



Reproductive parameters of the red-tailed parrot (*Amazona brasiliensis*) under ex situ conditions

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Received: 28 December 2021 / Revised: 26 December 2022 / Accepted: 2 January 2023 / Published online: 18 January 2023
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Abstract

The red-tailed parrot (*Amazona brasiliensis*) is a near-threatened endemic parrot species confined to the coastal area of southeastern Brazil. The species represents a successful chapter in global psittacine conservation. Due to the intensive conservation efforts of the past decades, including systematic field work, in situ nest monitoring, and education programs, the species population has shown a gradual increase from an all-time population low. The breeding biology of the species in the wild is reasonably well-known; however, some reproductive parameters of the species remain inadequately known to this date. Here, we provide a comprehensive account of the species reproductive parameters at the Association for the Conservation of Threatened Parrots e.V. (ACTP) facility in Germany, comparing our results with published and unpublished data for the closely related blue-cheeked (*A. dufresniana*) and red-browed parrot (*A. rhodocorytha*) in captivity. During the period of study for this species, we recorded a mean clutch size of 2.82 ± 0.75 eggs (2–4; $n = 11$) and a mean incubation period of 25.69 ± 0.72 days ($n = 6$). The average egg size and egg mass were $39.32 \pm 1.93 \times 30.07 \pm 1.12$ mm ($n = 40$) and 19.59 ± 2.11 g ($n = 50$), respectively. We observed chicks perform their first flights at an age of 55–57 days. After a total nestling period of 87–96 days, the chicks were fully independent. Chick growth patterns followed the typical logistical growth patterns reported for other congeneric species in the wild or in captivity.

Keywords Brazil · Breeding biology · Captivity · Post-natal development

Introduction

The red-tailed parrot (*Amazona brasiliensis*) forms a monotypic member of the genera *Amazona*, which is geographically confined to the coastal and mangrove forest of southeastern Brazil (Collar et al. 2020). Initial field work in the late 1980s unveiled the critical situation of this wild population, leading to the subsequent long-term conservation measurement efforts, which contributed progressively towards the sustainable increase of the historical overall low population (Collar et al. 1992). It comprised of less than 2000 individuals in 1991/1992 to a current estimated population size of 9000–10,000 individuals (Collar et al. 1992; Schunck et al. 2011; Waugh 2016; SPVS 2018; BirdLife

International 2022). Due to the positive development of population trends in the wild, the global status of the species was recently down listed from “Vulnerable” to “Near-threatened” (BirdLife International 2022).

Along a continuum of gradual loss and degradation of habitat, the outsized impact of wildlife trade posed a major threat for the wild populations of the red-tailed parrot (Collar et al. 1992; BirdLife International 2022). Martuscelli (1995), investigating the nesting success of the species in a field study, showed that 41 out of 49 actively monitored nest sites were poached during the study period, while only six failed due to natural predation. In other studies, assessing the species’ reproductive success resulted in an equally high nesting failure rate, primarily linked to nest robbing and poaching activity (Scherer Neto 1989; Collar et al. 1992; Martuscelli 1997; Low 2005; BirdLife International 2022). A long-term nest monitoring program along the implementation of artificial nest boxes helped to achieve a significant boost in the reproductive success of the species, reducing, simultaneously, predation pressure and counteracting the excessive numbers of chicks taken by poachers, which in a vast majority of cases

Communicated by: Lilian Manica (Associated Editor)

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lead to a gradual recovery of the wild populations (Sipinski et al. 2014; Waugh 2016; SPVS 2018).

An integral part of the international conservation action plan was the inclusion of an initial proposal for an ex situ breeding program, ensuring that in the case of a recurrent population trend, reintroduction of captive bred individuals to the remnant individuals in the wild would be possible (Lalime 1997; Lücker 2000; Low 2005). However, the breeding program faced several setbacks that decelerated the desired progress in the successful captive breeding of the species (Sweeney 1998; Waugh and Romero 2000). Despite small numbers of viable pairs producing clutches, low fertility proved to be a decisive conraindicator (Waugh and Romero 2000). A notable improvement in the breeding program was accomplished after using a novel alternative to force-mating and re-pairing mated individuals in a flocking setup under free-mate choice conditions (see Engebretson 2006; Luescher 2008), whereby respective birds were able to choose their preferred mates (Waugh and Romero 2000). Resulting pairs from such flocking aviaries have showed a significantly higher fertility rate and breeding readiness (Waugh and Romero 2000).

Currently, the red-tailed parrot is considered among the best studied Neotropical psittacines, with detailed information of their life history traits and demography being presented in several notable publications (Bertagnolio 1983; Scherer Neto 1989; Collar et al. 1992; Martuscelli 1995; Lalime 1997; Sipinski 2003; Cougill and Marsden 2004; Galetti et al. 2006; Popp et al. 2008; Schunck et al. 2011; Serafini et al. 2011; Abbud 2013; Sipinski et al. 2014). Some aspects of the breeding biology, however, remain undocumented or poorly known.

In this paper, we provide additional details about the reproductive biology of this species in captivity, expanding data on the egg characteristics, incubation patterns, and post-natal development. In addition, we collected published and unpublished data about the blue-cheeked (*A. dufresniana*) and red-browed parrot (*A. rhodocorytha*), which are considered to form a superspecies with the red-tailed parrot (Collar et al. 2020), for a comparative note of the breeding parameters of the three species under captive conditions, with the main objective to improve our general knowledge regarding the general biology of the red-tailed parrot and other congeneric species.

Material and methods

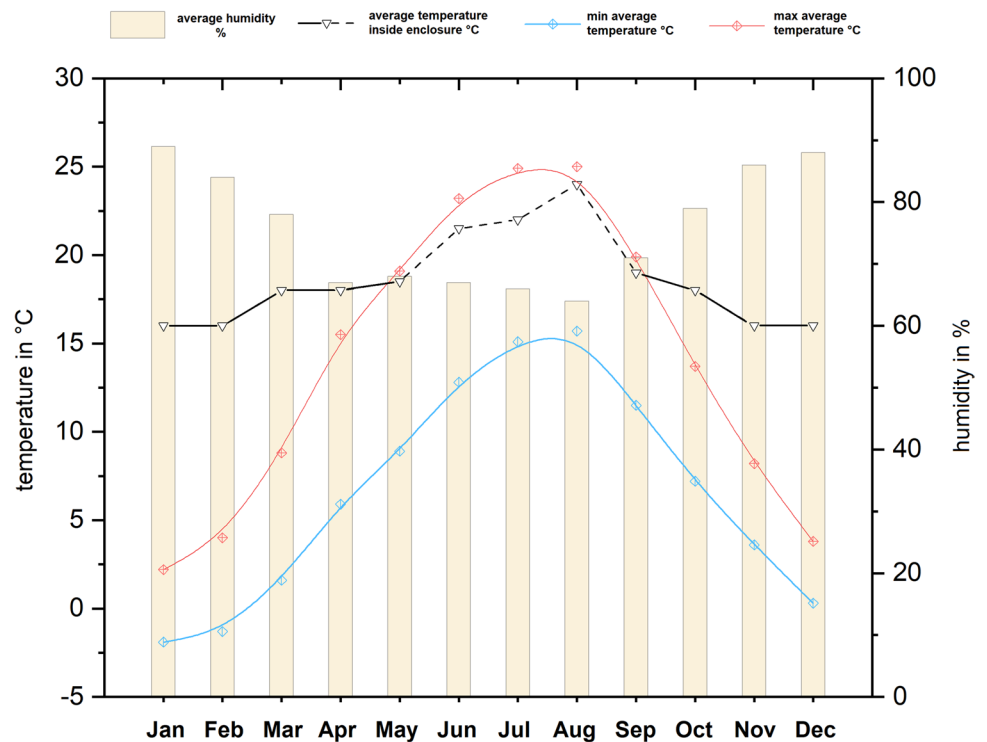
Husbandry

The data collection was conducted entirely at the facility of ACTP (Association for the Conservation of Threatened Parrots e.V. - <https://www.act-parrots.org>) in Tasdorf, Brandenburg (Germany). The Convention on International trade in Endangered Species (CITES) documents to keep the animals

were issued by the Bundesamt für Naturschutz (BfN, German Federal Agency for Nature Conservation for imported individuals) or need to be reported to the Landesamt für Umwelt (for individuals obtained within Germany), as required for most exotic parrots and is strictly controlled by the German authorities. The respective individuals were kept in two breeding complexes consisting of 12 or 13 breeding aviaries, respectively — with single species being housed under consideration of an inter-pair spatial gap ranging from three to five aviaries, to minimize the likelihood of redirected mate aggression. Each of the breeding aviaries is composed of a heated indoor enclosure (2×3.5×2.8 m) and fully planted outside enclosure (14×2×3 m, LBH). At ACTP Germany, two different types of dietary plans are used, of which one is implemented during the breeding season and the second for maintenance during the non-breeding period. As the vast majority of extant amazon species, the red-tailed parrot is prone to excessive weight gain under captive conditions, which will inevitably result in a poor reproductive performance and health issues on a long-term basis if not contemporarily counteracted. It is therefore crucial in the non-breeding season, to carry out all necessary precautions and steps to counteract progressive obesity.

Due to the changing environmental conditions in Central Europe (Fig. 1), the readiness of the birds to spend time in the outside enclosure drastically decreases in the autumn/winter months, thus leading to a successive reduction in the overall metabolic activity and would therefore encourage rapid weight gain if not counteracted in form of an adaption of the dietary plans. To evaluate the metabolic changes, the body weight and blood parameters are documented for each bird by the on-site veterinarian, in order to adjust the given quantities of food for each individual. During the non-breeding season, each individual is provided with two main feedings (morning 8:00 am and evening 4:00 pm) as well as one supportive feeding consisting of hypocaloric food items (e.g., salads, endives, cauliflower, broccoli). For the morning, a special mix of sprouted seeds and vegetables is used. The exact quantity is calculated for each single individual, considering the weight dynamics, activity level, and medical history. In the evening, a special seed mix is given and vice versa to the morning diet; the quantities are estimated and adjusted accordingly to the data available about the single individuals. Dietary changes are combined with the weekly provision of vibrant enrichment elements to encourage environmental interactions. Water is provided ad libitum. Two weeks prior to the onset of the breeding season (1.03), the food is successively increased over the course of two weeks, with all individuals starting to receive three main feedings (8:00 am, 11:30 am, and 5:00 pm) by the beginning of March. Despite a notable increase in quantities, several food items (e.g., boiled egg, cooked bean mixture, seasonal, and regional fruits) and supplements are added to the diet to stimulate prompt breeding.

Fig. 1 The average annual, minimum, maximum temperature, average annual humidity (all data: Deutscher Wetterdienst), and temperature maintained inside the indoor enclosure at Rüdersdorf, Brandenburg (--dotted line shows the average temperature maintained inside the enclosure, as the inside enclosures are not heated during the summer months)



The indoor enclosures are not heated during the late spring and summer season. Between March and October, the breeding pairs are able to use the outside enclosures without restrictions, while during the winter months, birds are closed during night or days with average temperatures below 0 °C, thunderstorms, or any other weather events posing a potential risk. A consistent temperature (Fig. 1) is maintained in the inside enclosures. The kept red-tailed parrots at ACTP tend to spend only short periods in the outside enclosures (less than one hour) during temperatures colder than 4 °C, with increasing outdoor activity with temperatures above 10 °C degrees.

Data collection and analysis

Behavioral observations were performed primarily using a non-invasive approach by analyzing short video sequences recorded by the indoor or intra-cavity cameras implemented in each nest box and were stored externally in a server, allowing the recording of the behavior patterns over several consecutive days (c. 14 days without overwriting). The behavior patterns were extracted using the backup function, converted from AVI to MP4 format and analyzed with Avidemux (version 2.7.1) for a more accurate time frame resolution. Durations of each behavior element were estimated to ± 0.01 s accuracy. Behavioral parameters were observed daily, during the active daytime period (light hours, approximately between 6:00 am and 20:00 pm). Incubation parameters were analyzed for the full day length (between

00:00 and 24:00). Data collection for this study was performed during two consecutive breeding seasons in 2016 to 2017, including in total the breeding activities of four pairs.

Data concerning incubation and post-natal growth were documented in accordance with the established protocols used at ACTP. Whenever possible, the egg mass was recorded shortly after the egg was laid (egg-laying was confirmed by observation through the intra-cavity cameras). Egg weights were taken using a KERN type PCD 100–3 precision scale (± 0.001 g SE error). Linear measurements were obtained with a digital caliper (GOSCIEN; $SE \pm 0.02$ mm). For the egg data set, the unpublished measurements of 28 eggs from the collection of Ralf and Rosina Neumeyer (pers. comm.; <https://www.papageien-neumeyer.com>) were included. In eggs, where the initial mass was not known ($n=6$, for example if the nest couldn't be accessed during the first days of the post-laying period), the egg mass was estimated using the Hoyt (1979) equation (where L is length, B is breadth or width, weight coefficient $K_w=0.548$; derived from fresh egg mass):

$$W = K_w * (L * B^2) \quad (1)$$

The egg weight loss was documented during artificial incubation on several occasions (during the early incubation stage at 2-day intervals, close to the pipping on a daily basis). After an incubation period of 16–18 days, the heart frequency and the vital parameters of the egg were visually or topically evaluated (e.g., development, air space, veins, approximate position of the chick), to ensure a contemporary

intervention or hatching assist if pre-natal complications were evident.

The hatchlings' weight was noted immediately after the chick emerged out of the shell, and the weight of post-natal growth was recorded for all hand-reared chicks before and after each feeding during the early post-natal period. This was successively reduced, and after a post-natal period of 45 days, weight was only recorded once per day. For the growth analysis, only the physiological weight prior to the first morning feed (8:00 am) with a completely empty crop was considered.

The growth parameters k and A , where k is the growth constant, A is the amplitude, and t is the time, were estimated using the logistical growth model after Ricklefs (1967):

$$y = \frac{A}{1 + e^{-k(t-b)}} \quad (2)$$

All statistical tests were performed in R (version 3.3.3, R Core Team, R Foundation for Statistical Computing, Vienna, Austria). For the visualization and fitting, we used OriginPro 2021b (64-bit) SR1 9.8.5.204 (Learning Edition, OriginLab Corporation, Northampton, USA). A two-tailed t test was used to compare the breeding parameters between the red-tailed, blue-cheeked, and red-browed parrot ($\alpha=0.05$).

Results

Sexual behavior

Breeding readiness is indicated by notable changes in the territorial presence and occurrence of socio-positive interactions (e.g., copulations, mutual feedings and prolonged allopreening duties) following by an evident increase in the nest attendance of the female. Following an intensification of socio-positive interactions and mutual feedings, a pre-copulatory display was observed in all four pairs (Fig. 2a). The initiator (in majority the male) pretends a copulation intention by flicking the wings in quick succession accompanied by a series of copulation calls. Wing flicks describe a rapid, usually repetitive pattern of singleton flicks of one wing, following by the second in quick continuation. The duration is short, in average lasting 0.34 ± 0.13 s (0.12 – 0.56 ; $n=14$). The female responds after a subtle delay vice versa by performing wing flicks (Fig. 2b) and lowering the upper body in horizontal position, indicating the copulation readiness. The wing-flicking persists during the copulation process and can occasionally occur post-copulation. Wing flicks were observed in 94 of 108 copulation initiations.

The male, often after several attempts, places one leg on the back of the female, without grabbing it (Fig. 2c). This is followed by the establishment of a cloacal contact;

where the male maintains the cloacal contact by lateral, pulsing movements of the lower body (tail, Fig. 2d), while holding balance with the other leg on the perch. Simultaneously, the male contracts the toes of the leg, which is placed on the back of the female, in an alternating pattern, with intervals between a single contraction averaged 4.14 ± 2.04 s (1.17 – 11.06 s; $n=39$) (Fig. 2d). The copulation termination is indicated by a sudden discontinuation of the pulsing bilateral movement of the tail and absence of copulation calls. The female usually remains stagnant in the horizontal position for a few seconds, leaving the copulation site and perching c. 5–10 cm in close proximity to the male.

Copulations were only observed during the active daytime period, with a substantial number of copulations occurred between 5:47 and 8:33 am (UTC + 1) (Fig. 3). Copulations lasted in average 87.52 ± 15.43 s (61.15 – 123.12 s; $n=100$). A copulation duration below 60 s was followed by a repeated copulation attempt, indicating that the preceding attempt was either incomplete or unsuccessful. Between 1 and 5, copulations were observed during the daytime period, with an evident peak approximately 3–4 days before the first egg was laid. The first egg was laid 31–36 days ($n=4$) after the first copulation was observed.

Diurnal roosting inside the nest habitually started 2 to 3 days prior to egg-laying. Close to oviposition (1–2 days before the first egg was laid), the female started to spend the night inside the nest. The nest attendance showed a steady increase, 6–8 days prior to egg-laying, while remaining inconclusive weeks before without notable trends.

Breeding parameters

Seasonality The breeding season at ACTP lasted during our study period from 8 April to 23 May (period between the first laid egg and the last fledged chick); with first copulations were documented in two pairs on the 14 March and 28 March and in the following season on 13 and 29 April, respectively.

Egg-laying The actual oviposition was indicated by a slow bilateral movement of the head in horizontal direction accompanied by vertical movement of the tail up and down, with the plumage remaining visibly ruffled. Immediately after the egg is successfully laid, the female rapidly sleeks the plumage, following by turning, after a short interruption of several seconds, to clean the egg surface with slow movement of the tongue. Based on the video frame recordings, the procedure of egg-laying takes between 10 and 15 min, if no subclinical complications are present (e.g., egg binding, egg shape malformation).

Clutch size and egg-laying interval A full clutch size held in average 2.82 ± 0.75 (2–4; $n=11$) eggs, with a modal clutch size of three. The mean laying interval was 3.13 ± 0.35 days

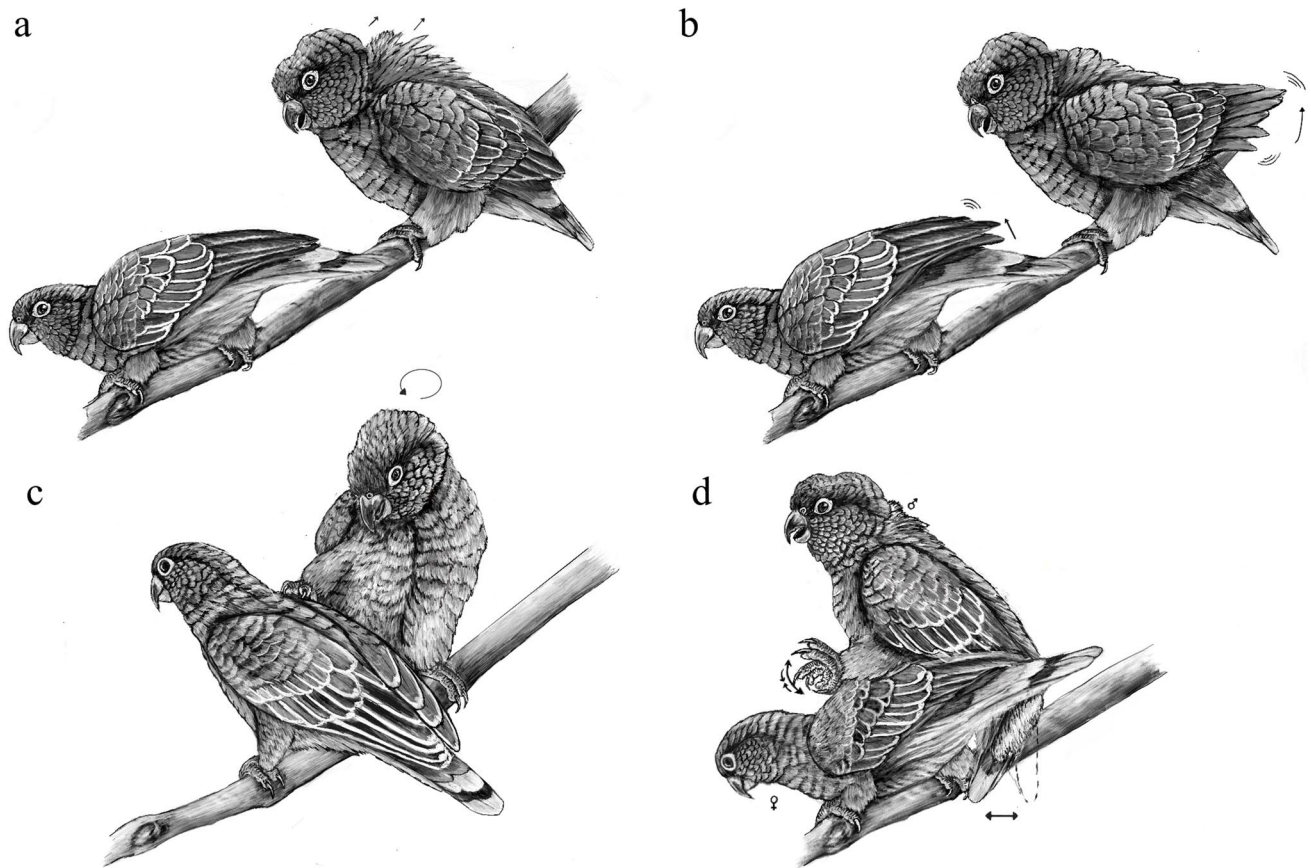


Fig. 2 **a** Copulation initiation, **b** wing-flicking, **c–d** copulation initiation with illustration of the alternating toe contraction and bilateral, pulsing tail movement in red-tailed parrot (*Amazona brasiliensis*). Illustrations by Vladislav Marcuk

(3–4; $n = 8$). In two clutches, the egg-laying intervals were determined accurately based on the exact time recorded when oviposition occurred: the average egg-laying interval here was 73.57 ± 3.54 h (70.20 – 77.26 ; $n = 4$).

If a full clutch was removed contemporary, for example if the eggs proved to be infertile, there was an increased likelihood that the pair will produce a replacement clutch. After the removal of the first clutch, the first egg of the second clutch was laid after a total period of 28 and 35 days ($n = 2$), respectively. A third clutch was never documented in any of the red-tailed parrot pairs.

Egg characteristics Eggs of red-tailed parrots are unremarkable white (Fig. 4a), round-ovate to elongated-ovate shaped. The linear measurements are given in the Table 1.

Incubation Incubation commenced shortly after the first egg was laid and was performed exclusively by the female. During the incubation period, the female demonstrated an overall high nest attendance rate of average $97.74 \pm 1.30\%$ (94.30 – 99.35 ; $n = 25$) (Fig. 5) of the daytime period. The

female left the nest during the incubation period usually only for a short period of several minutes (e.g., auto-preening, territorial defense or in rare occasions for water/food intake).

The nest attendance of the male fluctuated during the incubation period and attributed in total $1.09 \pm 0.93\%$ (0.47 – 5.07 ; $n = 25$) (Fig. 5) to the daytime period. During the incubation period, the male fed the female on average 6.46 ± 1.44 times (3 – 9 ; $n = 26$) during the active daytime period, ensuring sufficient food for the female during the entire incubation period. During the nocturnal period, mutual feedings were not observed, and the male roosted close to the nest, remaining usually on the preferred roosting site used by the respective pair during the non-breeding season.

Egg weight loss and hatching The egg weight loss was recorded for six eggs incubated by the female until the external pipping, resulting totally in a mean egg weight loss of $14.33 \pm 0.11\%$ (13.03 – 15.88 ; $n = 6$) over the incubation period. The hatching success was high overall, in total eight of nine chicks hatched autonomous and required no

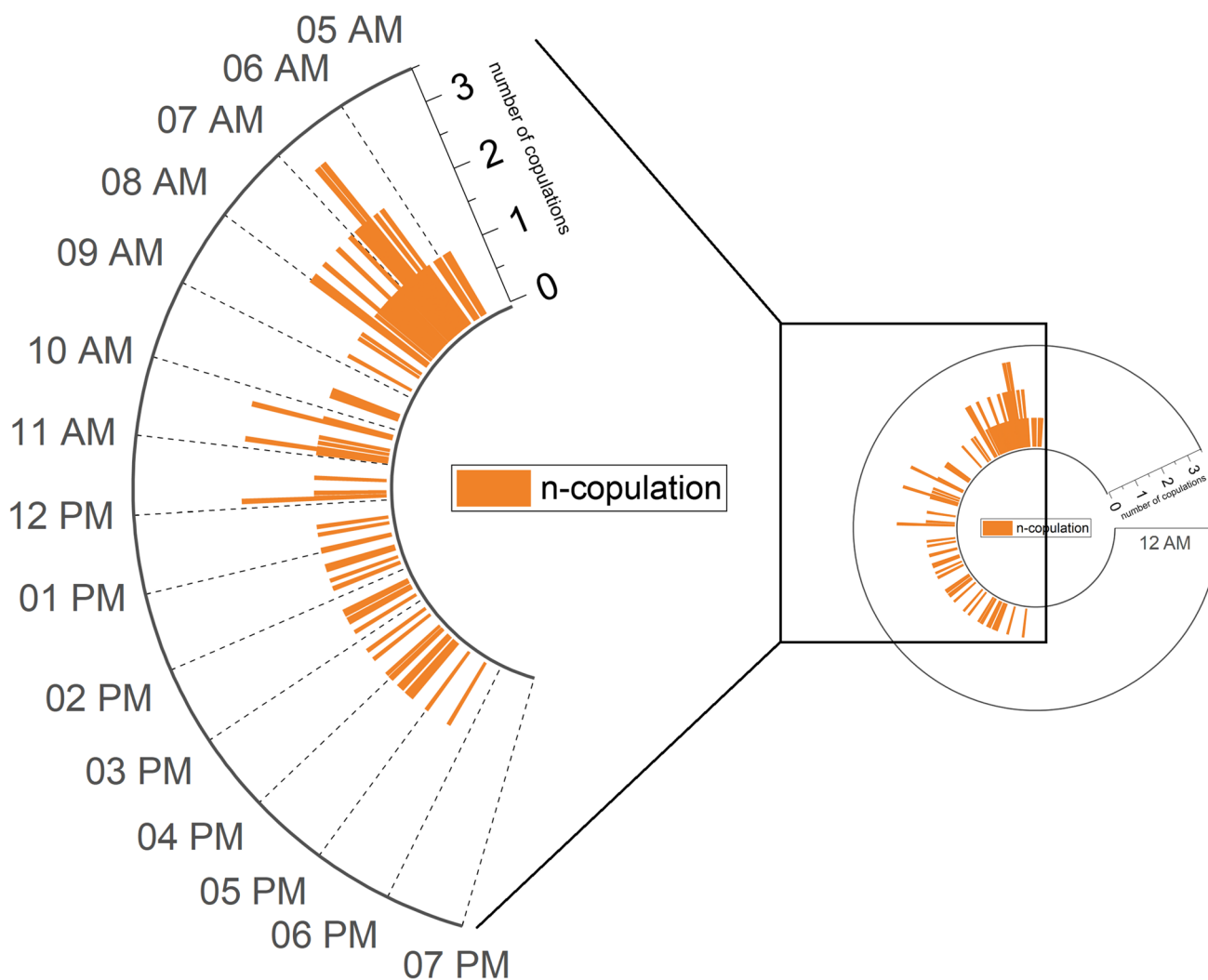


Fig. 3 Occurrence of copulation events from three different pairs of red-tailed parrots (*Amazona brasiliensis*) during the diurnal activity period (UTC+1)

intervention or hatching assistance. One chick died pre-natal within the first 15 day of incubation period.

Red-tailed parrot chicks hatched at ACTP after an incubation period of 25–26 days (artificial and natural incubation, $n=8$). The first external pip was recorded in average 49.08 ± 11.39 h (41.31–66.03; $n=4$) prior hatching. In two clutches, where exact time of the oviposition and hatching were documented, the chicks hatched after a mean incubation period of 25.69 ± 0.72 days (natural incubation, 24.41–26.28; $n=6$). The mean hatching mass was 12.58 ± 0.46 g (12.03–13.0; $n=8$). The average inter-sibling hatching interval was 62.66 ± 30.22 h (30.26–90.08; $n=4$).

Post-natal growth The post-natal weight gain followed the typical patterns of a logistical growth curve (after Ricklefs (1967)) with a growth constant of $k=0.143$ ($n=7$) (Fig. 6).

During the first 5 to 6 weeks of the post-natal development, the weight gain pursues an exponential growth trend, followed by a plateau period, which is characterized by an alternating weight increase and decrease until sufficient food intake is maintained, indicated in the graph by a stabilization of the weight. The peak weight of four chicks (three males and one female) was in average 416.73 ± 11.43 g (401–427; $n=4$) and was recorded at an age of 44–47 days. In contrast, the body mass documented for adult males in captivity averaged 426.15 ± 41.11 g (364–523; $n=13$) and for adult females 400.03 ± 46.74 g (313–495; $n=13$), respectively.

Freshly hatched red-tailed parrot chicks resemble — in various morphological characteristics — other *Amazona* spp. neonates, with their cream pink colored toes and tarsus. Dorsally, the chick is covered with c. 3 mm dense down.

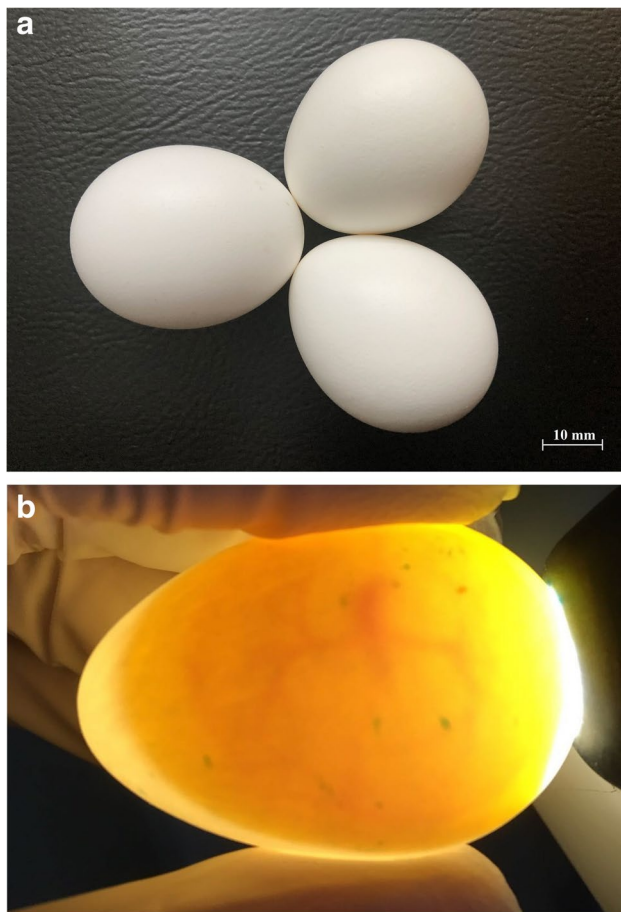


Fig. 4 **a** Clutch of a red-tailed parrot (*Amazona brasiliensis*). Photo by Vladislav Marcuk. **b** Fertilized red-tailed parrot egg with visible pre-natal embryonic development. Photo by Katrin Scholtyssek

Table 1 Overview of egg characteristics of the red-tailed parrot (*Amazona brasiliensis*) in captivity

Egg variables	\bar{x}	SD	Range	<i>n</i>
Mass (g)	19.59 ¹	2.11	16.66–24.16	50 *
Length (mm)	39.32	1.93	36.78–43.49	40
Width (mm)	30.07	1.12	27.61–32.41	40
Shell thickness (mm)	0.264	0.021	0.22–0.30	30

* *n* = 28 (R. & R. Neumeyer pers. comm.), remaining data from ACTP 1, estimation of egg mass after Hoyt (1979) for *n* = 6 eggs, as fresh egg mass was unknown

The beak is narrow and orange in color, with a prominent white egg tooth present on the culmen tip. After 8–9 days, an imperceptible trace of the pin feathers is detectable under the skin. The eyes are fully opened by a post-natal age of c. 21–22 days. With 22 days, the first pin feathers starting to erupt and getting denser around the wings. The follicles of the secondaries start to open after 25–26 days. At 33 days,

pin feathers start emerging around various body regions, including the head, underparts, crop, neck, and scapular region. When the chick is 38–40 days old, the majority of the pin feather growth is accomplished, despite some missing pin feathers around the neck. By an age of 55 days, the growth of the primaries and secondaries is accomplished, usually with the chicks starting at this age to practice their first flights. Stages of the post-natal growth are given in Fig. 7.

Comparative analysis of the breeding parameters between the red-tailed parrot and the closely related blue-cheeked and red-browed parrots

Published and unpublished data of the breeding parameters indicates that clutch size does not significantly differ between the three species (*A. dufresniana/brasiliensis*, $t = 0.43$, $P = 0.660$; *A. rhodocorytha/brasiliensis*, $t = 1.39$, $P = 0.173$) under captive conditions, while both congeneric species show significantly higher egg mass (*A. dufresniana/brasiliensis*: $t = 5.91$, $P < 0.00001$; *A. rhodocorytha/brasiliensis*, $t = 8.81$, $P < 0.00001$) and hatchling weight (*A. dufresniana/brasiliensis*, $t = 12.94$, $P < 0.00001$; *A. rhodocorytha/brasiliensis*, $t = 8.18$, $P < 0.00001$) in comparison to the red-tailed parrot. In Table 2, comparative details about the reproductive parameters are given, including results from this study and published/unpublished information about the closely related blue-cheeked and red-browed parrots in captivity.

Discussion

Despite adding novel information and details to the repository of information regarding the sexual behavior and breeding parameters of the red-tailed parrot, our study highlights the importance of conducting systematic data collection about the general biology of avian species under captive conditions. Due to the limited accessibility of wild nest cavities and logistical efforts to follow active pairs to investigate breeding behavior patterns over a consistent period, we especially encourage zoological collections to promote non-invasive scientific data collection about the breeding biology of extant psittacine breeding stocks that could contribute to the improvement of ex situ husbandry manuals and even support ongoing or proposed in situ efforts.

The wing-flicking was reported in a pre-copulative context in *Amazona ochrocephala*, *A. albifrons* and *A. vittata* (Arman and Arman 1980; Skeate 1984; Snyder et al. 1987). For *A. agilis*, the wing-flicking was not documented (Cruz and Gruber 1981). Our observations of this behavior element indicate that it plays a relevant role in the initiation

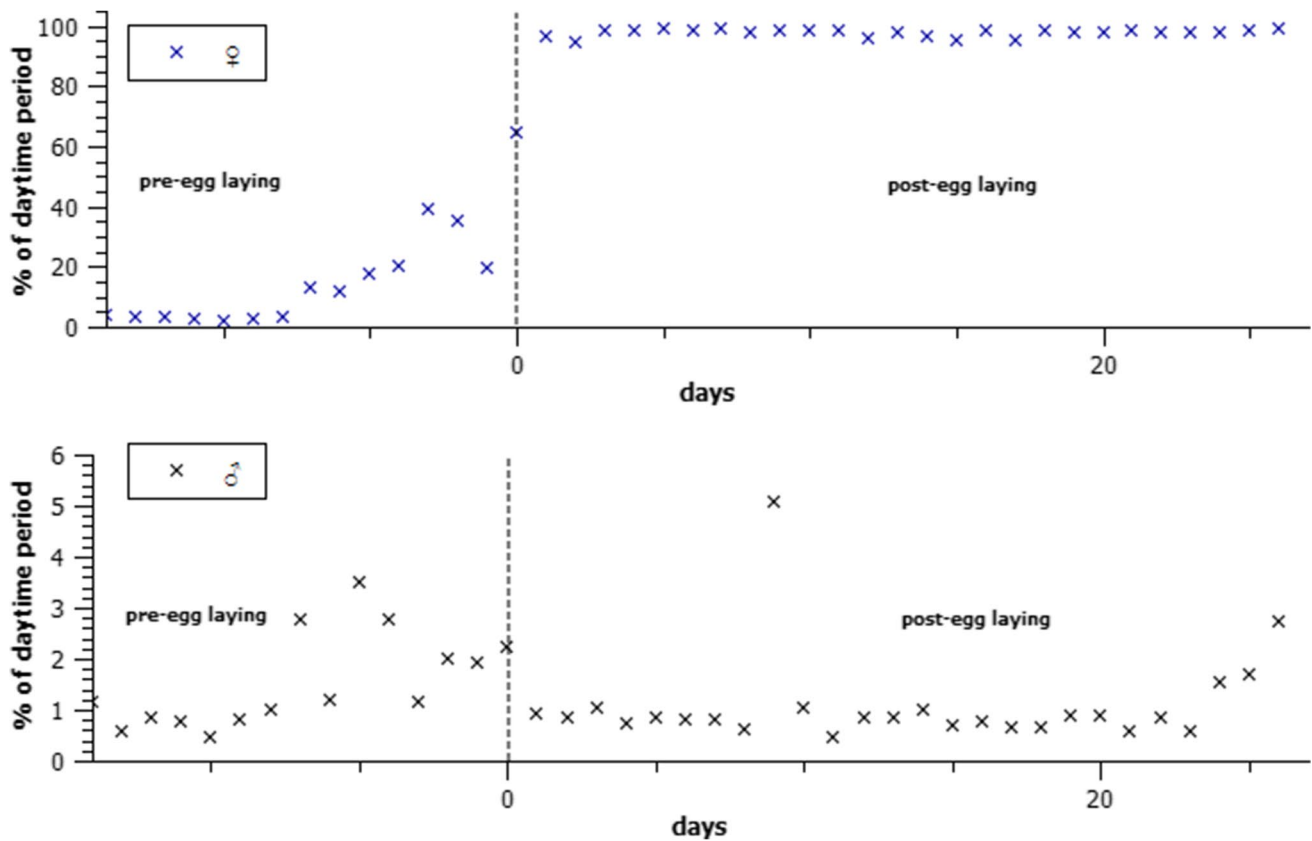


Fig. 5 Nest attendance during the pre-egg-laying (indicated by the dotted line) and incubation period for the female and male of a single pair of red-tailed parrots (*Amazona brasiliensis*)

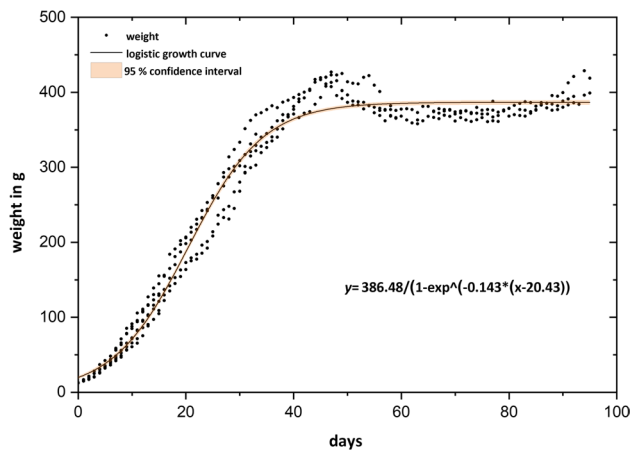


Fig. 6 Logistic weight gain curve for $n=7$ hand-reared red-tailed parrot chicks (*Amazona brasiliensis*) with 95% confidence intervals

of a copulation (pre-copulatory behavior). Wing flicks and copulation calls were observed inter alia in the pre-copulatory/peri-copulatory context in various other amazon species: *Amazona auropalliata*, *A. oratrix*, *A. autumnalis*, *A. aestiva*, *A. farinosa*, *A. guatemalae*, *A. vinacea*, *A. finschi*,

A. dufresniana, *A. amazonica*, *A. guildingii*, *A. versicolor*, and *A. arausiaca* (Marcuk pers. obs.).

The copulation duration of the red-tailed parrot differed slightly from copulation durations reported for other congeneric species. In the literature, the following durations are reported for different species; for the black-billed parrot (*A. agilis*), the duration of two copulations lasted 65 and 72 s, respectively (Koenig 2001). Four copulations documented in the Bahama (Abaco) parrot (*A. leucocephala bahamensis*) lasted between 30–120 s (Snyder et al. 1982). For the Puerto-Rican parrot (*A. vittata*), the copulation duration is well documented and averaged 70.7 s ($n=47$) in duration (Snyder et al. 1987). Contrary to these copulation durations, comparably long durations were documented in white-fronted parrots (*A. albifrons*) with an average duration of 3.4 min (Skeate 1984). While similar copulation durations over 3 min were not observed in the red-tailed parrot during our study period, copulations of > 2 min duration were observed occasionally in the red-tailed parrots (this study) and in the St. Vincent parrot (*A. guildingii*), where the mean duration of a copulation was 88.88 s (54.36–131.44 s; $n=202$) (Marcuk et al. 2020). For the closely related red-browed parrot, only an uncertain duration of approximately 60 s (1 min) is provided in the literature (Robiller 1990).

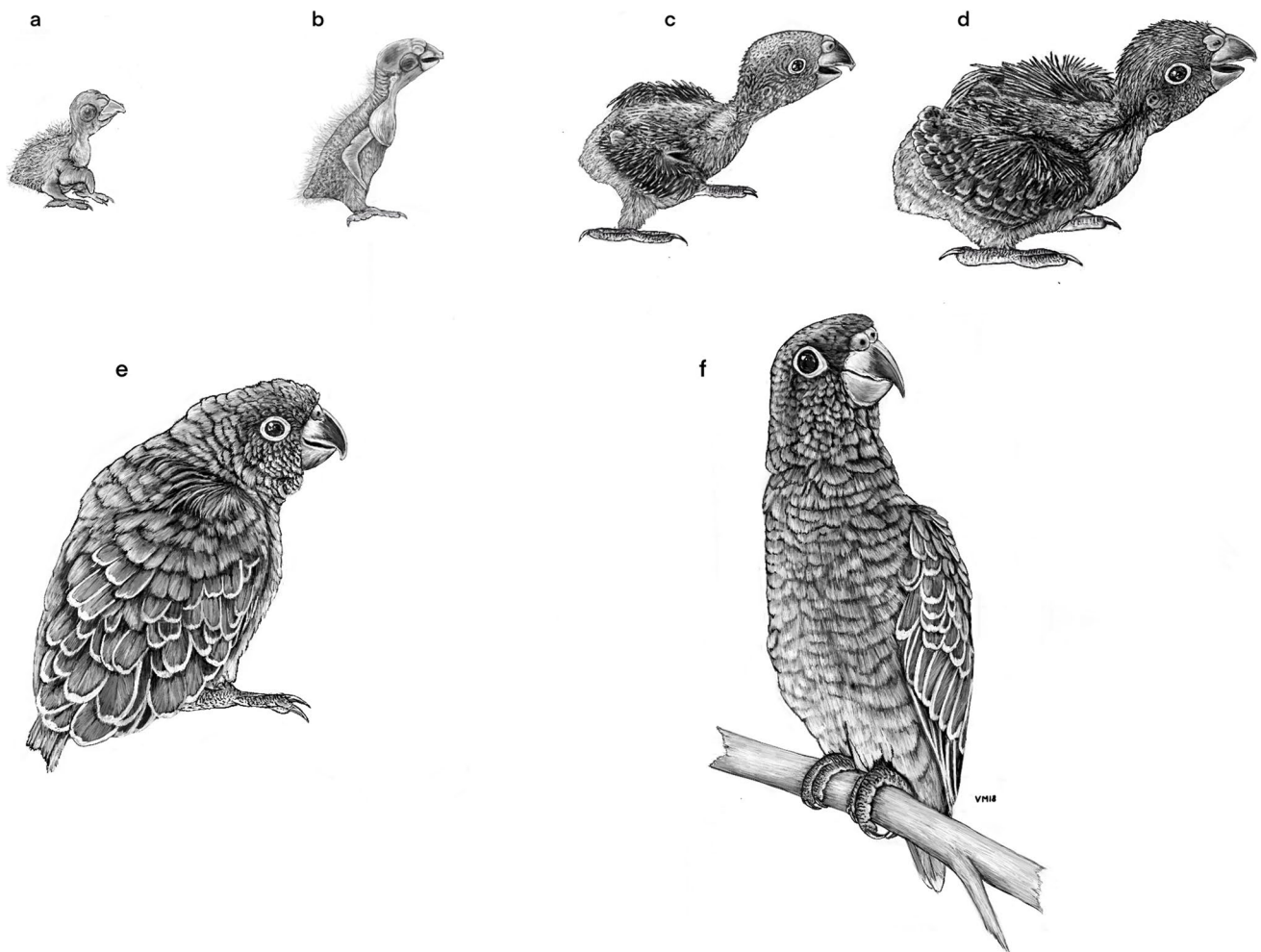


Fig. 7 Illustrations show post-natal development in red-tailed parrot (*Amazona brasiliensis*) chicks (biometric size of the illustrated chicks is not scaled) from 0 to 90 days. **a** Hatching (0. day), **b** 14 days, **c** 22 days, **d** 35 days, **e** 48 days, **f** 90 days. Illustrations by Vladislav Marcuk

Breeding seasonality in psittacines is in general affected by various ecological and abiotic factors, including the seasonal variation of food abundance/quality, age, and nest site availability (Snyder et al. 1987; Higgins 1999; Murphy et al. 2003; Sanz and Rodriguez-Ferraro 2006; Arndt and Reinschmidt 2009; Cameron 2009), so the breeding seasonality will unequivocally differ between an ex situ population outside its origin distribution range and a wild or ex situ population kept within or close to the native distribution range. The breeding season of wild red-tailed parrot populations lasts from October to November until February to March (Abbud 2013), contrary to the breeding season in Germany, which commenced between March and June. The differences in thermal amplitudes (the mesothermal subtropical humid climate in the Brazilian Atlantic Forest vs. temperate climate in Central Europe), humidity and perception rates (Kauano et al. 2012) in the native habitat have an impact on various ecosystem functions and phenology of important feeding resources/plants (Snyder et al. 1987;

Porfirio et al. 2016; Renton et al. 2018). Abiotic factors, like the average temperature and humidity, differ between the native environment and the temperate climate in Central Europe, which is characterized by a cold winter and hot sub-humid summer period. In addition, under captive conditions, the availability of food, levels of humidity, and other factors (e.g., light hours or inside temperature in the inside enclosure) can be adjusted without immerse effort. The breeding readiness of most parrots at ACTP is habitually triggered by seasonal increase of the food quantity, the availability of suitable nest boxes (which remain closed during the non-breeding season), and successive changes in abiotic conditions which occur during the spring and early summer period in Germany. However, in captivity, the increase in food quantity or modifications in food quality can be identified as proximate triggers for prompt breeding in parrots (pers. obs. authors; R. Neumeyer pers. comm.), as air temperatures can remain low until April in Central Europe.

Table 2 Comparative data on the reproductive parameters of *A. brasiliensis* and two closely related species, the blue-cheeked (*A. dufresniana*) and red-browed parrots (*A. rhodocorytha*) in captivity

Reproductive parameters	Species		
	<i>A. dufresniana</i>	<i>A. rhodocorytha</i>	<i>A. brasiliensis</i> ¹
Clutch size	3.0 ± 1.12 (2–5; n = 9) ^{3,8}	2.23 ± 1.28 (1–5; n = 26) ⁴	2.82 ± 0.75 (2–4; n = 11)
Egg measurements			
Length (in mm)	41.49 ± 1.73 ^{3,7} (39.07–43.00; n = 5)	42.33 ± 1.41* (39.23–44.00; n = 20)	39.32 ± 1.93 (36.78–43.49; n = 40)
Width (in mm)	32.17 ± 0.67 ^{3,7} (31.20–33.00; n = 5)	31.19 ± 0.89* (29.5–32.02; n = 20)	30.07 ± 1.12 (27.61–32.41; n = 40)
Egg mass (in g)	23.39 ± 1.41 ³ (20.99–25.60; n = 12)	23.25 ± 1.12 ³ (21.48–25.61; n = 30)	19.59 ± 2.11 (16.66–24.16; n = 50)
Hatchling weight (in g)	17.52 ± 1.65 ³ (14.40–19.40; n = 8)	16.89 ± 0.89 ³ (15.30–18.41; n = 20)	12.58 ± 0.46 (12.03–13.00; n = 8)
$\frac{\text{hatchling weight}}{\text{egg weight}}$ (in%)	74.30 ± 3.98 ³ (65.69–79.29; n = 8)	72.50 ± 2.65 ³ (68.99–77.36; n = 20)	70.84 ± 2.90 ³ (65.61–74.16; n = 8)
Hatching success (in %)	100 (8 of 8) ³	95 (19 of 20) ³	88.88 (8 of 9)
Incubation period (in days)	25.75 ± 0.5 ^{3,6} (25–26; n = 4)	25–26 (n = NA) ²	25.69 ± 0.72 (24.41–26.28; n = 6)
Nestling period (in days)	c. 8 weeks ³	54–55 (n = NA) ⁶	(55–57) ^{**}
Independent (in days)	95 (n = 1) ⁶	3–4 weeks after fledging ²	87–96 (n = 3)

1, this study; 2, Robiller (1990); 3, R. & R. Neumeyer pers. comm.; 4, Arndt and Reinschmidt (2009); 5, Low (2005); 6, Jordan (2006); 7, Olier (1995); 8, Glanzmann (2008)

* n = 3 Robiller (1990); Low (1996) n = 5; n = 12 VM unpublished

** period when first flights were observed

Information in the literature regarding the egg size and egg characteristics of the red-tailed parrot is limited; for 12 infertile eggs laid in captivity, a range of 38.5–40.9 × 29.3–31.2 mm is given (Sweeney 1998). No information about the egg mass or shell thickness is published and is currently absent for most members of the genus. The egg mass of red-tailed parrot was in direct comparison lower than the one recorded for other similar size species in captivity occurring in Brazil, like *A. vinacea* 21.73 ± 0.84 g (20.4–23.16; n = 16; R. & R. Neumeyer pers. comm.), *A. dufresniana*, or *A. rhodocorytha* (see Table 2) and, in average, higher than in other smaller species found in Brazil, like *A. pretrei* 12.78 ± 0.84 g (10.78–14.3; n = 36; R. & R. Neumeyer pers. comm.), *A. aestiva* 17.2 ± 0.84 g (15.3–19.2; n = 50; R. & R. Neumeyer pers. comm.), and *A. amazonica* 18.77 ± 1.21 g (17.34–21.05; n = 18; R. & R. Neumeyer pers. comm.).

In contrast to egg measurements, the clutch size is well documented for this species in the wild, with 958 full clutches recorded between 2003 and 2012 consisting in average of 2.15 ± 0.26 eggs (1–5; n = 958; Abbud 2013). In captivity, the average number of eggs laid in eight clutches was 2.86 ± 0.34 eggs (Arndt and Reinschmidt 2009). The egg-laying interval of 48 h reported in the literature (Martuscelli 1995) was not observed during our study period. However, for congeneric species, egg-laying intervals between 2

and 4 days are common (Robiller 1990) and with inter-pair differences observed by the authors for other Neotropical species.

For the incubation period, different values are given in the literature, ranging from 26 days (Arndt and Reinschmidt 2009) to over 27–28 days (Martuscelli 1995) and up to 28–30 days (Lalime 1997). The findings reported in this study were similar to the incubation period reported by Arndt and Reinschmidt (2009). Various factors could have an outsized impact on the incubation length, inter alia the egg mass, the incubation patterns, or setting used for the artificial incubation (Snyder et al. 1987; Robiller 1990; Arndt and Reinschmidt 2009), likely responsible for the variation among the provided values for the incubation period.

Chicks fledge according to the available literature data after a nestling period of 50–55 days (Scherer Neto 1989; Lalime 1997). In a single reported case study, the chicks left the nest after a nestling period of 60 days (Low 2005). These observations resemble our observations of the first flights in hand-reared chicks; however, these observations are still very subjective, and data from parent-reared chicks is required to determine the exact time fledging, as hand-reared chicks usually start to fly earlier than congeneric chicks required to leave the nest boxes.

Hatching weights reported in the literature does not differ from the hatching weights given in our study. Four freshly hatched chicks hatched at Loro Parque had a range between 10.0 and 12.9 g (Arndt and Reinschmidt 2009). Further, 12 chicks had an average hatching mass of 12.47 ± 0.86 g (10.86–13.95; R. & R. Neumeyer pers. comm.).

In the literature, growth characteristics for wild chicks ($n=2$) and a single captive bred chick are provided in detail (Scherer Neto 1989). The reported weight on the third day here ranged from 89 to 98 g (Scherer Neto 1989). In contrast, chicks in this study of the same age had an average weight of 22.95 g (20.2–28.09; $n=7$). The growth patterns of the wild and captive parent-reared chicks, however, show an overall higher daily weight gain in comparison to the data provided for hand-reared chicks here (see Eason and Moorhouse 2006). The divergence between the weight gain presented here and given for the wild chicks could be the result of multiple cumulative factors. In the first instance, the diet of wild nestlings will essentially differ from the selection of food items provided under captive conditions, as the majority or entire assortment of food items, identified *inter alia* for the red-tailed parrots in the wild (Serafini et al. 2011), is absent in captivity and replaced by commercial food mixtures. Divergence in food components and nutrition compensation can distort and alter growth characteristics. Another critical parameter is the frequency of food provision that notably differ between parent and hand raised neonates. Parent-reared St. Vincent chicks were fed during the first two weeks every hour by the parents, with regular nest controls indicating overtly high quantities of food found consistently present in the crop (on several occasions with > 20% of the body weight, Marcuk pers. obs.). While it is logistically and physiologically feasible to hand-feed chicks more frequently and increase the quantity of food, an overtly full crop failing to empty for a prolonged period can cause various complications, including the overstretching of the crop, crop stasis, crop infection, and gastrointestinal diseases (Duerr and Gauge 2020) — missing probably important components in conventional neonate formulas, like proenzymes and probiotics provided by the parents.

Estimations of growth parameters should preferably be performed in general, by biometric data obtained from wild chicks or parent-reared chicks. Significant differences are often present, comparing growth patterns of conspecific chicks raised by commercial hand-rearing formulas or by parents (authors pers. obs., Eason and Moorhouse 2006). Inappropriate husbandry manuals established in nurseries, like inappropriate feeding intervals or insufficient nutritional components, present possible constraints imposed on the growth rate of captive bred psittacine neonates. Growth parameters derived from a larger sample size including data from wild chicks along other parental parameters

(e.g., feeding rates) would be a desirable addition for more insightful understanding of the reported dynamics and deterministic factors among the growth characteristics of this or other closely related taxa.

Captive environments, despite possible extrinsic constraints and aversive effects imposed to animals' natural behavior, can provide an avid opportunity to unveil detailed insights of the species' general biology and behavioral traits. Combined *in situ* and *ex situ* research conducted on a focal species could proliferate the development of novel approaches that could be implemented in husbandry manuals to improve the reproductive performance, nutrition, post-natal growth, and animal welfare of the species under captive conditions. This would simultaneously contribute to a better understanding of the species' general biology, with possible implications of its *ex situ* and *in situ* conservation.

Acknowledgements The study was part of a B.Sc. internship research project conducted by VM. First, we would like to thank Mr. Martin Guth for funding the study and allowing us to obtain the relevant data used for the preparation of the manuscript. We would like to express our gratitude to Ralf and Rosina Neumeyer for providing us unpublished information about various *Amazona* species. We thank Vanessa Dörries and Marcellus Bürkle for their suggestions on the initial draft of the manuscript. Lastly, we would like to express our gratitude to the two anonymous reviewers, the editor in chief Sandra Maria Hartz, and the associate editor Lilian Manica for their comments that improved significantly the quality of the manuscript.

Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Research involving animals/ethics approval All procedures were non-invasive or were obtained during the internal standard procedures (e.g., using the standard requirements implemented in hand-rearing protocols) and the ethics for research using animals were followed (in accordance with the German Animal Welfare Act and Animal Ethics Laws). For the data collection, therefore, no approval from the Committee for Animal Welfare was required.

Consent to participate None.

Conflict of interest The authors declare no competing interests.

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