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Lizard life-history strategies

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INTRODUCTION

Plasticity in lizard life-history traits is influenced by environmental factors such as temperature variations and food availability, among others, as well as genetic factors (Dunham *et al.* 1988; Adolph & Porter 1993; Mesquita & Colli 2010). The first attempts to describe life-history patterns of lizards were performed by Donald Tinkle in the late 1960s and early 1970s (Tinkle 1969; Tinkle *et al.* 1970), and have received special attention ever since (Dunham & Miles 1985; Dunham *et al.* 1988; Charnov *et al.* 2007; Mesquita & Colli 2010; Meiri *et al.* 2012). Lizard life histories vary from species with genetically fixed clutch size (e.g. geckos and anoles) to species with more flexible patterns (Tinkle *et al.* 1970; Losos 2009). At least six reproductive strategies are recognized, varying from short-lived species with small clutches and early reproduction to comparatively long-lived species with relatively large clutches and delayed reproduction (Tinkle *et al.* 1970; Dunham *et al.* 1988). Live bearing (viviparity) has evolved repeatedly among lizards (Blackburn 1982; Blackburn *et al.* 1985; Shine 1985; Pyron & Burbrink 2014). This wide variation poses an interesting challenge to explain life-history patterns, which have been described for other clades, including plants, insects, fishes, birds and mammals (Grime 1977; Winemiller 1992; Winemiller & Rose 1992).

Using a multivariate approach to categorize life histories of fishes, Winemiller and Rose (1992) identified a two-dimensional life-history triangle in three-dimensional (3D) space with axes representing fecundity, age at reproduction and juvenile survivorship. They recognized three endpoints corresponding to opportunistic (small fish, like guppies with low fecundity, low juvenile and adult survivorship), equilibrium (large fish, like sharks with low fecundity but high longevity and high juvenile survivorship) and the so-called 'periodic' species (large fish, like the ocean sunfish *Mola mola* and sturgeon, with high fecundities, low juvenile survivorship, and long life spans). In a subsequent paper, Winemiller (1992) published a six-panelled figure, suggesting where insects, other invertebrates, birds, mammals and herpetofauna might be plotted, and his figure was partially reprinted in an ecology textbook (Molles 2010). Most higher vertebrate taxa tend to be dominated by only one or two dimensions of Winemiller's (1992) life-history strategies of fishes. However, amphibians and reptiles were lumped together, although they are not closely related (Rieppel & de Braga 1996; Hedges & Poling 1999; Coates *et al.* 2008), and Winemiller used a single rather unusual lizard genus, *Anolis*, in which all 300+ species have a clutch size of one egg resulting from allochronic ovulation, to represent a clade containing more than 5900 described species exhibiting great diversity in reproductive tactics. Our objective here is to improve and expand comparisons in Winemiller's triangular life-history continuum, using life-history information from 37 lizard families from all continents that contain extant lizards.

METHODS

We assembled a life-history database for 1029 lizard species representing 39 families, based on records we compiled from the literature (Meiri *et al.* 2012; Scharf *et al.* 2014) and our own records (Mesquita *et al.* 2015). The database contained the following life-history data: adult body mass, age at maturity (months), clutch size, foraging mode (active, mixed, sit-and-wait), hatchling mass, hatchling snout–vent length, longevity (years), relative clutch mass (RCM) and reproductive mode (oviparous, viviparous). We calculated RCM as (hatchling mass × clutch size)/female mass. When more than one data set presented data for the same species, parameters in the database were averaged. As usually happens with large databases, ours also had missing data. To prevent the decreased statistical power and biased estimates that result from incomplete observations (Rubin 1996; Schafer & Olsen 1998; Penone *et al.* 2014), we imputed missing observations using multiple imputation by chained equations (MICE) with R package *mice* (Van Buuren & Groothuis-Oudshoorn 2011). To improve the estimation of missing values (Guénard

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et al. 2013; Penone *et al.* 2014; Swenson 2014), we included phylogenetic information in the form of phylogenetic eigenvectors in the multiple imputation process. We calculated phylogenetic eigenvectors using the R package PVR (Diniz-Filho *et al.* 1998, 2012a,b) and the squamate phylogeny of Pyron *et al.* (2013), retaining the first 10 eigenvectors for multiple imputations, which captured 53.2% of the phylogenetic information. Because 204 species were not represented in the phylogeny, we excluded them with R package *picante* (Kembel *et al.* 2010), leaving 825 species for analysis representing 37 families. We conducted 100 multiple imputations with *mice* and used the average of estimates in our analysis. To estimate the position of lizard life-history information on the triangular life-history continuum, we calculated investment per progeny as the ratio of RCM divided by clutch size as suggested by Winemiller and Rose (1992). We also used published life-history information for guppies (García-Ulloa & García-Olea 2004; Hernández *et al.* 2004; Auer *et al.* 2010; Montag *et al.* 2011), white sharks (Gilmore 1993; Kohler *et al.* 1996; Lucifora *et al.* 2002), pallid sturgeon (Snyder 1999; Bryan *et al.* 2007; Steffensen *et al.* 2013), polar bear (Amstrup 2003), the deer mouse *Peromyscus leucopus* (Millar & Zammuto 1983), wild boar *Sus scrofa* (Millar & Zammuto 1983), ostrich (Selvan *et al.* 2013), domestic duck (Zammuto 1986; Rhymer 1988), the pigeon *Columba fasciata* (Zammuto 1986; Ibrahim & Sani 2010), the ranid frog *Rana temporaria* (Miaud *et al.* 1999) and the tree frog *Litoria dentata* (Greer & Mills 1998), coupled with lizard data. We plot 825 species of lizards and three extreme fishes (guppy, shark and sturgeon), some mammals (polar bear, deer mouse and wild boar), birds (ostrich, domestic duck and pigeon) and frogs (*Rana temporaria*, *Litoria dentata*), along the three dimensions of Winemiller and Rose's (1992) plot. We conducted all statistical analyses using R (R Core Team 2014). Throughout the text, means appear ± 1 SD. All data used are available in Appendix S1.

RESULTS

The smallest estimate for age at maturity was observed in Chamaeleonidae and the largest in Iguanidae (Table 1). Dactyloidae, Sphaerodactylidae and Anniellidae share the lowest fecundity values, whereas the highest fecundity values occurred in Iguanidae and Chaemeleonidae (Table 1). Varanidae and Corytophanidae had the lowest value for investment in progeny, whereas Sphaerodactylidae and Phyllodactylidae had the greatest (Table 1). Lizards occupy a very narrow zone on Winemiller's triangular 3D life-history surface for fishes. Essentially, all are concentrated near the origin at the guppy vertex corner, but with higher investment per progeny and smaller clutch size (Fig. 1). The ranid and the tree frog plotted in the graph were located between guppy and sturgeon vertices, with low investment per progeny and large clutch size (Fig. 1). Mammals are clumped within lizards, but the polar bear has a much greater age at maturity than wild boar (Fig. 1). Birds occupy a similar zone, with ostrich close to polar bear, but with larger clutch size; domestic ducks have a greater investment per progeny than other birds; and pigeons are close to some anoles (Fig. 1). Among lizards, there are no 'equilibrium' species (large long-lived low fecundity, high expenditure per progeny such as sharks). The species closest to the 'equilibrium' corner are the iguanids *Conolophus subcristatus*, *C. pallidus* and *Cyclura cychlura* (Fig. 1). Nor are there any large long-lived high fecundity 'periodic' species such as *Mola mola* or sturgeon (Fig. 1). A few lizard species, however, are outliers on each of the three axes. For example, chameleons and *Ctenosaura* are the most fecund lizards, but they are relatively short lived. The cordylid *Cordylus cataphractus*, the gecko *Phyllopezus periosus* and the sphaerodactylids *Saurodactylus mauritanicus* and *Sphaerodactylus notatus* exhibit high expenditure per progeny but are not particularly long lived. And the three lizards with the longest lives (*Conolophus* and *Cyclura*) are large, but they have relatively small clutch sizes and low expenditures per progeny.

DISCUSSION

Winemiller and Rose (1992) identified two gradients of life-history diversification in fishes: one associated with larger adult size, late maturity, long life, larger clutches of small eggs and reduced number of reproduction events; the other with presence of parental care, larger eggs, prolonged reproductive events and multiple reproductive episodes. When species belonging to these two gradients were clustered together, three life-history strategies were identified as endpoints of a trilateral continuum: equilibrium, opportunistic and periodic (Winemiller 1989, 1992; Winemiller & Rose 1992). Previous efforts have also reported similar patterns for plants (Grime 1977), zooplankton (Allan 1976), fishes (Baltz 1984), insects (Southwood 1977; Greenslade 1983) and reptiles (Tinkle *et al.* 1970; Dunham *et al.* 1988). This 3D model considers trade-offs among life-history parameters (fecundity, age of maturity and survivorship), making it possible to identify and describe three endpoints of reproductive strategies: (i) equilibrium, species with late maturity, small clutches, and high survivorship; (ii) opportunistic, which are species with early maturity, small clutches and low survivorship; and (iii) periodic, which are species with late maturity, large clutches and low survivorship (Winemiller 1992; Winemiller & Rose 1992).

While assembling an extensive database on lizard life histories for a phylogenetic comparative analysis to determine major determinants of these patterns (genetic or environmental), we noticed the paucity of lizard species in Winemiller's life-history plot (Winemiller & Rose 1992), and were unanimous that the common graph lumping one lizard (*Anolis*) with an amphibian (*Bufo*, a toad) and other non-squamate

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Table 1. Mean values and standard deviation for life-history variables based on lizard families

Family	Species	Age of maturity	Fecundity	Investment per progeny
Agamidae	72	19.3475 ± 8.5884	7.6810 ± 4.338	0.0377 ± 0.0196
Anguidae	18	21.7135 ± 5.6445	8.1936 ± 3.0880	0.0471 ± 0.0368
Anniellidae	2	21.0595 ± 2.4275	1.3063 ± 0.4331	0.0984 ± 0.0321
Bipedidae	3	12.8607 ± 1.0097	4.3111 ± 0.4087	0.0529 ± 0.0067
Blanidae	1	12.1020	3.1793	0.0794
Carphodactylidae	8	16.2345 ± 6.1713	1.9975 ± 0.0071	0.0836 ± 0.0304
Chamaeleonidae	20	13.4446 ± 10.8291	20.1855 ± 15.5731	0.0288 ± 0.0142
Cordylidae	12	21.8047 ± 6.0989	3.8905 ± 3.1907	0.0869 ± 0.0616
Corytophanidae	6	16.8322 ± 4.9662	7.2075 ± 2.6096	0.0279 ± 0.0133
Crotaphytidae	5	18.5494 ± 3.3445	4.7375 ± 1.3577	0.0576 ± 0.0277
Dactyloidae	36	11.7232 ± 3.2517	1.1929 ± 0.4877	0.0942 ± 0.0326
Diplodactylidae	23	22.5084 ± 14.7358	1.8926 ± 0.2421	0.0922 ± 0.0309
Eublepharidae	6	15.3902 ± 3.7159	2.0783 ± 0.2069	0.0670 ± 0.0140
Gekkonidae	98	15.6067 ± 5.1634	2.6369 ± 1.2923	0.0821 ± 0.0286
Gerrhosauridae	9	21.0588 ± 7.2014	5.5899 ± 2.8898	0.0447 ± 0.0121
Gymnophthalmidae	20	15.1009 ± 2.7907	2.3066 ± 0.6359	0.0722 ± 0.0234
Helodermatidae	2	53.3030 ± 43.4121	6.775 ± 1.7324	0.0555 ± 0.0418
Iguanidae	22	47.2115 ± 40.7177	14.6499 ± 12.0951	0.0286 ± 0.0204
Lacertidae	96	19.4084 ± 8.4344	4.7265 ± 2.3849	0.0577 ± 0.0270
Lanthanotidae	1	15.3420	4.0000	0.0380
Leiocephalidae	4	16.7628 ± 1.1663	2.65375 ± 0.9547	0.0765 ± 0.0145
Leiosauridae	1	16.7290	4.0000	0.0378
Liolaemidae	18	17.4184 ± 2.6825	4.2660 ± 1.3630	0.0652 ± 0.0147
Opluridae	2	15.4410 ± 0.1273	3.7500 ± 0.3535	0.0561 ± 0.0175
Phrynosomatidae	54	17.4541 ± 5.9473	7.3539 ± 4.7663	0.0547 ± 0.0199
Phyllodactylidae	17	19.4757 ± 12.2251	1.5706 ± 0.4043	0.1166 ± 0.0694
Polychrotidae	10	15.9352 ± 1.0815	3.8596 ± 0.5139	0.0466 ± 0.0076
Pygopodidae	8	17.2191 ± 5.5451	3.4901 ± 2.3531	0.0737 ± 0.0325
Scincidae	145	20.8535 ± 9.5836	4.5654 ± 2.5110	0.0580 ± 0.0267
Shinisauridae	1	20.5620	7.4000	0.0411
Sphaerodactylidae	18	15.0145 ± 4.7067	1.2739 ± 0.4097	0.1259 ± 0.0507
Teiidae	34	16.2292 ± 5.3259	5.9873 ± 6.4972	0.0456 ± 0.0189
Trogonophiidae	1	20.5620	3.7453	0.0847
Tropiduridae	15	14.7102 ± 3.5993	4.0746 ± 1.5072	0.0634 ± 0.0331
Varanidae	28	29.7724 ± 18.5481	11.6247 ± 6.6212	0.0258 ± 0.0204
Xantusiidae	7	23.6507 ± 8.5644	4.2907 ± 2.1698	0.0602 ± 0.0181
Xenosauridae	2	22.9405 ± 2.7202	3.3744 ± 1.2319	0.0740 ± 0.0271
All 37 families	825	19.3367 ± 12.0443	5.3586 ± 5.6238	0.0620 ± 0.0355

Age of maturity (months), fecundity was measured by mean clutch or litter size; and investment in progeny is the ratio of relative clutch mass (RCM) divided by clutch size.

reptiles, including two tortoises (*Geochelone* and *Gopherus*) and a crocodilian (*Crocodylus*, a 'bird'), could be challenged. In the present study, we plot only one monophyletic group, squamate lizards on Winemiller's herpetofauna plot. Our data reveal that with the exception of a few lizards (see Fig. 1), all are concentrated near and right below the guppy vertex corner, but with higher investment per progeny and smaller clutch size, similar to the three extreme mammals and birds plotted. The ranid and the tree frog plotted in the graph were located between guppy and sturgeon vertices, with low investment per progeny. The smaller investment per progeny of fishes compared with lizards can be related to their habit (Shine 1988). Because fishes are aquatic (with larval development), their investment per progeny should be smaller, because most produce very small larvae, which will grow up in aquatic environments (Shine 1988). The same argument could be applied to frogs. Although most frogs are terrestrial, they still depend on water for reproduction and larval development, which could result in their low investment per progeny. The lizard species closest to the 'equilibrium' corner are the iguanids *Conolophus subcristatus*, *C. pallidus* and *Cyclura cychlura* (Fig. 1). Among lizards, none is large, long-lived, high fecundity, 'periodic' species such as *Mola mola* or sturgeon (Fig. 1). A few lizard species, however, are outliers on each of the three axes, most iguanids, *Heloderma*, *Varanus komodoensis* (late maturity), the cordylid *Cordylus cataphractus*, the gecko *Phyllopezus periosus* and the sphaerodactylids *Saurodactylus mauritanicus* and *Sphaerodactylus notatus* exhibit high expenditure per progeny but are not particularly long lived.

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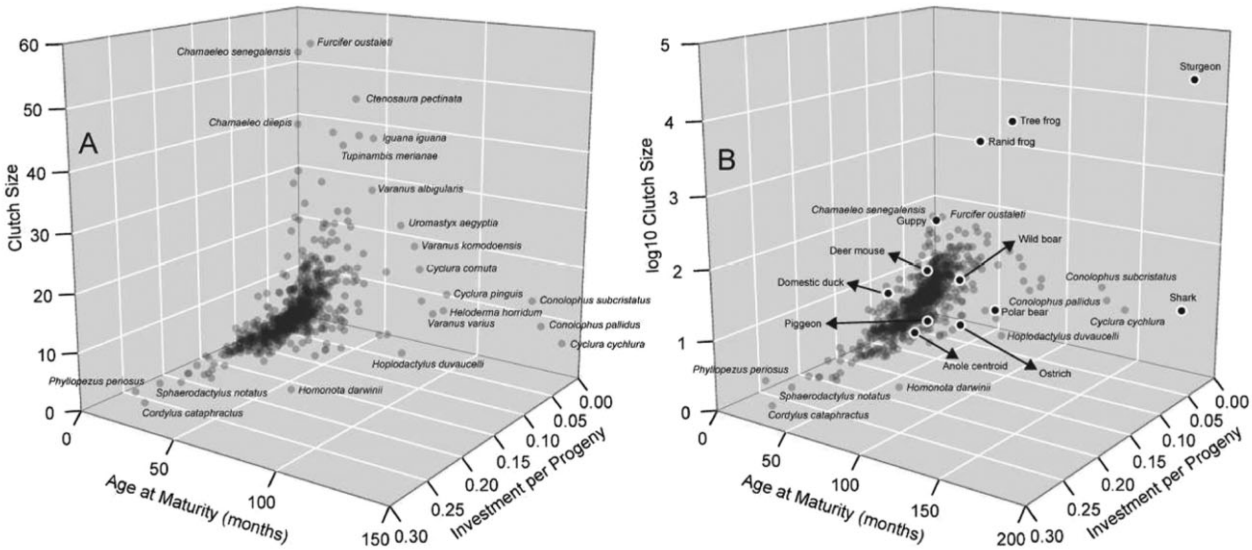

Fig. 1. (a) Positions of 825 species of lizards along the three dimensions of Winemiller and Rose's (1992) plot with outliers identified. (b) Clutch size is $\log_{10}$ transformed and the centroid for 45 species of anole lizards plus three extreme fishes (guppy, shark and sturgeon), mammals (polar bear, deer mouse and wild boar), birds (ostrich, domestic duck and pigeon) and frogs (ranid and tree frog) are plotted along with the 825 species of lizards.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Life-history data of 825 species of lizards used in the analysis.