<td>Greenwood 1986</td>
</tr>
<tr>
<td>Pheasant</td>
<td>fox</td>
<td></td>
<td>2.3 ± 0.6 (5)</td>
<td>4.2 ± 1.1 (5)</td>
<td></td>
<td></td>
<td>Trautman et al. 1974</td>
</tr>
<tr>
<td>Pheasant (Phasianus colchicus)</td>
<td>all carnivores</td>
<td>22.4 ± 7.6 (6)</td>
<td>21.7 ± 5.7 (6)</td>
<td>-0.10</td>
<td>SEC</td>
<td></td>
<td>Trautman et al. 1974</td>
</tr>
<tr>
<td>Golden Plover</td>
<td>crows &amp; gulls</td>
<td>20.5 ± 20.0 (5)</td>
<td>0 ± 0 (4)</td>
<td>1.20</td>
<td></td>
<td></td>
<td>Parr 1993</td>
</tr>
<tr>
<td>Wild Turkey</td>
<td>all carnivores</td>
<td></td>
<td>5.0 ± 7.1 (2)</td>
<td>20.5 ± 16.3 (2)</td>
<td></td>
<td></td>
<td>Beasom 1974</td>
</tr>
<tr>
<td>Bobwhite Quail</td>
<td>all carnivores</td>
<td>34.7 ± 29.4 (2)</td>
<td>45.8 ± 31.5 (2)</td>
<td>0.21</td>
<td>SEC</td>
<td></td>
<td>Beasom 1974</td>
</tr>
<tr>
<td>Various ducks</td>
<td>all carnivores</td>
<td>59.5 ± 12.0 (2)</td>
<td>88.5 ± 5.0 (2)</td>
<td>1.80</td>
<td></td>
<td></td>
<td>Duebbert &amp; Kantrud 1974</td>
</tr>
<tr>
<td>Various ducks</td>
<td>all carnivores</td>
<td>68.7 ± 9.5 (3)</td>
<td>94.0 ± 3.5 (3)</td>
<td>2.83</td>
<td></td>
<td></td>
<td>Duebbert &amp; Lokemoen 1980</td>
</tr>
<tr>
<td>Pheasant</td>
<td>all carnivores</td>
<td>18.3 ± 1.9 (3)</td>
<td>29.8 ± 6.7 (3)</td>
<td>1.87</td>
<td></td>
<td></td>
<td>Chesness et al. 1968</td>
</tr>
<tr>
<td>White-winged Dove (Zenaida asiatica)</td>
<td>Great-tailed Grackle (Cassidix mexicanus)</td>
<td>55.0 ± 14.1 (2)</td>
<td>67.0 ± 8.5 (2)</td>
<td>0.59</td>
<td>115.6 ± 4.7 (3)</td>
<td>742.1 ± 85.2 (2)</td>
<td>5.92</td>
</tr>
<tr>
<td>Fieldfare (Turdus pilaris)</td>
<td>Hooded Crow (Corvus corone)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Various tetraonids</td>
<td>fox &amp; martens</td>
<td></td>
<td>7.8 ± 1.8 (8)</td>
<td>8.4 ± 2.3 (8)</td>
<td>0.26</td>
<td></td>
<td>SEC</td>
</tr>
<tr>
<td>Capercaillie (Tetrao urogallus)</td>
<td>fox &amp; martens</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Marcström et al. 1988</td>
</tr>
<tr>
<td>Black Grouse (Tetrao tetrix)</td>
<td>fox &amp; martens</td>
<td></td>
<td></td>
<td></td>
<td>44.4 ± 13.7 (9)</td>
<td>83.2 ± 54.5 (9)</td>
<td>0.93 SEC</td>
</tr>
</tbody>
</table>
Table 1. Continued

<table>
<thead>
<tr>
<th>Target</th>
<th>Predator removed</th>
<th>Hatching success $b$</th>
<th>Post-breeding population size$^c$</th>
<th>Breeding population size</th>
<th>Type$^d$</th>
<th>Pop. trend$^e$</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Control Removal $d_i$</td>
<td>Control Removal $d_i$</td>
<td>Control Removal $d_i$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ruffed Grouse (Bonasa umbellus)</td>
<td>all carnivores</td>
<td>49.8 ± 15.8 (4)</td>
<td>79.2 ± 16.1 (4)</td>
<td>1.60 (4)</td>
<td>14.5 ± 4.2 (4)</td>
<td>13.9 ± 4.6 (4)</td>
<td>−0.12 (4) 0.04 SEC + Edminster 1939; Darrow 1947</td>
</tr>
<tr>
<td>Willow Ptarmigan (Lagopus lagopus)</td>
<td>corvids</td>
<td>62.3 ± 15.9 (4)</td>
<td>75.2 ± 11.8 (4)</td>
<td>0.80 (4)</td>
<td>—</td>
<td>—</td>
<td>+ Parker 1984</td>
</tr>
<tr>
<td>Various ducks</td>
<td>all carnivores</td>
<td>28.6 ± 32.2 (6)</td>
<td>58.7 ± 15.1 (6)</td>
<td>1.10 (6)</td>
<td>809.7 ± 678.2 (6)</td>
<td>1261.8 ± 1036.2 (6)</td>
<td>0.48 (6) 0.03 SEC S Balser et al. 1968</td>
</tr>
<tr>
<td>Ruffed Grouse</td>
<td>all carnivore</td>
<td>25.7 ± 0 (1)</td>
<td>45.2 ± 11.3 (3)</td>
<td>0.98 (3)</td>
<td>—</td>
<td>—</td>
<td>+ Darrow 1947</td>
</tr>
<tr>
<td>Grey Partridge (Perdix perdix)</td>
<td>fox &amp; corvids</td>
<td>—</td>
<td>147.5 ± 46.2 (6)</td>
<td>1.14 (6)</td>
<td>321.7 ± 73.1 (6)</td>
<td>2.62 (6) 97.5 ± 34.3 (6)</td>
<td>0.16 SEC S Tapper et al. 1991</td>
</tr>
<tr>
<td>Grey Partridge (Perdix perdix)</td>
<td>black rat</td>
<td>25.5 ± 21.7 (4)</td>
<td>60.5 ± 21.2 (4)</td>
<td>1.42 (4)</td>
<td>34.3 ± 4.7 (3)</td>
<td>47.7 ± 8.5 (3)</td>
<td>1.56 (3) 10.0 ± 1.0 (3) 1.13 BA − Robertson et al. 1994</td>
</tr>
<tr>
<td>Grey Partridge (Perdix perdix)</td>
<td>all carnivores</td>
<td>—</td>
<td>5.7 ± 2.5 (10)</td>
<td>1.08 (10)</td>
<td>—</td>
<td>—</td>
<td>SEC ? Frank 1970</td>
</tr>
<tr>
<td>Various ducks</td>
<td>all carnivores</td>
<td>12.1 ± 16.5 (15)</td>
<td>18.4 ± 16.9 (15)</td>
<td>0.37 (15)</td>
<td>—</td>
<td>—</td>
<td>SEC ? Sargeant et al. 1995</td>
</tr>
<tr>
<td>Wild turkey</td>
<td>coyote &amp; bobcat</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>94.5 ± 21.9 (2)</td>
<td>92.0 ± 5.7 (2)</td>
<td>−0.09 SEC − MacDonald 1966</td>
</tr>
</tbody>
</table>

$a$ Means are given ± 1 SD. Sample sizes (number of years or areas) are given in parentheses.

$b$ Hatching success was measured in percentages of successful nests (usually meaning fledging at least one young). Post breeding population size and breeding population sizes were measured as densities.

cPost-breeding population size and breeding population sizes were measured as densities.

d $d_i$ is the effect size for each individual study.

eType refers to the experimental design: BA, before-and-after comparison, and SEC, simultaneous experimental and control areas.

Population trend: $+$, increasing/large prey population; $-$, stable prey population; $-$, declining/small prey population.
size, where the effect size is much smaller (0.339 standard deviations) and the 95% CI overlaps, although barely, with zero (−0.022−0.700). This suggests that predator removal does not have a significant effect on breeding population sizes of target birds.

There was significant heterogeneity among studies in their effect on breeding population size ($Q = 25.13$, df = 13, $p = 0.02$). This heterogeneity was not due to experimental design because there was no significant difference in mean effect size between before-and-after studies and those with simultaneous experimental and control areas ($Q_B = 2.18$, df = 1, $p = 0.05$). Similarly, there was no difference between studies performed on islands or mainlands ($Q_B = 1.96$, df = 1, $p = 0.02$), between studies where all or only some of the predators had been removed ($Q_B = 0.64$, df = 1, $p = 0.40$), or between studies targeting game and non-game species ($Q_B = 0.13$, df = 1, $p = 0.70$). In addition, the migration behavior of the prey population did not affect effect sizes ($Q_B = 0.02$, df = 1, $p = 0.90$). There was a nearly significant tendency for studies performed on stable or increasing populations to show a higher mean effect size ($d_{1+} = 0.494$, 95% CI = 0.097–0.891) than studies performed on declining populations ($d_{1+} = -0.401$, 95% CI = -1.269–0.467; $Q_B = 3.39$, df = 1, $p = 0.07$).

**Fail-Safe Sample Sizes**

The fail-safe sample size, $N_n$, for our meta-analysis of the effect of predator removal on hatching success is 33.3, indicating that more than 33 additional, unpublished, non-significant studies would be required to overturn the results. $N_n$ for the meta-analysis of post-breeding population size is 45.2. The results of both of these meta-analyses are thus very robust.

The fail-safe sample size for the meta-analysis of breeding population size is 9.7. Nevertheless, because the results of this meta-analysis yielded a non-significant average effect size, the inclusion of additional non-significant studies would strengthen our results rather than overturn them. In this situation a relatively small, fail-safe value is not meaningful.
Discussion

Conservation biologists usually view the health of a population in terms of long-term trends in breeding numbers, hence their main concern is the impact of predation on the number of breeding individuals. In contrast, the objectives of game management focus on enabling the removal of as large a number of post-breeding (i.e., autumn) individuals as is sustainable. The effect of predation on post-breeding population size is therefore of concern to game managers. Newton (1993) pointed out that this discrepancy in objectives has led to misunderstandings between conservationists and game managers. Our review has shown that predator removal often fulfills the goal of the latter, but less frequently that of the former. Our meta-analysis of published studies revealed that predator removal can reduce early avian mortality considerably and significantly. Similarly, post-breeding population sizes are also significantly larger following the removal of predators. However, predator removal does not necessarily affect bird breeding population sizes to the same extent. Published studies are not consistent in their results, with some studies showing increased breeding populations following predator removal whereas others show no effect or decreases. This result is not completely unexpected if one considers how bird populations are regulated.

Bird populations may be limited by a variety of factors, including food supply, territorial space, nest sites, predation and parasites (reviewed by Newton 1994a). There are two particularly crucial times in avian life cycles where one or more of these factors can limit population densities: winter and breeding periods. There is good evidence for density-dependence operating on overwintering birds, where the number of birds dying from starvation or exposure increases with the size of the population entering winter (e.g., Goss-Custard et al. 1995). Experiments enhancing food supply in winter often result in increased breeding population sizes, usually as a result of better overwinter survival of first-year birds (e.g., Smith et al. 1980; van Balen 1980; Jansson et al. 1981). Juveniles thus appear to be particularly susceptible to density-dependent limitation in the winter.

Bird population densities may also be constrained during the breeding season, both by lack of nest sites and by territoriality. Newton (1994a) reported that all but 2 of 32 nest-site provision experiments resulted in increased breeding densities, suggesting that shortages of nest sites commonly limit populations of hole-nesting species. Studies focusing on other types of nests are more scarce, but they too tend to suggest that nest-site availability is important in determining breeding population sizes (Newton 1994b). Territoriality can exacerbate the problem of nest-site shortages. Territorial behavior often creates space shortages, resulting in large populations of “floating” individuals that are unable to obtain breeding territories (Newton 1992; Sutherland 1996). These floaters are often young, inexperienced individuals (Zack & Stutchbury 1992).

As a consequence of density-dependent processes occurring in winter and during the breeding season, and of the vulnerability of juveniles to such processes, an increase in hatching success as a result of predator control may influence the number of post-breeding (autumn) juveniles. Nevertheless, it should have little influence on the number of breeding adults because most juveniles will starve over the winter or fail to find a breeding territory. Our results are consistent with this scenario.

Predator removal programs may also fail to enhance bird breeding populations for reasons unrelated to life histories. Several of the studies included in the meta-analyses were carried out on game species whose autumn populations may have been reduced by hunting. The population entering winter in removal areas may thus have been similar in size to that on control areas, where fewer birds were hunted. This may have been the case in the study by Tapper et al. (1991), where an increase in autumn bag of Partridge (Perdix perdix) was noted on predator removal areas, but it does not appear to apply to most other studies of game species included in this study.

In addition, few, if any, of the studies managed to eliminate predators completely from removal areas, even when all predators were targeted. Edminster (1939), for example, concluded that fox control had been unsatisfactory on one of his selective removal areas when nest mortality proved higher than on the control area. Such incomplete predator removal may also be expected in many conservation exercises. It is possible that complete predator removal could have resulted in more significant findings in some of the studies.

The removal of predators may not affect bird populations if the empty niche left by a removed predator is filled by other predatory species that share the same diet. This has been documented several times, especially for introduced predators on oceanic islands. For example, an attempt to eradicate feral cats (Felis gatus) on Amsterdam Island in the Indian Ocean resulted in an increase in the numbers of black rats (Rattus rattus) and house mice (Mus musculus), which also preyed on endemic ground-nesting birds (Holdgate & Wace 1961; Holdgate 1967). Murphy and Bradfield (1992) also demonstrated that stoats (Mustela erminea) in New Zealand shifted their diet from rats, which had been removed by poisoning, to birds, causing some conservation concern.

Finally, it is possible that predator control does increase breeding bird populations, but that this results in migration to areas which are not monitored. If this occurs, predator control may contribute to overall metapopulation size without appearing to enhance local populations. This effect may be difficult to measure.

The status of the prey population appeared to affect
the magnitude of the effect of predator removal, with stable or increasing populations responding positively and declining populations declining further. This is unexpected because anecdotal evidence suggests that populations at peak densities are unaffected, or sometimes reduced, by predator removal (e.g. Edminster 1939). This may reveal the importance of factors other than predation in controlling bird breeding numbers. Predator removal failed to stem the decline of three of the four declining populations included in this meta-analysis. In one study (Parr 1993) population decline was ascribed specifically to adverse weather. Predator removal may thus be effective only when environmental conditions permit population growth.

In addition to its effectiveness, the costs of predator removal and its long-term effects will be factors in the decision to implement removal programs. On islands predator removal may be an effective solution with long-lasting effects if predators cannot recolonize the islands naturally. On the mainland the limited evidence available suggests that predator removal does not have long-lasting effects, and if not maintained, any benefit disappears quickly. Duebbert and Kantrud (1974) showed that hatching success of waterfowl nests decreased quickly to levels comparable to those on control areas in the year following cessation of predator removal. Higher numbers of breeding ducks remained on the experimental area in that year, but no information is available on longer-term effects. Duebbert and Lokemoen (1980) found that waterfowl hatching success and nesting density returned to pre-control levels within 2 years. Chesness et al. (1968) recorded predation rates comparable to pre-removal rates within a year after predator trapping had ceased. Greenwood (1986) found that two areas showed lower hatching rates (18%) in the year after predator removal was stopped, whereas a third area showed a slight increase in hatching success. Predator removal must therefore be a permanent management measure if no other measures, such as habitat improvement and/or creation, are undertaken.

This latter point was highlighted by many game biologists, who have long appreciated the fact that limited financial resources may be better spent on habitat improvement rather than continual predator removal (Lehmann 1946; Grange 1949; Duebbert & Kantrud 1974; Trautman et al. 1974). High rates of nest predation often occur in fragmented habitats, where the relative amount of edge habitat where predators can thrive is great (Paton 1994; Robinson et al. 1995). Reconnecting these habitats may reduce nest predation as well as provide other benefits to wildlife. Simple and inexpensive habitat modifications such as providing nest cover, by altering mowing regimes for example, can result in increased hatching success of a magnitude similar to the removal of predators (Duebbert & Kantrud 1974; Duebbert & Lokemoen 1980). Habitat improvement also removes the ethical problems of predator control and may benefit other fauna and flora.

In areas where the harvest of predatory species is permitted and on-going, hunting may be incorporated into a management strategy and restricted to effect specific changes in predator community structure. For example, Sovada et al. (1995) showed that duck nesting success was greater when coyotes (Canis latrans) were the dominant predator than when red foxes predominated. The protection of coyotes from harvest, but not of foxes, may thus result in safer nesting habitat for ground-nesting birds. Regulatory control of hunting may be achieved at little cost.

In summary, information currently available in the literature suggests that predator removal does not reliably increase bird breeding populations. This may be due to the action of density-dependence on avian populations, in which case predator removal will rarely result in more breeding birds except when density-dependent emigration occurs. Nevertheless, this has yet to be documented and should be a focus of future removal studies. Alternatively, the apparent failure to enhance breeding numbers may result from ineffective removal of predators from study areas or from recolonization by new predators of ecological niches emptied by removal programs. Whatever the exact mechanism underlying the results, these technical problems are likely to plague any removal study carried out by conservationists.

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