

Nestling Development of Ring-necked Parakeets (*Psittacula krameri*) in a Nest Box Population

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Abstract: Chick development of a population of non-native Ring-necked Parakeets (*Psittacula krameri*) (RNP) has been investigated between 2006 and 2008 in Heidelberg, Germany. In parrots hatching asynchrony is common. RNP chicks are under natural selection to fledge synchronously with their siblings, as parents return less often to the nest after the first chick has fledged and remaining chicks may starve. Female nestlings apparently outperform the males by about one d in body mass gain, but also had higher measurements in tarsus, wing and tail growth. This was unexpected as adult males are generally larger than females. First-hatched chicks showed lowest biometrical values as compared to their younger siblings in several characters like body mass gain, bill, wing, and tail length. This feature may contribute to a synchronization of fledging in an otherwise asynchronous brood.

Keywords: Parrots, Psittaciformes, fledging synchronization, invasive species.

INTRODUCTION

The Ring-necked Parakeet (RNP) (*Psittacula krameri*) is the most successful introduced parrot with established populations in at least 24 countries worldwide. In Europe, first breeding occurred in 1885 in Britain, with established and growing populations since the late 1960s mainly in Britain, Belgium, the Netherlands, Germany, Spain, Italy, Greece, and France [1-3].

The RNP is a strictly herbivorous parrot and feeds on buds, flowers, shoots, seeds, and fruits. It only rears one brood per year. In the natural range in India, RNP breed in cavities of trees, where the nest often contains a layer of debris or wood dust, and in crevices of buildings [4]. RNP breed both in single pairs and in colonies with up to nine couples in one tree [5]. The females occupy nests long before the 1st egg is laid and defend their cavities against competitors, especially other female RNP. The clutch size ranges from 2-6, but mostly 3-4 eggs are laid. Only the female incubates and incubation lasts 22-24 d. Chicks hatch asynchronously as the female starts incubation as soon as the 1st egg has been laid. The time lag between the laying of two subsequent eggs is 1-2 days. Chicks fledge at an age of six to seven weeks [4, 6-9]. After leaving the nest, the chicks are still being fed by their parents, especially by the father for at least two weeks. After that time, fledglings gather in groups, while parents separate themselves from the young, and later from each other [10].

Breeding performance, like clutch size and breeding period, is similar for introduced and native RNP [4, 6-9]. But a reduced hatching success has been registered in introduced RNP. However, non-native populations experience a reduced predation risk which balances the reduced hatching success [11]. The breeding period starts at earliest in February and ends in July [4, 12, Braun & Wink in prep.]. In Europe, RNP breed mostly in tree cavities and largely avoid nest boxes [13]. Breeding of non-native RNP in buildings has been reported only from Britain, Germany, Belgium, and Japan so far [14, 15, D. Strubbe, pers. comm.]. For this study, we could establish two colonies, which almost entirely breed in nest boxes on buildings in Heidelberg, Germany (Braun and Wink, in prep.). This allowed us for the first time to record the nestling development in detail.

Hatching in birds can be either synchronous or asynchronous. Asynchronous hatching may regularly be found among parrots as females usually start incubation after laying of the first egg [16, 17]. As a consequence nestlings which hatch last can experience a disadvantage. A decreased survival rate for last-hatched chicks could be found in some neotropical parrots [18, 19], while an evenly distributed mortality rate across hatching order has been reported for Australian *Platycercus* [20]. Hatching order in birds may have a great impact on the growth pattern and can differ considerably between age classes. In Burrowing Parrots body mass, wing length and tarsus were significantly higher in first- than in last-hatched chicks [40]. Krebs [21] stated that asymptotic mass for Crimson Rosellas was highest in middle-hatched male and first-hatched female chicks, and least in last-hatched male and middle-hatched female chicks. In Red Shining-parrots (*Prosopeia tabuensis*) the older chicks receive the double amount of food as compared to their

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younger siblings [42]. Older siblings have been observed to brood the younger nestlings, so a higher energy requirement in older chicks may explain this discrepancy. In Budgerigars (*Melopsittacus undulatus*), in which large clutch sizes and extreme hatching asynchrony occur, early-hatched young reduce their weight towards fledging and fledge early. The youngest siblings are known to beg the most, so they fledge with highest body mass. In Budgerigars, nestlings feed for themselves soon after fledging, thus the pressure of a synchronized fledging in this species is reduced [22]. A similar pattern is known from the Green-rumped Parrotlet (*Forpus passerinus*) in which smaller chicks of large broods were begging more often than their larger siblings and therefore received more food [43]. In some species, smaller and last-hatched nestlings suffer from the highest mortality. An increased mortality rate for the smallest chicks may be a result of hatching asynchrony. In Ouvea Horn Parakeet (*Eunymphicus cornutus uvaensis*) third siblings had a higher mortality in the first week due to hatching asynchrony [18]. As little is known about the fledging synchronization in wild parrots, we wanted to test if there is any sign of fledging synchronization in RNP.

In birds, both male and female chicks may outperform the other sex during development because of differing paternal investment, begging behaviour, or hormone level. Maternal investment may favour the males (smaller sex) like in Bengalese Finch [23]. In Wandering Albatross, male chicks received more food than female chicks [24]. In Black-headed Gull female chicks (smaller sex) were begging more often than male chicks, but males (larger sex) did have a higher asymptotic body mass [25]. An artificially increased corticosterone level prior to incubation slowed the growth of male, but not that of female chicks in Japanese Quail [26]. In chicken, higher amounts of growth hormone expression were found in male than in female chicks [27]. In the dimorphic Crimson Rosella (*Platycercus elegans*) adult males are larger than adult females. Male chicks grew faster and were larger at fledging than females [20]. In contrast, no differences in chick development related to sex were found in the monomorphic Burrowing Parrot (*Cyanoliseus patagonus*), where adult sexes are of similar size [19]. RNP shows plumage dimorphism but only a slight size dimorphism [28].

The aim of this study was to document and to analyse the growth pattern of RNP chicks in a nest box population in detail, in which male and female chicks were identified by molecular sexing. It was analysed whether chicks of different sex and hatching rank develop equally and if there is any sign of fledging synchronization. This is the first time that the development of RNP chicks has been investigated in detail.

MATERIALS AND METHODS

Study Colonies

Since 1974, *Psittacula krameri* is resident in the Rhine-Neckar-Region of Germany. The first breeding in the city of Heidelberg was recorded in 1990 [1]. At some buildings, Great spotted Woodpecker (*Dendrocopos major*) had pecked several holes into the Styrofoam layer of thermal insulation of houses. These hollows had been enlarged by RNP so that they expand up to 1.5 m in length and 40-50 litre in volume

[15]. In 2001, the first case of broods in such cavities was registered [29]. After the breeding season, nest boxes (18 x 18 x 45 cm, entrance diameter 5.5 cm) were placed in front of both, used and non-used, cavities in house insulations, so RNP were forced to breed in nest boxes the next season. In total, 40 nest boxes were thus installed on the walls of buildings in two localities since 2004 (20 boxes per site).

Catching of RNP

During 2006 to 2008, 25 adult females and 2 adult males were caught, sampled, measured and ringed (Series UA... and later UH..., Vogelwarte Radolfzell) for this study. Adults were mainly captured in April, some also in May. Males rarely visit the nest; this is the reason why only 2 adult males could be included in the dataset. As soon as the chicks hatched in April, adult female RNP were caught at their nests and sampled. Even several nest controls did not induce the females to abandon their chicks.

Sampling of Nestlings and Molecular Sexing

150 individual chicks have been sampled, measured and ringed. Blood or feather samples (2-4 growing feathers per chick) were collected from each individual. The brachial vein was punctured with a sterile needle and about 100 µl blood were collected and stored in a modified EDTA buffer [30, 31]. Samples were stored at -20 °C until DNA isolation. Total DNA was isolated from 100 µl of blood using standard proteinase K (Merck, Darmstadt) and phenol / chloroform protocols [32]. Molecular sexing was conducted following standard protocols established in our laboratory by amplification of DNA markers on the sex chromosomes [33]. In general, separation of the PCR products by high resolution polyacrylamide electrophoresis revealed one band in males and two bands in females.

Biometrics

The following morphological parameters were measured: body mass (g), bill length (mm), bill width (mm), tarsus (mm), toe span (mm), wing length (cm), and tail length (cm). For the measurements standardized methods have been used following Proctor and Lynch [34]. Bill and tarsus measures were taken sliding callipers (to nearest 0.1 mm) and wing and tail measures with a stiff metal ruler (to nearest 1 mm).

Bill length was measured from the distal edge of the cere to the tip of the upper mandible. Bill width was determined at the base (broadest part) of the bill. Young chicks carry a fleshy skin edging on the base of the bill, which contributed to its width.

Tarsus length is considered as the distance from the middle of the intertarsal joint to the distal edge of the last complete scale before the toes begin. As young parrots have very fleshy and short legs this measurement was sometimes difficult to take. Toe span was measured to nearest 1 mm as the maximum distance from the tip of digit 3 to the tip of digit 4 (the two longest digits). The foot was flattened on a paper board covered with millimetre paper. At a mean age of 34.6 (± 10.4) d chicks ($n=90$) had a mean toe span of 46.8 (± 2.8) mm when toes were cramped and 47.9 (± 2.8) mm when relaxed (corr. 0.924). The exclusion of the claw from toe

length measurements allowed a better comparison between the values of chicks and adult parakeets because adults often have lost their claws due to heavy frost bite in temperate zone winter.

Wing length was taken with a from wrist joint at the bend of the wing to the tip of the longest primary feather (p8). The wing was softly flattened on the ruler to standardise the measurements within the groups, according to Butler [35: 214]. Before feather growth started, the wing length was de-



Fig. (1). Contd.....

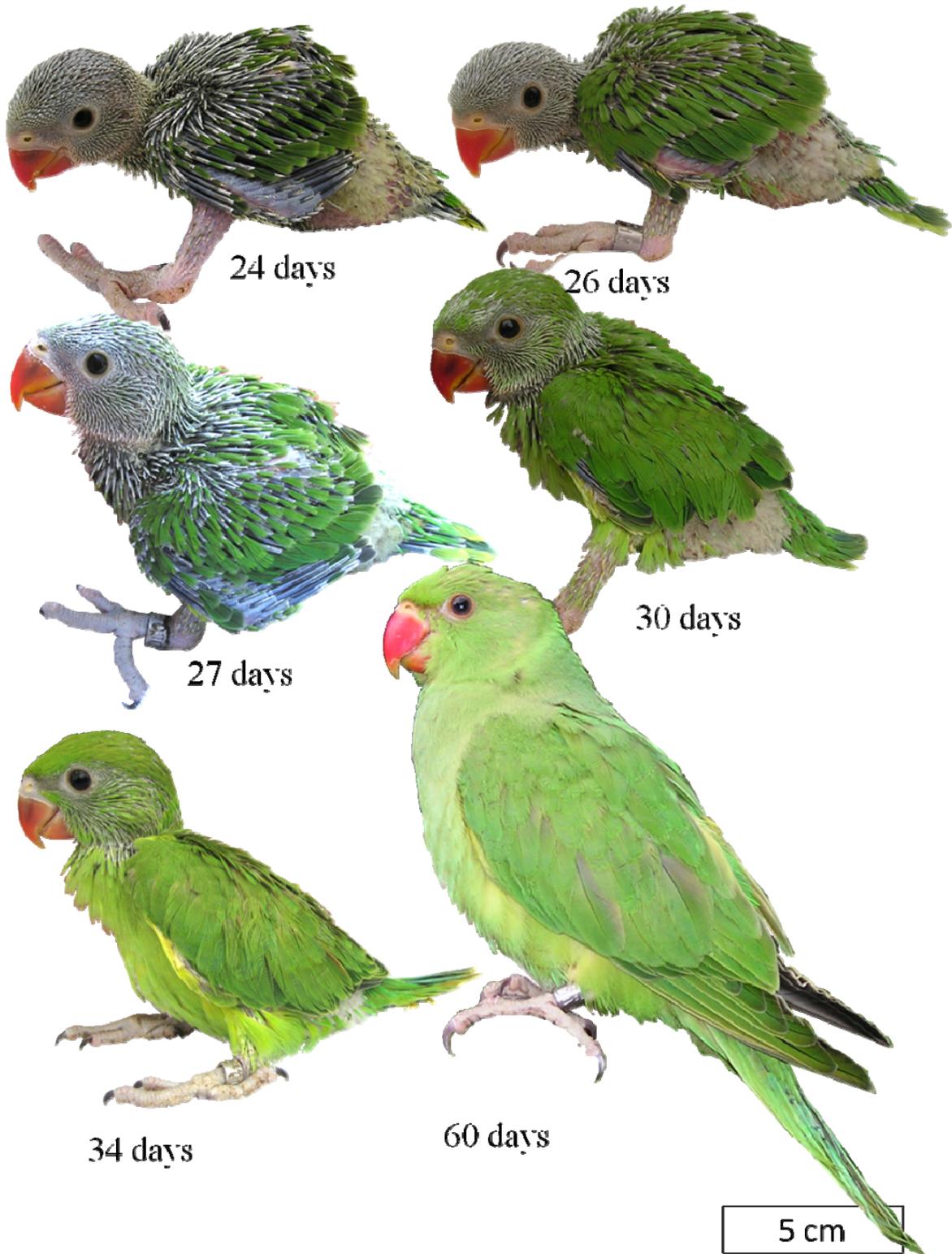


Fig. (1). Photographic documentation of chick development in Ring-necked Parakeet (3 to 60 days).

terminated as the maximum length of the naked wing. For tail length measurements (length of the longest feather) the distal tip of the ruler was placed between the two central tail feathers.

Body mass was measured using two Pesola scales (100 g to the nearest 1 g or 300 g to the nearest 2 g). For measurements, the birds were placed in a small cotton bag.

Fledging Age and Ageing of Chicks

Chicks could quite easily be aged between the age of 12 and 30 d according to the growth status of the feathers. We compared each chick with an age table containing photographs of a captive *P. krameri* chick from 4 to 44 d, for which photographs were taken every 2 d [36].

Growth Stages

According to the different shapes of growth curves, we divided nestling ages into different stages for our linear mixed-effect model which were derived from residual patterns. For better comparison (sex, hatching order) we took mean values at different stages (early, medium, late nestling phase). This distinction differed between characters, as outlined Table 1 and Table 2.

Statistical Analysis

Because many measurement data are dependent (chicks were measured several times), we used the linear mixed-effect model (lmer) of the Package lme4 in the 'R' version 2.7.2 for statistical analyses [37]. The developmental traits have been evaluated using individual and nest box as random effects in order to account for the specific pattern of dependence. The different biometrics (body mass, bill, tarsus, toe span, wing, tail) were regarded as dependent variables, while age, sex, and hatching order were used as fixed effects. Parameters have been calculated using the restricted maximum likelihood (REML) method. Models were tested using ANOVA.

RESULTS

Molecular Sexing

Nestlings (n=149) and adult birds (n=27) could be sexed by amplification of sex chromosome specific DNA markers

using blood or feather tissue as DNA source. Sex ratio of the chicks was 1:1 (74 females, 75 males).

Biometrics of Nestling Development

Development and growth of RNP nestlings is illustrated in Fig. (1). Both, sex and hatching order within a brood can influence nestling development (Table 1 and 2; Fig. 2-8).

Body mass shows a linear increase with time within the first 25 d, and then stays at a plateau for approximately 5-10 d before decreasing towards fledging. The development of body mass follows a quadratic regression and can be divided into two phases, the first phase being the mass gain phase and the second phase being the mass recession phase towards the end of the nestling stage (Fig. 2). The mass recession accounts for a weight loss of 23% in females and 19% in males (Table 2). The average body mass of adults is 149.2 ± 11.1 g (n=27) and is nearly reached, but not exceeded during the nestling stage.

Female chicks have an advance in body mass development of 1-2 d in the early nestling stage compared to males, but the mass recession is also higher in this group until fledging. As a consequence female nestlings are heavier than males in the first two growth stages, whereas at fledging males are 3% heavier than females (Table 2). Females also show higher growth rates in tarsus, wing and tail as compared to male chicks (Table 2). In first-hatched chicks only the body mass in the middle and late nestling age is higher as compared to the younger siblings. In nearly all other measurements intermediate-hatched chicks show the highest values except early bill length, which is highest for last-hatched chicks at an early nestling stage (Table 1).

No significant difference could be detected in the linear mixed model of the body mass development related to clutch size (ANOVA test, $p = 0.802$), or the calendar week of hatching (ANOVA test, $p = 0.53$), indicating that there is no

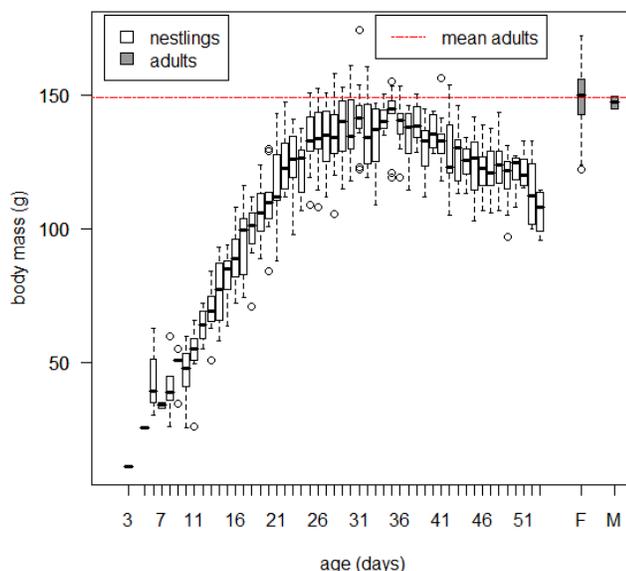


Fig. (2). Development of body mass during chick development (n=150) in Ring-necked Parakeets. For comparison adult values are given with females (F, n=25) and males (M, n=2) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

Table 1. ANOVA Test of Morphological Features between Chicks of Different Hatching Order. P-values and Significance Level Evaluate the Role of Hatching Order Used as a Main Factor in our Linear Mixed-effect Model. Stages are Divided by Changes in Growth Curves

Character	Age (Days)	1st Hatch (Mean)	Intermediate Hatch (Mean)	Last Hatch (Mean)	P-value	Stage	Daily Change Per Stage
Body mass (g)	15	79.37	83.01	80.18	0.001	0-25 days	5.55
	31	144.55	141.99	139.87	<0.001	30-55 days	-1.23
	50	121.21	118.61	116.45	<0.001	30-55 days	-1.23
Bill length (mm)	15	10.85	11.34	11.37	<0.001	0-30 days	0.35
	50	19.72	20.08	19.98	<0.001	31-55 days	0.18
Bill width (mm)	14	11.03	11.16	10.99	n.s.	0-25 days	0.22
	50	14.40	14.48	14.35	<0.001	26-55 days	0.10
Tarsus length (mm)	14	16.10	16.18	15.67	<0.001	0-23 days	0.35
	25	18.20	18.32	18.00	<0.05	24-55 days	-0.01
	50	17.88	17.99	17.69	<0.001	24-55 days	-0.01
Toe span (mm)	14	35.95	37.89	36.34	<0.001	0-23 days	1.48
	25	46.01	46.36	46.03	<0.001	24-55 days	0.05
	50	47.21	47.56	47.23	<0.001	24-55 days	0.05
Wing (cm)	10	2.22	2.35	2.29	n.s.	0-15 days	0.19
	50	16.53	16.90	16.81	<0.001	16-55 days	0.37
Tail (cm)	30	3.98	4.26	4.23	<0.001	18-55 days	0.33
	50	10.65	10.95	10.90	<0.001	18-55 days	0.33

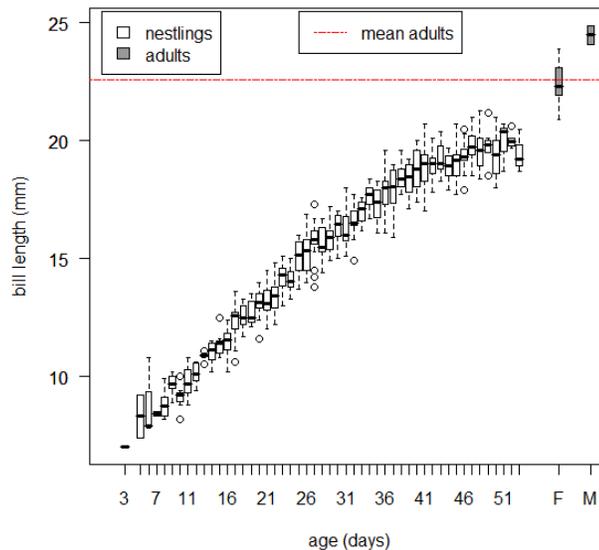


Fig. (3). Bill growth during chick development (n=150). For comparison adult values are given with females (F, n=25) and males (M, n=2) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

shortage of high quality food supply at any time of the breeding season.

Fig. (4). Growth of toe span (without claws) during chick development (n=150). For comparison adult values are given

with females (n=25) and males (n=1) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical

dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

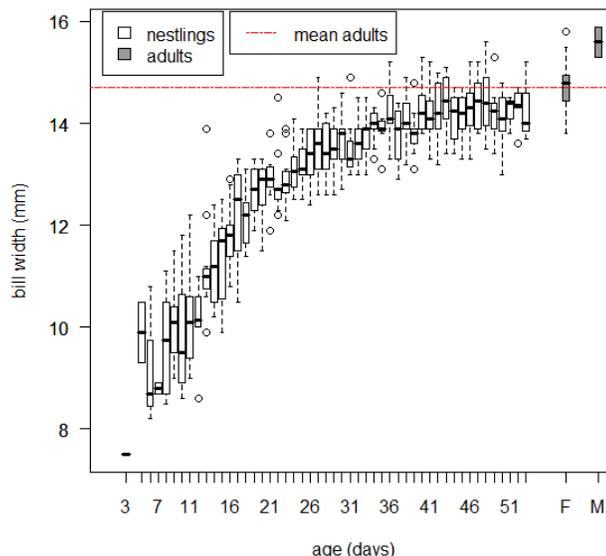


Fig. (4). Growth of bill width during chick development (n=150). For comparison adult values are given with females (F, n=25) and males (M, n=2) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

Table 2. ANOVA Test of Morphological Features between Female and Male Chicks. P-values and Significance Level Evaluate the Role of Sex Used as a Main Factor in Our Linear Mixed-effect Model. Stages are Divided by Changes in Growth Curves

Character	Age (Days)	Females (Mean)	Males (Mean)	P-value	Stage	Females Daily Change Per Stage	Males Daily Change Per Stage
Body mass (g)	15	89.40	83.78	<0.001	0-25 days	5.52	5.52
	31	148.52	145.07	<0.001	30-55 days	-1.78	-1.44
	50	114.64	118.05	<0.001	30-55 days	-1.78	-1.42
Bill length (mm)	15	11.10	11.15	<0.001	0-30 days	0.35	0.35
	50	19.64	19.85	<0.001	31-55 days	0.18	0.18
Bill width (mm)	14	11.03	11.07	<0.001	0-25 days	0.22	0.22
	50	14.13	14.32	<0.001	26-55 days	0.04	0.04
Tarsus length (mm)	14	16.95	16.26	<0.001	0-23 days	0.39	0.39
	25	18.41	18.27	<0.001	24-55 days	-0.01	-0.01
	50	18.09	17.94	<0.001	24-55 days	-0.01	-0.01
Toe span (mm)	14	37.13	36.88	n.s.	0-23 days	1.47	1.47
	25	45.69	46.03	n.s.	24-55 days	0.05	0.05
	50	46.86	47.24	n.s.	24-55 days	0.05	0.05
Wing (cm)	10	2.36	2.31	n.s.	0-15 days	0.18	0.18
	50	17.01	16.83	<0.001	16-55 days	0.37	0.37
Tail (cm)	30	4.46	4.25	<0.001	18-55 days	0.33	0.33
	50	11.12	10.93	<0.001	18-55 days	0.33	0.33

Bill Growth

Bill size of adult RNP males is larger than that of adult females (Fig. 3, 4) [12, 38]. Already during nestling development male chicks of all age stages have longer and broader bills than the female siblings (Table 2). The development of bill length is almost linear with time with a slow decrease in the growth rate towards the end of the nestling stage (Fig. 3). The average bill length of adult females (22.5 mm) is not reached during nestling stage, but young females attain 87% of the adult value by the age of 50 d.

The development of bill width is initially linear with time but flattens out towards the end of the nestling stage (Fig. 4). The average bill width of adult females (14.7 mm) is nearly attained by the end of the nestling stage with 96% in 50 d old females (mean values compared).

Tarsus and Toe Growth

Tarsus and toe length do not show a sexual dimorphism in adult RNP (Fig. 5,6). Tarsus length is significantly longer in female chicks as compared to male chicks in all three growth stages (Table 2). Tarsus growth is fastest in early chick development until the age of 20 d (Fig. 6) and follows a logarithmic growth pattern. The average tarsus length of adults (18.0 mm) is reached, even exceeded during the early nestling stage, with female chicks of 50 d of age reaching 100% of the adult tarsus length.

The growth of toe span occurs during the first 20 d (Fig. 6). The average toe span of adults (44.6 mm) is reached during early nestling stage of about 18 d of age and then exceeds this value after day 25 in both sexes and among all hatching orders (Tables 1, 2).

Wing Development

In RNP the first feathers appeared at an age of c. 14 d (Fig. 1). Primaries, which contribute to the wing length, started growing from day 16 onwards. Wing growth is almost linear over the nestling stage with a slow decrease of growth rate towards the end (Fig. 7). The average wing length of adult females (17.3 cm) is nearly reached by the end of the nestling stage, with female chicks reaching 17.0 cm (98%) at day 50 as compared to 16.8 cm in males (Table 2).

Tail Growth

The development of tail feathers is quite linear, starting at an age of c. 18 d (Fig. 8). The average tail length of adults (20.7 cm) is not reached by the end of the nestling stage. Females attain 11.1 cm (54%) at day 50 and males 10.9 cm which apparently have longer tails as adults (Fig. 8). Tail length may be underestimated because tips sometimes were broken due to nesting behaviour and limited space in nest boxes.

Influence of Hatching Order on Chick Development

Depending on the hatching order body mass of young RNP differed significantly (Tab. 1). On day 15 first-hatched chicks had a weight of 79.4 g whereas it was 80.2 g in last-hatched chicks and 83.0 g in intermediate-hatched chicks.

The daily increase of body mass in the early nestling stage (0-25 d) is 5.6 g d⁻¹ (Table 1; Fig. 9).

In the subsequent nestling phase (d 30-55, Fig. 10), first-hatched chicks attained a body mass of 144.6 g on d 31, last-hatched chicks of 139.9 g and intermediate chicks of 142.0 g (Table 1). Furthermore, intermediate-hatched chicks show significantly higher measurements in nearly all other characters, like bill length, bill width, tarsus, toe span, wing, and tail length than first- and last-hatched chicks (Table 1).

Sex-dependent Nestling Development

When 15 d old, female chicks weigh about 89.4 g, whereas males are 5.6 g lighter. The daily gain in weight is 5.5 g in both sexes in the early nestling stage (0-25 d). Differences between sexes are significant ($p < 0.001$). In the subsequent nestling phase (30-55 d) body mass decreases in both sexes, but the slopes are significantly different ($p < 0.05$). At an age of 31 d, females weigh 148.5 g and males 145.1 g. Females lose 1.7 g d⁻¹, whereas males only lose 1.4 g d⁻¹ (Table 2).

Adult RNP males have larger bills, wings and tails than females [7, 38]. Surprisingly our study shows, that female chicks are significantly heavier in the early nestling phase, which gives them an advance of 1-2 d as compared to male chicks. Furthermore, females show a significantly longer tarsus, wing and tail (Table 2). Bill length and width are the only characters in which male chicks outperform female chicks (Table 2) which agrees with the finding that adult RNP have bigger bills than females (s. above).

Breeding Success and Mortality

The average clutch size in 69 broods was 4.08 ± 1.42 eggs, with 61.3% of eggs hatching and 79.2% of all chicks surviving until fledging (3.5% of chicks have been rescued, hand raised and released). Total mortality of 173 chicks in the nest was 17.3%. After day 25, mortality of chicks was independent of hatching order.

DISCUSSION

Body mass data from this study were similar to those of the Asian *P. k. borealis* [7], and other RNP (n=292) breeding in Europe (UK) [35]. As compared to 141.7 g in Butler [35], birds in our study were heavier with 149.3 g. However, our data are biased as they derived almost completely from adult females caught at the beginning of the breeding season. Females in the egg-production period weigh more than after egg-laying as they carry the developing eggs. The heaviest recorded bird in literature (180 g) was a female in egg-laying stage caught in Southern England in March [35: 184]. The maximum body mass of a nestling, which exceeded the weight of any of our adult RNP, recorded in this study was 175 g; it came from a 31 d old female chick.

Normally, the body mass of bird nestlings does not exceed that of the adults. Exceptions are found in pelagic birds, swallows and swifts. These species have a long nestling stage, spend long times for foraging in flight, and nestlings may feed for themselves directly or soon after fledging. For these species a reduction of the overweight (produced as nes-

tlings) before fledging is common [39]. In parrots, a weight reduction before fledging has been found in cockatoos like *Cacatua tenuirostris* [40], *C. pastinator* [41], *Calyptorhynchus funereus* [42], *C. latirostris* [43], and neotropical parrots like *Myiopsitta monachus* [44], *Amazona viridigenalis* [45], *Rhynchopsitta* sp. [46], or Burrowing Parrots [47].

The body mass in RNP peaked at day 31, about 20 d prior to fledging. The mean body mass reduction in RNP

chicks accounted for 23% in females and 19% in males. Similar values have been reported for the Burrowing Parrot with a weight reduction of 23% [48]. Burrowing Parrots had maximum body mass at an age of 38 d, but chicks stay in the nest for 60 d [48]. Studies on other parrots, like cockatoos, *Myiopsitta monachus*, or *Rhynchopsitta pachyrhyncha*, show similar patterns [overview given in 48]. The pre-fledging weight peak of RNP occurs earlier than in Crimson Rosellas, in which the weight maximum was reached 10 d prior to

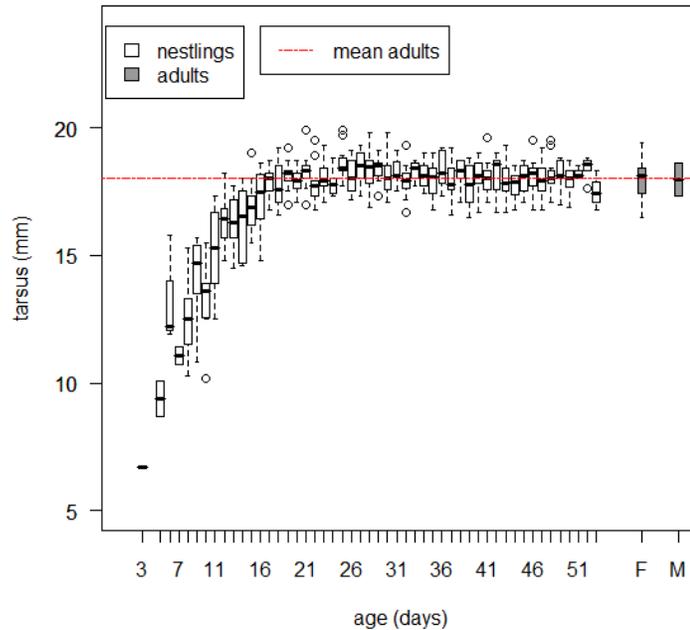


Fig. (5). Tarsus growth during chick development (n=150). For comparison adult values are given with females (F, n=25) and males (M, n=2) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

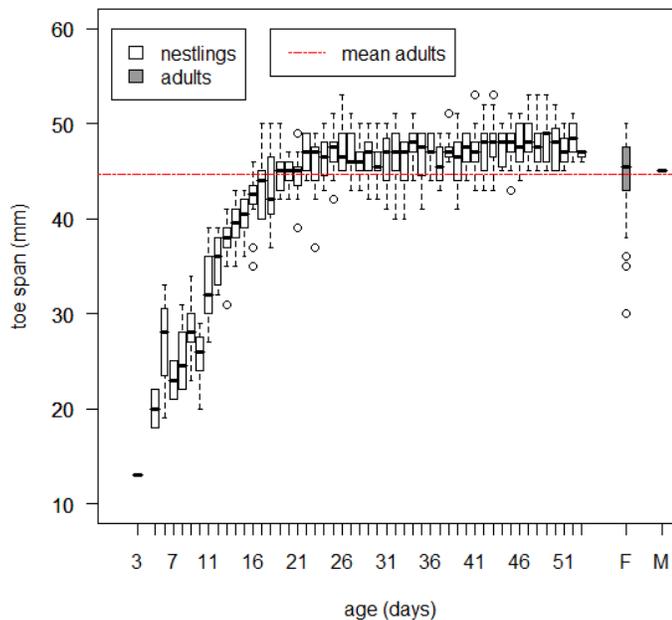


Fig. (6). Growth of toe span (without claws) during chick development (n=150). For comparison adult values are given with females (n=25) and males (n=1) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

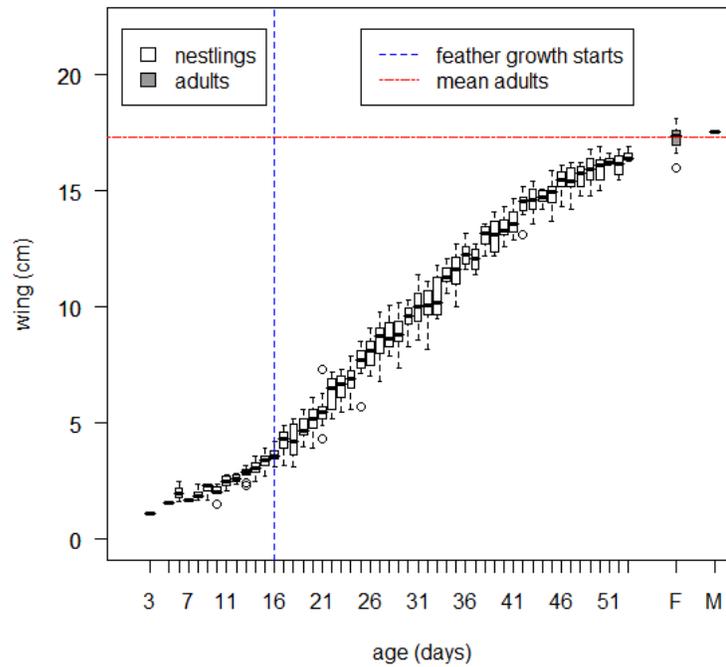


Fig. (7). Wing growth during chick development ($n=150$). For comparison adult values are given with females (F, $n=25$) and males (M, $n=2$) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

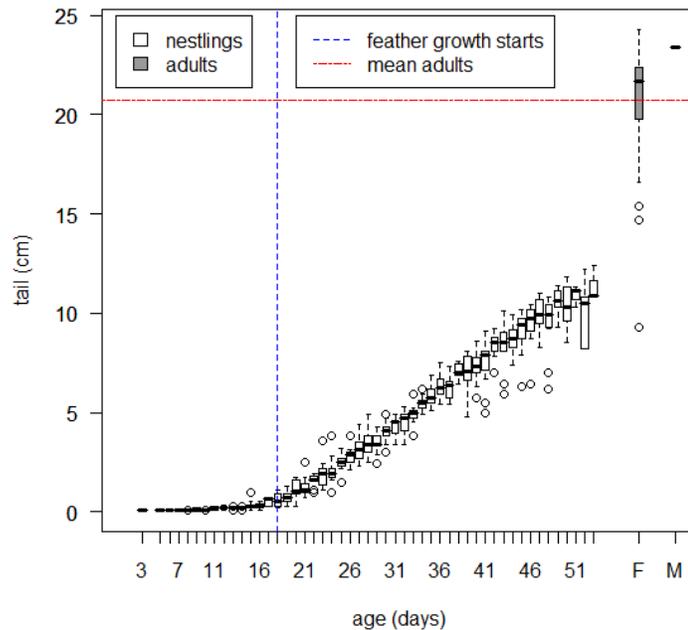


Fig. (8). Tail growth during chick development ($n=150$). For comparison adult values are given with females (F, $n=25$) and males (M, $n=1$) on the right side, the red dashed line shows the mean value of adults. boxplot: horizontal line shows the median; the top and the bottom of the box show the 25th and the 75th percentiles; the vertical dashed lines ('whiskers') show either maximum value or 1.5 times the quartile range; circles indicate outliers out of the 1.5 times quartile range.

fledging; but rosellas exhibit a shorter nestling stage of only 35 d [21, 49].

Tarsus length is the only other morphometric character (beside the body mass) which decreases (about 2% loss) at the end of the nestling stage. Young nestlings have a soft fleshy skin tissue covering their tarsus, which becomes dry

and solid, sometimes even skinny in light-weight chicks during the late nestling phase. For *P. k. borealis* similar data have been published [12]. A comparable pattern in tarsus development has been seen in Burrowing Parrots in which pre-fledging chicks have a similar tarsus length as adult birds [38]. Krebs [21] used the tibia as a measure for the overall skeletal size. The linear tibial growth phase was very short,

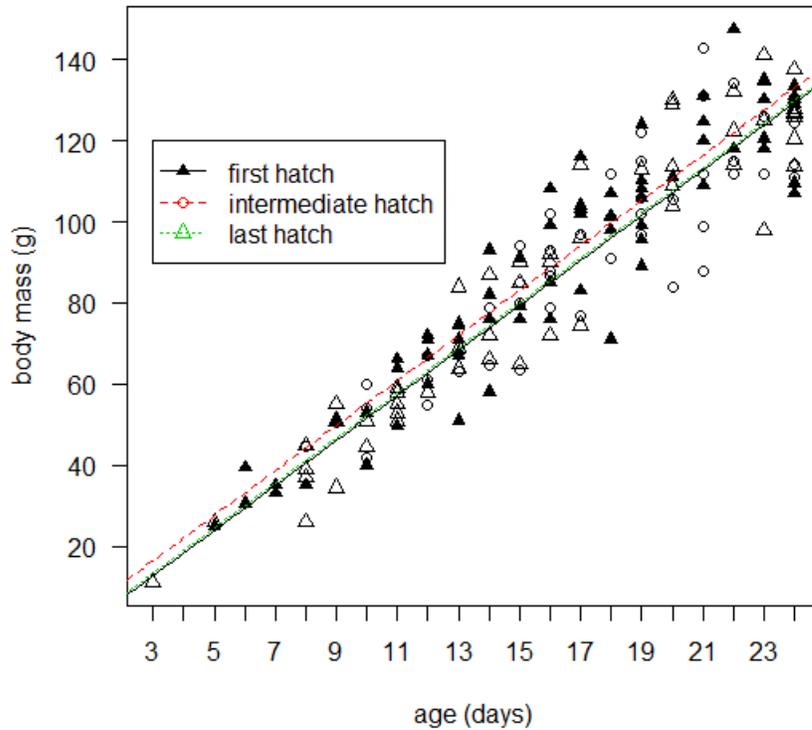


Fig. (9). Differences in body mass increase of in early chick development due to hatching order.

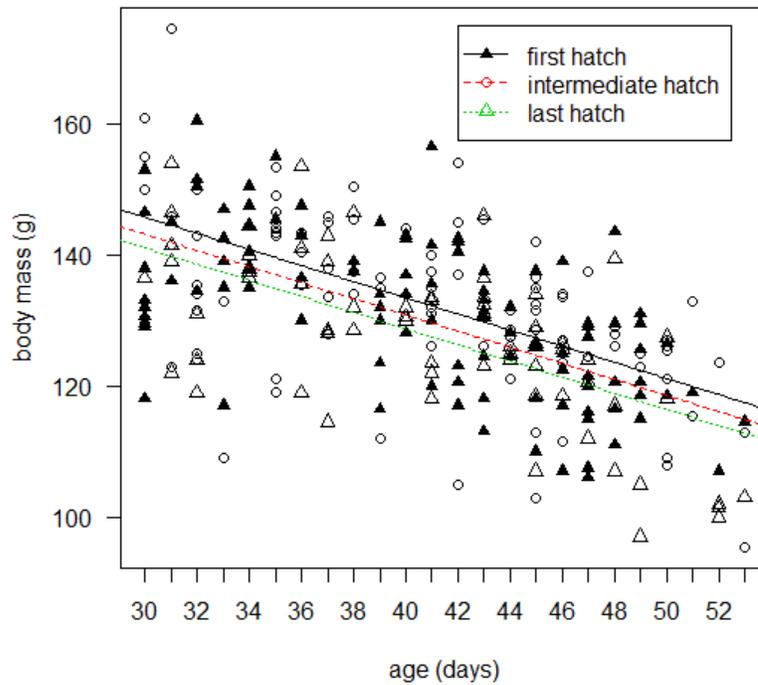


Fig. (10). Differences in body mass decrease in late chick development due to hatching order.

taking place only between 1 and 10 d in *Platycercus elegans*. This indicates that in parrots the development of skeletal structures is attained very quickly and basically before the start of feather growth (s. Fig. 1).

Males of nearly all investigated RNP subspecies except *parvirostris* have longer wings than females [12, 38]. Pre-fledglings of Burrowing Parrots reached 92% of the adult wing length [40]. Therefore pre-fledging female chicks of

RNP which reach 98% of the adult length apparently have excellent fledging conditions. Even a chick at only 43 d of age, attaining 86% of the adult wing length, was well capable of flying (Braun and Wink, in prep.). The mean growth rate for wing length in RNP nestlings was 3.7 mm d⁻¹, being 1.1 mm d⁻¹ less than in Burrowing Parrots [48]. This finding is not surprising as adults of the latter species nearly twice as heavy as adult RNP.

Tail length is dimorphic in RNP with males having longer tails in all subspecies [38]. In Burrowing Parrots tail growth started at an age of 25 d [40]. In RNP tail growth began at an age of 18 d, resulting in a slightly faster development than in Burrowing Parrots. Fledglings of Burrowing Parrots attain 72% of the adult tail length without significant differences between sexes or hatching order. Our findings are different: RNP fledglings only reach 54% of the adult tail length. This may be due to the relatively longer tail in RNP as compared to Burrowing Parrots, which makes up to 59% of the total body length as compared to 53% in Burrowing Parrots [max. values compared to body length in 50]. The average growth rate of tails in RNP was 3.4 mm d^{-1} , being about 0.6 mm d^{-1} lower as compared to the nearly double-sized Burrowing Parrot.

As chicks of both sexes fledged at about 50 d of age, the literature value of seven weeks is quite adequate [50], whereas Wilson and Roselaar [7] give a shorter range of 40 to 50 d. Benson *et al.* [51] mentioned the fledging age as spanning from 46 to 61 d for the African subspecies and 49 d for the Indian subspecies.

Masello and Quillfeldt [48] had proposed an allometric relationship of fledging age in relation to body mass for several parrot species. Burrowing Parrots stay 11 d longer in the nest than expected from the model. The authors concluded that the prolonged nestling stage did not pose an additional predation risk to the nestlings, but contributed to the magnitude of mass recession which was observed during their study. In RNP, fledging takes place 4 d after the expected date from allometric model of Masello and Quillfeldt.

Our finding that chick developmental traits are independent of clutch size and hatching date is surprising because environmental factors vary substantially during the breeding season. The hatching date of RNP extended over 10 calendar weeks (26th of March to 29th of May). The German spring season is characterized by an enormous change in food quality for RNP during flowering and fruiting time of 42 tree and shrub species (50% of which were non-native species) [14]. From May to September, RNP live mainly on fruits (90% of food items) [14], but use a high amount of buds, flowers, leaves, and shoots in preceding months [52]. RNP benefit from a high tree and shrub species diversity in urban areas with at least 85 recorded food plants in Germany with special focus on *Acer* spec., *Aesculus hippocastanum*, *Populus* spec., *Quercus* spec., *Hedera helix*, *Carpinus betulus*, *Malus* spec., and *Prunus* spec. [52].

In the mass gain phase, first-hatched chicks were lighter as compared to their younger siblings, and even lower than the last-hatched ones; the young that had hatched in the middle of the hatching order were the heaviest. In the mass recession phase, the results show another pattern: now the first-hatched chicks had an advantage as compared to their younger siblings. In the late nestling phase, parents feed less often (Braun & Wink, in prep.) and food supply decreases for all siblings at the same time, but now the eldest chicks benefit from being closer to fledging as compared to the younger ones. Chicks of intermediate hatching rank obtained the best values not only in body mass but also in the other morphological characters, such as growth of tarsus, toe span, wing and tail (Table 1). The only character that differed from

this pattern was bill development, as intermediate-hatched chicks show highest values both for bill length and width, except for the early development (5-30 d), when last-hatched chicks are having the highest growth rate in bill length (Table 1).

These data can be interpreted as a means to overcome hatching asynchrony and to synchronise fledging. In RNP, the chicks are dependent on their parents for about two weeks after fledging [53], so they have to move to the nearby feeding grounds. If chicks fail to fledge in time, they may starve, because the parents focus on the already fledged young and return less often to feed the remaining chicks in the nest (Braun and Wink in prep.). Our results thus agree with the hypothesis that RNP belong to those parrots which prefer feeding the younger chicks in order to synchronize fledging.

In contrast, in Burrowing Parrots first-hatched chicks produced the longest wing length and the last-hatched chicks the shortest one, whereas tail length was independent from hatching order [40]. For Crimson Rosellas [21] no significant differences in the linear growth rate of wing chord or other variables, neither in chicks of different sex nor of different hatching order, were found. In Green-rumped Parrotlets, parents of asynchronously hatched broods required significantly less energy than parents of artificially synchronized broods. Although the magnitude of peak energy demand was similar both in asynchronous and synchronous broods, the temporal duration of high energy demand was lower in asynchronous broods [54]. Experimentally synchronized broods in Green-rumped Parrotlets fledged as many or more young than asynchronous broods [55].

Mortality in RNP chicks was low and nestling mortality was not correlated with hatching order. Mortality in Burrowing Parrots tended to be higher in younger nestlings, but the survival rate between hatching and fledging was very high in this species (91%) [40]. Although some nest boxes of our RNP were in reach of Red Squirrels (*Sciurus vulgaris*), a known nest predator of birds, the nest safety of the study population was very high; not even a single registered case of nest predation was recorded.

CONCLUSION

Most biometric variables exhibited similar patterns during RNP nestling development. Female RNP chicks showed a faster growth as compared to their male siblings and first-hatched chicks were smaller as compared to their younger siblings.

In parrots, hatching and fledging asynchrony is common. In seed-eating species an unsynchronized fledging may not be of disadvantage, like in the budgerigar, in which chicks may feed independently soon after fledging. In the predominantly fruit-eating RNP with a wide variety of food plants, fledglings are fed by their parents for some time after leaving the nest and have to learn the selection of food items. Remaining siblings in the nest are under pressure to fledge quickly because the parents will return less often to the nest. Weakness and mortality may be the result of a delayed ability to fledge. Our study indicates that RNP is a species in which 'fledging synchronization' is operational.

CONFLICT OF INTEREST

The authors confirm that this article content has no conflicts of interest.

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