

LETTER

Foraging mode affects extinction risk of snakes and lizards, but in different ways

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Abstract

What factors render a species more vulnerable to extinction? In reptiles, foraging mode is a fundamental ecological dimension: some species actively search for immobile prey, whereas others ambush mobile prey. Foraging mode is linked to diet, morphology, movement ecology, and reproductive output, and hence plausibly might affect vulnerability to threatening processes. Our analyses of data on 1543 taxa revealed links between foraging mode and (IUCN) conservation status, but in opposite directions in the two main squamate groups. Ambush-foraging snakes were more threatened and with declining populations than were active searchers, whereas lizards showed the reverse pattern. This divergence may be linked to differing consequences of foraging mode for feeding rates and reproductive frequency in snakes versus lizards. Our findings underscore the need for taxon-specific conservation management, particularly in groups such as reptiles that have been neglected in global conservation prioritization.

KEYWORDS

endangered species, life history, phylogenetic comparative methods in conservation, sit-and-wait foraging, threatening processes

1 | INTRODUCTION

Global biodiversity is in steep decline, creating an urgent need for management (Tilman et al., 2017), but the resources available to identify which taxa are most at risk, and how we can best buffer those declines, are inadequate for the task (Caetano et al., 2022; Cardillo & Meijaard, 2012). Conservation biologists thus need tools with which to predict the taxa that are likely to survive anthropogenic threats versus those that are likely to go extinct unless managers intervene. The increasing availability of large

datasets on species attributes, and categorization of threat status by international agencies such as the International Union for Conservation of Nature (IUCN) (Mace et al., 2008), permits broadscale analyses of links between a species' attributes and its conservation status (Chichorro et al., 2022; Cox et al., 2022; Ducatez & Shine, 2017). Many such links have been identified; for example, a species may be most at risk of extinction if it has a small geographic range (e.g., Purvis et al., 2000), has a specialized diet or habitat (e.g., Safi & Kerth, 2004), or is restricted to islands (e.g., Slavenko et al., 2016). We explore the potential link

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between conservation status and a major dimension of ecological variation: the way in which an animal obtains its food.

Individual foraging tactics vary within a population (sometimes linked to ontogeny or sex: Shine & Wall, 2007) and geographic and temporal shifts in prey composition and predation behavior (e.g., Goodyear & Pianka, 2011). Studies on squamate reptiles have nonetheless identified a major dimension of variation that captures substantial interspecific variation: foraging mode (Glaudas et al., 2019; Huey & Pianka, 1981; Reilly et al., 2007; Vitt et al., 2003). At one extreme, reptiles, such as most chameleons and rattlesnakes, lie in ambush for long periods, remaining immobile until a prey item approaches closely enough to be seized. At the other extreme, reptiles such as *Gila* monsters and garter snakes search actively for hidden (generally immobile) prey. Although squamates occupy the full continuum between extreme ambush foraging and extreme active searching, most species are concentrated near one or the other end of that continuum and hence can be classified according to the foraging mode most often employed (Perry, 1999; Reilly et al., 2007).

Research has revealed strong links between foraging mode and several aspects of reptile biology, including aspects that might well affect a species' vulnerability to anthropogenic threats. For example, active searchers tend to be slender bodied (Meiri, 2010) and fast moving, are often seen in relatively open habitats, and produce relatively small clutches or litters (perhaps because a slender body shape provides less space to carry developing eggs: Du et al., 2005; Vitt & Congdon, 1978). Other correlates of foraging mode differ between lizards and snakes: for example, ambush-foraging snakes, such as pit-vipers, tend to take large mammalian prey infrequently (Glaudas et al., 2019), whereas ambush-foraging lizards (such as *Phrynosoma* or *Moloch*) take small insect prey (i.e., ants and termites) frequently (Huey & Pianka, 1981). Low feeding rates in ambush-foraging snakes have been implicated as causal factors for the evolution of "slow" life histories that involve delayed maturation and infrequent reproduction (e.g., *Hoplocephalus bungaroides*: Webb & Shine, 1998). The resultant low reproductive rate may predispose such taxa to extinction if prey abundance falls, whereas a sympatric active-searching snake can adjust its foraging rate to compensate for such a reduction in encounter rates with prey (Webb et al., 2002).

To our knowledge, only one prior analysis has looked for a link between foraging mode and endangerment in squamates. Based on data from 69 species of Australian elapid snakes, Reed and Shine (2002) concluded that ambush-foraging snakes were more vulnerable, perhaps because of "slow" life histories, combined with dependency on distinctive habitats (such as leaf-litter in which to lie in wait),

which were eliminated by agricultural activities. We now address this question with a dataset on more than 1500 species that incorporates information on lizards as well as snakes. We tested the prediction that foraging mode would be associated with its risk of extinction. We further hypothesized that this association might differ between lizards and snakes because of the different ecological correlates of foraging mode in the two groups.

2 | METHODS

2.1 | Data collection

We retrieved data on species foraging mode (active vs. sit-and-wait forager) from an updated version of Meiri (2018). Information on conservation status and geographic range size was obtained from the IUCN Red List of Threatened Species (www.iucnredlist.org; accessed August 2022), specifically species red-list category (i.e., least concern: LC; near threatened: NT; vulnerable: VU; endangered: EN; critically endangered: CR) and population trend (i.e., declining, stable, increasing, unknown). We used the IUCN data to generate the following three variables: (i) "extinction risk"—a continuous score, whereby LC = 0, NT = 1, VU = 2, EN = 3, and CR = 4; (ii) "threat status"—a binary trait, whereby species facing a high risk of extinction (i.e., classified as VU, EN, or CR) were considered "threatened" and species not under immediate risk (i.e., LC or NT) were considered "not threatened"; and (iii) for "population trend"—a binary trait—we merged species with a "stable" "increasing" population trend under a new category, namely, a "neutral" population trend. A "decreasing" population trend was considered "negative." Species scored as "unknown"—and those not scored at all—were not considered. In total, we collated published data on the foraging mode and conservation status of 1543 species belonging to 59 families (Table S3) that we could map to the squamate phylogeny proposed by Tonini et al. (2016)—the most complete time-calibrated phylogenetic tree available for squamates.

2.2 | Data analysis

Prior to phylogenetically informed data analysis, we explored frequency patterns of conservation status and foraging mode using traditional (nonphylogenetic) chi-square (χ^2) statistics. After pruning the phylogenetic tree to include only the species covered in this study, we tested for phylogenetic signal in foraging mode by calculating Fritz and Purvis' *D* (Fritz & Purvis, 2010) (1000 permutations; "phylo.d" function, "caper" package; Orme, 2012) and in extinction risk by calculating Pagel's λ and Blomberg's *K*

(using the “phyloglm” function in the “phytools” package; Revell, 2012). We then ran a series of phylogenetic generalized linear models (PGLM logistic regression using the “phyloglm” function; 2000 bootstraps; using the “phylom” package; Tong Ho & Ané, 2014) to test for the predictive power of foraging mode (as a binomial variable: active forager = 0; sit-and-wait forager = 1) on species threat status and population trends. Phylogenetic generalized least squares were performed to assess the link between foraging mode and extinction risk (using the “ppls” function in “phytools” with the lambda set to “ML” to optimize branch length transformations).

Next, we performed phylogenetic path analyses to assess the interrelation among foraging mode, threat status, and (log-transformed) geographic range size (“define_model_set” and “phylo_path” functions; “phylopath” package; van der Bijl, 2018). We included geographic range size given that it is a strong correlate of extinction risk in many terrestrial vertebrate taxa and is used by the IUCN as a listing criterion (Cox et al., 2022; Purvis et al., 2000)—and especially so for squamates (Meiri et al., 2023). We built structural equation models that compared three scenarios on how range size and foraging model can indirectly and directly affect the probability of being threatened (Figure S1). The highest ranked scenario (based on the C-statistics Information Criterion; Gonzalez-Voyer & Hardenberg, 2014) was considered the most likely causal scenario. All analyses were run three times: (1) on the dataset containing all squamates, (2) solely on ophidian squamates (“snakes”), and (3) exclusively on nonophidian squamates (“lizards”).

3 | RESULTS

Of the 1543 squamate species in this study, 62.2% were reported as active foragers and 37.8% as sit-and-wait foragers (Fig. 1; Table S1). A total of 11.3% of the squamates in our dataset are considered threatened and 18.5% show negative population trends, while most squamates are not threatened (88.7%) and show stable (and rarely, increasing) population trends (81.5%). The near 3/2 ratio of number of species that are active versus sit-and-wait foragers as observed in the global dataset was also seen in the threatened species (63.2% vs. 36.8%) and species with negative population trends (59.2% vs. 40.8%), and not under threat (62.0% vs. 38%) and with stable or positive population trends (62.2% vs. 37.8%) (threat status: $\chi^2 = 0.05$, $p = 0.822$; population trend: $\chi^2 = 0.51$, $p = 0.476$).

When we considered lizards and snakes separately, ratios slightly shifted but importantly revealed opposite patterns in the two lineages. In lizards, the proportion of species under threat that are active foragers (14.1%)

was approximately 1.4 times higher than the proportion of sit-and-wait foragers under threat (10.1%) ($\chi^2 = 3.38$, $p = 0.066$). Likewise, the proportion of active-foraging lizards with a negative population trend (20.0%) was 1.4 times higher than the proportion of sit-and-wait foragers with a negative population trend (14.3%) ($\chi^2 = 3.65$, $p = 0.056$). The opposite was true in snakes, where the proportion of sit-and-wait foragers under threat (14.0%) was about twice the proportion of active foragers that are under threat (7.6%) ($\chi^2 = 3.84$, $p = 0.049$), and the proportion of sit-and-wait foraging snakes with a negative population trend (42%) was nearly three times the proportion of active-foraging snakes with a negative population trend (14.7%) ($\chi^2 = 26.70$, $p < 0.001$).

Tests for phylogenetic signal revealed a slightly negative D value for squamate foraging mode (-0.05), which significantly differed from the value of 1 expected at random ($p < 0.001$), but not from 0 expected under Brownian motion ($p = 0.666$), indicating a clumped phylogenetic pattern. Conservation status, in contrast, was unrelated to phylogeny (threat status: $D = 0.71$, $p_0 < 0.001$, $p_1 < 0.001$; population trend: $D = 0.69$, $p_0 < 0.001$, $p_1 < 0.001$; extinction risk, $\lambda = 0.39$, $p_0 < 0.001$ and $K = 0.11$, $p_0 = 0.13$).

The opposing trends in lizards versus snakes meant that, in squamates overall, foraging mode failed to predict threat status (binomial; $n = 1543$, $\beta \pm SE: 0.307 \pm 0.185$, $z = 1.656$, $p = 0.098$), population trend (negative or stable; $n = 1085$, $\beta \pm SE: 0.086 \pm 0.181$, $z = 0.476$, $p = 0.634$), or extinction risk category ($n = 1543$, $\beta \pm SE: -0.139 \pm 0.072$, $t = -1.934$, $p = 0.053$). However, foraging mode was a significant predictor of species conservation status when we considered lizards and snakes separately. Lizard active foragers were more often threatened ($n = 1029$, $\beta \pm SE: -0.562 \pm 0.216$, $z = -2.598$, $p = 0.009$), experienced high risks of extinction ($n = 1029$, $\beta \pm SE: -0.214 \pm 0.087$, $z = -2.472$, $p = 0.014$), and had negative population trends ($n = 725$, $\beta \pm SE: -0.592 \pm 0.232$, $z = -2.558$, $p = 0.011$). In contrast, sit-and-wait snakes were more likely to be under threat ($n = 514$, $\beta \pm SE: 1.087 \pm 0.401$, $z = 2.708$, $p = 0.007$) and show declining populations ($n = 360$, $\beta \pm SE: 1.161 \pm 0.316$, $z = 3.674$, $p < 0.001$). Snake extinction risk category was not significantly linked to foraging mode ($n = 514$, $\beta \pm SE: 0.004 \pm 0.131$, $t = 0.034$, $p = 0.973$).

Based on phylogenetic path analyses that incorporated range size, the most plausible links between foraging mode and threat status differed between lizards and snakes (Fig. 2; Table S2). In lizards, the best-fit scenario was one in which foraging mode affected threat status indirectly through range size: active-foraging lizards exhibited smaller ranges (standardized estimate: $+0.153 \pm 0.087$), which negatively affected threat status (-1.599 ± 0.135). Indeed, when statistically correcting for range size ($\beta \pm SE: -0.892 \pm 0.105$, $z = -8.480$, $p < 0.001$), foraging mode

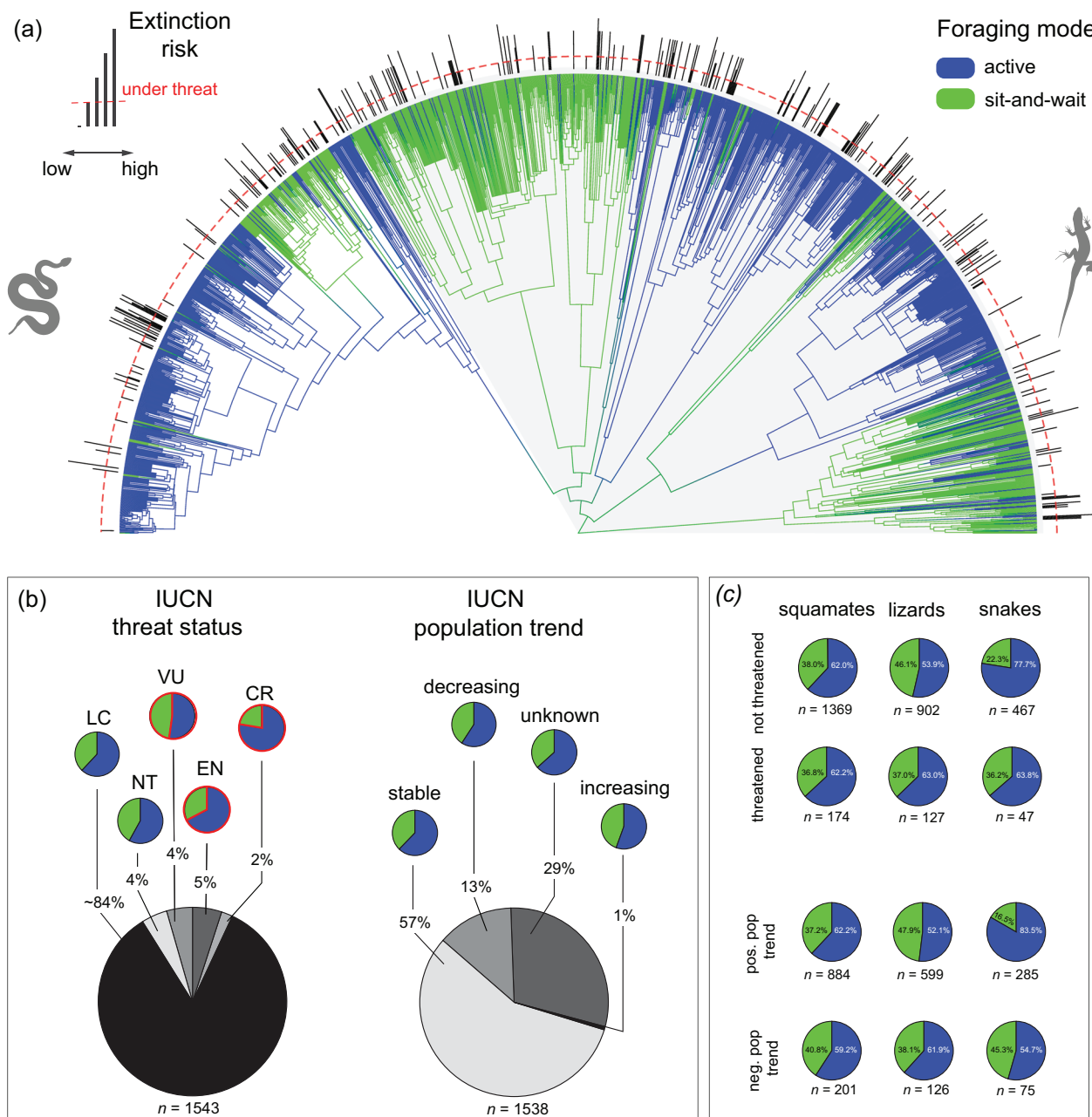


FIGURE 1 (a) Phylogenetic relationships among the 1543 squamate species included in this study with branch colors showing ancestral character state estimation of foraging mode along the branches. Bars at the tree tips denote species' risk of extinction; species with bars crossing the red dotted line indicate that they are under threat. The gray overlay indicates the lizard clade in the phylogenetic tree. (b) Diagrams visualizing proportions of species as categorized under IUCN Red List of Threatened Species. (c) Diagrams visualizing the proportions of active (blue) and sit-and-wait (green) foragers under threat (top) and showing a neutral or negative population trend (bottom) for squamates, and for lizards and snakes separately.

was no longer a significant predictor of threat status in lizards ($\beta \pm SE: -0.350 \pm 0.202, z = -1.732, p = 0.083$). In snakes, the best-supported scenario has range size and foraging mode independently affecting threat status: an ambush foraging mode increased the probability of being threatened ($+0.891 \pm 0.434$), as did a small range size (-1.419 ± 0.183). Correcting for range size ($\beta \pm SE: -1.148 \pm 0.150, z = -7.648, p < 0.001$), thus, did not alter

the significant effect of foraging mode on threat status in snakes ($\beta \pm SE: 0.976 \pm 0.434, z = 2.249, p = 0.025$).

4 | DISCUSSION

A central goal of contemporary conservation research is to identify what makes one species more prone to extinction

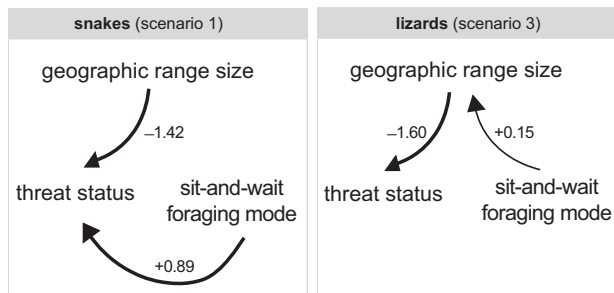


FIGURE 2 Illustration of the best-supported phylogenetic path for snakes (left) and lizard (right) explaining how foraging mode and geographic range size directly or indirectly affect species' probability of being threatened.

than another, particularly in taxa historically neglected in global conservation assessments, such as reptiles (Böhm et al., 2013; Cox et al., 2022; Luiselli, 2006; Roll et al., 2017). Focusing on squamates, we examined the predictive value of a key, yet largely overlooked, ecological trait—foraging mode—on species' threat status. Our analyses on snakes revealed the same pattern already reported in Reed and Shine's (2002) study of Australian elapids: that is, ambush-foraging snakes are more at risk than active searchers. Our study is based on >20 times more species (1543 vs. 69), is distributed globally (rather than in one continent), and shows that ambush-foraging snakes exhibit a higher proportion of declining populations as well as a higher level of threat to population persistence compared to actively foraging ones. Surprisingly, however, we found the reverse pattern in lizards: ambush foraging was associated with a lower not higher risk of extinction and population decline.

The analyses in which we incorporated geographic range size reinforce the different pathways to endangerment in lizards versus snakes. In lizards, range sizes were smaller in active foragers than in ambush foragers, and foraging mode had no significant effect on conservation status if we included range size in the analysis. The apparent link between active foraging and endangerment in lizards may be an indirect consequence of links between foraging mode and ecosystem type rather than directly causal. In snakes, on the other hand, foraging mode was not linked to range size and remained a significant predictor of endangerment even when range size was included in the analysis.

Why did lizards and snakes show such different patterns in our analysis? One clue to that divergence may lie in the biology of ambush predation. In particular, the link between ambush predation and low feeding rates seen in snakes that take relatively large and rare vertebrate prey (Glaudias et al., 2019) may not apply to many ambush-foraging lizards that feed on small abundant invertebrate prey (i.e., social insects). For example, the ambush-foraging horned lizards (*Phrynosoma*) are

renowned for high rates of feeding, and field observations have recorded the ingestion of hundreds of prey items per hour by lizards that wait beside ant trails (Huey & Pianka, 1981). Consistent with that idea, rates of reproduction (number of clutches or litters per year) are high in many ambush-foraging lizards (Huey & Pianka, 1981; Vitt & Congdon, 1978), but low in ambush-foraging snakes (Reed & Shine, 2002). Indeed, in our data, ambush-foraging lizards have clutch sizes that are, on average, 1.7 times higher than those of actively searching ones, whereas in snakes the ratio is 0.77. A direct link driven by trophic level is also possible: many ambush-foraging snakes eat mostly active-searching lizards (Huey & Pianka, 1981), so threats to the latter group may imperil the former.

The causal links between foraging mode and conservation status undoubtedly differ within as well as between clades. For example, research on snakes of both foraging modes in southeastern Australia suggests that the ambush-foraging *H. bungaroides* is at risk because of low feeding rates (and thus, low reproductive rates), low dispersal rates (and thus, inability to recolonize areas from which it has been extirpated), and reliance upon scarce and highly specific (but seasonally divergent) habitats for predation (Webb et al., 2002a). However, this ambush-forager species was less affected by an intense wildfire than was a sympatric active-searching taxon (*Cryptophis nigrescens*) because the resultant lack of tree cover increased vulnerability of the more mobile species to avian predation (Webb & Shine, 2008). In contrast, the high vulnerability of an imperiled ambush forager in tropical Australia (*Acanthophis praelongus*) to a lethally toxic invasive amphibian (the cane toad *Rhinella marina*) was mediated by the snake's use of caudal luring to attract prey. Cane toads were more likely to stimulate luring, and to approach such a lure, than were native frogs or lizards (Hagman et al., 2009). Unlike many other ambush-foraging snakes, this species also exhibits fast growth and early maturation (Webb et al., 2002b). Thus, ambush foraging imperils these two ambush-foraging snakes via different mechanisms.

Large-scale analyses such as our own are valuable for identifying patterns but have limited power to tease apart causal effects (Cardillo & Meijaard, 2012). The correlations that we identified suggest that a reptile's foraging mode influences its conservation status, but do not identify the precise pathways by which such effects occur. In the case of squamates, complex links between foraging mode and behavior, physiology, ecology, and life history (Reilly et al., 2007; Vitt et al., 2003) render many causal effects plausible. At present, all we can do is document the patterns and speculate on reasons for the associations that emerge. Future work could usefully examine these links in more detail and especially look at the ecology of threatened species to document foraging modes and life histories

with greater precision. The way in which a snake or lizard obtains its food appears to influence its vulnerability to extinction, but the reasons for that link remain elusive.

Our findings may have implications for reptile conservation policies and management practices. We suggest that data on foraging mode should be incorporated into reptile vulnerability assessments. Approximately 28% of all reptile species remain unassessed and about 14% of those assessed are “data deficient” (i.e., not assigned a risk category) (Caetano et al., 2022). Knowing the foraging mode of such nonclassifiable species can be a first proxy for their true threat status. An understanding of mechanistic links between foraging mode and extinction risk can clarify potential impacts of threats such as extreme wildfires and climatic events (e.g., foraging mode may affect how changes in vegetation density affect feeding rate and exposure to predation: Webb et al., 2002a). The sedentary nature, low rates of prey encounter, and high fecundity of many ambush-foraging snakes make them ideal candidates for setting up “insurance” captive populations whereby individuals can be maintained in small enclosures and induced to reproduce at high rates by provision of abundant prey, or such prey can be provided to free-ranging individuals in the field (e.g., Shine et al., 2002; Taylor et al., 2005).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data can be found in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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