Scientific Reports

https://doi.org/10.1038/s41598-026-44759-z

Article in Press

Reproductive strategies of the most geographically isolated *Trachylepis* support predictions of the island syndrome

Received: 28 July 2025

Accepted: 13 March 2026

Published online: 19 March 2026

Cite this article as: Migliore S.N., Braz H.B., Gasparotto V.P.O. *et al.* Reproductive strategies of the most geographically isolated *Trachylepis* support predictions of the island syndrome. *Sci Rep* (2026). https://doi.org/10.1038/s41598-026-44759-z

Serena N. Migliore, Henrique B. Braz, Vinicius P. O. Gasparotto, Cybele S. Lisboa, Ricardo A. Dias, Gabrieli S. Araújo, Renan A. Ramalho & Selma Maria Almeida-Santos

We are providing an unedited version of this manuscript to give early access to its findings. Before final publication, the manuscript will undergo further editing. Please note there may be errors present which affect the content, and all legal disclaimers apply.

If this paper is publishing under a Transparent Peer Review model then Peer Review reports will publish with the final article.

ARTICLE IN PRESS

© The Author(s) 2026. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by-nc-nd/4.0/.

Reproductive strategies of the most geographically isolated *Trachylepis* support predictions of the island syndrome

Serena N. Migliore[1,2], Henrique B. Braz[1]*; Vinicius P. O. Gasparotto[3,4], Cybele S. Lisboa[5], Ricardo A. Dias[3], Gabrieli S. Araújo[1], Renan A. Ramalho[1], Selma Maria de Almeida-Santos[1]

[1]Laboratório de Ecologia e Evolução, Instituto Butantan, São Paulo, Brazil

[2]Programa de Pós-graduação em Anatomia dos Animais Domésticos e Silvestres, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Brazil

[3]Laboratório de Epidemiologia e Bioestatística, Departamento de Medicina Veterinária Preventiva e Saúde Animal, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, Brazil

[4] Tríade - Instituto Brasileiro para Medicina da Conservação, Recife, Brazil

[5] Setor de Herpetofauna, Zoológico de São Paulo - Reserva Paulista, São Paulo, Brazil

*Corresponding author: h.braz@hotmail.com

ABSTRACT

The island syndrome hypothesis predicts that insular organisms exhibit phenotypic differences from their mainland counterparts, particularly in reproductive strategies. Island populations are expected to have shorter breeding seasons, smaller clutches, larger offspring, and lower reproductive frequency. Although these patterns are well-documented in birds and mammals, evidence from island squamates is conflicting. The skink genus *Trachylepis*, which includes many island endemics in the Atlantic and Indian oceans, offers a model for testing these predictions in squamates. However, robust reproductive data are scarce for most insular *Trachylepis*. We characterized the reproductive phenology and output of the Noronha skink (*Trachylepis atlantica*), an endemic species to the remote Fernando de Noronha Archipelago (northeastern Brazil) and the westernmost dispersion of the genus in the Atlantic. We analyzed macroscopic and microscopic data from free-ranging, museum, and zoo-housed individuals, and compared our findings with available data for other *Trachylepis* species. Our results support the predictions of the island syndrome. Both sexes show a seasonal breeding pattern concentrated in the dry season, lasting approximately seven months—substantially shorter than in most tropical mainland congeners. Free-ranging females produce the smallest clutches (typically two eggs) and the largest eggs relative to body size in the genus. Female reproduction occurs at least biennially, which is lower than in most congeners. These reproductive patterns primarily reflect evolutionary responses to an insular environment historically characterized by low predation pressure and high intraspecific competition. These patterns are further shaped by resource seasonality and phylogenetic constraints, illustrating the multifactorial nature of reproductive evolution in insular reptiles. However, these same reproductive traits may also reduce the species’ resilience to increasing threats that are already impacting the population, including invasive predators and environmental change. Conservation actions are therefore needed to protect this evolutionary unique insular lineage.

Keywords: island syndrome; clutch size–egg size trade-off; reproductive cycle; conservation; slow life history

INTRODUCTION

Insular organisms often differ from their mainland relatives in demographic, morphological, behavioral, physiological, and ecological traits[1,2]. This suite of changes was first described in rodents and termed the ‘island syndrome’[3], and has since been documented in other mammals, birds, lizards, invertebrates, and plants[4–10]. Its repeated occurrence across diverse taxa suggests that islands impose similar selective pressures on colonizing species. Due to geographic isolation and limited area, islands typically house fewer species than the mainland, and therefore, insular species coexist with fewer predators and interspecific competitors[2,11]. Insular environments also tend to have milder, more predictable climates[2]. These conditions relax anti-predatory behaviors and favor niche expansion, ultimately resulting in high population densities and intensified intraspecific competition[3,12,13]. These dynamics are thought to drive the convergent phenotypic shifts seen in insular populations[1–3].

A central prediction of the island syndrome in vertebrates is reduced reproductive output, expressed as delayed maturity, lower reproductive frequency, fewer but larger offspring, or shorter breeding seasons[2,4,7]. Under high population density and intraspecific competition, these reproductive adjustments may increase offspring survival by enhancing their ability to cope with conspecific aggression[3,11,14]. The extent of these changes is expected to increase on smaller, more isolated islands[2,3]. Although lower reproductive frequency and the production of fewer but larger offspring are widely documented[3,7,15], the length of the breeding season is understudied in the context of the island syndrome. Nonetheless, some studies report shorter breeding seasons in insular mammals and birds than in their mainland counterparts[16–18]. Whether similar shifts occur in other vertebrates remains an important research gap, evidencing the need to include reproductive phenology in studies of insular life-history evolution.

In squamates, research on reproductive strategies under insularity shows mixed results. For instance, some insular lacertids produce larger clutches of smaller eggs, whereas others produce larger clutches of larger eggs than their mainland counterparts[19,20], contrary to the prediction of reduced reproductive output. However, broader phylogenetic analyses mostly support the island syndrome: insular lizards generally produce fewer but larger offspring than mainland relatives, especially on oceanic islands[4,21]. Reproductive frequency, however, is higher in insular lizards, but this difference disappears when controlling for phylogeny[4,21]. Comparative data on reproductive phenology of insular lizards are largely underexplored; however, insular lacertids have longer breeding seasons than mainland populations[19,20], contrary to the expectation of shorter breeding seasons. Given these conflicting findings, systematic efforts are recommended to describe the components of the insular syndrome more comprehensively, assess their generality across taxa, and identify underlying causes[22].

The skink genus *Trachylepis* offers an excellent system to investigate the effects of insularity on reproductive strategies. This genus occurs mainly in Africa and includes 97 species[23], about 20 of which have independently colonized islands in the Indian and Atlantic oceans[24], thus providing multiple replicates for testing evolutionary responses to insular environments. One interesting species is the Noronha skink, *Trachylepis atlantica* (Figure 1), endemic to the Fernando de Noronha Archipelago off northeastern Brazil. This species represents the westernmost distribution of the genus in the Atlantic[24,25]. It likely diverged from the '*T. maculilabris* group' 18.8–26.4 million years ago and colonized the archipelago through long-distance transoceanic dispersal (~3000 km) no more than 12 million years ago[24–26]. *Trachylepis atlantica* exhibits several traits consistent with the island syndrome, such as high population density, reduced wariness, and omnivory with substantial plant consumption[27–31]. Despite these well-documented ecological traits, its reproductive strategies—key components of the island syndrome—remain largely unknown, apart from a few isolated observations[32–34]. Understanding reproductive strategies may also inform assessments of population resilience in insular systems[2]. Although *T. atlantica* is currently listed as Least Concern[35], the archipelago has experienced increasing anthropogenic pressures, and the species has recently been classified as threatened in a regional assessment[36].

We characterized the reproductive phenology and output of *T. atlantica* using macroscopic and microscopic data from free-ranging, museum, and zoo-housed specimens. We then compared our findings with existing literature on other *Trachylepis*. Based on the island syndrome hypothesis, we predicted that *T. atlantica*, as an oceanic island endemic, produces smaller clutches of larger eggs with longer intervals between reproductive events than its mainland and continental-island congeners. We also predicted a shorter breeding season than that of its tropical mainland relatives. Finally, we discuss the implications of these reproductive traits for conservation amid ongoing anthropogenic threats to the species' habitat.

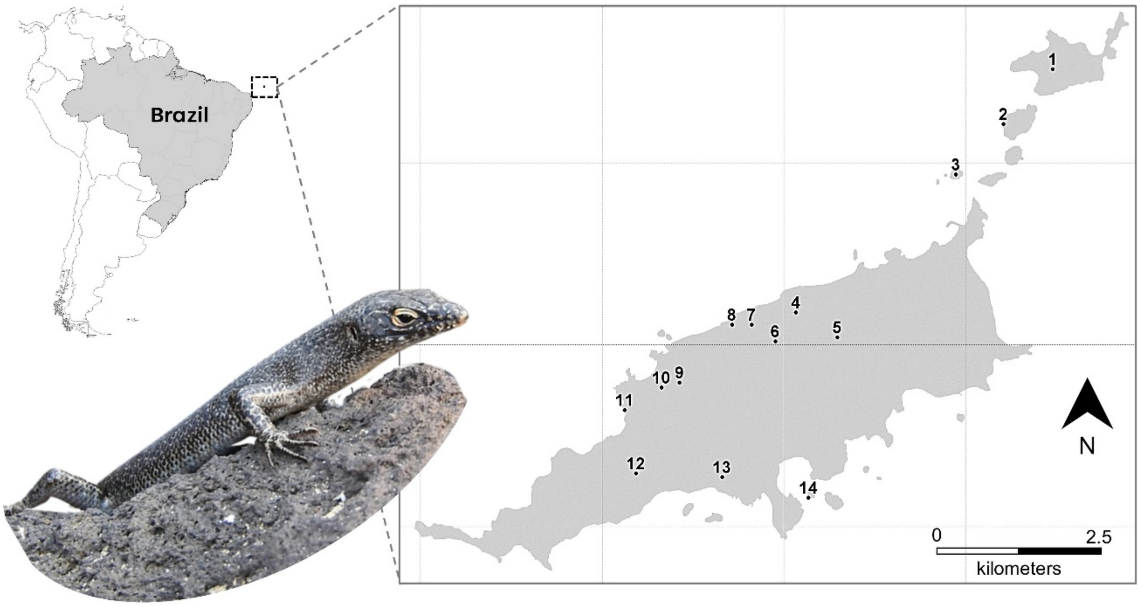


Figure 1. Map showing the location of the Fernando de Noronha Archipelago in northeastern Brazil and the collection sites of the examined specimens of the Noronha skink (*Trachylepis atlantica*). Mapped localities include free-ranging individuals collected for the present study as well as preserved museum specimens for which specific collection localities were available. (1) Ilha da Rata, n = 5; (2) Ilha do Meio, n = 2; (3) Ilha São José, n = 2, (4) Pedra da Cebola, n = 4, (5) Casa da Polícia, n = 2, (6) ICMBio, n = 1, (7) Boldró, n = 5; (8) Praia do Americano, n = 21; (9) Praia do Sancho, n = 2; (10) Trilha do Golfinho, n = 1; (11) Baía dos Golfinhos, n = 1; (12) Capim Açu, n = 1; (13) Praia do Leão, n = 1; and (14) Ilha do Chapéu, n = 2. In addition, 17 preserved museum specimens from Fernando de Noronha lacked specific locality information and are therefore not represented on the map.

RESULTS

Male reproductive cycle

Of the 39 dissected males, 33 (84.6%) were sexually mature. The smallest sexually mature male measured 80 mm SVL. We identified three testicular stages: quiescence (n = 7), spermiogenesis (n = 12), and regression (n = 4). No individuals showed testicular recrudescence. Quiescence was observed in both seasons, including the wet–dry transition

(Figure 2A, B). Spermiogenesis was recorded from mid- to late dry season (Figure 2A, C). Testicular regression was observed in both seasons, including the wet–dry transition (Figure 2A, D).

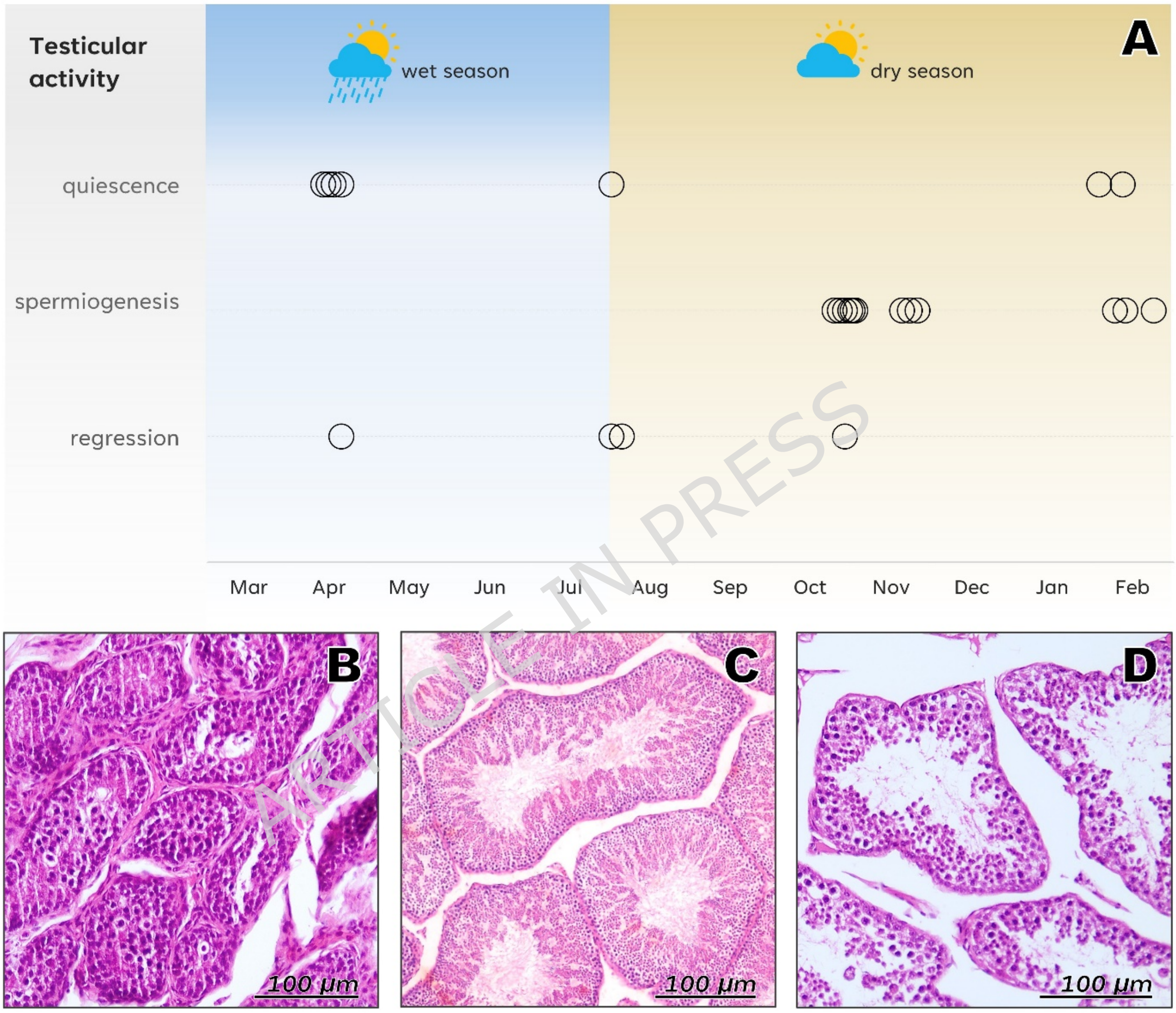


Figure 2. (A) Seasonal variation in testicular activity in the Noronha skink (*Trachylepis atlantica*) and representative histological sections (hematoxylin-eosin) of the testes of in (B) quiescence, (C) spermiogenesis, and (D) regression.

Males undergoing spermiogenesis had epididymides and ductus deferentia packed with sperm, and hypertrophied SSKs (Figure 3A-C). In contrast, males with regressed testes had moderate to sparse sperm in the epididymides and ductus deferentia, as well as hypertrophied to regressed SSKs. During quiescence, epididymides were empty and SSKs regressed. Only one quiescent male had vestigial sperm in the ductus deferentia; all others had empty ducts (Figure 3D-F).

Secretory granules in the apical portion of hypertrophied SSK cells reacted positively to Coomassie blue (proteins) but negatively to Alcian blue (acidic carbohydrates) and PAS (neutral carbohydrates) (Figure 3G-I). Collecting ducts reacted negatively to Coomassie blue but positively to Alcian blue and PAS (Figure 3G-I). No positive reactions were found in the testes, epididymides, and ductus deferentia for any histochemical tests.

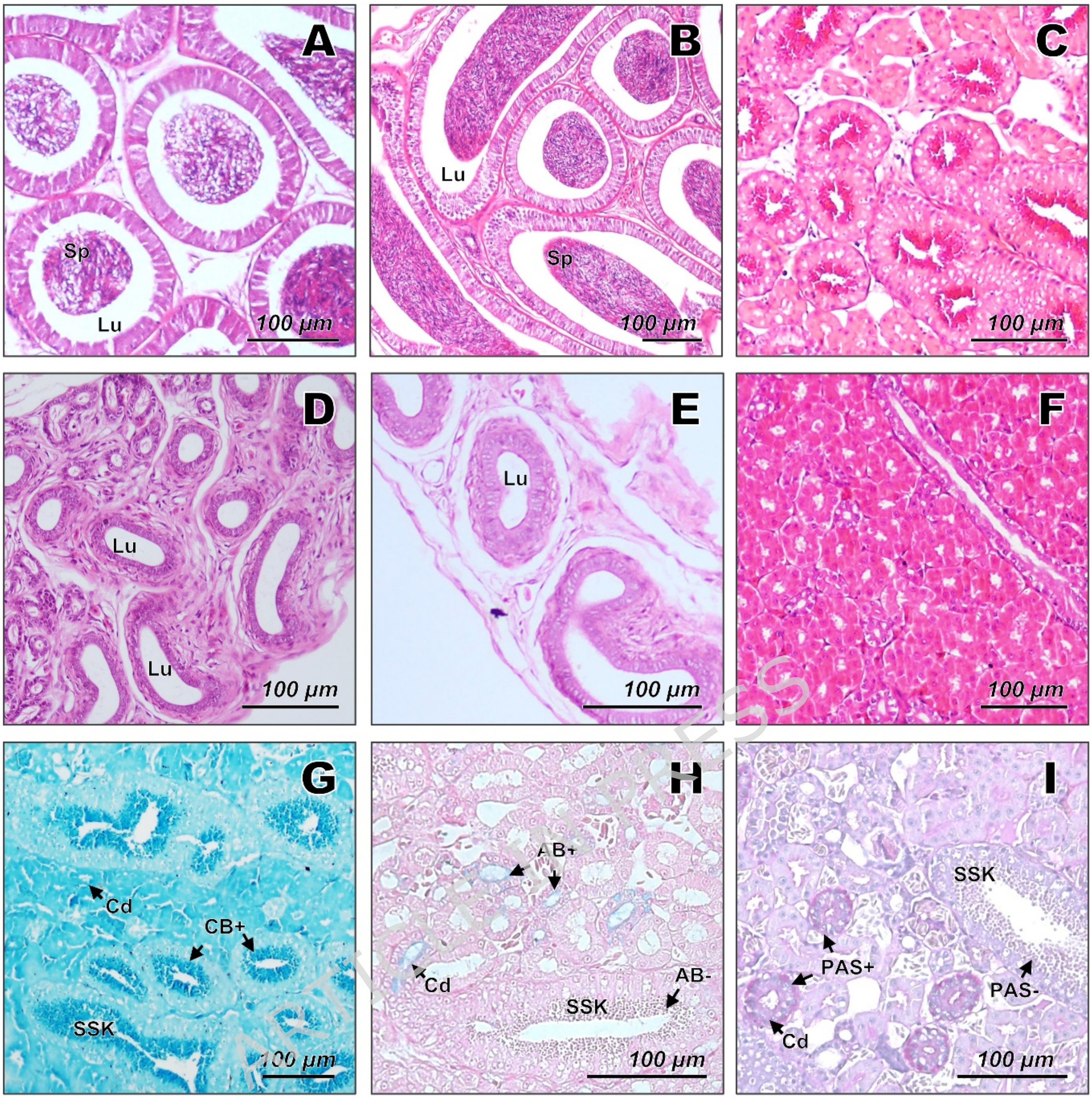


Figure 3. Histological and histochemical analysis of the male urogenital tract of the Noronha skink (*Trachylepis atlantica*). Individuals with (A) epididymides and (B) ductus deferentia densely packed with sperm also showed (C) hypertrophied sexual segment of the kidney (SSK). In contrast, individuals with (D) epididymides and (E) ductus deferentia with few or no sperm in the lumen showed (F) regressed SSKs. Panels A–F: hematoxylin–eosin. The secretion granules in the apical portion of hypertrophied SSK cells reacted positively to (G) Coomassie blue, indicating protein content, but negatively to (H) Alcian blue and (I) PAS, indicating the absence of acidic and neutral carbohydrates, respectively. The collecting ducts reacted (G) negatively to Coomassie blue but positively to (H) Alcian blue and (I) PAS. Abbreviations: AB, Alcian blue; CB, Coomassie blue; Cd, collecting ducts; Lu, lumen; PAS, Periodic Acid–Schiff; Sp, spermatozoa.

Female reproductive cycle

Of the 28 dissected females, 27 (96.4%) were sexually mature. The smallest sexually mature female measured 71 mm SVL. Ovarian follicles ranged from 0.95 to 8.54 mm in diameter. The smallest vitellogenic follicle (4.14 mm) was recorded in a female captured in the early to mid-wet season but showed signs of degeneration (heterogeneous central region and disrupted yolk vesicles), unlike the typical vitellogenic pattern. This female also had reduced uterine glands. The largest follicle (8.54 mm) was observed in the late dry season. Vitellogenic follicles had a granulosa layer thinner than non-vitellogenic follicles ($W = 73$, $p = 0.0014$). Vitellogenic females had taller infundibular epithelium ($W = 18$, $p = 0.0507$) and larger uterine glands ($W = 4$, $p = 0.0001$) than non-vitellogenic ones, but uterine epithelial height was similar in both reproductive stages ($W = 55$, $p = 0.8907$). In vitellogenic females, the luminal epithelium of the glandular uterus stained uniformly positive with Alcian blue (carboxylated glycosaminoglycans) and PAS (neutral carbohydrates) (Supplementary Figure S1A-B). Uterine glands stained positively with Coomassie blue for proteins (Supplementary Figure S1C). In the nonglandular uterus, staining with Alcian blue and PAS was restricted to secretory cells (Supplementary Figure S1D-E).

Nonvitellogenic females occurred in all sampled months (Figure 4A). Most vitellogenic females (85.7%) were captured during the dry season, and two gravid females were collected during mid- and late dry season (Figure 4A). No sperm were detected in any oviducts. The zoo-housed female laid seven infertile clutches between October and May and seven fertile clutches between November and June (Table 1). Fertile clutches were produced only after she was paired with the male. Three eggs laid on 29 March 2015 hatched on 12-13 July 2015, after 105-106 days of incubation. One egg from a clutch laid on 16 November 2015 hatched on 8 February 2016 (84 days of incubation); another egg from the same clutch contained a full-term but malformed and dead young. All other incubated eggs spoiled. A hatchling male (50 mm SVL) was collected in mid-wet season (31 May 2016).

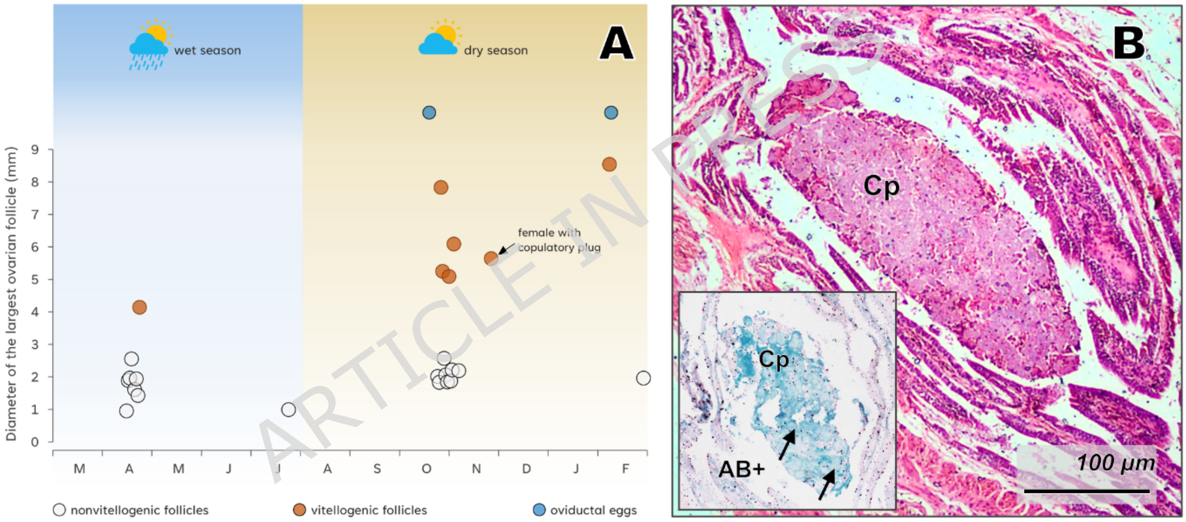


Figure 4. (A) Seasonal variation in the diameter of the largest ovarian follicle and occurrence of gravid females of the Noronha skink (*Trachylepis atlantica*) from the Fernando de Noronha Archipelago. (B) A copulatory plug (Cp) observed in the non-glandular uterus of a vitellogenic female collected during the mid–late dry season, providing direct evidence of mating during this period. hematoxylin and eosin. Inset shows AB+ staining, indicating acidic carbohydrates; spermatozoa were absent within the plug.

Mating season

Courtship was observed in the wild on 8 November 2019 (mid-dry season), at 12:30 p.m., at Praia do Sancho (D. Granville, pers. comm.; Supplementary Figure S2). We found a copulatory plug in the non-glandular uterus of a female in early vitellogenesis (follicle = 5.64 mm) collected during mid- to late dry season (23 November 2016; Figure 5). The plug stained positively with Alcian blue (Figure 4B), but no spermatozoa were detected in it. The zoo-housed lizards were seen copulating on 31 January 2016, 18 March 2016, and 30 October 2016.

Reproductive output

Ten of 27 females (37%) were reproductive. Considering the period during which reproductive females were observed (October–April), 8 of 17 females (47%) were reproductive. No female had vitellogenic follicles and oviductal eggs simultaneously. All seven vitellogenic females had two developing follicles, one per ovary. Three gravid females carried two shelled eggs each, one per oviduct. Over ~6.5 years, the zoo-housed female laid 14 clutches (averaging 2.6 clutches per year) of 2–3 eggs, with three-egg clutches occurring more frequently (64%, Table 1).

In free-ranging females, eggs averaged 19.66 ± 0.76 mm in length, 8.41 ± 1.19 mm in width, 0.64 ± 0.08 g in mass, and 735.27 ± 182.00 mm^3 in volume (n = 6 eggs from 3 clutches). In the zoo-housed female, eggs averaged 21.06 ± 1.67 mm in length, 11.15 ± 0.61 mm in width, 1.35 ± 0.22 g in mass, and 1375.62 ± 184.03 mm^3 in volume (n = 12 eggs from 5 clutches). Egg volume in free-living females (measured from oviductal eggs) was significantly smaller than that produced by the zoo-housed female (measured from freshly laid eggs; W = 72, p = 0.0009).

Interspecific comparison of reproductive traits in *Trachylepis*

We compiled data for 51 species of *Trachylepis* from mainland (n = 38) and island environments (n = 13; Supplementary Table S2). After accounting for female body size, *T. atlantica* showed the smallest relative clutch size and the largest relative egg size among congeners (Figure 5). Mainland species showed a broad range of relative clutch and egg sizes, whereas island endemics tended to cluster toward smaller relative clutch sizes and larger relative egg sizes. These patterns place *T. atlantica*, an oceanic island endemic, at the extreme end of the clutch size–egg size continuum within the genus.

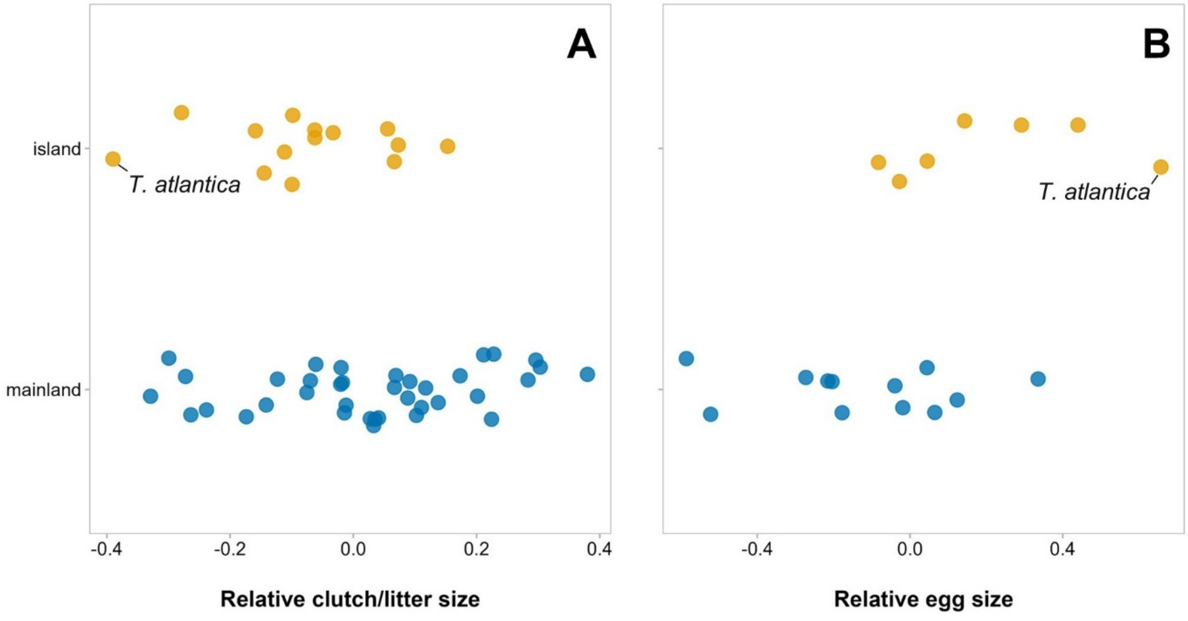


Figure 5. Relative clutch/litter size and egg size in mainland and island *Trachylepis* species. (A) Relative clutch/litter size; (B) Relative egg size. Relative values were calculated as residuals from log–log regressions of mean clutch/litter size and mean egg volume (a proxy for egg size), respectively, on mean female body size (SVL). The focal species, *Trachylepis atlantica*, an oceanic island endemic from the Fernando de Noronha Archipelago (Brazil), shows the smallest relative clutch size (A) and the largest relative egg size (B) among congeners. Data were compiled from published sources (see Methods and Supplementary Table S2). The comparison is descriptive, and values show substantial overlap between groups.

DISCUSSION

We present the first comprehensive investigation of the reproductive strategies in an insular species of *Trachylepis*, focusing on *T. atlantica* from the Fernando de Noronha Archipelago, the westernmost-dispersed lineage of the genus in the Atlantic Ocean. Based on the island syndrome hypothesis, we predicted that *T. atlantica* would exhibit a shorter breeding season than its tropical congeners, as well as smaller clutches with larger eggs and lower reproductive frequency than its mainland and continental-island congeners. The reproductive traits of *T. atlantica* are largely consistent with these predictions. The species shows a shorter breeding season than most tropical congeners. It also exhibits the smallest relative clutch size, the largest relative egg size, and one of the lowest reproductive frequencies reported for the genus.

Reproductive strategies of *Trachylepis atlantica*

Male reproductive activity in *T. atlantica* is seasonal and concentrated in the dry season (Figure 6). During the wet season, males had quiescent testes, empty ducts, and regressed SSKs, indicating reproductive inactivity. The absence of recrudescent testes suggests that testicular activation occurs rapidly and synchronously, likely at the onset of the dry season. During the dry season, males showed full mating capacity, as evidenced by spermiogenesis, sperm-filled ducts, and hypertrophied SSKs. Mating coincides with sperm production (Figure 6). Most matings and all mating-related behaviors have been recorded during the dry season (present study; see also [34]). The presence of a copulatory plug in a female captured during the dry season further confirms mating during this period. These plugs are common in lacertid lizards[37] but appear to be rare in scincids, and their role in *T. atlantica* warrants further investigation. Some males showed residual sperm and partially functional SSKs into the early wet season, which may explain the mating event observed during this time[28], outside the spermiogenesis period.

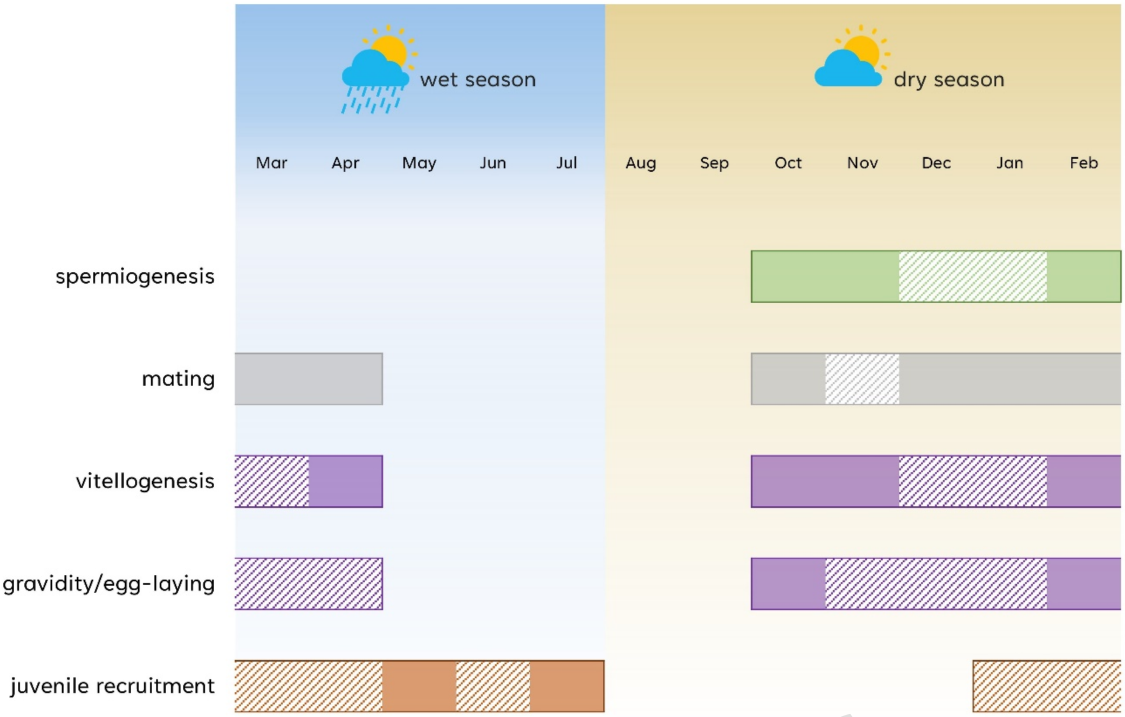


Figure 6. Overview of the reproductive events in the Noronha skink (*Trachylepis atlantica*) from the Fernando de Noronha Archipelago. Observations from the present study are complemented with published data on courtship and mating[28,34], hatching[32], and the record of a hatchling-sized individual[38]. Hatched areas represent inferred periods based on the available evidence.

Female reproductive activity was also concentrated in the dry season, although vitellogenesis and oviposition may extend into early wet months (Figure 6). Based on laboratory incubation duration (3–4 months), hatching is expected from late dry to mid-wet season (Figure 6), consistent with a field record[32]. The pronounced size gap between the largest vitellogenic follicles (~8.5 mm) and mean oviductal eggs (~ 21 mm) means that these follicles would have to almost double in size before they were ready for ovulation. Histological and histochemical analyses confirmed the vitellogenic status of these females by revealing morphological and secretory patterns consistent with a reproductive tract preparing for egg reception[39,40]. Two hypotheses may explain the absence of late-vitellogenic or preovulatory females in our sample. First, the final phase of yolk deposition may occur rapidly. This explanation is partially supported by observations of the zoo-housed female, which laid successive clutches over a short time frame, suggesting rapid follicular maturation, at least under favorable conditions. Second, females nearing ovulation may reduce activity and become less detectable in the field. However, we find this less likely, as vitellogenesis coincides with the mating season, and females must remain active to access male territories[34]. We found no evidence of female sperm storage. Because mating and vitellogenesis/ovulation are synchronous, sperm storage may be unnecessary. Supporting this interpretation, the zoo-housed female only produced fertile eggs after a male was introduced.

All reproductive females carried either two vitellogenic follicles or two shelled eggs, matching previous records[29,32]. These data suggest a fixed clutch size of two eggs in free-ranging females. However, the zoo-housed female laid multiple clutches of 2−3 eggs, most often three. This higher reproductive output likely reflects favorable captive conditions (see below). Nonetheless, clutch size in *T. atlantica* is consistently small and appears to vary little. Oviductal eggs from free-ranging females were smaller than those laid by the zoo-housed female, probably due to greater food availability in captivity, pre-laying water uptake, or both. Their smaller size compared with eggs from a near-hatching clutch found in the wild (31 × 17 mm; [32]) likely reflects post-laying water uptake. Reproductive frequency was low. No females were simultaneously vitellogenic and gravid, and only 37–47% of sampled females were reproductive, implying biennial or even triennial reproduction under natural conditions.

The reproductive strategies of *Trachylepis atlantica* are consistent with island syndrome predictions

Consistent with island syndrome predictions, the 7-month breeding season of female *T. atlantica* is shorter than the year-round breeding reported for most tropical mainland congeners, including *T. maculilabris* (its closest mainland relative), *T. affinis*, *T. striata*, and *T. varia*[41–44]. Only two tropical mainland species, *T. quinquetaeniata* and *T. mlanjensis*, have similar breeding season durations[44,45]; however, *T. mlanjensis* inhabits high-elevation regions (~2080 m a.s.l.) where lower temperatures likely influence its seasonal breeding[45]. The only tropical congener with a shorter breeding season is *T. buettneri*, which reproduces over just two months[43]. Overall, the female breeding season in *T. atlantica* resembles that of subtropical congeners such as *T. capensis*, *T. margaritifer, T. punctatissima*, and *T. spilogaster* (7–8 months)[46–52], and is longer than that of *T. sulcata*, *T. variegata*, and *T. occidentalis* (4–6 months)[48,52–56]. However, these comparisons are secondary, as the climate of Fernando de Noronha resembles lowland tropical environments. Similarly, the 7-month breeding season of male *T. atlantica* is shorter than the year-round breeding reported for tropical mainland males of *T. striata* and *T. quinquetaeniata*[44] and for tropical-subtropical *T. variegata*[57], and shorter than the 9-month season of tropical-subtropical *T. sparsa*[58], while closely matching that of subtropical *T. capensis* and *T. spilogaster*[50,52]. These comparisons support the inference that *T. atlantica* has evolved a shorter breeding season than its tropical mainland relatives.

In line with island syndrome predictions, *T. atlantica* also exhibits lower reproductive output than its mainland congeners. Free-ranging females produce two-egg clutches—the smallest relative to body size among *Trachylepis* species. The occasional three-egg clutch recorded in the zoo-housed female does not alter this pattern. In contrast, *T. atlantica* lays the largest eggs relative to body size in the genus, consistent with the expected egg size–clutch size trade-off in island populations. Its biennial (perhaps triennial) reproduction is markedly lower than the annual or multi-annual clutches reported for its closest mainland relative (*T. maculilabris*) and oviparous mainland congeners (*T. affinis*, *T. striata*, and *T. mlanjensis*)[42–45]. Among *Trachylepis*, only the viviparous *T. spilogaster* reproduces less than annually[52], likely due to the high energetic cost of gestation[59]. These patterns indicate that *T. atlantica* has evolved a suite of reproductive adjustments typical of insular environments. The extremity of these traits likely reflects the species' exceptional biogeographic context as the most geographically isolated species in the genus, restricted to a small oceanic archipelago over 2,500 km from the African center of radiation. This combination of low reproductive frequency, small clutch size, and large eggs—although adaptive in historically stable insular environments—is generally associated with reduced demographic resilience and may limit recovery from abrupt environmental changes, with potential consequences for long-term persistence[60–62]. In this context, these biological constraints, combined with escalating anthropogenic threats, corroborate the suggestion that *T. atlantica* is more threatened than currently recognized[36].

Selective drivers of reproductive adjustments in *Trachylepis atlantica* and other island congeners

The reproductive strategies of *T. atlantica* likely reflect adaptations to long-term island isolation. As documented in various vertebrates, such adaptations are primarily driven by ecological release from predation and interspecific competition, combined with intensified intraspecific competition[2–4,15,63–65]. Under these conditions, low extrinsic mortality and high population density tend to favor life histories that prioritize offspring quality over quantity[11,65,66]. This appears to apply to *T. atlantica*. The species has no confirmed native predators, indicating historical ecological release from predation[67,68], and interspecific competition is likely minimal, as the only other native lizard, *Amphisbaena ridley*, is fossorial and ecologically distinct[69,70]. On the other hand, intraspecific competition appears intense, particularly early in life, as evidenced by frequent reports of adults attacking or consuming eggs and juveniles[34,38,67]. These pressures may favor larger eggs and hatchlings that are more competitive in crowded environments[11,65,66].

In addition to ecological release and intraspecific competition, resource seasonality may also contribute to shaping the reproductive strategies in *T. atlantica*. The Fernando de Noronha Archipelago has a short, intense wet season followed by a prolonged dry period[71], restricting resource abundance to a narrow temporal window. In other tropical oceanic islands, arthropod abundance peaks during the wet season (e.g., [72]), a pattern also presumed for Fernando de Noronha[68]. Because arthropods are a key energy source for lizards[73,74], this resource seasonality is ecologically significant. During the dry season, *T. atlantica* faces nutritionally constrained conditions, with individuals relying heavily on ants and plant material—resources with lower energetic yields that are rarely exploited by mainland congeners[29,31]. These constraints likely intensify selection for energy-efficient reproductive strategies and contribute to reduced clutch size and extended inter-clutch intervals. Females probably accumulate energy reserves during the wet season to fuel reproduction early in the dry season, thereby timing hatching with the subsequent resource peak. Similar reliance on stored energy has been reported in another long-lived skink[75]. Seasonal food availability may also influence clutch frequency, size, and egg size. Although the broad dietary niche of *T. atlantica* may buffer prey fluctuations[29,31,67,68], this remains uncertain because dietary data are currently restricted to dry-season sampling.

Observations from the zoo-housed female support the role of food availability and reduced intraspecific competition in shaping reproductive output. Under food-rich, non-competitive conditions, this female produced larger and more frequent clutches over an extended period—far exceeding the output inferred for free-ranging individuals. Although based on a single individual, these observations suggest that reproductive traits in *T. atlantica* are phenotypically plastic and respond flexibly to local conditions. Similar plasticity has been documented in other lizard species, in which enhanced food availability increases reproductive output[76,77].

How broadly do these patterns apply to other insular *Trachylepis*? Comparative data from other insular *Trachylepis* are heterogeneous and often restricted to few species and small samples to provide robust comparisons, but they still provide useful context for evaluating insularity-driven reproductive trends in the genus. Differences in clutch size between island and mainland species show substantial overlap (Figure 5A), whereas relative egg size tends to be larger in island species (Figure 5B). These descriptive patterns should be interpreted cautiously, given uneven data availability. Formal phylogenetically informed analyses will be needed to assess the generality of these trends as additional data accumulate. Like *T. atlantica*, low reproductive frequency has been reported in *T. sechellensis* and *T. wrightii* from Cousin Island, Seychelles, where 50% and 21% of females, respectively, were reproductive[78], suggesting biennial and triennial (or lower) reproduction. In contrast, *T. lavarambo* from Madagascar may produce multiple clutches per season, as one female carried vitellogenic follicles and oviductal eggs[79]. However, given its large size and ecological complexity, Madagascar is expected to resemble mainland systems more than typical oceanic islands, which may explain this deviation. Data on breeding season length in insular *Trachylepis* are scarce. In *T. sechellensis*, reproduction has been proposed to occur year-round, yet "developed eggs" were recorded over only five months[78], implying a shorter breeding season than in mainland congeners.

While resource seasonality may influence breeding cycle length, phylogenetic history may constrain seasonal timing. Besides *T. atlantica*, several island species within the *maculilabris* clade (*T. albotaeniata*, *T. principensis*, and *T. thomensis*) reproduce during the dry season[24,80,81]. The same pattern occurs in *T. sechellensis* and *T. wrightii*[78], members of the Seychelles clade sister to *maculilabris*[24]. In contrast, Malagasy clade species (*T. vato*, *T. boettgeri*, and *T. gravenhorstii*) reproduce exclusively during the wet season[82,83].

In summary, the reproductive adjustments of *T. atlantica* likely result from the combined effects of ecological release, strong intraspecific competition, seasonal resource dynamics, and phylogenetic constraints. Its reproductive strategies align with island syndrome predictions and illustrate the multifactorial nature of reproductive evolution in insular reptiles. Future studies integrating seasonal variation in diet, body condition, and reproductive endocrinology will help clarify the relative importance of these selective pressures.

METHODS

Study area

Fernando de Noronha (3° 51' S, 32° 25' W; elevation: 0–323 m a.s.l.; Figure 1) is a volcanic archipelago in the Atlantic Ocean, located approximately 545 km off the coast of Pernambuco state (northeastern Brazil) and 2,600 km from Africa[84]. The archipelago spans 26 km^2 and consists of a main island (~17 km^2) surrounded by 20 smaller islands, islets, and rocks (Figure 1). Only the main island is inhabited, with approximately 3,167 residents[84]. The vegetation is primarily xeromorphic and seasonally deciduous, comprising herbaceous, shrub, and forest formations[85].

The climate is tropical wet and dry ("As" type in the Köppen-Geiger system), with consistently high annual temperatures averaging 27 °C (range: 26.0−27.5 °C; [71]). Annual rainfall averages 1,260 mm, and two well-marked seasons are evident: a dry season from August to February (mean monthly rainfall = 37 mm) and a wet season from March to July, which accounts for approximately 80% of the annual precipitation (mean monthly rainfall = 200 mm; [71]). Fernando de Noronha is recognized for its ecological importance and is protected as a Marine National Park and UNESCO World Heritage Site.

Specimens

We dissected 67 specimens (28 females and 39 males) of *T. atlantica* collected in the Fernando de Noronha Archipelago (Figure 1), including two previously reported gravid females[33]. Of these, 35 were collected between 2014–2018 for this study. These lizards were captured using nooses, anesthetized with an intramuscular injection of 10% ketamine hydrochloride (50 mg/kg) combined with 2% xylazine hydrochloride (2 mg/kg), and euthanized by an intracranial injection of 1% lidocaine hydrochloride. All these procedures were conducted in accordance with relevant institutional and national guidelines and regulations, with approval from the Ethics Committee on Animal Use of the School of Veterinary Medicine and Animal Science at the University of São Paulo (protocol 1827250515), and collection authorized by the Instituto Chico Mendes de Conservação da Biodiversidade (Brazilian Ministry of Environment, SISBio 41682-1 to 41682-5). The remaining 32 specimens were obtained from museums and dissected as available (Supplementary Material, Table S1).

To gain insights into the reproductive patterns of the species under controlled conditions, we also obtained data from a pair of *T. atlantica* kept at São Paulo Zoo. These individuals were inadvertently transported from the archipelago by tourists in their luggage, an event that occurs relatively frequently due to the species' docile and curious behavior[86]. The female (snout-vent length [SVL] = 87 mm) was received on 23 September 2010, and the male (SVL = 103 mm, measured on 20 March 2020) on 15 January 2015. The female was initially housed alone and later paired with the male in a fiberglass terrarium (90 × 60 × 60 cm) furnished with sand, rocks, logs, and vegetation for environmental enrichment. A heating rock was provided year-round, and ceramic heaters were used additionally during winter. The mean air temperature in the enclosure averaged 22.6 ± 2.6 °C (range = 21.0–24.4 °C), and relative humidity averaged 66.1 ± 11.3% (range = 59.8–72.1%). The animals were fed crickets twice weekly and fruits and vegetables once weekly. The male is still alive after ten years, but the female died on 26 March 2017, after ~ 6.5 years in the zoo. Fertile eggs (determined via candling) were incubated in moistened sand inside plastic containers (23 × 15 × 6 cm) with perforated lids in a heated room (mean = 23.6 ± 2.4 °C; range = 18.9–28.3 °C). All methods involving live animals are reported in accordance with the ARRIVE guidelines (https://arriveguidelines.org).

Data collection

In free-ranging and museum specimens, we measured SVL for all individuals. In females, we then recorded (1) the number of ovarian follicles; (2) the diameter of the largest ovarian follicle; and (3) the length, width, and mass of oviductal eggs. In males, we recorded whether the testes were undeveloped or turgid. Next, we sampled the right side of the reproductive tract for histological analyses. We collected the testis, epididymis, distal ductus deferens, and anterior kidney from males and the ovary, infundibulum, glandular uterus, and non-glandular uterus from females. Tissues were processed using standard paraffin protocols for light microscopy[87], cut at 5 μm thick with a rotary microtome, and stained with hematoxylin and eosin.

Histological sections of testes were examined to assess spermatogenic activity, including the presence and relative abundance of spermatogonia, spermatocytes, spermatids, and spermatozoa, as well as the structure of the germinal epithelium. Epididymides and ductus deferentia were examined to evaluate sperm content within the lumen.

Kidney sections were evaluated for hypertrophy and secretory activity of the sexual segment of the kidney (SSK), known to play a role in male reproductive physiology[88]. The infundibulum and uterus were checked for sperm presence. Secretory activity was assessed using histochemical stains: Alcian blue (pH 2.5) for carboxylated glycosaminoglycans, Periodic Acid–Schiff (PAS) for neutral carbohydrates, and Coomassie blue for proteins.

Photomicrographs were taken with an Olympus Q-Color5™ digital camera mounted on an Olympus BX51 light microscope (Olympus Corporation, Tokyo, Japan) using Image-Pro Express, version 5(Media Cybernetics, 2004). Photomicrographs were minimally processed for brightness and contrast using Microsoft PowerPoint (Microsoft 365). To assess female reproductive status, we measured granulosa layer thickness, infundibular and uterine epithelial height, and uterine gland diameter[39]. For each structure, 10–20 measurements were taken using cellSens software (Olympus Corporation, Tokyo, Japan). Uterine gland diameter was calculated as the average of two measurements taken along perpendicular axes.

Comparative data and interspecific comparisons

We conducted an interspecific descriptive comparison within the genus *Trachylepis*. We compiled data on female SVL, clutch or litter size, and egg size (length and width) from published sources for mainland species and island endemics (Supplementary Table S2). When mean values were not explicitly reported, they were calculated from available published data. We then calculated egg volume (V) using the prolate spheroid equation: $V = 4/3\pi(\text{width}/2)(\text{length}/2)^2$. Cases reporting a single egg dimension were excluded. To account for body size effects, relative clutch/litter size and relative egg size were calculated as residuals from log–log regressions of mean clutch/litter size and mean egg volume, respectively, on mean female SVL. Species were classified according to geographic context as mainland, continental island, or oceanic island endemics. These comparisons were intended as descriptive and exploratory, given the heterogeneity of data sources, variation in sample sizes among species, and the absence of formal phylogenetic correction.

Data analysis

Males were considered sexually mature if they had enlarged, turgid testes, and sperm in the seminiferous ducts. Testicular sections were categorized into four activity stages: (1) quiescence (no spermatogenic activity, only Sertoli cells and sparse spermatogonia), (2) recrudescence (presence of spermatogonia, spermatocytes, and spermatids), (3) spermiogenesis (metamorphosing spermatids and spermatozoa in the lumen), and (4) regression (thin germinal epithelium, few germ cells and Sertoli cells)[89]. Epididymides and ductus deferentia were classified based on sperm content as empty, sparsely to moderately filled, or densely packed[90]. Females were considered sexually mature if they had sperm in the oviducts, vitellogenic follicles, oviductal eggs, or folded oviducts. Ovarian follicles were categorized as non-vitellogenic (small, whitish follicles with thicker granulosa layer) or vitellogenic (enlarged, yellowish follicles with a thinner granulosa layer)[91,92]. Enlarged uterine glands, typically observed during vitellogenesis[93], were also used to determine the vitellogenic stage. Egg volume (V) was calculated using the prolate spheroid equation: $V = 4/3\pi(\text{width}/2)(\text{length}/2)^2$. We used R v4.4.2[94] in RStudio 2024.09.1 (RStudio Inc., Boston, MA, USA) to perform Mann-Whitney U tests to compare the volume of eggs produced by free-ranging females and the zoo-housed female, as well as histological variables (granulosa thickness, infundibular and uterine epithelial height, and uterine gland diameter) between reproductive stages. Values are presented as mean ± standard deviation, with significance at $\alpha = 0.05$.

DATA AVAILABILITY

The data supporting the findings of this study are available within the manuscript or supplementary information files, as well as from the corresponding authors upon reasonable request.

REFERENCES

1. Baeckens, S. & Van Damme, R. The island syndrome. *Current Biology* **30**, R338–R339 (2020).
2. Whittaker, R. J., Fernández-Palacios, J. M. & Matthews, T. J. *Island Biogeography: Geo-Environmental Dynamics, Ecology, Evolution,*

Human Impact, and Conservation. (Oxford University PressOxford, Oxford, 2023). doi:10.1093/oso/9780198868569.001.0001.

3. Adler, G. H. & Levins, R. The island syndrome in rodent populations. *The Quarterly Review of Biology* **69**, 473–490 (1994).
4. Novosolov, M., Raia, P. & Meiri, S. The island syndrome in lizards. *Global Ecology and Biogeography* **22**, 184–191 (2013).
5. Goltsman, M., Kruchenkova, E. P., Sergeev, S., Volodin, I. & Macdonald, D. W. 'Island syndrome' in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island. *Journal of Zoology* **267**, 405–418 (2005).
6. Nieberding, C., Morand, S., Libois, R. & Michaux, J. R. Parasites and the island syndrome: the colonization of the western Mediterranean islands by *Heligmosomoides polygyrus* (Dujardin, 1845). *Journal of Biogeography* **33**, 1212–1222 (2006).
7. Jezierski, M. T., Smith, W. J. & Clegg, S. M. The island syndrome in birds. *Journal of Biogeography* **51**, 1607–1622 (2024).
8. Burns, K. C. *Evolution in Isolation*. (Cambridge University Press, Cambridge, 2019). doi:10.1017/9781108379953.
9. Leihy, R. I. & Chown, S. L. Wind plays a major but not exclusive role in the prevalence of insect flight loss on remote islands. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20202121 (2020).
10. Lomolino, M. V. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* **32**, 1683–1699 (2005).
11. MacArthur, R. A. & Wilson, E. O. *The Theory of Island Biogeography*. (Princeton University Press, Princeton, 2001).

12. Buckley, L. B. & Jetz, W. Insularity and the determinants of lizard population density. *Ecology Letters* **10**, 481–489 (2007).
13. Case, T. J. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* **56**, 3–18 (1975).
14. Cooper, W. E., Dimopoulos, I. & Pafilis, P. Sex, age, and population density affect aggressive behaviors in island lizards promoting cannibalism. *Ethology* **121**, 260–269 (2015).
15. Covas, R. Evolution of reproductive life histories in island birds worldwide. *Proceedings of the Royal Society B: Biological Sciences* **279**, 1531–1537 (2012).
16. Mills, H. R., Bradshaw, F. J., Lambert, C., Bradshaw, S. D. & Bencini, R. Reproduction in the marsupial dibbler, *Parantechinus apicalis*; differences between island and mainland populations. *General and Comparative Endocrinology* **178**, 347–354 (2012).
17. Shield, J. A breeding season difference in two populations of the Australian macropod marsupial (*Setonix brachyurus*). *Journal of Mammalogy* **45**, 616–625 (1964).
18. Blondel, J. Breeding strategies of the blue tit and coal tit (*Parus*) in mainland and island Mediterranean habitats: a comparison. *The Journal of Animal Ecology* **54**, 531–556 (1985).
19. Carretero, M. A. Reproductive cycles in Mediterranean lacertids: plasticity and constraints. in *Mainland and insular lacertid lizards: a mediterranean perspective* (eds Corti, C., Lo Cascio, P. & Biaggini, M.) 33–54 (Firenze University Press, Firenze, 2006).

20. Sagonas, K., Pafilis, P., Lymberakis, P. & Valakos, D. Sexual maturation and reproduction of the Balkan green lizard Lacerta trilineata specimens in mainland and island populations from Greece. *North-Western Journal of Zoology* **15**, e171511 (2019).
21. Novosolov, M. & Meiri, S. The effect of island type on lizard reproductive traits. *Journal of Biogeography* **40**, 2385–2395 (2013).
22. Whittaker, R. J., Fernández-Palacios, J. M., Matthews, T. J., Borregaard, M. K. & Triantis, K. A. Island biogeography: Taking the long view of nature's laboratories. *Science* **357**, eaam8326 (2017).
23. Uetz, P. *et al.* The Reptile Database. http://www.reptile-database.org/ (2025).
24. Weinell, J. L. *et al.* A species-level phylogeny of *Trachylepis* (Scincidae: Mabuyinae) provides insight into their reproductive mode evolution. *Molecular Phylogenetics and Evolution* **136**, 183–195 (2019).
25. Mausfeld, P. *et al.* Phylogenetic affinities of *Mabuya atlantica* Schmidt, 1945, endemic to the Atlantic Ocean Archipelago of Fernando de Noronha (Brazil): necessity of partitioning the genus *Mabuya* Fitzinger, 1826 (Scincidae: Lygosominae). *Zoologischer Anzeiger* **241**, 281–293 (2002).
26. Carranza, S. & Arnold, E. N. Investigating the origin of transoceanic distributions: Mtdna shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. *Systematics and Biodiversity* **1**, 275–282 (2003).
27. Branner, J. C. Notes on the Fauna of the Islands of Fernando de Noronha. *The American Naturalist* **22**, 861–871 (1888).

28. Lyra, M. L. & Vences, M. Preliminary assessment of mitochondrial variation in the insular endemic, biogeographically enigmatic Noronha skink, <I>Trachylepis atlantica</i> (Squamata: Scincidae). *Salamandra* **54**, 229–232 (2018).
29. Rocha, C. F. D., Vrcibradic, D., Menezes, V. A. & Ariani, C. V. Ecology and natural history of the easternmost native lizard species in South America, *Trachylepis atlantica* (Scincidae), from the Fernando de Noronha Archipelago, Brazil. *Journal of Herpetology* **43**, 450–459 (2009).
30. Travassos, H. Estudo da variação de *Mabuya punctata* (Gray, 1839). *Boletim do Museu Nacional* **60**, 1–56 (1946).
31. Sazima, I., Sazima, C. & Sazima, M. Little dragons prefer flowers to maidens: a lizard that laps nectar and pollinates trees. *Biota Neotropica* **5**, 185–192 (2005).
32. Silva-Neto, A. M., Mendes, D. M. M., Sobral, R. & Rafael, J. A. *Trachylepis atlantica* (Noronha skink). Nest site and hatchling. *Herpetological Review* **51**, 132–132 (2020).
33. Migliore, S. N., Braz, H. B., Gasparotto, V. P., Dias, R. & Almeida-Santos, S. M. *Trachylepis atlantica* (Noronha skink). Reproduction. *Herpetological Review* **51**, 132–133 (2020).
34. Gasparotto, V., Migliore, S. N., Pinheiro, R., Dias, R. A. & Almeida-Santos, S. M. Agonistic and mating behaviour of the endemic lizard Trachylepis atlantica from the Fernando de Noronha archipelago, Brazil. *Herpetological Bulletin* **158**, 16–23 (2021).

35. Colli, G. R. *et al.* Trachylepis atlantica: *IUCN Red List of Threatened Species* (2014) doi:10.2305/IUCN.UK.2019-1.RLTS.T120689136A134890404.pt.
36. Moura, G. J. B. & Tavares, P. *Avaliação Do Estado de Conservação Dos an Bios e Répteis de Pernambuco: Protegendo as Espécies Ameaçadas.* (Secretaria de Meio Ambiente e Sustentabilidade de Pernambuco, Recife, 2022).
37. in den Bosch, H. A. J. First record of mating plugs in lizards. *Amphibia-Reptilia* **15**, 89–93 (1994).
38. Ribeiro, P. & Oliveira, R. M. *Trachylepis atlantica* (Noronha skink). Cannibalism attempt. *Herpetological Review* **49**, 122–122 (2018).
39. Guillette, L. J., Fox, S. L. & Palmer, B. D. Oviductal morphology and egg shelling in the oviparous lizards *Crotaphytus collaris* and *Eumeces obsoletus*. *Journal of Morphology* **201**, 145–159 (1989).
40. Stewart, J. R. *et al.* Uterine and eggshell structure and histochemistry in a lizard with prolonged uterine egg retention (Lacertilia, Scincidae, *Saiphos*). *Journal of Morphology* **271**, 1342–1351 (2010).
41. Robertson, I. A. D., Chapman, B. M. & Chapman, R. F. Notes on the biology of the lizards *Agama cyanogaster* and *Mabuya striata striata* collected in the Rukwa Valley, southwest Tanganyika. *Proceedings of the Zoological Society of London* **145**, 305–320 (1965).
42. Barbault, R. Écologie comparée des lézards *Mabuya blandingi* (Hallowell) et *Panaspis kitsoni* (Boulenger) dans les forêts de Lamto (Côte-d'Ivoire). *Revue d'Écologie* 272–295 (1974).

43. Barbault, R. Population dynamics and reproductive patterns of three African skinks. *Copeia* **1976**, 483–490 (1976).
44. Simbotwe, M. P. Reproductive biology of the skinks *Mabuya striata* and *Mabuya quinquetaeniata* in Zambia. *Herpetologica* **36**, 99–104 (1980).
45. Patterson, J. W. Female reproductive cycles in two subspecies of the tropical lizard *Mabuya striata*. *Oecologia* **84**, 232–237 (1990).
46. Loveridge, A. Scientific results of an expedition to rain forest regions in eastern Africa. V. Reptiles. *Bulletin of the Museum of Comparative Zoology at Harvard College* **79**, 209–337 (1936).
47. Visser, J. Oviparity in two South African skinks of the genus *Mabuya*, with notes on hatching. *Zoologica Africana* **10**, 209–213 (1975).
48. de Waal, S. W. P. The Squamata (Reptilia) of the Orange Free State, South Africa. (University of Natal, Pietermaritzburg, 1977).
49. Mouton, P. I. F. N. & Van Wyk, J. H. Reptile fauna of the Katse Dam catchment area and a biogeographical assessment of species composition in the Lesotho Highlands. *Koedoe* **36**, 67–78 (1993).
50. Flemming, A. F. Male and female reproductive cycles of the viviparous lizard, *Mabuya capensis* (Sauria: Scincidae) from South Africa. *Journal of Herpetology* **28**, 334–341 (1994).
51. Wymann, M. & Whiting, M. J. Foraging ecology of rainbow skinks (*Mabuya margaritifer*) in southern Africa. *Copeia* **2002**, 943–957 (2002).
52. Goldberg, S. R. Reproductive cycle of the Kalahari tree skink, *Trachylepis spilogaster* (Squamata: Scincidae) from southern Africa. *Texas Journal of Science* **58**, 291–298 (2006).

53. Bates, M. F. *Mabuya sulcata sulcata*. Western rock skink. Reproduction. *African Herp News* **24**, 23–24 (1995).
54. Branch, W. R. & Bauer, A. M. Herpetofauna of the Little Karoo, western Cape, South Africa with notes on life history and taxonomy. *Herpetological Natural History* **3**, 47–89 (1995).
55. Goldberg, S. R. Reproductive cycle of the western three-striped skink, *Trachylepis occidentalis* (Squamata: Scincidae) from southern Africa. *Salamandra* **44**, 123–126 (2008).
56. Kopij, G. & Buiswalelo, B. Notes on reproduction of *Trachylepis* species in Namibia. *African Herp News* **80**, 34–39 (2022).
57. Goldberg, S. R. Notes on the reproductive biology of the variegated skink, *Trachylepis variegata* (Squamata: Scincidae), from southern Africa. *Bulletin of the Chicago Herpetological Society* **41**, 168–169 (2006).
58. Goldberg, S. R. Reproductive cycle of the Namibian striped skink, *Trachylepis sparsa* (Squamata: Scincidae) from southern Africa. *African Zoology* **42**, 289–293 (2007).
59. Foucart, T., Lourdais, O., DeNardo, D. F. & Heulin, B. Influence of reproductive mode on metabolic costs of reproduction: insight from the bimodal lizard *Zootoca vivipara*. *Journal of Experimental Biology* **217**, 4049–4056 (2014).
60. Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences* **267**, 1947–1952 (2000).

61. Webb, J. K., Brook, B. W. & Shine, R. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research* **17**, 59–67 (2002).
62. Fernández-Palacios, J. M. *et al.* Scientists' warning – The outstanding biodiversity of islands is in peril. *Global Ecology and Conservation* **31**, e01847 (2021).
63. Blondel, J. Evolution and ecology of birds on islands: trends and prospects. *Vie et Milieu* **50**, 205–220 (2000).
64. Schwarz, R. & Meiri, S. The fast-slow life-history continuum in insular lizards: a comparison between species with invariant and variable clutch sizes. *Journal of Biogeography* **44**, 2808–2815 (2017).
65. Schwarz, R. *et al.* Isolation and predation drive gecko life-history evolution on islands. *Biological Journal of the Linnean Society* **129**, 618–629 (2020).
66. Slavenko, A., Itescu, Y., Foufopoulos, J., Pafilis, P. & Meiri, S. Clutch size variability in an ostensibly fix-clutched lizard: effects of insularity on a Mediterranean gecko. *Evolutionary Biology* **42**, 129–136 (2015).
67. Silva-Jr, J. M., Péres-Jr, A. K. & Sazima, I. *Euprepis atlanticus* (Noronha Skink). Predation. *Herpetological Review* **36**, 62–63 (2005).
68. Gasparini, J. L., Peloso, P. L. & Sazima, I. New opportunities and hazards brought by humans to the island habitat of the skink <I>Euprepis atlanticus</i>. *Herpetological Bulletin* **100**, 30–33 (2007).
69. Finley, R. B. Notes on lizards from Fernando Noronha. *Copeia* **1945**, 162–164 (1945).

70. Pregill, G. Durophagous feeding adaptations in an amphisbaenid. *Journal of Herpetology* **18**, 186–191 (1984).
71. APAC. *Atlas Climatológico Do Estado de Pernambuco: Normais Climatológicas 1991-2020*. (Agência Pernambucana de Águas e Clima & Gerência de Meteorologia e Mudanças Climáticas, Recife, 2023).
72. Tanaka, L. K. & Tanaka, S. K. Rainfall and seasonal changes in arthropod abundance on a tropical oceanic island. *Biotropica* **14**, 114–123 (1982).
73. Cooper, W. E. & Vitt, L. J. Distribution, extent, and evolution of plant consumption by lizards. *Journal of Zoology* **257**, 487–517 (2002).
74. Vitt, L. J. & Pianka, E. R. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences* **102**, 7877–7881 (2005).
75. Doughty, P. & Shine, R. Reproductive energy allocation and long-term energy stores in a viviparous lizard (*Eulamprus tympanum*). *Ecology* **79**, 1073–1083 (1998).
76. Olsson, M. & Shine, R. Plasticity in frequency of reproduction in an alpine lizard, *Niveoscincus microlepidotus*. *Copeia* **1999**, 794–796 (1999).
77. Du, W. Phenotypic plasticity in reproductive traits induced by food availability in a lacertid lizard, *Takydromus septentrionalis*. *Oikos* **112**, 363–369 (2006).
78. Brooke, M. L. & Houston, D. C. The biology and biomass of the skinks *Mabuya sechellensis* and *Mabuya wrightii* on Cousin Island, Seychelles (Reptilia: Scincidae). *Journal of Zoology* **200**, 179–195 (1983).

79. Nussbaum, R. A. & Raxworthy, C. J. New long-tailed *Mabuya* Fitzinger from Lokobe Reserve, Nosy Be, Madagascar (Reptilia: Squamata: Scincidae). *Copeia* **1998**, 114–119 (1998).
80. Pakenham, R. H. W. The reptiles and amphibians of Zanzibar and Pemba islands (with a note on the freshwater fishes). *Journal of the East Africa natural History Society and National Museum* **177**, 1–40 (1983).
81. Ceríaco, L. M. P., Marques, M. P. & Bauer, A. M. A review of the genus *Trachylepis* (Sauria: Scincidae) from the Gulf of Guinea, with descriptions of two new species in the Trachylepis maculilabris (Gray, 1845) species complex. *Zootaxa* **4109**, 284–314 (2016).
82. Nussbaum, R. A. & Raxworthy, C. J. A new species of *Mabuya* Fitzinger (Reptilia: Squamata: Scincidae) from southern Madagascar. *Herpetologica* **50**, 309–319 (1994).
83. Andreone, F. & Greer, A. E. Malagasy scincid lizards: descriptions of nine new species, with notes on the morphology, reproduction and taxonomy of some previously described species (Reptilia, Squamata: Scincidae). *Journal of Zoology* **258**, 139–181 (2002).
84. IBGE. Fernando de Noronha. *https://cidades.ibge.gov.br/brasil/pe/fernando-de-noronha/panorama* (2022).
85. Mello, T. J. & Oliveira, A. A. de. Making a bad situation worse: an invasive species altering the balance of interactions between local species. *PLoS ONE* **11**, e0152070 (2016).

86. Toledo, L. F., Zanotti, A. P., Bezerra, L. M. L. S., Abrahão, C. & Lisboa, C. S. Occasional herpetofaunal introductions into and from the archipelago of Fernando de Noronha, Brazil. *Spixiana* **45**, 271–275 (2023).
87. Junqueira, L. C. & Carneiro, J. *Histologia Básica*. (Guanabara Koogan, Rio de Janeiro, 2008).
88. Sever, D. M. & Hopkins, W. A. Renal sexual segment of the ground skink, *Scincella laterale* (Reptilia, Squamata, Scincidae). *Journal of Morphology* **266**, 46–59 (2005).
89. Méndez-de la Cruz, F. R., Manríquez-Morán, N. L., Ríos, E. A. & Ibargüengoytía, N. Male reproductive cycles in lizards. in *Reproductive biology and phylogeny of lizards and tuatara* (eds Rheubert, J. L., Siegel, D. S. & Trauth, S. E.) 302–339 (CRC Press, Boca Raton, 2014).
90. Silva, K. M. P., Braz, H. B., Kasperoviczus, K. N., Marques, O. A. V. & Almeida-Santos, S. M. Reproduction in the pitviper *Bothrops jararacussu*: large females increase their reproductive output while small males increase their potential to mate. *Zoology* **142**, 125816 (2020).
91. Ramírez-Pinilla, M. P. Biología reproductiva y placentotrofía en lagartijas del género *Mabuya*. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* **38**, 106–117 (2014).
92. Braz, H. B., Kasperoviczus, K. N. & Guedes, T. B. Reproductive biology of the fossorial snake *Apostolepis gaboi* (Elapomorphini): a threatened and poorly known species from the Caatinga region. *South American Journal of Herpetology* **14**, 37–47 (2019).

93. Braz, H. B., Almeida-Santos, S. M., Murphy, C. R. & Thompson, M. B. Uterine and eggshell modifications associated with the evolution of viviparity in South American water snakes (*Helicops* spp.). *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* **330**, 165–180 (2018).
94. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing (2024).

ACKNOWLEDGMENTS

We thank Paulo Passos, Renato Feio, Paulo Manzani, and Karina Rebelo for allowing us to examine specimens under their care; Rafaela Coeti for helping with data collection; and Marta Antoniazzi, Carlos Jared, and Luciana Sato for kindly allowing access to microscopic equipment. We also thank Mariana Lyra and Daniel de Granville for providing information on courtship and mating, and the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Parque Nacional Marinho de Fernando de Noronha, and Centro Nacional de Pesquisa e Conservação de Répteis e Anfíbios (RAN/ICMBio) for their support.

FUNDING

This study was supported by the Coordination for the Improvement of Higher Education Personnel– CAPES (Finance Code 001), The Rufford Foundation (grant number 18890-1), and CAPES (PVE Project number 88881.065000/2014-1). S.M. Almeida-Santos holds a research fellowship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq; process number 312325/2022-3).

FIGURE LEGENDS

Figure 1. Map showing the location of the Fernando de Noronha Archipelago in northeastern Brazil and the collection sites of the examined specimens of the Noronha skink (*Trachylepis atlantica*). Mapped localities include free-ranging individuals collected for the present study as well as preserved museum specimens for which specific collection localities were available. (1) Ilha da Rata, n = 5; (2) Ilha do Meio, n = 2; (3) Ilha São José, n = 2, (4) Pedra da Cebola, n = 4, (5) Casa da Polícia, n = 2, (6) ICMBio, n = 1, (7) Boldró, n = 5; (8) Praia do Americano, n = 21; (9) Praia do Sancho, n = 2; (10) Trilha do Golfinho, n = 1; (11) Baía dos Golfinhos, n = 1; (12) Capim Açu, n = 1; (13) Praia do Leão, n = 1; and (14) Ilha do Chapéu, n = 2. In addition, 17 preserved museum specimens from Fernando de Noronha lacked specific locality information and are therefore not represented on the map.

Figure 2. (A) Seasonal variation in testicular activity in the Noronha skink (*Trachylepis atlantica*) and representative histological sections (hematoxylin-eosin) of the testes of in (B) quiescence, (C) spermiogenesis, and (D) regression.

Figure 3. Histological and histochemical analysis of the male urogenital tract of the Noronha skink (*Trachylepis atlantica*). Individuals with (A) epididymides and (B) ductus deferentia densely packed with sperm also showed (C) hypertrophied sexual segment of the kidney (SSK). In contrast, individuals with (D) epididymides and (E) ductus deferentia with few or no sperm in the lumen showed (F) regressed SSKs. Panels A–F: hematoxylin–eosin. The secretion granules in the apical portion of hypertrophied SSK cells reacted positively to (G) Coomassie blue, indicating protein content, but negatively to (H) Alcian blue and (I) PAS, indicating the absence of acidic and neutral carbohydrates, respectively. The collecting ducts reacted (G) negatively to Coomassie blue but positively to (H) Alcian blue and (I) PAS. Abbreviations: AB, Alcian blue; CB, Coomassie blue; Cd, collecting ducts; Lu, lumen; PAS, Periodic Acid–Schiff; Sp, spermatozoa.

Figure 4. (A) Seasonal variation in the diameter of the largest ovarian follicle and occurrence of gravid females of the Noronha skink (*Trachylepis atlantica*) from the Fernando de Noronha Archipelago. (B) A copulatory plug (Cp) observed in the non-glandular uterus of a vitellogenic female collected during the mid–late dry season, providing direct evidence of mating during this period. hematoxylin and eosin. Inset shows AB+ staining, indicating acidic carbohydrates; spermatozoa were absent within the plug.

Figure 5. Relative clutch/litter size and egg size in mainland and island *Trachylepis* species. (A) Relative clutch/litter size; (B) Relative egg size. Relative values were calculated as residuals from log–log regressions of mean clutch/litter size and mean egg volume (a proxy for egg size), respectively, on mean female body size (SVL). The focal species, *Trachylepis atlantica*, an oceanic island endemic from the Fernando de Noronha Archipelago (Brazil), shows the smallest relative clutch size (A) and the largest relative egg size (B) among congeners. Data were compiled from published sources (see Methods and Supplementary Table S2). The comparison is descriptive, and values show substantial overlap between groups.

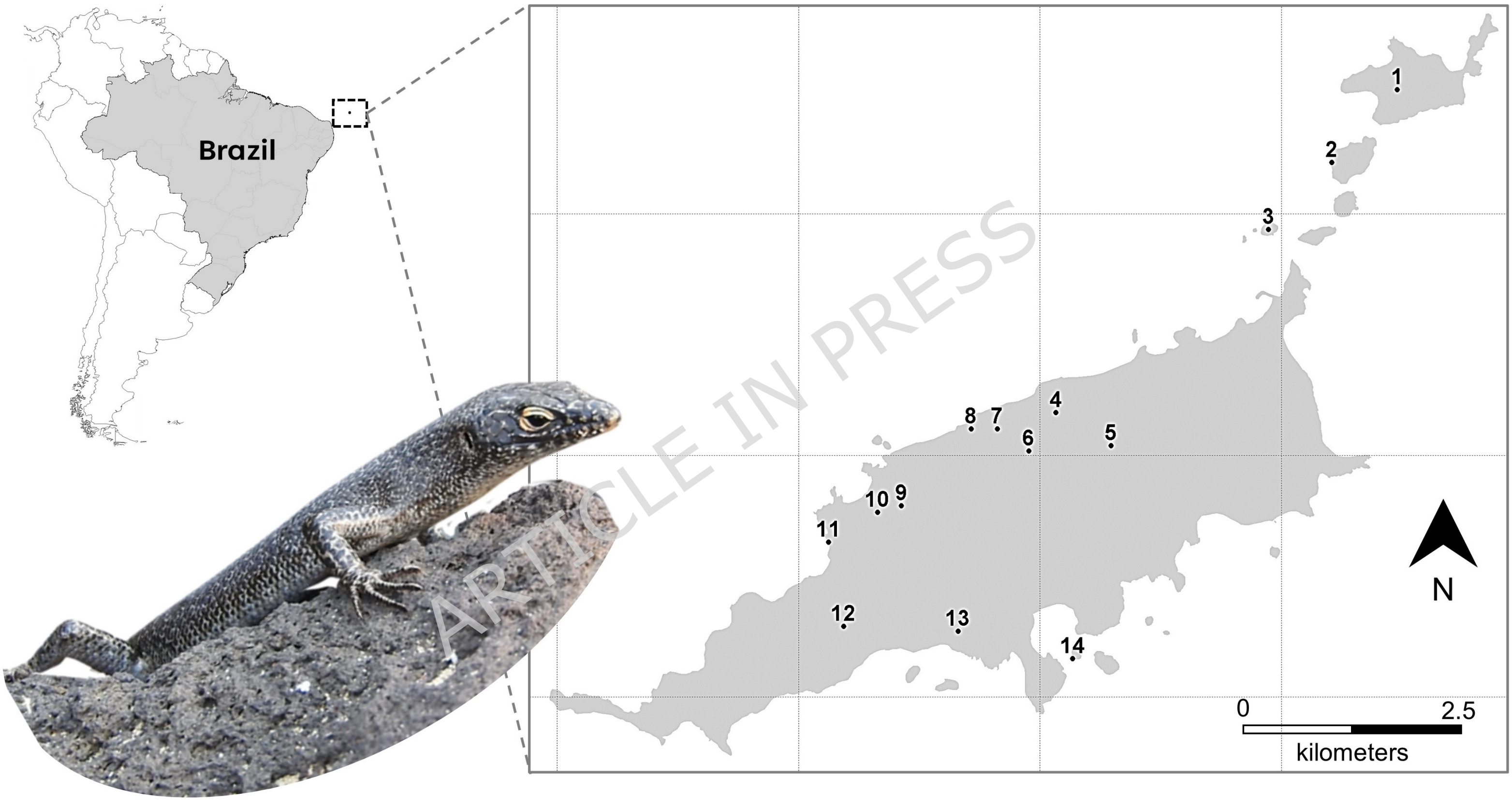
Figure 6. Overview of the reproductive events in the Noronha skink (*Trachylepis atlantica*) from the Fernando de Noronha Archipelago. Observations from the present study are complemented with published data on courtship and mating[28,34], hatching[32], and the record of a hatchling-sized individual[38]. Hatched areas represent inferred periods based on the available evidence.

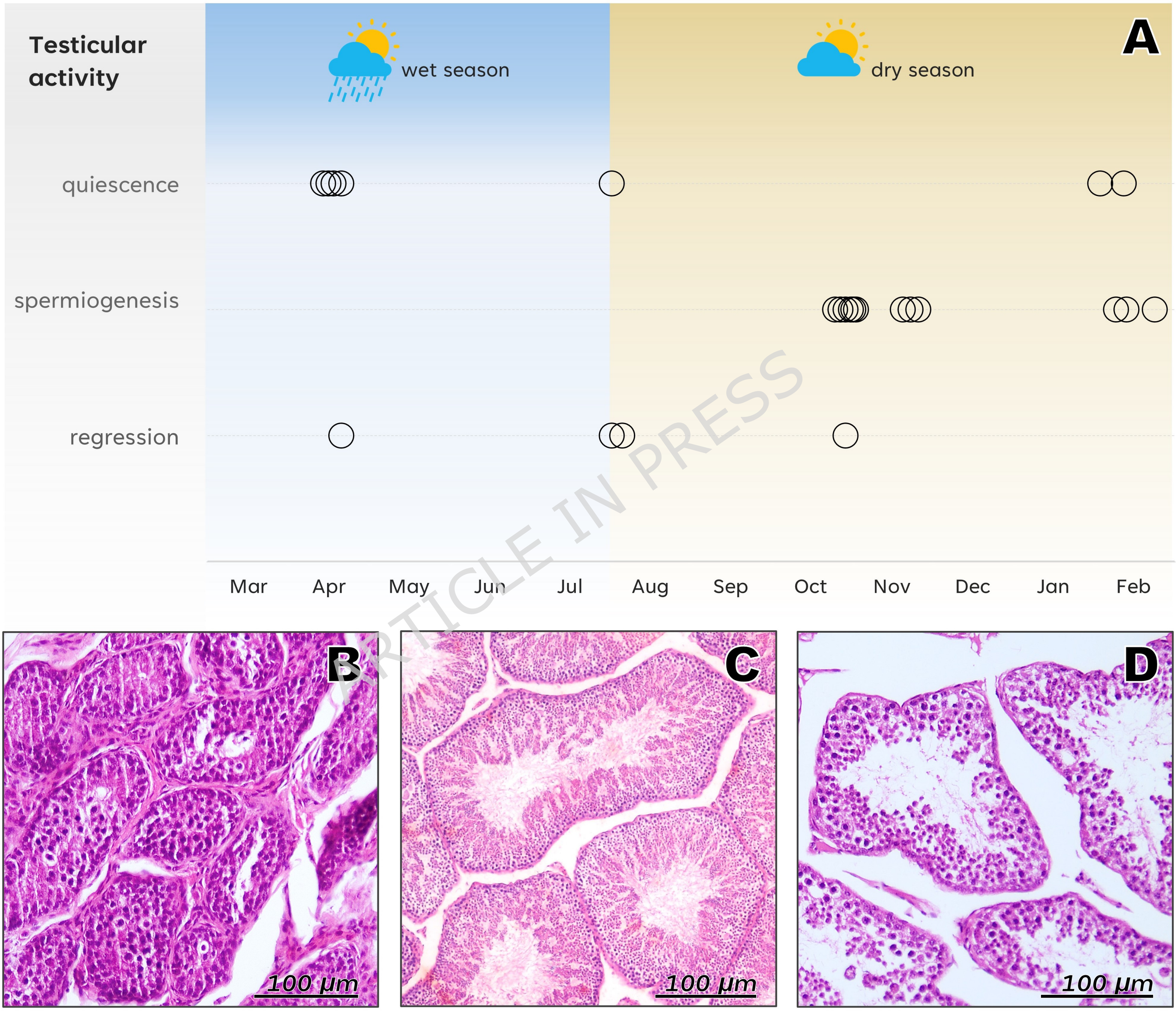
TABLES

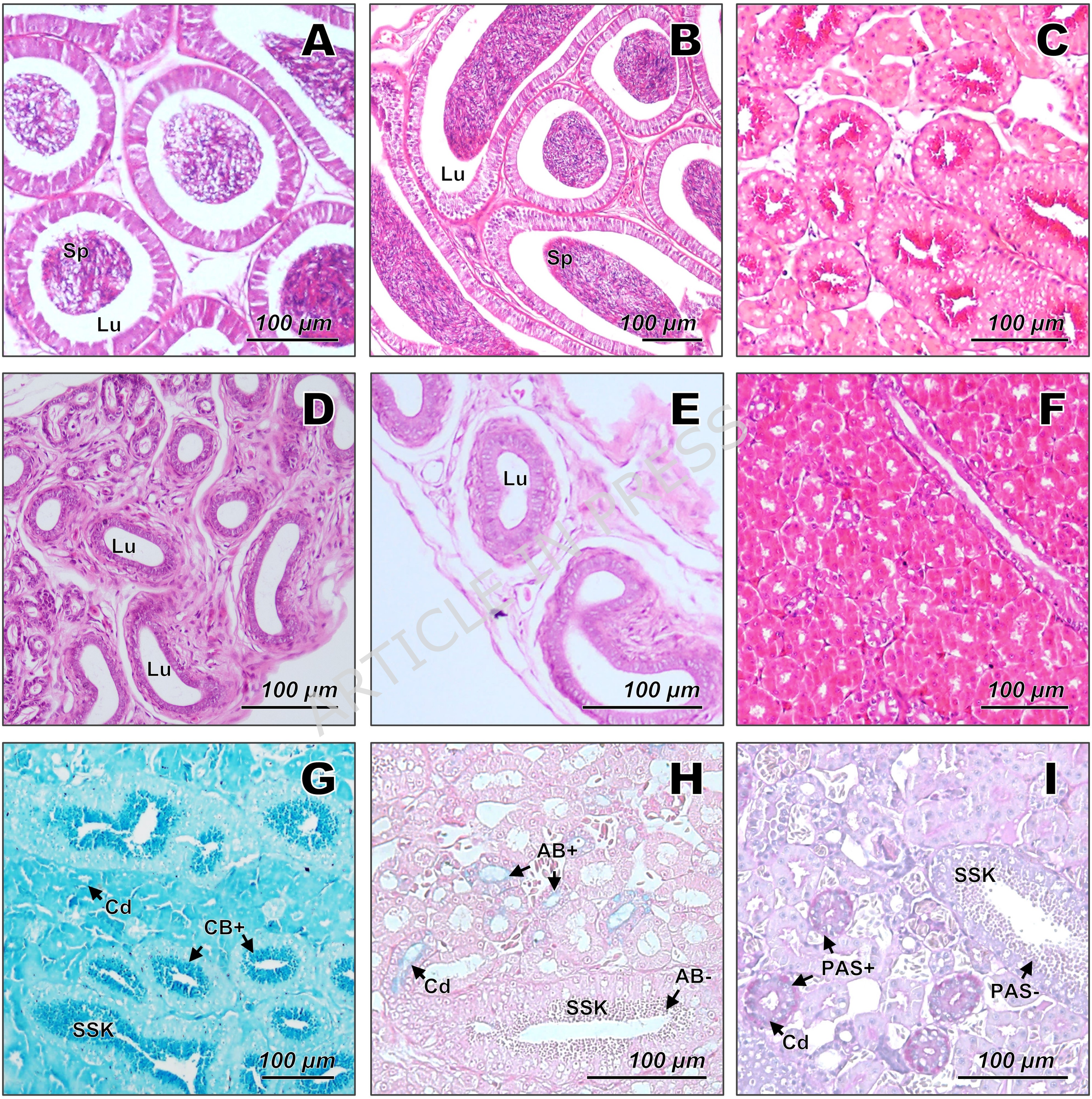
Table 1. Clutches laid by a zoo-housed female of the Noronha skink (Trachylepis atlantica). The asterisk indicates the first clutch laid after pairing with a male. For each clutch, date of egg-laying, clutch size, and

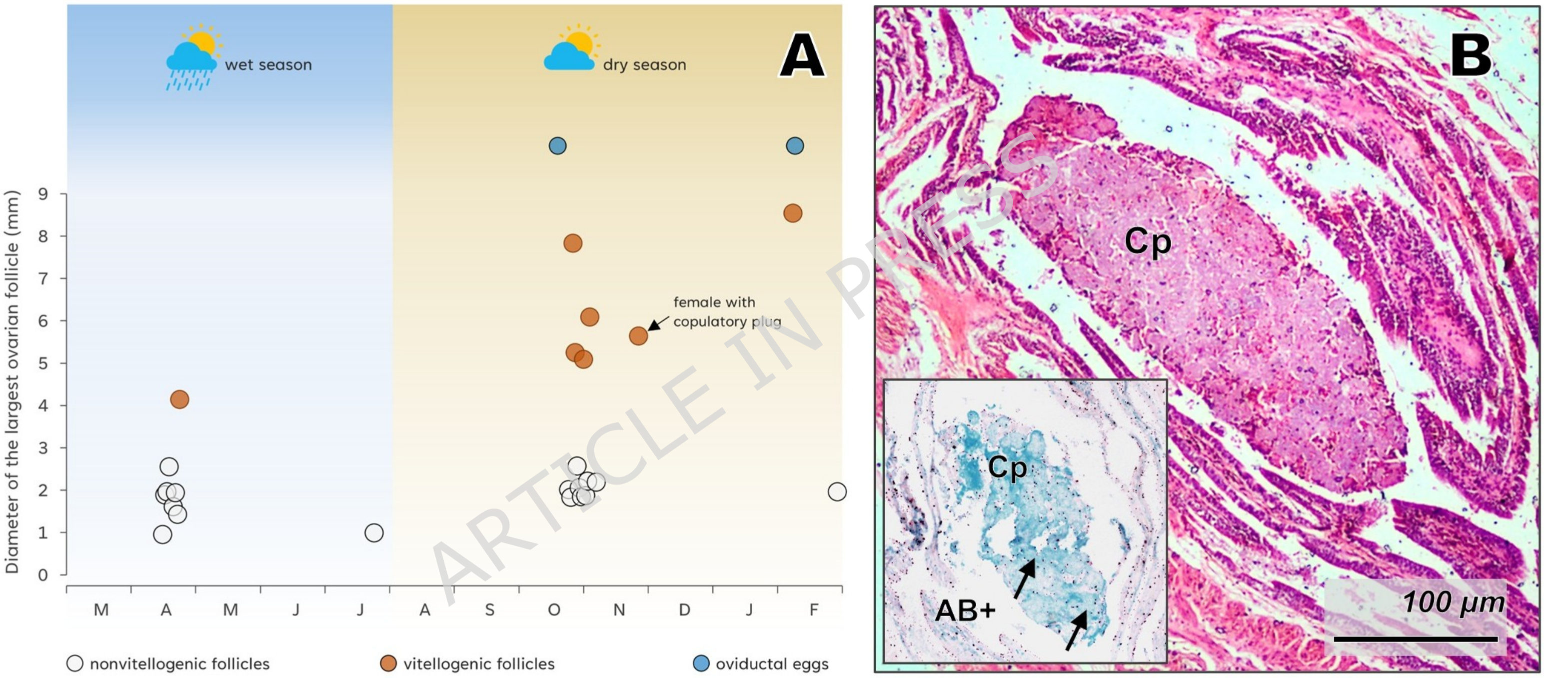
condition/fate of the eggs are shown.

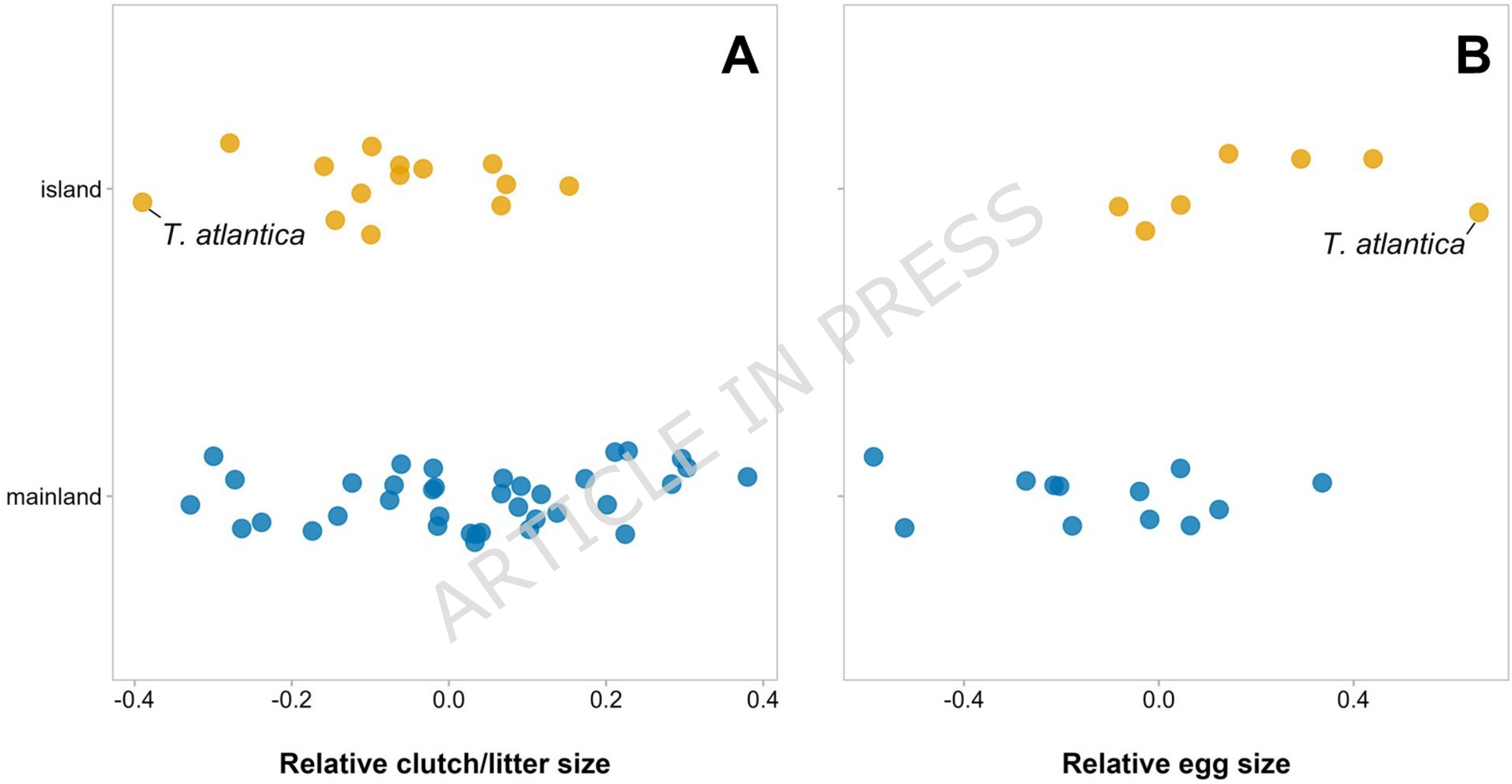
Clutch ID	Date of egg-laying	Clutch size	Clutch condition and fate
1	20 April 2012	3	infertile
2	3-5 October 2012	3	infertile
3	3 December 2012	2	infertile
4	1-2 May 2014	3	infertile
5	28 October 2014	3	infertile
6	2 December 2014	3	infertile
7	21-23 January 2015	2	infertile
8	29 March 2015*	3	fertile, hatched
9	16 November 2015	3	fertile, hatched
10	3 January 2016	2	fertile, spoiled
11	25 February 2016	2	fertile, spoiled
12	15 April 2016	2	fertile, spoiled
13	16-18 June 2016	3	fertile, spoiled
14	21 February 2017	3	fertile, spoiled


Brazil
1
2
3
4
5
6
7
8
9
10
11
12
13
14
N
0
2.5
kilometers


Testicular activity
wet season
dry season
A
quiescence
spermiogenesis
regression
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
B
100 µm
C
100 µm
D
100 µm


A
Sp
Lu
100 µm
B
Lu
Sp
100 µm
C
100 µm
D
Lu
Lu
100 µm
E
Lu
100 µm
F
100 µm
G
Cd
CB+
SSK
100 µm
H
AB+
Cd
AB-
SSK
100 µm
I
SSK
PAS+
PAS-
Cd
100 µm


A
wet season
dry season
female with
copulatory plug
Diameter of the largest ovarian follicle (mm)
0
1
2
3
4
5
6
7
8
9
M
A
M
J
J
A
S
O
N
D
J
F
○ nonvitellogenic follicles
● vitellogenic follicles
● oviductal eggs
B
Cp
Cp
AB+
100 µm


A
B
island
mainland
T. atlantica
T. atlantica
-0.4
-0.2
0.0
0.2
0.4
-0.4
0.0
0.4
Relative clutch/litter size
Relative egg size

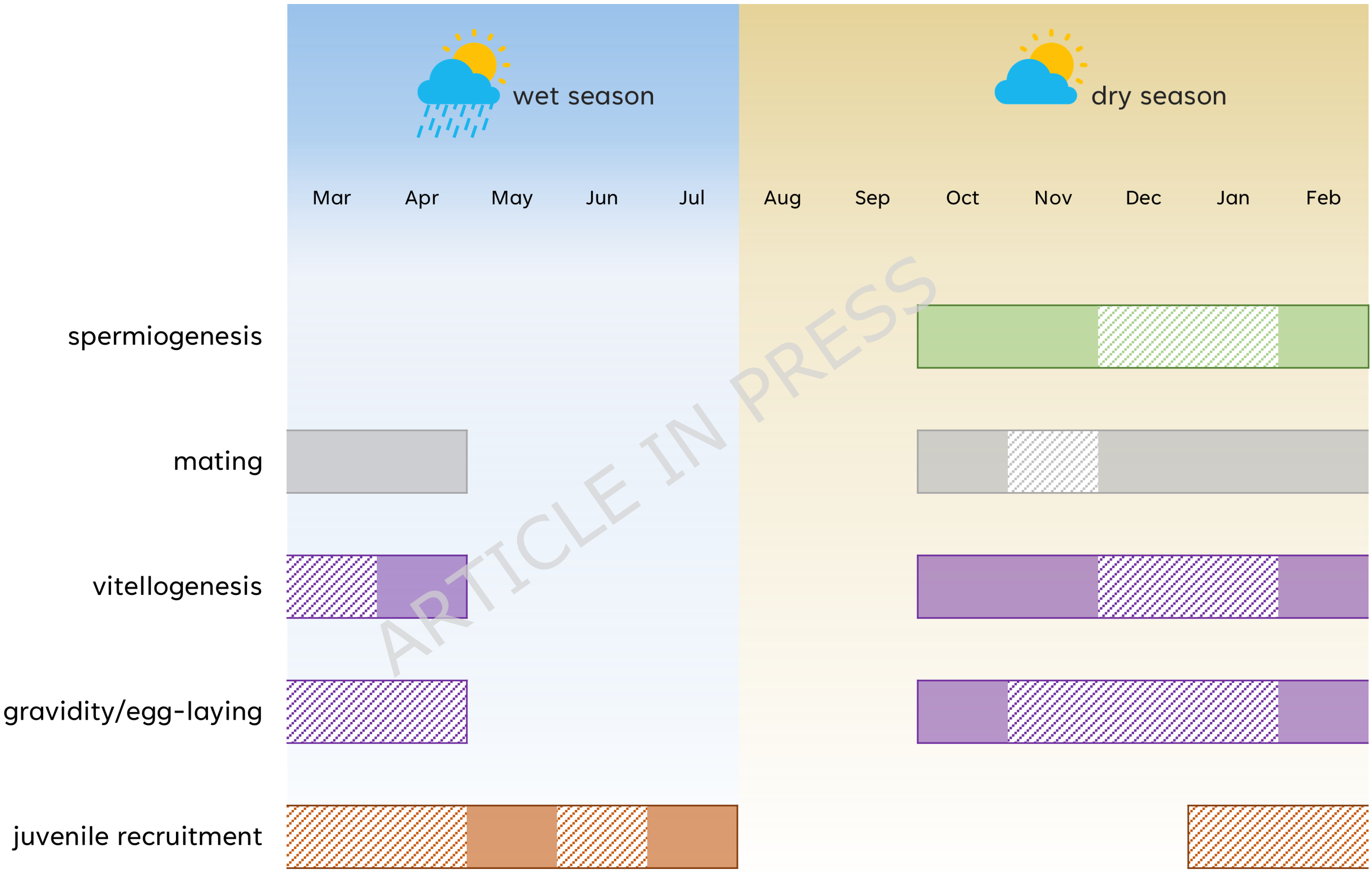

wet season
dry season
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
spermiogenesis
mating
vitellogenesis
gravidity/egg-laying
juvenile recruitment

Table 1. Clutches laid by a zoo-housed female of the Noronha skink (*Trachylepis atlantica*). The asterisk indicates the first clutch laid after pairing with a male. For each clutch, date of egg-laying, clutch size, and condition/fate of the eggs are shown.

Clutch ID	Date of egg-laying	Clutch size	Clutch condition and fate
1	20 April 2012	3	infertile
2	3-5 October 2012	3	infertile
3	3 December 2012	2	infertile
4	1-2 May 2014	3	infertile
5	28 October 2014	3	infertile
6	2 December 2014	3	infertile
7	21-23 January 2015	2	infertile
8	29 March 2015*	3	fertile, hatched
9	16 November 2015	3	fertile, hatched
10	3 January 2016	2	fertile, spoiled
11	25 February 2016	2	fertile, spoiled
12	15 April 2016	2	fertile, spoiled
13	16-18 June 2016	3	fertile, spoiled
14	21 February 2017	3	fertile, spoiled