RESEARCH ARTICLE

Adaptive seasonal shift towards investment in fewer, larger offspring: Evidence from field and laboratory studies

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Abstract

1. Seasonal changes in reproduction have been described for many taxa. As reproductive seasons progress, females often shift from greater energetic investment in many small offspring towards investing less total energy into fewer, better provisioned (i.e. larger) offspring. The underlying causes of this pattern have not been assessed in many systems.

2. Two primary hypotheses have been proposed to explain these patterns. The first is an adaptive hypothesis from life-history theory: early offspring have a survival advantage over those produced later. Accordingly, selection favours females that invest in offspring quantity early in the season and offspring quality later. The second hypothesis suggests these patterns are not intrinsic but result from passive responses to seasonal changes in the environment experienced by reproducing females (i.e. maternal environment).

3. To disentangle the causes underlying this pattern, which has been reported in brown anole lizards (*Anolis sagrei*), we performed complementary field and laboratory studies. The laboratory study carefully controlled maternal environments and quantified reproductive patterns throughout the reproductive season for each female. The field study measured similar metrics from free ranging lizards across an entire reproductive season.

4. In the laboratory, females increased relative effort per offspring as the reproductive season progressed; smaller eggs were laid earlier, larger eggs were laid later. Moreover, we observed significant among-individual variation in seasonal changes in reproduction, which is necessary for traits to evolve via natural selection. Because these patterns consistently emerge under controlled laboratory conditions, they likely represent an intrinsic and potentially adaptive adjustment of reproductive effort as predicted by life-history theory.

5. The field study revealed similar trends, further suggesting that intrinsic patterns observed in the laboratory are strong enough to persist despite the environmental variability that characterizes natural habitats. The observed patterns are indicative of an adaptive seasonal shift in parental investment in response to a deteriorating offspring environment: allocating greater resources to late-produced offspring likely enhances maternal fitness.

1 | INTRODUCTION

In seasonal environments, the timing of reproduction is important for fitness because early-produced offspring often have higher survival compared to those produced later (Anderson, Faulds, Atlas, Pess, & Quinn, 2010; Varpe, Jørgensen, Tarling, & Fiksen, 2007; Warner & Shine, 2007). This trend occurs in a variety of taxa and is attributed to a seasonal decline in the quality of the offspring environment (Varpe, 2017). For example, late-produced offspring must compete with larger, earlier produced conspecifics and have less time to grow prior to winter or the dry season (Harriman, Dawson, Bortolotti, & Clark, 2017; Verhulst & Nilsson, 2008). For species that reproduce repeatedly over a long reproductive season, females should invest more total energy in early-season clutches/litters than those produced late (Nussbaum, 1981). Indeed, seasonal changes in clutch/litter mass and size occur in a diversity of animals (e.g. spiders: Iida, Kohno, & Takeda, 2016; fish: Heins, Baker, & Guill, 2004; frogs: Williamson & Bull, 1995; lizards: DeMarco, 1989; birds: Du, Liu, et al., 2014 and mammals: Singleton, Krebs, Davis, Chambers, & Brown, 2001). These changes are often expressed as trade-offs between offspring size and number as the season progresses (Smith & Fretwell, 1974): females shift from investing in many, smaller offspring to allocating less total energy into fewer, better provisioned offspring (Nussbaum, 1981). The causes of these trends are uncertain in many systems (e.g. Mitchell, Hall, & Warner, 2018; Öberg, Pärt, Arlt, Laugen, & Low, 2014) but may represent an intrinsic, adaptive shift in parental investment that maximizes offspring number when conditions for offspring are good and maximizes offspring quality when conditions for offspring are poor. Alternatively, this seasonal shift may be a passive response to changes in the environment experienced by reproducing females (henceforth 'maternal environment'; Nussbaum, 1981).

Disentangling the effects of multiple variables that correlate with seasonal fitness declines is a major challenge for empirical tests of life-history theory (Harriman et al., 2017; Pärt, Knape, Low, Öberg, & Arlt, 2017). Because many environmental variables change with season (e.g. rainfall, food availability), the factors that drive seasonal shifts in reproduction are difficult to assess from field studies alone. For example, many bird species exhibit a seasonal decline in fitness (Öberg et al., 2014), and whether this is driven by seasonal timing of reproduction, per se, or due to other factors (e.g. parental quality, territory quality) is often unknown (Pärt et al., 2017). One way to assess the strength of these shifts and determine their underlying causes is with laboratory studies that tightly control the maternal environment (Ferguson & Snell, 1986). Laboratory studies, however, have limitations because many factors that influence reproduction (e.g. hormonal cycles, circadian rhythms) differ between animals in the laboratory and field (Calisi & Bentley, 2009). Thus, leveraging field and laboratory studies will illuminate ecologically relevant patterns of seasonal shifts in reproduction and identify causal factors, respectively.

Studies of oviparous lizards have greatly enhanced our understanding of investment in offspring size and number (e.g. DeMarco, 1989; Du, Robbins, Warner, Langkilde, & Shine, 2014; Mitchell et al., 2018; Uller et al., 2009). Many species produce young over an extended breeding season, and their life history is characterized by a seasonal fitness decline (Pearson & Warner, 2018; Qualls & Shine, 2000; Warner & Shine, 2007). Because most lizards provide no parental care, trade-offs between offspring size and number equate to simple measures of egg mass versus number. Moreover, the effects of a changing environment (e.g. decline in food supply) are somewhat decoupled for parents and offspring. Most oviparous lizards studied lay only one or two clutches per year, which limits the power for assessing seasonal trends in reproduction and makes it difficult to determine whether patterns of reproduction are intrinsic or driven by seasonal shifts in the maternal environment. Furthermore, species that lay multi-egg clutches have a limited capacity to differentially invest energy towards each offspring (i.e. clutch size and egg mass may be coupled). *Anolis* lizards alleviate these problems because they produce frequent, single-egg clutches across an extended reproductive season.

Brown anoles (*Anolis sagrei*) are relatively small (2–6 g; Stroud, Giery, & Outerbridge, 2017), tropical lizards with short life spans (1–2 years). They lay a single egg every 4–14 days from March to October (Lee, Clayton, Eisenstein, & Perez, 1989). Egg production alternates between ovaries, so each egg is yolked, shelled and laid separately from others (i.e. monoallochronic ovulation, Smith, Sinelnik, Fawcett, & Jones, 1972). This allows females to adjust the effort among offspring at a fine scale as the environment changes (Hall, Buckelew, Lovern, Secor, & Warner, 2018). Hatchling survival is higher for early-produced individuals than those produced later in the season (Pearson & Warner, 2018), and, accordingly, females invest greater total energy earlier in the season by producing relatively many, smaller offspring and less energy later by producing relatively few, larger offspring (Mitchell et al., 2018; Pearson & Warner, 2018). They make excellent models for this work (see Warner, 2014) because protocols for captive breeding and incubating eggs are established, wild populations are large and dense, and standard methods are available for monitoring reproduction in the field (Lee et al., 1989).

Past studies of brown anoles have used cohorts of females captured at different times during the same reproductive season and bred in the laboratory (Mitchell et al., 2018; Pearson & Warner, 2018). Thus, complementary work is needed to address three issues,

all of which we address in this study. First, because mating and reproduction occurred in the laboratory under relatively good conditions (e.g. high-quality diet, no predation pressure), the direction or strength of the observed trends may differ from what occurs in the field. Second, because cohorts were captured at different times in the year, some previously observed trends may be driven by environmental entrainment rather than inherent, evolved responses to a deteriorating offspring environment. To control for this, all individuals must be captured at the same time and their reproduction monitored in a constant laboratory setting for the entire season. Finally, while many studies have explored population-level patterns of seasonal shifts in reproduction in lizards (e.g. Du, Robbins, et al., 2014; Ferguson & Snell, 1986), we know comparatively little about individual variation in seasonal patterns of reproduction. Quantifying existing variation within populations can provide insight into the evolutionary potential of seasonal investment patterns.

Our goals were to: (1) quantify temporal reproductive shifts when females are bred in a controlled laboratory setting across the full reproductive season, (2) characterize among-individual variation in reproduction across the season and (3) determine how seasonal shifts in reproduction occur in the field. To accomplish the first and second goals, we conducted a laboratory study that carefully monitored reproduction and growth of females for an entire breeding season. To accomplish the third goal, we routinely captured mature females across the entire reproductive season and, via necropsy, assessed their reproductive status and effort. Goals one and three assess the parental investment hypothesis that mothers intrinsically increase their per offspring investment as the season progresses under controlled and natural settings, respectively. Goal two assesses the potential for seasonal reproductive patterns to vary among individuals, providing opportunity for natural selection to shape life-history traits. Finally, replication of studies of ecology and evolution is rare (Nakagawa & Parker, 2015), so we make quantitative comparisons between our laboratory and field data to evaluate the strength and consistency of the ecological patterns we observe.

2 | MATERIALS AND METHODS

2.1 | Laboratory study

On 4 March 2017, we collected 30 adult *A. sagrei* females and 15 males from a suburban area (Lat: 25.676355, Long: −80.284321) in Pinecrest, Florida, USA. We measured each lizard's mass (to nearest 0.01 g) and snout to vent length (SVL, to the nearest 1 mm). Females were housed individually per standard husbandry conditions (details in Supplemental Methods). We fed lizards three crickets each (dusted with vitamins and calcium) two times per week and misted cages with water daily.

We checked the nest pots three times per week (each Monday, Wednesday, Friday) from 10 March to 23 October 2017. Thus, oviposition dates are only accurate for 3 days; however, our large sample size (n = 718 eggs) increases the accuracy of estimates of reproduction (e.g. egg size, oviposition rate). For each egg, we recorded the mass, date of oviposition and maternal identity. We placed eggs in individual Petri dishes (60 × 15 mm) half-filled with moist vermiculite (−150 kPa), wrapped the dish with parafilm to prevent evaporation and incubated them at temperatures measured from nest sites in the field (Figure S1); however, some eggs (n = 450) were used in a separate study to determine the effects of extreme temperatures on development. These eggs were randomly selected across the duration of the breeding season and subjected to extremely warm temperatures for 2 hr on only 1 or 2 days during development. Thus, they experienced suitable temperatures for more than 99% of development. These treatments somewhat slowed developmental rates but had no statistically clear effects on the hatchling body size (see Hall & Warner, 2019). For analysis of hatchling mass, we include incubation treatment as a factor in our statistical analyses. At hatching, we recorded each lizard's mass (to 0.0001 g).

To account for maternal growth, we measured each female's SVL (to 0.01 mm) immediately following each time we collected an egg. At the end of the study, we measured the mass and SVL of all surviving females (n = 26) and then euthanized them by intraperitoneal injection of a 1:1 mixture of Sleepaway Beuthanasia (sodium pentobarbitol) and deionized water. We dissected each female, massed (to 0.0001 g) her abdominal fat bodies and assigned her to one of four reproductive stages by examining her ovaries and oviducts (Sexton, Ortleb, Hathaway, Ballinger, & Licht, 1971): (I) no enlarged ovarian follicle and no oviductal eggs (i.e. reproductively inactive); (II) one enlarged ovarian follicle; (III) one enlarged ovarian follicle and one oviductal egg; (IV) one enlarged ovarian follicle and two oviductal eggs. Because anoles alternate egg production between left and right ovaries, stage IV is suspected to represent the highest rate of egg production (Sexton et al., 1971).

2.2 | Field study

The following year (2018), we collected females (~10 per sample) from the same population weekly from 13 February to 27 March and monthly thereafter until 10 January 2019. Lizards were shipped overnight to Auburn University on the day of or the day after capture and euthanized immediately as previously described. No females were reproductive in December of 2018 (n = 9) or January of 2019 (n = 19); thus, we only include females collected from February to November in analyses. Table S1 provides sample sizes and collection dates.

We measured each female's SVL (to 0.01 mm) and abdominal fat mass (to 0.0001 g) and assigned each to a reproductive stage (as previously described). To assess seasonal changes in egg size, we removed and massed (to 0.0001 g) mature eggs (i.e. white and shelled; n = 53) from the oviducts. Mature eggs do not appreciably increase in size when retained in the oviducts (Stamps, 1975), but once laid, eggs increase in size via water uptake. In our laboratory conditions, this increase equates to 6.38 (±0.21 *SE*) mg of water per day (see Supplemental Methods).

2.3 | Statistical analyses

All data analyses were performed in R (ver. 3.5.1; R Core Team, 2018). We analysed egg mass, hatchling mass and inter-egg interval (IEI) for the laboratory study. The IEI is the number of days between each oviposition; thus, a smaller IEI indicates a more rapid rate of reproduction. Because we egg-checked three times per week, for each egg we estimated the maximum and minimum possible IEI and analysed these as well. Oviposition dates were expressed as Julian day (henceforth 'Day') for analysis.

Prior to analysis, we scaled and centred continuous variables. We followed Zuur, Ieno, Walker, Saveliev, and Smith (2009) to determine random effects and fixed effects structures for our models. For each trait, we fit three supermaximal models to determine the appropriate random effects structure: one included maternal ID as a random effect (i.e. random intercept), one included the interaction between maternal ID and Day (i.e. random intercept and random slope) and one included the interaction between maternal ID and Day + Day^2 (i.e. random intercept and random coefficients). We used likelihood ratio tests to determine the best fit. Significant test results ($p < .05$) indicated that allowing intercepts and/or slopes to vary among females significantly improved the fit of the model; thus, these analyses determined if the relationship between each trait and Day differed among females and whether this difference was linear or curvilinear. Using the preferred random effects structure, we fit two new models for each trait: one assumed the relationship with Day was linear and the other assumed it was curvilinear (i.e. included a linear and quadratic term). Comparing these models with a likelihood ratio test determined if a trait varied linearly or curvilinearly with Day. We removed all non-significant interaction terms in stepwise fashion to arrive at final models and assessed models for violations of assumptions by visually inspecting residuals. Egg and hatchling mass were fit with linear mixed effects models, and IEI was fit with a generalized linear model with a Poisson distribution. To assess the relative importance of among-individual variation, we calculated the proportion of residual variance explained by the random effects (i.e. repeatability estimates of the intercept and slope; Nakagawa & Schielzeth, 2010).

For analyses of IEI and egg mass, fixed effects were maternal SVL, Day and Day^2. For hatchling mass, fixed effects were initial egg mass, Day, Day^2 and incubation treatment. Because this analysis included egg mass as a covariate, larger residuals represent hatchlings that are large relative to their egg size, which is an index of 'egg quality' (Mitchell et al., 2018).

Egg size covaries with maternal SVL, and females grew substantially in the laboratory. We performed two analyses to assess the influence of growth on seasonal changes in reproduction. First, to compare patterns of maternal growth with seasonal changes in reproduction, we used the process of model selection previously described to analyse female body size. Maternal SVL was the response variable and Day and Day^2 were fixed effects. Second, for each female, we calculated a seasonal increase in egg size (i.e. slope of egg size vs. time) and her total growth in SVL (final measure minus initial). We performed a simple regression between these variables to determine how growth in SVL might covary with seasonal changes in offspring provisioning.

Because body size influences reproduction and our studies were conducted in different years (i.e. temporally isolated populations), the SVL of laboratory females at the time of capture (4 March) was compared to field females collected on 28 February and 6 March with a t test. Moreover, because females grew substantially in the laboratory, we used a t test to compare final measures of SVL, fat mass and reproductive stage for the laboratory colony (measured on 23 October) with those of females collected from the field on 4 October and 5 November, combined. For fat mass, we performed a general linear model with SVL and source (laboratory vs. field) as fixed effects. Reproductive stage was analysed with an ordinal regression and included source and SVL as fixed effects.

To compare seasonal increases in egg size between laboratory and field samples, we generated 95% prediction intervals for the SVL of females housed in the laboratory across the study period and selected females from the field whose SVL fell within this interval. We compared mass of their eggs to those produced by laboratory females on similar days. This approach resulted in similar sample sizes for females from the laboratory ($n = 57$) and field ($n = 43$; Figure S2). We performed a linear mixed model with egg mass as the response variable and maternal SVL, source, date and an interaction between source and date as fixed effects. Maternal ID was a random effect.

Measurements of reproduction differed between laboratory and field datasets. Thus, to compare seasonal rates of reproduction between studies, we assessed the relationship between weekly egg production and Day for our laboratory colony and mean reproductive stage and Day for field collected lizards. Weekly egg production was the total number of eggs produced each week divided by the number of females alive in the breeding colony during that time. For the field data, the mean reproductive stage was the mean stage of all females collected on each date. For weekly egg production and mean stage, we compared models assuming the relationship with day was linear versus curvilinear (as previously described). To determine if seasonal trends in egg production differed between the laboratory and field, we tested for differences between the quadratic coefficients (i.e. the shape of the curve; Zar, 1984).

3 | RESULTS

3.1 | Reproduction in the laboratory

Egg mass increased linearly by 0.1033 mg/day (0.0533–0.1533, 95% CI) throughout the study (Table 3; Figure 1a). With a mean egg mass of 142.1 mg at the beginning of the study, this seasonal change equates to a 16.2% increase. Egg size also covaried with maternal SVL: egg mass increased by 2.01 mg (0.72–3.29; 95% CI) for each 1 mm increase in maternal SVL (Table 3); thus, the largest females (48 mm) lay eggs as much as 23.9% larger than the smallest females (34 mm). Egg mass increased with time for most females, but slopes significantly varied among individuals (Figure 1a; Table 1): some females exhibited no increase or a decline in egg mass. The proportion of residual variance accounted for by the random intercepts
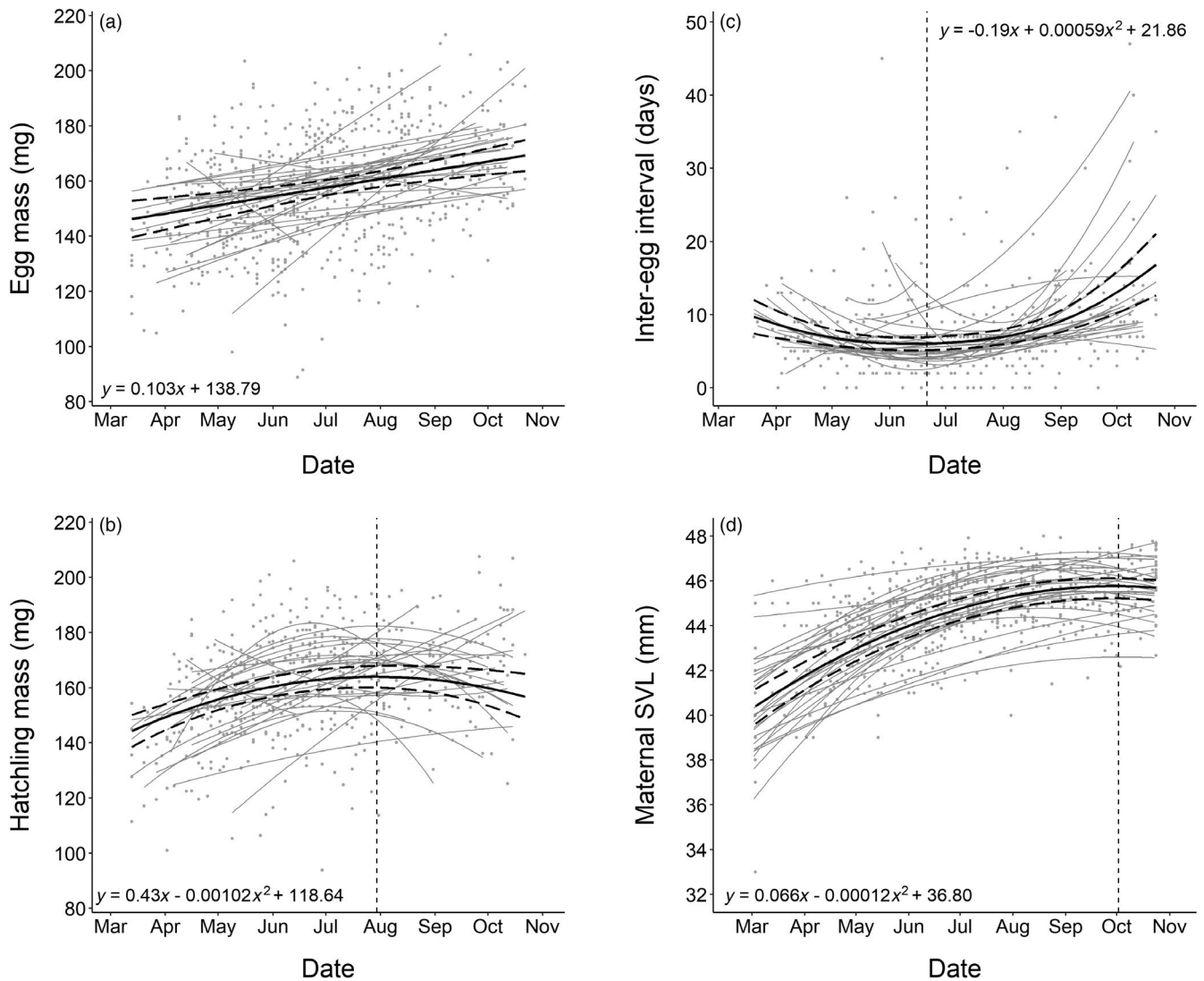
FIGURE 1 Changes in reproduction and snout to vent length (SVL) of *Anolis sagrei* females maintained in the laboratory. Solid black lines show the relationship between each response variable and Day from final models (see text), and dashed black lines show the 95% CI. Equations are given for each line and assume a mean value for covariates. Grey circles are the raw data. Grey lines show, for each female, the fitted values from regressions that include Day of the year (a) or Day + Day^2 (b)–(d) as fixed effects. Dashed vertical lines (b)–(d) show the highest or lowest point of curves (see Section 3)

(i.e. maternal ID) and slope (i.e. interaction between maternal ID and time) were 13.0% and 6.8% respectively.

The relationship between Day and hatchling mass was curvilinear (Tables 1 and 3): hatchling mass increased until 30 July (i.e. Day 211; Figure 1b) when it reached 164.0 mg (±2.01 *SE*) and then declined. The shapes of curves differed among females (Figure 1b; Table 1). For some females, hatchling mass increased through the study, for others it increased and became relatively constant, while for others, it increased and then declined. The proportion of residual variance accounted for by the random intercepts and the random curves (i.e. interaction between maternal ID and day = linear + quadratic components) were 31.0% and 4.1% respectively.

The IEI also shifted curvilinearly through time (Tables 1 and 3), with the minimum (5.50 days ± 0.53 *SE*) being reached on 20 June (i.e. Day 171; Figure 1c). This trend significantly differed among

females (Figure 1c; Table 1), but for most, IEI decreased at the start of the study and then increased towards the end. The mean number of eggs laid per female was 25.74 (±7.33 *SE*; range = 9–38 eggs). See Table S2 for summary statistics of reproduction for each female. At the end of the study, dissections revealed that 19 of 25 females (76%) were still reproductive (stage I, *n* = 6; stage II, *n* = 4; stage III, *n* = 7; stage IV, *n* = 8). There was no clear relationship between maternal SVL and the IEI (Table 3). Final model structures for the IEI were identical, regardless of which IEI was used (raw vs. estimated minimum/maximum). Estimates of the lowest IEI were 3.1 (±0.42 *SE*) and 7.98 (±0.60 *SE*) days for the minimum and maximum estimated IEI respectively (Figure S3). All three estimates of the lowest IEI are similar to those reported previously (Fetters & McGlothlin, 2017). The proportion of residual variance accounted for by the random intercepts and the random curves were 14.7% and 6.4% respectively.

TABLE 1 Results from model comparisons for measures of reproduction and snout to vent length (SVL) of *Anolis sagrei* females in the laboratory. Bold type denotes the model selected at each step via likelihood ratio test

Response	Model	K	LogLik	df	χ^2	p	Test
Egg mass	**Maternal ID × Day**	10	−2853.6				Random effects
	Maternal ID × (Day + Day^2)	13	−2852.6	3	1.95	.583	
	Maternal ID	8	−2863.4				Random effects
	Maternal ID × Day	10	−2853.6	2	19.66	.000	
	Day	8	−2858.9				Fixed effects
	Day + Day^2	10	−2858.7	2	0.38	.825	
Final model	Maternal SVL + Day + (random effect = Maternal ID × Day)						
Hatchling mass	Maternal ID × Day	28	−2018.2				Random effects
	Maternal ID × (Day + Day^2)	31	−2012.4	3	11.41	.001	
	Maternal ID	26	−2023.5				Random effects
	Maternal ID × (Day + Day^2)	31	−2012.4	5	22.20	.0004	
	Day	23	−2067.1				Fixed effects
	Day + Day^2	31	−2057.7	8	18.78	.016	
Final model	Egg mass + Incubation treatment + Day + Day^2 + (random effect = Maternal ID × (Day + Day^2))						
Inter-egg interval	Maternal ID × Day	9	−1932.4				Random effects
	Maternal ID × (Day + Day^2)	12	−1909.5	3	45.85	<.0001	
	Maternal ID	7	−1965.1				Random effects
	Maternal ID × (Day + Day^2)	12	−1909.5	5	111.25	<.0001	
	Day	10	−1919.5				Fixed effects
	Day + Day^2	12	−1909.5	2	20.08	<.0001	
Final model	Maternal SVL + Day + Day^2 + (random effect = Maternal ID × (Day + Day^2))						
Maternal SVL	Maternal ID × Day	7	−1057.8				Random effects
	Maternal ID × (Day + Day^2)	10	−1037.8	3	40.07	<.0001	
	Maternal ID	5	−1109.9				Random effects
	Maternal ID × (Day + Day^2)	10	−1037.8	5	144.18	<.0001	
	Day	9	−1052.9				Fixed effects
	Day + Day^2	10	−1033.3	1	39.25	<.0001	
Final model	Day + Day^2 + (random effect = Maternal ID × (Day + Day^2))						

Abbreviations: LogLik = log-likelihood; Model = shows only what differed between the two models; K = number of model parameters.

Maternal SVL changed nonlinearly through time and this relationship differed among females (Tables 1 and 3): for most, SVL increased rapidly at the start of the study but slowed as time progressed (Figure 1d). A maximum size of 45.76 was reached on 1 October (Day 274). The proportion of residual variance accounted for by the random intercepts and the random curves were 63.1% and 19.4% respectively. We observed no relationship between the seasonal increase in egg size and the total growth of females (β = 0.004, SE = 0.033, df = 25, t = 0.123, p = .90; Figure S4).

3.2 | Reproduction in the field

Egg mass from field-caught females increased linearly with time (Tables 2 and 4), and we observed a significant interaction between female SVL and Day (Table 4). To assess this interaction, we split the dataset into females larger than or smaller than the mean SVL. For larger females, egg mass increased by 0.1950 mg/day (0.1334–0.2565, 95% CI; t_{25} = 6.21, p < .0001), but smaller females showed no appreciable increase in egg mass (slope = 0.0163 mg/day; −0.0679–0.1006, 95% CI; t_{22} = 0.38, p = .71; Figure 2a).

3.3 | Comparisons of data from the laboratory and field

Laboratory and field females did not differ in SVL at the beginning of the season (β = −0.61; SE = 0.77; t_{45} = −0.80; p = .43); however, SVL of laboratory females was 6.36 mm (4.82–7.90, 95% CI) greater than field females at the end of the studies (t_{36} = 8.4; p < .0001; Figure S5a). Abdominal fat mass did not covary with SVL (t_{49} = −1.83; p = .07) but was 0.0533 g (0.0222–0.0843, 95% CI) greater for

TABLE 2 Results from model comparisons for measures of reproduction for *Anolis sagrei* females collected routinely from the field. Models compared linear versus curvilinear effects of collection date. Bold type denotes the model selected via likelihood ratio test

Response	Model	K	LogLik	df	χ^2	p
Egg mass	**Day**	5	−202.5			
	Day + Day^2	7	−202.1	2	0.89	.640
Final model	Maternal SVL + Day + Maternal SVL × Day					
Reproductive stage	Day	3	−18.0			
	Day + Day^2	4	−8.5	1	18.89	<.0001
Final model	Day + Day^2					

Abbreviations: LogLik = log-likelihood; Model = shows only what differed between the two models; K = number of model parameters.
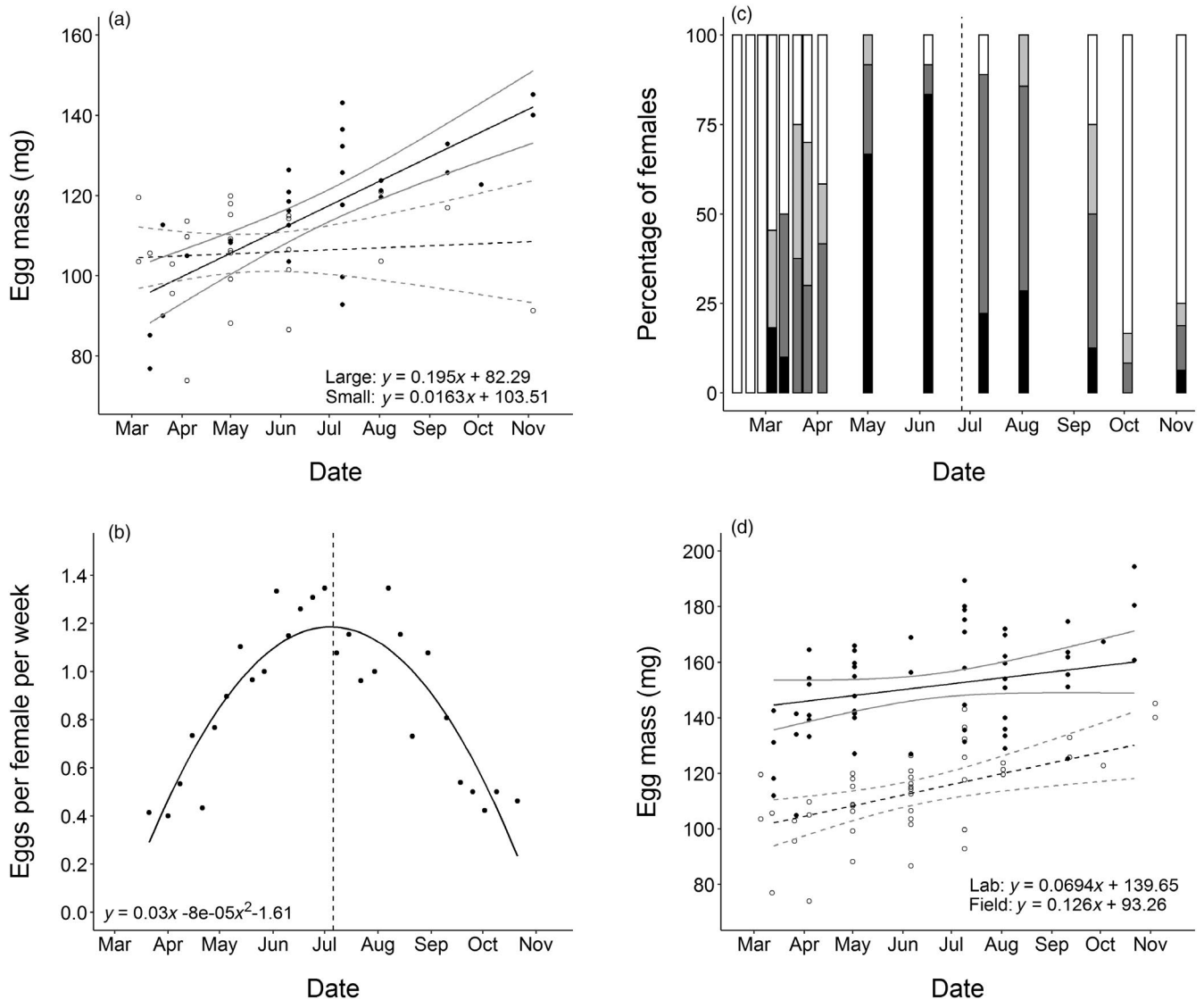

FIGURE 2 Seasonal changes in reproductive traits of *Anolis sagrei* females in the laboratory and field. (a) Mass of eggs removed from the oviducts of females that were collected from the field. Solid and dashed black lines show model fits for large (i.e. greater than the mean) and small (i.e. smaller than the mean) females, respectively. Grey lines show 95% CI's. Closed and open circles are raw data for large and small females respectively. (b) Weekly egg production of laboratory females. Closed circles show raw data, and the line is the model fit. (c) Percentage of field females that were assigned to each reproductive stage: Stage I (not reproductive)—white; Stage II—light grey; Stage III—dark grey; Stage IV (highest reproductive output)—black. (d) Seasonal increase in egg mass for laboratory and field females. The solid and dashed black lines show model fits for laboratory and field, respectively. Grey lines show 95% CI's. Closed and open circles show raw data for laboratory and field respectively. For (b) and (c), dashed vertical lines indicate the estimated peak of reproduction (see text)

TABLE 3 Results from final models analysing reproductive traits of female *Anolis sagrei* in the laboratory. Bold text denotes statistical significance (α = .05). For egg quality, 'Treatments' were incubation treatments for a study not described here (see text for details). See Table 1 for model comparisons made to determine the random and fixed effects structure for each model. Asterisk denotes a z-value test statistic rather than a t-value. Estimates of coefficients shown were calculated using unscaled data

Response	Fixed effect	df	Estimate	SE	t-value	p-value
Egg mass (mg)	**Maternal SVL**	641	2.0048	0.6552	3.06	.002
	Day	641	0.1033	0.0251	4.12	<.0001
Hatchling mass (mg)	Treatment 2	480	1.8195	1.3859	1.31	.19
	Treatment 3	480	−0.7657	1.4681	−0.52	.60
	Treatment 4	480	−6.8680	2.6529	−2.59	.01
	Egg mass	480	0.3437	0.0356	9.64	<.0001
	Day	480	0.4299	0.0786	5.47	<.0001
	Day^2	480	−0.0010	0.0002	−4.59	<.0001
Inter-egg interval (log counts of days)	**Maternal SVL**	648	0.04199	0.03136	1.34*	.18
	Day	648	0.08981	0.03836	2.34*	.019
	Day^2	648	0.16917	0.03261	5.12*	<.0001
Weekly egg production (eggs per female)	**Day**	26	3.006e−02	3.068e−03	9.80	<.0001
	Day^2	26	−8.064e−05	8.081e−06	−9.98	<.0001
Maternal SVL (mm)	**Day**	740	0.0656	0.0059	11.15	<.0001
	Day^2	740	−0.0001	0.00001	−9.14	<.0001

TABLE 4 Results from final models analysing egg mass and reproductive stage of female *Anolis sagrei* collected periodically from the field. Bold text denotes statistical significance (α = .05). See Table 2 for model comparisons that determined the fixed effects structure for each model. Estimates of coefficients shown were calculated using unscaled data

Response	Fixed effect	df	Estimate	SE	t-value	p-value
Egg mass (mg)	Maternal SVL	49	−2.5094	1.6718	−1.5	.14
	Day	49	−1.0233	0.3634	−2.82	.007
	SVL × Day	49	0.0269	0.0086	3.15	.003
Mean reproductive stage	**Day**	12	0.0484	0.00668	7.26	<.0001
	Day^2	12	−0.00014	2.00E-05	−7.02	<.0001

laboratory than field females (t_{49} = 3.359; p = .002; Figure S5b; i.e. 105% greater). In the field, females were not reproductive until early March. Similarly, oviposition in the laboratory began on 14 March. In the laboratory, weekly egg production increased until 5 July (i.e. Day 186), at which point the rate was 1.19 eggs per female per week (±0.042 SE), then declined (Table 3; Figure 2b). Mean reproductive stage of field females peaked on 25 June (i.e. Day 176) at a mean stage of 3.27 (±0.20 SE), then declined (Figure 2c; Tables 2 and 4). However, the distribution is slightly right-skewed with the greatest rates of reproduction in May and June (Figure 2c). Reproduction peaked at similar times for laboratory and field females (5 July and 25 June, respectively; Figure 2b,c). At the end of the studies, laboratory females ranked at a higher reproductive stage than field females (laboratory = 2.68; field = 1.41), but this difference was not statistically significant (β = −0.904, SE = 0.882, z = 1.03, p = .31; Figure S5c).

Egg mass was 44.47 mg (±8.35 SE) greater for laboratory females than field females (df = 64, t = 5.33, p < .0001); however, much of this difference could be due to water uptake prior to collection (see Supplemental Methods). Moreover, egg mass increased by 2.72 mg (±1.21 SE) and 0.13 mg (±0.04 SE) for each 1 mm increase in maternal SVL (df = 31, t = 2.25, p = .03) and each 1-day increase in the oviposition date (df = 31, t = 3.01, p = .005), respectively. However, we observed no interaction between female source and Day for egg mass (β = −0.0561, SE = 0.0484, df = 31, t = −1.16, p = .26): thus, although egg mass increased at a greater rate in the field compared to the laboratory (Figure 2d), the difference in slopes was not statistically clear. Moreover, the rise and fall in reproductive rate was similar in the laboratory and field: the quadratic coefficients (i.e. shape of the curve; field: β = 0.000123, SE = 0.0000223; laboratory: β = 0.0000806, SE = 0.00000808) were not statistically different (t_{40} = −1.77677, p = .083).

4 | DISCUSSION

When the quality of the offspring environment declines through the season, selection should favour temporal shifts in maternal provisioning to offspring in ways that have season-specific benefits to maternal

fitness. Our longitudinal laboratory study demonstrates that egg size and the IEI are greatest at the end of the reproductive season. Because we tightly controlled the maternal environment, such seasonal shifts in reproduction represent an intrinsic adjustment by females, rather than a passive response to a changing maternal environment. Moreover, we detected among-individual variation in these seasonal trends which demonstrates the opportunity for selection to shape seasonal shifts in reproductive life-history traits. Our complementary field study corroborates the laboratory results by showing that seasonal shifts are present in the field. Overall, these results reveal an intrinsic seasonal shift towards the production of fewer, larger offspring late in the season when the quality of the offspring environment is relatively poor (Pearson & Warner, 2018).

Though past studies reveal a seasonal increase in egg size in the laboratory (e.g. Delaney, Lovern, & Warner, 2016; Hall et al., 2018; Warner & Lovern, 2014; but see Fetters & McGlothlin, 2017), our study was unique because we bred females over the entire season and carefully monitored maternal growth. We are confident that seasonal increases in egg mass were due to shifts in the relative amount of energy allocated to each offspring rather than maternal growth because the relationship between growth and time differed from that between egg mass and time (Figure 1a,d), and we observed no direct relationship between maternal growth and seasonal changes in egg mass (Figure S4). Seasonal changes in egg size are assumed to be adaptive shifts in parental investment for some study systems (e.g. Du, Liu, et al., 2014; Mitchell et al., 2018); however, for many species, such changes appear to be passive responses to environmental conditions (e.g. temperature; Heins et al., 2004; Magrath, 1992; Williamson & Bull, 1995). Because we controlled the maternal environment, the trends we observe are likely intrinsic and represent an adaptive shift in parental investment. Similarly, the lizard *Sceloporus undulatus garmani* increases egg size of late-season clutches even under controlled laboratory conditions (Ferguson & Snell, 1986); thus, endogenous control of seasonal changes in egg size may be prevalent across squamates, but more study is needed to assess the generality of this conclusion.

Although many species exhibit seasonal increases in egg size, egg size seasonally declines for some taxa (e.g. Heins et al., 2004; Iida et al., 2016; MacGregor, While, & Uller, 2017). A seasonal increase in egg size can be adaptive if greater provisioning to late-produced offspring confers a fitness benefit (Nussbaum, 1981); however, a seasonal reduction in egg size can also be adaptive if it allows females to produce eggs earlier and earlier produced offspring have a survival advantage over those produced late (Birkhead & Nettleship, 1982). For most lizards studied, earlier produced offspring have higher survival than those produced later in the season (e.g. Pearson & Warner, 2018; Qualls & Shine, 2000; Warner & Shine, 2007), yet many lizards show a seasonal increase in egg size (see Ferguson & Snell, 1986 and citations therein). Thus, for late-season clutches, the benefits of producing larger eggs must outweigh the benefits of advancing lay-date via reductions in egg size. This is likely related to the absence of parental care. In other taxa (e.g. birds), advancing lay-date at a cost to egg size may be adaptive because parents can adjust care of offspring in accordance with seasonal changes in the environment (e.g. predation risk, food resources; Du, Liu, et al., 2014).

Past studies reveal that late-season eggs are not only bigger but produce larger hatchlings for their size (i.e. greater egg quality; Mitchell et al., 2018; Pearson & Warner, 2018). In our laboratory study, hatchling mass increased until August, at which point it did not increase further. Thus, the quality of eggs began to decline over the last 2 months of the study. Though females may be intrinsically predisposed (e.g. by genetics) to increase egg quality through the season, doing so may be influenced by cues (e.g. photoperiod, temperature) or resources (e.g. micronutrients) from natural environments. The mechanisms by which females seasonally alter egg quality are poorly understood, but many aspects of maternal provisioning (e.g. hormones, vitamins) influence offspring phenotypes (e.g. Bowden, Ewert, & Nelson, 2000; Parolini, Romano, Caprioli, Rubolini, & Saino, 2015; Ruuskanen & Hsu, 2018). In addition, seasonal shifts in water availability to mothers could impact the hydration (and mass) of eggs at oviposition (Brusch, Heulin, & DeNardo, 2019), which might explain our observed seasonal changes in egg quality (i.e. consistent yolk provisioning, but more water allocation later in the season). Indeed, we observed a greater proportion of unexplained residual variance in egg mass than hatchling mass, which could be due to variation in water allocation by females and/or water uptake by the eggs prior to discovery. Yolk energy content varies little with oviposition sequence in anoles (Hall et al., 2018) and is unlikely to modulate changes in egg quality. Studies examining variation in yolk contents and hormones are generally conducted in the laboratory; more field data are needed to understand seasonal changes in reproductive allocation.

A central prediction of life-history theory involves a trade-off between offspring size and number (Roff, 2002; Uller et al., 2009). For organisms that produce one egg at a time, this would entail a seasonal increase in egg size with a concomitant increase in the IEI. Though IEI was lowest mid-season, it was greatest at the end of the season when egg size was largest. Thus, our results show a relatively weak relationship between the size and number of offsprings compared with other studies (e.g. Pearson & Warner, 2018). Egg size and clutch size are assumed to be tightly and inversely correlated; however, some studies find only a weak relationship between the two (e.g. Ferguson & Snell, 1986). A possible explanation for the relatively weak relationship between egg size and IEI might be the warmer and less seasonal climate where this study took place (~4° south of populations used by Mitchell et al., 2018; Pearson & Warner, 2018; mean annual temperatures of 25°C vs. 20°C respectively). Because the strength of seasonal changes in reproduction should increase with latitude (Du, Robbins, et al., 2014; Varpe, 2017), for our population, selection on life-history traits may favour individuals that invest more in growth versus reproduction early in the season, which could generate a mid-season peak in reproductive effort.

Like our laboratory study, our field study revealed a seasonal increase in per-offspring effort, which demonstrates the patterns we observed in the laboratory are detectible in the field in spite of changing environmental conditions. However, unlike the laboratory study, the slope of the seasonal increase in egg size scaled positively with female SVL in the field (Figure 2a). This interaction between season and SVL may be due to physiological and morphological constraints on egg size: there is likely a minimum provisioning required to produce a viable egg (Warner & Lovern, 2014) which sets the lower bound of egg size, while the size of the pelvic aperture limits the upper bound (Michaud & Echternacht, 1995). Together these factors might generate relatively low variance in egg size for small females. Additionally, small females tend to allocate more resources towards growth than to reproduction compared to larger females (Andrews & Rand, 1974). Regardless, this hints at a twofold reproductive benefit of large maternal body size: larger females can produce larger eggs and are better able to modify the size of eggs to compensate for a changing environment.

Rates of seasonal changes in reproduction were comparable in the laboratory and field which further illustrates the endogenous control of these life-history traits; however, there were some notable differences. Laboratory females were bigger, had larger fat reserves and produced bigger eggs which reflects their high-calorie diet and low activity levels. Some of the difference in egg size can be attributed to water uptake by eggs in the laboratory (as much as 43%, see Supplemental Methods) since we only egg-checked thrice per week. Although the egg size by Day slope did not statistically differ between studies, it was nearly twice as great in the field. Moreover, in the field, the highest rate of egg production occurred earlier in the year compared to the laboratory (Figure 2b,c). Thus, overall, field data better conform to the parental investment hypothesis. Even if seasonal shifts in reproduction are intrinsic, they may be enhanced by field conditions. Seasonal variation in photoperiod, rainfall, humidity and temperature heavily influence reproductive phenology (Lee et al., 1989) and, thus, seasonal changes in reproduction may result from adaptation to seasonality and passive responses to changing maternal conditions (i.e. these hypotheses are not mutually exclusive). Finally, the interaction between maternal SVL and season on egg size observed in the field could likely not be detected in a longitudinal laboratory study because small females are not present late in the experiment due to growth. These results demonstrate how important aspects of reproduction can differ between laboratory and field studies, and we urge researchers to integrate studies when possible. An important caveat is that our studies were conducted during different years which may explain some of these differences. For example, although weather conditions leading up to the field and laboratory studies and during the field study were representative of historic conditions, the months leading up to the field study were somewhat cooler and drier compared to the laboratory study (see Supplemental Methods).

Variation among females in reproductive trajectories provides insight into the evolutionary potential of seasonal reproductive allocation. Although we detected statistically significant variation among females, the variation does not appear large, biologically. For example, the random slopes and intercepts explained relatively little

residual variance compared to the amount of unexplained variation. This could indicate that there has been strong selection against individuals that exhibit certain seasonal reproductive trajectories (e.g. that exhibit a decline in egg size); however, strong directional selection is particularly rare for phenological traits (Kingsolver et al., 2001). Though the shapes of curves for IEI are similar among females, the greater variation in IEI late in the season suggests more opportunity for selection to shape late-season allocation patterns than early or mid-season patterns. Despite this possibility, we do not know the strength of genetic correlations between IEI and other aspects of reproduction (e.g. egg size), which could constrain the evolution of these traits. Still, similarities in individual reproductive trajectories suggest that populations have evolved to change reproductive allocation throughout the season via changes in egg size and the rate of egg production. Given that late-produced offspring have lower survival than early-season offspring, the seasonal shift in parental investment observed here seems to maximize offspring number when conditions for offspring are good and maximize offspring quality when conditions for offspring are poor.

Finally, replication of studies of ecology and evolution is rare (Nakagawa & Parker, 2015). Four studies using three distinct experimental designs have quantified seasonal changes in the reproduction of brown anoles (temporally separated breeding cohorts—Mitchell et al., 2018, Pearson & Warner, 2018; longitudinal laboratory studies—Hall et al., 2018, this study; cross-sectional field study—this study). All four studies reveal a seasonal increase in egg size; however, the extent to which egg quality changes with season and how well females align reproductive effort with seasonal changes in habitat quality is less consistent. Despite logistical challenges, ecologists and evolutionary biologists strongly advocate for replication to (a) assess the validity of past work and (b) determine the generality of results (e.g. Nakagawa & Parker, 2015). The present work makes progress towards each goal by corroborating previously established trends with different methods and a different population.

A central goal of life-history theory is to understand how reproductive strategies evolve. In seasonal environments, aligning changes in reproductive effort with changes in environmental conditions is important for fitness in a diversity of species. Our results reveal an endogenous control of seasonal increases in egg size, and this is likely an adaptive response to a seasonal decline in the quality of the offspring environment. Animals with extended reproductive seasons and invariant clutch sizes afford great opportunities to evaluate the role of seasonality in life-history evolution, and integrating results from both laboratory and field studies of reproduction will be a necessary step towards achieving this goal.

Auburn University Museum of Natural History. The authors declare they have no conflict of interest.

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