

DRIVERS OF FECUNDITY IN OVIPAROUS LIZARDS FROM ARID ANDEAN FOOTHILLS: THE CASE OF A *LIOLAEMUS* CLADE

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Abstract.—Environmental, morphological, and phylogenetic agents may explain the clutch size in lizards. Some lineages do not fit the established correlates, however, and the causes of the variations are poorly understood. We evaluated the fecundity (in terms of clutch size) of 20 oviparous *Liolaemus* lizards of the *boulengeri* group using environmental variables under a phylogenetic framework. We used Pagel's Phylogenetic Signal Test to determine if the patterns observed respond to phylogenetic relatedness or other factors. We also ran phylogenetic generalized least squares models to determine which variable better explains differences in clutch size in these species. We found that female body size showed a strong phylogenetic signal. The clutch size of these lizards is mainly related to the daily thermal amplitude and showed a weak phylogenetic signal. Female body size weakly explains fecundity at the lineage level. It seems that thermal amplitude and, to a lesser degree, female body size and relative humidity are the critical factors for clutch size in these lizards, probably because it provides the females the conditions to reach a better body condition for reproduction.

Key Words.—clutch size; *Liolaemus boulengeri* group; reproduction; South America; thermal amplitude

INTRODUCTION

The clutch size of lizards is generally variable among different species; however, in lineages with fixed clutch size, such as Eublepharidae, Gymnophthalmidae, and *Anolis*, only one or two eggs are produced per reproductive bout (Fitch 1985; Vitt 1986; Colli et al. 2003). Variable clutch size is widespread in Squamata and is observed in most lineages (Meiri et al. 2020). Intrinsic and/or extrinsic factors can explain litter size variation, among the latter, rainfall was related to the number of clutches per season (Rocha, 1982; Magnusson 1987; Mesquita and Colli 2003; Mesquita et al. 2016). Additionally, rainfall may also influence female body size and indirectly clutch size (Brandt and Navas 2011; Padilla-Pérez and Angilletta 2022) of squamates; however, rainfall may have a negative effect on offspring size (Padilla-Pérez and Angilletta 2022). The availability of energy in the rainy season increases with temperature and humidity and food resources increase during the rainy season, which can be used for reproductive investment (Cox et al. 2021). Thus, females may allocate energy for reproduction when environmental quality improves (Mitchell et al. 2018). Temperature may also affect the number of clutches per season, such as in the Eastern Fence Lizard (*Sceloporus undulatus*), a broadly distributed lizard (Du et al. 2014).

The intrinsic factors phylogeny and body size of the females can affect clutch size of squamates (Dunham and Miles 1985; Baxter-Gilbert et al. 2018). The Fecundity Advantage Hypothesis (Darwin 1871; Fairbairn 1997; Mesquita et al. 2016) posits that larger females can produce significantly more eggs than smaller females because they possess larger abdominal cavities. Abdominal cavity size is not only dependent on body size of a species but body shape also can affect cavity size. For example, abdominal capacity and reproductive mode (oviparous/viviparous) were positively associated in species of *Liolaemus* (Cei et al. 2003); however, this relationship was not supported under a phylogenetically based study on a specific clade of *Liolaemus*, the *L. darwini* clade (Cabrera et al. 2013). Nevertheless, Iguanian lizards have oblong body shapes with broad bellies (Vitt and Congdon 1978), which is a phylogenetic characteristic.

With nearly 290 described species (Abdala and Quinteros 2014; Uetz et al. 2021), the genus *Liolaemus* is one of the most speciose in the world. This genus has broad latitudinal and elevational distributions, from central Western Perú in the North to Tierra del Fuego in the South and from the Pacific to Atlantic coasts (Cruz et al. 2022). Most species occur in the Andes and the Andean foothills, occupying arid ecoregions, such as High Andes, Puna, Chaco, Monte and the Steppe

(Burkart et al. 1999; Abdala et al. 2022). The activity season for most *Liolaemus* species is up to six months (Meiri et al. 2020); however, juveniles may be active also in fall (Fitzgerald et al. 1999).

We studied 20 oviparous lizard species of the *Liolaemus boulengeri* clade (Abdala 2007) that occur east of the Andes, where 67 of 74 species are oviparous (Abdala et al. 2022). We examined the effects of maternal body size, environmental factors (rainfall, temperature, thermal amplitude, and relative humidity), and phylogeny on the reproductive output (clutch size) in one-third of the oviparous species (20 of 67 oviparous species) of this clade. We were interested in determining whether intrinsic aspects, such as body size and phylogeny, or extrinsic factors (mean air temperature, daily thermal amplitude, relative humidity, rainfall), affected the clutch size in oviparous species of the *Liolaemus boulengeri* group.

MATERIALS AND METHODS

We used clutch size (CS) data from the literature and data we collected. We collected data mainly for *Liolaemus cuyanus* (no common name: NCN), *L. laurenti* (NCN), and *L. koslowskyi* (NCN; Fig. 1), which occur in the Monte region (Burkart, et al. 1999) in the nearby Antinaco, Department of Famatina, La Rioja Province, Argentina (28°49'13"S, 67°18'53"W, 1,100 m elevation). For these three species, we recorded the snout-vent length (SVL) with a digital caliper (Model CD-6" CX; Mitutoyo; Kanagawa, Japan), and we used



FIGURE 1. *Liolaemus koslowskyi* (no common name) from the Monte region in nearby Antinaco, Department of Famatina, La Rioja Province, Argentina. (Photographed by Gabriela Gallardo).

SVL as the estimate of body size. We captured lizards by noosing, and we transferred them to the laboratory at Chilecito National University, Chilecito, La Rioja, Argentina. We euthanized lizards with a lethal dose (approximately 60–100 mg per kg) of pentothal (Euthanyle; Brower S.A., Buenos Aires, Argentina). Later, we dissected lizards and recorded the number of vitellogenic follicles (only yellowish follicles of least 4 mm diameter) or eggs in the oviduct. Finally, we fixed lizards in 4% formalin and transferred them to 75% ethanol after 48 h.

We also searched for studies on the reproductive cycles of *Liolaemus* species with precise data on clutch size (CS) and female body size (snout-vent length; SVL). Most of these studies correspond to single species research (e.g., the Chaco Tree Iguana, *L. chacoensis*, Cruz and Ramírez Pinilla 1996; *L. espinozai*, NCN, Cabrera and Scrocchi 2019). From these studies, we used CS information based on vitellogenic follicles and oviductal egg counting (see Ramírez Pinilla 1991 as an example). If both data were recorded, we used the mean value from the source with a larger value. Our final database comprised 20 of the 67 recognized oviparous species of the *Liolaemus boulengeri* monophyletic group (Abdala 2007; Abdala et al. 2022) and one of the oviparous species is parthenogenic (Abdala et al. 2016, 2022). Thus, we studied nearly one-third of the oviparous species in this group. We did not pool populations of the same species; instead, we considered the population with larger sample size and its locality. In all cases, the CS corresponded to the mean value of the number of oviductal eggs and/or vitellogenic follicles.

We extracted data from the U.S. National Aeronautics and Space Administration (NASA) website: average daily temperature, thermal amplitude (the result from the maximum temperature minus the minimum temperature each day), average precipitation, and ambient relative humidity (<https://power.larc.nasa.gov/data-access-viewer/>), corresponding to the period between 1993 and 2015. We eliminated data between April 16 and October 14 of each year because we considered this as a period of inactivity of adults (fall and winter in the Southern Hemisphere) after Ramírez Pinilla (1991). These authors collected data on the length of the reproductive cycle in several *Liolaemus* species from different phylogenetic groups (*Eulemus* and *Liolaemus sensu stricto*; Laurent 1983; Ruiz Monachesi et al. 2022) and distant localities (Chubut in the south and Salta in the north), which showed that reproductive activity falls ends during the colder months of the year in all oviparous species, that is from April till October (Meiri et al. 2020, Appendix 4). Finally, we discarded year-round abiotic data because of the high correlation with the more meaningful seasonal data, similar to Cruz et al. (2022).

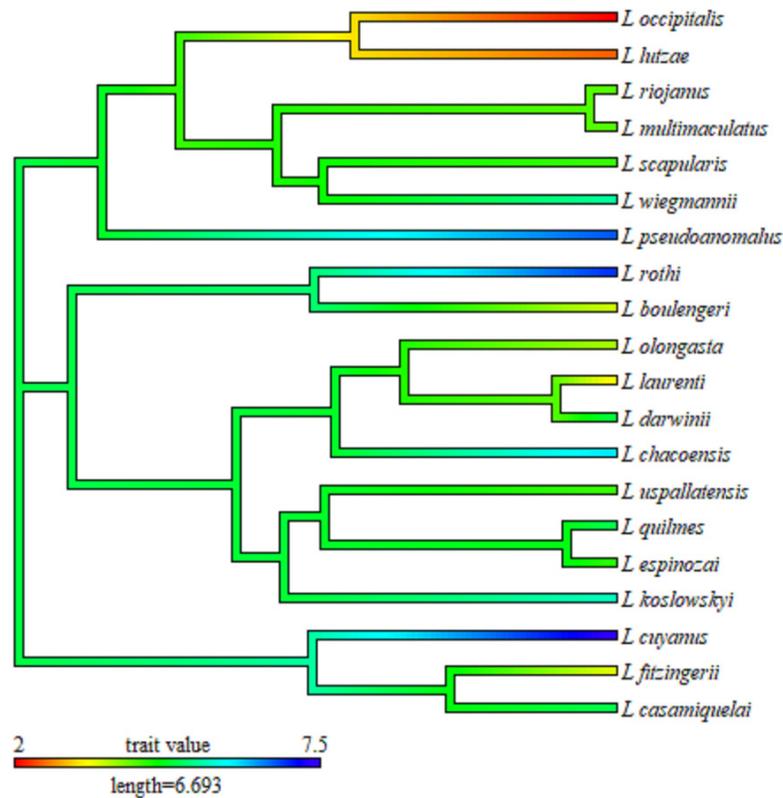


FIGURE 2. Traitgram of the *Liolaemus* species studied here. We used the function contMap in the package phytools (Revell, 2012) to portray the changes in clutch size in the tree. Colors represent variations in trait values.

Because the relatedness among species varies with the phylogenetic structure, species cannot be taken as independent datum (Felsenstein 1985). Thus, we used a phylogenetic tree to gauge the comparisons between the species studied here. First, we filtered the 20 oviparous species of *Liolaemus* of the *L. boulengeri* group (see Appendix Table 1) corresponding to our study from the Esquerré et al. (2019) phylogenetic tree. For this, we used the functions drop.tip and extract.clade of the ape package (Paradis and Schliep 2019) and obtained a calibrated tree (Fig. 2), including only the species for which we had reproductive data. Then, we accounted for the phylogenetic signal (a measurement of resemblance among species due to their shared evolutionary history), for which we used the module phylosig from phytools R package (Revell 2012). Then, to determine which variable affects CS, we used the multispecies analysis Phylogenetic Generalized Least Squares (PGLS; Orme et al. 2013). Clutch size was the resulting variable, whereas, mean seasonal air temperature (TaS), mean seasonal thermal amplitude (AmpS), mean seasonal rainfall (Rfalls), mean seasonal relative humidity (RHS), and SVL were the predictive variables. We analyzed the broad model (CS~SVL+TaS+AmpS+Rfalls+RHS) and all the possible combinations (Appendix Table 2). Thus, we searched for better fitted models to build our results.

For this, we selected the most plausible model based on the Akaike Information Criterion (AIC; Burnham and Andersson 2004), considering a $\Delta AICc < 2$ as the limit to consider the most informative models (Mazerolle 2006). We performed all analyses using R v 4.1.3 (R Core Team 2018).

RESULTS

Mean clutch size varied between 2.0 and 7.5 eggs (*L. occipitalis* and *L. cayanus*, respectively; Appendix Table 1). The mean body size of reproductive females varied between 46.5 and 78.83 mm SVL (*L. chacoensis* and *L. cayanus*, respectively; Appendix Table 1). Body size (SVL) showed a high phylogenetic signal ($\lambda = 0.99$; $P = 0.001$); whereas CS showed a low phylogenetic signal ($\lambda = 0.002$; $P = 0.98$). Five models were equally plausible from the 31 possible models obtained (Appendix Table 2) based on the $\Delta AICc$ values (Appendix Table 2). The data corresponding to the activity season shows that thermal amplitude (AmpS) was essential in most models and showed a significant relationship with clutch size (Table 1). Only one of the best-fit models did not include AmpS as a predictive variable. Body size was also important, but to a lesser degree (Table 1) because this variable was not significant in two of the five of the

TABLE 1. Best-fitted models among those produced based on the relationships between clutch size (CS) and different variables: (SVL = snout-vent length; AmpS = daily thermal amplitude (the difference between maximum and minimum temperature °C during the day); TaS = daily mean air temperature °C; RfallS = mean precipitation; and RHS = daily mean ambient relative humidity. The period considered was from 1993 to 2015. Symbols and acronyms are λ = phylogenetic signal corresponding to the relationship between variables, r^2 = coefficient of determination; Int = intercept; Var = variable; Slope = slope, Pvar = significance for each variable in the model, and PM = total significance of the model. Asterisks (*) denote those models that are significant ($P < 0.05$).

Model	λ	r^2	Int.	Var	Slope	Pvar	PM
CS~SVL+AmpS	0.00	0.381	-1.904	SVL	0.068	0.057	0.006*
				AmpS	0.205	0.015*	
CS~SVL+RfallS+RHS	0.00	0.413	3.593	SVL	0.090	0.018*	0.008*
				RfallS	0.737	0.038*	
				RHS	-0.107	0.008*	
CS~SVL+AmpS+TaS	0.00	0.404	-4.016	SVL	0.078	0.034*	0.011*
				AmpS	0.223	0.009*	
				TaS	0.068	0.218	
CS~AmpS	0.00	0.273	1.624	AmpS	0.232	0.011*	0.011*
CS~SVL+AmpS+RfallS	0.00	0.374	-3.425	SVL	0.077	0.043*	0.014*
				AmpS	0.250	0.014*	
				RfallS	0.177	0.385	

best-fit models. Finally, relative humidity and rainfall showed significant relationships with clutch size; however, in only one of the five best-fit models (Table 1). Additionally, thermal amplitude showed steeper slopes, suggesting that this variable may be the most important to define the litter size in the 20 *Liolaemus* species of the *boulengeri* group we studied; however, SVL should not be ruled out as a guide to clutch size. Mean annual temperature, rainfall, and relative humidity showed little effect on litter size (Table 1).

DISCUSSION

Our results show that clutch size in oviparous species of the *Liolaemus* of the *boulengeri* species group is mainly affected by the daily thermal amplitude and secondly by the body size of the females that also showed a high phylogenetic signal. Rainfall and relative humidity were less critical for CS, and surprisingly mean air temperature did not show any effect. Day and night differences in temperature may affect some aspects of the life history of lizards; however, clutch size was not severely affected in the Side-blotched Lizard, *Uta stansburiana* (Clarke and Zani 2012). Other studies have shown that climate, and more importantly, environmental temperature, affects clutch size, egg size, and the fitness of hatchlings in reptiles (Atkinson et al. 2001; Bownds et al. 2010). High temperatures may produce reabsorption of follicles to adjust the balance between clutch and egg size (Bonnet et al. 2008). It is also possible that temperature, as well as the extension

of the favorable conditions during the reproductive and activity season, may increase the number of clutches per reproductive event. This has been observed in some *Liolaemus* species (*L. chacoensis*, *L. longasta*, NCN, and *L. koslowskyi*; see Cruz and Ramírez Pinilla 1996; Cánovas et al. 2006; Martori and Aùn 2010), as well as other iguanian lizards, such as the Spiny Lava Lizard (*Tropidurus spinulosus*; Cruz 1998) and the Amazon Lava Lizard (*T. torquatus*; Ortiz et al. 2014) that lay more than one clutch per season in northern localities or just one clutch per season in the southern population of *T. spinulosus* (Martori and Aùn 1994).

Regarding temperature, the thermal biology of the genus *Liolaemus* is labile; the average body temperature varies with the ecological gradients of the ambient temperature (Labra 1998; Medina et al. 2009; Rodríguez Serrano et al. 2009; Bonino et al. 2015). On the other hand, environments with more significant rainfall have enabled the evolution of larger maternal size and bigger mothers produce larger clutches of larger offspring (Brandt and Navas 2011). Annual precipitation may negatively affect offspring size, however, despite the positive indirect effect mediated by maternal size (Padilla Pérez and Angilletta 2022). There may be a trade-off between some environmental aspects (air temperature, rainfall, seasonality, thermal amplitude) and clutch size or offspring size. Probably a climatic bottleneck may induce maximizing the reproductive output in certain conditions. It can be reasonably expected, however, that the temporal distribution of adequate thermal resources during the post-reproductive period should be favorable

for females and their offspring. This has been observed in species of *Liolaemus* (e.g., *L. koslowskyi*, Martori et al. 2002; *L. chacoensis*, Astudillo et al. 2009; the, *L. wiegmannii*, NCN, Stelletti et al. 2013; *L. parvus*, NCN, Gómez Alés et al. 2017). The high variability of clutch size of the oviparous species within the *Liolaemus* of the *boulengeri* group (from two to eight eggs) reveals the influence of the environment on this trait as more important than phylogenetic history.

When considering the whole Liolaemidae family (*Ctenoblepharys*, *Liolaemus*, and *Phymaturus* species), most species produce one clutch per season (Ramírez Pinilla 1991). Some species may lay more than one clutch per season, such as *L. chacoensis*, *L. olongasta* and *L. koslowskyi* (Cruz and Ramírez Pinilla 1996; Cánovas et al. 2006; Martori and Aùn 2010), and other species produce a single clutch or brood every 2–3 y, such as the Painted Tree Iguana (*L. pictus*; Ibargüengoytia and Cussac 1996), *Phymaturus tenebrosus* (NCN; Ibargüengoytia 2004), and several *Phymaturus* species (Boretto and Ibargüengoytia 2009). Reproductive maturity in Liolaemid lizards may be reached in the second year (*L. chacoensis*; Cruz and Ramírez Pinilla 1996) and between the fourth and sixth year (*L. irregularis*, NCN, and *L. multicolor*, NCN, respectively; Valdecantos et al. 2007). In this latter study, the authors found that the life span of one species is up to 19 y (*L. multicolor*) and up to 10 y in *L. irregularis*, one of the viviparous species in the *L. boulengeri* group. All the studies on Liolaemid species skeletochronology correspond to viviparous species in Liolaemidae (*Liolaemus* and *Phymaturus*; Piantoni et al. 2006; Valdecantos et al. 2007; Cabezas-Cartés et al. 2015). Some of the species studied here may probably live nearly 5–7 y and generally lay a clutch per season and reach maturity in their second season in most cases (unpubl. data). Clutch size in the *Liolaemus* species corresponds to the mean clutch size for lizards (Mesquita et al. 2016). The species (and their populations) of this clade (the *Liolaemus boulengeri* group) are distributed between 23° and 35° South Latitude in Argentina, Brazil, and Uruguay, occur primarily in highly continental arid and semiarid ecoregions in South America, and produce clutch sizes between two and eight eggs. We observed that the smaller clutch sizes in the *Liolaemus boulengeri* species group (*L. occipitalis*) occur where favorable climatic conditions are more extended; for example, in the coastal dunes of Brazil (latitude 30° S, mean annual temperature above 20° C). Additionally, under this extended reproductive period, *L. occipitalis* lays several small clutches every season (Verrastro and Rauber 2013). Conversely, the closest related species among the species studied here (*L. multimaculatus*, see Esquerré et al. 2019) occurs on the coast of Buenos Aires province, Argentina (Latitude 38° S and a mean

air temperature of 13.5° C) and show a relatively short activity period, where a single and large clutch (mean = 4.2 eggs, range 3–7 eggs) per season is produced (Vega 1997). Thus, despite the close relatedness (phylogeny), climate may play an important role in the size and frequency of clutches produced in these species.

The Fecundity Advantage hypothesis (Darwin 1871; Fairbairn 1997) proposes that litters of larger females should be more numerous than clutches of smaller females because they may acquire more nutritional resources before reproduction and also have a larger abdominal capacity (Fitch 1985; Cei et al. 2003; Pincheira-Donoso and Tregenza 2011). Additionally, larger females may have a lower impact concerning their body mass and the energetic reproductive investment per clutch (Rossi 2022). Our results, however, suggest partial support for body size as a driver of clutch size in the oviparous species of the *Liolaemus* species of the *boulengeri* group. We found that snout-vent length affects the clutch size in the oviparous species of the *Liolaemus boulengeri* group; however, with less impact than thermal amplitude during the activity season of these species. Additionally, we found that the phylogenetic signal in female body size is high in the species we studied. In habitats where water and food are scarce, fluctuations in the availability of these resources are marked as a result of slight variations in precipitation, which markedly increase primary productivity, the composition and abundance of primary consumers, and their predators (Polis 1991). For example, in the tropical Madagascar Ground Gecko (*Paroedura picta*), females tend to produce larger clutches of smaller eggs when temperatures increase (Starostova et al. 2012). This flexibility could be advantageous in fluctuating and extreme environmental conditions (Castro-Franco et al. 2011). Additionally, smaller hatchlings show a higher survival success when eggs are laid early in the season when resources are more abundant (Rodríguez-Díaz and Braña 2012).

Species occurring in arid environments may have a high reproductive output despite the limited resources, such as the studied *Liolaemus* species here, which suggests new questions about how the environment affects clutch size in oviparous species. Our study showed that in the *Liolaemus boulengeri* clade, a group mainly distributed in arid regions, clutch size is primarily driven by thermal amplitude and, secondly, by female body size. The pattern of the phylogenetic signal of female body size prevents us from considering this aspect as a more important variable. Surprisingly, in the species studied here, the role of rainfall and mean air temperature were not significant, despite the effect of these variables on resources, such as humidity for egg laying or food abundance for hatchlings and adults.

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APPENDIX TABLE 1. List of species analyzed in this study. Abbreviations are CS = mean clutch size, in some cases \pm standard deviation, and SVL is mean snout-vent length, in some cases \pm standard deviation. Asterisks (*) denote those species that may be present in Patagonia, Argentina. Data of Blanco et al. (2001 and 2003) correspond to IV Congreso Argentino de Herpetología, Argentina, and XVII Reunión de Comunicaciones Herpetológicas, Argentina, respectively.

Species	CS	SVL	Source
<i>Liolaemus boulengeri</i> *	3.6 \pm 0.4	57.1 \pm 0.62	Medina and Ibarquengoytía 2010
<i>L. casamiquelae</i> *	5.0 \pm 0.7	63.0 \pm 1.34	Félix Cruz, unpubl. data
<i>L. cf. uspallatensis</i>	4.3	55.0	Castro 2019
<i>L. chacoensis</i>	6.1 \pm 1.43	46.5 \pm 0.98	Cruz and Ramírez-Pinilla 1996
<i>L. cuyanus</i> *	7.5 \pm 3.02	78.8 \pm 2.38	This study
<i>L. darwini</i>	4.9	53.6	Blanco et al. 2001
<i>L. espinozai</i>	4.4 \pm 1.34	55.3 \pm 5.07	Cabrera and Scrocchi 2019
<i>L. fitzingerii</i> *	3.5	68.0	Scolaro 2005
<i>L. koslowskyi</i>	6.5 \pm 1.28	59.7 \pm 3.78	This study
<i>L. laurenti</i>	3.3 \pm 1.5	52.2 \pm 3.67	This study
<i>L. lutzae</i>	2.5 \pm 0.61	56.2	Duarte Rocha 1992
<i>L. multimaculatus</i>	4.2 \pm 1.22	54.6 \pm 3.97	Vega 1997
<i>L. occipitalis</i>	2.0	53.0	Verrastro and Rauber 2013
<i>L. olongasta</i>	3.8	52.2	Cánovas et al. 2006
<i>L. pseudoanomalous</i>	6.8 \pm 2.4	63.5	Villavicencio et. al. 2007
<i>L. quilmes</i>	5.0 \pm 1.42	52.2	Ramírez-Pinilla 1992
<i>L. riojanus</i>	4.2	52.3	Blanco et al. 2003
<i>L. rothi</i> *	7.0	71.0	Scolaro 2006
<i>L. scapularis</i>	4.4 \pm 0.88	59.8	Ramírez-Pinilla 1994
<i>L. wiegmannii</i>	5.4 \pm 1.19	48.4 \pm 3.1	Martori and Aùn 1997

APPENDIX TABLE 2. Phylogenetic generalized linear models (PGLS) for the set of species studied here. Acronyms are AICc = Akaike Information Criterion value for the small sample size for each model, Δ AIC is the delta Akaike, the difference concerning the smallest AIC value, Wi is Akaike weights, CS = clutch size; SVL = snout-vent length, AmpS = daily thermal amplitude (the difference between maximum and minimum temperature °C during the day, TaS = daily mean air temperature °C, RfallS = mean precipitation, and RHS = daily mean ambient relative humidity. Boldface corresponds to the models with lower than 2 Δ AICc, which are the best-fitted models.

Model	AICc	Δ AICc	Wi
CS~SVL+AmpS	65.92776	0	0.20045
CS~SVL+RfallS+RHS	66.81359	0.88582	0.12872
CS~SVL+AmpS+TaS	67.13923	1.21147	0.10938
CS~AmpS	67.48685	1.55908	0.09193
CS~SVL+AmpS+RfallS	68.12495	2.19718	0.06682
CS~SVL+AmpS+RHS	69.01809	3.09032	0.04275
CS~SVL+RHS	69.14763	3.21986	0.04007
CS~SVL+AmpS+TaS+RfallS	69.48413	3.55636	0.03386
CS~AmpS+TaS	69.75329	3.82552	0.02960
CS~RHS	69.93395	4.00618	0.02704
CS~SVL+AmpS+TaS+RHS	70.04135	4.11358	0.02563
CS~SVL+AmpS+RfallS+RHS	70.05475	4.12698	0.02546
CS~AmpS+RfallS	70.22910	4.30133	0.02333
CS~SVL	70.26636	4.33860	0.02290
CS~AmpS+RHS	70.27400	4.34623	0.02282
CS~SVL+TaS+RfallS+RHS	70.34142	4.41365	0.02206
CS~RfallS+RHS	70.75140	4.82363	0.01797
CS~SVL+TaS+RHS	71.88647	5.95871	0.01019
CS~SVL+RfallS	72.60757	6.67980	0.00710
CS~SVL+TaS	72.61381	6.68604	0.00708
CS~TaS+RHS	72.72001	6.79223	0.00672
CS~AmpS+TaS+RfallS	72.87186	6.94409	0.00622
CS~AmpS+TaS+RHS	72.90150	6.97374	0.00613
CS~AmpS+RfallS+RHS	73.03509	7.10732	0.00574
CS~RfallS	73.29352	7.36575	0.00504
CS~SVL+AmpS+TaS+RfallS+RHS	73.42248	7.49472	0.00473
CS~TaS+RfallS+RHS	73.84733	7.91957	0.00382
CS~TaS	74.91080	8.98303	0.00225
CS~SVL+TaS+RfallS	75.26531	9.33754	0.00188
CS~TaS+RfallS	76.04181	10.11404	0.00128
CS~AmpS+TaS+RfallS+RHS	76.45962	10.53185	0.00104