

Figure 7. % nest depredation in relation to nest type. The bars represent means \pm 1 SE. Sample sizes are given above the error bars. One-way ANOVA, $F_{4,93} = 6.65$, $p = 0.0001$. Cavity nesters have significantly lower rates of nest predation than either open or ground nesters (Scheffe's tests, $p < 0.005$).

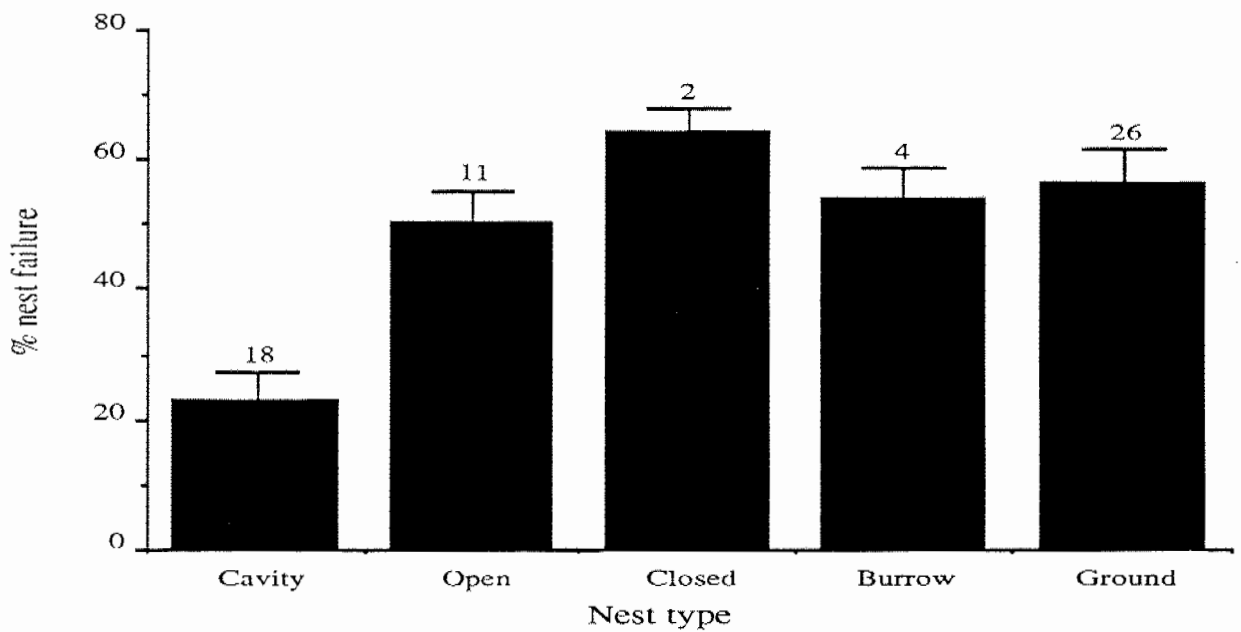


Figure 8. % nest failure (all causes combined) in relation to nest type. The bars represent means \pm 1 SE. Sample sizes are given above the error bars. One-way ANOVA, $F_{4,56} = 7.05$, $p = 0.0001$. Cavity nesters have significantly lower rates of nest predation than ground nesters (Scheffe's test, $p < 0.005$).

Total nest failure was also lowest among cavity nesters, but rates of nest failure were similar among other nest types (Figure 8). Interestingly, predation accounted for a similar proportion of nest failures for all nest types ($F_{4,52} = 0.90$, $p = 0.47$). This suggests that nests with high rates of predation also have high rates of failure from other causes.

Contrary to popular dogma, ground-nesting species do not appear to be more susceptible to nest predation than species nesting off the ground in open or closed nests, although cavity nesters show significantly lower predation rates than species breeding in any other nest type. Martin (1993) also failed to find higher predation rates on ground-nesting species, but only in forests. He recorded higher nest predation on ground-nesting birds in shrub and grassland habitats, but we did not find this difference in our data when considering only those habitats (Figure 9).

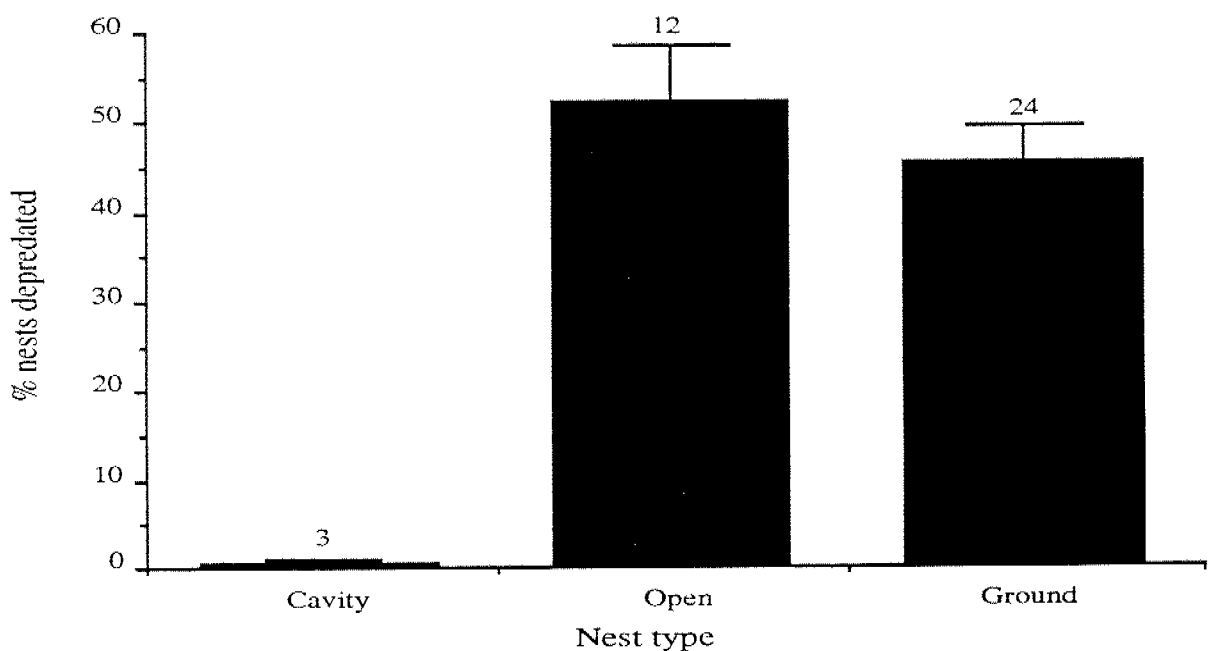


Figure 9. % nest predation in relation to nest type for species breeding in grasslands and shrub habitats (Data from Table 1). The bars represent means \pm 1 SE. Sample sizes are given above the error bars. One-way ANOVA, $F_{2,36} = 8.19$, $p = 0.0012$. Cavity nesters have significantly lower rates of nest predation than ground and open-cup nesters (Scheffe's test, $p < 0.005$).

3.2.1 Compensatory or additive nest mortality ?

The impact of nest predation on bird populations may be reduced if predators prey preferentially on nests that would otherwise fail. Although nest predators are sometimes opportunistic, many predators are attracted to nests because of the feeding activity of parents or the begging calls of young. Evidence is mounting that begging activity can increase predation rate. Redondo and Castro (1992) documented this in magpies *Pica pica*. Haskell (1994) showed experimentally that begging noises made the nests of ground-nesting birds up to three times more vulnerable than silent nests. Evans et al. (in press) found that Cirl bunting (*Emberiza cirlus*) chicks that were preyed upon were experiencing significantly slower growth rates. The chicks were probably discovered by predators as a result of increased begging activity, but Evans et al. believe that they would have starved had they not been preyed upon.

This may be a general phenomenon which reduces to a certain extent the impact of nest predation. However, in many bird species, the bulk of nest predation occurs at the egg rather than the chick stage. It is conceivable that predators might prey preferentially on eggs that will fail, due to differences in parental behaviour.

3.2.2 Predation on breeding adults

Another impact of predation on breeding success can occur through predation on nesting birds. Estimates of mortality of incubating adults caused by predation are relatively scarce in the literature. Table 2 shows 12 estimates, mostly for ground-nesting seabirds.

Predation on breeding adults occurs more rarely than predation on eggs or nestlings. Nevertheless, in some instances, predators can remove an apparently significant number of breeding birds (e.g. 24% of forked-tailed storm-petrels in 2 breeding seasons, 23% of rhinoceros auklets in a single season). The impact of predation on breeding adults for long-term population viability was not assessed in any of the studies, in part due to their short-term nature (average length: 2.3 years) and the long life-span of the prey studied.

3.2.3 Compensatory or additive mortality on adults?

In some cases, predation mortality on adult birds may replace mortality due to other causes

Table 2. Estimates of predation on breeding adults.

Prey	Predator	Location	Length of study	Predation rate	Source
Fork-tailed storm-petrel <i>Oceanodroma furcata</i>	River otter + avian pred. <i>Lutra canadensis</i>	Alaska USA	2 seasons	24 % of breeding adults	Quinlan 1983
Tufted puffin <i>Lunda cirrhata</i>	Red fox <i>Vulpes vulpes</i>	Northwest Territories Canada	1 season	8.3 % of breeding adults	Petersen 1982
Heerman's gull <i>Larus heermanni</i>	Peregrine <i>Falco peregrinus</i>	California USA	1 season	0.02 % of breeding adults	Velarde 1993
Elegant tern <i>Sterna elegans</i>	Peregrine <i>Falco peregrinus</i>	California USA	1 season	0.03 % of breeding adults	Velarde 1993
Royal tern <i>Sterna maxima</i>	Peregrine <i>Falco peregrinus</i>	California USA	1 season	0.005 % of breeding adults	Velarde 1993
Sand martin <i>Riparia riparia</i>	Hobby <i>Falco subbuteo</i>	Hungary	6 season	10 adults/week maximum	Szep & Barta 1992
Rhinoceros auklet <i>Cerorhinca monocerata</i>	Peregrine <i>Falco peregrinus</i>	Washington USA	1 season	23 % of breeding adults	Paine et al. 1990
Cassin's auklet <i>Ptychoramphus aleuticus</i>	Western gull <i>Larus occidentalis</i>	California USA	1 season	3.7 % of subadults and breeding adults	Nelson 1989
California gull <i>Larus californicus</i>	Unspecified avian predators	Utah USA	6 seasons	0.3-0.9 % of breeding adults	Jehl 1989

Table 2 (continued). Estimates of predation on breeding adults

Prey	Predator	Location	Length of study	Predation rate	Source
Great tit <i>Parus major</i>	Sparrowhawk <i>Accipiter nisus</i>	Oxfordshire England	2 seasons	14.4 % of breeding adults	Gray 1987, cited in McCleery & Perrins 1989
Grey partridge <i>Perdix perdix</i>	Fox <i>Vulpes vulpes</i>	Sussex England	2 seasons	10-26% of brooding females	Potts 1986
Pheasant <i>Phasianus colchicus</i>	Fox <i>Vulpes vulpes</i>	Sweden	3 seasons	15% of brooding females	Brittas et al. 1992

rather than add to it. Hudson et al. (1992) found that red grouse (*Lagopus lagopus scoticus*) killed by predators had significantly higher burdens of parasitic nematodes than grouse shot by hunters. Grouse that had died of 'natural' causes had even more parasites than predated individuals. Infection by parasites may thus make grouse vulnerable to predators. It is believed that intestinal nematodes disrupt the normal metabolism by which grouse hens can stop emitting scent during nesting. Indeed, dogs were less likely to find hens that had been treated with an anti-parasite drug than parasitised birds. It is particularly interesting that grouse had more parasites on intensively kept estates. By preying preferentially on parasitised individuals, predators may improve overall prey population health, and the authors showed that a low predation rate could theoretically lead to higher prey population sizes.

3.3 Impact of predators on long-term population viability

The importance of predation on nests and breeding adults can only be evaluated in relation to its impacts on long-term population viability. Few of the studies reviewed in Table 1 related predation rate to population dynamics. This is due, in large part, to the short-term nature of these studies (average length: 4.3 years). Long-term studies are thus necessary to evaluate the impact of predators on prey population viability.

Table 3 summarises the population trends and possible role of predation for 16 long-term studies of bird species. Predation was implicated in only 13% (2/16) of cases of declining bird populations, and may have played a role, albeit indirectly, in another 31% (5/16) of cases. Predation was ruled out as a cause of prey population decline in 50% (8/16) of the studies. In one study, greater predation on the predators of guillemots (*Uria aalge*) is believed to have caused an *increase* in population size of guillemots (Paine et al. 1990). These single-species studies therefore suggest that the impact of predation on long-term prey population viability is species-specific, or at least context-specific. The ultimate causes of decline are, more often than not, human-induced (e.g. changes in agricultural practices, habitat fragmentation, use of pesticides).

Studies of long-term trends of abundance of groups of functionally similar species, obtained from national ornithological recording schemes, also give equivocal evidence for a long-term effect of predation. For example, Gooch et al. (1991) examined the relationships between population densities of 15 common British songbirds, based on Common Bird

Table 3. Long-term studies of bird populations

Target species	Years and location	Population trends and ultimate causes of change	Role for predation?	Source
Lesser snow goose <i>Chen caerulescens caerulescens</i>	1968-89 Manitoba Canada	Breeding population size increasing, but declining fecundity (now 16% of initial annual mean). Annual rates of egg predation unchanged. Probable cause: intraspecific competition for food	No	Cooch et al. 1989
Greenshank <i>Tringa nebularia</i>	1964-90 Britain	Breeding population size declining since 80s. No adverse weather, no increase in nest predation, increase in numbers over-wintering. Probable cause: unknown	No	Thompson & Thompson 1991
Canada goose <i>Branta canadensis</i>	1953-1994 USA	64% decline in breeding population 1960-75 attributed to coyote predation. Increasing population since 1975 owing to shift to coyote-free habitat	Yes	Fitzner et al. 1994
Rock ptarmigan <i>Lagopus mutus</i>	1960-1969 Alaska	Cyclically declining and increasing population. Cycle paralleled by changes in clutch size, nest failure, and winter juvenile survival. No evidence of food shortage in decline years. Increased nest predation in decline years, but may not be a direct effect.	Possible (indirect?)	Weeden & Theberge 1972
Guillemot <i>Uria aalge</i>	1977-88 Washington USA	Increasing population size while peregrine population increased. Probably occurred in response to peregrine predation on northwestern crow, predators of guillemot eggs	Yes (indirect)	Paine et al. 1990
Wood thrush <i>Hylocichla mustelina</i>	1974-90 Delaware USA	3.5 % decline per year in adult numbers from 1978 to 1987. Rates of return declined, probably due to emigration. High rates of nest failure in decline years, assumed to be predator-induced, exacerbated by cowbird parasitism.	Possible	Roth and Johnson 1993
Kentucky warbler <i>Oporornis formosus</i>	1979-93 Virginia USA	40% decline in number of territories. Rates of predation, brood parasitism, and number of young fledged per pair unchanged. Probable cause: unknown	No	McDonald & Morton, unpubl., cited in Rappole & McDonald 1994

Table 3 (continued). Long-term studies of bird populations

Target species	Years and location	Population trends and ultimate causes of change	Role for predation?	Source
Cassin's auklet <i>Ptychorampus aleuticus</i>	1977-88 Washington USA	Declining breeding population. Rate of decline correlated with increasing abundance of peregrines	Yes	Paine et al. 1990
Fork-tailed storm-petrel <i>Oceanodroma furcata</i>	1977-88 Washington USA	Stable population size while peregrine population increased	No	Paine et al. 1990
Golden plover <i>Pluvialis apricaria</i>	1973-1990 Scotland	Breeding population size increased till 1977, followed by decline to extinction. No loss of breeding habitat. Predators rose during decline years. Probable cause: cold weather causing low overwinter survival	Yes (but not ultimate cause)	Parr 1992
Grey partridge <i>Perdix perdix</i>	1950-1986 England	Declining population since 1950's, correlating with increased predation, use of pesticides and decreased nesting cover. Probable cause: pesticides, perhaps exacerbated by predation	Possible (but not ultimate cause)	Potts 1986
Yellowhammer <i>Emberiza citrinella</i>	1924-1992 England	12% decline in population size between 1968-1991. Causes of nest failure (including predation) relatively unchanged through this period.	No	Crick et al. 1994
Reed bunting <i>Emberiza schoeniclus</i>	1924-1992 England	61% decline in population size between 1968-1991. Causes of nest failure (including predation) relatively unchanged through this period.	No	Crick et al. 1994
Corn bunting <i>Miliaria calandra</i>	1924-1992 England	74% decline in population size between 1968-1991. Predation has become less important as a cause of nest failure, but losses due to farming processes became higher.	No	Crick et al. 1994
Common tern <i>Sterna hirundo</i>	1950-1986 Germany	Population declined from 1950 to 1970, due mainly to pesticides. No change in nest predation rates throughout this period.	No	Becker 1991
Great tit <i>Parus major</i>	1960-1989 England	Some declines correlate with high predation by weasels. Release of weasel predation resulted in population increase.	Possible	McCleery & Perrins 1989

Censuses and Nest Record Schemes, and magpie population densities. While magpie populations increased 4-5% per year from 1966 to 1986, populations of songbirds either increased, decreased, or stayed stable during that time period. There was no systematic correlation between songbird densities or nesting success and magpie densities. By contrast, Böhning-Gaese et al. (1993) found that nest vulnerability to predation was significantly related to population declines in North American insectivorous songbirds over a 20-year period. Note that nest vulnerability was an index comprising nest type, nest height, and susceptibility to cowbird parasitism. Habitat fragmentation, which results in increased predation due to edge effects (Paton 1994), is believed to be the ultimate cause of decline of these North American songbirds.

4. REVIEW OF EMPIRICAL EVIDENCE FOR THE EFFECTS OF PREDATOR CONTROL ON BIRD POPULATIONS

The goal of this section was originally to review the evidence for the idea that appropriate predator control measures can reverse downward trends in prey populations caused by predation. However, after a thorough search of the literature, it became apparent that many predator control experiments had been carried out on populations of game birds and waterfowl that were not necessarily declining. Our objective was therefore broadened to examine the effects of such studies.

We assessed the effectiveness of predator removal and of alternative methods of predator control separately because predator removal studies generally lasted longer and assessed various prey population parameters. The testing of alternative methods of predator control, however, was not as rigorous.

4.1 Predator removal

The results of 35 studies of predator removal are summarised in Table 4. The effectiveness of predator removal programmes may be measured in a number of ways. Short-term benefits include increased hatching success, fledging success and brood size. Longer-term benefits include increased breeding and post-breeding population sizes.

The majority of predator removal experiments resulted in short-term gains for the target species (Table 5). Two-thirds of the studies showed increased breeding success, either

Table 4. Results of predator removal experiments

Prey	Predator(s)	Location	Length of study	Experimental design	Effects of predator removal	Source
Mallard <i>Anas platyrhynchos</i> and other ducks	Red fox, striped skunk, raccoon, badger	S. Dakota USA	6 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 27% increase in hatching success • 2.6-fold increase in density of nests 	Duebber & Lokemoen 1980
Dabbling ducks	Striped skunk	N. Dakota USA	2 years	Before and after comparison	<ul style="list-style-type: none"> • Decrease in nest predation from 30+% to 7-13% 	Kalmbach 1939
Various ducks	Red fox, raccoon, striped skunks badgers	S. Dakota USA	5 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 24-34% increase in hatching success • 39% increase in density of breeding pairs 	Duebber & Kantrud 1974
Dabbling ducks	Striped skunk	N. Dakota USA	3 years	Simultaneous experimental and control areas with replicates and treatment reversal	<ul style="list-style-type: none"> • 10% increase in hatching success (2 of 5 experimental areas showed no benefit) 	Greenwood 1986
Dabbling ducks	Striped skunk, raccoon, Franklin's ground squirrel	Manitoba Canada	1 year	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 18% increase in nest success (measured on artificial nests) 	Lynch 1972
Dabbling ducks	Red fox, raccoon, striped skunks badgers	N. Dakota USA	2 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 26% increase in nest success (measured on artificial nests) 	Schranck 1972

Table 4 (continued). Predator removal experiments

Prey	Predator(s)	Location	Length of study	Experimental design	Effects of predator removal	Source
Dabbling ducks	Striped skunk	Alberta Canada	5 years	Before and after comparison	<ul style="list-style-type: none"> • No reduction in nest predation 	Keith 1961
Dabbling ducks	Skunk, raccoon, fox (main)	Minnesota USA	6 years	Simultaneous experimental and control areas with treatment reversal	<ul style="list-style-type: none"> • 30% increase in hatching success • No effect on number of breeding pairs 	Balser et al. 1968
Wild turkey <i>Meleagris gallopavo</i>	Coyote, bobcat, raccoon, striped skunk, badger, opossum	S. Texas USA	2 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 2-7 fold increase in number of young per hen • Increase in autumn numbers • No effect on number of hens 	Beasom 1974
Pheasant <i>Phasianus colchicus</i>	Red fox, raccoon, striped skunk, badger	S. Dakota USA	7 years	Simultaneous experimental and control areas, with replicates	<ul style="list-style-type: none"> • No change in % nests hatched or % nest destroyed • 2.8-fold increase in number of pheasants 	Trautman et al. 1974
Pheasant <i>Phasianus colchicus</i>	Striped and spotted skunk, raccoon, crow (main)	Minnesota USA	5 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 10% increase in hatching success • 2-fold increase in chick production • No effect on nest density • No effect on adult population 	Chesness et al. 1968
Pheasant <i>Phasianus colchicus</i>	Fox	New York USA	4 years	Before and after comparison	<ul style="list-style-type: none"> • Increased number of nests • No effect on chick mortality • Increased number of breeders 	NY Conservation Dept 1951
Pheasant <i>Phasianus colchicus</i>	Avian	Washington USA	Not reported	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • No effect on production 	Lauckhart and McKean 1956

Table 4 (continued). Predator removal experiments

Prey	Predator(s)	Location	Length of study	Experimental design	Effects of predator removal	Source
Pheasant <i>Phasianus colchicus</i>	Cats, hawks	Washington USA	4 years	Before and after comparison	<ul style="list-style-type: none"> • More nests but brood size and hatching success constant • 20-50% increased summer survival of hens • Increased post-breeding population 	Einarsen 1950
Pheasant <i>Phasianus colchicus</i>	Domestic cat, skunk, raccoon,	California USA	4 years	Before and after comparison (control area in 1yr)	<ul style="list-style-type: none"> • 12-33% reduction in nest predation (50% reduction relative to control) 	Hart et al. 1956
Pheasant <i>Phasianus colchicus</i> and Grey partridge <i>Perdrix perdrix</i>	Fox	Denmark	11 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 50-100% increase in autumn population (measure by bag size) 	Jensen 1970
Pheasant <i>Phasianus colchicus</i> and Grey partridge <i>Perdrix perdrix</i>	All predators	Germany	11 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • Increased post-breeding population size 	Frank 1970
Grey partridge <i>Perdrix perdrix</i>	Crow, magpie, fox	England	6 years	Simultaneous experimental and control areas with treatment reversal	<ul style="list-style-type: none"> • Increased hatching success • Increased brood size • Increased autumn population size • No effect on breeding population 	Tapper et al. 1991
Grey partridge <i>Perdrix perdrix</i>	Crow, stoat, fox	England	17 years	Simultaneous experimental and control areas with treatment reversal	<ul style="list-style-type: none"> • Decreased nest losses • Nest predation no longer density-dependent 	Potts 1986

Table 4 (continued). Predator removal experiments

Prey	Predator(s)	Location	Length of study	Experimental design	Effects of predator removal	Source
Grey partridge <i>Perdix perdix</i>	Crow, stoat, fox	England	38 years	Before and after comparison	<ul style="list-style-type: none"> • Decreased nest losses • Nest predation no longer density-dependent 	Potts 1986
Grey partridge <i>Perdix perdix</i>	Crow, stoat, fox	England	20+ years	Before and after comparison	<ul style="list-style-type: none"> • Decreased nest losses • Nest predation no longer density-dependent 	Potts 1986
Red grouse <i>Lagopus l. scotticus</i>	Fox, carrion crow	Wales (Ireland moor)	5 years (on-going)	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 3-4-fold increase in number of grouse (but burning undertaken simultaneously) 	I. Williams, RSPB pers. comm.
Willow grouse <i>Lagopus l. lagopus</i> Black grouse <i>Lyurus tetrix</i>	Hooded crow, black-billed magpie	Norway	4 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • No effect on nest predation in willow, slight decrease in black • No effect on brood size • No effect on nesting density 	Parker 1984
Ruffed grouse <i>Bonasa umbellus</i>	Raptors, corvids, fox, skunk, mustelids, cat, raccoon, woodchuck	New York USA	4 years	Simultaneous experimental and control areas with treatment reversal	<ul style="list-style-type: none"> • 50% reduction in nest mortality • No effect on juvenile or adult mortality • Higher autumn grouse density in some years • No effect on breeding population 	Edminster 1939

Table 4 (continued). Predator removal experiments

Prey	Predator(s)	Location	Length of study	Experimental design	Effects of predator removal	Source
Capercaillie, black grouse, hazel grouse, willow grouse	Fox, marten	Sweden	9 years	Simultaneous experimental and control areas with treatment reversal	<ul style="list-style-type: none"> • Increased brood size • 2.2-fold increase in chick production • 56% increase in breeding population size of capercaillie, 80% of black grouse 	Mareström et al. 1988
Capercaillie	Fox, carrion crow	Scotland (Abermethy)	4 years (on-going)	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • Increased number of chicks per hen (coinciding with good weather) 	Anon. 1995
Bobwhite quail <i>Colinus virginianus</i>	Coyote, bobcat, raccoon, striped skunk, badger, opossum	S. Texas USA	2 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • 1-2 fold increase in number of young per hen • No effect on brood size • 33-69% increase in number of hens • 60% increase in population size 	Beasom 1974
Bobwhite quail <i>Colinus virginianus</i>	Coyote <i>Canis latrans</i>	S. Texas USA	2 years	Before and after comparison	<ul style="list-style-type: none"> • 20% increase in hatching success 	Lehmann 1946
White-winged dove <i>Zenaida asiata</i>	Great-tailed grackle	Texas USA	2 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • Increased number of nests, eggs, and young • No effect on hatching success 	Blankinship 1966
Fieldfare <i>Turdus pilaris</i>	Hooded crow	Norway	6 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • Decrease in nest predation (measured on artificial nests) • Increased population size 	Slagsvold 1978, 1980

Table 4 (continued). Predator removal experiments

Prey	Predator(s)	Location	Length of study	Experimental design	Effects of predator removal	Source
Songbirds	Corvids, magpies	England	2 years	Before and after comparison	<ul style="list-style-type: none"> • 32% increase in nest success of blackbird, song thrush and chaffinch • No effect on nest success of dunnoek, whitethroat and blackcap 	Stoate & Szczur 1993
Kakerori flycatcher (<i>Pomarea dimidiata</i>)	Rats (introduced)	Cook Islands	6 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • Nesting success increased 2.5 fold • 3 fold reduction in adult mortality • 1.5-fold increase in breeding population size 	Robertson et al. 1994
Fulmar, gulls	Brown rat	Scotland	6 years	Before and after comparison	<ul style="list-style-type: none"> • 100% increase in nesting success 	P. Monaghan, U. Glasgow pers. comm.
Golden plover, lapwing, redshank, snipe, curlew	Carriion crow, common gull	Scotland	4 years	Simultaneous experimental and control areas	<ul style="list-style-type: none"> • No effect on hatching success of golden plover, snipe and oystercatcher • Increased hatching success of redshank, lapwing and curlew after removal, but not relative to control • No effect on population sizes 	Parr, 1993
Wading birds	Fox, carrion crow, magpie	England (Scott Head)	4 years (on-going)	Before and after comparison	<ul style="list-style-type: none"> • Increased fledging success of lapwings and other waders 	Harold, 1994