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Life-history strategies are decoupled from ecomorphological convergence in two *Anolis* lizards

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ABSTRACT

Convergence is considered powerful evidence for adaptation to similar natural selection pressures. However, for many ecologically and morphologically convergent species, it remains unclear whether convergence extends to reproductive strategies, which are particularly important because of their tight connection to fitness. Here, by measuring key life-history traits (e.g. reproductive status, egg size, oviposition frequency, reproductive effort) across a full annual cycle comprising both reproductive and non-reproductive seasons, we discover divergence in reproductive strategies in two *Anolis* lizards that are otherwise strikingly convergent in ecology, morphology, and behaviour. The Cuban brown anole (*Anolis sagrei*) rapidly produces many small eggs during a concentrated summer reproductive season, whereas the Puerto Rican crested anole (*Anolis cristatellus*) produces comparatively fewer, larger eggs over a longer period. Thus, despite evolving highly convergent ecomorphological phenotypes and both being constrained to a single-egg clutch, these species exhibit marked divergence in life-history trade-off strategies along the fast–slow continuum. Our results indicate that ecomorphological convergence evolved uncoupled from life-history pathways in these species.

Keywords: convergent evolution; divergent evolution; fast–slow continuum; life-history evolution; reproductive phenology; reproductive effort; trade-offs

INTRODUCTION

Phenotypic convergence among unrelated species experiencing similar environmental conditions is widely taken as evidence for adaptation by natural selection (Losos 2009). However, most comparative studies of convergence focus on species' similarities in morphology (Muschick *et al.* 2012, Mahler *et al.* 2013, Pigot *et al.* 2020), ecology (Losos 1992, Winemiller *et al.* 2015), behaviour (Blackledge and Gillespie 2004, Ord *et al.* 2013), and physiology (Chen *et al.* 1997, Bernal *et al.* 2001). Often overlooked are other key traits associated with biological fitness, such as reproductive strategies (but see Johnson and Belk 2001, Ibargüengoytía and Casalins 2007). Such traits are key components of life-history theory, which seeks to explain how natural selection optimizes reproductive success in organisms, considering environmental selective pressures (e.g. mortality) and intrinsic factors (e.g. trade-offs, constraints) that impact survival and reproduction. Life-history theory, therefore, is widely considered essential to understanding phenotypic evolution (Husak and Lailvaux 2022). As such, it may be expected (perhaps assumed) that highly convergent species share similar life-history strategies; however, few empirical studies have investigated this directly.

Life-history theory predicts the optimal allocation of resources to growth, maintenance, and reproduction (i.e. fitness) in response to the environment (Roff 1993, Stearns 1998). Such allocation can be situated on a 'fast' to 'slow' continuum, whereby 'fast' species mature quickly at a small size, have relatively low annual survival, and exhibit high annual reproductive effort, often via the production of many small offspring. 'Slow' species exhibit the opposite (Stearns 1983). This continuum explains variation in reproductive traits across a diversity of organisms (Stearns 1983, Salguero-Gómez *et al.* 2016, Schwarz and Meiri 2017) and illuminates a variety of ecological phenomena, such as invasion dynamics (Allen *et al.* 2017), migration distance (Winger and Pegan 2021), hibernation (Turbill *et al.* 2011), extinction risk (Purvis *et al.* 2000), and adaptation to climate (Wiersma *et al.* 2007). Life histories can evolve along the fast–slow continuum in predictable ways; for example, becoming faster in response to

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high predation pressure (Reznick *et al.* 2001), slower in response to living on an island ('island syndrome'; Adler and Levins 1994), or slower in response to a tropical climate (Wiersma *et al.* 2007). Notably, such pressures also shape other phenotypes, such as morphology, behaviour, and physiology (e.g. Cooper and Pérez-Mellado 2010). Therefore, one avenue to convergence might occur if species share similar life-history tactics; establishing an evolutionary pathway by which reproductive strategies influence other aspects of the phenotype or vice versa (Wilbur *et al.* 1974). For example, in response to predation, fish convergently evolve similar phenotypes, including key life-history traits related to reproduction (Johnson and Belk 2001, Reznick *et al.* 2001), suggesting that morphology and physiology might evolve in tandem with life-history tactics. Identifying life-history trade-offs and reproductive strategies is therefore an important step towards predicting evolutionary outcomes and in understanding how and when phenotypic convergence occurs (Lande and Arnold 1983).

Anolis lizards (anoles) are an excellent system in which to study the interaction of reproductive strategies and evolutionary convergence (Losos 2009, Stroud and Losos 2020). Across the Greater Antilles, anoles have radiated into similar sets of habitat specialists that are convergent in ecology, morphology, and behaviour ('ecomorphs'; Williams 1972). However, unlike most lizards, which produce between one and three multi-egg clutches per year, all anoles produce multiple single-egg clutches throughout the reproductive season (Andrews and Rand 1974, Mesquita *et al.* 2015, Meiri 2018). Thus, *Anolis* reproductive strategies are assumed to be similar across species (Kratochvíl and Kubička 2007, Meiri *et al.* 2015), although other aspects of their biology (i.e. ecology, morphology, behaviour) can be highly divergent (Losos 1992, 2009). Generally, lizards evolve faster life histories in response to warmer, stable climates and in response to increased predation pressure (i.e. diverse predator communities in mainland regions vs. depauperate predator communities on islands) (Mesquita *et al.* 2015, Schwarz and Meiri 2017, Meiri *et al.* 2020); thus, we should expect variation in life-history traits and reproductive strategies among anoles as they occupy a diversity of habitats. Anole ecomorphological diversity is extensive and varies across environmental contexts, and it is possible that life-history traits evolve decoupled from these other aspects of the phenotype that are most commonly considered in studies of convergent evolution.

Detailed data on seasonal reproductive patterns and life-history traits of Caribbean anoles are limited (Gorman and Licht 1974, 1975, Andrews 1979, Mitchell *et al.* 2018, Hall *et al.* 2020). Several studies have explored the reproductive biology of individual species across seasons (Gorman and Licht 1974, Lee *et al.* 1989, Hall *et al.* 2018, 2020), and others have considered how reproductive traits of anoles differ from other major squamate lineages (i.e. those with multi-egg clutches; Andrews and Rand 1974, Kratochvíl and Kubička 2007, Meiri *et al.* 2015). However, there has not been a comparative assessment of whether ecomorphologically convergent anoles (i.e. distantly related species classified in the same ecomorph class) are also similar in fundamental life-history traits.

Here, we assess the reproductive ecology of two convergent *Anolis* lizards: the Cuban brown anole (*Anolis sagrei*) and the Puerto Rican crested anole (*Anolis cristatellus*) (Fig. 1). These species are convergent not only in morphology but also in many

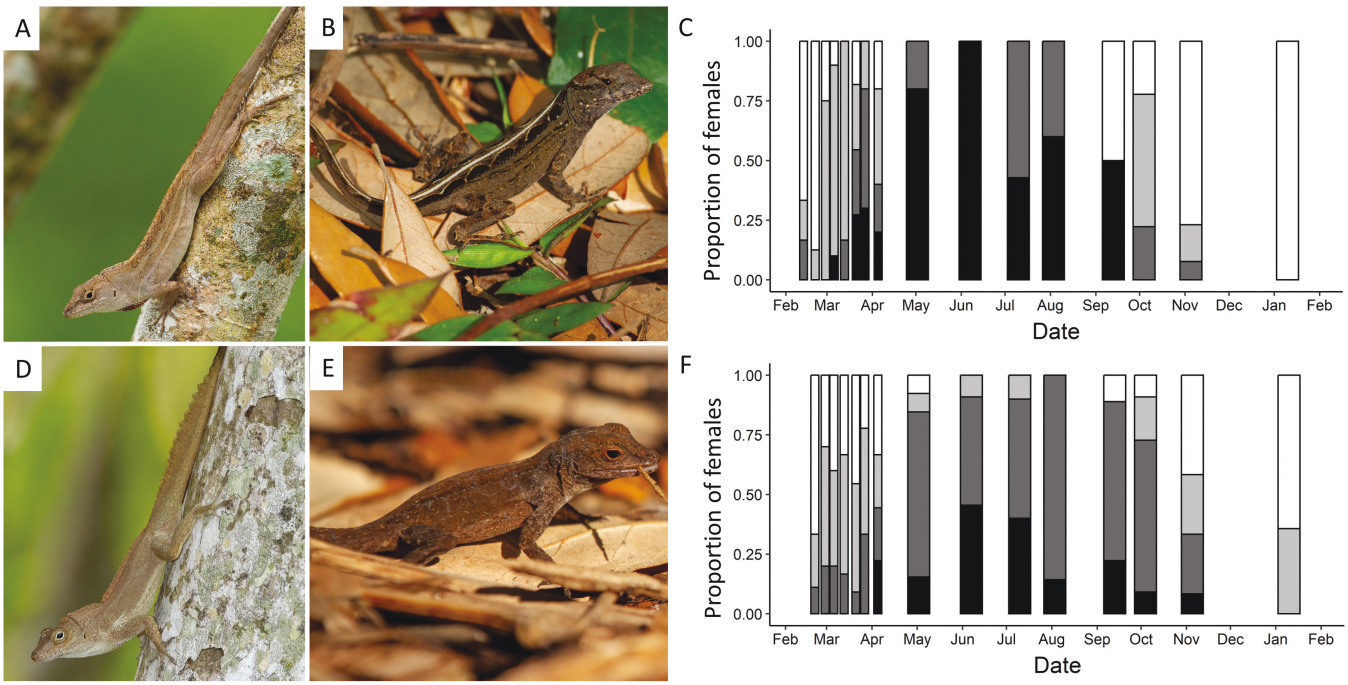

Figure 1. The Cuban brown anole (*Anolis sagrei*) and the Puerto Rican crested anole (*Anolis cristatellus*) are convergent species (i.e. members of the same 'trunk–ground' ecomorph class) but differ in key reproductive traits. *Anolis sagrei* adult male (A) and female (B). *Anolis cristatellus* adult male (D) and female (E). Photographs: Neil Losin/Day's Edge Productions. Seasonal variation in reproductive stage differs between *A. sagrei* (C) and *A. cristatellus* (F). White, light grey, dark grey, and black bars denote the proportion of females in stages I, II, III, and IV, respectively.

other aspects of the phenotype, including behaviours that might be expected to influence reproductive strategies, such as territorial display rate (Johnson *et al.* 2010b), signal size allometry (Stroud *et al.* 2023b), foraging rate (Johnson *et al.* 2008), sexual dimorphism (Butler *et al.* 2000), and habitat use (Kolbe *et al.* 2016). We combined field and laboratory approaches to evaluate the reproductive strategies of these two otherwise highly ecomorphologically convergent species. Specifically, we assessed: (i) reproductive status (reproductive stage, egg and maternal fat mass, and relative reproductive effort) of wild-caught female lizards throughout the course of an entire calendar year; and (ii) reproductive effort of wild-collected females housed in common garden conditions in the laboratory. Our approach, which combines cross-sectional and longitudinal study designs, provides a rare opportunity to investigate these topics at both the population and the individual levels for single bouts of reproduction and for total seasonal effort.

MATERIALS AND METHODS

Study species and sites

Anolis sagrei and *A. cristatellus* (Duméril & Bibron, 1837) are similar-sized, diurnal tropical lizards (for description, see Table 1) and originate from independent Caribbean island adaptive radiations (divergence occurred ~40–45 Mya; Poe *et al.* 2017). Both species are considered 'trunk–ground' ecomorphs (Losos 2009, Kolbe *et al.* 2016): predominantly brown lizards (Fig. 1) that most commonly occupy broad, low surfaces, such as the ground and lower portions of tree trunks, in both their native and introduced Florida range (Salzburg 1984, Kolbe *et al.* 2016, 2021, Stroud 2018, Stroud *et al.* 2019). Females excavate holes in the ground to deposit single-egg clutches and cover eggs with the displaced substrate (Pruett *et al.* 2022). These species are excellent candidates for this research because they are highly abundant in Florida, allowing for robust sample sizes (Stroud *et al.* 2023a, b), and protocols for studying their reproductive ecology in the wild are available (Sexton *et al.* 1971, Gorman and Licht 1974, 1975, Lee *et al.* 1989, Otero *et al.* 2015). Additionally, they are suitable for laboratory common garden studies owing to their hardiness in captivity, in concert with well-developed captive husbandry protocols (Sanger *et al.* 2008). Moreover, these species are highly fecund in captivity and have been used in a host of laboratory studies to learn about reproduction and life-history evolution (Fetters and McGlothlin 2017, Hall *et al.* 2018, 2020, Mitchell *et al.* 2018, Pearson and Warner 2018, Sanger *et al.* 2018, 2021). Although other non-native anoles of the same ecomorph class exist in south Florida [e.g. trunk–crown: *Anolis allisoni* (Cuba) and *Anolis chlorocyanus* (Hispaniola); crown–giant: *Anolis equestris* (Cuba) and *Anolis garmani* (Jamaica)], most of these species exist in small and geographically localized

Table 1. Comparisons between *Anolis sagrei* and *Anolis cristatellus* in field and laboratory studies. Values are the mean ± 95% confidence intervals, or confidence limits if in parentheses. For reproductive stages, relative effort, and fat mass in the field study, values are calculated at the mid-season for each species (21 June for *A. sagrei* and 30 July for *A. cristatellus*).

Comparison	*Anolis sagrei*	*Anolis cristatellus*
Native islands	Cuba and Bahamas	Puerto Rico
Ecomorph	Trunk–ground	Trunk–ground
Introduced to Florida	1940s	1970s
Wild-collected lizards		
Body size (snout–vent length; mm)	42.1 ± 0.5	45.8 ± 0.4
Body mass (g)	1.93 ± 0.08	2.72 ± 0.07
Reproductive season: start date	20 February	2 March
Reproductive season: end date	21 October	27 December
Reproductive season: Total days	243 ± 10	300 ± 7
Size vs. reproductive probability (odds ratio)	1.11 (0.92–1.35)	1.49 (1.26–1.81)
Egg mass (mg)	114.3 ± 5.7	184.2 ± 6.5
Probability of stage I	0.00 (0.00–0.01)	0.02 (0.00–0.04)
Probability of stage II	0.04 (0.00–0.08)	0.08 (0.02–0.13)
Probability of stage III	0.17 (0.06–0.29)	0.57 (0.45–0.69)
Probability of stage IV	0.78 (0.64–0.92)	0.33 (0.20–0.47)
Relative effort (egg mass/body mass)	0.13 ± 0.01	0.15 ± 0.01
Fat mass (mg)	18.7 ± 10.4	15.4 ± 11.2
Laboratory common garden		
Body size (snout–vent length; mm)	43.6 ± 0.19	46.0 ± 0.20
Body mass (g)	2.50 ± 0.04	2.82 ± 0.04
Egg mass (mg)	161.5 ± 3.2	240.4 ± 5.5
Inter-egg interval (days)	6.6 ± 0.7	9.9 ± 0.8
Total eggs per female	17.5 ± 1.7	7.4 ± 1.2
Effort per female (egg mass/body mass)	1.07 ± 0.14	0.60 ± 0.10

populations (Krysko *et al.* 2019); *A. sagrei* and *A. cristatellus* are the only two introduced species of the same ecomorph class that are well established and that co-occur broadly across the region. For these reasons, *A. sagrei* and *A. cristatellus* represent an excellent pair of candidate species for this comparative research.

We adopted two approaches to study temporal patterns of reproductive activity. First, lizards were collected from a wild population in Miami, FL, USA (Fairchild Tropical Botanic Gardens; 25.675837, −80.271684), where both species have occurred in sympatry for ~50 years (Kolbe *et al.* 2016). Therefore, despite being introduced from separate Caribbean islands, our wild population provides a scenario analogous to a natural common garden study: both species are experiencing the same environmental conditions (e.g. rainfall, photoperiod, temperature, and food availability) that contribute to reproductive output and seasonal reproductive cycles in anoles (Gorman and Licht 1974, Lee *et al.* 1989, Otero *et al.* 2015, Hall *et al.* 2018). Second, we leverage reproductive data from a large breeding colony of both species wild-collected from our field study area and subjected to common garden conditions in the laboratory (Hall and Warner 2019).

Study design

To demarcate the start of reproductive activity, we collected female *A. sagrei* and *A. cristatellus* weekly from 13 February to 27 March 2018; we then collected females every 2–4 weeks thereafter until 10 January 2019 (Supporting Information, Table S1). We attempted to capture every female of potential reproductive size that we encountered [i.e. >34 mm snout–vent length (SVL)] until reaching a target sample of ~10 individuals per species during each effort (Supporting Information, Table S1). Lizards were immediately shipped overnight to Auburn University and euthanized by intraperitoneal injection of a 1:1 mixture of Sleepaway Beuthanasia (sodium pentobarbital) and deionized water. We measured SVL (to 0.01 mm) and mass (to 0.01 g), then via post-mortem examination, we measured abdominal fat mass (to 0.0001 g) and examined oviducts and ovaries to assign each female to one of the following four reproductive stages (Sexton *et al.* 1971): stage I, no yolky ovarian follicles and no oviductal eggs (i.e. reproductively inactive); stage II, one yolky ovarian follicle (i.e. yellow in colour); stage III, one yolky ovarian follicle and one oviductal egg; or stage IV, one yolky ovarian follicle and two oviductal eggs. Anoles alternate egg production between left and right ovaries; thus, the rate of reproductive output is suspected to be greatest when an egg is present in each oviduct (i.e. stage IV; Sexton *et al.* 1971). To assess interspecific variation in egg mass, we removed mature eggs (i.e. white and shelled; *A. sagrei*, $N = 49$; *A. cristatellus*, $N = 38$) from the oviducts and recorded their mass (to 0.0001 g).

Full details of the common garden breeding project are reported elsewhere (Hall and Warner 2019). Briefly, in 2017, we wild-collected adult *A. sagrei* ($N = 30$ females; $N = 15$ males) and *A. cristatellus* ($N = 64$ females; $N = 34$ males) from the same area as our field study. Lizards were transported to Auburn University and maintained in identical conditions in the same room, following established protocols for housing and breeding *Anolis* lizards (Sanger *et al.* 2008). Lizards were housed in cages constructed from plastic bins (29 cm × 26 cm × 39 cm, height × width × depth). Ambient cage temperature was 28°C, with basking spots of 31°C–33°C, which is similar to body temperatures in South Florida (Battles and Kolbe 2019). We misted cages with water daily and provided each lizard with three crickets dusted with vitamins and calcium twice per week. We illuminated cages with a 12 h–12 h light–dark cycle using UVB bulbs. We provided each enclosure with two bamboo perches and multiple fake plants to disrupt lines of sight within and across cages, reducing stress imposed by sighting other lizards. Eggs were collected and weighed (to 0.0001 g) 3 days per week from 7 June to 25 October 2017. Females were housed individually, allowing for estimates of egg size, number, and reproductive effort. Because we had half as many males as females, we moved males among cages approximately every 2 weeks to ensure that eggs were fertile. Females can store sperm for several weeks (Calsbeek *et al.* 2007).

Statistical methods

For the field study, we removed all females from our dataset that were smaller than the smallest reproductive female we collected (i.e. reproductive stage II or above; *A. sagrei* SVL limit = 37 mm, *A. cristatellus* = 39mm). To assess interspecific differences in reproductive phenology, we categorized females as being either reproductive (stages II–IV) or not (stage I). We used a generalized linear model with a binomial distribution; reproductive status was the response variable (1 = reproductive, 0 = not reproductive) and SVL, date, and species were fixed effects. For this model and subsequent analyses, collection date (hereafter, 'date') was modelled as a second-degree polynomial, because we expected the probability of being in any particular stage to scale curvilinearly with time (i.e. reproductive activity peak in summer months; Gorman and Licht 1974, Lee *et al.* 1989). To compare phenology between species, we used the *predict* function to estimate the earliest and latest dates at which the probability of a female being reproductive was ≥.50 (i.e. half the population reproductive).

To determine species differences in offspring size, we used egg mass (which accurately predicts hatchling mass; Hall *et al.* 2018, 2020) as a response variable in a general linear model, with maternal SVL, species, and date as fixed effects. Egg mass was log-transformed to reduce heteroscedasticity. Date was modelled linearly (Hall *et al.* 2018, 2020). To determine species differences in the number of offspring produced, we analysed reproductive stage (I, II, III, or IV) with an ordinal regression, assuming that higher values for reproductive stage (e.g. stage IV vs. stage III) indicate a greater rate of egg production, which is correlated with a greater number of offspring produced. In the ordinal regression, reproductive stage, as an ordered factor, served as the response variable, and maternal SVL, species, and date were fixed effects.

To compare individual reproductive effort (i.e. total egg mass divided by body mass) between species, we estimated the typical egg mass for every female using coefficients from species-specific models of egg mass (described above) and multiplied this value by the number of eggs each female could produce. We excluded non-reproductive females (i.e. stage I) from the analysis because they had a relative effort of zero. To calculate the number of eggs, we assigned each female a number of eggs based on reproductive stage: stages II, III, and IV females were equated with one, two, and three eggs, respectively. These values represent the total number of eggs that each female could produce

given her reproductive status at the time of capture. We used a general linear model to analyse reproductive effort, with species and date as fixed effects. We did not include SVL as a covariate because it was used to estimate the response variable.

To assess variation in fat mass between species, we performed a general linear model, with abdominal fat mass as the response variable and with species, date, and body mass (minus fat mass) as fixed effects. To account for the high frequency of females with zero fat mass during the peak of the reproductive season (i.e. avoid boundary issues), we used mean values of fat and body mass from each collection date. To account for unequal sample sizes, we weighted the regression by the sample size of each collection date.

For the laboratory study, we analysed egg mass with a general linear mixed effects model, with date, species, and SVL as fixed effects and with maternal identity as a random effect. Egg number and the mean inter-egg interval (i.e. average number of days between clutches) were analysed with general linear models, with species and SVL as fixed effects, and we weighted the inter-egg intervals by the sample size (i.e. number of eggs). Egg mass and inter-egg interval were log-transformed to reduce heteroscedasticity. To assess species differences in reproductive effort, we divided the sum of all egg masses for each female by her body mass and made comparisons with a *t*-test.

We used SVL as a covariate in analyses rather than body mass for several reasons. First, SVL is recorded more often than body mass (Meiri 2018), which makes our work more comparable to other studies. Second, SVL is less variable than body mass in response to immediate environmental conditions, such as food availability (Hall *et al.* 2018). Moreover, body mass can vary substantially according to lean mass, fat reserves, or water content (Warner *et al.* 2016), and these might differ in their influence on reproduction. Finally, body mass of females is heavily influenced by reproductive status, which was unknown in our laboratory study when females were measured. Thus, SVL was more comparable than body mass between our laboratory and field data.

Finally, to understand how reproduction in the invasive range compares with native populations, we compared published data for *A. sagrei* in Jamaica (Licht and Gorman 1970) and *A. cristatellus* in Puerto Rico (Otero *et al.* 2015) using similar analyses to those above for reproductive phenology and reproductive stage. No data were given for egg size. For *A. sagrei*, body size was not provided; therefore, our models for phenology and reproductive stage included a location variable (Florida vs. Jamaica) and date as a second-degree polynomial. For *A. cristatellus*, we used the 'open canopy' sites from the study by Otero *et al.* (2015) because these are most comparable to our field site in Florida. They reported data from two locations: Monagas and Punta Salinas. To compare phenology, our initial model included location (Florida vs. Monagas vs. Punta Salinas), SVL, and date as a second-degree polynomial. Otero *et al.* (2015) do not differentiate between stage III and stage IV females in their published dataset; however, they report the overall incidence of stage IV females in the main text. Thus, we could not analyse reproductive stage according to body size and date, but we could perform an ordinal regression with location (Florida vs. Monagas vs. Punta Salinas) as a fixed effect to determine whether populations differed in the probability of each reproductive stage.

For all models, we included all two-way interaction terms and dropped non-significant interactions in a stepwise fashion via likelihood ratio tests. To explore remaining interactions, we split the dataset by species and re-ran the final models excluding a species factor. Continuous fixed effects were centred prior to analysis; therefore, species effects are meaningful even in the presence of interactions. Owing to species differences in body size, maternal SVL was centred separately for each species. Date was coded as Julian day of the year; however, the January field sample was considered day 375 because it followed samples from the previous year. For log-transformed variables, we re-reran final models with untransformed data to calculate model coefficients (i.e. beta values; β). Likelihood ratio tests and mixed effects models used the 'lmtest' package (Zeilis and Hothorn 2002) and the 'lme4' package (Bates *et al.* 2015), respectively. Estimates (β ± 1 SE) were calculated using the 'summary' function in R. Ordinal regression was performed using the package 'ordinal'. All analyses were performed in R (R Core Team 2021). Although our analyses correct for SVL, to correct conservatively for species differences in body size, we reduced both field and laboratory data to include only females between 42 and 45 mm SVL (i.e. similar-sized females; Supporting Information, Figs S1A, S2A) and repeated analyses for measures of egg size, number of eggs (i.e. reproductive stage and inter-egg interval), and reproductive effort.

RESULTS

Reproductive phenology

We detected clear seasonality in reproduction for both species, indicated by consistent periods of low vs. high reproductive output (Fig. 1). However, the overall pattern of reproductive phenology differed between species ($\chi^2 = 33.2$, $P < .001$; Fig. 2; Supporting Information, Table S2). Specifically, the reproductive season (as determined by >.50 probability of a female being reproductive) of *A. sagrei* was 57 days shorter than that of *A. cristatellus* (Table 1), which is driven primarily by *A. cristatellus* extending their reproductive season later in the year (Fig. 1). Additionally, the effect of body size on the probability of being reproductive differed between species ($\chi^2 = 4.8$, $P = .03$; Supporting Information, Table S2): larger females were more likely to be reproductive for *A. cristatellus* ($t = 4.3$, $P < .001$; Supporting Information, Table S3) but not *A. sagrei* ($t = 1.1$, $P = .265$; Supporting Information, Table S3). Specifically, the largest *A. cristatellus* females (~50 mm) were 54.1 times as likely to be reproductive (stages II–IV) as the smallest females (~40 mm) (Table 1).

Egg mass (offspring size)

Egg mass was substantially larger for *A. cristatellus* than *A. sagrei* in both the field ($F_{1,83} = 228.5$, $P < .001$; Fig. 3A; Supporting Information, Tables S2 and S3) and the laboratory ($F_{1,81} = 16.8$, $P < .001$; Fig. 4A; Supporting Information, Tables S4 and S5) even when constraining the data to females of comparable body size (Supporting Information, Figs S1B, S2B; Tables S6 and S7). Although egg mass was greater in the laboratory for both species owing to water uptake from the nest pots, the difference in mass between species was comparable in both studies

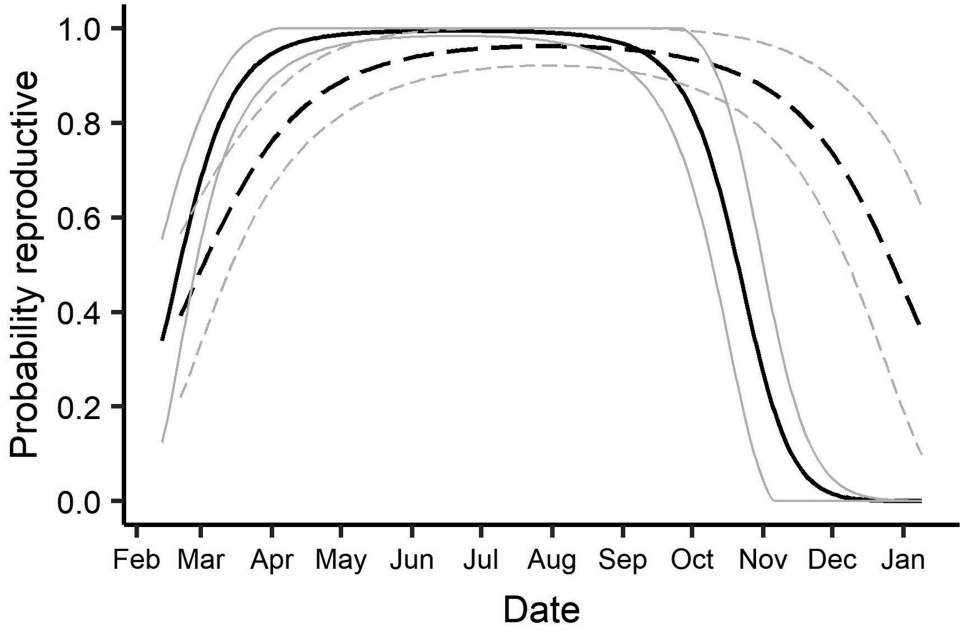

Figure 2. Reproductive phenology of *Anolis sagrei* (continuous lines) and *Anolis cristatellus* (dashed lines). Grey lines show the 95% confidence intervals. All lines were generated using the individual species models that included snout–vent length and collection date (as a second-degree polynomial) as fixed effects.

(Table 1). Furthermore, egg mass increased across the breeding season for both species in the field ($F_{1,83}$ =17.7, P < .001; Fig. 3A; Supporting Information, Table S2) and the laboratory ($F_{1,749}$ = 64.1, P < .001; Fig. 4A; Supporting Information, Table S4); but scaled with body size only in the field study (Figs 3B, 4B; Supporting Information, Tables S2 and S4).

Reproductive rate and number of offspring

Seasonal patterns of reproductive stage differed between species (χ^2 = 23.8, P < .001; Fig. 5A–D; Supporting Information, Table S2). In the middle of the season (21 June and 30 July for *A. sagrei* and *A. cristatellus*, respectively), the probability of being non-reproductive (i.e. stage I) or in the early stages of reproductive activity (i.e. stage II) was similar between species (Table 1; Fig. 5A, B). However, *A. cristatellus* was more likely to have a single oviductal egg (i.e. stage III) than *A. sagrei* (Table 1; Fig. 5C), whereas *A. sagrei* had a higher probability of having two oviductal eggs (i.e. stage IV) (Table 1; Fig. 5D). Thus, *A. sagrei* consistently exhibited a higher rate of egg production than *A. cristatellus* even when comparing females of similar size (Supporting Information, Fig. S1C; Table S6). Moreover, for both species, the probability of being in a higher reproductive stage increased with body size (χ^2 = 24.6, P < .001; Supporting Information, Table S2); however, at the height of the reproductive season, even the smallest mature *A. sagrei* had a greater probability (~50%) of being stage IV than the largest *A. cristatellus* (~40% probability) (Fig. 5E, F).

Results from the laboratory aligned with those from the field: *A. sagrei* females produced, on average, 10 eggs more than *A. cristatellus* across the entirety of the laboratory study ($F_{1,77}$ = 90.7, P < .001; Supporting Information, Table S4), which was driven by *A. sagrei* exhibiting an inter-egg interval that was ~3 days shorter than *A. cristatellus* ($F_{1,77}$ = 39.0, P < .001; Supporting Information, Table S4) (Table 1; Fig. 4C). These differences remained for females of comparable size (Supporting Information, Fig. S2C; Table S7).

Reproductive effort and energy reserves

In the wild, *A. sagrei* and *A. cristatellus* exhibited similar levels of reproductive effort (Fig. 3C; Supporting Information, Fig. S1D; Table S6); however, the species differed in seasonal patterns of effort ($F_{2,198}$ = 4.6, P = .011) and fat mass ($F_{2,22}$ = 11.0, P < .001) (Fig. 3C, D; Supporting Information, Table S2). Although effort and fat mass were comparable for most of the season (Table 1), in August *A. sagrei* decreased effort relative to *A. cristatellus* (Fig. 3C, D). Fat mass shifted in concert with changes in reproductive effort, with *A. sagrei* having higher fat mass than *A. cristatellus* from August onwards, when *A. sagrei* reproductive output decreased while output of *A. cristatellus* remained higher (Fig. 3D). Owing to differences in the number of eggs produced (see above), in the laboratory, reproductive effort was ~0.47 greater for *A. sagrei* than for *A. cristatellus* ($F_{1,82}$ = 29.75, P < .001; Table 1; Fig. 4D; Supporting Information, Table S4) even when comparing females of similar body size (Supporting Information, Fig. S2D; Table S7). Thus, *A. sagrei* produced about half their body mass more in total egg mass than did *A. cristatellus*.

Comparison with the native range

Anolis sagrei reproduction differed substantially between the native and invasive range for both phenology and reproductive stage (Supporting Information, Tables S8 and S9); however, *A. cristatellus* reproduction was similar across populations (Supporting Information, Tables S8 and S9). Specifically, *A. sagrei* exhibited a longer reproductive season in Jamaica, such that >50% of females were reproductive year-round, whereas in Florida reproduction ceased during the winter months

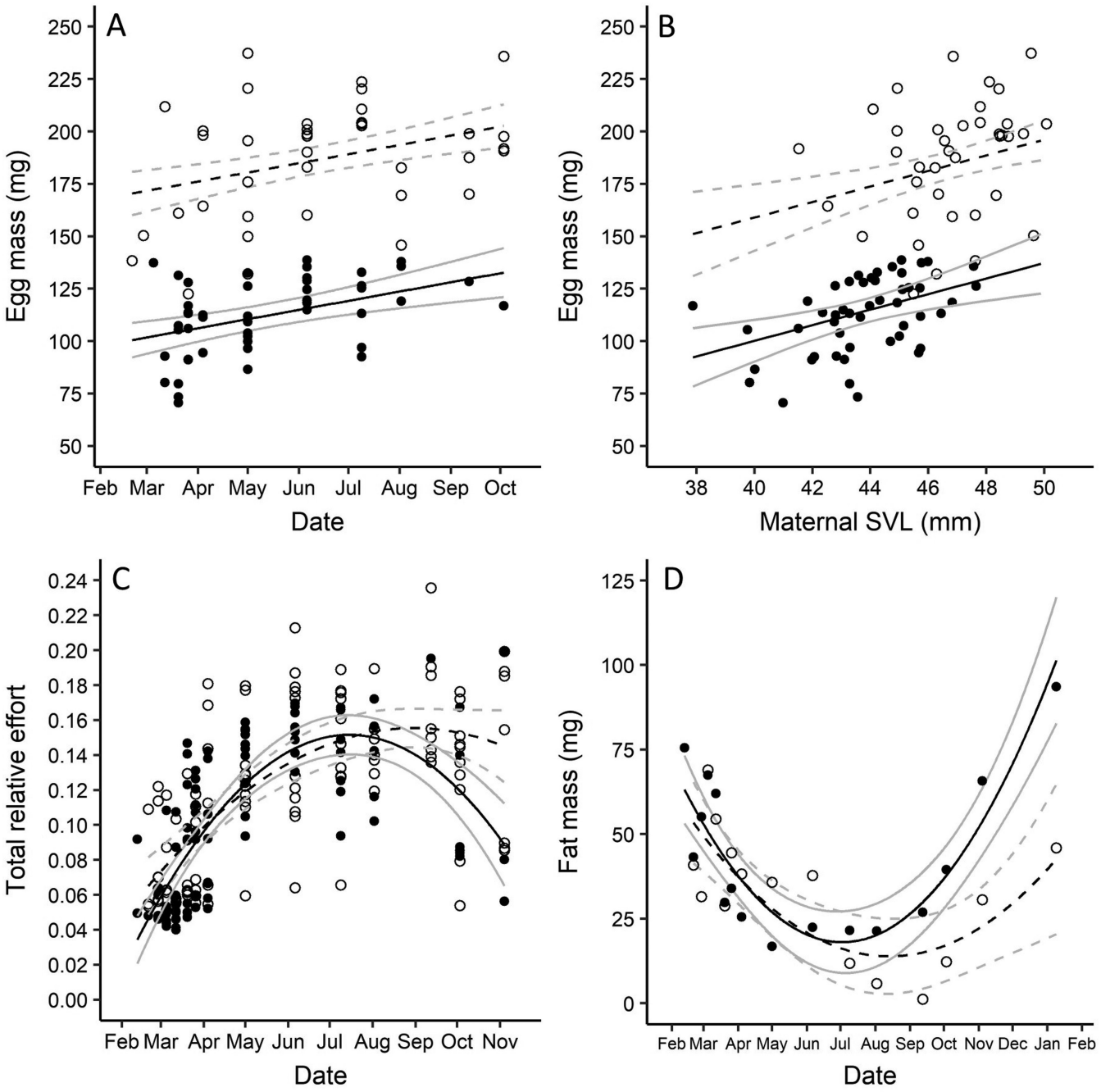

Figure 3. Reproductive traits for *Anolis sagrei* and *Anolis cristatellus* females in the field. Relationships between egg mass and season (A), egg mass and maternal snout–vent length (SVL; B), total relative effort across the reproductive season (C), and seasonal changes in energy reserves (i.e. fat mass; D). Open circles and dashed lines show raw data and trend line for *A. cristatellus*. Filled circles and continuous lines show raw data and trend line for *A. sagrei*. Grey lines show the 95% confidence intervals.

(Supporting Information, Fig. S3A). Moreover, in Jamaica, *A. sagrei* females were much less likely to reach stage IV compared with those in Florida, indicating a slower rate of egg production in the native range (Supporting Information, Fig. S4). For *A. cristatellus*, we did not observe population-specific phenology (i.e. no location by date interaction; Supporting Information, Table S8), indicating that seasonal trends in reproduction are similar between the native and invasive range (Supporting Information, Fig. S3B). Although Florida *A. cristatellus* were less likely to be stage IV than females from Monagas (Supporting Information, Fig. S5), the difference was slight. Additionally, Florida *A. cristatellus* did not differ in reproductive stage from females in Punta Salinas (Supporting Information, Fig. S5), indicating that rates of egg production were comparable between the native and invasive ranges.

DISCUSSION

Phenotypic convergence is often taken as evidence for adaptation and the predictability of evolution in response to

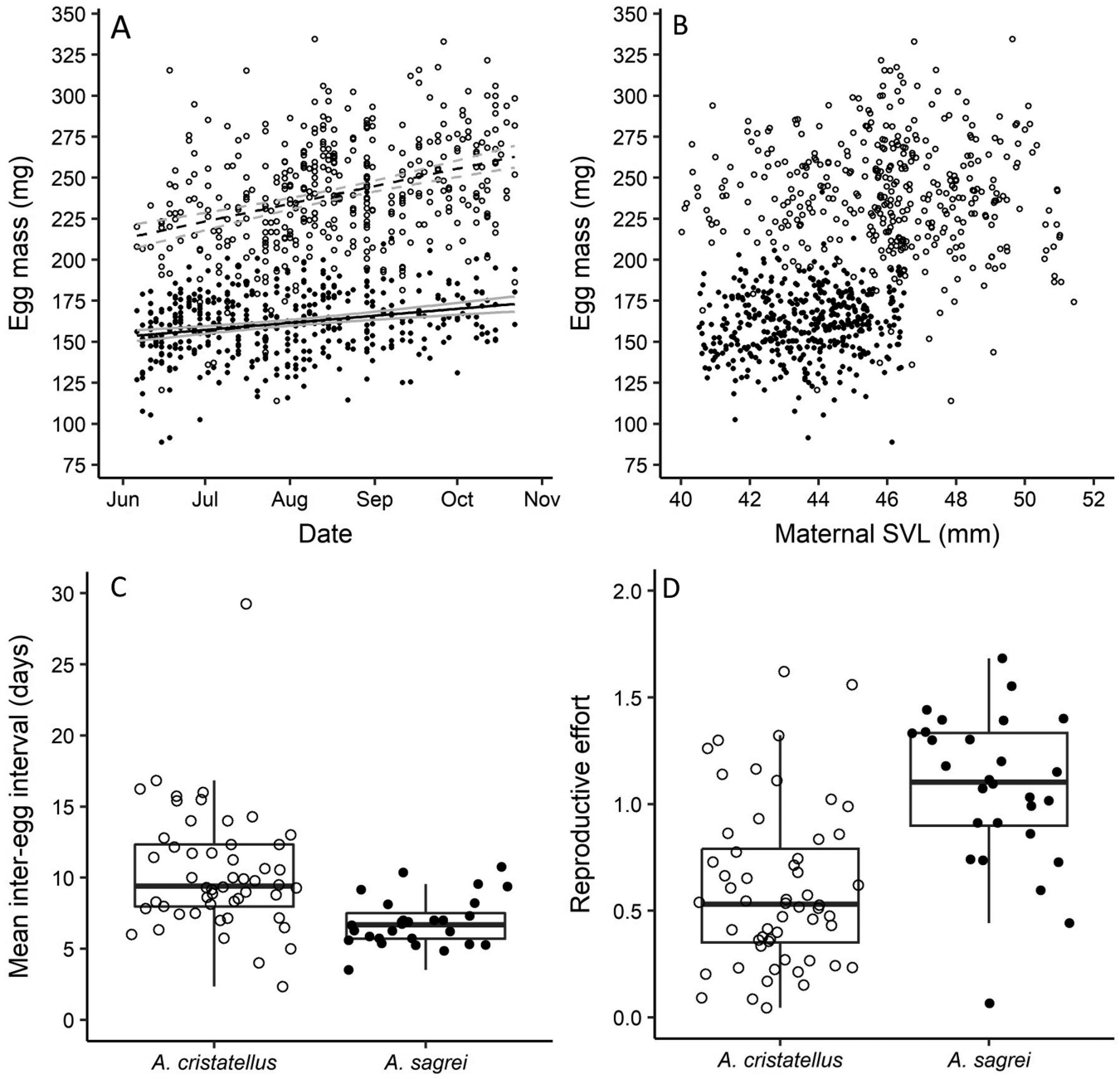

Figure 4. Reproductive traits for *Anolis sagrei* and *Anolis cristatellus* females from the laboratory common garden study. A, B, relationships between egg mass and season (A) or maternal snout–vent length (B). C, D, Species differences in the inter-egg interval (C) and reproductive effort (D). Open circles and dashed lines show raw data and trend line for *A. cristatellus*. Filled circles and continuous lines show raw data and trend line for *A. sagrei*. A and B show data for each egg, whereas C and D show a single value for each female.

similar environmental conditions. We show that two *Anolis* lizard species, each originating from different Caribbean islands yet strikingly convergent in ecology and morphology, differ in key reproductive traits, such as egg size, clutch frequency, and reproductive phenology; traits that are often overlooked in studies of convergent evolution. Our results indicate that life-history evolution can be uncoupled from the evolutionary trajectory of other aspects of the phenotype, providing an integrative insight into how organismal evolution, particularly through the lens of convergent evolution, unfolds in the wild.

Divergent reproductive phenology

Given that anoles produce single-egg clutches, total reproductive effort across the lifespan of a lizard is intrinsically related to the length of the reproductive season (i.e. the annual duration of female egg production). In their native ranges, reproduction is continuous for both *A. sagrei* and *A. cristatellus*, although fewer females are reproducing during the cooler months (34%–66% of the population, from November to March; Licht and Gorman 1970, Gorman and Licht 1974, Otero *et al.* 2015). Our results identify clear periods of reproductive inactivity in *A. sagrei* but not *A. cristatellus* in Florida: *A. sagrei* cease reproduction

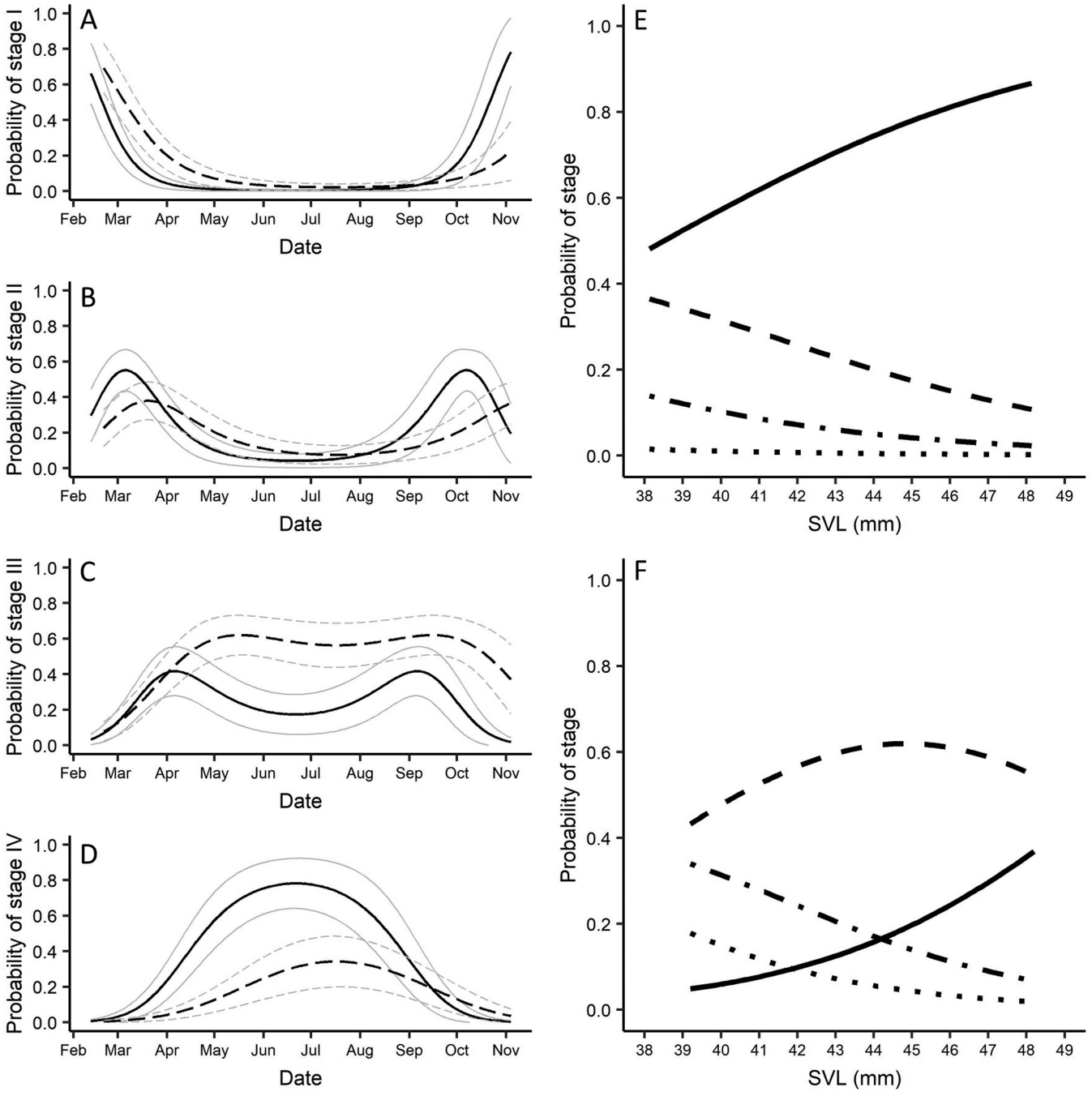

Figure 5. Probability of female *Anolis sagrei* and *Anolis cristatellus* being in a particular reproductive stage (A–D) and relationship between stage and body size (E, F). A–D, probabilities of a female being in stage I, II, III, and IV, respectively. Continuous black line and dashed black line show model estimates for *A. sagrei* and *A. cristatellus*, respectively. Grey lines show the 95% confidence intervals. In E, F, lines are model predictions of each stage at the midpoint of the reproductive season for *A. sagrei* (E) and *A. cristatellus* (F): dotted line is stage I, dash and dot line is stage II, dashed line is stage III, and continuous line is stage IV.

in the winter (the majority of adult females are stage I from November to February), whereas *A. cristatellus* maintain moderate reproductive activity during the same period (i.e. many females are stages II and III). Thus, patterns between the native and non-native range are more similar in *A. cristatellus* than in *A. sagrei*.

Three non-mutually exclusive reasons could explain our results. First, *A. sagrei* might have adapted locally to south Florida environmental conditions, owing to its relatively longer period of establishment (~80–90 vs. 30–40 generations; Kolbe *et al.* 2007a, 2007b), whereas *A. cristatellus* has not. For example, in other Florida populations, *A. sagrei* that hatch earlier in the year have greater survival relative to those that hatch later (Pearson and Warner 2018). It is possible, therefore, that a shorter reproductive season has evolved in response to this seasonal fitness decline of offspring (Hall *et al.* 2020). Second, alternatively, *A. sagrei* might possess greater inherent phenological plasticity of reproduction in response to local environmental conditions.

For example, *A. sagrei* might reduce reproductive activity owing to lower temperatures or decreased food availability in winter (Ballinger 1977). Indeed, *A. sagrei* exhibit marked variation in seasonal reproduction across their range (Belize, Sexton and Brown 1977; Hawaii, Goldberg *et al.* 2002; Taiwan, Norval *et al.* 2012). Alternatively, given that plasticity is expected to evolve in response to variable or cyclical environments (Price *et al.* 2003) [e.g. the transition from native (non-seasonal) tropical islands, such as *A. sagrei*'s native Cuba, to seasonally subtropical south Florida], such phenological plasticity could result from divergent adaptive evolution owing to the longer establishment of *A. sagrei* in south Florida. Third, seasonal selective pressures might differ between species such that the seasonal decline in fitness is weaker for *A. cristatellus*. Although such differences have not been assessed explicitly, these species might be experiencing divergent selective pressures in south Florida despite their convergence (e.g. via differential parasitism loads; Thawley *et al.* 2019). Alternatively, *A. cristatellus* reproductive activity might be prolonged through winter because eggs are less sensitive to cold temperatures than those of *A. sagrei* (Hall and Warner 2019), and cool incubation temperatures might drive seasonal reproduction in anoles (Gorman and Licht 1974).

Body size, egg mass, and the 'fast–slow' continuum

Life-history traits are often situated on a 'fast–slow' continuum: 'faster' species exhibit short lifespans, smaller size at maturity, and production of relatively many, lower-quality (e.g. smaller) offspring, whereas 'slower' species exhibit the opposite traits (Pianka 1970, MacArthur and Wilson 2001, Schwarz and Meiri 2017). Our results indicate that *A. sagrei*, which is marginally smaller and potentially shorter lived (see below), produces smaller eggs at a faster rate than *A. cristatellus*. Importantly, these differences in offspring size/number contrast with both our original hypothesis (i.e. similar ecomorphs have similar reproductive traits) and the null expectation (i.e. larger anoles lay relatively smaller eggs; Meiri *et al.* 2015).

There are several functional and selective agents operating on egg size in *Anolis*. For example, although bigger eggs result in larger, potentially more robust offspring, there are anatomical limits to egg size (i.e. pelvic aperture), and females might not produce the largest egg possible because carrying even a single egg impairs locomotion (Cox and Calsbeek 2010; Johnson *et al.* 2010a). Moreover, lizards might produce relatively small eggs to increase the total number of offspring (i.e. invest in quantity over quality; Hall *et al.* 2020). Life-history theory suggests that such investment is preferable when offspring survival is low and increasing offspring size does not appreciably enhance offspring survival (Winkler and Wallin 1987). Our results indicate that the reproductive value of *A. sagrei* offspring is considerably lower than those of *A. cristatellus*. Indeed, annual female survival is lower for *A. sagrei* than for *A. cristatellus* at our field site (16% vs. 32%, respectively; J. Stroud, unpublished data). The reasons for this difference are not clear; however, female survival in the native range is also greater for *A. cristatellus* than for *A. sagrei* (Wright *et al.* 2013, Otero López and Sabat 2015), which might reflect our proposed divergence on the fast–slow continuum.

Alternatively, selection might favour the production of larger offspring if larger size confers a significant advantage (e.g. higher survival probability); however, empirical evidence for this in lizards is mixed and likely to be context dependent (Sinervo *et al.* 1992, Warner and Shine 2007, Pearson and Warner 2018). Although insular lizards typically evolve a slower life history (including lower rate of egg production; Powell and Watkins 2014), it has been suggested that insular anoles exhibit 'reverse island syndrome' (Schwarz and Meiri 2017) by evolving a faster rate of egg production as an adaptation to Caribbean islands, where high population densities result in low offspring survival owing to cannibalism (Powell and Watkins 2014), depredation by other predators (including other anoles; Gerber and Echternacht 2000), or extreme climate events (Donihue *et al.* 2018, 2020, Stroud *et al.* 2020). Additionally, the evolutionary history of insular anoles is one of repeated island colonization and adaptive radiation. High clutch frequencies might benefit species constrained to single-egg clutches during natural dispersal and establishment events between islands (Fetters and McGlothlin 2017). Over the past century, these reproductive traits might be responsible for the success of anoles in establishing populations outside of their native range (Kraus 2015). For example, *A. sagrei* has the highest rate of egg production recorded in anoles, with some females laying an egg every 4 days (Fig. 4C), and is also one of the most successful invaders, with a growing, global distribution (Stroud *et al.* 2017, 2018, 2019, Hulbert *et al.* 2020). Although invasive populations of *A. sagrei* exhibit faster rates of egg production than native populations (Fetters and McGlothlin 2017), past work aligning anole phenotypes with invasion success did not include reproductive traits (Latella *et al.* 2011); therefore, this hypothesis has not been tested with a multi-species dataset.

Further evidence of divergence on the fast–slow continuum comes from effects of body size on reproduction. For *A. sagrei*, the relationship between reproduction and size appears binary: once females achieve reproductive size, they initiate reproduction. For *A. cristatellus*, the probability of a female reproducing increased with body size. Moreover, body size appears less important for *A. sagrei* to achieve maximal reproductive output (i.e. stage IV): the smallest *A. sagrei* had a probability of .5 of being stage IV, whereas *A. cristatellus* require growth to near-maximal size to exhibit a similar rate (Fig. 5). These results indicate that *A. sagrei* initiate maximal reproductive effort as soon as females are reproductively viable, whereas *A. cristatellus* exhibit a more conservative relationship of body size with reproductive effort, possibly to increase longevity or achieve larger body sizes. Taken altogether, these results highlight that, despite being constrained to a single-egg clutch, very similar, convergent species can clearly diverge in reproductive ecology and life-history strategies. Such life-history traits are often overlooked yet could be a powerful influence on evolutionary change given their direct connection with fitness.

Reproductive effort

Reproductive effort represents the relative amount of energy a female dedicates to production of offspring and can be calculated for a single reproductive bout, an entire season, or a lifetime. The cost of present reproductive effort is often calculated as the amount of future reproduction that must be sacrificed to achieve it (Hirshfield and Tinkle 1975). However, for short-lived species, such as anoles, reproductive effort is influenced primarily by the effect of reproduction on survival rather than a trade-off between current and future reproduction (Shine and Schwarzkopf 1992).

Thus, both species have probably maximized their per bout reproductive effort, and reproduction responds to selection only via small adjustments to the number and size of offspring based on slight differences in annual survival. Anoles possess multiple traits associated with high reproductive effort, including frequent egg production in a single season, aggressive behaviour towards conspecifics, and a high degree of sexual dimorphism (Andrews and Rand 1974, Hirshfield and Tinkle 1975, Butler *et al.* 2000, Reedy *et al.* 2017, Stroud 2018, Hall *et al.* 2020).

Given that both species in our study are experiencing similar environmental conditions and access to resources, equal effort for a reproductive bout is expected, because anoles are primarily income breeders (i.e. the size and number of eggs scale with food availability; Hall *et al.* 2018). However, owing to the near-continuous production of single-egg clutches during the breeding season, seasonal and lifetime effort scale with phenology and lifespan (Hall *et al.* 2018). Likewise, our results demonstrate that the per-bout effort is similar between species, as expected (Fig. 3C); however, total effort in a season appears greater for *A. sagrei* owing to the lower overall egg production of *A. cristatellus* (Fig. 4D). Effort, therefore, appears to be distributed as expected across the fast–slow continuum: *A. sagrei* exhibits high effort during a single, relatively short season via the production of many small offspring, whereas *A. cristatellus* expends less effort over a longer period (both phenology and lifetime) via production of relatively fewer, larger eggs.

CONCLUSION

Convergent species (those similar in ecology, morphology, and other phenotypic traits) might be expected also to share reproductive ecology and life-history strategies. Our data indicate that this is not true for two strongly convergent Caribbean *Anolis* lizards, which diverge on the fast–slow life-history continuum. Although reproductive strategies are tightly linked to fitness, and therefore have substantial influence on evolutionary trajectories, it appears that phenotypic convergence can manifest uncoupled from life-history convergence. To gain a better understanding of how and why convergence evolves, integrative studies are needed to investigate multiple axes of species phenotypes, spanning ecological, morphological, physiological, behavioural, and life-history traits.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

All authors conceived of the project and developed hypotheses. Christopher J. Thawley and James T. Stroud conducted fieldwork. Joshua M. Hall conducted laboratory work. Joshua M. Hall analyzed data. All authors contributed to manuscript writing and development.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

Data are available via AUrora: Auburn University's scholarly digital repository (https://doi.org/10.35099/85f3-h106).

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