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REPRODUCTIVE TRAITS OF THE SÃO NICOLAU WALL GECKO, *TARENTOLA NICOLAUENSIS* (GEKKOTA, PHYLLODACTYLIDAE)

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Reproductive traits of the São Nicolau wall gecko, *Tarentola nicolauensis* (Gekkota, Phyllodactylidae). Rösler, H. & Wolfgang Wranik, W. — This study provides information on main reproductive characteristics of *Tarentola nicolauensis*. Egg-laying behaviour, clutch size, reproductive effort, size, weight, incubation period and post-oviparous weight loss of eggs as well as hatching characteristics of offspring in captivity were described. Our study revealed that *T. nicolauensis* produces relatively few clutches in the course of a laying season and that the majority of clutches contain a single large egg rather than two comparatively small eggs. Hatching size and hatching weight of the hatchlings correspond to the egg sizes. These reproductive traits are characteristic of many endemic species of *Tarentola* of the Cape Verde Islands. Studies on life history and ecology of animals are important for species conservation. Such studies are unfortunately limited for reptiles. Therefore, studies in captivity are important and complement field studies.

Key words: Cape Verde, *Tarentola nicolauensis*, reproductive studies.

Introduction

As part of a faunistic survey of vertebrates on the islands of Santiago and São Nicolau, which belong to the Cape Verde Islands, one of the authors (W.W.) had the opportunity to carry out zoological field studies on the terrestrial fauna (Wranik, 2007). During the stay on the island of São Nicolau, different taxa of amphibians and reptiles were observed, of which we have described various features of their life cycle (Wranik & Rösler, 2007; Rösler & Wranik, 2008, 2009). However, as the research stay

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Fig. 1. Adult female of *Tarentola nicolauensis* (São Nicolau, Ribeira Brava). © H. Rösler

on São Nicolau was limited in time, there was no opportunity to study the habits of the local lizard fauna intensively. In particular, only sporadic studies on reproductive biology could be carried out. The following study is a continuation of our earlier investigations on the biology of Cape Verdean lizards and thus a further addition to the field studies carried out on São Nicolau from October 21 to 28, 2006.

Certain reproductive characteristics of reptiles can only be obtained to a limited extent through field observations. Ex situ breeding expands the possibilities of accurately recording, storing and processing important reproductive data. Precise knowledge of species-specific reproductive traits is of central importance for the reconstruction of the life-history-evolution of Squamata and can provide valuable information on phyletic relationships. Finally, reproductive traits are also meaningful indicators that can provide reliable information on the stability and resilience of island populations under changing environmental conditions in the context of current global climate change (López-Alcaide & Macip-Ríos, 2011; Ualiyeva & Khan, 2022).

In this study, we describe aspects of the reproductive biology of the gecko *Tarentola* (*Makariogecko*) *nicolauensis* found on the island of São Nicolau (Fig. 1). The reproduction of this species took place under controlled laboratory conditions and data of various reproductive traits were recorded over the course of several years and then evaluated.

Material and Methods

Two males and four females of *T. (M.) nicolauensis* were used for the reproduction studies (taxonomy according to Vasconcelos et al., 2012). Both males and two females were wild-caught from the island of São Nicolau, the other two females were captive-bred (F₁ and F₂ generation). During captivity in the terrarium, all females used for the study were measured and weighed once a year outside the breeding season. Mean values were then calculated from the size and weight data obtained and used for the statistical analyses. The reproductive data of *T. (M.) nicolauensis* were recorded in the years 2007–2013, 2016, 2017, 2019, 2020 and 2024.

Tarentola (M.) nicolauensis was kept individually in lighted and heated terraria and the two males were alternately socialized with the four females during the breeding season. The terraria used were identical in construction, made of glass and measured 40 × 25 × 25 cm. They were equipped with a 4–5 cm layer of sand as a substrate. As hiding places and shelter the geckos used curved pieces of bark scattered on the ground or crevices under flat stone slabs as well as plastic tubes with an internal diameter of 3 cm, which were leant against the walls at an angle.

The conditions in the terraria were roughly based on the climatic conditions of São Nicolau. The temperature and humidity in the terrarium were approximately adapted to the natural annual cycle of São Nicolau (Grünwald et al., 1983, <https://meteoatlas.de/kap-verde/tarrafal-de-sao-nicolau-11362>). In addition to natural daylight, the terraria were illuminated with fluorescent lamps (36 W, 5–12 hours) and heated with spotlights (20 W, 1–3 hours). Water was sprayed into the terraria at intervals of 4–5 days (November to June) and 2–3 days (July to October).

The geckos were fed alternately with all developmental stages of the yellow mealworm (*Tenebrio molitor*), crickets (*Gryllus assimilis*), woodlice (*Porcellionides pruinosus*) and occasionally “meadow plankton”, including in particular wolf spiders (*Pardosa* sp.) and various species of grasshoppers (*Chorthippus* sp.). Feeding took place twice a week and all food animals were powdered with a vitamin-mineral preparation (MYKOSTIN®) before being placed in the terrarium. A small water container gave the geckos the opportunity to drink daily.

Egg-laying sites of *T. (M.) nicolauensis* were apparently easy to recognise on the basis of local changes in the soil surface. All eggs were dug out, carefully brushed off the surface with a soft-bristled brush, and then measured and weighed.

Egg length and egg width were measured manually with a digital caliper (Format, ± 0.1 mm) and the egg weight and hatching weight of the offspring were determined with an electric analytical balance (Freiberg, ± 0.0002 g). In newly hatched young, the head-body length and tail length were measured with a standard ruler (±1 mm).

The first data collection on the eggs took place immediately after the eggshell had fully hardened on the day of egg laying, or on the following day at the latest. All subsequent egg weight checks were carried out at intervals of 10 days. The young specimens were measured and weighed immediately after hatching.

For the calculation of the reproductive effort (RCM), the index clutch weight/female weight was used (see Vitt & Congdon, 1978; Shine, 1992). The egg volume was determined from the long (horizontal, EL) and both short (horizontal/vertical EW1, EW2) semi-axes using the traditional volume formula for a symmetric ellipsoid:

$$V = 4/3 \times \pi \times EL/2 \times EW1/2 \times EW2/2.$$

The egg surface area was calculated using the formula:

$$A \approx 4\pi \times \left[\left((EL/2 \times EW1/2)^{1.6075} + (EL/2 \times EW2)^{1.6075} + (EW1/2 \times EW2)^{1.6075} \right) / 3^{1/1.6075} \right].$$

For incubation, all eggs of *T. (M.) nicolauensis* were placed separately in small plastic tins. During the entire incubation period, the eggs lay freely on a dry bed of

sand. Air temperature and humidity were monitored locally using an electronic multifunctional measuring device (Typtechno line).

The eggs of *T. (M.) nicolauensis* were incubated under different temperature and humidity conditions. Some of the eggs were hatched in identical incubators at constant temperatures of 27 °C or 31 °C. Incubation of the eggs at fluctuating temperatures was used as another incubation variant. In this method, the plastic tins with the eggs were placed in selected locations that guaranteed average temperatures in the range of 27–31 °C for 10–16 hours during the day and allowed a gradual reduction in temperature of 5–10 °C at night. The daily average values of the incubation temperature were calculated from the maximum and minimum temperatures per day (24.6, 25.6, 25.9, 26.6, 26.9, 27.2 °C).

In the plastic tins containers for egg incubation, the relative humidity (r.h.) was either constant at 75% or > 90% or fluctuated between 45–87% (daily mean 61.3% r. h.). In the following text, the term “wet” is used for eggs hatched at 75% r.h. or > 90% r.h. and “dry” for eggs hatched at fluctuating relative humidity.

All statistical analyses were carried out using the software PAST version 4.17 (Øyvind Hammer, 1999–2021 ©). The individual results of the comparative tests are listed in the appendix.

Abbreviations used

- CS — clutch size
- EL — egg length
- EW — egg width
- EM — egg mass
- RCM — relative clutch mass (= reproductive effort)
- IT — incubation temperature
- IP — incubation period
- HM — hatchling mass
- SVL — snout vent length
- TL — tail length

Results

Tarentola (M.) nicolauensis produced calcium-rich, hard-shelled eggs. They were laid in the terrarium from late March to early August. For oviposition, all females dug 2–3 cm deep holes in the dry sandy soil, which were covered with sand again immediately after oviposition. The eggshell, which was still flexible immediately after the eggs were pressed out, was very sticky, so that a relatively large amount of substrate adhered firmly to the shell surface during the shell hardening process. The clutches were occasionally buried under the objects present in the terrarium (e. g. curved bark), but the majority of the females used free surface sections of the substrate for this purpose.

The females of *T. (M.) nicolauensis* produced 52 clutches during the study period. Egg laying always took place at night and both eggs of a double egg clutch were laid during one laying cycle. The overall percentage of single-egg clutches, compared to double-egg clutches was 67% (Table 1). In total, the females laid 69 eggs over the

course of 12 years, of which 64 were fertilized (fertility rate 93%). During a laying season, the females produced 1–7 clutches (\bar{x} 2.9 ± 1.7, n = 52) at intervals of 7–40 days (\bar{x} 16.2 ± 9.0 d, n = 24).

For the production of one clutch, the females of *T. (M.) nicolauensis* invested a reproductive effort of 0.098–0.320 (\bar{x} 0.165 ± 0.054, n = 31). The individual data of the females for the production of one clutch are summarized in Table 2. Three females invested more endogenous resources in a double egg clutch than in a single egg clutch. The RCM value for two eggs was 0.152–0.320 (\bar{x} 0.213 ± 0.045, n = 13) and for a single egg 0.098–0.185 (\bar{x} 0.132 ± 0.024, n = 17). The effort values for double egg clutches versus single egg clutches differed significantly ($p < 0.01$, see Appendix).

The egg shape of *T. (M.) nicolauensis* was slightly oval (index EL/EW 1.52–1.06, \bar{x} 1.25 ± 0.10, n = 54). Egg length varied between 13.40–17.05 millimetres (\bar{x} 15.20 ± 0.89 mm, n = 54), egg width 9.85–14.30 millimetres (\bar{x} 12.19 ± 0.93 mm, n = 54) and egg weight immediately after oviposition 0.7926–1.7720 grams (\bar{x} 1.0875 ± 0.1923 g, n = 49). Eggs from single egg clutches were larger and heavier than eggs from double egg clutches. For eggs from single egg clutches, the egg length was 14.20–17.05 millimetres (\bar{x} 15.78 ± 0.73 mm, n = 26), the egg width was 11.05–14.30 millimetres (\bar{x} 12.70 ± 0.83, n = 26) and the egg weight was 0.9821–1.4872 grams (\bar{x} 1.1898 ± 0.1719 g, n = 18) and for eggs from double egg clutches, the egg length was 13.40–15.80 millimetres (\bar{x} 14.67 ± 0.67 mm, n = 28), the egg width was 9.85–13.05 millimetres (\bar{x} 11.73 ± 0.77, n = 28) and the egg weight 0.7926–1.7720 grams (\bar{x} 1.0218 ± 1.7720 g, n = 28). The individual data of the females on egg sizes and egg weights are summarized in Table 3. Egg sizes and egg weights differed significantly depending on the clutch size and the difference in significance was the same for all three variables ($p < 0.01$, see Appendix).

Table 1. Clutch size of four *Tarentola nicolauensis* females

| Female | Reproductive period | Clutches, n | Single egg clutches, n | Double egg clutches, n | Double egg clutches, % |
|--------|---------------------|-------------|------------------------|------------------------|------------------------|
| 1 | 2007–2011 | 17 | 14 | 3 | 17.6 |
| 2 | 2009–2012 | 14 | 10 | 4 | 28.6 |
| 3 | 2011–2020 | 19 | 12 | 7 | 36.8 |
| 4 | 2024 | 2 | 0 | 2 | 100 |

Table 2. Reproductive effort (RCM) of four *Tarentola nicolauensis* females.

Abbreviations: see text

| Female | SVL (mm) | Mass, g | Clutch size | RCM single egg clutch | RCM double egg clutch |
|--------|----------|---------|----------------------|------------------------|------------------------|
| | | | | 0.133–0.185 | |
| 1 | 56 | 7.81 | 1.17 ± 0.39 (n = 18) | (0.155 ± 0.019, n = 8) | 0.258 (n = 1) |
| | | | | 0.107–0.110 | 0.199–0.320 |
| 2 | 61 | 9.19 | 1.29 ± 0.47 (n = 14) | (0.108 ± 0.001, n = 3) | (0.237 ± 0.056, n = 4) |
| | | | | 0.098–0.143 | 0.152–0.205 |
| 3 | 63 | 10.40 | 1.42 ± 0.51 (n = 19) | (0.117 ± 0.018, n = 6) | (0.184 ± 0.023, n = 6) |
| | | | | | 0.239–0.247 |
| 4 | 57 | 8.89 | 2 | – | (0.243 ± 0.005, n = 2) |

Table 3. Egg sizes and egg weights of four *Tarentola nicolauensis* females.
Abbreviations: see text, measurements in mm, weight in grams

| Female | Single egg clutches | | | Double egg clutches | | |
|--------|---------------------------------------|---------------------------------------|---|---------------------------------------|--------------------------------------|--|
| | EL | EW | EM | EL | EW | EM |
| 1 | 14.20–16.40 (15.74 ± 0.63, n = 12) | 11.60–14.30 (12.79 ± 0.83, n = 12) | 1.0349–1.4453 (1.2122 ± 0.1490, n = 8) | 13.40–16.50 (14.80 ± 1.28, n = 4) | 11.50–13.00 (12.13 ± 0.64, n = 4) | 0.9870–1.4114 (1.1267 ± 0.1937, n = 4) |
| 2 | 14.90–17.05 (15.76 ± 0.85, n = 5) | 11.05–13.60 (12.37 ± 0.95, n = 5) | 0.9821–1.0079 (0.9922 ± 0.0183, n = 5) | 13.55–15.80 (14.99 ± 0.79, n = 8) | 10.30–12.65 (11.46 ± 0.83, n = 8) | 0.8955–1.7720 (1.0870 ± 0.2893, n = 8) |
| 3 | 14.40–16.85 (15.75 ± 0.88, n = 8) | 11.55–16.80 (12.72 ± 0.87, n = 8) | 1.0200–1.4872 (1.2217 ± 0.1844, n = 6) | 13.44–15.60 (14.54 ± 0.63, n = 13) | 9.85–12.55 (11.67 ± 0.80, n = 13) | 0.7926–1.1215 (0.9618 ± 0.1129, n = 13) |
| 4 | – | – | – | 14.30–15.00 (14.76 ± 0.32, n = 4) | 11.85–13.05 (12.38 ± 0.52, n = 4) | 1.0014–1.1570 (1.07090 ± 0.0731, n = 4) |

Table 4. Incubation period of *Tarentola nicolauensis* eggs at different temperatures.
Abbreviations: n = number of eggs, min. = minimum, max. = maximum, others see text

| IT (min.–max.) °C | n | Mean | SD | min.–max |
|-------------------|----|-------|------|----------|
| 27 | 4 | 111.8 | 8.0 | 103–122 |
| 31 | 4 | 81.5 | 1.7 | 80–84 |
| 24.6 (21.2–27.5) | 3 | 109.0 | 11.5 | 100–122 |
| 25.6 (22.6–28.3) | 5 | 87.4 | 9.4 | 78–98 |
| 25.9 (22.8–29.3) | 4 | 84.0 | 17.3 | 64–99 |
| 26.6 (23.5–29.4) | 12 | 76.1 | 12.7 | 56–95 |
| 26.9 (23.6–29.6) | 5 | 73.8 | 14.5 | 57–89 |
| 27.2 (24.3–29.8) | 8 | 73.6 | 9.3 | 61–85 |

The incubation time of the eggs was influenced by the incubation temperature. Juveniles of *T. (M.) nicolauensis* hatched after 56–122 days (\bar{x} 83.2 ± 16.8 d, n = 45). Table 4 summarizes the extracorporeal development times of the eggs incubated at different temperatures. Constant and fluctuating temperatures had different effects on the duration of extracorporeal egg development. Juveniles from eggs that were incubated at a constant 27 °C hatched around 30 days later than those incubated at 31 °C. With fluctuating incubation temperatures, the incubation time shortened linearly with the gradually increasing mean incubation temperatures. From eggs that were incubated at average temperatures of 26.6, 26.9 and 27.2 °C, the young hatched earlier than from eggs incubated at a constant 31 °C. With a difference of 2.6 °C between the lowest and highest mean temperature, the average hatching interval was around 35 days. Furthermore, the relationship between extracorporeal development time and egg size/egg weight was investigated in *T. (M.) nicolauensis*. Scaled into two size groups, relatively large eggs from single egg clutches (mean volume 1343 mm³, n = 16) incubated at an average temperature of 27.9 °C required 80.3 days and relatively small eggs from double egg clutches (average volume 1074 mm³, n = 22) incubated at an average temperature of 25.8 °C required 88.1 days to hatch. Despite the

relatively large hatching interval of about eight days, the two egg groups did not differ significantly during the incubation period ($p > 0.05$, see Appendix).

Freshly laid *T. (M.) nicolauensis* eggs were usually pure white, with a few exceptions where the egg already had a distinct pale pink shimmer. In the early phase of embryogenesis, the colour of the initially white eggs changed from initially pale to later bright pink (= formation of the blood vessel system). Subsequently, the embryonic development of pigments, starting at the eyes and followed by the epidermis, produced a graduated grey tint.

Roughly linked to the colour changes of the eggs were the physiological weight changes recorded during extracorporeal egg development, which occurred as a result of water vapor losses through the eggshell. Regardless of starting egg weight, incubation temperature and relative humidity, the weight of *T. (M.) nicolauensis* eggs decreased by 0.0428–0.2520 g (\bar{x} 0.1360 \pm 0.0597 g, $n = 15$) or $\sim 12\%$ of the starting egg weight during incubation. In larger eggs from single egg clutches (mean volume 1302 mm³, mean shell surface 579 mm², $n = 5$), the weight decreased during the incubation process by 3.8–18.9% (\bar{x} 11.8 \pm 5.4%, $n = 5$) with a mean incubation time of 104 days, and in smaller eggs from double egg clutches (mean volume 1165 mm³ and mean shell surface 538 mm², $n = 10$) by 6.5–21.5% (\bar{x} 12.6 \pm 5.1%, $n = 10$) with a mean incubation time of 101 days. The percentage weight losses of the eggs from both size groups that occurred during extracorporeal development did not differ significantly ($p > 0.05$, see Appendix).

In the course of extracorporeal egg development, a cyclical weight loss was diagnosed. The egg mass usually decreased rapidly during the first 10–30 days of incubation. The weight of the eggs decreased by 0.29–1.78 % (\bar{x} 0.92 \pm 0.35 %) during this period. In the subsequent incubation period, which extended over a period of 30–70 days depending on the incubation time, the weight loss of the eggs decreased to 0.28–1.31% (\bar{x} 0.64 \pm 0.25%). An exponential increase in weight loss rates of 0.91–8.50 % (\bar{x} 2.61 \pm 1.83 %) occurred at the last 20–50 days before the hatching of the young (Diagram 1).

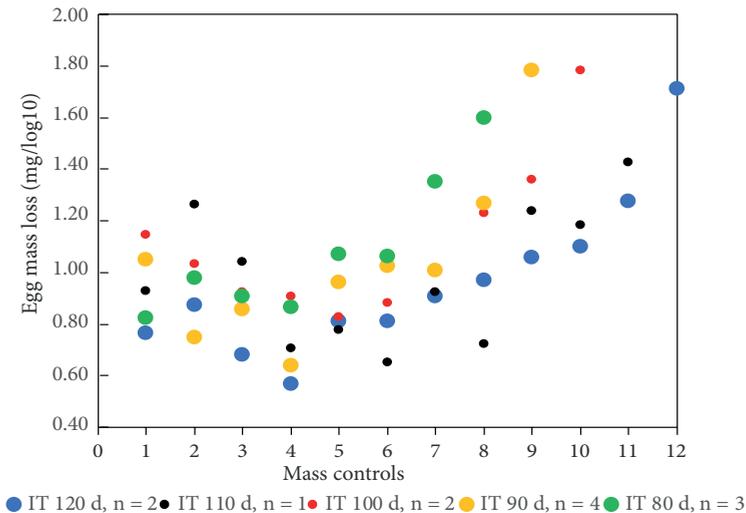


Diagram 1. Weight loss of *Tarentola nicolauensis* eggs ($n=12$) after egg laying until hatching of the young. The individual markings are based on the mean weight loss of the eggs each within a decade of the incubation period.

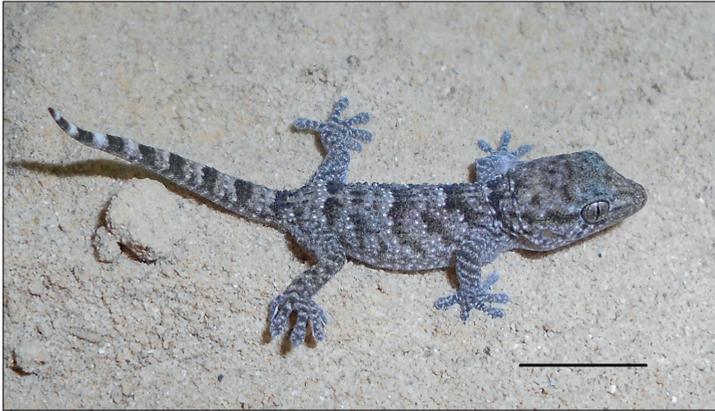


Fig. 2. Young of *Tarentola nicolauensis* on the day of hatching. Measuring bar 10 mm. © H. Rösler

It was also investigated whether the ambient humidity during incubation has an influence on the daily water loss rate of the eggs of *T. (M.) nicolauensis*. The weight of eggs hatched under moist conditions decreased by 0.80–2.43mg/d (\bar{x} 1.41 ± 0.71 mg/d, n = 4) and in dry conditions by 0.93–2.52mg/d (\bar{x} 1.47 ± 0.55mg/d, n = 8). The mean daily weight losses of eggs laid relatively dry or relatively wet did not differ statistically significantly ($p > 0.05$, see Appendix).

Newly hatched juveniles measured 24.0–37.5 millimeters in head-body length (\bar{x} 27.8 ± 1.9 mm, n = 51) and in tail length 21.0–37.0 millimeters (\bar{x} 27.6 ± 2.8 mm, n = 51). The hatching weight on the day of hatching was 0.4562–0.9962 grams (\bar{x} 0.7094 ± 0.1069 g, n = 51). The individual data on hatch sizes and hatch weights of the young animals are summarized in Table 5. The size ratio of both body measurements was relatively balanced (index SVL/TL 0.90–1.29, \bar{x} 1.01 ± 0.07, n = 51). There was no statistically significant difference in the body proportions of head-body length and tail length between the young from single clutches and double clutches ($p > 0.05$, see Appendix).

Table 5. Size and weight of the hatchlings of four *Tarentola nicolauensis* females.

Abbreviations: see text, measurements in mm, weight in grams

| Fe-male | Hatchlings of single egg clutches | | | Hatchlings of double egg clutches | | |
|---------|-------------------------------------|-------------------------------------|--|-------------------------------------|-------------------------------------|--|
| | SVL | TL | HM | SVL | TL | HM |
| 1 | 27.5–30.0 (28.41 ± 0.92, n = 11) | 24.0–32.0 (28.27 ± 2.27, n = 11) | 0.6021–0.9962 (0.7735 ± 0.1218, n = 11) | 27.0–30.0 (28.50 ± 2.12, n = 2) | 25.0–32.0 (28.50 ± 4.85, n = 2) | 0.6421–0.8358 (0.7390 ± 0.1370, n = 2) |
| 2 | 26.0–29.0 (27.43 ± 1.30, n = 7) | 24.5–30.0 (27.43 ± 2.09, n = 7) | 0.5681–0.8805 (0.6950 ± 0.11212, n = 7) | 26.0–29.0 (27.13 ± 0.88, n = 8) | 25.0–30.0 (27.69 ± 1.67, n = 8) | 0.6000–0.7535 (0.6655 ± 0.0532, n = 8) |
| 3 | 27.0–37.5 (29.45 ± 3.04, n = 10) | 27.0–37.0 (29.75 ± 2.94, n = 10) | 0.6527–0.9244 (0.7648 ± 0.0912, n = 10) | 24.0–28.0 (26.50 ± 1.32, n = 11) | 22.5–28.0 (25.73 ± 2.20, n = 11) | 0.4562–0.7634 (0.6410 ± 0.0822, n = 11) |
| 4 | – | – | – | 27.0–28.0 (27.50 ± 0.71, n = 2) | 21.0–24.0 (22.50 ± 2.12, n = 2) | 0.6268–0.6805 (0.6537 ± 0.0379, n = 2) |

The hatchlings from eggs from single-egg clutches were larger and heavier than those from eggs from double egg clutches (Fig. 2). Hatchlings from eggs of single egg clutches had a head-body length of 26.0–37.5 millimeters (\bar{x} 28.6 \pm 2.1 mm, $n = 29$), tail length of 24.0–37.0 millimeters (\bar{x} 28.7 \pm 2.6 mm, $n = 29$) and a hatching weight of 0.5681–0.9962 grams (\bar{x} 0.7537 \pm 0.1114 g, $n = 29$). In the case of hatchlings from eggs of double egg clutches, these were in the same order of traits, 24.0–29.0 millimeters (\bar{x} 26.8 \pm 1.1 mm, $n = 22$), 21.0–30.0 millimeters (\bar{x} 26.1 \pm 2.4 mm, $n = 22$) and 0.4562–0.7634 grams (\bar{x} 0.6510 \pm 0.0660 g, $n = 22$). Hatchling size and weight were correlated with the clutch size. Depending on the egg size and the egg weight, all three variables of the hatchlings differed significantly at the same level ($p < 0.01$, see Appendix).

Discussion

Tarentola is a genus of the Phyllodactylidae (Gamble et al., 2008). As part of a taxonomic revision, Joger (1984) subdivided the genus *Tarentola* subgenerically and established several subgenera (*Makariogecko*, *Neotarentola*, *Saharogecko*, *Sahelogecko*, *Tarentola*).

Tarentola nicolauensis is the basal species of a phylogenetically relatively young kinship group within the Canarian-Cape Verdean subgenus *Makariogecko* (Vasconcelos et al. 2012). It is an endemic species of the island of São Nicolau, where it inhabits the western part (*T. bocagei* lives in the eastern part of the island) (Mateo et al., 2022). *Tarentola nicolauensis* is a nocturnal, insectivorous ground-dwelling gecko in stony/rocky areas, partly with a finely structured substrate. Similar to *T. (M.) delalandii* on the Canary Islands, which has been observed on cisterns and laying stone walls (Bischoff, 1985), *T. (M.) nicolauensis* could also occur in anthropogenic environment on house walls (Wranik & Rösler, 2007).

Common reproductive traits that *Tarentola* species share with all other phyllodactylid taxa include apotypically highly calcified eggshells and post-oviparous egg weight loss (Rösler, 2020 a, 2021, 2022). A selective factor that has significantly contributed to the intrageneric modification of reproductive traits in *Tarentola* is the transmarine migration of ancestors of the species complexes *Makariogecko* and *Neotarentola*. Modified reproductive patterns are known from island-dwelling lizards, in which they differ from mainland relatives. Extensive studies have shown that the laying frequency of island species decreases within a reproductive season and that they produce smaller clutches with larger eggs and stronger hatchlings (e.g. Fitch, 1985; Novosolov & Meiri, 2013; Novosolov et al., 2013; Schwarz & Meiri, 2017).

Island geckos of the genus *Tarentola* have narrower toes than species from the mainland and are predominantly nocturnal ground dwellers. According to Meiri et al. (2020), microhabitat preferences can be strong drivers of clutch size reduction in non-geckonid lizards. *Tarentola (M.) nicolauensis* does not appear to be continuously distributed on São Nicolau (Wranik & Rösler, 2007) and Mateo et al. (2022) also refer to spatially limited high population densities in rocky areas. Similar information is given by Bischoff et al. (1979) for *Tarentola boettgeri hierrensis* (as *Tarentola*

delalandii), who also found the species in large densities only in places on the island of El Hierro (Canary Islands). Density and population boundaries could be co-determined by habitat structures insofar as they must offer sufficient adequate opportunities for species-typical egg burying. However, whether they have also contributed significantly to the reduction in clutch size in the species of the subgenus *Makariogecko* can only be clarified by further field studies.

With the exception of *T. (M.) chazaliae*, which occurs on the North African mainland (see Carranza et al., 2002), all other species of the subgenus *Makariogecko* are distributed on many islands of Macaronesia. As islanders, many species of this lineage reduced clutch size by increasing the number of clutches containing only a single egg, thereby significantly reducing reproductive effort. The strategy results in more vigorous offspring, which are better able to assert themselves in the competition for food resources and in intra-species conflicts (Henle, 1990). In addition to *T. (M.) nicolauensis*, *T. (M.) darwini* and *T. (M.) rudis* of the Cape Verdean species as well as most of the species of the same subgenus distributed in the Canary Islands follow this strategy (Nettmann & Rykena, 1985; Hielen, 1993).

The reproductive effort required by geckos for clutch production is correlated with body size, body weight and clutch size (Rösler, 2020 b and references cited therein). As a central component of lifelong reproductive performance, the reproductive effort of *Tarentola* species varies considerably for various reasons. Females of most species of the subgenus *Makariogecko* often produce less expensive single-egg clutches, but this is not a strategy influenced by the age or size of the island and only to a limited extent by body size or weight (Novosolov & Meiri, 2013). The relatively small species *T. substituta* (SVL up to 57 mm, São Vicente, 227 km²) and *T. delalandii* (SVL up to 64 mm, Tenerife, 2034 km²) produce a relatively large number of double egg clutches and thus have a much greater reproductive effort than the huge *T. gigas brancoensis* (SVL up to 110 mm, Ilhéu Branco, 3 km²) (Rösler & Wranik, in press). According to Hielen (1993), the island forms of *Tarentola* generally have a higher reproductive effort per clutch compared to the mainland forms, but considering an overall lower clutch production during a reproductive season, their total reproductive effort is lower.

Several factors have a direct or indirect effect on the extracorporeal development time of gecko eggs (Rösler, 2005). The subterranean temperature gradient of natural egg-laying sites of *Makariogecko* species is unknown, but it is to be expected that the upper soil layers heat up or cool down to varying degrees during the course of the day, both depending on the season and the locality. For the artificial incubation of the eggs, rhythmically fluctuating temperatures during the day correspond more reliably to the local conditions than constant incubation temperatures. Eggs of *T. (M.) nicolauensis* often required a longer development time when incubated at relatively high, constant temperatures and, conversely, sometimes a shorter development time at fluctuating temperatures with lower daily averages. Similar results were obtained by Hielen (1991), who incubated eggs of *T. (T.) angustimentalis* and *T. (T.) mauritanica* at both constant and fluctuating temperatures. She assumes that embryonic development accelerates with fluctuating temperatures and earlier hatching occurs if the regular temperature fluctuations each day include sufficiently long periods of sufficiently high temperatures.

In addition, Hielen (1993) found that the heavy eggs of species of the subgenus *Makariogecko* require a longer period of extracorporeal development than the light eggs of species of the subgenus *Tarentola*. Intraspecifically, this effect was not found in *T. (M.) nicolauensis* during the present study. In addition to the varying real exposure times to daily mean temperatures, advanced embryonic developmental stages during egg-laying (see above) could also have been partly responsible for the earlier hatching from heavy eggs in *T. (M.) nicolauensis*.

Concluding remarks

The reproductive pattern of *T. (M.) nicolauensis* corresponds to the life-course characteristics of the classical rules of the “islet syndrome”. It is generally agreed that many other species of the subgenus *Makariogecko* produce competitive young at the expense of small clutch sizes, heavy eggs and a reduced laying frequency. In relation to the number of offspring and the entire reproductive lifespan, the survival rate is high enough to establish and maintain stable populations. Most species of *Tarentola* from continental subgenera have a more basic reproductive strategy. They compensate a higher mortality rate of relatively smaller and lighter juveniles by producing proportionately more double egg clutches, smaller egg sizes and an increased number of clutches. More recent dispersals from the African mainland to Macaronesia still pursue this reproductive strategy (e. g. *T. (T.) angustimentalis*).

There are many studies on phylogeny and taxonomy of diverse gecko species, but relatively few on their ecology and reproductive strategies. However, such studies are crucial to understand species needs in the wild and in captivity also in view of the one plan approach. We hope that our data on the reproduction of *T. (M.) nicolauensis* will stimulate further research on the impressive geckos of the genus *Tarentola* from the Cape Verde Islands. One focus of this research could be to use field studies to find out whether reproduction under natural environmental conditions yields results similar to those obtained under laboratory conditions.

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Appendix

Statistical results on selected reproductive traits of *Tarentola nicolauensis*.

A Mann-Whitney U test was used for the two-sided comparisons.

Significant differences $p < 0.05$ are highlighted. For abbreviations and further information see text.

| Feature | U | z | p |
|--|-------|--------|-----------------|
| RCM | 6.5 | 4.3336 | 1.47E-05 |
| EL | 95.5 | 4.6418 | 3.45E-06 |
| EW | 149.5 | 3.7071 | 2.10E-04 |
| EM | 105 | 3.2974 | 0.0010 |
| Incubation period depends on egg size | 114.5 | 1.8054 | 0.0710 |
| Weight loss of eggs depending on egg size | 21 | 0.4287 | 0.6682 |
| Weight loss of eggs depending on relative humidity | 14 | 0.2548 | 0.7989 |
| SVL | 120.5 | 3.7989 | 1.45E-04 |
| TL | 141 | 3.3927 | 0.0007 |
| HM | 147 | 3.2617 | 0.0011 |
| SVL/TL | 245.5 | 1.4037 | 0.1604 |