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Article

Age and terminal reproductive attempt influence laying date in the thorn-tailed rayadito

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Age-specific variation in reproductive effort can affect population dynamics, and is a key component of the evolution of reproductive tactics. Late-life declines are a typical feature of variation in reproduction. However, the cause of these declines, and thus their implications for the evolution of life-history tactics, may differ. Some prior studies have shown late-life reproductive declines to be tied to chronological age, whereas other studies have found declines associated with terminal reproduction irrespective of chronological age. We investigated the extent to which declines in late life reproduction are related to chronological age, terminal reproductive attempt or a combination of both in the thorn-tailed rayadito *Aphrastura spinicauda*, a small passerine bird that inhabits the temperate forest of South America. To this end we used long-term data (10 years) obtained on reproductive success (laying date, clutch size and nestling weight) of females in a Chilean population. Neither chronological age nor terminal reproductive attempt explained variation in clutch size or nestling weight, however we observed that during the terminal reproductive attempt older females tended to lay later in the breeding season and younger females laid early in the breeding season, but this was not the case when the reproductive attempt was not the last. These results suggests that both age-dependent and age-independent effects influence reproductive output and therefore that the combined effects of age and physiological condition may be more relevant than previously thought.

Keywords: age-dependence, age-independence, clutch size, nestlings, reproductive performance

Introduction

Understanding age-specific variation in reproductive effort and breeding success is fundamental to our understanding of the ecology and evolution of iteroparous species (Rose 1991, Roff 2002). Most studies that have investigated the variation in



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reproductive success with age have shown a pattern of increasing reproductive performance in early adulthood followed by a decline in later life (Nussey et al. 2013, Mourocq et al. 2016). Such late-life declines may be tied directly to age, either through loss of physiological function (senescence hypothesis; Kirkwood and Austad 2000, Mysterud et al. 2001), or as a reproductive strategy that maintains survival when physiological condition declines ('allocation hypothesis'; McNamara et al. 2009). Late-life declines in reproductive success may be gradual (Møller and Nielsen 2014) or abrupt, when individuals show signs of reproductive decline close to their death (Coulson and Fairweather 2001, Rattiste 2004) (i.e. terminal reproductive attempt) (Hammers et al. 2012). Such variation in late-life declines could be explained because the rate of damage accumulation is affected by factors (e.g. oxidative damage) that depend on the environment and as a consequence individuals may senesce and die at different chronological ages (i.e. age-independent) (Ricklefs 2008, McNamara et al. 2009). Therefore, age-independent late-life decreases in physiological condition could increase late-life age-dependent reproductive declines, producing an abrupt change in reproductive output in the last reproductive attempt (Hammers et al. 2012). For example, in bighorn sheep *Ovis canadensis* reproductive allocation decreased in the last two reproductive attempts independent of age, and fecundity was lower in the last two years of life, particularly for older individuals (Martin and Festa-Bianchet 2011).

One way to evaluate whether age-dependent and age-independent effects are acting simultaneously is to incorporate into the analysis a term that distinguishes whether the reproductive event is the last (terminal) or not (non-terminal). We make the following predictions: 1) if reproductive output is independent of age and independent of the terminal reproductive attempt, we expect to observe absence of correlation between age and reproduction in the terminal and in non-terminal reproductive attempts (Fig. 1a); 2) if reproductive output is independent of age but dependent on the terminal reproductive attempt, we expect to observe lower reproductive output in the terminal reproductive attempt compared to the non-terminal reproductive attempt (Fig. 1b); 3) if reproductive output depends only on age, we expect to observe the same decreasing pattern in the terminal reproductive attempt and in the non-terminal attempts (Fig. 1c) and 4) if the age-dependent pattern differs between the terminal and non-terminal reproductive attempts (i.e. significant interaction between age and terminal reproductive attempt), it would suggest that both age-dependent and age-independent effects shape reproductive output simultaneously (Fig. 1d).

To our knowledge the only study that has used this approach (i.e. to include in the analysis a term that accounts for the terminal event) is the study of Hammers et al. (2012) in Seychelles warblers *Acrocephalus sechellensis*; post-peak reproductive output declined with age, but this pattern differed between terminal and non-terminal reproductive attempts (Fig. 1d), suggesting that both age-dependent and age-independent effects influence reproductive output. In order to increase our understanding of the influence of age

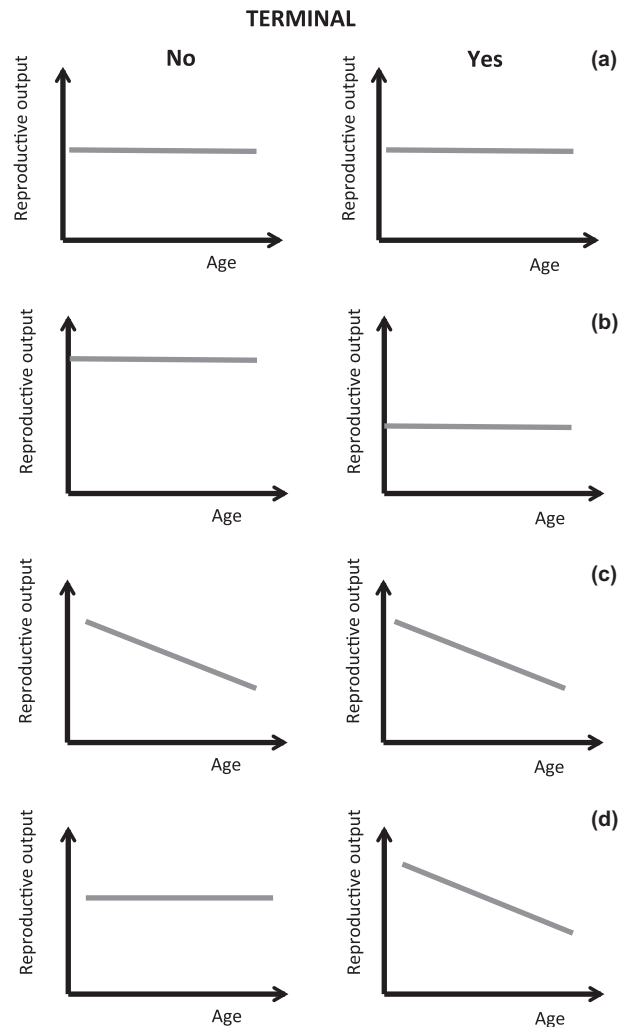


Figure 1. Schematic representation of the four alternative hypotheses for the effects of female age and terminal reproduction (terminal or non-terminal) on reproduction: (a) independent of age and terminal reproductive attempt, (b) independent of age and dependent of the terminal reproductive attempt, (c) dependent on age and independent of the terminal reproductive attempt and (d) age-dependent and age-independent effect on terminal reproductive attempt.

dependent and age-independent effects on reproductive output (laying date, clutch size and nestling weight), we used longitudinal data (10 yr) collected on a population of the thorn-tailed rayadito *Aphrastura spinicauda*, a small passerine bird that inhabits the temperate forest of South America (Chile and Argentina) and tested the predictions of Fig. 1.

Material and methods

The thorn-tailed rayadito and the study population

The thorn-tailed rayadito (Furnariidae: Passeriformes) is a small (~11 g) endemic insectivorous species residing in temperate forests in Argentina and Chile (Remsen 2003). The species is socially monogamous; both members of the pair

contribute to nest building, incubation and the feeding of nestlings (Moreno et al. 2007, Espíndola-Hernández et al. 2017). Females lay one clutch per breeding season, during the austral spring, from October to December (Moreno et al. 2005). Nest construction takes 9–20 d, the incubation period is 15–22 d and fledging occurs 20–21 d after hatching (Altamirano et al. 2015). Eggs are laid on alternate days and incubation is delayed until the clutch is completed (Moreno et al. 2005). Clutch size varies according to latitude, with a mean clutch size of 2.5 eggs at lower latitudes and 4.5 eggs at higher latitudes (Quirici et al. 2014). Thorn-tailed Rayaditos can live at least nine years (nestlings marked and recaptured nine years later) and their mean the lifespan (based on individuals of known ages) is 4.8 yr, so this pattern of longer lifespan is similar to what is found in other Southern Hemisphere species (Martin 1995).

Because thorn-tailed rayaditos are secondary cavity nesters (Remsen 2003), they easily adopt to nesting in artificial nest boxes. As part of a long-term study, we have monitored nest boxes in different populations throughout Chile. In the present study we report data from Fray Jorge National Park (30°38'S, 71°40'W), a low-latitude population (101–157 nest boxes available annually in 2006–2017) (Botero-Delgadillo et al. 2017) that represents the northern limit of the species' distribution. The forest of Fray Jorge is a relic forest from the Pleistocene period composed mainly of olivillo *Aextoxicon punctatum* occurring in patches at the top of the coastal mountain range, where fog-induced microclimatic conditions allow the forest to exist in this semiarid region (Villagrán et al. 2004). Because xeric shrub matrixes that surround the forest represent a barrier for dispersal (movement of breeders of rayaditos out of or into the study population has not been recorded) (Cornelius 2007), this population is genetically isolated from the other populations in Chile (González and Wink 2010, Yañez et al. 2015). A recent study (Bottero-Delgadillo et al. 2017) showed that in our study population thorn-tailed rayaditos are highly philopatric, and that breeding dispersal is not frequent (~30%) and involves short movements (commonly < 100 m). Vital rates calculated with static life tables in Fray Jorge National Park indicated that fledgling survival is approximately 23% and the recovery rate of marked fledglings is approximately 26%.

Field methods and molecular sexing

Data for our study were obtained during ten consecutive breeding seasons (2008–2017) (Table 1). Nest boxes were monitored on a weekly basis to check for nest box occupation, and when occupied, checked daily to record the laying date (date of laying of the first egg of the clutch), clutch size, hatching date and brood size at hatching. When nestlings were 12 d old they were weighed and banded with individual metal bands (National Band and Tag Co., Newport, Kentucky, USA and Porzana Ltd, UK). Adults were captured in their nests with a manually-triggered metal trap that sealed the entrance hole when adults entered to feed their 12-d-old nestlings.

We weighted adults and obtained a small blood sample (ca 15 µl) by puncturing the brachial vein with a sterile needle. Blood samples were stored on filter paper (FTA Classic Cards, Whatman) for subsequent molecular sexing. Similar to nestlings, adults were banded with individual metal bands.

Because thorn-tailed rayaditos are sexually monomorphic externally, we used molecular methods to determine the sex of nestlings and adults. The sex was determined using 2550F and 2718R primers (Fridolfsson and Ellegren 1999). PCR products were run in 1% agarose gels, pre-stained with ethidium-bromide and detected in a Fluorimager (Vilber Lourmat). Birds were sexed as females (heterogametic: WZ) when the CHD1W of 450 bp and CHD1Z of 600 bp fragments were amplified, and identified as males (homogametic: ZZ) when only the CHD1Z fragment was present. Details of the protocol and validation of this method in the thorn-tailed rayadito are described in Quirici et al. (2014).

Age determination and data processing

During the ten reproductive seasons of our study (2008–2017) we captured 207 males, 210 females and 702 nestlings (Table 1). In total, 11.66% (73: 31 females and 35 males) of the 626 marked nestlings that were ringed between during 2008 and 2016 were recaptured as breeding adults in our study population and thus their exact age was known. Of the 31 females of known age, one female reached a maximum age of one year, seven a maximum age of two years, four a maximum age of three years, three a maximum age of four years, seven a maximum age of five years, zero a maximum age of six years, two a maximum age of seven years, three a maximum age of eight years and four reached a maximum age of nine years. We also included in our analysis those females that, although they were captured for the first time as adults and were thus of unknown age, reached at least a maximum age of five years: 16 females reached at least a maximum age of five years, 10 reached at least a maximum age of six years, two reached at least a maximum age of seven years and one reached at least a maximum age of eight years, so we included 26 additional long-lived females. The number of recapture occasions

Table 1. Number of occupied nest boxes with their clutch size, number of reproductive males and females and number of nestlings of the thorn-tailed rayadito in Fray Jorge National Park (30°38'S, 71°40'W).

Year	Nest boxes	Clutch size (±SD)	Males	Females	Nestlings
2008	43	2.48 (±0.83)	32	37	107
2009	14	2.64 (±0.63)	12	12	36
2010	36	2.61 (±0.90)	13	15	93
2011	31	2.58 (±0.72)	27	27	79
2012	30	2.59 (±0.67)	17	17	82
2013	27	2.48 (±0.64)	24	21	66
2014	17	2.06 (±0.70)	17	15	50
2015	24	2.48 (±0.51)	25	27	61
2016	21	2.65 (±0.88)	20	19	52
2017	37	3.16 (±0.83)	20	20	76
Total			207	210	702

Table 2. Model list for the influence of age, age² and terminal attempt on laying date in female thorn-tailed rayadito.

Model	Female age	Female age ²	Terminal	Female age×terminal	Female age ² ×terminal	AICc	ΔAICc	AICc weight
1	Yes	Yes	Yes	Yes	No	941.87	0.00	0.91
2	Yes	Yes	Yes	Yes	Yes	946.39	4.52	0.09

Model list includes models that represent > 95% of the cumulative weight. Yes indicates that the term was included in the model, No indicates that the term was not included in the model.

(e.g. 1001001100, where 1 indicates that the female was captured and 0 indicates that the female was not captured) per individual ranged from 1 to 5 (1=17, 2=12, 3=11, 4=12 and 5=5), resulting in a total of 147 observations of 57 females. Since females that were captured twice may have different capture histories, e.g. 1010000000, 1000000010, sample sizes of age 1–9 were 17, 30, 25, 24, 22, 9, 9, 7 and 4, respectively. Because our objective was to evaluate the interaction between age and the terminal reproductive attempt and in order to have a balanced design in the interaction term, we combined the ages of the extremes 1 + 2 and 6–9 yr, therefore the sample sizes for ages 1 + 2, 3, 4, 5 and 6+ were 47, 25, 25, 22 and 29, respectively. Although our study population is isolated by the xeric environment that surrounds Fray Jorge National Park (genetically closed population – Yañez et al. 2015), not finding a female nesting in a nest box in a year does not necessarily mean that the female has died (e.g. it may be nesting in a natural cavity instead of in a nest box).

Statistical analyses

In order to test whether reproductive output differs with age and the terminal breeding attempt (predictions of Fig. 1), we included a binary factor to categorize each breeding attempt as being the terminal reproductive attempt or not (Hammers et al. 2012) and included the interaction between age (continuous variable) and the terminal breeding attempt. We included the linear and quadratic effects of age (age²) as predictors (Martin and Festa-Bianchet 2011, Hammers et al. 2012, Tarwater and Arcese 2017). Prior to the analyses, we mean-centered age to reduce collinearity between the linear and quadratic terms. Reproductive output included laying date (the date the first egg was laid) (n = 147 observations of 57 females), clutch size (n = 147 observations of 57 females, mean clutch size = 2.57, SD = 0.98, range = 1–4) and nestling weight (n = 147 nest, n = 294 nestlings). The distributions of the variables were tested with the *fitdistrplus* package (Delignette-Muller and Dutang 2015). Mixed models were fitted using a REML maximization with the ‘*lmer*’ function of the *lme4* package, which allows for unbalanced datasets (Bates et al. 2008). Random effects were breeding year and female identity (to account for multiple observations of the same female), and nest identity for the nestling weight analysis (to account for the fact that multiple nestlings come from the same nest). We used a linear mixed model (LMM) for laying date and nestling weight and a generalized linear mixed model (GLMM) with a Poisson error structure and a log link for clutch size. For each reproductive output we first assessed

whether the saturated model, i.e. the model that included all fixed effects (age, age², terminal and interactions between these variables) and random effects, explained the variance better than the null model (that considers only the intercept and the random effects), with the likelihood ratio test (LRT). In those cases in which the saturated model explained the variance better than the null model ($p < 0.05$), we proceeded to perform model selection using Akaike’s information criterion corrected for small sample sizes (AICc) as implemented in the package *MuMIn* (Bartoń 2014). Following Tarwater and Arcese (2017), we: 1) tested all nested models from the global model, except that random effects were retained in all models and the quadratic effect of age was only included with the linear effect of age; and 2) the model set used for model averaging were those with the lowest AICc until the cumulative model weight exceeded 0.95 (Burnham and Anderson 2002). All statistical tests were performed using $\alpha = 0.05$ for hypothesis testing, and were performed in R ver. 3.2.2 (R Development Core Team).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.bq468qc>> (Quirici et al. 2019).

Results

The model that included all the fixed effects explained variation in laying date better than the null model (LRT: Chi-squared = 23.20, df = 5, $p < 0.001$). Two averaged models (cumulative weight of 1.00) each included female age, female age squared, terminal attempt and the interaction between age and terminal attempt (Table 2). We observed a significant interaction between age and the terminal attempt (Table 3).

Table 3. Model-averaged results of the influence of age on laying date in female thorn-tailed rayadito.

Traits	β Estimate	SE	Lower CI	Upper CI
Intercept	27.49	6.45	14.72	40.26*
Age	-0.98	1.38	-3.72	1.77
Age ²	0.59	1.02	-1.43	2.59
Terminal	-12.19	9.61	-31.18	6.82
Age×terminal	-3.57	1.76	-7.05	-0.89*

* Confidence intervals (CI) do not cross 0. Terms whose CI do not cross 0 have a p value of < 0.05 for the model averaged model. The variances for random effects were 0.00, 105.3 and 176.4 for female identity, year and residual variance, respectively.

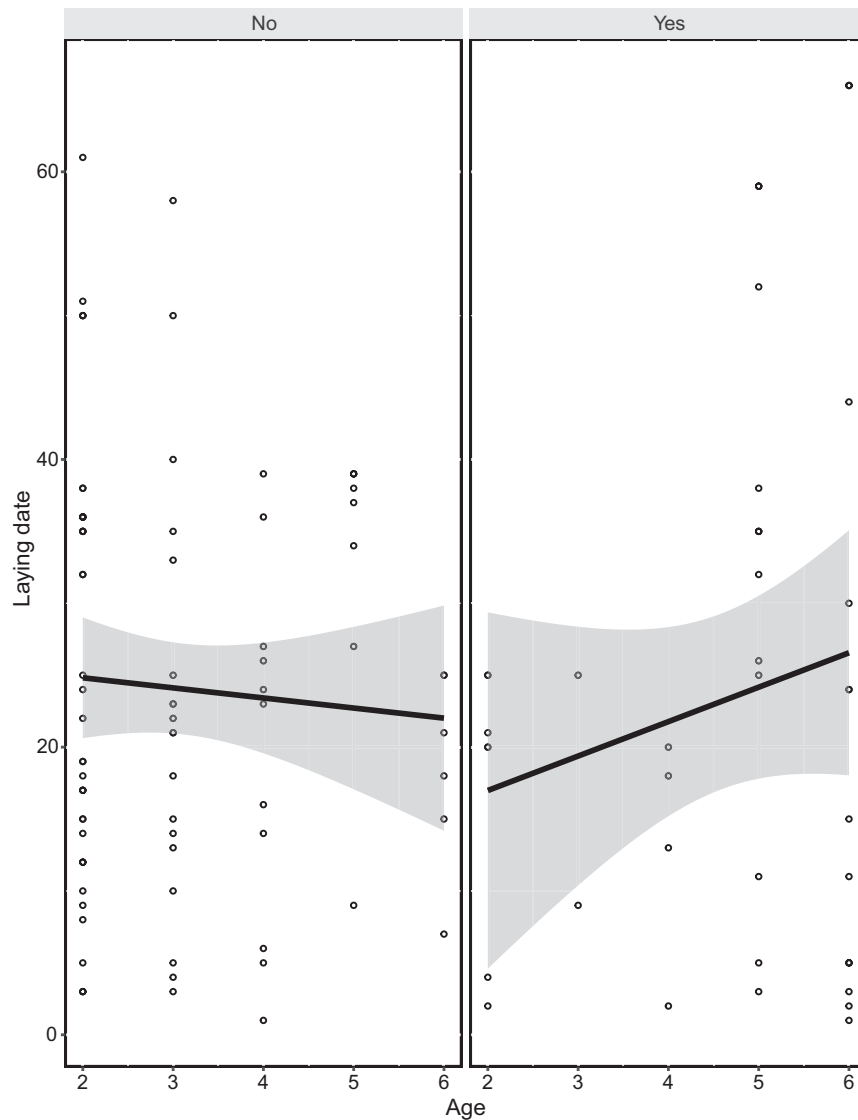


Figure 2. Laying date of females of the thorn-tailed rayadito in relation to age in the terminal attempt (yes: right panel) or not (no: left panel). Ages of 1 and 2 (age=2) and ages of 6, 7, 8 and 9 (age=6) were lumped. Sample sizes of ages in the terminal attempt samples were as follows: no: age 2=23, age 3=20, age 4=11, age 5=7, age 6=6; yes: age 2=7, age 3=4, age 5=11, age 6=11.

During the final breeding attempt, older females laid later in the breeding season but this was not the case when the breeding attempt was not the last (Fig. 2). Younger females laid sooner during the final breeding attempt, but this was not the case when the breeding attempt was not the last (Fig. 2).

The models that included all the fixed effects did not explain variation in clutch size or nestling weight better than the null model (LTR: Chi-squared=2.11, df=6, $p=0.91$; Chi-squared=2.23, df=6, $p=0.89$, respectively).

Discussion

We have found that both age-dependent and age-independent factors played roles in determining the laying date of female thorn-tailed rayaditos in their terminal nesting attempt.

The terminal nesting attempts of younger females are earlier than non-terminal nesting by females of the same age, whereas terminal nesting of older females was later than non-terminal nesting. However, no effects of age and terminal nesting were found for clutch sizes or nestlings weights for these same females. It is interesting to note that although laying date is an important trait (van der Jeugd and McCleery 2002, Amininasab et al. 2016, Amininasa et al. 2017), comparing with other traits (e.g. brood size, progeny weight and fledging) fewer studies have evaluated laying date in relation to age and age-independent events. In similar studies of laying date, in wandering albatrosses (Froy et al. 2013) and goshawks (Møller and Nielsen 2014), laying date varied only with respect to age (no age-independent effect) and similar to our study older females started to lay later in the breeding season.

The combination of age-dependent and age-independent effects on reproductive output have been observed for other reproductive traits in other studies (Martin and Festa-Bianchet 2011, Hammers et al. 2012, Froy et al. 2013, Tarwater and Arcese 2017). The only study that was similar to ours methodologically (included a binary factor to categorize each breeding attempt as being the terminal reproductive attempt or not) is that Hammers et al. (2012) in Seychelles warblers: similar to our study, they observed a significant interaction term in relation to age and the terminal reproductive attempt, but differed from our results in that the significant interaction was observed in the age squared term. In the Seychelles warblers study, reproductive success in the terminal reproductive attempt peaked at an intermediate age (seven years) and then declined with age (between 8 and 14 yr); in our study the relationship between age and reproductive output (laying date) in the terminal reproductive attempt was linear (i.e. we did not observe a peak of reproductive output).

It is important to point out that both the senescence hypothesis and the allocation hypothesis predict the same pattern (decrease of reproductive success at older age). Therefore, like Hammers et al. (2012), we cannot conclude which of these mechanisms have affected the terminal reproduction of the rayadito. However we speculate about different scenarios, which could be tested in future studies. We observed that during the last reproductive event the youngest females began to lay earlier in the reproductive season and older females tended to lay later in the breeding seasons. Laying date is an important predictor of fitness (van der Jeugd and McCleery 2002, Amininasab et al. 2016, Amininasa et al. 2017), since the females that start laying earlier in the breeding seasons have greater availability of food or could have more than one clutch in the breeding season. Our observation of both age-dependent and age independent effects suggests that the physical/metabolic condition of rayadito females could play an important role in reproductive success. For example, a young female who has some malignant condition (e.g. disease, high level of oxidative stress and/or large telomere shortening) and therefore a low probability of future reproduction is expected to invest all her energy in the last reproductive event (terminal investment hypothesis, Velando et al. 2006, McNamara et al. 2009). Future studies on this species should focus on determining both the cost associated with laying date (for example if there is competition for nesting site, territory or mate) and investigating which age-independent factors (e.g. disease, glucocorticoids and oxidative stress) affect reproductive success.

Conclusions

Long-term studies are a fundamental tool to study life history traits, however they require time, which is often difficult to record, especially in long-life species. This type of study has indicated that contrary to what was thought, physiological deterioration is an important aspect to consider

(Hammers et al. 2012) given the effect that the age structure has on the dynamics of the population and its evolution. As in Seychelles warblers (Hammers et al. 2012), reproductive output in the thorn-tailed rayadito could be both age-dependent and age-independent.

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