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 Paseridae 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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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. Fi-
ally, most parrots are long lived com-
pared 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 pre-
dator and is mainly responsible for the
extirpation of 9 of 13 native forest birds,
having eaten its way through eggs, nest-
lings, and adults. One species became
extinct before the snake arrived and three
others persist by the slimmest of margins.
The island swiftlet (Aerodramus vaniko-
rensis bartschi) survives by nesting in caves
that snakes do not penetrate, and the
Micronesian starling (Apolos apoca) per-
sists 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 larg-
est forest bird. The Aga survived because
it typically grows too big for the snake to
eat! Down to less than one dozen individ-
uals, 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 demog-
raphy 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 threat-
ened principally by habitat loss exhibited
ecological correlates that differed from
lineages suffering because of human per-
secution and introduced predators. Ex-
tinction risk from habitat loss dispropor-
tionately affected birds that were small,
short generation times, and were hab-
itat 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 elu-
cidated. Conservation biologists have typ-
ically 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 mi-
grate 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 Ben-
nett as affected only by habitat destruction
are primarily composed of frugivores or
nectivores, which could be more suscepti-
table 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 inter-
action between threats and diverse but
specific ecological variables. The result-
ing elucidation of risk to species and
lineages would contribute a theoretical
component that the “declining popula-
tion paradigm,” which identifies and
ameliorates threats, currently lacks and
would complement the burgeoning the-
ory of genetic and demographic risks of
smallness, which composes the “small
population paradigm” (25).

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