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The scientific basis for predator control for bird conservation

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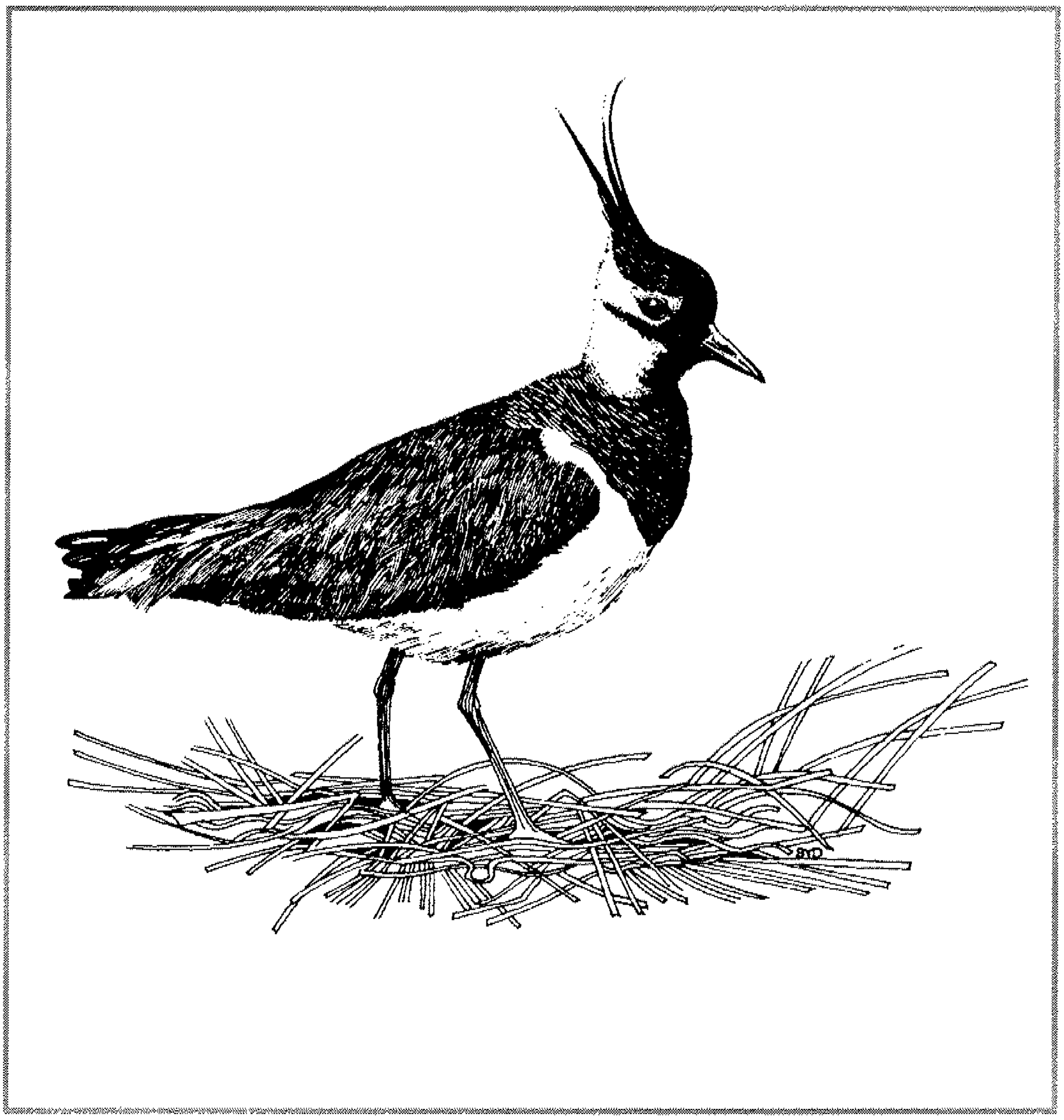

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THE SCIENTIFIC BASIS FOR PREDATOR CONTROL FOR BIRD CONSERVATION

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1. INTRODUCTION

Predation is widely believed to have shaped every aspect of the life histories and behaviour of birds. Indeed, mortality due to predation can be high, particularly in early avian life stages. For example, Lack (1954) estimated that 75% of all nests and nestlings lost from open-cup nests are taken by predators. Ricklefs (1969) estimated that predation accounted for 55% of egg losses and 66% of nestling losses in six species of passerines. Such rates of mortality can generate strong selection on reproductive behaviour 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 alien predators. The loss of at least 34 of 110 (31%) species of birds which have become extinct since c.1600 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 thus lacked defensive behaviours. 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 behaviours evolved to defend nests and self against native predators may have also given some protection against aliens (Atkinson 1985).

The impact of non-introduced predators on bird populations is far less clear. Many avian populations appear able to withstand high rates of egg predation without detrimental effects on population size, and there are few declines in bird populations that have been ascribed unequivocally to the sole action of native predators. The more common explanation for declines in 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. Nevertheless, 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 controlled if necessary.

Several countries, such as Great Britain and the United States, have a long history of controlling predators to increase populations of game birds and waterfowl for hunting purposes. Recently, predator control has been suggested (and in some cases, implemented) for conservation purposes (Anonynous 1995, Musgrave 1993, Harold 1994). In Britain, the growing populations 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.

The goals of this report are thus:

(1) to review relevant theoretical aspects of predator-prey relationships,
(2) to assess critically the literature pertaining to the impact of predators on bird populations, and
(3) to evaluate the effectiveness of predator control programmes on declining prey populations.

The ethics of predator control are beyond the scope of this report.

2. VERTEBRATE PREY-PREDATOR RELATIONSHIPS: REVIEW OF THEORY

To develop clear policies on predator control, it is necessary to understand the effects of predators on the distribution and abundance of their prey populations. Case studies are invaluable for illustrating these impacts. However, case studies are of limited general use as both the level of predation and its consequences are often specific to the predator and prey involved. Results may not even be applicable to other populations of the same species.

The aim of this section is to consider the relationship between mortality through predation and ecological characteristics such as population size and range. Four theoretical issues relevant to the question of predator control are discussed below: (1) how prey populations are regulated, (2) whether predation can drive prey populations to extinction, (3) how prey populations may act as sources or sinks, and (4) how prey populations may or may not behave as metapopulations.

2.1 Population regulation and the impact of predation

Predicting the consequences of predation requires an understanding of the way in which prey populations are regulated. The relationship between the size of a post-breeding (autumn) population and the number of individuals that breed in the following year is typically curvilinear (Figure 1). At low population sizes, post-breeding and breeding numbers are directly related; hence, a doubling of the post-breeding population size results, on average, in a doubling of the numbers that will breed. At such low population levels, the effects of density-dependent factors, such as competition for limiting resources, are negligible and populations can grow unchecked. At higher population sizes, this cannot be the case. Doubling an already large post-breeding population will result in competition for territories or food and, as a result, a large number of individuals will starve or fail to obtain territories. The breeding population size may therefore increase slightly, but cannot double.

The exact shape of the relationship will be determined by the ecology and behaviour of the species. If the number of breeding territories is fixed or if resources permit only a fixed number of individuals to avoid starvation, the relationship will plateau abruptly such that breeding population will remain constant for a large range of post-breeding population sizes

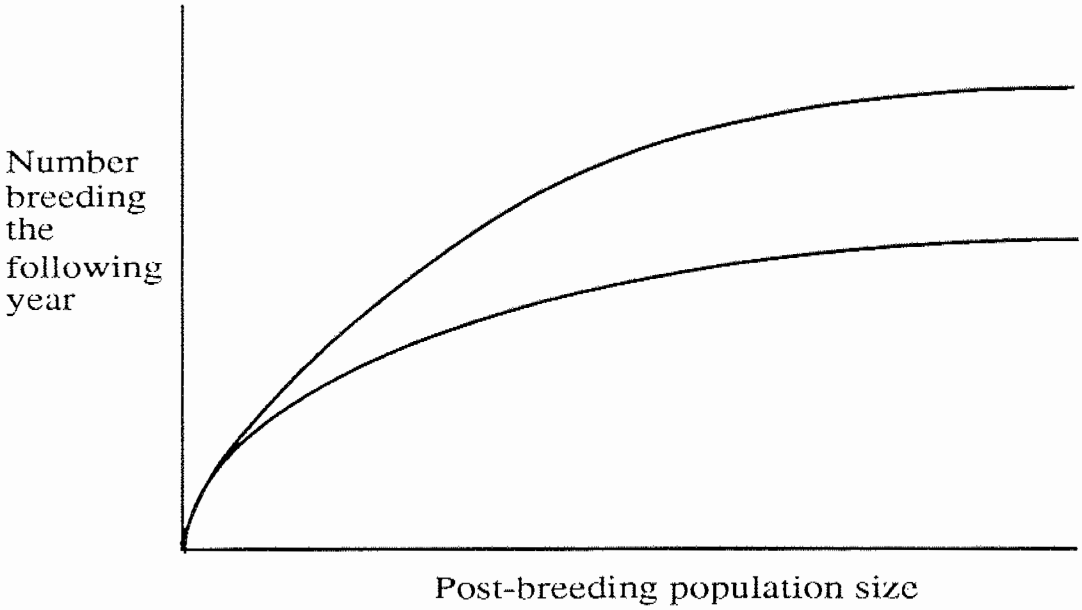

Figure 1. The relationship between post-breeding population size and the number breeding the following year in the presence of compensatory (lower curve) and under-compensatory (upper curve) processes.

(Figure 1, lower curve). This is known as 'compensation' and indicates that there is an absolute maximum in the numbers breeding. By contrast, if at high densities territory size is reduced or if starvation increases with population size (but not at such a rate as to limit the population), the number of breeding individuals will increase with increasing post-breeding population size, although at a decreasing rate (Figure 1, upper curve). We will call this 'under-compensation'.

Whether a prey population is regulated in a compensatory or under-compensatory fashion will have a profound effect on how it responds to predation. In the case of compensation, a considerable decrease in post-breeding population size caused by predation may have a negligible impact on breeding numbers (Figure 2, lower curve). However, the same predation rate on an under-compensating population results in a greater decrease in breeding population size (Figure 2, upper curve).

Note that in Figure 2, the decrease in post-breeding numbers results in a smaller decrease in breeding population size. This may not always be the case. If there is no compensation at all (i.e. there is a direct relationship between post-breeding and breeding numbers), then any decline in post-breeding number caused by predation will result in a nearly equal decline in breeding population. It is important to note that this situation will often occur at low post-breeding population sizes (Figure 3), when resources and habitats are plentiful. Small post-breeding populations will be affected to a greater extent by equal rates of predation than large ones. Predation may thus compound the inherent risk of extinction faced by small populations because of chance demographic or environmental events (Pimm et al. 1988, Rosenzweig & Clark 1994). The populations of ground-nesting species that are the target of conservation efforts in Britain are typically in this situation.

We have so far focused on only two late life stages, but the principle of compensation may act with differing intensity at all life history stages. Figure 4 shows how this may operate by breaking down the different stages of a bird's life into a series of relationships similar to that shown in Figure 1. We have used a range of relationships to describe the different stages but the actual relationships will, of course, vary between species and ecological circumstances.

The consequences of a 50% reduction in egg number, as a result of predation, can now be traced through the population. As the birds pass through the different life stages, the impact of egg mortality becomes gradually reduced, so that breeding population size is ultimately

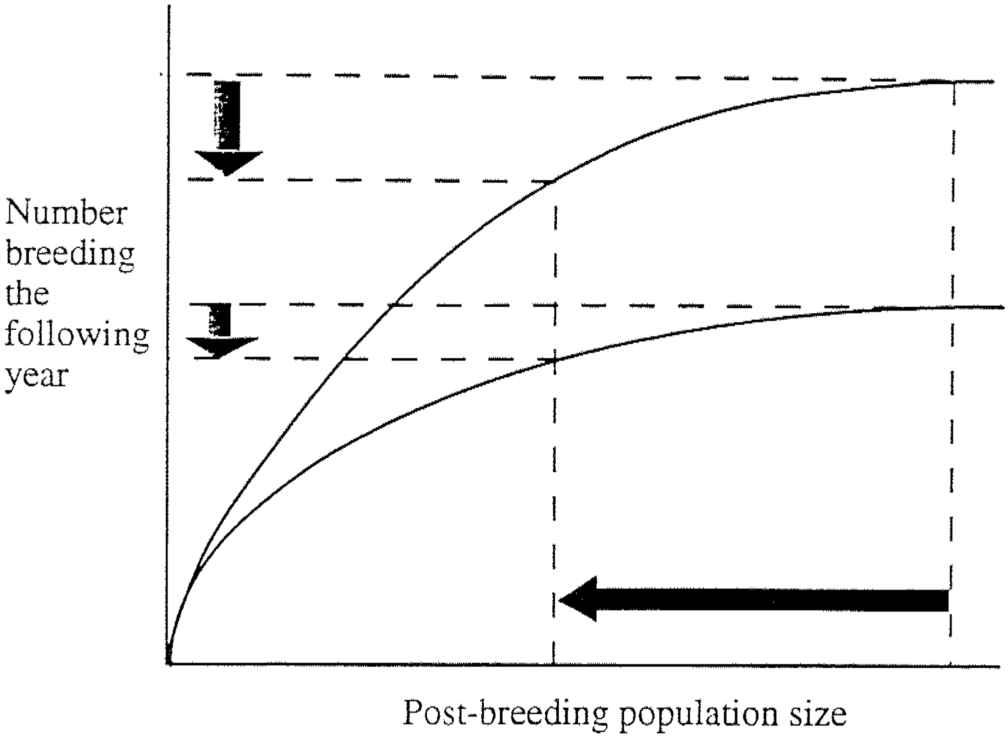

Figure 2. The relationship between post-breeding population size and the number breeding the following year as shown in Figure 1. Here, reduction of an initially large post-breeding population, because of predation, results in slightly lower breeding numbers. The effect is more marked in the undercompensated (upper curve) than the compensated (lower curve) population.

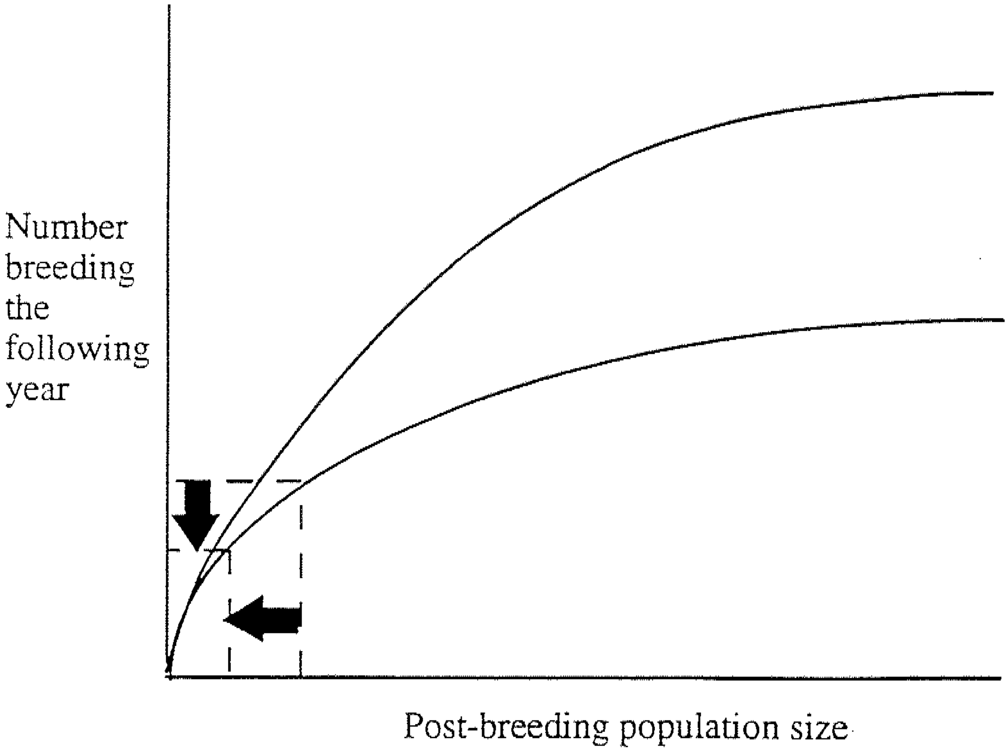

Figure 3. The effect on the numbers breeding of mortality in the post-breeding population is shown as in Figure 2, but for an initially small post-breeding population size. In this case, losing the same proportion of the post-breeding population as in Figure 2 results in a greater proportional impact on breeding number.

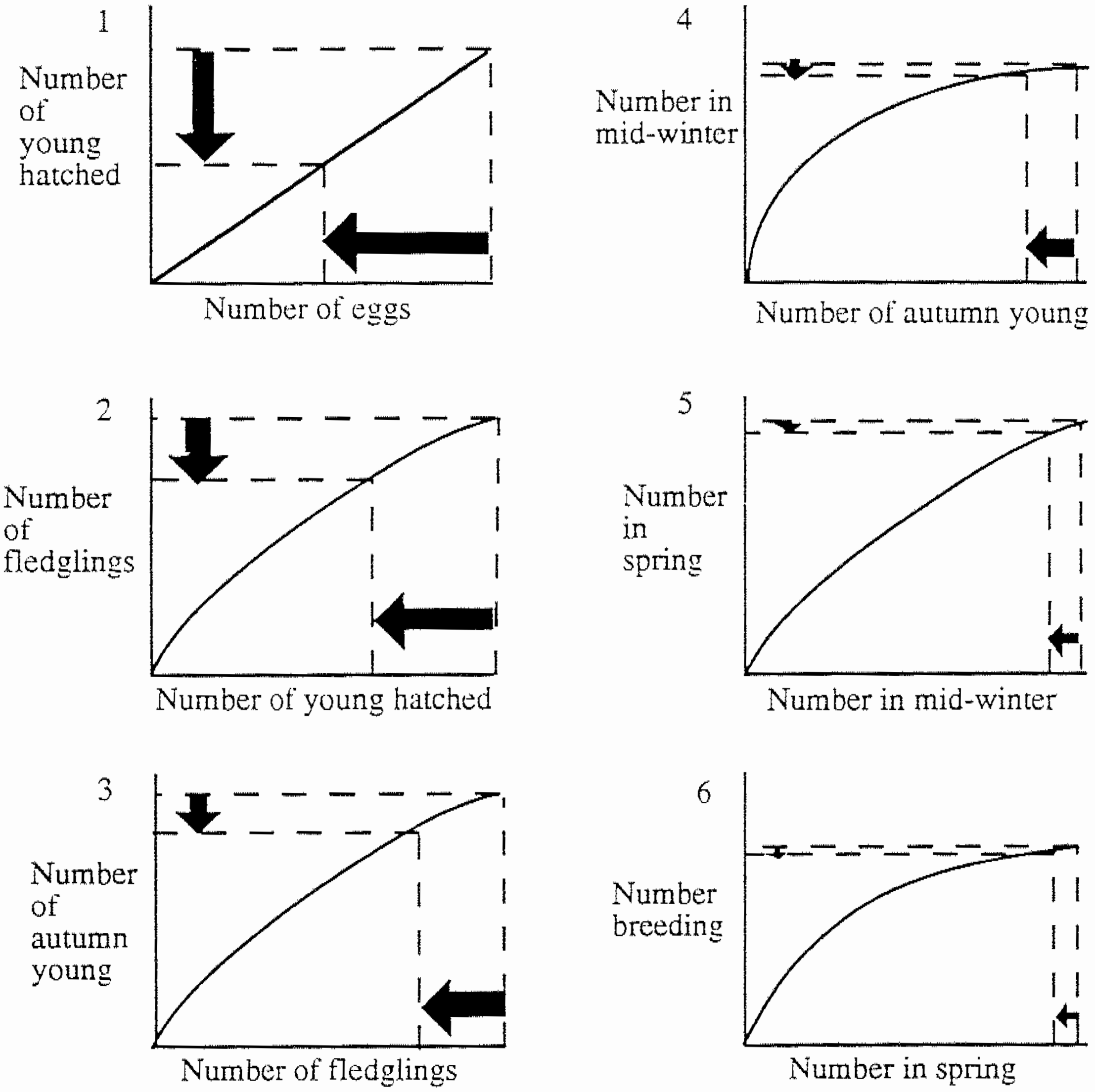

Figure 4. The sequence of regulatory stages acting upon a population. The consequence of a 50% loss in the number of eggs is followed through the various stages, ultimately resulting in a minor decrease in breeding number. The sensitivity of the population to predation therefore depends greatly on the timing of predation.

influenced very little. By contrast, a similar mortality imposed on pre-breeding individuals in the spring would have considerable consequences for breeding numbers. This model therefore predicts that predation on younger individuals will affect breeding population size less than equal predation occurring later in life. Compensation operating at each life stage can effectively dilute the effects of mortality in the previous stages. Thus sparrowhawks may kill large numbers of juvenile great tits in Wytham Wood, yet have no noticeable impact on the breeding population (McCleery and Perrins 1991).

The impact of predation will also depend on the extent to which compensation operates at each stage of the life cycle. For example, in Figure 4, we assumed that there was high compensation between autumn and mid-winter populations, but little compensation between mid-winter and spring populations. In this situation, predation in mid-winter would have a greater impact on breeding numbers than predation in autumn.

Another topical issue can be addressed with our model. Conservationists usually view the health of a population in terms of breeding numbers, and hence their main concern is the impact of predation on the number of breeding individuals. By 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 model shows that this misunderstanding is not a simple matter of semantics. The loss of eggs to predation shown in Figure 4 results in an appreciable decrease in number of autumn young, reducing the number harvestable by hunters, but has little effect on breeding population size. The same rate of predation may thus be important to game managers but relatively unimportant to conservationists.

2.1.1 Summary of the effects of predation on population regulation

- The effects of predation will depend on whether there is compensating or under-compensating mortality . This will need to be determined empirically.

- Predation on young individuals is likely to influence breeding population size less than predation on later stages.

- Predation is likely to be more important where populations are already reduced by other processes.

- Predation may increase the probability of extinction of small populations.

- Predators may reduce prey autumn populations but have no impact on breeding populations. Thus, predation may have considerable consequences for game managers but not for conservationists.

2.2 Can predators drive their prey to extinction?

We suggested above that predation, because of its relatively greater impact on small populations, could increase the probability of extinction of small populations. In practice, however, predators are unlikely to drive their prey to extinction, except under special circumstances (for example, when predators kill more prey than they can eat).

Specialist predators, which rely on a single prey species, are unlikely to cause the extinction of prey populations. Their abundance is closely linked to the abundance of their prey, and their numbers are likely to fall before their prey is eliminated completely. The populations of such specialist predators often oscillates in cycles with those of their prey.

On the other hand, many predators of birds are generalists which feed on a variety of prey. They are not usually affected greatly by shortages of any prey species as they can switch to more abundant species, but they will take any prey that is encountered (e.g. Vickery et al. 1992). Since some prey species are inherently more vulnerable to predation, as a result of their behaviour or less developed escape responses, these may be taken in disproportionate numbers relative to their abundance (Tinbergen 1946). As a result, the abundance of such species can be severely reduced, possibly leading to extinction, usually as a result of stochastic events (Pimm et al. 1988, Rosenzweig and Clark 1994).

The life-history of the prey species may also play a role in the likelihood of extinction as a result of predation. Prey species with life-history characteristics such as late maturation, high natural survival, and low fecundity, may be particularly vulnerable to the impact of predation. An example may be the common skate (*Raja batis*), which reaches maturity late and spawns only a few eggs each year. Fishing pressure (which is a form of predation) has all but extirpated this species from the Irish Sea (Brander 1981).

The responses of predators to prey density can have important repercussions for habitat management. For example, providing suitable breeding habitat which results in attracting birds from a wide area to breed in high densities may, if predation increases with density, result in a decrease in average breeding success. This may be the case of little terns (*Sterna* *albifrons*) in England, where habitat creation has resulted in an increasing colony size at Great Yarmouth, Suffolk, while colonies at other sites on the East Anglian coast have been declining steadily (C. Durdin, pers. comm.). The mean fledging success of breeding pairs at Great Yarmouth fell with increasing colony size over several years, until predator control was implemented (Joyce 1993).

2.2.1 Summary of the effects of predation on prey extinction

- Predators feeding on single species of prey are unlikely to drive them to extinction or to very low levels.
- Predators feeding on a range of species may drive a prey species to very low levels or even extinction if the species is particularly vulnerable to predation or if it possesses certain life history characteristics, such as late maturity and low fecundity.
- Habitat management programmes, particularly those which result in breeding birds aggregating in a few sites, should take into account the potential responses of predators to increased prey density.

2.3 Sources and sinks

It is becoming increasingly clear that populations of a species should not be considered in isolation but as part of a network of populations sharing individuals. Pulliam and Danielson (1991) suggested that it might be useful to consider habitats as comprising regions known as sources and sinks. In source populations, the birth rate exceeds the death rate, and a surplus of individuals are produced which can emigrate (Figure 5a). In sink populations, the death rate exceeds the birth rate and populations may be maintained by immigration. Thus, due to immigration, the species may occur over a greater area than if there were no immigration. A balance between sources and sinks is crucial to overall population stability. Although sources and sinks undoubtedly occur, there are technical problems associated with identifying them (Watkinson and Sutherland 1995), but this does not affect the arguments described here.

Predation may affect the balance of sources and sinks in one of two ways. First, predation may reduce the birth rate or increase the death rate in sinks, making them even deeper sinks (Figure 5b). Alternatively, predation may increase the size of the sinks relative to the sources (Figure 5c). This will have population consequences as the density of immigrants into the sinks will be reduced due to a decreased area of sources and an increased area of

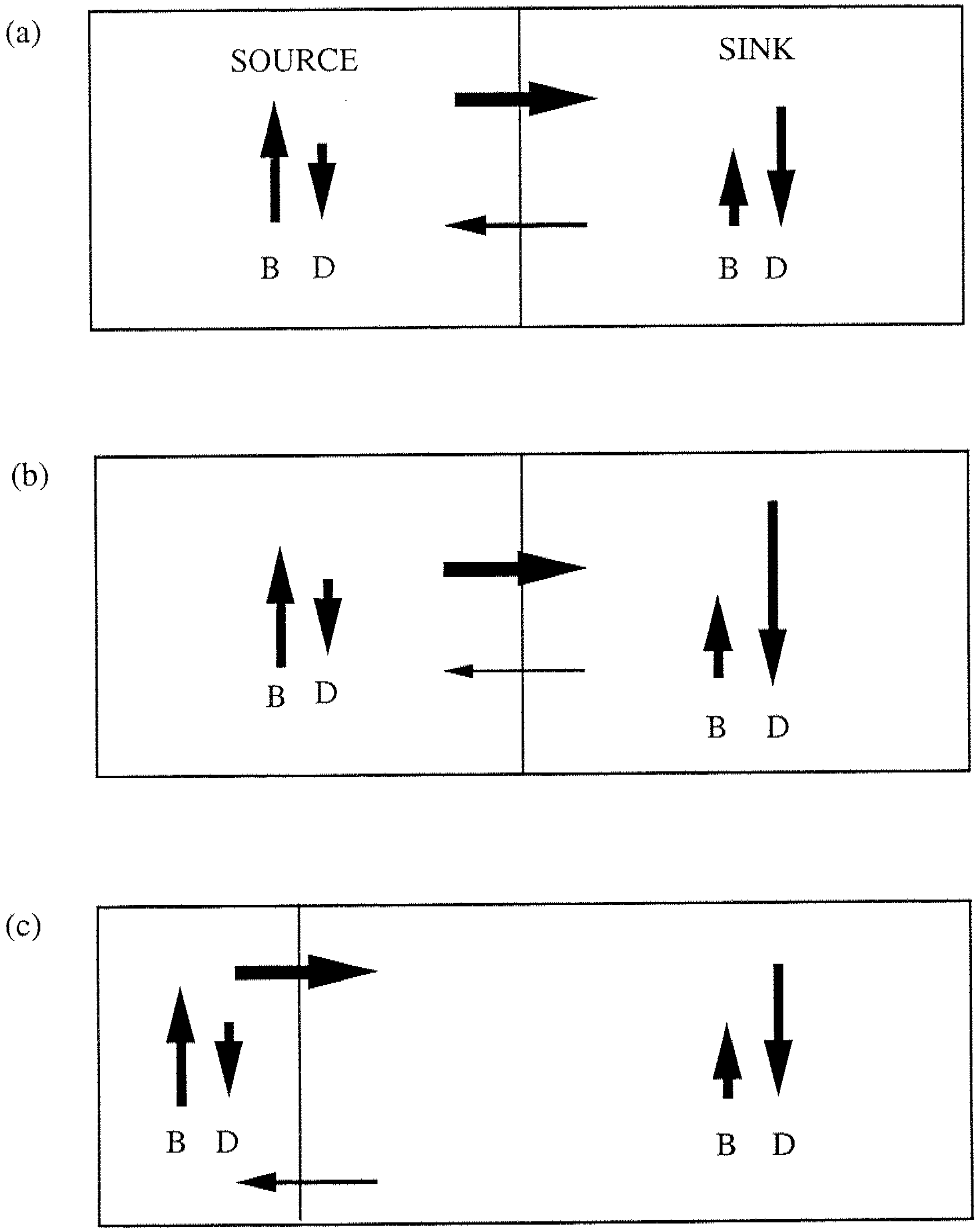

Figure 5. Source and sink populations. (a) Each population has a birth rate and a death rate with the discrepancy being made up through immigration or emigration. (b) Predation may reduce the birth rate or increase the death rate in sinks, making them deepers sinks. (c) Predation may increase the size of sinks relative to sources.

sinks.

It is possible that habitat management (e.g. on nature reserves) in areas of high predation risk may increase the apparent attractiveness of sinks and could thus result in a reduction in total population size.

2.3.1 Summary of the effects of predation on prey population sources and sinks

- Predation may alter the size of sinks or the extent to which mortality exceeds birth rate in sinks. This could alter total population size and population ranges.

- Habitat management may increase the attractiveness of sinks and thus reduce total population size.

2.4 Metapopulations

Recent theory suggests that localised populations may go extinct and then be recolonised by individuals dispersing from other populations. With this framework a species in a large area is considered as a metapopulation comprising a number of populations which go extinct and are re-established again.

Figure 6 shows a very simplified version of the possible consequences of having one of the sites act as a sink due to predation, such that it never produces dispersing individuals. Nee and May (1992) have shown the consequences of such loss in more detail.

In practice, metapopulation models are not good descriptors of the way in which most populations behave (Harrison 1994). Metapopulation models require that populations be sufficiently connected so as to be recolonised after extinction, yet sufficiently isolated that groups can be considered as separate populations.

2.4.1 Summary of the effects of predation on metapopulations

- Predation may increase the probability of extinction of prey populations which may affect the size and range of prey metapopulations.

- Metapopulations models probably provide a poor description of the population ecology of British birds.

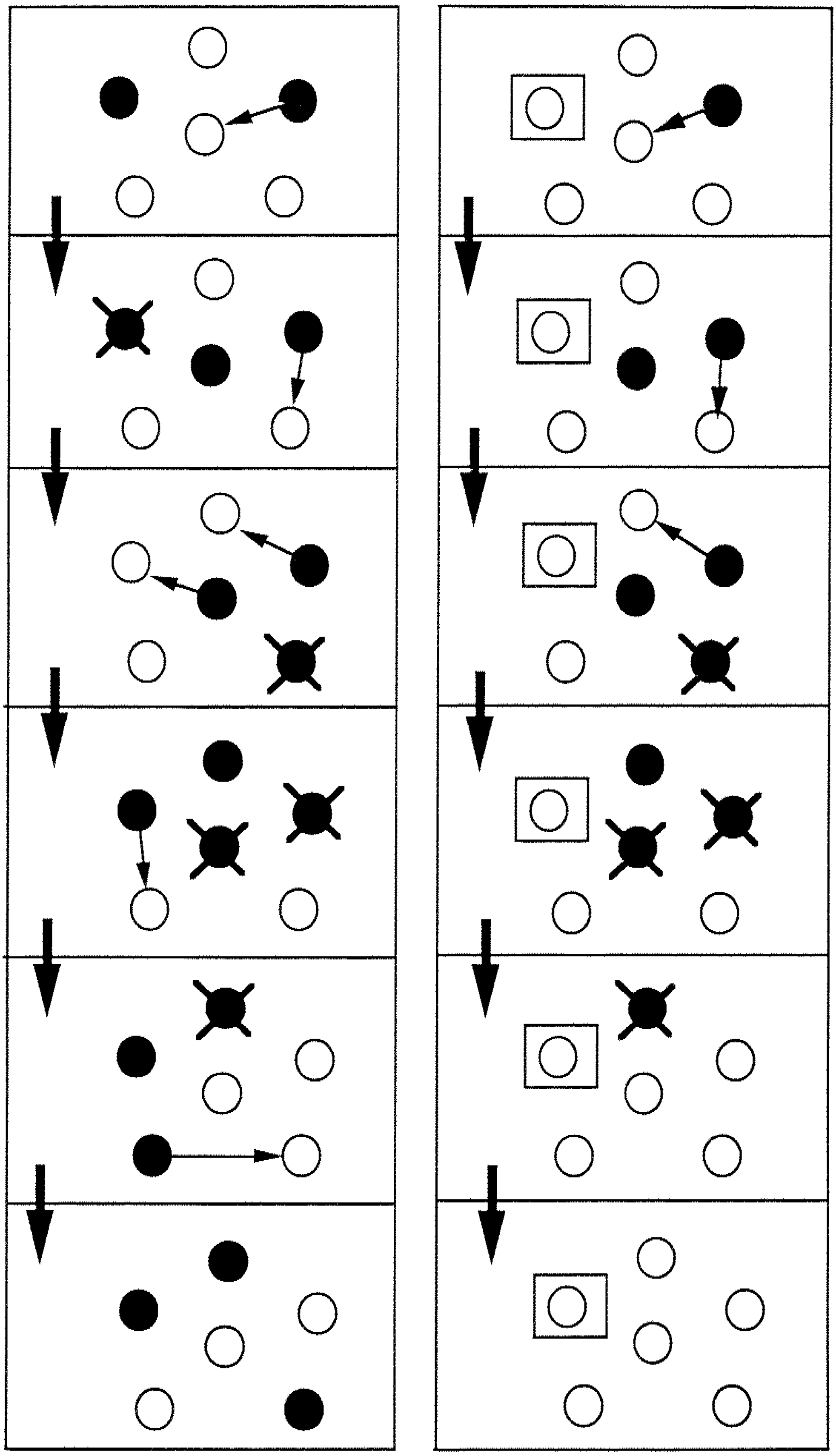

Figure 6. The left-hand column shows a metapopulation at different time intervals. It consists of a range of sites which may be occupied by a population (•) or unoccupied (o). Populations may go extinct (✖) or sites may be colonised (→). The right hand column shows the same events, only with one site (⊡) not suitable as a result of predation.

3. REVIEW OF EMPIRICAL EVIDENCE FOR THE EFFECTS OF PREDATORS ON BIRD POPULATIONS

To document the impact of predators on bird populations, we reviewed systematically the 5-8 most recent volumes of the following journals: *The Auk, Ardea, Condor, Ibis, Oikos, Ornis Scandinavica*, and *Wilson Bulletin*. In addition, we included results obtained from other articles and book chapters that were readily available to us. We focused on three specific effects of predation on birds: (1) the impact on distribution, (2) the impact on breeding success, and (3) the impact on long-term viability. To review the impact of predation on bird breeding success, we recorded only studies where predation rate was expressed in proportion of nests lost to predation. This was by far the most common measure of predation. Other less common measures were the proportion of eggs or chicks lost. When more than one estimate of predation was available per bird species, the estimates were averaged. We also recorded, when possible, the total proportion of nests that failed, from all mortality sources combined. Few studies provided estimates of nesting success that were corrected for the time each nest was exposed to predation (Mayfield, 1975), thus the rates of predation and nest failure reported are probably under-estimates.

3.1 Impact of predators on prey distribution

Predators can potentially affect both the fine-scale and large-scale distribution of their prey. Within a habitat, there is ample evidence that predators influence nest-site selection in birds, with several studies showing increased rates of predation on nests placed in atypical locations (Collias and Collias 1984). The shape and height of nests off the ground may be responses to minimise predation pressure.

The risk of predation may also restrict breeding birds to certain predator-free habitats. Seabirds are a well-known example. It is widely believed that seabirds nest on islands to avoid predators (Burger and Gotchfeld 1994).

Predators can potentially cause local extinction of prey, resulting in a fragmented prey distribution across an otherwise suitable habitat. This has been documented in a few cases. For example, Florida white-crowned pigeons (*Columba leucocephala*), which are particularly susceptible to predation by raccoons (*Procyon lotor*), were found nesting in only 6 of 33 mangrove keys which offered potentially suitable habitat but which had raccoons (Strong et al. 1991). A 40-year study of Canada geese (*Branta canadensis*) in the

Columbia River valley (USA) showed a shift in distribution on islands downstream of the initial centre of distribution, presumably in response to high predation by coyotes (*Canis latrans*) (Fitzner et al. 1994). There are also several cases of bird species, endemic to groups of small neighbouring islands, which have disappeared from those islands where predators have been introduced but persist on predator-free islands (e.g. Lovegrove, in press).

3.2 Impact of predators on prey breeding success

3.2.1 Nest predation

We reviewed 110 studies which reported predation rates on nests for 98 species of birds belonging to 17 orders (Table 1). Seventy -eight species inhabit temperate regions, six were from tropical areas, and 14 from polar regions. For 61 species, both estimates of nest predation and total nest failure were available.

Nest predation is widely regarded as the most important cause of reproductive failure in birds (Ricklefs 1969, Skutch 1985, Martin 1988, Rotenberry and Weins 1989). Our results confirm this view. The overall rate of nest predation was 38.4% (± 27.1 % SD). The overall rate of nest failure, from all causes, was 45.5% (± 26.3% SD), suggesting that predation accounts, on average, for over 80% of all nest failures. These estimates are similar to those found by O'Connor (1991), who reviewed 74 studies published prior to 1980 (not included this review) and found an average nest predation rate of 32.8% ± 22% and a total nest failure rate of 49.9% ± 20 %.

Further analyses allowed us to investigate other patterns of nest predation. For example, it is widely believed that ground-nesting birds are more susceptible to nest predation than birds that nest off the ground (e.g. Ricklefs 1969, Collias and Collias 1984). However, our data suggest otherwise. Each species was assigned to one of five categories of nest types: cavity nests (including boxes), open nests off the ground, closed nests off the ground, nests in burrows or crevices, and ground nests. As expected, cavity nesters had a significantly lower nest predation rate than species with any other nest type (Figure 7), but predation rates were similar among all other nest types.

Table 1. Estimates of nest predation. Predation rate is expressed in percentage of nests depredated. Failure rate is the percentage of nests failing from all causes combined.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
ORDER PSITTACIFORMES								
Bahama parrot *Amazona leucocephala*	Feral cat *Felis* + other mammals	Bahamas	Forest	Crevice	4 years	50	58	Gnam & Rockwell 1991
ORDER PASSERIFORMES								
Jackdaw *Corvus monedula*	Pine marten	C. Sweden	?	Cavity	6 years	33	44	Johnsson 1994
Black-billed magpie *Pica pica*	Unspecified	Denmark	Farmland	Cup in tree	8 years	68.3	?	Møller 1991
Florida scrub jay *Aphelocoma coerulescens*	Snakes, raptors	Florida, USA	Forest	Cup in tree	13 years	33.0	44.0	Schaub et al. 1992
Chaffinch *Fringilla coelebs*	Unspecified	S. Finland	Forest	Cup in tree	2 years	57.2	?	Hanski & Lavrila 1993, Møller 1991
Blackbird *Turdus merula*	Unspecified	Denmark	Farmland	Cup in tree	8 years	56	?	Møller 1991,
Yellowhammer *Emberiza citrinella*	Unspecified	Denmark	Farmland	Cup in tree	8 years	28.9	?	Møller 1991
Swallow *Hirundo rustica*	Unspecified	Denmark	Farmland	Cavity (box)	8 years	0	?	Møller 1991

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Great tit *Parus major*	Unspecified	Denmark	Farmland	Cavity	8 years	1.6	?	Møller 1991
House sparrow *Passer domesticus*	Unspecified	Denmark	Farmland	Cavity	8 years	0	?	Møller 1991
Black-throated sparrow *Amphispiza bilineata*	Loggerhead shrike, corvids, cactus wren, grey thrasher	California USA	Forest	Cup in tree	2 years	66.5	70.5	George 1987
Verdin *Auriparus flaviceps*	Loggerheaad shrike, corvids, cactus wren, grey thrasher	California USA	Forest	Closed cup in tree	2 years	63.5	68	George 1987
(several grassland birds)	Striped skunk	Maine USA	Grassland	Ground	3 years	58	58	Vickery et al. 1992
Thekla lark *Galerida theklae*	Corvids, fox, mustelid, reptiles	Spain	Shrubsteppe	Ground	1 years	51.6	83.2	Suarez & Manrique 1992
Lesser short-toed lark *Calandrella rufescens*	Corvids, fox, mustelid, reptiles	Spain	Shrubsteppe	Ground	2 years	71	80.8	Suarez & Manrique 1992
Black-eared wheatear *Oenanthe hispanica*	Fox, reptiles	Spain	Shrubsteppe	Ground	4 years	50	67.9	Suarez & Manrique 1992
(4 species of tits)	Weasel	England	Forest	Cavity (box)	29 years	21.6	?	Dunn 1977
Corn bunting *Miliaria calandra*	Gull, rat	Scotland	Grassland	Ground	4 years	23.2	44.1	Hartley & Shepherc 1994
Eurasian nuthatch *Sitta europaea asiatica*	Weasel	Siberia, Russia	Forest	Cavity	5 years	5.4	24.3	Pradosudov 1993

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Redbreasted nuthatch *Sitta canadensis*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	27.3	27.3	Li & Martin 1991
Pygmy nuthatch *Sitta pygmaea*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	11.1	11.1	Li & Martin 1991
Cordilleran flycatcher	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	62.5	62.5	Li & Martin 1991
Mountain chickadee *Parus gambeli*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	25.0	25.0	Li & Martin 1991
White-breasted nuthatch *Sitta carolinensis*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	33.3	33.3	Li & Martin 1991
Brown creeper *Certhis americana*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	20.0	20.0	Li & Martin 1991
Western bluebird *Sialia mexicana*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	25.0	25.0	Li & Martin 1991
House wren *Troglodytes aedon*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	18.3	18.3	Li & Martin 1991
House wren *Troglodytes aedon*	Red squirrels, raccoons, weasels, snakes	Wyoming, USA	Forest	Cavity (box)	4 years	19.2	27.3	Finch 1990
Honeyeaters *Phylidonyris* spp.	Brown tree snake, rats, cats, corvids	Australia	Heathland	Cup in bush	2 years	44.6	58.0	Armstrong & Pyke 1991
Red-winged blackbird *Agelaius phoeniceus*	Snakes, raccoon, mustelids	Kansas, USA	Marsh	Cup	2 years	50.5	?	Shipley 1979

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Red-winged blackbird *Agelaius phoeniceus*	Raptors, corvids, snake, raccoon, cat, fox	Connecticut, USA	Marsh	Cup	3 years	32.9	?	Robertson 1972
Red-winged blackbird *Agelaius phoeniceus*	Snake, raccoon, squirrel	Illinois, USA	Marsh	Cup	3 years	57.0	66.7	Strehl & White 1986
Mockingbird *Mimus polyglottus*	Corvids, snakes, oppossum, raccoon, squirrel, cat	Louisiana, USA	Grassland	Cup	2 years	43.5	43.5	Joern & Jackson 1983
Savannah sparrow *Passerculus sandwichensis*	Crow, snake	West Virginia, USA	Grassland	Ground	3 years	36.6	48.8	Wray et al. 1982
Savannah sparrow *Passerculus sandwichensis*	Gulls, grackles, red-winged blackbird	Nova Scotia, Canada	Grassland	Ground	Dune	4.8	18.0	Ross 1980
Savannah sparrow *Passerculus sandwichensis*	Unspecified	Alaska	Grassland	Ground	3 years	0.7	0.7	Miller & Knight 1993
Savannah sparrow *Passerculus sandwichensis*	Gull, crow	New Brunswick, Canada	Grassland	Ground	5 years	50.5	60.3	Dixon 1978
Savannah sparrow *Passerculus sandwichensis*	Corvids, mustelids, cat	Quebec, Canada	Grassland	Ground	2 years	22.4	?	Lapointe & Bedard 1986
White-crowned sparrow *Zonotrichia leucophrys*	Gulls, finches, ground-squirrels	California, USA	Forest	Cup in bush	19 years	30.0	?	Morton et al. 1993
White-crowned sparrow *Zonotrichia leucophrys*	None	Northwest Territories, Canada	Tundra	Cup in bush	3 years	0	?	Norment 1992

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Field sparrow *Spizella pusilla*	Crow, snake	West Virginia, USA	Grassland	Ground	3 years	34.8	34.8	Wray et al. 1982
Field sparrow *Spizella pusilla*	Corvids, snakes, raccoons, mustelids, foxes, squirrels		Grassland	Ground		69.7	?	Nolan 1963
Field sparrow *Spizella pusilla*	Snakes, oppossum, raccoon, cat, fox	Illinois, USA	Grassland	Gound	2 years	76.2	89.8	Best 1978
Dark-eyed junco *Junco hyemalis*	Mustelids, deermice	Utah, USA	Forest	Ground	3 years	32.4	?	Smith & Anderson 1982
Black-throated blue warbler *Dendroica caerulescens*	Blue jay, squirrel	New Hampshire, USA	Forest	Cup in tree	4 years	22.0	28.0	Holmes et al. 1992
Black-throated blue warbler *Dendroica caerulescens*	Unspecified	New Hampshire, USA	Forest	Cup in tree	2 years	41.1	?	Holway 1991
Hermit thrush *Catharus guttatus*	Red squirrels, chipmunk, weasel, wren, jay	Arizona, USA	Forest	Ground	3 years	84.0	84.0	Martin & Roper 1988
Yellow-breasted chat *Icteria virens*	Corvids, snakes, raccoons, mustelids, foxes, squirrels		Grassland	Cup in shrub		89.5	?	Nolan 1963
Cardinal *Cardinalis cardinalis*	Corvids, snakes, raccoons, mustelids, foxes, squirrels		Grassland	Cup in tree		80	?	Nolan 1963
American goldfinch *Carduelis tristis*	Corvids, snakes, raccoons, mustelids, foxes, squirrels		Grassland	Cup in shrub		66.7	?	Nolan 1963

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Indigo bunting *Passerina cyanea*	Corvids, snakes, raccoons, mustelids, foxes, squirrels		Grassland	Cup in shrub		60.0	?	Nolan 1963
Prairie warbler *Dendroica discolor*	Corvids, snakes, raccoons, mustelids, foxes, squirrels		Grassland	Cup in shrub		45.5	?	Nolan 1963
Loggerhead shrike *Lanius ludovicianus*	Cats, snakes, grackles	Oklahoma, USA	Grassland	Cup in tree	4 years	9.2	17.4	Tyler 1992
Seaside sparrow *Ammodramus maritimus*	American crow, grackle	Massachussetts USA	Saltmarsh	Ground	2 years	6.7	61.7	Marshall & Reinert 1990
Grasshopper sparrow *Ammodramus savannarum*	Crow, snake	West Virginia, USA	Grassland	Ground	3 years	56.9	60.8	Wray et al. 1982
Vesper sparrow *Pooecetes gramineus*	Crow, snake	West Virginia, USA	Grassland	Ground	3 years	54.3	68.6	Wray et al. 1982
Tree swallow *Tachycineta bicolor*	Red squirrels, raccoons, weasels, snakes	Wyoming, USA	Forest	Cavity (box)	4 years	27.6	69.0	Finch 1990
Sage sparrow *Amphispiza belli*	Snakes, corvids, weasel	Washington, Oregon, Nevada, USA	Shrub-steppe	Ground	5 years	33.3	?	Rotenberry & Wier 1989
Brewers sparrow *Spizella breweri*	Snakes, corvids, weasel	Washington, Oregon, Nevada, USA	Shrub-steppe	Ground	5 years	14.1	?	Rotenberry & Wier 1989
Sage thrasher *Oreoscoptes montanus*	Snakes, corvids, weasel	Washington, Oregon, Nevada, USA	Shrub-steppe	Ground	5 years	32.0	?	Rotenberry & Wier 1989
Harris sparrow *Zonotrichia querula*	Ground-squirrels, weasel	Northwest Territories, Canada	Tundra	Cup in shrub	3 years	34.4	?	Norment 1992

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
McCown's longspur *Calcarius mccownii*	Ground-squirrel	Colorado, USA	Grassland	Ground	2 years	52.6	?	With 1994
Dusky flycatcher *Empidonax oberholseri*	Chipmunks, ground-squirrels, magpie, raven	Wyoming	Forest	Cup in bush	3 years	53.0	59.4	Kelly 1993
Yellow-throated euphonia *Euphonia hirundicacea*	Unspecified	Costa Rica	Forest	Covered cup	4 years	53.7	61.0	Sargent 1993
ORDER APODIFORMES								
Costa's hummingbird *Calypte costae*	Loggerheaad shrike, corvids, cactus wren, grey thrasher	California USA	Forest	Cup in tree	2 years	62.5	67	George 1987
ORDER CHARADRIIFORMES								
Red-necked phalarope *Phalaropus lobatus*	Unspecified	Manitoba Canada	Tundra	Ground	5 years	35.1	43.7	Reynolds 1987
Wilson's phalarope *Phalaropus tricolor*	Mammalian	Saskatchewan, Canada	Wetland	Ground	2 years	47.0	78.8	Colwell 1992
Common murre *Uria aalgae*	Fox	Northwest Territories, Canada	Island	Ground	1 year	100.0	100.0	Petersen 1982
Pigeon guillemot *Cepphus columba*	Crows, garter snakes	British Columbia, Canada	Island	Burrow	2 years	60.5	?	Emms & Verbeek 1989

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Spotted sandpiper *Actitis macularia*	Turnstones, mink, gull, grackles	Minnesota, USA	Island beach	Ground	16 years	34.3	?	Alberico et al. 1991
Buff-breasted sandpiper *Tryngites subruficollis*	Unspecified	Alaska, USA	Tundra	Ground	2 years	72.0	?	Pruett-Jones 1988
Semi-palmated plover *Charadrius semipalmatus*	Raptors, skuas, gulls, foxes	Manitoba, Canada	Tundra	Ground	2 years	27.9	27.9	Armstrong & Nol 1993
Piping plover *Charadrius melodus*	Unspecified	Virginia, USA	Island beach	Ground	2 years	49.9	?	Patterson et al. 1991
Piping plover *Charadrius melodus*	Unspecified	Massachussetts USA	Beach	Ground	4 years	70.8	?	Rimmer & Deblinger 1990
Snowy plover *Charadrius alexandrinus*	Corvids	Oregon	Beach	Ground	2 years	26.4	?	Wilson-Jacobs & Meslow 1984
Ringed plover *Charadrius hiaticula*	Arctic fox, stoat, skua, gull, raven	Greenland	Tundra	Ground	1 year	62.0	62.0	Pienkowski 1984
Greater golden plover *Pluvialis apricaria*	Red fox, gull, raven	Norway	Tundra	Ground	7 years	52.9	?	Byrkjedal 1987
Long-billed curlew *Numenius americanus*	Badger, coyotes, corvids	Oregon, USA	Grassland	Ground	2 years	12.5	?	Pampush & Anthony 1993
Eurasian dotterel *Charadrius morinellus*	Red fox, gull, raven	Norway	Tundra	Ground	7 years	30.2	?	Byrkjedal 1987
Pied stilt *Himanthopus himanthopus*	Feral mammals	New Zealand	Wetland	Ground	3 years	99.0	?	Pierce 1986

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
Black stilt *Himanthopus novaezelandiae*	Feral mammals	New Zealand	Wetland	Ground	3 years	92.0	?	Pierce 1986
Herring gull *Larus argentatus*	Fox	Michigan, USA	Island	Ground	1 year	45.0	?	Shugart & Scharf 1977
Glaucous-winged gull *Larus glaucescens*	Fox	Northwest Territories, Canada	Island	Ground	1 year	100.0	100.0	Petersen 1982
Long-tailed skua *Stercorarius longicaudus*	Arctic fox	Greenland	Tundra	Ground	3 years	89.0	?	De Korte 1986
ORDER GALLIFORMES								
Ruffed grouse *Bonasa umbellus*	Fox (main)	New York State, USA	Forest	Ground	13 years	34.4	38.6	Darrow 1947
Grey partridge *Perdrix perdrix*	Not specified	Norfolk, UK	Farmland	Ground	1 year	33.3	42.9	Rands 1988
Red-legged partridge *Alectoris rufa*	Not specified	Norfolk, UK	Farmland	Ground	1 year	38.8	64.2	Rands 1988
Black grouse *Tetrao tetrix*	Not specified	Sweden	Forest	Ground	4 years	38.4	38.4	Brittas & Willebrand 1991
ORDER CICONIIFORMES								
Various ibises, herons & egrets	Snakes, mammals	Florida, USA	Marsh	Platform in tree	2 years	1.3	54.7	Frederick & Collopy 1989a, b

Table 1 (continued). Estimates of nest predation

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
ORDER CORACIIFORMES								
Kingfisher *Alcedo atthis*	Fox, mustelids, voles, mice, moles	Germany	Streamside	Burrow	12 years	5.0	41.5	Bunzel & Druke 1989
White-fronted bee-eater *Merops bullockoides*	Snakes, mongoose	Kenya	?	Cavity	8 years	1.2	17.4	Wrege & Emlen 1991
ORDER FALCONIFORMES								
Sparrowhawk *Accipiter nisus*	Unspecified	Scotland	Forests	Platform	14 years	4.0	43.0	Newton 1988
ORDER GRUIFORMES								
Sandhill crane *Grus canadensis pratensis*	Raccoon, fish crow	Florida	Marsh	Ground	2 years	4.5	29.7	Dwyer & Tanner 1992
ORDER PROCELLARIIFORMES								
Tristam's storm-petrel *Oceanodroma tristami*	Laysan finch	Hawaii, USA	Island	Burrow	1 year	59.9	66.7	Marks & Leasure 1992
Shearwaters *Calonectris* sp. & *Puffinus* spp.	Gulls	France	Island	Ground	?	0	0	Fernandez 1982

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
ORDER PICIFORMES								
Northern flicker *Colaptes auratus*	None	Arizona, USA	Forest	Cavity	3 years	0	0	Li & Martin 1991
Red-napped sapsucker *Sphyrapicus nuchalis*	None	Arizona, USA	Forest	Cavity	3 years	0	0	Li & Martin 1991
Williamson's sapsucker *Sphyrapicus thyroideus*	None	Arizona, USA	Forest	Cavity	3 years	0	5.6	Li & Martin 1991
Hairy woodpecker *Picoides villosus*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	12.5	12.5	Li & Martin 1991
Downy woodpecker *Picoides pubescens*	None	Arizona, USA	Forest	Cavity	3 years	0	0	Li & Martin 1991
Acorn woodpecker *Melanerpes formicivorus*	Squirrels, chipmunks	Arizona, USA	Forest	Cavity	3 years	8.3	8.3	Li & Martin 1991
ORDER GAVIIFORMES								
Red-throated diver *Gavia stellata*	Fox, wolf, gull, skuas	Northwest Territories, Canada	Wetland	Ground	2 years	18.6	18.6	Eberl & Picman 1993
ORDER STRIGIFORMES								
Burrowing owl *Athene cunicularia*	Badger, coyote, dog	Oregon, USA	Shrub-steppe	Burrow	2 years	14.4	48.9	Green & Anthony 1989

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
ORDER COLUMBIFORMES								
Rufus turtle dove *Streptopelia orientalis*	Corvids, cats, snakes	Japan	Forest (urban)	Cup in tree	4 years	60.4	?	Wada 1994
ORDER ANSERIFORMES								
Emperor goose *Chen canagicus*	Arctic fox	Alaska, USA	Tundra	Ground	5 years	33.7	?	Petersen 1992
Canada goose *Branta canadensis*	Unspecified	Oregon, USA	Islands	Ground	10 years	8.4	?	Fitzner et al. 1994
Lesser scaup *Aythia affinis*	Skunk, crow	Saskatchewan, Canada	Marsh	Ground	?	24.3	24.3	Hines 1977
Common eider *Somateria mollissima*	Fox	Northwest Territories, Canada	Island	ground	1 year	100.0	100.0	Petersen 1982
ORDER PELECANIFORMES								
Double-crested cormorant *Phalacocorax auritus*	Fish crow	South Carolina USA	Wetland	Ground	1 year	45.0	?	Post & Seals 1991

Table 1 (continued). Estimates of nest predation.

Prey	Predator	Location	Habitat	Nest type	Length of study	Predation rate	Total failure rate	Source
ORDER PODICIPEDIFORMES								
Eared grebe *Podiceps nigricollis*	Coots	Minnesota, USA	Wetland	Ground	3 years	3.0	?	Boe 1993