Ecological mechanisms of extinction

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Ecological theory offers predictions, sometimes conflicting, about the ecological characteristics of species that correlate with their risk of extinction. It is generally agreed that risk should be higher for species with small populations, small geographic ranges, and poor dispersal ability than for their ecological counterparts (1–3). How suites of life history characteristics affect risk of extinction is less clear. Species with high variance in the intrinsic rate of population increase (r), which is often associated with high fecundity, moderate to low survival rates, short generation times, and small body size, are predicted to be more susceptible to extinction because they are prone to large stochastic population fluctuations (4). Alternatively, species with a low r (because of low fecundity, high survival, and long generation times) are predicted to be at increased risk, because they would recover slowly from a severe reduction in population size and remain threatened longer by demographic and genetic stochasticity (5, 6). Such species are typically large. Thus, it is unclear whether the "fast lifestyle" associated with small body size and short generation times or the "slow lifestyle" represented by large organisms with long generation times makes species and lineages more or less likely to become extinct. Empirical studies of island fauna yielded contradictory conclusions about the effects of body size and lifestyle on the risk of extinction and produced conflicting explanations to account for the mechanisms underlying the patterns (5, 7–11). Resolution of such issues transcends academic debates, as governments and conservation organizations struggle to apply laws, like the United States Endangered Species Act, and decide how to rank threats and allocate funds among taxa that may differ in risk (12).

Now Owens and Bennett (13) present new evidence that the ecological mechanisms underlying extinction may differ for lineages of birds threatened by habitat loss and for lineages threatened by human persecution and introduced predators. The study both supports and challenges current thinking in extinction theory and raises a number of intriguing issues. The authors tested predictions about extinction theory on a database of 95 avian families using phylogenetic comparative methods. Birds are one of the few taxa whose species are well enough described, whose phylogeny has been widely investigated (14), and whose ecology is sufficiently known to permit a global analysis. The outstanding scholarship of Collar *et al.* (15), who compiled life history accounts of all 1,111 species of birds in the world thought to be at risk, made possible this and similar analyses (16).

Multiple factors may interact to threaten species. About one-third of the world's threatened bird species are at risk from direct mortality because of human persecution, including harvesting, poisoning, egg collecting, and capture for trade, and by predation from introduced predators, which has been especially devastating to fauna and flora on island ecosystems. These factors directly reduce survival and/or reproduction, to result in population declines. Birds are primarily threatened by habitat loss because of habitat destruction and habitat degradation from agricultural practices and water management, which affects over two-thirds of the threatened species. For birds, habitat loss may not result in direct mortality unless the impacts destroy active nests. However, mortality may occur after habitat has been lost through starvation, accidents, and predation caused when birds must disperse in search of unspoiled areas to live in and from crowding into remaining habitats (17). The impacts of habitat loss, however, are likely to be different for less vagile or smaller animals and plants, which may suffer more immediate mortality. Although habitat loss and human persecution/introduced predators can occur simultaneously to drive a species toward extinction, Owens and Bennett (13) found that they often acted independently on lineages, as there was no correlation between the percentage of species within a family threatened by one force or the other.

Could differences among species in extinction risk be caused by differential vulnerability of lineages to habitat loss vs. persecution/predation as a result of the differing ecological pathways that these forces affect? Owens and Bennett's (13) results suggest they could. Extinction risks through human persecution and introduced predators were associated with birds that had large body size and long generation times. This result is entirely expected, because rate of population change (r) of long-lived and slowly reproducing species and lineages is especially sensitive to small perturbations to adult survival (18). For example, factors that lowered the survival of long-lived adult California condors (*Gymnogyps californianus*) or albatrosses would have a far greater impact on population change than proportional changes in their reproductive success, which is limited by a clutch size of one egg annually. Thus, slow lifestyle species and lineages should be more susceptible to human persecution and introduced predators if the impact primarily affects survival, compared to their fast-lifestyle counterparts.

This phenomenon is illustrated effectively by the differential vulnerability of parrots and finches harvested as adults for the international pet trade (Table 1). Between 1,600,000 and 3,200,000 birds were taken annually from wild populations for the live bird industry in the 1990s (19). Finches of the families *Passeridae* and *Fringillidae* composed 70% of the trade, and parrots (*Psittacidae*) accounted for 25% of the volume. The body mass of a typical finch is nearly 10 times smaller than the mass of a modal parrot. Despite the large numbers of finches traded, parrots suffer over three times the rate of threat that finches incur from trade (Table 1), making *Psittacidae* among the most threatened families of birds (6). Many parrots are threatened by a combination of trade and habitat destruction (20), but trade may be more threatening because often species persist in a variety of disturbed habitats (21). Life history differences partly explain why parrots are more susceptible to overharvesting than finches (Table 1). Annual fecundity of parrots is much less than that of finches by virtue of smaller clutch sizes and fewer broods per year. Finches do not require specialized structures for nesting, whereas parrots typically nest in tree cavities, which are often in short supply. This results in large

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Table 1. Comparison of levels of threat and ecology between parrots (*Psittacidae*) and finches (*Passeridae* and *Fringillidae*), the two most traded groups of birds

Category	Comparison	Parrots	Finches
Threat	No. of species	358	1,379
	No. of endangered and threatened species	103	90
	% endangered and threatened species	28.7	6.5
	% endangered and threatened affected by trade	47.5	13.3
Ecology	Clutch size	small	large
	No. of broods per year	single	multiple
	Nest type	cavity	open cup/hanging
	Age of first breeding	delayed	rapid
	Adult survivorship rate	high	intermediate

Endangered and threatened species are those listed by IUCN–The World Conservation Union as critically endangered, endangered, or vulnerable (19).

proportions of nonbreeding individuals parrots (22) that could create a surplus for harvesting, but also contributes to low rates of population growth. Furthermore, medium- and large-sized parrots do not breed until 2–5 years of age, whereas finches usually mature within a year. Finally, most parrots are long lived compared to finches. Thus, high reproductive effort and moderate survival make finches less susceptible to overharvesting than parrots.

A classic example of the impact of an introduced predator on island birds also provides an interesting exception to the rule that larger slowly reproducing species become extinct faster than smaller more fecund ones. The brown tree snake (*Boiga irregularis*) was accidentally introduced to Guam, the largest island of Micronesia, around 1950 (23). It is a voracious predator and is mainly responsible for the extirpation of 9 of 13 native forest birds, having eaten its way through eggs, nestlings, and adults. One species became extinct before the snake arrived and three others persist by the slimmest of margins. The island swiftlet (*Aerodramus vanikorensis bartschi*) survives by nesting in caves that snakes do not penetrate, and the Micronesian starling (*Aplonis opaca*) persists in urban areas where snake densities are low. Practically the only native bird remaining in the forest is the Aga or Mariana Crow (*Corvus kubaryi*), the largest forest bird. The Aga survived because it typically grows too big for the snake to eat! Down to less than one dozen individuals, the Aga has produced only two young in the wild over the past dozen years (24). This example illustrates the importance of understanding how threats act on demography and the ecological mechanisms of extinction if we are to predict successfully the differential vulnerability of species and lineages.

The most surprising result of Owens and Bennett's work was that lineages threatened principally by habitat loss exhibited ecological correlates that differed from lineages suffering because of human persecution and introduced predators. Extinction risk from habitat loss disproportionately affected birds that were small, had short generation times, and were habitat specialists. The latter trait was to be expected, but the mechanisms of habitat destruction that would promote extinction of small and short-lived birds over large and long-lived lineages remain to be elucidated. Conservation biologists have typically worked under the assumption that habitat destruction will first extirpate large species because they require large home ranges and occur at lower densities. The ability to traverse landscapes may assist large species to escape harm and find new homes when their habitats are destroyed. However, many small birds migrate thousands of kilometers and possess the ability to search for remaining suitable habitat. It is notable that the families of small birds identified by Owens and Bennett as affected only by habitat destruction are primarily composed of frugivores or nectivores, which could be more susceptible to changes in the spatial arrangement of habitats because they depend on ephemeral and specialized food resources.

Because the role of body size and life history traits in determining extinction risk varies, future research might be more fruitful if it focused on the interaction between threats and diverse but specific ecological variables. The resulting elucidation of risk to species and lineages would contribute a theoretical component that the "declining population paradigm," which identifies and ameliorates threats, currently lacks and would complement the burgeoning theory of genetic and demographic risks of smallness, which composes the "small population paradigm" (25).

COMMENTARY

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