Lying in Wait for Extinction: Ecological Correlates of Conservation Status among Australian Elapid Snakes

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Abstract: *Why do some species decline rapidly with anthropogenic disturbance, whereas others readily exploit disturbed habitats? It is possible that the ecological characteristics of some species render them especially vulnerable to extinction. Previous analyses of a diverse array of taxa have identified a number of intrinsic ecological predictors of vulnerability, but snakes have not been studied in this respect. We collated ecological data on Australian venomous snake species in the family Elapidae, based primarily on examination of preserved specimens in museums, to investigate possible differences between threatened and nonthreatened taxa. We also used comparative (phylogenetically based) analyses to identify functional associations with endangerment. Correlates of conservation vulnerability identified in previous studies did not discriminate successfully between threatened and nonthreatened elapid species. However, threatened and nonthreatened elapids differed significantly in two main respects. First, threatened species tended to rely on ambush foraging rather than actively searching for prey. Sit-and-wait foragers may be vulnerable because (1) they rely on sites with specific types of ground cover, and anthropogenic activities disrupt these habitat features, and (2) ambush foraging is associated with a suite of life-history traits that involve low rates of feeding, growth, and reproduction. The second major correlate of endangerment involves the mating system. Endangered species typically lacked male-male combat: In such taxa, females grow larger than males and are more vulnerable to human predation (as judged by the composition of museum collections). Our analysis also identified taxa that, although not currently listed as threatened, share many of the ecological traits of the endangered group. Our results may facilitate future attempts to prioritize conservation actions for Australian snakes.*

Esperando la Extinción: Correlaciones Ecológicas de Estatus de Conservación entre Serpientes Elápidas Australianas

Resumen: *¿Porqué unas especies declinan rápidamente con la perturbación antropogénica, mientras que otras rápidamente explotan los hábitats perturbados? Razonablemente las características ecológicas de algunas especies las hacen especialmente vulnerables a la extinción. Los análisis previos de un conjunto de taxones diversos han identificado numerosos predictores ecológicos intrínsecos de vulnerabilidad, pero las serpientes no han sido estudiadas al respecto. Comparamos datos ecológicos de especies Australianas de serpientes venenosas de la familia Elapidae, con base en el examen de especímenes preservados en museos, para investigar posibles diferencias entre taxones amenazados y no amenazados. También utilizamos análisis comparativos (basados filogenéticamente) para identificar asociaciones funcionales en peligro de extinción. Correlaciones de vulnerabilidad de conservación identificadas en estudios previos no discriminaron con éxito entre especies de elápidos amenazadas versus no amenazadas. Sin embargo, elápidos amenazados y no amenazados difirieron significativamente en dos aspectos principales. Primero, las especies amenazadas tienden a utilizar el forrajeo de emboscada en lugar de buscar a sus presas activamente. Los forrajeros que se "sientan y esperan" pueden ser vulnerables porque (1) dependen de sitios con tipos específicos de cobertura del suelo, y las actividades antropogénicas trastornan esas características del hábitat y (2) el forrajeo de emboscada se asocia con un conjunto de características de la historia de vida que implican bajas tasas de alimentación, crecimiento y reproducción. La segunda mayor correlación de peligro involucra el sistema de apareamiento. Las especies amenazadas típicamente carecen de combate macho-macho; en tales taxones, las hembras crecen más que los machos y son más vulnerables a la depredación humana (a juzgar por la composición de*

colecciones de museo). Nuestro análisis también identificó taxones que, aunque actualmente no estén incluídas en las listas como amenazadas, comparten muchas de las características ecológicas del grupo en peligro. Nuestros resultados pueden facilitar futuros intentos para priorizar acciones para la conservación de serpientes australianas.

Introduction

Anthropogenic degradation of natural systems has led to a massive and ongoing worldwide loss of biodiversity (Soulé 1985; Wilcove et al. 1986). Species do not respond equally to habitat alteration and disturbance, however. Instead, they are affected to different degrees. If we can understand the intrinsic ecological factors that predispose a species to endangerment, we may be able to predict declines before they occur and hence ameliorate them more effectively (Angermeier 1995). For this reason, several workers have attempted to identify the determinants of vulnerability, generally by comparing threatened taxa with related species that have not suffered major population declines. The factors that have been identified in this way include small local population sizes, small geographic-range size, large body size, low reproductive investment, specialized niche requirements, insular endemism, and the tendency to form aggregations (Primack 1993; Hanski et al. 1996; Gaston & Kunin 1997; Meffe & Carroll 1997). Species that display these traits may be disproportionately sensitive to habitat disturbance.

Humans have greatly altered habitats over much of Australia (Adamson & Fox 1982). Agriculture, fire, grazing, urbanization, and the introduction of exotic organisms have fragmented ecosystems both in the arid interior and the more mesic coastal areas (Hobbs & Hopkins 1990; Covacevich et al. 1998). As a result, almost 300 of Australia's 1600 species of terrestrial vertebrates may be threatened with extinction (Kennedy 1990; Recher & Lim 1990). The loss of native mammals has been particularly well documented; at least 22 species have become extinct since European settlement (Recher & Lim 1990). Declines and apparent extinctions of numerous Australian frogs have also been documented in the past two decades, with habitat loss, global climate change, disease, and pollution implicated as possible causes (Laurance et al. 1996; Tyler 1997). In contrast, the effects of human activities on reptiles are poorly known. Australia has a diverse reptile fauna (approximately 700 species of terrestrial lizards and snakes, compared to <250 species in the United States, a country of similar area), and basic natural-history data are lacking for many taxa (Cogger et al. 1993). Gathering detailed autecological data based on field observations of habitat use, behavior, and temporal variation in population sizes for each species of Austra-

lian reptile is a daunting task, and one that is unlikely to be completed in the foreseeable future. This situation leaves land managers without the knowledge necessary to adequately plan for the conservation of reptiles, with the result that they are often overlooked. In the state of New South Wales, for example, 59% of mammals, 23% of birds, 27% of frogs, and 13% of reptiles are considered threatened or vulnerable. But knowledge available for accurate assessment of the status of reptiles has been deemed "inadequate" for >75% of reptiles, compared with 34% of mammals, 45% of birds, and 62% of frogs (Lunney et al. 1997).

One partial solution to this dilemma is to identify ecological differences between species thought to be vulnerable and those that presently appear to be secure (Angermeier 1995; Jennings et al. 1998, 1999). These comparisons allow testing of general hypotheses about the factors contributing to vulnerability. Perhaps more important, however, such an analysis may reveal previously unsuspected patterns, thus pinpointing taxon-specific variables affecting conservation status. Policy and legislation will be most effective if they incorporate information not only on the nature of anthropogenic threats, but also on intrinsic predictors of a species' vulnerability to such threats.

We examined differences in ecology and behavior between threatened and nonthreatened proteroglyphous (elapid) snakes of Australia. Terrestrial members of the family Elapidae total about 75 species spanning virtually every habitat type. Elapids comprise >75% of the terrestrial macrostomatan snake fauna (Cogger 2000). Species range in adult body length from <25 cm to >3 m and vary widely in reproductive mode, diet, behavior, and other traits (Shine 1991; Greer 1997). Australian elapids prey almost exclusively on vertebrates, so comparative analyses are not complicated by major differences in trophic level (Damuth 1987). Our study was facilitated by the availability of a large data set on ecological attributes of Australian elapids (for additional references see Shine 1994*a*), based largely on data from preserved museum specimens. This data set offers an opportunity to quantify many life-history traits to a degree not yet possible for most reptiles.

Our first goal was to evaluate the degree to which oft-cited predictors of anthropogenic vulnerability successfully predict endangerment in the elapids. It is possible that taxon-specific phenomena may reduce the general-

ity of such hypotheses. Our second goal was to identify the suite of ecological variables best able to discriminate between threatened and nonthreatened elapid species. Third, we examined these data in a comparative (phylogenetically based) framework to look for functional associations between endangerment and other traits. Lastly, we identified a number of species that, although not currently regarded as threatened, share many of the characteristics of threatened taxa and hence may deserve increased conservation scrutiny.

Methods

In compiling our data, we relied on the taxonomy of Cogger (2000). Because the taxonomy of Australian elapids is undergoing constant revision, our database does not include all currently recognized species of Australian elapids (e.g., Shea 1998). Also, some taxa presently regarded as single, wide-ranging species undoubtedly will be split into a series of sister species by more detailed taxonomic investigation. Fortunately, such closely related taxa generally show many similarities in major life-history features (e.g., Shine 1989), so our analyses should not be greatly affected by such revisions. We restricted attention to species found in mainland Australia to avoid problematical issues concerning the taxonomic status of insular populations.

Life-History Data

Life-history data were obtained via dissection of >18,000 preserved specimens from various institutions; procedural details are discussed elsewhere (Shine 1994*a*). We used raw data from the original studies to recalculate variables as necessary to account for recent taxonomic changes. A small number of variables were estimated for poorly known species from congeners of similar size, a conservative practice that should minimize the chance of introducing Type I errors into analyses of differences between threatened and nonthreatened taxa. We used 19 variables in our analyses.

We determined adult sex ratio by dividing the number of adult males in museum collections by the total number of adult specimens. This variable reflects both underlying sex-ratio biases (due to, for example, differential mortality or differential ages at maturation) and collecting bias (adult males may be more vulnerable to collection in some species, females in others). Regardless, it offers an index of the degree to which predation by humans is concentrated on either adult males or adult females (Shine 1996).

The proportion of the museum sample composed of juvenile rather than adult specimens was calculated as described above for adult sex ratio. This variable may offer an indicator of underlying age structure, but it will be affected strongly by the differential observability—and hence vulnerability to collection—of juvenile versus adult snakes.

Male combat was dichotomously scored as 0 if combat had not been observed for a species within the genus, or was scored as 1 if combat had been observed. We used genus- rather than species-levels records of combat because this trait shows strong phylogenetic conservatism in Australian elapids and behavioral data are lacking for some species (Shine 1994*c*).

Ambush predation was dichotomously scored as for combat. Foraging modes in snakes range from extremes of sedentary ambush predation to active pursuit, but most snake species occupy positions close to either end of the continuum (Greene 1997). Our classification was based on behavioral observations in the field (Greer 1997).

We used both mean adult snout-vent length (adult SVL) and sexual size dimorphism (SSD) as independent variables. The SSD was calculated following the method of Lovich and Gibbons (1992). The mean adult SVL of the larger sex was divided by that of the smaller sex, and the difference between this value and 1.0 was used as an index of dimorphism (assigned to be positive if females are larger and negative if males are larger). This procedure minimizes problems associated with statistical analyses on ratio-based measures (Lovich & Gibbons 1992).

For each species, we determined the percentage of total prey items composed of each of four vertebrate classes, amphibians (represented in Australia by frogs), reptiles, birds, and mammals. We then calculated Shannon-Weiner diversity indices for prey from these proportions as a measure of dietary specialization.

We calculated mean clutch size and mean neonate size (SVL) for each species. Reproductive mode was scored as 0 for oviparous taxa and 1 for viviparous taxa. For each species, the body size of the smallest reproductively mature individual of each sex (as determined by dissection) was considered the minimum SVL at sexual maturity. This minimum SVL was divided by mean adult SVL to yield the percentage of mean adult body size at maturation. This variable quantifies the amount of growth that occurs after sexual maturity and is tied to mating system and female reproductive parameters (Shine 1996).

We scored habitat use by counting the number of habitat types used by each species, following Cogger et al. (1983). For each species, Cogger et al. listed each habitat type in which individuals have been observed or collected; habitat types were taken from a standardized list. Examples of habitat types include closed forest, hummock grassland, open heath, and swamp (totaling about 25 types).

As measures of climatic tolerances, we recorded the annual temperature and precipitation range to which each species is exposed across its entire range. Annual temperature range was defined as the maximum average

temperature of the warmest month, minus the minimum average temperature of the coolest month. We similarly defined annual precipitation range using average values from the wettest and driest months (data from Appendix 3 of Longmore 1989). These values overestimate the range of climatic values experienced by any individual snake, but allow interspecific comparisons of specialization for certain thermal or hydric zones.

Statistical Analysis

Our dependent variable for all analyses was the conservation status of the species in question. We took this classification from the Action Plan for Australian Reptiles (Cogger et al. 1993). This listing is based on an extensive series of surveys of the herpetological community and information from state and territorial agencies. Final conservation status was estimated by a panel of herpetologists using the ranking system of Millsap et al. (1990). In choosing variables for use in the present study, we were careful to avoid circularity. Thus, we did not use ecological variables (such as geographic range size) that had been explicitly used to determine conservation status by Cogger et al. (1993). The action plan lists 16 mainland elapid species, subspecies, or populations as either "endangered," "vulnerable," or "rare or insufficiently known." We excluded three poorly known species (*Furina dunmalli, Paraplocephalus* [formerly *Echiopsis*] *atriceps*, and *Simoselaps minimus*) and one undescribed species (*Rhinoplocephalus* sp. Eyre Peninsula) for which ecological data were not available. Two populations or subspecies of wider-ranging species also were included in the action plan (*Notechis ater ater* from the Flinders Ranges of South Australia and *Echiopsis curta* from east of Adelaide); again, these were deleted from our species-level analysis. The remaining 10 species from the action plan were classified as "threatened" in our analyses, whereas all other taxa were "nonthreatened." The following species were classified as threatened: *Acanthophis antarcticus, Austrelaps labialis, Denisonia maculata, Elapognathus minor, Furina barnardi, Hoplocephalus bungaroides, Hoplocephalus stephensii, Simoselaps calonotus, Simoselaps warro*, and *Vermicella annulata.*

Our database of nonthreatened elapids included 59 species. We excluded nine mainland taxa (*Acanthophis praelongus, Cacophis churchilli, Demansia reticulata, D. simplex, Pseudonaja inframacula, Simoselaps incinctus, S. morrisi, Suta ordensis*, and *Vermicella intermedia*) for which we had insufficient ecological or climatic information. We considered all mainland *Notechis* to comprise one variable species (Schwaner 1985). Because ecological data were lacking for recently described bandy-bandy species (*Vermicella* spp., Keogh & Smith 1996), we treated *V. annulata, V. vermiformis*, and *V. snelli* as a single, threatened taxon.

We performed statistical analyses using both univariate and multivariate approaches. We first performed univariate comparisons between threatened and nonthreatened taxa (a "tips" analysis, which does not consider possible phylogenetic effects on trait values). Effects of conservation status on dichotomous variables (male combat, ambush, and reproductive mode) were analyzed with 2×2 contingency tables. All other variables were analyzed with unpaired *t* tests, with species status as the grouping variable. We applied a Bonferroni correction to all univariate results to minimize the risk of Type I error. We then used linear discriminant-function analysis (LDFA) to assess our ability to discriminate between threatened and nonthreatened species based entirely on ecological variables.

These analyses treat each species as an independent data point. However, closely related species may share traits due to common descent rather than through independent evolution (Harvey & Pagel 1991). We therefore repeated our analyses using the comparative method to see whether we could identify functional associations—that is, ecological traits whose evolution has been consistently followed by a shift in endangerment. These tests also clarify the effects of phylogenetic conservatism on our tips analyses. We assembled a hypothesis of elapid relationships from several published and unpublished phylogenies (Mengden 1985; Keogh 1998; Keogh et al. 1998, 2000; J. S. Keogh, personal communication). The resultant cladogram was well resolved at the generic and deeper nodes, but incompletely resolved at the species level (Fig. 1).

Different methods were employed to analyze continuous variables and dichotomous (categorical) variables. For continuous variables we used the computer program CAIC v.2.6.1 (Purvis & Rambaut 1995). We assumed equal branch lengths (corresponding to a punctuational model of evolution; Purvis et al. 1994) and used the Brunch algorithm to calculate independent contrasts for each continuous variable, with species status as the dichotomous independent variable. We then regressed standardized independent contrasts of the variable of interest against contrasts of conservation status (regression forced through the origin) to test the null hypothesis that evolutionary changes in ecological traits have not been accompanied consistently by changes in conservation status (Garland et al. 1992).

To analyze categorical variables, we used the program MacClade (v.3.08; Maddison & Maddison 1992). Concentrated-changes character-correlation tests allowed us to determine whether changes in one character (e.g., conservation status) were significantly concentrated on those branches on which the second character (e.g., male combat) had a specified state (Maddison 1990). This test operates under the null expectation that changes are randomly distributed over the cladogram; statistically significant results indicate that changes in
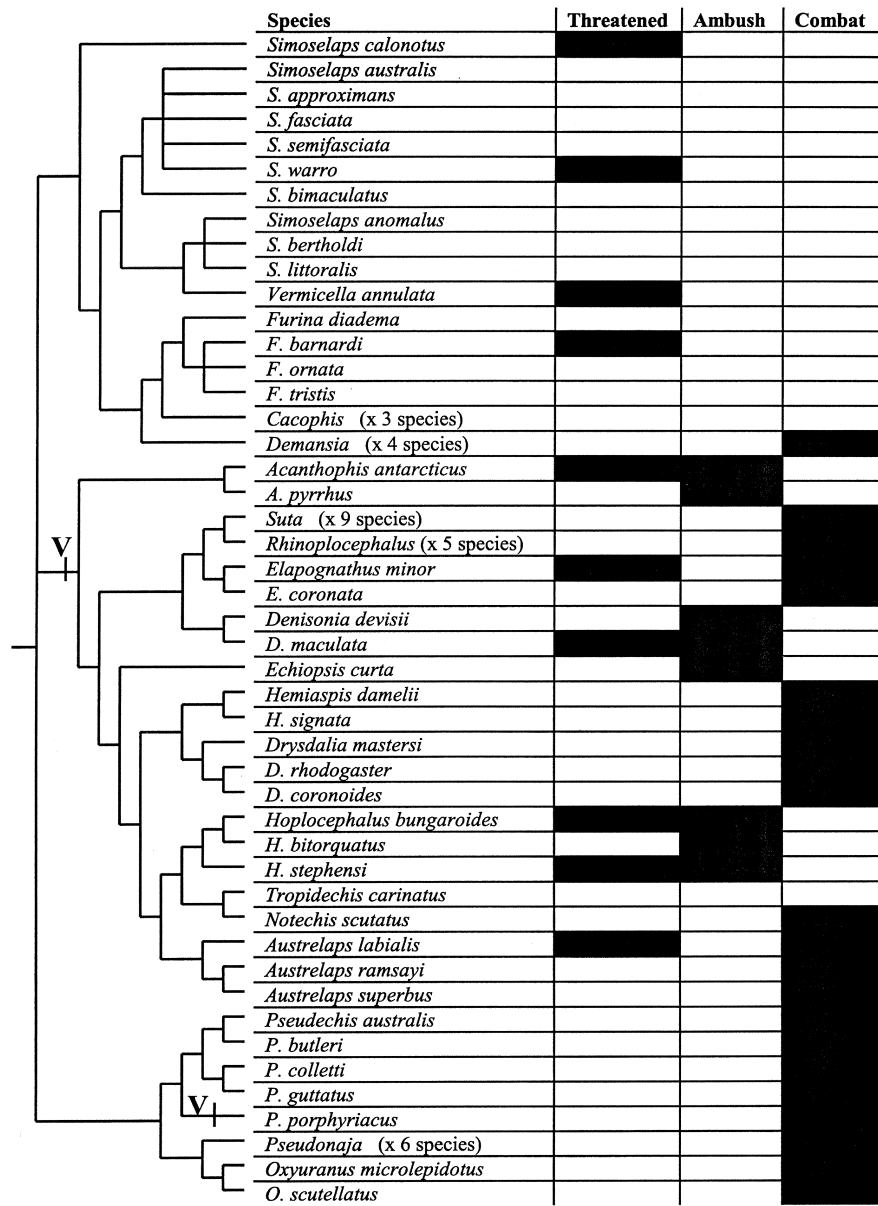
Figure 1. Phylogenetic relationships of taxa used in our analyses (assembled from various sources; see text) with assignment of conservation status and presence or absence of both ambush predation and male combat. Shaded cells respectively indicate threatened status, classification as an ambush predator, or documentation of male combat in a species. Some genera were unresolved. The number of species in our analyses is included after the generic name, for example, "Rhinocephalus (× 5 species)." The most parsimonious evolution of viviparity from oviparity is also mapped onto the tree (shown by a V at the node leading to the large clade of viviparous elapids and along the branch leading to P. porphyriacus within the genus Pseudechis).

the first character may be influenced by the state of the second character. Because the concentrated-changes tests cannot operate on incompletely resolved phylogenies, we arbitrarily resolved polytomies on our tree before performing these tests. To ensure that this procedure did not influence our results, we used multiple possible configurations of the tree to test each dichotomous variable. Results were similar among alternate topologies, and alphas we report are the mean values for all topologies.

We transformed variables as necessary to satisfy assumptions of normality in linear analyses. Proportional and percentage variables were subjected to arcsine-square-root transformation, and non-normal continuous variables were subjected to Box-Cox transformation, a procedure determining the power function resulting in

the best approximation of normality. We set alpha equal to 0.05 in all significance tests. Analyses were performed with Systat (v.7) or BIOMstat (v.3.3).

Results

Of the 19 ecological variables included in our univariate comparisons, five differed significantly between threatened and nonthreatened Australian elapids. Compared with nonthreatened taxa, threatened species were less likely to display male combat and more likely to ambush rather than search actively for prey (Table 1). Female body size was higher than male body size in threatened species, and museum specimens typically contained more adult females than adult males (Table 1). Lastly,

Table 1.   Univariate results (ranked by significance of test) of variables used in analyses of ecological differences between threatened and nonthreatened Australian elapid snakes.[a]

Variable[b]	Mean (nonthreatened)	SD	Mean (threatened)	SD	Statistic (t or χ^2)	p
Male combat	0.678	0.471	0.100	0.316	11.85	0.001[c]
Adult sex ratio	56.9	11.1	43.6	11.8	3.47	0.001[c]
Ambush predation	0.068	0.254	0.40	0.516	9.21	0.002[c]
Sexual dimorphism	0.009	0.14	0.170	0.181	−3.12	0.003[c]
Annual tempature (°C)	30.4	3.54	27.3	3.74	2.45	0.02
Male SVL at maturation (%)	72.4	11.6	79.1	11.9	−1.69	0.09
Age structure	35.5	11.9	29.7	16.2	1.67	0.10
Clutch size	6.90	4.27	7.52	3.19	1.09	0.28
Frogs in diet (%)	13.1	23.6	20.1	33.2	−0.84	0.40
Habitat types used	4.23	2.31	3.70	2.67	0.847	0.43
Neonate SVL (cm)	15.22	5.90	13.62	4.04	−0.69	0.51
Mammals in diet (%)	12.6	25.9	7.0	15.0	0.659	0.51
Adult SVL (cm)	53.30	37.57	41.88	13.95	−0.643	0.52
Reproductive mode	0.492	0.504	0.600	0.516	0.40	0.53
Annual precipitation (mm)	328	198	349	165	−0.60	0.55
Female SVL at maturation (%)	76.7	9.8	74.8	9.7	0.556	0.58
Reptiles in diet (%)	67.1	37.7	71.0	35.9	−0.37	0.71
Birds in diet (%)	5.0	1.6	0.80	2.5	−0.33	0.74
Diet diversity index	0.308	0.380	0.336	0.448	−0.214	0.83

[a]*Means and standard deviations are calculated from untransformed data, whereas analyses of differences between threatened and nonthreatened species are based on transformed data.*
[b]*See text for explanation of variables. Adult sex ratio is expressed as the percentage of males among museum specimens, and age structure is expressed as the percentage of juveniles among museum specimens. For all variables, SVL indicates snout-vent length in centimeters. The SVL at maturation (%) for both males and females refers to minimum SVL at sexual maturity, divided by mean adult SVL, yielding the percentage of mean adult body size at maturation. The SSD refers to sexual size dimorphism, calculated following Lovich and Gibbons (1992). Diet diversity index refers to results of a Shannon-Weiner analysis of diet diversity, calculated for each species from the percentage of diet composed of each major prey class. Annual temperature and annual precipitation refer to the mean annual temperature and precipitation ranges experienced by each species across its geographic range. Male combat and ambush predation were dichotomous variables, with 0 and 1 indicating the absence and presence of a trait, respectively. Means for these variables were thus calculated from relative numbers of 0s and 1s. Reproductive mode was also dichotomous, with 0 and 1 indicating oviparity and viviparity, respectively.*
[c]*Analyses remaining significant (p < 0.05) after experiment-wise Bonferroni correction.*

threatened taxa tended to occur over a narrower range of annual temperatures than did nonthreatened taxa (Table 1). Of these, all but annual temperature range retained a significant alpha after Bonferroni correction for multiple tests. Some of the trends were strong. For example, fully half of the ambush predators included in our analyses were classified as threatened, whereas <10% of active predators fell into this category.

Because many of these effects were very clear, the ability of the LDFA to classify species as threatened or nonthreatened, based only on ecological data, was excellent (overall model: Wilks's lambda = 0.545, approximate $F_{19,49} = 2.15$, $p = 0.016$). The LDFA incorrectly classified 6 nonthreatened species (*Acanthophis pyrrhus, Denisonia devisi, Echiopsis curta, Furina tristis, Hoplocephalus bitorquatus,* and *Simoselaps bimaculatus*) as being threatened, but correctly classified 53 species in this category. The LDFA incorrectly classified the dwarf copperhead (*Austrelaps labialis*) as nonthreatened, but the other nine threatened taxa were classified correctly.

The patterns were less robust with phylogenetically based analysis. Conservation status was not subject to strong phylogenetic conservatism (Fig. 1). The 10 threat-

ened taxa belonged to eight different genera, widely scattered among the lineages of Australian proteroglyphous snakes. However, many of the ecological variables, such as foraging mode and mating system, showed stronger conservatism (Fig. 1; Shine 1994*a*). Thus, the degree of freedom for most of our phylogenetically based tests was much lower than for our tips analyses. Evolutionary changes in ecological variables were not consistently accompanied by concurrent shifts in conservation status ($p > 0.05$ in all tests; Table 2). However, we found nonsignificant trends toward relationships between contrasts in conservation status and contrasts in sexual size dimorphism, annual temperature range, clutch size, and the proportion of diet composed of mammals (Table 2).

Results of concentrated-changes character-correlation tests indicate that the probability of a species being classified as threatened was evolutionarily correlated with both male combat and ambush predation. Threatened species were more likely to be ambush predators than expected by chance ($p = 0.036$) and less likely to display male combat ($p = 0.022$; Fig. 1). That is, the probability of a species becoming endangered was enhanced after ambush foraging evolved in the lineage and was re-

Table 2. Results of comparative analysis using independent contrasts (CAIC) (ranked by statistical significance of regression) of the evolutionary relationships between species conservation status and ecological variables among Australian elapid snakes.

Variable*	R^2	$F_{1,8}$	p
SSD	0.35	4.29	0.072
Annual temperature (°C)	0.33	3.95	0.082
Clutch size	0.31	3.6	0.094
Mammals in diet (%)	0.31	3.58	0.095
Age structure	0.25	2.71	0.138
Adult sex ratio	0.25	2.63	0.143
Combat	0.17	1.67	0.233
Annual precipitation (mm)	0.14	1.29	0.288
Male SVL at maturation (%)	0.13	1.23	0.300
Birds in diet (%)	0.11	1.00	0.347
Reptiles in diet (%)	0.05	0.40	0.546
Frog in diet (%)	0.02	0.14	0.722
Habitat types used	0.01	0.04	0.841
Neonate SVL (cm)	0.00	0.02	0.884
Adult SVL (cm)	0.00	0.02	0.888
Female SVL at maturation (%)	0.00	0.00	0.982
Diet diversity index	0.00	0.00	0.999

Refer to footnotes of Table 1 for definitions of variables.

duced after male-male combat evolved. Interestingly, these two traits rarely co-occur within Australian snakes, although this is not true for snakes in other parts of the world (e.g., Gillingham et al. 1983). Ambush predation was never observed in elapid species with male combat: across the entire phylogeny, the probability of male combat arising in ambush predators was low (concentrated-changes test, $p = 0.071$; Fig. 1). The probability of a species attaining threatened status was not correlated evolutionarily with its reproductive mode ($p = 0.23$).

Discussion

The Australian elapid snakes comprise a large and ecologically diverse assemblage of taxa. Even within the relatively small sample of 10 species of threatened snakes, mean adult snout-vent lengths varied from 21 to 66 cm, diets from highly specialized to broad, and mean clutch sizes from 3.5 to >15 (Shine 1991, 1994a). This ecological diversity mirrors the wide phylogenetic distribution of threatened taxa (Fig. 1). Despite this diversity, however, the elapid species identified as threatened by Cogger et al. (1993) share a number of ecological features that distinguish them from the other (presumably less threatened) confamilial taxa. The clearest evidence for the ecological distinctiveness of the threatened taxa comes from the ability of the LDFA analysis to unambiguously assign 90% of species to the "correct" category.

The ecological attributes that distinguish the threatened species do not accord well, however, with published conclusions on the nature of such attributes. This conflict strongly suggests that generally applicable pre-

dictors of vulnerability to anthropogenic threats may prove to be elusive or nonexistent. In other types of organisms, traits such as body size and degree of dietary specialization appear to predispose species toward endangerment, but our analysis does not suggest any such role within the Australian elapid snakes. Presumably, taxon-specific features of biology mean that different kinds of predictors are needed for different kinds of organisms.

Body Size and Reproduction

Of the traits believed to increase a species' vulnerability to habitat disturbance, perhaps the most widely cited is absolute body size (Pimm et al. 1988; Lunney et al. 1997; Jennings et al. 1999). Adult body size influences many ecological and life-history traits in Australian elapids (Shine 1994a), as in other types of organisms (Peters 1983). Large organisms require more resources per individual than do small organisms, and thus may require large individual activity ranges to meet energetic requirements. Large activity ranges are postulated to result in low densities of individuals, so large-bodied species may require large geographic ranges to maintain minimum viable populations (Brown & Maurer 1989; Brown 1995). Large animals also generally have low intrinsic rates of population growth, requiring long periods of time to recover from perturbations (Peters 1983; Pimm et al. 1988). Thus, the effects of human activities are predicted to be greater for large organisms. These predicted relationships were generated mostly from studies on endotherms, however. In contrast, reptiles require little energy per individual (Pough 1983), breaking down causal relationships between body size and range size. Also, clutch size tends to increase with body size among snakes (Shine et al. 1998), possibly allowing some species of large snakes to persist in extremely fragmented habitats (Shine & Fitzgerald 1996). Some of the largest Australian elapids have benefited from human activities. Taipans (*Oxyuranus scutellatus*) and eastern brown snakes (*Pseudonaja textilis*) appear to have increased population sizes above historical levels as a result of the clearing of forest for agriculture and high densities of introduced rodents (Shine & Covacevich 1983; Shine 1989). Thus, whereas big, fierce animals are generally rare (Colinvaux 1980), big, fierce Australian elapids are rarely rare.

Vulnerability due to low reproductive investment is tied closely to arguments invoking intrinsic rates of population increase. As with body size, mean clutch size did not differ between threatened and nonthreatened elapids, contrary to the results of studies on other taxa (Glazier 1980; Paine 1990). Clutch size alone may not be an adequate indicator of reproductive output in snakes, however, because females of many species (especially those of large body size) reproduce less than annually.

Indeed, variation in reproductive frequency has been identified as a major axis of interspecific variation in the reproductive biology of snakes (Seigel & Ford 1987). Because of shifts in behavior during pregnancy, actual reproductive frequencies are difficult to estimate for free-ranging snakes without long-term mark-recapture programs (e.g., Bonnet & Naulleau 1996). Thus, available data do not allow us to robustly test the proposition that species with low reproductive frequencies are more vulnerable to anthropogenic disturbance.

Specialization

Reliance on a small range of habitat types or prey species may be an important contributor to endangerment; specialists are unlikely to be able to use alternative resources in response to changing environmental conditions (Terborgh & Winter 1980; Gaston 1994). We found no differences, however, between threatened and nonthreatened elapids in either number of habitat types utilized or diet diversity, although our measure of dietary specialization was somewhat crude. By considering only four dietary categories, we necessarily overlooked specialists within each category. For example, bandy bandy snakes (*Vermicella* sp.) feed exclusively on blindsnakes (*Ramphotyphlops* sp.; Keogh & Smith 1996), which comprise an extremely small subset of our "reptile" diet class. Similarly, our methods did not allow for ontogenetic changes in diet specialization. A taxon may become endangered due to declines in a specific prey resource needed by a particular age/size class of snakes within the population. For example, juvenile broad-headed snakes (*Hoplocephalus bungaroides*) rely on velvet geckos (*Oedura lesueurii*), but adults consume a wider range of prey (Webb & Shine 1998). Our analysis treated this species as a generalist feeder, ignoring the potential role of a narrower trophic niche during early ontogeny.

Habitat specialization explains a significant amount of variation in the rates of extinction of reptile species from islands in the Mediterranean (Foufopoulos & Ives 1999). Trends observed in insular systems may not be applicable to many Australian taxa, however, where habitat specialization does not necessarily equate to a patchy distribution or small geographic range size. The arid interior of the continent is composed of a small number of major desert habitat types, allowing habitat "specialists" to range over large areas (James & Shine 2000). These species may actually be less vulnerable to local habitat disturbance, because the vast size of their geographic ranges increases the likelihood of multiple refugia for recolonization.

Foraging Mode and Mating Systems

Although the threatened Australian elapid species do not display the ecological characteristics noted among threatened taxa in other types of organisms, they nonetheless comprise a highly nonrandom assemblage with respect to foraging modes and mating systems. In keeping with a preliminary analysis by Webb and Shine (1998), our study revealed a strong association between endangerment and foraging mode. Sit-and-wait (ambush) foragers were disproportionately represented among the threatened taxa. There are two plausible reasons for this association. First, ambushing snakes require specific ground cover, usually either thick leaf litter (e.g., *Acanthophis* [Cogger 2000]) or thin, exfoliated rocks (e.g., *Hoplocephalus bungaroides* [Webb & Shine 1998]). Agricultural and urban activities frequently modify ground cover dramatically, which eliminates ambush sites and increases exposure to predators. For example, broad-scale clearing and frequent fire have reduced ground cover over much of semiarid Australia and hence have contributed to the decline of ambush-foraging pythons (Shine 1994*b*). The same python species remain abundant in mesic areas, where they are restricted largely to sites with enough ground and vegetative cover to provide successful ambush sites (Shine & Fitzgerald 1996). Wide-foraging snakes may be less dependent on the exact nature of ground cover as long as appropriate prey species remain available.

The second aspect of ambush foraging that may influence vulnerability to extinction involves the low rate of food acquisition typically associated with this foraging mode. Because the snake must wait for the close approach of prey, it may have few opportunities to feed and little opportunity to facultatively increase feeding rates in times of prey scarcity (Webb & Shine 1998). Low rates of food intake in turn result in slow growth, delayed maturation, and infrequent reproduction relative to sympatric active foragers (Shine 1980). The problems are exacerbated in Australia because low and variable ecosystem productivity has produced a prey resource largely composed of small, relatively sedentary animals (frogs, reptiles) rather than large, highly mobile animals (birds, mammals: Flannery 1994). Perhaps for this reason, ambush foragers comprise a much lower proportion of the snake fauna in Australia than in other well-studied areas such as Europe and North America, where ambush-foraging viperid snakes are a conspicuous component of the snake fauna (e.g., Klauber 1972).

Threatened species of Australian elapids tend to lack male-male combat, to have much larger body sizes in females than in males, and to have female-biased adult sex ratios in museum collections (Table 1). These attributes represent a single, functionally linked suite of traits. Sexual size dimorphism reflects the mating system, with male snakes being smaller than conspecific females if the mating system does not confer a mating advantage to larger male size via male-male combat (Shine 1994*c*). The larger size of females in these species may make them more obvious to humans (because of size and be-

cause of the thermoregulatory and trophic consequences of larger size), thus generating female-biased samples in museum collections. The same sex bias in vulnerability may mean that direct killing by humans (and perhaps by other predators) is concentrated on adult females, the most important age/sex class in terms of the population's ability to withstand anthropogenic mortality (Caughley & Gunn 1995). Although the influences of snake mating systems on a species' vulnerability to anthropogenic disturbance may not be immediately intuitive, they are not without precedent. Mating behaviors and other social factors are often significant contributors to population declines (Beissinger 1997) and may be most important for those species unable to behaviorally adapt to anthropogenic pressures (Reed 1999).

Conservation Recommendations and Conclusions

Lastly, we turn to the cases where our LDFA analysis incorrectly classified species as either threatened or nonthreatened. Such "mistakes" may provide insight into taxa for which current conservation classifications in the Action Plan for Australian Reptiles (Cogger et al. 1993) are suspect. The one threatened taxon incorrectly classified as nonthreatened by the LDFA was the dwarf copperhead (*Austrelaps labialis*). This species has the second-smallest range size known for any terrestrial Australian elapid, and most of its range is restricted to highly disturbed montane sites close to the city of Adelaide (Cogger et al. 1993). Hence, its threatened status reflects limited distribution and unlucky proximity to threatening processes rather than intrinsic ecological attributes.

More interesting are the six cases where the LDFA analysis classified a taxon as threatened although the action plan did not. These cases may potentially involve species that are susceptible to anthropogenic disturbance but have not yet revealed that sensitivity clearly enough for conservation problems to have become apparent. If so, they warrant close scrutiny from management agencies. In the absence of long-term survey data (unavailable for virtually all Australian snakes), declines may be difficult to assess until they have progressed to the point where remedial actions are difficult or impossible.

Given the strong phylogenetic conservatism in many ecological traits among the elapids (Shine 1994*a*), it is not surprising that five of the six "potentially vulnerable" taxa are congeners of species already identified as being of conservation concern. Four of these six species are ambush predators, and one of the six species is listed in the action plan, although only for a single geographic area (*Echiopsis curta*, Cogger et al. 1993). Another taxon (*Hoplocephalus bitorquatus*) is currently receiving increasing attention from wildlife managers, with recent survey work suggesting that it is probably more at risk than either of its congeners, both of which are "officially" classified as threatened species (M. Fitzgerald,

personal communication). We have no equivalent data on the other four taxa, but we suggest their conservation status warrants careful attention.

Endangered populations of birds and mammals often attract substantial research effort, with funding for detailed population-level surveys (e.g., Root 1988). Given the relative paucity of funding for conservation-oriented research on reptiles (Mittermeier et al. 1992) and other noncharismatic taxa (Ponder & Lunney 1999), however, this approach is unlikely to be feasible for most taxa at potential risk. Fortunately, low-cost shortcuts may be available, as demonstrated by our study. The dearth of information on basic ecological attributes can be remedied by cost-effective techniques such as the examination of museum specimens. One can use such information to identify variables that correlate with (and hence perhaps influence) a species' conservation status. The results from such analyses could be used to gain insight into the determinants of vulnerability and eventually to assign research priorities on a proactive rather than a reactive basis.

Acknowledgments

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