

Running title: Evolution of reproductive effort

32 **Abstract**

33 Life-history theory predicts that the optimal reproductive effort of an organism is affected by
34 factors such as energy acquisition and predation risk. Although this is a major focus of study in
35 evolutionary ecology, the empirical evidence consists of conflicting data on a few organisms. For
36 instance, theoretical models within the foraging mode paradigm suggest that widely foraging
37 females have evolved low reproductive effort, because a heavy reproductive load decreases their
38 ability to escape from predators. By contrast, a long-standing prediction of evolutionary theory
39 indicates that organisms subject to high mortality due to predation, as suggested for widely
40 foraging species, should increase their reproductive investment. Here, we revise the available
41 literature on the relationship between foraging mode and reproductive effort of lizards. In doing
42 so, we present evidence that widely foraging species have evolved greater reproductive effort
43 than sit-and wait species. This is the largest comparative analysis of foraging mode and
44 reproductive effort to date: 485 species grouped in 32 families. Based on our findings, we
45 propose a theoretical model derived from the optimal foraging theory that potentially explains the
46 observed patterns in lizards, paving the way for ecologist to test mechanistic hypotheses at the
47 intraspecific level.

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49 **Main Text**

50 **Introduction**

51

52 The foraging behaviors of vertebrates lie along a continuum, ranging from the energetically
53 demanding strategy of foraging actively to the energetically conservative strategy of sit-and-wait
54 foraging (Pianka 1966; Perry 1999). Over the past 50 years, ecologists have developed a set of
55 hypotheses about how an organism's foraging mode relates to its life history (Vitt & Congdon
56 1978; Vitt & Price 1982; Dunham *et al.* 1988; Webb *et al.* 2003). These relationships stem from
57 two major assumptions (Fig. 1). First, widely foraging animals spend more energy to forage than
58 a sit-and-wait foragers, but might also consume enough food to have more surplus energy
59 (Anderson & Karasov 1981, 1988; Huey & Pianka 1981; Nagy *et al.* 1984; Stuginski *et al.* 2018;
60 Bury 2021). However, sit-and-wait foragers might exhibit wider diet breadths, because they
61 encounter prey less frequently compared to active foragers (Glaudas *et al.* 2019). Second, a
62 widely foraging animal could suffer a greater risk of mortality because its movements are
63 conspicuous to predators (Cooper & Perez-Mellado 2004). Both a greater energy supply and a
64 greater mortality risk would select for genotypes that allocate more energy to reproduction,
65 manifested as more or larger offspring (Bonnet *et al.* 2001; Silva *et al.* 2020). The evolution of
66 greater reproductive effort could feed back on the energy gain and mortality risk if a female
67 carrying a greater mass of offspring tends to chase prey (Shine 1980). Similarly, the load
68 associated with food consumption may compromise the locomotion of individuals, increasing the
69 vulnerability to predators (Werner & Anholt 1993; Cooper 2000). In this model, a suite of traits
70 associated with foraging mode would coadapt to the spatiotemporal distributions of prey and
71 predators.

72

73 Despite the wealth of conjecture, these hypothetical relationships among foraging mode
74 and other traits have been assessed in only a handful of cases, as described above. Ideally, one
75 would isolate each relationship and conduct experiments to quantify the evolution of traits in

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76 controlled environments (Huey & Bennet 1986). However, such data are difficult to gather for
77 many species and will probably remain rare. For instance, limited circumstantial evidence exists
78 for the putative relationship between foraging mode and predation risk. Data on stomach contents
79 of field-collected vipers suggested that widely foraging lacertids are more vulnerable to predators
80 than sedentary species (Huey & Pianka 1981), but a number of confounding factors can explain
81 this observation as well as foraging mode can. Alternatively, researchers have evaluated the
82 relationship between mortality and life-history traits with no emphasis on foraging behavior. For
83 example, experimental evolution with guppies and fruit flies revealed that genotypes that evolved
84 in risky environments developed more rapidly, matured at a smaller size, and reached their peak
85 of fecundity faster than did genotypes that evolved in safe environments (Stearns 2000; Reznick
86 *et al.* 2001). From these results, we expect that a high rate of predation selects for greater
87 reproductive effort, but given the scarce evidence, it is still uncertain whether foraging mode
88 generally affects predation risk or net energy gain.

89

90 Although experimental data are lacking, comparative methods have been used to explore
91 how foraging mode and life-history traits have evolved. These interspecific analyses have
92 focused mostly on the reproductive effort of lizards. The earliest analysis of 22 species revealed
93 an unexpected pattern: sit-and-wait species had a greater reproductive effort than widely foraging
94 species (Vitt & Congdon 1978). The authors suggested that widely foraging species might be
95 forced to carry fewer or smaller offspring, because moving long distances with a voluminous
96 clutch decreases the chance of escaping from a predator. A subsequent analysis of data for 50
97 species of lizards supports this result by testing a model in which predation risk increased with
98 increasing reproductive effort (Vitt & Price 1982). Consecutively, Roff (2002) extended support for
99 this model in a comparative analysis of 130 lizard species. However, none of these early
100 analyses controlled for potential phylogenetic correlations that might generate spurious
101 relationships between foraging mode and reproductive effort (Felsenstein 1985), especially
102 because foraging could vary greatly among but little within families. A more recent analysis, using

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103 phylogenetic comparative methods, failed to detect a significant relationship between foraging
104 mode and reproductive effort (Mesquita *et al.* 2016). Thus, despite several attempts to establish a
105 relationship between foraging mode and the life history, we still lack support for a long-standing
106 prediction of the foraging-mode paradigm.

107

108 Here, we present the first evidence that widely foraging species have evolved greater
109 reproductive effort than sit-and wait species. This evidence comes from the largest comparative
110 analysis of foraging mode and reproductive effort to date: 485 species of lizards representing 32
111 families. In this analysis, we inferred the evolutionary history of foraging modes, complementing
112 on past reconstructions of ancestral states (Miles *et al.* 2007). In contrast to previous analyses,
113 our study supports the prediction of theoretical models of the optimal reproductive effort, paving
114 the way for ecologists to test mechanistic hypotheses at the intraspecific level.

115

116 **Materials and Methods**

117

118 ***Data source and description of variables***

119 We used published estimates of life history and foraging behavior for 485 species of lizards
120 grouped in 32 families, excluding amphisbaenians and snakes. These data represent a subset of
121 a data assembled from primary and secondary literature on lizards' traits published during the last
122 12 years (Meiri 2018). The reproductive effort of the species was defined as the product of the
123 mean snout-vent length of hatchlings or neonates (mm) and the mean clutch or litter size. Given
124 the limited data available for clutch frequency in widely foraging and sit-and-wait species, we
125 could not examine the lifetime reproductive effort of lizards. Instead, our measure represents the
126 investment of females in a single reproductive event. Our measure of maternal size consisted of
127 the mean snout-vent length of adult females. We used the length of hatchlings rather than the
128 mass of eggs, because the latter might reflect high water content rather than energy content in

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129 lizards that lay poorly calcified eggs (Deeming 2004; Meiri *et al.* 2015). Moreover, hatchling size
130 can be measured for viviparous species as well as oviparous species.

131

132 Although relative clutch mass is commonly reported as an index of reproductive effort, we
133 used a different index to avoid statistical issues associated with analyzing a ratio. Ratios of
134 random numbers regressed against their denominator will automatically yield negative
135 correlations (Atchley *et al.* 1876; Packard & Boardman 1988). For example, a comparative study
136 of 551 species of lizards revealed a negative effect of maternal size on relative clutch mass (Meiri
137 *et al.* 2012). This result is difficult to interpret as it contrasts with most theoretical models, which
138 predict that relative clutch mass should increase with maternal size (Roff 2002)—a pattern
139 observed in many organisms (e.g., Primack 1979; Barneche *et al.* 2018; Marshall *et al.* 2021).

140

141 We defined the foraging mode of a species based on whether it has been reported as an
142 ambush predator (“sit-and-wait”), an active forager (“widely foraging”), or uses a mixed strategy
143 (“mixed”). Although this categorization seems somewhat artificial and simplistic, numerous
144 species of lizards clearly belong to one of these categories (Huey & Pianka 1981; Perry 1999).
145 We focused our analyses only on carnivores, because herbivores do not fit into the classical
146 paradigm of foraging modes (Pianka & Vitt 2003).

147

148 ***Ancestral character and phylogenetic signal estimates***

149 To determine the appropriate model of evolution, we used a set of continuous-time discrete-state
150 Markov chain models to sample the character histories from their posterior probability distribution
151 (Huelsenbeck *et al.* 2003), and a time-calibrated phylogeny of squamate reptiles (Zheng & Wiens
152 2016). We rooted the tree with the Tuatara (*Sphenodon punctatus*) as the outgroup for our study
153 taxa. Based on previous analyses, we coded this outgroup as a sit-and-wait forager (Pianka & Vitt
154 2003; Vitt *et al.* 2003). We fitted three different models to our data, using the function
155 *make.simmap* from the R package “phytools” version 0.7.80 (Revell 2012; R Core Team 2021).

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156 These models were as follows: 1) an equal rates model (ER), in which the rate of change
157 between all three states of the character are assumed to be equivalent; 2) an all-rates-different
158 model (ARD), which allows the transitions among states to have different rates; 3) and a
159 symmetrical model (SYM), which allows different rates of change between pairs of states but
160 changes between all states are theoretically possible. For each model, we estimated the
161 stationary distribution by numerical solving for ρ_i ($\rho_i = \text{'estimated'}$), and this was used as prior
162 distribution on the root node of the tree. These models sample the character histories conditioned
163 on the transition matrix (Q matrix) and use the phylogenetic tree with annotated tips to create
164 stochastic simulation maps for the potential evolutionary transitions between foraging modes. To
165 describe the variation in reproductive effort across the study taxa, we plotted bars adjacent to the
166 tips of the phylogeny representing values of species reproductive effort. We selected the most
167 likely model of evolution based on the Akaike Information Criterion (AIC). Lastly, we generated
168 10000 trees of the most-likely model and used the *summary* function to count the total number of
169 transitions that occurred between character states (see supporting material for detailed
170 information).

171

172 We computed our measure of phylogenetic signal (or character dispersion on a
173 phylogeny) by using the Fritz and Purvis' *D test*, available through the function *phylo.d* in the R
174 package "caper" version 1.0.1 (Fritz & Purvis 2010; Orme *et al.* 2018; R Core Team 2021). This
175 parameter is calculated as follows:

176

177
$$D = \frac{[\sum d_{obs} - \text{mean}(\sum d_b)]}{[\text{mean}(\sum d_r) - \text{mean}(\sum d_b)]}$$

178

179 where d_{obs} equals the number of character-state changes required to get the observed
180 distribution of character states at the tips of the phylogeny. The d_{obs} is then scaled using two null
181 distributions. The first distribution, d_r , comprises d values obtained from permutations where the

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182 number of species with each character state is kept constant, but the values are shuffled on the
183 tips of the phylogeny. Thus, d_r is the expected distribution of d values if character states are
184 randomly distributed among species without respect to phylogeny. The second distribution, d_b ,
185 comprises the d values expected if character states are distributed among species under the
186 expectations of the Brownian motion model of evolution. We generated d_b by simulating a
187 continuous trait along the phylogeny, then defining the character state at each tip according to
188 some threshold value of the continuous trait (Fritz & Purvis 2010). The value of D equals 1 if the
189 distribution of the binary trait is random with respect to phylogeny, and exceeds 1 if the
190 distribution of the trait is more overdispersed than the random expectation. The value of D equals
191 0 if the binary trait is distributed as expected under the Brownian motion model of evolution, and
192 is less than 0 if the binary trait is more phylogenetically conserved than the Brownian expectation.
193 The distributions d_r and d_b were used to assign p – values to d_{obs} . Accordingly, if d_{obs} is larger
194 than 95% of d_r values, the distribution of the trait would be significantly more overdispersed than
195 the random expectation, if d_{obs} is less than 95% of d_b values, the character would be significantly
196 more clumped than the Brownian expectation.

197

198 ***Effects of body length and foraging mode on reproductive effort***

199 We fitted Phylogenetic Generalized Least Squares models (PGLS) to test our prediction on the
200 relationship among body length, foraging mode, and the reproductive effort of lizards. In
201 comparative biology, normal regression models cannot be used because the assumption of
202 independence of residuals is violated (Felsenstein 1985; Harvey & Pagel 1991). This problem can
203 be corrected using phylogenetic comparative methods. We fitted the models using the function
204 *gls* from the R package “nlme” version 3.1-152 (Pinheiro *et al.* 2021; R Core Team 2021). We
205 adopted the reproductive effort of lizards as our response variable. Similarly, maternal length and
206 foraging mode corresponded to our predictor variables. We fitted the models assuming two ways
207 in which the tree structure was expected to affect the covariance in trait values across taxa
208 (corBrownian and corPagel —value = 0— error structures, using the R package “ape”). We

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209 selected the best-fit model based on the AIC values (see supporting material for detailed
210 information). To avoid confounding results due to a potential large variation in maternal length
211 among species, we not only tested our prediction for all lizards in our data set (Fig. 3A), but also
212 examined the data at lower taxonomic scales (e.g., within the superfamily Scincoidea; Fig. 3B).
213 Analyzing the data at different taxonomic scales enabled us to better investigate the level of
214 support for the prediction tested.

215

216 **Results**

217

218 The evolutionary transitions in foraging modes among lizards were best described by a model in
219 which rates of evolution differ among modes, referred to as the all-rates-different model. Despite
220 a slightly difference with the widely foraging state, our analysis revealed that sit-and-wait foraging
221 is the most likely ancestral state of all lacertilians (Fig. 2). Sit-and-wait foraging has evolved in two
222 major clades of lizards; near the root of the tree, we found strong evidence suggesting that the
223 ancestor of Gekkota was a sit-and-wait predator. Likewise, the ancestor of iguanians was a sit-
224 and-wait predator. Iguanians included in our analysis are part of both the Acrodonta and
225 Pleurodonta clades. During the early Jurassic (≈ 200 mya), a major transition from sit-and-wait to
226 widely foraging occurred in the ancestor of Anguimorpha, Lacertoidea, and Scincoidea. Since
227 then, a reverse transition from widely foraging to sit-and-wait foraging occurred within Scincoidea,
228 in the ancestor of spiny-tailed lizards and night lizards (Cordylidae and Xantusiidae). The
229 estimate of the D test for phylogenetic signal indicated that foraging mode is phylogenetically
230 conserved as expected under a Brownian motion model of evolution ($D = -0.14$, $p[D < 1] = 0$,
231 $p[D > 0] = 0.80$).

232

233 Our analyses show that widely foraging species have evolved greater reproductive effort
234 than sit-and-wait species. However, the mechanism underlying this pattern is mediated by a
235 complex interaction between foraging mode and maternal length (Table 1). In Lacertilia, widely

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236 foraging species have greater reproductive effort for two reasons: 1) they are larger in size, and
237 2) on average, they give birth to a higher number of offspring for a given size (Fig. 3A). In the
238 superfamily Scincoidea, widely foraging species evolved greater reproductive effort despite
239 having a smaller mean body length (Fig. 3B). Interestingly, skinks that adopt a mixed foraging
240 behavior have also evolved greater reproductive effort than sit-and-wait skinks.

241

242 **Discussion**

243

244 Our results show that widely foraging species have evolved a greater reproductive effort than sit-
245 and-wait species. Presumably, the ability of widely foraging lizards to harvest and assimilate more
246 resources might explain this pattern. Studies on field metabolic rate of free-ranging lizards
247 suggest that an average widely foraging species spends 32% more daily energy than a sit-and-
248 wait lizard, but this extra energy expenditure is probably paid off with greater daily food
249 consumption (Brown & Nagy 2007). Food consumption may play an important role in determining
250 the reproductive effort of lizards in three ways: 1) it promotes follicular growth during the
251 reproductive season; 2) in the long term, it increases energy stores to initiate reproduction (e.g.,
252 vitellogenesis). and 3) it may also reduce age at first reproduction. Consistent with these ideas,
253 Bonnet and colleagues found that female vipers that had good body condition early in
254 vitellogenesis produced large litters (Bonnet *et al.* 2001). Similarly, vipers that gained more mass
255 during follicular growth produced larger offspring. Early reproduction gives offspring sufficient time
256 to mature in the same year that they hatched, which enables them to participate as adults in the
257 subsequent breeding season (Hahn & Tinkle 1965). Therefore, the foraging behavior of a widely
258 foraging female can increase the amount of gametic resources gathered before and during each
259 reproductive bout, potentially resulting in more energy to invest in reproduction.

260

261 Additionally, maternal size also plays an important role in determining the reproductive
262 effort of lizards. Among many ectotherms and plants, a common pattern is that reproductive effort

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263 increases with size (Tinkle 1967; Primack 1979; Bownds *et al.* 2010; Barneche *et al.* 2018;
264 Marshall *et al.* 2018, 2021). This observation indicates that increased size might evolve by natural
265 selection, because it increases the fitness of individuals. Interestingly, our results paint a more
266 complex picture of the effect of body size on reproductive effort. We found that the relationship
267 between maternal length and reproductive effort depends on foraging mode. The most complex
268 form of relationship occurs when small widely-foraging females have a greater reproductive effort
269 than large sit-and-wait females (Fig. 3B). A model of the evolution of optimal reproductive effort
270 predicts this pattern (Parker & Begon 1986). This model suggests that the total energy
271 accumulated for reproduction (m) depends on the time spent foraging (t) and maternal size.
272 Assuming that females have the same foraging efficiency, smaller females would reach their
273 maximum capacity to accumulate resources at lower values of m , producing fewer or smaller
274 offspring than larger females (Fig. 4A). However, if a widely foraging female has a smaller body
275 size but a higher foraging efficiency, she may have greater reproductive investment than a large
276 sit-and-wait female (Fig. 4B). The same outcome should be observed if a widely foraging female
277 is both a larger and more efficient forager than a sit-and-wait female (Fig. 4C). Furthermore, if
278 widely foraging females are more efficient at foraging, they may have both a shorter foraging time
279 and a reduced interclutch interval. Therefore, widely foraging females might not only produce
280 larger or more offspring in a single clutch, but they might also increase the number of clutches
281 throughout their lifetime.

282

283 Because the risk of predation presumably depends on the time spent foraging, individuals
284 that require less time to accumulate the optimal amount of resources should incur a lower
285 probability of death. Based on the theory of foraging by Schoener, the energy accumulated from
286 foraging increases monotonically toward an asymptote (Schoener 1971). In such cases, the law
287 of diminishing returns implies that foraging for twice as long would not result in twice the energetic
288 return (Fig. 4B). Therefore, greater foraging efficiency (more energy gain per foraging time)
289 should enable an organism to survive better in environments with high predation risk. Consistent

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290 with this idea, a study on foraging efficiency (defined as ratio of metabolizable energy gained
291 while foraging to the energy spent while foraging) partially indicates that widely foraging lizards
292 spent less time foraging but grew larger than did sit-and-wait lizards (Nagy *et al.* 1984). Indeed,
293 our results show that widely foraging lizards are, on average, larger than sit-and-wait lizards (Fig.
294 3A). The ability of widely foraging species to rapidly outgrow a sit-and-wait species may also
295 enable them to outgrow the gape limitations of predators (Lynch 1980; Reznick & Endler 1982).
296 Furthermore, when competition for mates is crucial, the winner of a mating-contest between two
297 competitors is generally the larger individual (Roff 2002). Therefore, if body size is critical to
298 outperform predators and outcompete conspecifics, the optimal pattern may be to grow to the
299 maximal size that leads to the greatest reproductive effort.

300

301 The foraging mode paradigm is mostly focused on dichotomous variation, yet plastic
302 variation in foraging mode may drive the evolution of the reproductive effort in some species.
303 Recent studies have revealed that the foraging mode of an organism depends on the ecological
304 context, such as presence of predators, abundance of prey, or habitat degradation (Greef &
305 Whiting 2000; Hawlena & Perez-Mellado 2009; Wasiolka *et al.* 2009; Donihue 2016). Such
306 plasticity could precede rapid evolutionary change and local adaptation of the life history
307 (Richardson *et al.* 2014). Our results show a strong presence of species that adopt a mixed
308 foraging strategy in the superfamilies Anguimorpha, Gekkota, Iguania, and Scincoidea (Fig. 2).
309 Interestingly, these lizards have greater reproductive effort than do sit-and-wait lizards,
310 specifically for species of relative small size (Fig. 3B). Because mixed foraging species are often
311 exposed to a wide range of environments with different selective pressures, these species might
312 actively select habitats that maximize their reproductive effort, indirectly resulting in local
313 adaptation (Richardson *et al.* 2014). Our analysis, which provides the first evidence that a mixed
314 foraging strategy can lead to greater reproductive effort, should encourage others to address the
315 questions raised by this discovery.

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317 Our study presents the first evidence that the early shift in foraging mode—from sit-and-
318 wait to widely foraging—in the evolutionary history of lacertilians was accompanied by the
319 evolution of a greater reproductive effort in most widely foraging species (Fig. 3). Based on the
320 theory of optimal foraging, we propose a theoretical model that potentially helps to better
321 understand the evolution of the optimal life-history strategy. This model is emphasized on a
322 complex covariation between energy gain, maternal size, and foraging mode. Investigating how
323 much energy an individual obtains from the environment is crucial in life-history analysis because
324 the flux of energy within an organism not only determines its survival, but also whether it can
325 engage in reproduction, a very evolutionarily important activity. Currently, analyses of the
326 energetics of foraging modes stem from measures of a few species in short periods of a season.
327 Such data overlook the physiological and ecological constraints of seasonality on some
328 organisms. For example, widely foraging lizards in the Kalahari Desert consume more food during
329 the summer, but stop eating during winter as they hibernate. By contrast, sit-and-wait lizards
330 probably forage during both seasons as they remain active during winter (Huey *et al.* 2021).
331 Evidence of this nature is still rare in the current literature, revealing the need for long-term
332 studies on the energetics of foraging modes. Similarly, direct comparisons of mortality rates in
333 widely foraging versus sit-and-wait species are required, as the existing data prevent us from
334 making convincing conclusions on the relationship between foraging mode and vulnerability to
335 predation. Finally, our study captured the effects of foraging plasticity on the evolution of the
336 reproductive effort of lizards. Overall, lizards that adopt a mixed foraging strategy also have
337 greater reproductive effort than do sit-and-wait species. This result suggests that foraging
338 plasticity can result in differential reproductive effort and opens the question for future studies of
339 whether the foraging efficiency and predation risk of each mode influence the evolution of
340 fecundity in species that forage plastically.

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344 **Acknowledgments**

345

346 We thank Mark O'Shea for providing us with lizard photos for data visualization. We also thank

347 Gustavo Burin for his valuable comments on an early draft of our manuscript.

348

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350

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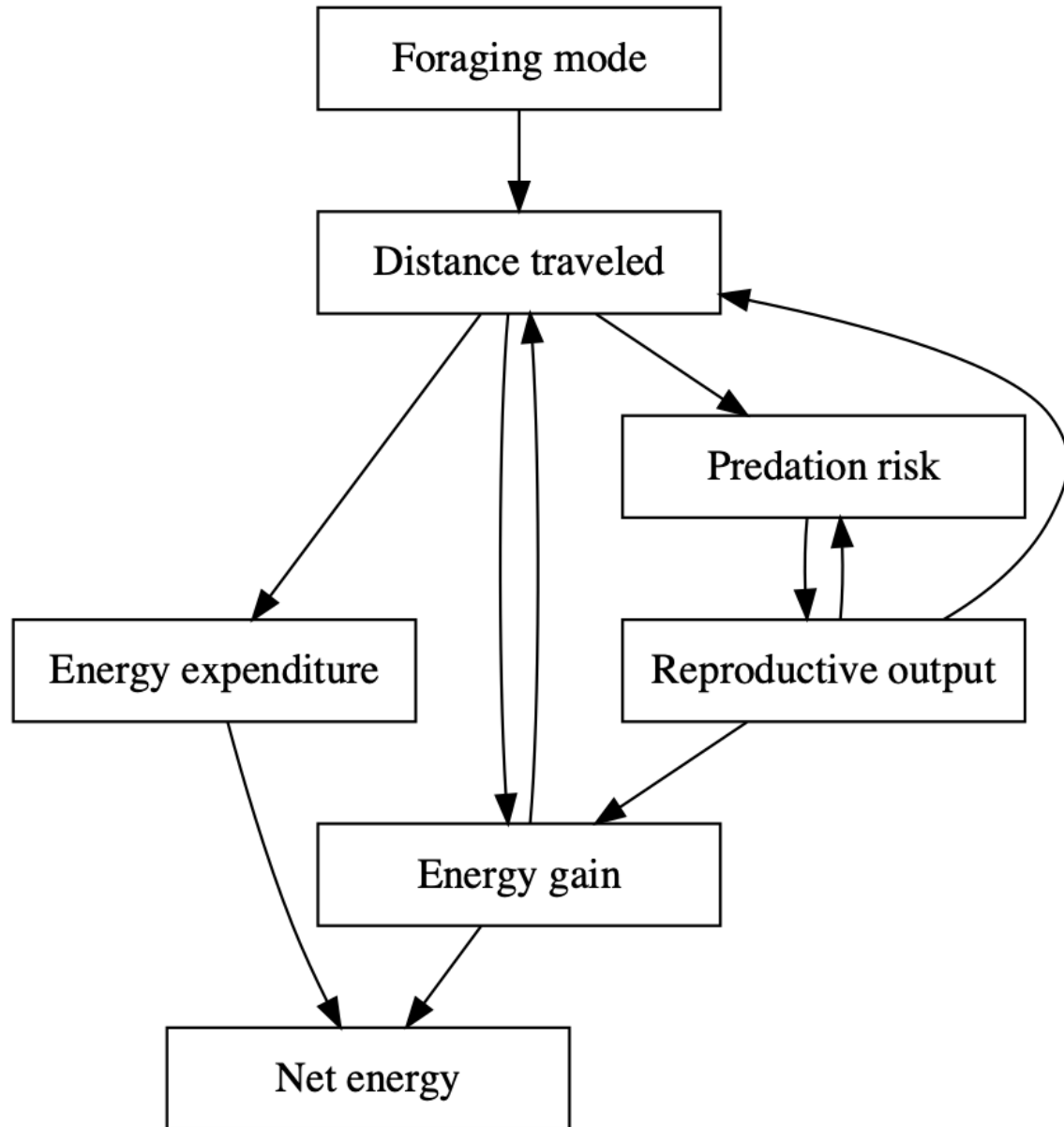
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484 **Figures and Tables**

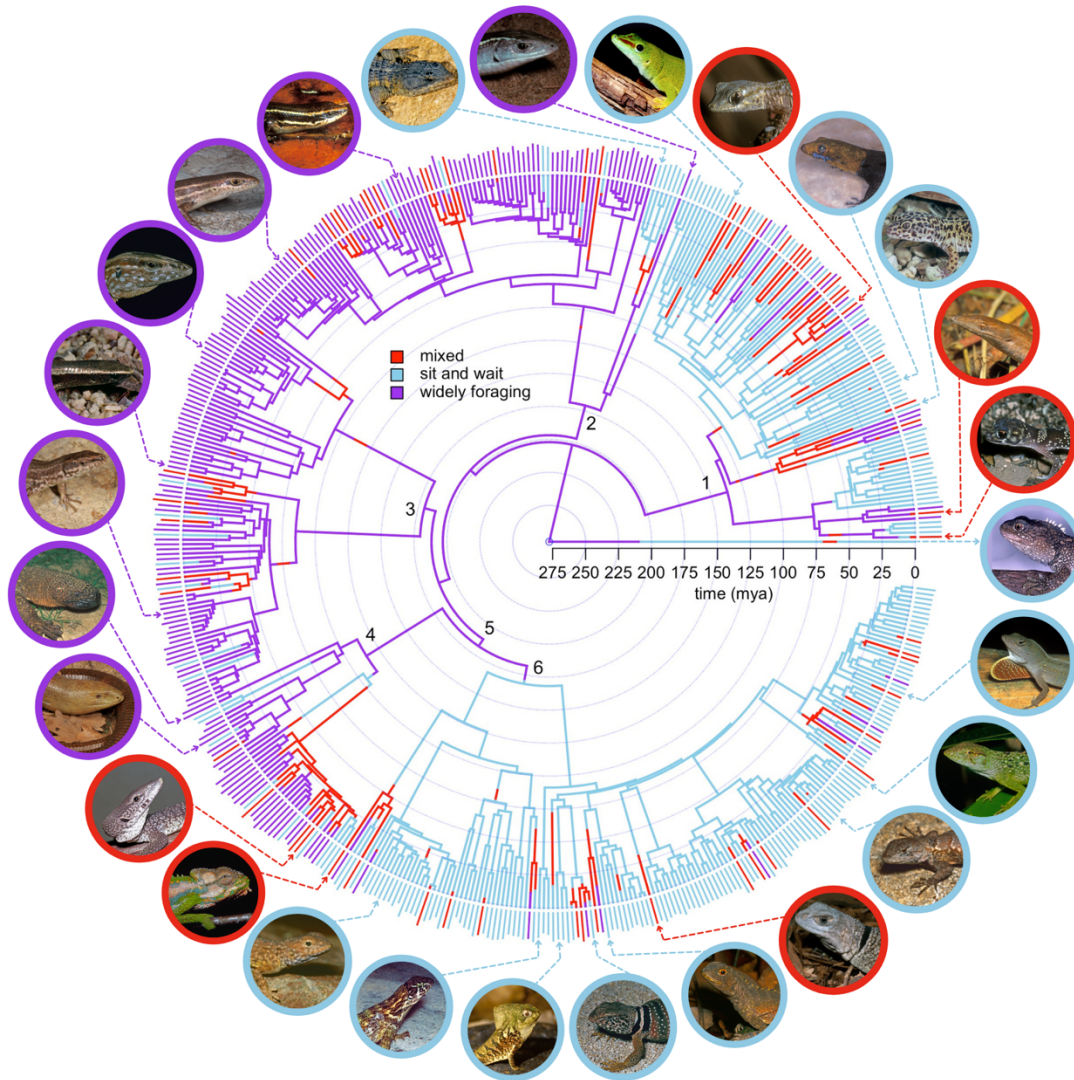
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487 **Fig. 1.** Conceptual model depicting potential relationships between foraging behavior, energetics,
488 predation risk, and reproductive effort. The predicted relationships derived from long-standing
489 models of life-history theory (see text).

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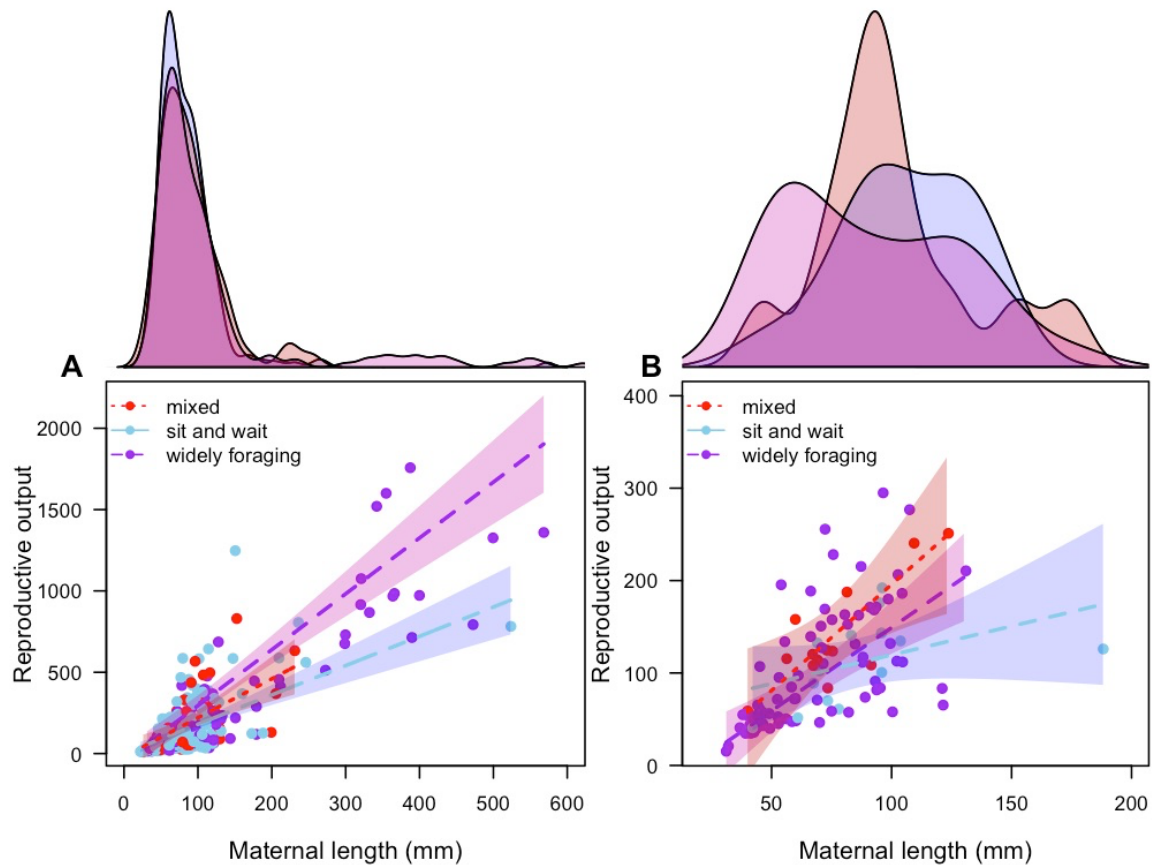
490

491 **Fig. 2.** Random sample of stochastic character maps depicting the evolution of foraging mode in
492 485 species of lizards (see supporting material for estimates of ancestral states in each internal
493 node). Bars at the tips of the phylogeny represent log-transformed values of reproductive effort
494 for all lizards, but not the outgroup *Sphenodon punctatus*. Major clades are enumerated as
495 follows: 1) Gekkota, 2) Scincoidea, 3) Lacertoidea, 4) Anguimorpha, 5) Toxicofera, and 6)
496 Iguania. Lizard photos by Mark O'Shea.

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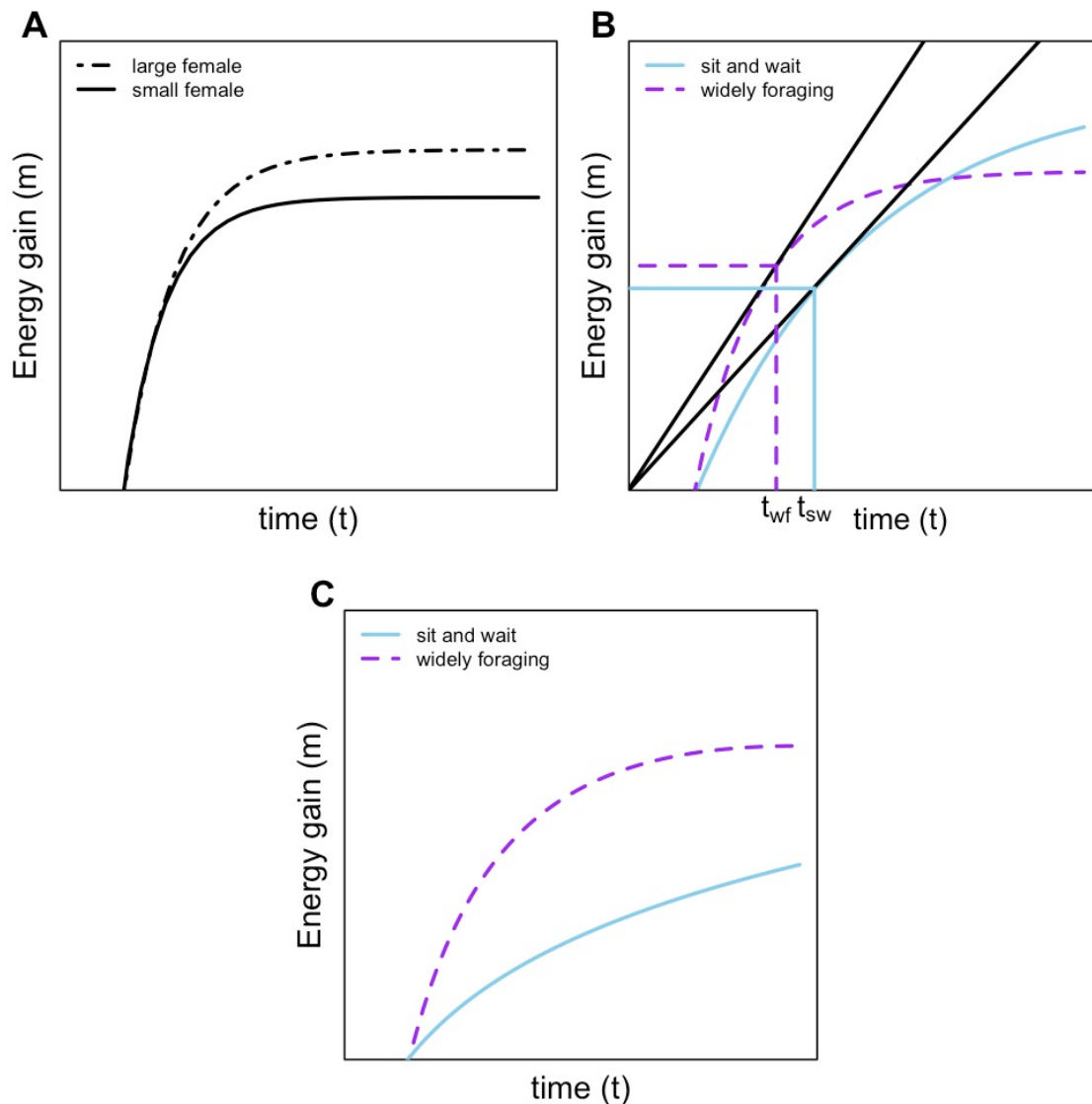


499

500 **Fig. 3.** Effects of maternal length and foraging mode on the evolution of the reproductive effort of
501 lizards, as determined by phylogenetic generalized least squares analysis. A) In Lacertilians,
502 widely foraging species have evolved the greatest reproductive effort. However, our analysis
503 revealed a right-skewed distribution of body length in this clade. B) The same pattern holds in
504 lizards with small and normal-distributed body length, such as skinks. According to the estimated
505 parameters of the model, sit-and-wait species have the lowest reproductive effort
506 ($\beta = -1.026, Std. Error = 0.507, t - value = -2.021, p = 0.046$).

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508

509 **Fig. 4.** Theoretical model relating the amount of energy gain for reproduction, m , as a function of
510 time spent foraging, t , and maternal size. A) Larger females reach their maximum capacity at a
511 higher value of m than small females. B) Widely foraging females that are smaller but more
512 efficient foragers may produce a greater reproductive effort than larger sit-and-wait females. C)
513 Widely foraging females may also produce a greater reproductive effort than sit-and-wait females
514 if they are both larger and more efficient foragers. t_{wf} and t_{sw} in (B) represent the optimal
515 foraging time of widely foraging females and sit-and-wait females, respectively.

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517 **Table 1.** Summary statistics for the most likely model of evolution of the reproductive effort,
518 based on the ranking of AICc for potential candidate models included in our analyses.

Terms	numDF	F-value	p-value
(Intercept)	1	27.560	<.0001
female.SVL	1	533.959	<.0001
foraging.mode	2	0.533	0.587
female.SVL:foraging.mode	2	19.910	<.0001

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