Table 5. Summary of results of 35 predator removal experiments.

	Short-term benefits	Long-term benefits	
	Increased hatching success or brood size	Increased autumn population size	Increased breeding population size
Yes	24	8	8
No	8	6	8
Not reported	3	21	19

in terms of greater hatching success or brood sizes. The magnitude of these short-term gains can sometimes be impressive. For example, Dr P. Monaghan witnessed a switch from 0% to 100% nesting success of fulmars after the eradication of rats from a small Scottish island.

Evidence for longer-term benefits is more limited, in part because the data necessary to evaluate these benefits were often not provided. Larger post-breeding (autumn) population sizes are documented in only 8 studies (23%), but over half the studies did not give the necessary data. Six studies (17%) found no effect of predator removal on post-breeding population size. Finally, 23% of studies found increases in breeding population size, while a similar number showed no effect. Again, over half the studies did not assess this parameter.

4.1.1 Problems with interpreting the results of predator removal studies: experimental design

The interpretation of the results of predator removal studies was often complicated by confounding factors owing to poor experimental design. Eleven of the studies (31%) were simple before-and-after comparisons. Although eight of these studies found increases in hatching success, it is impossible to attribute these differences solely to predator removal.

The use of controls reduces the effect of confounding factors and is relatively widespread in predator removal studies with 24 of 35 studies claiming a control area in their experimental design. However, while control areas were sometimes chosen that matched as best as possible the ecological and environmental characteristics of the experimental area (e.g.

Beasom 1974, Greenwood 1986), the validity of control areas was sometimes dubious for various reasons. The control area in the red grouse study reported by Williams, for example, was under a different kind of management (mowing) than the experimental area (burning twice), and second burns are known to remove *Sphagnum* mosses. This promotes the growth of heather on which grouse feed (Williams, 1994a). In Parr's (1993) study of waders in Scotland, the control area had no avian predators, while in the experimental area, avian predators were removed. Waders in the control area also had higher nesting success than in the experimental area before the experiment began. 'Light' predator removal was conducted on the control area in Beasom's (1974) study in late autumn and winter, while this was not performed on the experimental area.

Close proximity between control and experimental areas may reduce the effectiveness of predator removal if predators from control areas can easily move into removal areas. Although control areas were usually 7+ km (5+ miles) away from experimental areas, which may preclude movement of most territorial predators, control and experimental areas were adjacent to one another in at least 2 studies (Edminster 1939, Balser et al. 1968), or less than 3 km apart in another (Chesness et al. 1968).

The results of predator removal studies are strengthened by experimental designs which allow for replication and treatment reversal. By replication, we mean spatial replication, with more than one set of control and experimental plots. Temporal replication is common in removal experiments, whereby a single set of control and experimental areas is studied for several years. However, if the data for each year are considered independent from other years, the sample size is artificially inflated, and the problem of pseudoreplication occurs (Hurlburt 1984). Keeping this in mind, it is nevertheless valuable to run a removal experiment for several years. The experimental effects may take some time to appear as the efficiency of removing predators often increases through the study, and the longer-term benefits, such as increased breeding population size, may only be measured after several years.

A single study, by Greenwood (1986), incorporated both treatment reversal and replication. Four studies had treatment reversal and one replication. The experimental design and results of these studies are reviewed in detail below.

Replication

1. Trautman et al. 1974 - Pheasant

This 5-year study consisted of four replicated units, each comprising a control area, a fox-reduction area, and a small-carnivore reduction area. The small-carnivore reduction area was added 2 years after the onset of the experiment. (One small-carnivore reduction area in one unit was abandoned half-way through the study because of land-owner pressure.) Areas within a unit were located from 5 -15 miles apart, and were chosen for their similarity in climate, geography, and land use. Variation in climate and agricultural practice among units was sought to represent variation encountered within pheasant range.

Surprisingly, Trautman et al. found no reduction in the percentage of nests destroyed or in the percentage of nests hatched, despite estimated yearly reductions of 58-74% of the small carnivore populations. However, late summer pheasant populations were on average 19% higher each year on the fox reduction areas than on the control areas. On the small-carnivore reduction areas, post-breeding pheasant numbers were 132% higher, on average, each year than on the control areas. The authors believe that the major impact of predator control was related to improved rates of juvenile and adult pheasant survival.

Treatment reversal

1. Edminster 1939 - Ruffed grouse

Two areas of similar size and containing a similar amount of habitat suitable for ruffed grouse were chosen adjacent to each other. An attempt was made at removing all potential predators of grouse on one area, while keeping the other area as a control. After two years, predator removal was allowed to lapse for a year. The experiment then resumed for another year, with the original control area becoming the removal area and vice-versa. That year, an additional experimental area was chosen 5 miles from the main site, where selective removal of only fox and weasels was performed. In the fifth and final year of the experiment, three smaller areas were monitored on the main site: a control, a complete predator removal, and a selective predator removal area. This final year was of particular interest since grouse density on the complete predator removal area was the highest ever recorded. The goal of the experiment that year was therefore to examine whether predator control could help maintain high grouse densities.

In the first two years, nest mortality was reduced by 30%, while brood mortality remained constant. Adult losses were slightly lower and grouse autumn density higher on the removal area in the first year, but not in the second year. Treatment reversal generated results similar to the second year: reduced nest mortality, unchanged brood mortality, slightly higher adult survival, unchanged autumn density. Edminster argues that the lack of an effect on autumn numbers in the second year and in the reversal year stems from the fact that these were peak grouse years and that grouse populations were already at carrying capacity. Interestingly, in the last year when grouse densities were at their highest ever, although complete and partial predator removal resulted in lower nest mortality, adult losses were much greater on the complete removal area (72% of adults) than on the control area (49% of adults). Predators took 20% of adults on the complete removal area compared to 13% on the control area. This, compounded by increased emigration, resulted in a drop in density of 46% on the complete predator removal area compared with a 21% drop on the control area. Selective predator removal had a similar effect to complete predator removal.

2. Balser et al. 1968 - Waterfowl

A wildlife refuge was divided into two equal-sized (19,000 acres) areas. Nest predators were removed for three years in one area, with the other area serving as a control. The treatment was then reversed, and predator removal was carried out on the former control area. All predators were targeted, except for snapping turtle (*Chelydra serpentina*) and northern pike (*Esox lucius*).

Seventy-five of 132 nests (56.8%) hatched successfully in the predator-removal area in the first three years, compared with 22 of 37 nests (59.5%) in the control area. Following treatment reversal, hatching success was 62.6% (72 of 115 nests) on the predator-removal area and 17.3% (13 of 75 nests) on the control. The lack of an effect in the first half of the experiment was blamed on the inadequate intensity and duration of predator control. The average number of chicks produced per year was 1783 in the removal area vs 1258 in the control area in the first three years, and 740 in the removal area and 361 in the control area in the last three years. The average number of breeding pairs was 734 (removal) vs 454 (control) before treatment reversal, and 325 (removal) vs 592 (control) after reversal. This study exemplifies the need for good controls, since one of the two areas offered significantly more suitable habitat for breeding waterfowl than the other.

3. Tapper et al. 1991 - Grey partridge

Two partridge beats of similar area, amount of farmland, and partridge number were selected. The areas were 6 km apart. Trapping of crows, magpies, and foxes (with occasional stoats and rats) was carried out for 3 years on one area. Treatment was then reversed and trapping carried out on the initial control area for 3 years.

In all years, the area with predator removal had more broods, and larger broods, than the control area. Larger brood sizes probably arose because fewer hens had to re-nest in the removal areas and second clutches are usually smaller. Over six years, autumn population in the removal areas was more than twice the size of that in the control areas (1896 birds vs 874). Breeding bird densities appeared unaffected (approximately 615 birds in removal area vs 585 birds in control area; numbers extracted from Figure 3 in Tapper et al.), although the authors claim that breeding densities increased on the removal areas by an average of 11% compared with 24% decrease in years without predator removal.

4. Marcström et al. 1988 - Tetraonids (capercaillie, black grouse, hazel grouse, willow grouse)

Two study islands were chosen which lay 3-4 km from the mainland and a similar distance apart. Both islands had similar tree cover and vegetation. The main predators, foxes and martens, were killed on one island for five consecutive winters. The treatments were then reversed and predators removed from the other island for four winters.

Reproduction was affected in several ways. On average, broods contained 68% more young on the removal island than on the control. The proportion of females with broods was also higher on the removal island in 8 of the 9 years of the study. Productivity was 2.2 times higher (4.25 vs 1.94 young per hen) on the removal island. The number of adults increased by 56% for capercaillie and by 80% for black grouse on the experimental island, relative to the control. Counts at leks were even more remarkable, with increases of 174% for capercaillie and 166% for black grouse.

Replication and treatment reversal

1. Greenwood 1986 - Waterfowl

Six study areas were selected that consisted mainly of retired cropland and mixed-grass prairie and were more than 3.2 km apart. The areas were grouped into two sets of three, the first set being studied for all three years of the study and the second set for the latter two years. Striped skunks were removed from a different area in each set each year with a second area in each set serving as a control. Removal and control areas were chosen randomly at the beginning of the study, with the stipulation that a removal area could not serve as a control area the year following removal.

The average percentage of nests hatching in removal areas (15%) was significantly higher than on the control areas (average: 5%); however, two of the five removal areas studied showed no increase in hatching success. On those two areas, other waterfowl nest predators, such as fox and Franklin's ground squirrel, were abundant.

The results of these 6 well-designed studies mirror largely the results of the other studies. Most predator removal experiments resulted in increased hatching success and/or reproduction. Five of these 6 studies found increased post-breeding success, but effects on breeding population size were more elusive, with only Marcström et al. (1988) finding increases in tetraonid lek size. However, even in this case, it is difficult to know whether the increased lek size resulted from increased breeding success in previous years or increased immigration into a predator-free environment.

If predator removal leads to increased breeding success, as most of the studies in Table 4 suggest, why are longer-term effects not detected? We can suggest two potential reasons, based on the theory outlined in Section 2. First, it is possible that higher hatching success leads to lower juvenile survival because of density-dependent processes unrelated to predation (e.g. competition for food with adults, other juveniles, etc.). In a situation of resource limitation for the prey, reducing predation will not greatly affect population sizes. Second, if resources do not limit juvenile survival, it is possible that areas of high chick production, because of predator removal, become sources of colonists for other areas. Changes in population sizes may thus occur, but away from the experimental population. Such an effect has not yet been documented and would be, in any case, difficult to measure.

4.1.2 Factors reducing the efficiency of predator removal

Several factors were noted from the studies in Table 4, which could have reduced the efficiency of predator removal and hence affected the results.

Incomplete predator removal

Few, if any, of the studies above or in Table 4, managed to eliminate predators completely from removal areas. Complete eradication may be done more successfully on islands, yet Marcström et al (1988) were aware of the presence of at least one or two foxes and a weasel on their experimental island in some years. Edminster (1939) concluded that fox control had been unsatisfactory on one of his selective removal areas when nest mortality proved higher than on the control area.

It is possible that complete predator removal could have resulted in more significant findings in some of the studies.

Targeting one of a suite of predators

Predator removal appears to be more efficient when a whole suite of predators is removed rather than a single species. Two studies examined this issue experimentally. Although Edminster (1939) found similar results on his selective (fox and weasel only) and total removal areas, Trautman et al (1974) recorded 19% more pheasants per year on fox-removal areas, but 132% more pheasants on areas where small carnivores (including foxes, raccoons, striped skunk, and badgers) were removed. Part of the latter increase was probably due to better conditions since there was a 53% increase in pheasant numbers on the control areas in those years.

Several studies which failed to find an effect of predator removal had targeted a single predatory species for removal. This was the case for Kalbach (1939), Keith (1961), Wagner et al. (1965), and McDonald (1966). Greenwood (1986) found only a slight increase in hatching success of waterfowl after skunks were removed, but fox and ground squirrels became major egg predators during the study and were uncontrolled. Both Parr (1992) and Parker (1984) removed only avian predators, but found increased predation by mammalian species.

These studies illustrate the important fact that compensatory predation by other species can occur if a key predator is removed.

Prey cycles

The efficiency of predator removal appears linked, in some instances, to prey population cycles, with predator removal showing positive effects in some parts of the prey's cycle but not in others. This was suggested by Edminster (1939) and Parker (1984) in pheasants and tetraonids respectively. In peak prey years, both failed to find any effect of predator removal on prey production and survival. Edminster actually found enhanced nest predation and lower adult survival in predator removal areas than in control areas.

Predator removal may be most efficient at time of low prey population numbers.

Renesting

Renesting following failure of a first clutch is a common feature in birds. If it occurs often, it can lead to an overestimate of the importance of predation. For example, if three-quarters of the nests found by the observers are depredated, hatching success may still be greater than 25% if birds can renest. This problem can be avoided by measuring breeding success in terms of post-hatch brood size, as Marcström et al. did, rather than simple hatching success.

4.1.3 What is the long-term effectiveness of predator removal?

On islands, predator removal appears to be an effective solution with long-lasting effects, providing predators cannot recolonise the islands naturally. On mainlands, what limited evidence exists 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 quickly decreased 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 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 2 areas showed lower hatching rates (18%) in the year after predator removal was stopped, while 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.

4.1.4 Can predator removal reverse trends in declining bird populations?

The strongest case for the use of predator removal for conservation purposes is made by considering the response of threatened island bird species to the eradication of introduced predators. In such cases, predator removal has often led to increases in breeding numbers which had been depressed as the result of predation. Dr P. Monaghan reports a change from 100% hatching failure to 100% hatching success of fulmars on a small Scottish island after the complete eradication of introduced rats (pers. comm.). Similarly, after the removal of domestic cats from the single island where New Zealand stitchbirds (*Notiomystis cincta*) survived, the population has increased to a point where it can now repopulate neighbouring islands (Griffin et al. 1988). Although these experiments are not controlled and the effects of other factors cannot be ruled out, it seems likely that most of the increases in breeding population can be ascribed to predator removal.

As discussed in the introduction, island birds may have been particularly vulnerable to the introduction of new predators. Islands also provide a better setting for predator removal than mainland sites, since they are less accessible to new predators seeking to fill empty territories. This may be the main reason why the results of predator removal studies on mainlands have been mixed.

On mainlands, most predator removal studies were undertaken to enhance game bird and waterfowl populations, rather than for conservation purposes. The study by Parr (1992) was an exception, as he undertook corvid and gull control to stem the decline of a golden plover population. In this case, predator removal did not increase plover nesting success or population size, in part because of nest predation by foxes which became more prevalent during the experiment. The ultimate cause of decline in this population of plovers appears to have been cold weather, which appeared to reduce drastically over-winter survival. Other uncontrolled removal studies seeking to protect songbirds (Stoate and Szczur 1993) and wading birds (Harold 1994) did achieve success at increasing nest success for some (but not all) of the species targetted.

Although most studies carried out on mainlands succeeded in enhancing hatching success of the prey species, post-breeding population sizes were only sometimes increased and breeding population sizes remained largely unchanged. These results support the predictions of the simple population regulation model presented in Section 2. From a game management perspective, predator control may therefore be beneficial, under some circumstances. From a conservation perspective, the evidence at hand suggests that predator control does not systematically increase bird breeding populations. It is possible, however, that conservation bodies may benefit from increased post-breeding bird populations if these attract visitors to reserves.

4.2 Alternative methods of predator control

4.2.1 Predator exclosures

Fences around nests or around nesting areas have been used with some success, particularly in North America, to reduce predation on ground-nesting birds. Fork-tailed storm-petrel nesting inside a fence that excluded river otter (*Lutra canadensis*) enjoyed a 44% higher nesting success than storm-petrels nesting in similar habitat outside the exclosure (Quinlan 1983). Similarly, 24 of 26 nests of the endangered piping plover (*Charadrius melodus*) that were surrounded by wire mesh hatched at least one egg, compared with 6 of 24 unprotected nests, with predation accounting for 94% of failures in the latter group (Rimmer and Deblinger 1990). There was no indication that increased hatching success resulted in greater population sizes in either of these two species.

By contrast, electrified fences failed to keep foxes from entering an important Sandwich tern (*Sterna sandvicensis*) at Scolt Head, Norfolk (Musgrave 1993). Fences may also, inadvertently, be detrimental to the very species they are supposed to protect. Keith (1961) found lower hatching success of dabbling ducks in fenced than unfenced areas. Although the fenced areas offered better nest cover for ducks because large grazers were excluded, striped skunks also preferred these areas.

4.2.2 Habitat manipulation

Bird populations may be enhanced by manipulating breeding habitats to reduce predation. Several studies have shown increased hatching success of waterfowl nests when more cover in the form of vegetation was provided (e.g. Schrank 1972). This was successful in reducing predation by visual predators. The effects on population size are unknown.

The success of cavity-nesting species can also be improved by providing predator-proof boxes. The fledging success of blue tits in Wytham Wood, Oxfordshire, increased significantly after the wooden nest boxes, which were accessible to weasels, were replaced by concrete boxes (Dunn 1977). Similarly, on New Zealand offshore islands, the provision of roost and nest boxes off the ground decreased the rate of population decline of the endangered North Island saddleback (*Philesturnus carunculatus*) by reducing predation by rats (Lovegrove, in press).

4.2.3 Conditioned taste aversion

When predators become ill after a meal, they often form a conditioned taste aversion to the taste of the food that preceded the illness. This reaction may be exploited for conservation purposes, by exposing predators to prey tainted with illness-producing substances (e.g. injected eggs). Conditioned aversion can then protect other prey from further predation.

There have been few tests of this principle under natural conditions, but the preliminary results are encouraging. Dimmick and Nikolaus (1990) offered chicken eggs containing Landrin, a tasteless but nauseous substance, in artificial nests to crows in the wild. The rate of egg predation on artificial nests was significantly lower after aversive conditioning, while it remained the same at sites where no conditioning occurred. At Landrin sites where crows returned the following year, taste aversion was retained without further training. Similar results have been obtained with free-ranging mongoose (Nikolaus and Nellis 1987).

Conditioned taste aversion offers a significant advantage over predator removal when dealing with territorial predators. A conditioned predator that is allowed to continue defending its territory and exclude conspecific intruders may incidentally protect resident breeding birds from further predation. By contrast, predator removal, particularly on mainlands, invariably results in new predators invading the vacant territory.

4.2.4 Predator dissuasion

Low-tech methods of deterrence may provide some protection for ground-nesting birds. Following two years of problematic cat predation on the Great Yarmouth little tern colony, plastic carrier bags were attached to the fence delineating the colony in 1994. On breezy nights, the bags rustled in the wind, and no cat tracks could be found the following mornings. Cat tracks were only seen after calm, dry nights (Rondel and Durdin 1994). The carrier-bag method was used in conjunction with infra-red sensors which emitted bursts of ultrasounds, irritating to cats, when detecting motion. Because the sensors were activated almost continually by movement of marram grass on the dunes, it is difficult to evaluate the effectiveness of either method. Nonetheless, no cat predation was observed in 1994 (Rondel and Durdin 1994).

By contrast, rags soaked in renardine, a pungent, fox-repelling chemical, placed around hen harrier (*Circus cyaneus*) nests in Wales failed to prevent predation (Williams 1994b). During 1988-1993, 56% of nests protected with renardine were successful, compared with 58% for unprotected nests. The experiment is continuing.

4.2.5 Supplemental feeding of predators

There is at least one reported case of supplemental feeding of predators to reduce predation on ground-nesting birds. In 1992, frozen laboratory mice were provided to two pairs of kestrels (*Falco tinnunculus*) nesting near the UK's largest colony of little terns (*Sterna albifrons*) at Great Yarmouth, Norfolk. Mice were put directly into the kestrels' nests 3-4 times a day. Supplementary feeding was withheld experimentally once during the breeding season, and the rate of kestrel predation appeared to increase, until supplementary feeding was resumed. Little tern fledging success was much higher in 1992 (0.71 chick per pair) than in 1991 (0.04 chick per pair) (Paget-Wilkes 1992, Durdin 1993), but it is impossible to determine the role of supplemental feeding in this increase. In addition to supplemental feeding, chick shelters were introduced and cloth rags soaked in renardine (repellent) were tied at intervals to the protective fence around the colony. The little tern colony at Great Yarmouth has been increased over the past 8 years, but it is not known whether this due to predator control methods or to increase immigration from other Norfolk sites.

4.2.6 Can alternative methods of predator control reverse trends in declining bird populations?

Alternative methods of predator control have been used more widely to protect vulnerable or endangered species on mainlands than predator removal. Based on the information at hand, there is no evidence that such methods can reverse trends in declining bird populations. Studies using these methods have focused only on documenting increased hatching success of the prey species, but no long-term effects have been monitored. Some alternative methods, such as nest fencing and conditioned taste aversion, have been successful in providing the short-term gain of increased hatching success. More research is needed into the long-term benefit of these methods for prey population size.

5. RECOMMENDATIONS FOR FUTURE RESEARCH

Our review uncovered several gaps in our knowledge of the impacts of predators and of predator control on prey populations.

- Our simplistic model predicted fairly accurately the effects of predation and of predator removal. More detailed population models can be created to consider more realistically the consequences of predation. This will require a detailed knowledge of the population dynamics of the prey.

- Most predator removal experiments reported in the literature had poor experimental designs which made the interpretation of results difficult. Well-designed predator removal experiments need to be carried out, which will include treatment reversal half-way through the study and adequate replication of sites. The experiments should run over several years, preferably in conjunction with a ringing programme, to allow the quantification of long-term population changes.

- The effectiveness of alternative methods of predator control, in particular the use of fences around nests and conditioned taste-aversion, should be tested more rigorously under natural conditions. The long-term effects of these methods on prey breeding populations are unknown. If successful, they could prove a cost-efficient and ethical means of reducing predation on vulnerable birds.

6. SUMMARY

Predator control on nature reserves is an increasingly contentious issue. The growing populations of a number of predator species, such as foxes, minks, sparrowhawks, goshawks, magpies and gulls, have led to concerns about their impact on vulnerable prey species, particularly songbirds and ground-nesters such as terns and waders. Many conservation bodies have begun small-scale control of corvids, gulls, foxes, mink and stoats on their reserves, but this policy is increasingly being questioned on both scientific and ethical grounds.

To inform the debate about predator control, Côté and Sutherland (1995), under a contract with English Nature, reviewed the literature pertaining to the impacts of predation on bird breeding success and long-term population viability and the effectiveness of predator control programmes for bird conservation. The main findings of this review are summarised below.

The impacts of predation on birds

A review of 110 recent studies which reported nest predation rates for 98 species of birds revealed that, on average, one in three nests fails because of predation. This is similar to other estimates from reviews (O'Connor 1991). Nest predation rate can vary widely, from 0% to 100% of nests within a species. Interestingly, ground-nesting birds are not more at risk of predation than other species. The rate of predation on ground-nesters (45%) was similar to that on open-cup nesters (46%) and burrowing species (38%). Cavity-nesting birds experienced significantly less predation (15% of nests lost). Similar results were also observed by Martin (1993). The overall rate of failure from all causes combined for the 98 species was 46%. Predation therefore accounts, on average, for 84% of all nests lost, supporting the widely held notion that nest predation is the most important cause of reproductive failure in birds (Ricklefs 1969, Skutch 1985).

However, many avian populations appear able to withstand high rates of egg predation without detrimental effects on population size, and there are indeed few declines in bird populations that have been ascribed unequivocally to the sole action of native predators. In 16 long-term studies of declining bird populations, only 2 implicated predation as the ultimate cause of population decline (Canada goose and Cassin's auklet, both from the USA). Eight of the studies clearly showed that predation pressure did not change while populations were declining (including studies of greenshank, corn bunting, reed bunting, yellowhammer in Britain). In the remaining six studies, ultimate causes of decline (such as cold weather, changing agricultural practices, use of pesticides, brood parasitism) were identified, but predation appears to have contributed to population decline by exacerbating these problems (e.g. for some golden plover and grey partridge populations in Britain). The role of predation in causing long-term declines of bird populations is therefore far from universal.

The effectiveness of predator removal programmes

Thirty-five studies of predator removal programmes were reviewed. The majority were aimed at game birds and waterfowl to increase autumn population size.

Two-thirds of the studies (24/35 or 69%) resulted in increased breeding success or increased brood size of the target species. The magnitude of these short-term gains were sometimes impressive. Evidence for longer-term benefits, such as increased post-breeding and breeding population sizes, is more limited, in part because the data to evaluate these benefits were often not provided. Larger post-breeding (autumn) population sizes were found in only 8 studies (23%), while 6 studies documented no effect (20 studies did not record post-breeding population sizes). Larger breeding (spring) population sizes were also found in only 8 studies, with a similar number recording no increase in breeding population.

The strongest case for the use of predator removal for bird conservation is the response of small island bird species to the eradication of introduced predators. In such cases, predator removal has often led to significant increases in breeding numbers which had been depressed as the result of predation. Dr P. Monaghan reports a change from 100% hatching failure to 100% hatching success of fulmars on a small Scottish island after the complete eradication of introduced rats. Similarly, after the removal of domestic cats from the single island where New Zealand stitchbirds (*Notiomystis cincta*) survived, the population has increased to a point where it can now repopulate neighbouring islands (Griffin et al. 1988). Although these experiments are not controlled and the effects of other factors cannot be ruled out, it seems likely that most of the increases in breeding population can be ascribed to predator removal.

Islands provide a better setting for predator removal than mainland sites, since they are less accessible to new predators seeking to fill empty territories. This may be the main reason why the results of predator removal studies on mainlands have been mixed. On mainlands, most predator removal studies reviewed were undertaken to enhance game bird and waterfowl populations, rather than for conservation purposes. The study by Parr (1992) was an exception, as he undertook corvid and gull control to stem the decline of a golden plover population. In this case, predator removal did not increase plover nesting success or population size, in part because of nest predation by foxes which became more prevalent during the experiment. The ultimate cause of decline in this population of plovers appears to have been cold weather, which appeared to reduce drastically over-winter survival. Other uncontrolled removal studies seeking to protect songbirds (Stoate and Szczur 1993) and wading birds (Harold 1994) did achieve success at increasing nest success for some (but not all) of the species targeted.

Although most studies carried out on mainlands succeeded in enhancing hatching success of the prey species, post-breeding population sizes were only sometimes increased and breeding population sizes remained largely unchanged. From a game management perspective (i.e. when the aim is to create a larger autumn populations), predator control may therefore be beneficial, under some circumstances. From a conservation perspective (i.e. when the number of breeding birds is important), the evidence at hand suggests that predator control does not systematically increase bird breeding populations. It is possible, however, that conservation bodies may benefit from increased post-breeding bird populations if these attract visitors to reserves.

Several factors were noted which appeared to reduce the potential effectiveness of predator removal. These included (1) incomplete predator removal as a result of inefficient trapping or poisoning, or as a result of recolonisation by predators, (2) targeting only one of a suite of predators, which allowed compensatory predation by other species, (3) the presence of prey cycles whereby predator removal appeared to increase post-breeding populations at times of low abundance but was ineffective during periods of high abundance, and (4) renesting, which leads to an overestimate of the importance of predation.

Predator removal is an effective solution with long-lasting effects on islands, providing predators cannot recolonise the islands naturally. On mainlands, however, predator removal does not have long-lasting effects, and if not maintained, any benefit disappears quickly. For example, Duebbert and Lokemoen (1980) found that 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 2 areas showed lower hatching rates (18%) in the year after predator removal was stopped, while 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.

The effectiveness of alternative methods of predator control

Alternative methods of predator control have been used more widely to protect vulnerable or endangered species on mainlands than predator removal, but the results have been mixed. For example, fences around nests have increased hatching success of the endangered North American piping plover (Rimmer & Deblinger 1990), but they did not prevent access of foxes to the Sandwich tern colony at Scolt Head, Norfolk (Musgrave 1993). There is even one documented instance of fences inadvertently increasing predation on dabbling duck nests (Keith 1961). Some success has been obtained with conditioned taste aversion, a method which consists in exposing predators to prey tainted with illness-producing substances (e.g. injected eggs) to illicit avoidance to the taste or sight of that prey. There have been few tests of this principle under natural conditions, but the preliminary results are encouraging. Dimmick and Nikolaus (1990) offered chicken eggs containing Landrin, a tasteless but nauseous substance, in artificial nests to crows in the wild. The rate of egg predation on artificial nests was significantly lower after aversive conditioning, while it remained the same at sites where no conditioning occurred. At Landrin sites where crows returned the following year, taste aversion was retained without further training. Conditioned taste aversion offers a significant advantage over predator removal when dealing with territorial predators. A conditioned predator that is allowed to continue defending its territory and exclude conspecific intruders may incidentally protect resident breeding birds from further predation. By contrast, predator removal, particularly on mainlands, invariably results in new predators invading the vacant territory.

Based on the information at hand, there is no evidence that alternative methods can actually reverse trends in declining bird populations. However, studies using these methods have so far focused only on documenting increased hatching success of the prey species, and no long-term effects have been monitored. More research is needed into the long-term benefit of these methods for prey population size.

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