14

Mechanisms of extinction in birds: phylogeny, ecology and threats

PETER M. BENNETT, IAN P. F. OWENS, DANIEL NUSSEY,
STEPHEN T. GARNETT AND GABRIEL M. CROWLEY

INTRODUCTION

Effective conservation action and biodiversity management requires an understanding of the mechanisms that cause extinction (Caughley 1994). Theoretical treatments have suggested that these mechanisms are complex. They emphasise the interactions among factors such as the intrinsic biology of species, phylogeny, ecological relationships, environmental variation, human influences and chance catastrophes (see, for example, Diamond 1989; Pimm 1991; Lande 1998). Most conservation projects focus on protecting particular species or particular areas. This focus on the specific problems of particular species or areas can be successful in identifying the *idiosyncratic* extinction mechanisms operating at a local scale; however, much can also be learned by using comparative methods to synthesise information across taxa and regions. The major strength of formal comparative methods is that they allow us to test whether there are *general* processes that determine interspecific variation in vulnerability to extinction (Bennett & Owens 1997, 2002).

In this chapter we present a framework for investigating variation in extinction risk that emphasises the interactions between evolutionary history, ecological processes and contemporary threats. We will illustrate this framework by using our work on birds, which are arguably the best-studied vertebrate class and are therefore highly suitable for large-scale comparative analyses (Bennett & Owens 2002). We will discuss how the main extrinsic causes of extinction risk to birds, such as habitat loss and human persecution, have predictable outcomes due to differences between species in intrinsic biological attributes, such as life history and ecology. Some birds are especially vulnerable to human persecution and introduced predators, whereas others are more sensitive to habitat loss. Many birds show remarkable resilience to these threats, with some groups apparently able to circumvent these mechanisms of extinction by their ability to exploit modified habitats. The overall aim of our framework is to explore the relative roles of, and interactions between, extrinsic causes of extinction risk and intrinsic characteristics of individual species.

EXTINCTION IN BIRDS

All species eventually become extinct, yet we know remarkably little about the processes that cause extinction (Lawton 1995; May 1999). What we do know is based on combining the available information from three incomplete sources: real extinctions based on fossil evidence; real extinctions based on historical records; and predicted extinctions based on studies of currently threatened species. Combining information across these sources is challenging, however, because all these sources of data are imperfect sources of information, and each of them is imperfect in a different way (Bennett *et al.* 2001). In fact, there are marked differences in our knowledge of extinction across these time periods. Differences in sampling effort and methodology, and in the survival and distribution of evidence, mean that we have an incomplete and biased record of extinction. This problem is exacerbated by our uneven knowledge of species diversity and extinction rates across taxonomic groups and habitats. For example, we can be reasonably sure that most extant species of bird and mammal have been described and that their current risk of extinction has been assessed. However, this is not the case with marine organisms or the majority of invertebrate taxa (Roberts & Hawkins 1999).

The fossil record of avian extinctions is poor, even though it includes famous examples such as *Archaeopteryx*, and has recently benefited from a spate of new exciting finds (Feduccia 2003). Elsewhere we have examined the likely causes of avian extinction in historical times (Bennett *et al.* 2001). Three main causes of extinction were identified for 79 bird species that have become extinct since AD 1600 (Fig. 14.1). These were habitat loss, human persecution and introduced predators, which appear to have had roughly equal impact in driving these species extinct. When we examine the causes of threat among living bird species, the same three processes are involved, but habitat loss in particular appears to represent the most important threat now. This interpretation must be viewed with caution, however, owing to differences in sampling methodology over these time periods and the large

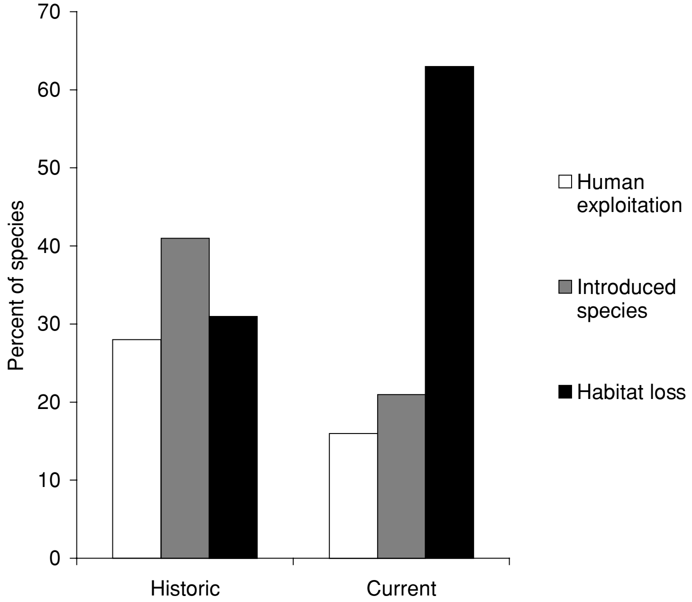

Figure 14.1. Frequency histogram comparing presumed main causes of extinction in historic times ($n = 79$ species in past 400 years) with current threats to living birds ($n = 1111$ species). From Bennett *et al.* (2001).

proportion of island species in the record of historical extinctions (Bibby 1995; Manne *et al.* 1999; Baillie 2001; Bennett *et al.* 2001). Recent evidence suggests that mainland passerine birds are particularly at risk from habitat loss and fragmentation (Manne *et al.* 1999).

Because of the difficulties of interpreting the avian fossil record, in this chapter we will concentrate on examining variation in extinction risk among currently threatened species. The conservation status of all living bird species has been assessed by BirdLife International using quantitative criteria. They estimate that 12% of bird species are threatened with global extinction (BirdLife International 2000). The criteria used to make these assessments include: small population size (affecting 961 species), small range size (856 species) and extent of population decline (425 species). Furthermore, BirdLife International has also estimated the relative importance of the main threats to birds for each species. Habitat loss impacts the most species (1008 species) and is caused by increasing levels of human activity, including agricultural expansion, resource extraction, infrastructure growth and urbanisation. Human exploitation by direct hunting and capture for the pet trade (367 species), and introduced predators and competitors (298 species), are the next most important threats to living birds.

COMPARATIVE APPROACHES TO STUDYING EXTINCTION

There is no shortage of hypotheses that have sought to find general explanations for variation in extinction risk among birds. Characteristics that have been hypothesised to be associated with an increased risk of extinction in birds include large body size (Terborgh 1974; Pimm *et al.* 1988; Gaston & Blackburn 1995), low fecundity (Pimm *et al.* 1988; Garnett 1992, 1993), ecological specialisation (Bibby 1995), high trophic levels (Terborgh 1974; Diamond 1984), colonial nesting (Terborgh 1974), migratory species (Pimm *et al.* 1988), heightened secondary sexual characteristics (McLain *et al.* 1995; Møller 2000, 2003; Bessa-Gomes *et al.* 2003; Morrow & Pitcher 2003), low genetic variability (Frankham 1998), species-poor lineages (Russell *et al.* 1998), increased evolutionary age (Gaston & Blackburn 1997), small population size (MacArthur & Wilson 1967), and species with high population fluctuation (Leigh 1981; Pimm *et al.* 1988; Lande 1993).

We have attempted to test some of these theories by focusing on a number of questions about extinction risk in living birds. These questions include:

- Are threatened species simply a phylogenetically random sample of unlucky birds?
- Are some taxa predisposed to extinction through their intrinsic biological characteristics? If so, how and why?
- Do different intrinsic characteristics predispose species to extinction via different extrinsic threatening processes?
- Have some taxa benefited from anthropogenic changes and, if so, why?

More generally, we have been interested in whether evolutionary and ecological processes help to explain variation in extinction risk among birds (Bennett & Owens 1997, 2002; Owens & Bennett 2000; Bennett *et al.* 2001). Our approach has been to use the comparative method, which uses comparisons across species to test evolutionary and ecological hypotheses about the reasons for diversity among organisms (Harvey & Pagel 1991). It has been used successfully to explain the adaptive reasons for variation in a host of morphological, physiological, behavioural and ecological traits across a wide range of taxonomic groups.

Our first question was to ask whether threatened birds are randomly distributed across taxonomic families (Bennett & Owens 1997). This is important because threatened species may just be unlucky and become threatened owing to chance encounters with threatening processes, such as catastrophes and human persecution. If chance plays the main role in

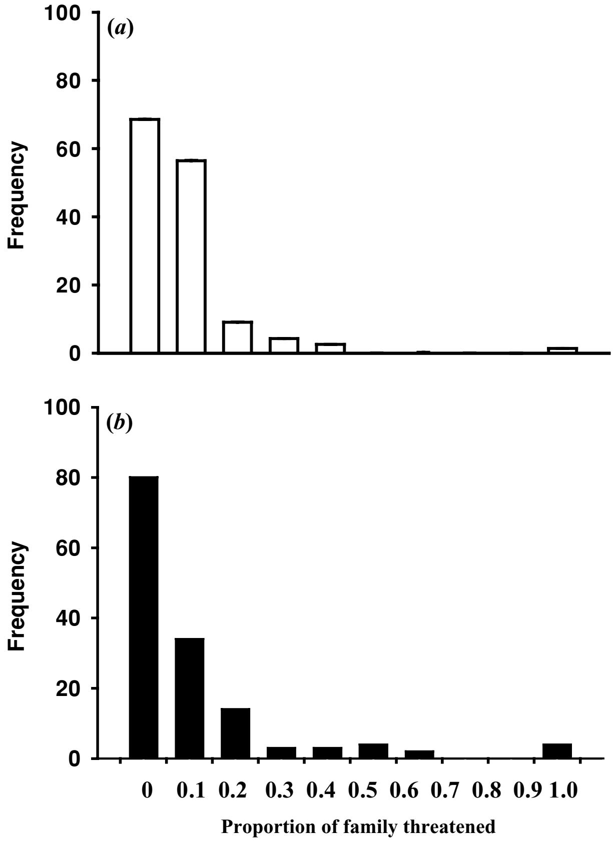

Figure 14.2. Frequency histogram across families of the proportion of species in a family that are classified as being threatened by extinction ($n = 143$ families). (*a*) Predicted frequency distribution based on Monte Carlo simulations. (*b*) Observed frequency distribution. Adapted from Bennett & Owens (1997) and updated with data from BirdLife International (2000).

determining extinction patterns in birds, then there would be little point in seeking biological and ecological explanations for why some species are threatened and others secure. We used a Monte Carlo simulation to predict the random distribution of threatened species across avian families. We then tested whether the random and observed distributions of threatened species across avian families are significantly different (Bennett & Owens 1997). We found that the distributions were significantly different, with some families having significantly more threatened species than expected by chance, whereas other families had significantly fewer threatened species than expected (Fig. 14.2). These analyses have been updated

Table 14.1. Highly threatened and secure avian families

Family	No. of threatened species	% of total species in family
(a) Families with significantly ***more*** *threatened species than expected by chance*		
Parrots	94	26
Albatrosses	55	48
Pheasants	44	25
Rails	33	23
Penguins	10	59
Cranes	9	60
(b) Families with significantly ***fewer*** *threatened species than expected by chance*		
Woodpeckers	11	5
Cuckoos	2	2
Tyrant flycatchers	47	9
Titmice	1	2
Hummingbirds	29	9

here to include the latest list of threatened bird species from BirdLife International (2000). This finding that extinction risk is not randomly distributed with respect to taxonomy has proved to be remarkably consistent across different groups of animals and plants, for both currently threatened species and extinct taxa (see, for example, McKinney 1997; Russell *et al.* 1998; Lockwood *et al.* 2000; Purvis *et al.* 2000a; Schwartz & Simberloff 2001).

We then used the binomial distribution to identify those avian families that had either more or fewer threatened species than would be expected by chance (Table 14.1). The parrot (Psittacidae), albatross (Procellaridae), pheasant (Phasianidae), rail (Rallidae), penguin (Spheniscidae) and crane (Gruidae) families all have significantly more threatened species than expected by chance. In contrast, the woodpecker (Picidae), Old World cuckoo (Cuculidae), tyrant flycatcher (Tyrannidae), titmouse (Paridae) and hummingbird (Trochilidae) families all have significantly fewer threatened species than expected by chance. Again, these results have proved to be consistent when different statistical methods have been used to identify threatened avian lineages (Russell *et al.* 1998; Lockwood *et al.* 2000) and when the list of threatened species was updated with information from BirdLife International (2000) here. It is this variation in extinction risk across taxa that we aim to explore in the next sections of this chapter.

A number of studies have now used comparisons across species to identify morphological, behavioural, ecological and environmental factors that correlate with increasing vulnerability to extinction in different vertebrate groups (see, for example, Bennett & Owens 1997, 2002; McKinney 1997; Russell *et al.* 1998; Owens & Bennett 2000; Purvis *et al.* 2000b; Cardillo & Bromham 2001; Duncan & Lockwood 2001; Dulvy & Reynolds 2002, 2003; Johnson 2002; Johnson *et al.* 2002; Harcourt *et al.* 2002; Reynolds *et al.* 2002; Fisher *et al.* 2003; Jones *et al.* 2003). However, it is important to recognise that the comparative method is not the only approach to investigating extinction mechanisms (see, for example, Saccheri *et al.* 1998; Davies *et al.* 2000; Nieminen *et al.* 2001).

EVOLUTIONARY PREDISPOSITION TO EXTINCTION

Birds vary considerably in life-history characters (Lack 1968). We investigated the history of avian diversification and found that the greatest variation in many key life-history traits, including adult body size and annual fecundity, evolved more than 40 million years ago (Owens & Bennett 1995; Bennett & Owens 2002). Furthermore, these traits co-vary among these ancient lineages in a manner that is consistent with the predictions of classic models of life history evolution (see, for example, Cole 1954). For example, families that experience heavy mortality of young and adults also have fast growth rates, low survival and high annual fecundity. Among birds, these ‘fast’ life histories are typical of species that nest in locations subject to high nest losses, such as ground or cup nests. In contrast, families that nest in more safe locations, such as tree holes, tend to have ‘slow’ life histories characterised by higher survival, slow development and low annual fecundity (Bennett & Owens 2002). Overall, in many natural populations of birds, mortality and fecundity tend to balance such that stable populations persist (Bennett & Harvey 1988).

The fossil evidence, molecular extrapolations and our phylogenetic studies all suggest that the ancestors of most of the modern orders of bird had evolved by the Eocene (Sibley & Ahlquist 1990; Feduccia 1995, 2003; Bennett & Owens 2002). During this ancient period of diversifying evolution, avian families radiated into a range of different niches; we have identified nest type as the key ecological factor that promoted divergent life-history patterns. We asked whether these findings predispose some families to heightened extinction risk. Do living birds inherit traits from their ancient ancestors that make them vulnerable to extinction?

In order to investigate whether ancient evolutionary changes in life-history variation have influenced vulnerability to extinction in living birds, we collated a database of life-history traits, including adult body mass and measures of fecundity, such as clutch size and number of clutches laid per year. We multiplied the latter two variables together to obtain an index of annual fecundity. Using a phylogenetic comparative method, we then examined whether variation in extinction risk was correlated with variation in adult body size and annual fecundity (Bennett & Owens 1997, 2002). We found that both body size and annual fecundity are independently associated with variation in extinction risk among birds but in opposite directions. Larger body size and low fecundity are associated with heightened extinction risk (Fig. 14.3). We illustrate these findings here using an analysis of more than 2,000 species, but elsewhere we have used phylogenetic comparative methods to demonstrate that these patterns also exist using independent contrasts (Bennett & Owens 1997).

We know that large body size and low fecundity evolved deep in the evolutionary history of birds. Living birds possessing these traits are predisposed to extinction through their ancient evolutionary heritage. This heritage imposes limitations on their ability to respond to anthropogenic change. To illustrate how divergent life-history patterns in birds influence extinction risk, consider the life histories of the Californian quail (*Lophortyx californica*) and the wandering albatross (*Diomedea exulans*). The quail breeds within its first year of life and produces over 20 eggs per year, but only one third of adult birds survive each year. The albatross, in contrast, waits over ten years before it breeds for the first time, then produces a single chick every two years; over 98% of adult birds survive each year (data collated in Owens & Bennett 1995). The quail is hunted for sport by humans and is a typical gamebird, being able to respond to heavy unnatural mortality owing to its naturally high fecundity. The albatross, however, is not capable of sustaining artificially increased rates of mortality. A ‘slow’ life history and extremely low fecundity hamper its ability to respond to population crashes; many albatross species are currently threatened by commercial fisheries, with long-lining causing artificially high seabird mortality (see, for example, Barnes *et al.* 1997). Unfortunately, albatrosses and their allies are predisposed to anthropogenic extinction by their extreme life history.

When heavy artificial mortality disrupts the natural fecundity–mortality balance that evolved millions of years ago, then populations of slowly reproducing species can rapidly decline or be driven to extinction. Remnant small populations of slowly reproducing species are especially vulnerable to extinction from catastrophes such as hurricanes (Pimm *et al.* 1988).

Another example of how life histories affect extinction risk is provided by the blue macaws. There are four species of blue macaw, all of which have

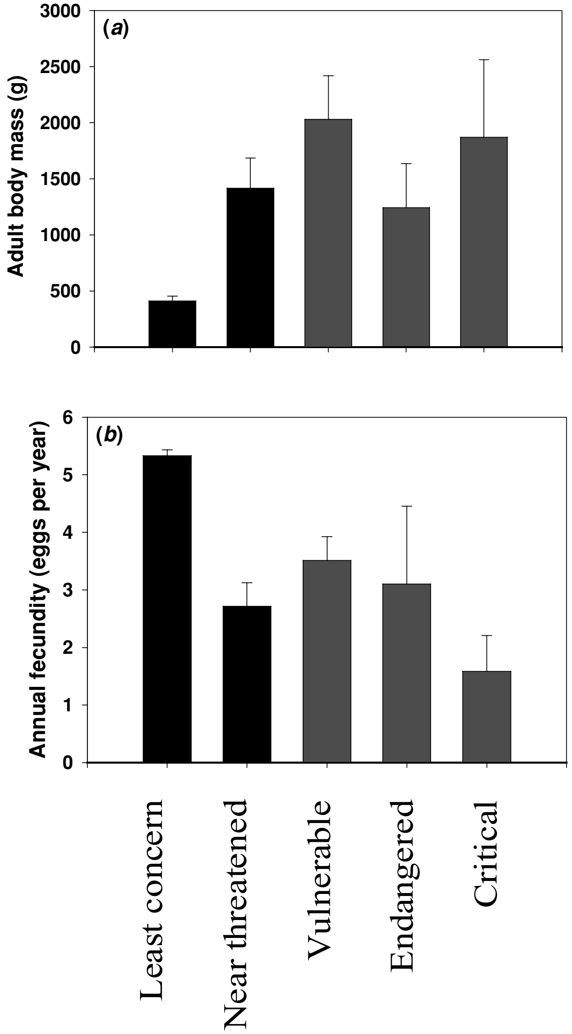

Figure 14.3. Frequency histogram of the mean adult body mass (*a*) and mean annual fecundity (*b*) for species with different levels of extinction risk. Data are from over 2000 species (Bennett & Owens 2002).

slow life histories and are either recently extinct in the wild or threatened with extinction (BirdLife International 2000). Spix's macaw (*Cyanopsitta spixii*) is believed to be extinct in the wild; the last wild bird disappeared in 2001 (Juniper 2002). There are around 60 surviving captive birds, mostly in the hands of collectors. The glaucous macaw (*Anodorhynchus glaucus*) is critically endangered and possibly extinct. The Lear's macaw (*Anodorhynchus* *leari*) is critically endangered, with a few hundred birds surviving. The hyacinth macaw (*Anodorhynchus hyacinthus*) is listed as endangered, with possibly up to 10 000 birds remaining in the wild. The macaws are vanishing because of capture for pets and habitat loss (BirdLife International 2000). The pet trade is a source of heavy anthropogenic mortality, resulting in the loss of adults and chicks, which cannot be sustained by the naturally low fecundity of many parrot species (Beissinger 2000, 2001). Unfortunately, the blue macaws are among the largest parrots with the slowest life histories, and are unable to respond to the illegal harvest of birds stimulated by collectors. The glorious blue macaws, among the most magnificent bird species ever to have lived, are doomed unless the threats to their survival, including capture for the pet trade, are removed.

Other forms of evolutionary predisposition to extinction have been identified in birds. The most famous examples are of the dodo and other flightless island birds that were driven to rapid extinction by humans and introduced predators (Bibby 1995). Again, their evolutionary history resulted in extreme morphological and behavioural specialisation that hampered their ability to respond to anthropogenic changes.

INTERACTIONS BETWEEN EXTRINSIC THREATS AND INTRINSIC BIOLOGY

In the previous section we discussed how two traits, body size and annual fecundity, are associated with vulnerability to extinction in birds. Although these traits have also been shown to correlate with extinction risk in a similar manner in some other animal groups, we found that they did not explain a large proportion of the variation in extinction risk in birds (Bennett & Owens 1997). We wondered whether this was because different taxa are threatened by different ecological mechanisms (Diamond 1984; Pimm 1991). We will now discuss whether this is the case by considering how phylogenetic history, ecological mechanisms and anthropogenic threats can interact and result in multiple routes to extinction among birds.

Models of extinction have predicted that different taxa are vulnerable to different threats and that different ecological factors predispose taxa to different extinction mechanisms. Human persecution and introduced predators should impact slowly reproducing taxa, because these sources of extinction risk disrupt the natural balance between fecundity and mortality in stable populations (Brown 1971; Diamond 1984; Pimm *et al.* 1988). Habitat loss, in contrast, should affect ecologically specialised species, because it leads to reduced niche availability (Brown 1971; Diamond 1984;

Bibby 1995). We tested these ideas by using a database of species from 95 avian families (Owens & Bennett 2000).

Our analyses supported the contention that different families are threatened by different mechanisms of extinction. Habitat loss affected 70% of species in our sample, whereas 35% of species were affected by human persecution or introduced predators. Although these threats were the most important in our database, we found that one of these threats, rather than both, was the primary source of extinction in many species. Twice as many species (54%) were threatened by one source of extinction, habitat loss alone or human persecution/introduced predators alone, than were threatened by both threats together. These results suggested that different ecological factors may predispose taxa to different extinction mechanisms.

To investigate whether different threats are associated with different ecological factors, we performed separate tests of whether body size, residual generation time and degree of breeding habitat specialisation are associated with habitat loss or human persecution/introduced predators, respectively (Fig. 14.4). For body size, we found that large-bodied taxa are more vulnerable to human persecution or introduced predators than are small-bodied taxa (Fig. 14.4*b*), but in contrast small-bodied taxa are more vulnerable to habitat loss than are large-bodied taxa (Fig. 14.4*a*). For residual generation time, we found that taxa with long generation times (after correcting for the scaling effects of body size) were threatened by human persecution or introduced predators (Fig. 14.4*d*) but not by habitat loss (Fig. 14.4*c*). For degree of breeding habitat specialisation, we found that more specialised species that typically utilise only one type of breeding habitat were threatened by habitat loss (Fig. 14.4*e*) but not by human persecution or introduced predators (Fig. 14.4*f*).

These contrasting patterns of association between ecological factors and sources of extinction threat provide support for the contention that there are multiple routes to extinction among birds (Bennett & Owens 1997, 2002; Owens & Bennett 2000). One route is for slowly reproducing large-bodied species to become threatened when an external threat, such as human persecution or introduced predators, leads to unusual mortality and disrupts the fecundity–mortality balance. We have already discussed this route to extinction above, with the albatrosses and blue macaws as examples. Other taxa affected include the kiwis (Apterygidae), cassowaries (Casuariidae) and penguins (Spheniscidae). Another route is for ecologically specialised species to become threatened by habitat loss. Taxa affected include the logrunners (Orthonychidae), trogons (Trogonidae) and scrub-birds (Menuridae). We will explore the importance of ecological specialisation

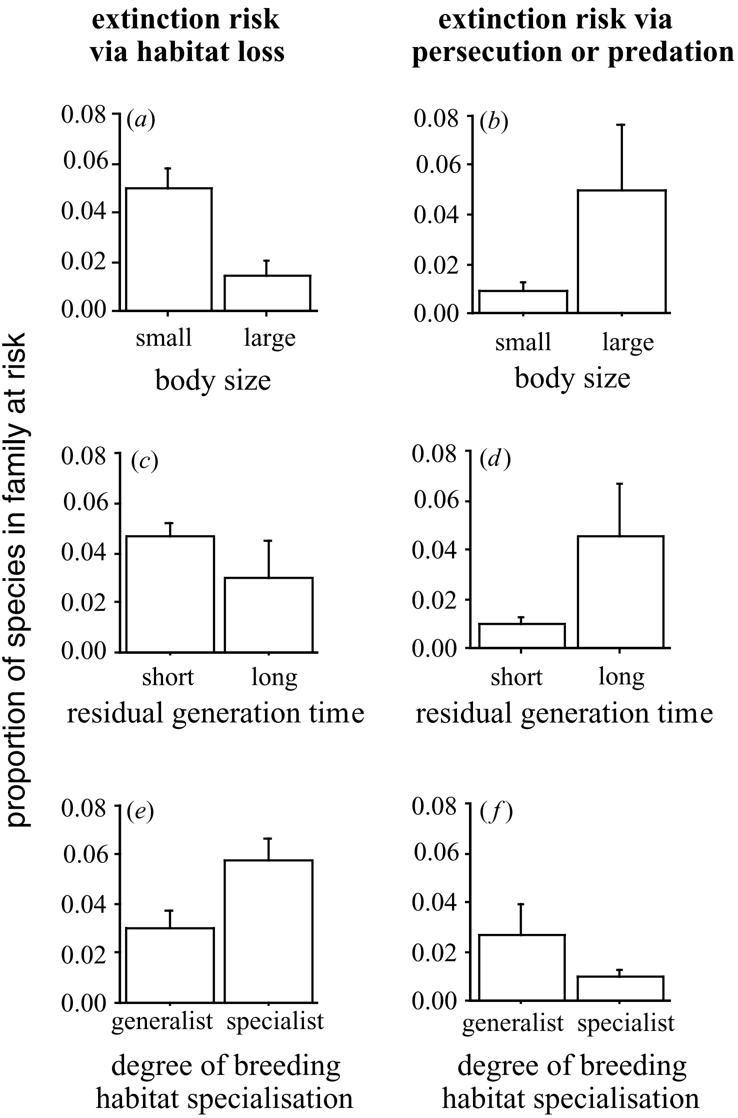

Figure 14.4. Associations between ecology and extinction risk across avian families, with separate analyses for extinction risk via habitat loss versus extinction risk via human persecution or introduced predators. On the vertical axis of each graph, the proportion of each family threatened by extinction risk is the proportion of species in that family classified as being threatened by extinction via the appropriate source of threat. All analyses are based on raw family-typical values for 95 avian families. Error bars show standard errors. Statistics show results of one-way ANOVAs: (*a*) $F = 8.61$, $p = 0.004$; (*b*) $F = 5.36$, $p = 0.02$; (*c*) $F = 1.06$, $p = 0.31$; (*d*) $F = 4.13$, $p = 0.04$; (*e*) $F = 5.87$, $p = 0.01$; (*f*) $F = 1.05$, $p = 0.31$. Degrees of freedom in all ANOVAs = 1, 93. From Owens & Bennett (2000), where more details can be found.

further in the next section of this chapter. Unfortunately, some avian families are predisposed to both of these routes to extinction, and it is no surprise that these are the same families that statistical analyses reveal to contain unusually large numbers of threatened species. They include the parrots (Psittacidae), pheasants (Phasianidae), rails (Rallidae), pigeons (Columbidae) and cranes (Gruidae).

The fact that taxa respond to threats in different ways because of differences in their evolutionary history, intrinsic biology and ecology has also being demonstrated in recent studies of mammals. The ecological factors that predispose primates to extinction risk (Purvis *et al.* 2000b) are different from those found in bats (Jones *et al.* 2003). In Australian marsupials one extrinsic factor, geographic range overlap with sheep, explains most variation in extinction risk (Fisher *et al.* 2003). Blackburn & Gaston (2002) and Reynolds (2003) also discuss the importance of examining different threats and how they interact with life-history traits to influence population vulnerability and extinction risk.

In this section we have discussed the evidence in support of the hypothesis that interactions between phylogenetic history, contemporary ecological factors and anthropogenic threats help to explain variation in extinction risk among birds. Multiple mechanisms underlie patterns of extinction risk; we have identified some of the general ecological mechanisms that are apparent from broad-scale analyses across avian families and regions. More refined tests are now needed to investigate these questions in greater detail within regions.

ECOLOGICAL FLEXIBILITY IN AUSTRALIAN BIRDS

Our analyses across avian families demonstrated that ecologically specialised taxa are prone to extinction from habitat loss. Habitat loss is the single most important threat to the survival of birds (BirdLife International 2000). Here we examine the impact of habitat loss further by asking two questions. First, does the ability to respond to rapid habitat modification help to explain extinction risk in Australasian parrots? Second, does feeding habitat specialisation influence extinction risk in Australian birds in general?

Australian birds have been subject to rapid changes in habitat, especially the conversion of land for grazing and crops, since the arrival of Europeans in the eighteenth century (Garnett & Crowley 2000). Moreover, although some bird species have suffered as a result of these anthropogenic changes, others have expanded their ranges. Recent work has suggested

Table 14.2. Correlates of extinction-risk in Australian parrots

Number of taxa included (n) = 50+ *species, 100 sub-species.*

Variables	Threatened	Non-threatened	Probability
Auto-correlated			
Geographic range size	Smaller	Greater	$p < 0.001$
Range/abundance trend	Decreasing	Stable, increasing	$p < 0.001$
Size			
Female body mass	Greater	Smaller	$p < 0.05$
Reproductive flexibility			
Clutch size range	Smaller	Greater	$p < 0.01$
Multiple broods per year	Rare, absent	Common	$p < 0.05$
Ecological flexibility			
No. of feeding habitats	Fewer	Greater	$p < 0.01$
Use of modified habitats for feeding	Rare, absent	Common	$p < 0.01$
Use of modified habitats for nesting	Rare, absent	Common	$p < 0.05$

Source: D. Nussey *et al.* (in preparation).

that behavioural flexibility may be an important factor in influencing invasion success in birds (Sol *et al.* 2002); however, these authors found no evidence that it is associated with extinction risk (Nicolakakis *et al.* 2003). Reed (1999) has also discussed the influence of behaviour on extinction in birds.

We asked whether flexibility in life history, ecology or behaviour might influence the ability of species to deal with these anthropogenic changes (D. Nussey *et al.*, in preparation). Parrots were chosen for study because they exhibit variation in many of the variables in which we were interested (Garnett *et al.* 1992; Garnett & Crowley 2000). There are over 50 species of Australian parrot and they vary greatly in extinction risk (some species are critically endangered whereas others are so abundant they are regarded as pests), clutch size (varies from 1 to 6 eggs), number of feeding habitats (varies from 1 to 9 habitats) and a range of other variables. Some parrot species also use anthropogenically modified habitats for feeding (e.g. crops, orchards, gardens, alien palms/pines/weeds), nesting (e.g. fence posts, houses, alien trees) and/or roosting (e.g. telegraph wires, gardens, alien trees).

The results of our statistical analyses of the correlates of extinction risk in Australian parrots are summarised in Table 14.2 (D. Nussey *et al.*, in preparation). As in our previous studies of extinction risk across avian families (Bennett & Owens 1997, 2002; Owens & Bennett 2000), we found that threatened parrots were larger than non-threatened parrots. We also found that our indices of reproductive and ecological flexibility were correlated with variation in extinction risk. Clutch size range was greater and multiple brooding was common in non-threatened parrots, whereas threatened parrots had a narrow clutch size range and rarely or never raised multiple broods in a year. Reproductive flexibility is likely to be advantageous in arid-zone parrots that rely on unpredictable rainfall to promote the right environmental conditions for successful breeding. Our indices of ecological flexibility were also correlated with variation in extinction risk in these parrots. Non-threatened parrots utilised a greater number of feeding habitats than did threatened species. Furthermore, non-threatened species commonly used anthropogenically modified habitats for feeding, nesting and/or roosting. Among threatened parrot species the use of these artificial habitats was either rare or absent (D. Nussey *et al.*, in preparation).

These results provide some useful insights into the impact of threats, especially habitat loss, on extinction risk in a specific avian family and region, the Australian parrots. First, they are consistent with the results of our wider analyses of extinction risk across families and regions discussed above. Second, they suggest that reproductive and ecological flexibility are important characteristics for species survival in the face of rapid habitat modification. Specialisation, through either life history or ecology, hampers the ability of species to deal with anthropogenic threats. Species that are able to utilise a variety of feeding habitats, and/or the artificial characteristics of agricultural or urban landscapes, may actually benefit from anthropogenic changes (D. Nussey *et al.*, in preparation).

We performed a second analysis of Australian birds to establish whether these results were peculiar to parrots or whether they could be generalised across all Australian species. To do this we analysed a database updated from Garnett *et al.* (1992) which listed the number of feeding habitats utilised by all species recorded on the Australian mainland (828 species). There were eleven possible feeding habitats: grassland, heath, spinifex, acacia scrub, chenopod scrub, mallee, tropical woodland/forest, temperate forest, rainforest, mangrove, and cultivated land (Garnett *et al.* 1992). We found that the number of feeding habitats utilised by species is closely associated with extinction risk in Australian birds (Fig. 14.5). Vulnerable, endangered, critically endangered and extinct species (data from Garnett & Crowley 2000) used fewer than two feeding habitats on average. In contrast, successful species (defined here as species that are not currently threatened) and introduced species, used two or more feeding habitats on average. These results are consistent with the hypothesis that ecological

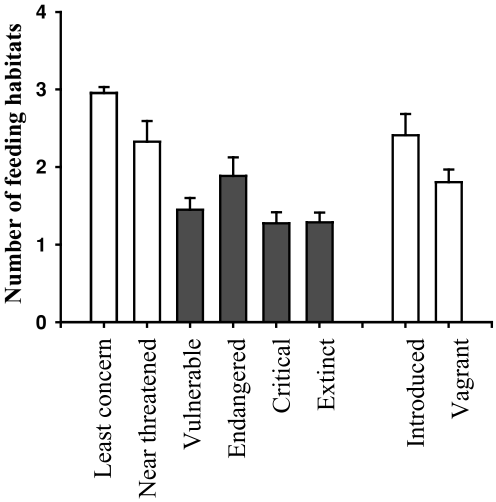

Figure 14.5. Frequency histogram of the number of feeding habitats used by all recorded Australian mainland bird species according to level of extinction risk. The histogram also includes introduced and vagrant species. Error bars show standard errors. From D. Nussey *et al.* (in preparation).

specialisation is associated with elevated threat levels and extinction across all Australian birds (D. Nussey *et al.*, in preparation).

One finding that remains to be discussed is the relation we found between small body size and habitat loss across avian families (Owens & Bennett 2000). Why should small-bodied birds be vulnerable to habitat loss? It is possible that ecological specialisation may also explain this finding. Some evidence is now emerging that small-bodied birds are more specialised than large-bodied forms. Sekercioglu *et al.* (2002) investigated the response of insectivorous forest birds to habitat fragmentation in Costa Rica. They found that small-bodied species are less able to disperse through deforested areas than are large-bodied species. More work is required to establish the importance of dispersal ability and the other characteristics of small-bodied species that render them prone to extinction from habitat loss.

CONCLUSIONS

We have argued that an evolutionary approach is necessary to understand variation in extinction risk among living birds. Ancient evolutionary history predisposes some taxa to extinction, especially those with large body sizes, low fecundity and long generation times. We identified interactions between threats and ecological mechanisms that were predicted by theory. Species with slow life histories are vulnerable to human persecution and introduced predators. Habitat specialists and inflexible species are vulnerable to habitat loss and modification. Future work will consider how ecological specialisation can result in population declines. For example, are some species vulnerable because they exploit restricted resources at one point in their life cycle (e.g. the breeding season), but otherwise are ecological generalists? In addition, can we use the results of comparative studies of extinction risk to help in the formulation of recovery plans where there is little species-specific information available or when there are two or more putative threats?

REFERENCES

Baillie, J. E. M. 2001 *Persistence and vulnerability of island endemic birds.* Ph.D. thesis, University of London.

Barnes, K. N., Ryan, P. G. & BoixHinzen, C. 1997 The impact of the hake *Merluccius* spp. longline fishery off South Africa on Procellariiform seabirds. *Biological Conservation* **82**, 227–34.

Bennett, P. M. & Harvey, P. H. 1988 How mortality balances fecundity in birds. *Nature* **333**, 216.

Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. Lond.* B**264**, 401–8.

2002 *Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction.* Oxford: Oxford University Press.

Bennett, P. M., Owens, I. P. F. & Baillie, J. E. M. 2001 The history and ecological basis of extinction and speciation in birds. In *Biological Homogenization: the Loss of Diversity through Invasion and Extinction* (ed. J. L. Lockwood & M. L. McKinney), pp. 201–22. Dordrecht: Kluwer Academic/Plenum Press.

Beissinger, S. R. 2000 Ecological mechanisms of extinction. *Proceedings of the National Academy of Sciences, USA* **97**, 11688–9.

2001 Trade of live wild birds: potentials, principles and practices of sustainable use. In *Conservation of Exploited Species* (ed. J. D. Reynolds, G. M. Mace, K. H. Redford & J. G. Robinson), pp. 182–202. Cambridge: Cambridge University Press.

Bessa-Gomes, C., Daek-Gontard, M., Cassey, P., Møller, A. P., Legendre, S. & Clobert, J. 2003 Mating behaviour influences extinction risk: insights from demographic modelling and comparative analyses of extinction risk. *Annales Zoologici Fennici* **40**, 231–45.

Bibby, C. J. 1995 Recent, past and future extinctions in birds. In *Extinction rates* (ed. J. H. Lawton & R. M. May), pp. 98–110. Oxford: Oxford University Press.

BirdLife International 2000 *Threatened Birds of the World.* Barcelona: Lynx Edicions.

Blackburn, T. M. & Gaston, K. J. 2002 Extrinsic factors and the population sizes of threatened birds. *Ecology Letters* **5**, 568–576.

Brown, J. H. 1971 Mammals on mountaintops: nonequilibrium insular biogeography. *American Naturalist* **105**, 467–78.

Cardillo, M. & Bromham, L. 2001 Body size and risk of extinction in Australian mammals. *Conservation Biology* **15**, 1435–40.

Caughley, G. 1994 Directions in conservation biology. *Journal of Animal Ecology* **63**, 215–44.

Cole, L. C. 1954 The population consequences of life history phenomena. *Quarterly Review of Biology* **29**, 103–37.

Davies, K. F., Margules, C. R. & Lawrence, K. F. 2000 Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**, 1450–61.

Diamond, J. M. 1984 'Normal' extinctions of isolated populations. In *Extinctions* (ed. M. U. Nitecki), pp. 191–246. Chicago: University of Chicago Press.

1989 Overview of recent extinctions. In *Conservation for the Twenty-first Century* (ed. D. Western & M. Pearl), pp. 824–62. Tucson, AZ: University of Arizona Press.

Dulvy, N. K. & Reynolds, J. D. 2002 Predicting extinction vulnerability in skates. *Conservation Biology* **16**, 440–50.

Duncan, J. R. & Lockwood, J. L. 2001 Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological Conservation* **102**, 97–105.

Feduccia, A. 1995 Explosive evolution in tertiary birds and mammals. *Science* **267**, 637–8.

2003 'Big bang' for Tertiary birds? *Trends in Ecology and Evolution* **18**, 172–6.

Fisher, D. O., Blomberg, S. P. & Owens, I. P. F. 2003 Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proceedings of the Royal Society of London* B**270**, 1801–8.

Frankham, R. 1998 Inbreeding and extinction: island populations. *Conservation Biology* **12**, 665–75.

Garnett, S. T. 1992 *An Action Plan for Australian Birds*. Canberra: Australian Parks and Wildlife.

1993 *Threatened and extinct birds of Australia*, 2nd edn. Melbourne: Royal Australian Ornithological Union (RAOU).

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

Garnett, S. T., Crowley, G. M., Fitzherbert, K. & Bennett, S. 1992 *Life History Characteristics of Australian Birds*. Melbourne and Canberra: Royal Australian Ornithologists Union & Australian National Parks and Wildlife Service.

Gaston, K. J. & Blackburn, T. M. 1995. Birds, body-size and the threat of extinction. *Philosophical Transactions of the Royal Society of London* B**347**, 205–12.

1997 Evolutionary age and risk of extinction in the global avifauna. *Evolutionary Ecology* **11**, 557–65.

Harcourt, A. H., Coppeto, S. A. & Parks, S. A. 2002 Rarity, specialization and extinction in primates. *Journal of Biogeography* **29**, 445–56.

Harvey, P. H. & Pagel, M. D. 1991 *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Johnson, C. N. 2002 Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proceedings of the Royal Society of London* B**269**, 2221–7.

Johnson, C. N., Delean, S. & Balmford, A. 2002 Phylogeny and the selectivity of extinction in Australian marsupials. *Animal Conservation* **5**, 135–2.

Jones, K. E., Purvis, A. & Gittleman, J. L. 2003 Biological correlates of extinction risk in bats. *American Naturalist* **161**, 601–14.

Juniper, T. 2002 *Spix's Macaw: The Race to Save the World's Rarest Birds*. London: Fourth Estate.

Lack, D. 1968 *Ecological Adaptations for Breeding in Birds*. London: Chapman and Hall.

Lande, R. 1993 Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**, 911–27.

1998 Anthropogenic, ecological and genetic factors in extinction and conservation. *Researches in Population Ecology* **40**, 259–69.

Lawton, J. H. 1995 Population dynamic principles. In *Extinction Rates* (ed. J. H. Lawton & R. M. May), pp. 147–63. Oxford: Oxford University Press.

Leigh, E. G. 1981 The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* **90**, 213–39.

Lockwood, J. L., Brooks, T. M. & McKinney, M. L. 2000 Taxonomic homogenization of the global avifauna. *Animal Conservation* **3**, 27–35.

MacArthur, R. H. & Wilson, E. O. 1967 *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Manne, L. L., Brooks, T. M. & Pimm, S. L. 1999 Relative risk of extinction of passerine birds on continents and islands. *Nature* **399**, 258–61.

May, R. M. 1999 Unanswered questions in ecology. *Philosophical Transactions of the Royal Society of London* B**354**, 1951–9.

McKinney, M. L. 1997 Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annual Review of Ecology and Systematics* **28**, 495–516.

McLain, D. K., Moulton, M. P. & Redfearn, T. P. 1995 Sexual selection and the risk of extinction of introduced birds on oceanic islands. *Oikos* **74**, 27–34.

Møller, A. P. 2000 Sexual selection and conservation. In *Behavior and Conservation* (ed. L. M. Gosling & W. J. Sutherland), pp. 161–71. Cambridge: Cambridge University Press.

2003 Sexual selection and extinction: why sex matters and why asexual models are insufficient. *Annales Zoologici Fennici* **40**, 221–30.

Morrow, E. H. & Pitcher, T. E. 2003 Sexual selection and the risk of extinction in birds. *Proceedings of the Royal Society of London* B**270**, 1793–9.

Nicolakakis, N., Sol, D. & Lefebvre, L. 2003 Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour* **65**, 445–52.

Nieminen, M., Singer, M. C., Fortelius, W., Schops, K. & Hanski, I. 2001 Experimental confirmation that inbreeding depression increases extinction risk in butterfly populations. *American Naturalist* **157**, 237–44.

Owens, I. P. F. & Bennett, P. M. 1995 Ancient ecological diversification explains life history variation among living birds. *Proceedings of the Royal Society of London* B**261**, 227–32.

Owens, I. P. F. & Bennett, P. M. 2000 Ecological basis of extinction risk in birds: Habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences, USA* **97**, 12144–8.

Pimm, S. L. 1991 *The Balance of Nature*. Chicago: The University of Chicago Press.

Pimm, S. L., Jones, H. L. & Diamond, J. 1988 On the risk of extinction. *American Naturalist* **132**, 757–85.

Purvis, A., Agapow, P. M., Gittleman, J. L. & Mace, G. M. 2000a Nonrandom extinction and the loss of evolutionary history. *Science* **288**, 328–30.

Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000b Predicting extinction risk in declining species. *Proceedings of the Royal Society of London* B**267**, 1947–52.

Reed, J. M. 1999 The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* **13**, 232–41.

Reynolds, J. D. 2003 Life histories and extinction risk. In *Macroecology: Concepts and Consequences* (ed. T. M. Blackburn & K. J. Gaston). Oxford: Blackwell.

Reynolds, J. D., Dulvy, N. K. & Roberts, C. M. 2002 Exploitation and other threats to fish conservation. In *Handbook of Fish Biology and Fisheries,* Volume 2, *Fisheries* (ed. P. J. B. Hart & J. D. Sutherland), pp. 319–41. Oxford: Blackwell.

Roberts, C. M. & Hawkins, J. P. 1999 Extinction risk in the sea. *Trends in Ecology and Evolution* **14**, 241–6.

Russell, G. J., Brooks, T. M., McKinney, M. L. & Anderson, C. G. 1998 Change in taxonomic selectivity in the future extinction crisis. *Conservation Biology* **12**, 1365–76.

Saccheri, I., Kuussaari, M., Kankare, M. *et al.* 1998 Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**, 491–4.

Schwartz, M. W. & Simberloff, D. 2001 Taxon size predicts rates of rarity in vascular plants. *Ecology Letters* **4**, 464–9.

Sekercioglu, C. H., Ehrlich, P. R., Daily, G. C. *et al.* 2002 Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences, USA* **99**, 263–7.

Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. New Haven, CT: Yale University Press.

Sol, D., Timmermans, S. & Lefebvre, L. 2002 Behavioural flexibility and invasion success in birds. *Animal Behaviour* **63**, 495–502. (Erratum: **64**, 516.)

Terborgh, J. 1974 Preservation of natural diversity: the problem of extinction prone species. *BioScience* **24**, 715–22.

CAMBRIDGE UNIVERSITY PRESS
Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo

Cambridge University Press
The Edinburgh Building, Cambridge CB2 2RU, UK
Published in the United States of America by Cambridge University Press, New York
www.cambridge.org
Information on this title: www.cambridge.org/9780521825023

First published in print format 2005

ISBN-13 978-0-511-12869-1 eBook (Adobe Reader)

ISBN-13 978-0-521-82502-3 hardback
ISBN-10 0-521-82502-4 hardback

ISBN-13 978-0-521-53200-6 paperback
ISBN-10 0-521-53200-0 paperback