Raptors in changing West African savannas : the impact of anthropogenic land transformation on populations of Palearctic and Afrotropical raptors in northern Cameroon

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Chapter 3

Breeding biology and nestling development of the Grasshopper Buzzard

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Abstract

Research into the effect of environmental variables on reproductive success of tropical raptors is often constrained by the lack of information on breeding biology. We provide the first detailed information of the breeding biology and nestling development of the Grasshopper Buzzard *Butastur rufipennis*, an Afrotropical migratory raptor threatened by extensive land transformation in its breeding range. Breeding coincided with the transition from the dry to the wet season. The mean incubation period was 30 days and mean fledging period 36 days. The breeding period was characterized by rapid establishment of territories and short post-fledging dependency periods related to the onset of migration shortly after breeding. Growth rate of body mass, tarsus, wing and primary feathers were similar between sexes, which showed significant but moderate body mass dimorphism at fledging (♂85-90% of ♀). Second hatchlings were smaller in body mass and structural dimensions compared to similarly-aged first hatchlings and singles of the same sex. Survival of second hatchlings was related to body mass ratio with first hatchlings, while brood reduction occurred through food competition and siblicide. We provide ageing formulae and photographic records to facilitate further studies of Grasshopper Buzzard nestling development and reproductive success in the region.

Left: Grasshopper Buzzard at perch in Waza National Park.

3.1 Introduction

Little quantitative information exists on the breeding biology, nestling growth and development of the majority of raptors in tropical Africa (Virani & Watson 1998), despite the importance of such information for conservation management of threatened species (Steenhof & Newton 2007). The breeding biology and nestling development of the Grasshopper Buzzard *Butastur rufipennis* are largely undescribed, apart from anecdotal accounts of nests in Niger and Mali (Cheke 1995, Brouwer *et al.* 2000), and despite its status as the second most common Afrotropical raptor in western Africa (Ferguson-Lees & Christie 2001). Grasshopper Buzzard populations migrate roughly between 7-18ºN in West Africa, exploiting abundant and easily accessible prey following rains northwards and increasing prey availability, notably grasshoppers, as dry season fires and grazing reduce grass cover southwards (Thiollay 1978a). During the breeding season, insects and reptiles are the most commonly taken prey, but reptiles, mammals, and amphibians dominate the prey biomass (Chapter 4). The species' main breeding area ranges between 9-15ºN (Ferguson-Lees & Christie 2001) and coincides almost entirely with the Sudano-Sahelian and Sahelian climate zones, exposing it to the rapidly changing and increasingly deteriorating breeding conditions for raptors in this region (Thiollay 2006a, 2007a). The widespread over-exploitation of the habitat following explosive human population growth in this region contributed to significant Grasshopper Buzzard population declines such as those reported in protected (-33%) and cultivated areas (-57%) in a large region of Sudano-Sahelian West Africa between 1969 and 2004 (Thiollay 2006a). In light of these declines, detailed information on the breeding biology of the species is urgently required to assist studies that attempt to evaluate reproductive output in the increasingly transformed breeding habitats.

In this chapter, we describe for the first time aspects of the breeding biology of the Grasshopper Buzzard based on 2 years of observations (2009 and 2010) in northern Cameroon. We quantify growth and development of nestlings, including the timing of plumage development and growth rate of different body parts. We investigate the influence of sex on body and feather growth, and how nestlings order in the hatching sequence influences growth, development, and survival. Lastly, we present a morphological guide and develop ageing formulae that will aid further studies into reproductive success in this species.

3.2 Materials and methods

The study was conducted between 2 May and 22 July 2009 and 3 May and 25 July 2010, in and southwest of the Waza National Park in the Far North of Cameroon (11°00'N-11°40'N and 14°20'E-15°00'E), covering *c*. 14 km^2 (2009) and 20 km^2 (2010) inside the National Park and 32 km^2 (2009) and 20 km^2 (2010) in the cultivated habitat. The topography of the area is generally flat with some gentle slopes and rocky outcrops. The vegetation is characterized by open woodland dominated by *Sclerocarya birrea*, *Anogeissus leiocarpus*, and *Balanites aegyptiaca*. The habitat inside Waza National Park consists of mature and

largely intact woodland savanna, whereas the human-dominated, disturbed habitat outside Waza National Park is characterized by a mosaic of cultivated fields (notably sorghum and millet), settlements, and fragments of heavily exploited woodland. The climate is semi-arid with a dry season from November to April, when the first rains occur, followed by a wet season from May into October, with a mean annual precipitation of *c*. 500 mm. Mean annual temperature is 28 ºC and peaks before the rainy season from March-May when temperatures of 47 ºC are reached, with a mean daily minimum of 21 ºC and mean daily maximum of 41 ºC.

Nestling measurements and growth patterns

The study area was intensively searched for Grasshopper Buzzard nests between 2 and 18 May in 2009 and between 3 and 16 May in 2010, which coincided with the first half of the incubation period for three nests at this latitude in 2008 (R. Buij pers. obs.). All occupied Grasshopper Buzzard nests, defined as those nests lined with green leaves and/or containing one or more eggs or nestlings, were GPS marked and their status (e.g. green lining, number of eggs) recorded. Additional nest searches in the second half of May and June were combined with visits to occupied nests. Nests without eggs were revisited at 1-week intervals to determine their status until 4 weeks after discovery and were declared abandoned in the absence of adults attending. Nests which had failed early in the breeding season (first two weeks of May) were revisited 2-3 times at later stages (20 May-15 June) to investigate whether renesting had occurred. We used a mirror on a pole to record the clutch size in order to reduce time spent at the nest and subsequent disturbance to a minimum. At later stages, nests were accessed by climbing the trees.

Occupied nests were revisited at approximately two-weekly intervals during incubation, at averagely 7-day intervals following hatching in 2009, and at averagely 5-day intervals (due to increased human resources) following hatching in 2010. The morphological and morphometric development of nestlings was studied from hatching to nestling death or fledging, or later until it became impossible to capture the young. In case nestlings fledged prematurely as a result of our actions, they were returned to the nest. Nests were not visited at higher intensity during hatching to avoid unnecessary disturbance. Nestlings still damp when first measured were classified as hatching on the day of the visit, while dry nestlings were classified as having hatched either the day before or two days previous to the visit depending on features of nestlings of known age, such as opening of the eyes, posture and coordination. Eggs that were opened on the day of the visit were noted as hatching the same day or the day after the visit depending on the size of the opening (crack or larger opening). Hatch date was taken as day 0. When additional nestlings or eggs were present on the nests, nestlings were marked on the right or left tarsus using a waterproof marker pen, which was repeated on subsequent visits. Photographic records (dorsolateral view) were made of the body plumage development of all nestlings in 2010 at each measurement, allowing estimation of the timing of the emergence of second down and appearance of body feathers. As nestlings were not inspected at daily intervals, feather development data for each feature were estimated from a proportion of nestlings (25-30%; n = 224).

We measured body mass, tarsus, wing length, and length 8th primary for each nestling at each visit. The terminology for body parts follows Boal (1994). Wing length was measured to the nearest mm as the chord between the carpal joint and the tip of the 8th or longest primary when flattened against a stopped ruler. Prior to the emergence of flight feathers the distance between the tip of the radius ulna and the carpal joint was measured. Length of the 8th primary was measured as the distance between the tip and base of the 8th primary. Tarsus length was measured to the nearest mm with a caliper. Body mass was measured using digital scales accurate to 0.1 g. The wing and 8th primary length were thought to potentially aid in aging nestlings. Wing measurement used to generate age formulae were restricted to those nestlings for which hatch dates were known to the nearest day and which fledged. Incubation periods were calculated for nine breeding pairs with known laying and hatching dates. Hatch dates of nestlings of unknown age were calculated from wing measurements and were used to calculate mean laying date (cf. Olsen & Olsen 1987). Fledging periods were assessed from nests which were visited until all nestlings had fledged.

To sex nestlings, a small blood sample (0.01 ml) from the alar vein was obtained from the nestling when it was older than *c.* 15 days. All nestlings surviving to that age were molecularly sexed in 2009 and 2010 using the primers described in Fridolfsson & Ellegren (1999) and an adjusted version of their PCR methods. PCR products were separated by electrophoresis on a 2% agarose gel, and visualized by ethidiumbromide staining. Females could be identified by two bands on the agarose gel, while males showed only one, which concurred with results in the majority of species (Kahn *et al.* 1998, Fridolfsson & Ellegren 1999).

Individual growth curves were graphically fitted (Ricklefs 1967) to body mass, tarsus, and wing measurements for 50 male and 36 female nestlings at 73 nests measured in 2009 and 2010. Curves were not fitted to data for nestlings when early measurements were missing or asymptotes were difficult to estimate due to premature death of the nestling, as this reduces the reliability of estimating growth parameters. The growth pattern of nestlings was defined by asymptote values for body mass, tarsus, and wing length estimated by fitting Gompertz and logistic equations to the growth data following the method proposed by Ricklefs (1967). These models fitted the data better than von Bertalanffy models, which were also tried. Similarly, we estimated the time interval for growth from 10 to 90% of the body mass asymptote ($W_{10\text{-}90}$), tarsus ($T_{10\text{-}90}$), and wing ($Wi_{10\text{-}90}$) asymptote; and the body mass, tarsus, and wing growth rate between 0-10, 11-20, 21-30 days. These were estimated considering 18.5 g (18/19 g) as the average body mass at hatching (age = 0 days) for first-hatch nestlings, and 18 g (17.5/18.5 g) for second-hatched nestlings, based on two nests containing two hatchlings each which were weighed when still wet. The wing length at hatching was 16 mm for first hatchlings/singles and 15 mm for second hatchlings, and tarsus length was 18 mm for first hatchlings/singles and 17 mm for second hatchlings. Fledging body mass was the body mass at the last check prior to fledging, and body mass recession rate was calculated as the slope of the line fitted to the body mass values from the date that maximum body mass was reached. For the growth rate of the 8th primary, we fitted the primary length measurements to a line, allowing estimation of primary emergence (i.e.

when the line intersects the X-axis), and the age at which the 8th primary reaches the length necessary for fledging (i.e. the known age of first flight with this feather length).

Breeding behaviour

Observations of display, nest construction, and incubation behaviour were made from end March in 2009 and 2010, from a vehicle at 14 territories in April 2009 and 2010 and in combination with nest searches in May. The behavioral data during the nestling phase were based on 105 h of observation at 29 nests, 20 in 2009 and 9 in 2010, 17 in cultivated areas and 12 in Waza National Park. Observations were conducted at nests with a full view of the nest and the immediate surroundings (< 200 m), by two observers using binoculars and a telescope from a concealed position or using a car as a hide at 75-150 m from the nest tree. Observations were made between 06:00 and 11:00, which incorporated daily peak activity hours (*c*. 07:00-10:00). Day-long observations at five nests had indicated a sharp decline in activity from *c*. 10:00-10:30 and significantly fewer displacements and food deliveries during the afternoon activity peak (from 16:00-17:00) compared to morning hours. Records were made at 5-min intervals of the position of the male and the female in relation to the nest tree (distance to nest tree in m), attendance at the nest, display flights, courtship, response to conspecifics, other raptors and potential mammalian predators.

Statistical analyses

Analyses were conducted in SPSS 19.0 (SPSS Inc., Chicago, IL, USA). Mann-Whitney *U*-tests were used for investigating differences in laying dates, nestling development, growth parameters. Kruskal-Wallis tests were used to examine whether median laying or hatch dates of respectively the first egg or hatchling were different for nests with different clutch size (n = 1, 2, or 3), hatchling number (n = 1, 2, or 3), and fledgling number (n = 0, 1, or 2); laying or hatch dates were calculated as the number of days from the first recorded laying or hatch date in the study area for 2009 and 2010 separately. The sequential Bonferroni correction was used to adjust the significance level when multiple tests were performed on the same data set (Rice 1989). Spearman Rank Order and Pearson correlation were used to explore associations. Chi-square goodness-of-fit tests were used to test for difference in sex ratios between nestlings. We used χ^2 contingency tables to test for an interaction between nestling mortality and hatch order; and for an interaction between male and female nestlings that survived to fledging and hatch order. For nests with two nestlings, the effect of the independent variables sex of the first and second hatchling on dependent variable nestling mortality was examined using logistic regression. The relationship between age and growth parameters was investigated using linear regression. Kolmogorov-Smirnov and Shapiro-Wilk tests were used to test for normality. All data are expressed as means ±S.D. unless indicated otherwise and all tests are two-tailed.

3.3 Results

Egg laying, incubation and fledging periods

In total, 268 occupied Grasshopper Buzzard nests were discovered, 138 in 2009 and 130 in 2010. Laying was surprisingly synchronous between and within years: laying date for the first egg was estimated at 5 May for 2009 (± 3.6 days; range: 21 April-15 May; n = 86) and 9 May for 2010 (± 7.1 days; range: 25 April-28 May; n = 66; U = 1799, Z = -3.88, P < 0.001). Laying succeeded the first seasonal rains in the study area in both years (2009: 8 April, 2010: 22 April). No significant relationship existed between clutch size and laying date (χ^2_2 = 4.13, n = 152, P = 0.13). The incubation period from laying to hatching of the last egg could be assessed at 30.1 days (± 0.87 days; range: 29-32 days; n = 9). We recorded no incidents of renesting at nests which had failed. First and second nestlings hatched 1.9 days apart (± 0.85 days, n = 50; range: 1-4 days). The fledging period, i.e. the period from hatching to the first flights and roosting away from the nest tree, was 35.9 days (± 4.3 days; range: 30-57 days; n = 64) and did not differ between first and second hatchlings ($U_{51,13}$ = 219, Z = -0.58, P = 0.34). Fledging period and hatch date were unrelated for first hatchlings (r_s = -0.03, n = 51, P = 0.79). Observations of juvenile Grasshopper Buzzards (n = 6) capturing termites in the absence of adults and at least 400 m from the nearest nest site on 15 July 2009 suggests that foraging independence was achieved within at most 16-18 days after dispersal from the nest territory (i.e. at an age of *c*. 58 days), assuming that these juveniles were among the earliest recorded hatchlings in 2009.

Nestling sex ratio

Of the nestlings sexed (n = 153), 42% (2009: 38%; 2010: 45%) were females and 58% (2009: 62%; 2010: 55%) were males. Sex ratios did not differ significantly from parity during the first half of the nestling phase for both years combined (nestling age ≤ 18 days, 57% ♂ vs. 43% ♀; χ^2_1 = 1.85, n = 106, P = 0.17), but sex ratios were significantly male-biased (61% ♂ vs. 39% ♀) at fledging (nestling age ≥ 29 days; χ^2_1 = 6.14, n = 137, P < 0.05). No relationship was recorded between sex and hatch order for first and second hatchlings that fledged (χ^2_1 = 0.35, n = 136, P = 0.56).

Breeding behaviour

Courtship and territorial display flights were recorded from the last week of March and characterized by slow flapping and soaring flights, by both partners above the nesting territory. The earliest nest building was recorded on 5 April (n = 2). Of 93 nests occupied in 2009, 6.5% were reused in 2010. The nests were shallow structures *c*. 30-40 cm across and lined with green leaves (usually of *Sclerocarya birrea*) in the majority of nests (> 96%; n = 244). Nests were placed in the fork of small side branches or on top of larger side branches (98%; n = 244), rarely in the tree top (2%). Males were seen to provide food to the incubating female. Female time spent at the nest declined with age of the first nestlings (r_s = -0.52, n = 29, P < 0.01), as did time spent at < 50 m from the nest tree (r_s = -0.57, n = 29, P

< 0.01). Males were observed up to 1 km from the nest; their time spent < 50 m from the nest was not related to age of the nestlings (r_s = -0.17, n = 29, P = 0.22). Throughout the nesting cycle, females spent 75.2% (± 24.4, n = 29) and males spent 25.6% (± 21.9, n = 29) of the peak morning activity hours < 200 m from the nest tree. Females participated in hunting for the nestlings from age 4-5 days but possibly earlier. The majority of prey captured by females was in the immediate vicinity (< 100 m) of the nest tree (87%; n = 22 captures), while males captured 66% (n = 29 captures) of prey items < 200 m from the nest. Both parents defended the nest territory against conspecifics up to *c*. 50-200 m from the nest, by flying straight at them followed by parallel gliding or tail chasing. Larger raptors, corvids, and potential mammalian predators (Patas Monkey *Erythrocebus patas*, Serval *Felis serval*) were harassed up to *c*. 400 m from the nest; an African Hawk Eagle *Hieraaetus spilogaster* was simultaneously chased by three pairs on one occasion. The majority of food items (mostly insects, grasshoppers, skinks) were swallowed whole by the nestlings from *c*. 10 days, while larger items (rodents, frogs, snakes, agamas) were (partly) dismembered and occasionally fed to the nestlings up to age 20-25 days. Older nestlings often claimed small prey and larger food items dropped at the nest by both parents, as well as smaller portions presented during feeding sessions. Females dismembered prey for the nestlings, but on two occasions, males were observed feeding the nestlings, once simultaneously with the female. Nestlings frequently roosted on branches near the nest before fledging (30-34 days), which commenced with short flights to neighboring trees. In four instances the nest area (< 100 m from the nest tree) was found vacated 3-5 days after all nestlings had fledged.

Nestling development: plumage and bare parts

Measurements were conducted on a total of 121 nestlings at 74 nests in 2009 and 103 nestlings at 65 nests in 2010. Figure 1 shows the general appearance of the nestlings at different ages. The first week after hatching, nestlings were covered in buffish-white prepennae down, variable in the intensity of the buff coloration (pale buff to tawny buff), which was most intense on the crown and wings. The iris is dark grayish brown throughout the nestling phase. By day 5 (5-7) a light greyish-white second (preplumulae) down gradually replaced the first down, reducing buffish coloration which was to a variable degree retained until day 14-18 on the majority of nestlings (80%; n = 46), particularly on the head, neck, back and wings, until the second down was fully developed. The pink skin was clearly visible through the second down. The remiges emerged at day 8-10 in most nestlings, later in three second hatchlings (13-15 days). The retrices emerged a day later. The timing of the emergence of body feathers was highly variable and related to hatching order; first body feathers emerged later in second than in first hatchlings ($U_{34,18}$ = 70, Z = -4.60, P < 0.001). No relationship was found between the emergence of body feathers and sex ($U_{25,27}$ = 264, Z = -1.37, P = 0.17). Body feathers first emerged on the scapulars at day 11-15 (as late as 19-21 days in six second hatchlings). Pins on the breast normally emerged at day 15-18 (but as late as day 22 and 24 for two second hatchlings), those on the cheeks at days 15-22 (but as late as day 25 and 26 in two second hatchlings), and those on the crown at day 16-23. Pins appeared last on the tarsi, at the earliest on day 18 and at the latest on day 26. The majority of nestlings (71%; n = 41) fledged while down was still visible on the

crown and breast. The egg tooth was lost at day 10-12 (n = 8), although four nestlings retained a clearly visible egg tooth until day 14-16. At hatching, the legs were a pinkish color, the cere light yellow and the talons whitish. The legs gradually lost their pinkish tinge and turned light yellow at 3-6 days, while the talons turned grey at 10-12 days (n = 8) and gradually uniform dark grey thereafter. The cere and legs turned darker yellow with age although the intensity of the coloration of both differed between nestlings. The bill was grey upon hatching and darker at the tip of the upper mandible, turning into a more uniform dark grey at 12-16 days (n = 13).

Figure 1. Grasshopper Buzzard nestlings at different ages (number of days indicated) in northern Cameroon, May-July 2010.

Nestling growth parameters

Table 1 presents the data for the growth equation parameters *t*, *a*, and growth rates for body mass, wing, and tarsus from day 0-10, 11-20, 21-30 for 86 nestlings that survived to fledge, by sex and hatching order. As brood size had no significant effect on their growth parameters ($P > 0.05$), data for first and single hatchlings were grouped. The body mass asymptote was strongly correlated for females with the values of *t* ($r = 0.50$, $n = 36$, $P < 0.01$) but not for males ($r = 0.23$, $n = 50$, $P = 0.06$). $W_{10\text{-}90}$ and *t* were highly significantly correlated for males ($r_s = 0.94$, $n = 50$, $P < 0.001$) and females ($r_s = 0.91$, $n = 36$, $P < 0.001$). $W_{10\text{-}90}$ was strongly correlated with $Wi_{10\text{-}90}$ ($r_s = 0.63$, $n = 86$, $P < 0.001$), $T_{10\text{-}90}$ ($r_s = 0.59$, $n = 86$, $P < 0.001$), and the intercepts of the 8th primary regressions ($r_s = 0.65$, $n = 60$, $P < 0.001$). The slopes of the 8th primary regression were not correlated to $W_{10\text{-}90}$ ($r_s = -0.07$, $n = 60$, $P = 0.25$). Figure 2 presents body mass, tarsus and wing growth curves for all measured nestlings (i.e. including those that died prematurely). As differences between the growth rates of the wings were absent between the sexes for first and second hatchlings (Table 1, Figure 2f), these measures can be used to assess the age of unsexed nestlings. After the emergence of the 8th primary at day 8 for first hatchlings and day 10 for second hatchlings the wing length is linear up to approximately day 30. The age of hatchlings can then be determined by the following formulae: age first hatchling (days) = 0.119 x wing length (mm) + 4.519 ($F_{1,350} = 6555$, $r^2 = 0.95$, $P < 0.0001$); age second hatchling (days) = 0.116 x wing length (mm) + 7.844 ($F_{1,100} = 508$, $r^2 = 0.84$, $P < 0.0001$). For both sexes, the growth of the wing at nest departure was not yet fully completed. Comparison of wing length with asymptotic length reveals that wing length was at 84% (80-86%) of mature length, and further advanced in first hatchlings compared to second hatchlings.

In nests with more than one nestling, a greater proportion of second hatchlings died (62.5%, $n = 56$) compared to first hatchlings (23.2%, $n = 56$; $\chi^2_1 = 17.6$, $P < 0.001$). Of 16 nests with third-hatched nestlings, only two survived to fledge (i.e. 87.5% died). Second and third nestlings died at a mean age of 9 days (± 5.7; range 1-24; $n = 22$). A logistic regression analysis for nests with two nestlings of known sex ($n = 27$) showed no significant effect of sex of the first and second hatchling on nestling mortality from the age of 15 days ($\chi^2_2 = 1.42$, $n = 54$, $P = 0.42$). For second nestlings for which circumstantial evidence suggested starvation and/or siblicide (weak, hardly responsive, large wounds to neck and head from attacks by the one to two day older sibling), death was related to the ratio of their body mass to the older nestling: the body mass ratio of first to second nestlings that survived was significantly lower compared to the body mass ratio of similarly-aged first to second nestlings that died (Figure 3; $U_{22,22} = 83.5$, $Z = -3.72$, $P < 0.001$). In one nest with a day-old and two-day old nestling, the latter was observed attacking the younger bird by pecking at its back and head, which bore large wounds (cf. Figure 3c,d to Chapter 5). The second nestling died after 1-3 days. The surviving first hatchling on this nest was atypical for its extremely long fledging period (57 days; the longest reported), suggesting growth was severely retarded and siblicide was related to suboptimal food supply.

Table 1. Growth equation parameters *a* (the asymptote of growth curves), *t* (the inflection point), and growth rates for body mass, wing, and tarsus during 0-10, 11-20, and 21-30 days after hatching for 86 nestlings in 2009 and 2010. Data were fitted separately for first hatchlings/singles (38 males, 30 females) and second hatchlings (12 males, 6 females). As brood size had no significant effect on their growth parameters ($P > 0.05$), data for first and single hatchlings were grouped. Letters (a, b, c) indicate significant differences ($P < 0.05$) between hatchling groups after Mann-Whitney *U*-tests with sequential Bonferroni correction.

Growth parameters	Males 1st	Females 1st	Males 2nd	Females 2nd
Body mass[1]				
a (g)	314.8±42.9[a]	360.1±45.9[b]	276.7±54.4[a]	269.7±51.9[a]
t (d)	12.6±2.3	12.7±2.0	14.5±3.8	13.3±3.7
$W_{10\text{-}90}$ (d)	21.0±3.7	20.3±3.3	25.7±7.4	24.2±8.2
body mass gain 0-10 (g/d)	10.8±2.7[ac]	12.0±2.1[a]	7.9±2.6[b]	8.6±2.6[bc]
body mass gain 11-20 (g/d)	13.6±2.4[a]	16.1±2.3[b]	10.9±2.2[c]	11.1±3.5[ac]
body mass gain 21-30 (g/d)	4.3±2.3	5.1±2.7	5.0±3.5	4.4±3.3
body mass max (g)	310.4±39.2[a]	357.6±34.0[b]	263.0±41.0[c]	294.4±62.5[ac]
fledge body mass (g)	301.0±44.6[a]	353.1±44.5[b]	255.6±46.5[c]	284.3±64.1[abc]
body mass recess (g/d)	1.7±2.4	1.5±2.9	2.3±4.0	0.8±1.8
Tarsus length[2]				
a (mm)	58.2±2.6[a]	58.5±2.4[a]	55.0±2.6[b]	55.6±3.5[ab]
t (d)	6.0±1.1	6.1±1.1	6.7±1.4	6.3±2.0
$T_{10\text{-}90}$ (d)	29.3±4.9[ab]	28.8±3.6[a]	34.6±6.8[b]	35.7±6.4[b]
tarsus gain 0-10 (mm/d)	1.9±0.3[a]	2.0±0.2[a]	1.5±0.3[b]	1.6±0.2[b]
tarsus gain 11-20 (mm/d)	1.4±0.1[a]	1.4±0.1[a]	1.3±0.1[b]	1.3±0.1[ab]
tarsus gain 21-30 (mm/d)	0.5±0.2	0.5±0.1	0.6±0.2	0.6±0.2
tarsus max (mm)	55.9±2.2[ac]	56.3±1.6[a]	52.5±2.4[b]	53.3±2.2[bc]
Wing length[2]				
a (mm)	251.2±15.1	253.5±17.2	244.5±22.8	232.2±29.0
t (d)	19.5±2.3[a]	19.2±1.6[a]	23.0±4.0[b]	20.6±4.0[ab]
$Wi_{10\text{-}90}$ (d)	30.7±3.5[ab]	30.1±2.0[a]	35.3±5.7[b]	32.6±5.9[ab]
wing gain 0-10 (mm/d)	3.6±0.8[a]	3.6±0.6[a]	2.4±0.8[b]	2.7±0.9[ab]
wing gain 11-20 (mm/d)	8.0±1.1[ac]	8.1±0.6[a]	6.2±1.5[b]	6.6±1.4[bc]
wing gain 21-30 (mm/d)	7.3±0.7	7.5±0.7	7.1±0.9	6.8±1.6
wing max (mm)	216.2±14.4[a]	216.1±21.0[a]	196.6±17.2[b]	192.0±30.8[ab]
Primary length[3]				
primary growth rate (mm/d)	6.3±0.8	6.4±0.4	5.7±0.8	6.0±0.8
primary emergence (d)	8.3±1.3	8.3±1.0	10.2±2.6	9.1±3.0
primary flight (d)*	34.3±4.3[a]	33.4±1.7[a]	38.9±4.8[b]	36.1±2.3[ab]

[1] Data were fitted to Gompertz and logistic models.
[2] Data were fitted to logistic models.
[3] Linear regression equations were fitted for the relationship between age and length of the 8th primary for day 11-30 when wing growth is approximately linear (cf. Figure 2f,g), for 40 first hatchlings/singles and 11 second hatchlings of known age measured in 6 age periods at 4-day intervals in 2010.
* The age at which primaries achieved length for first flight was determined at 160 mm ($n = 9$ nestlings).

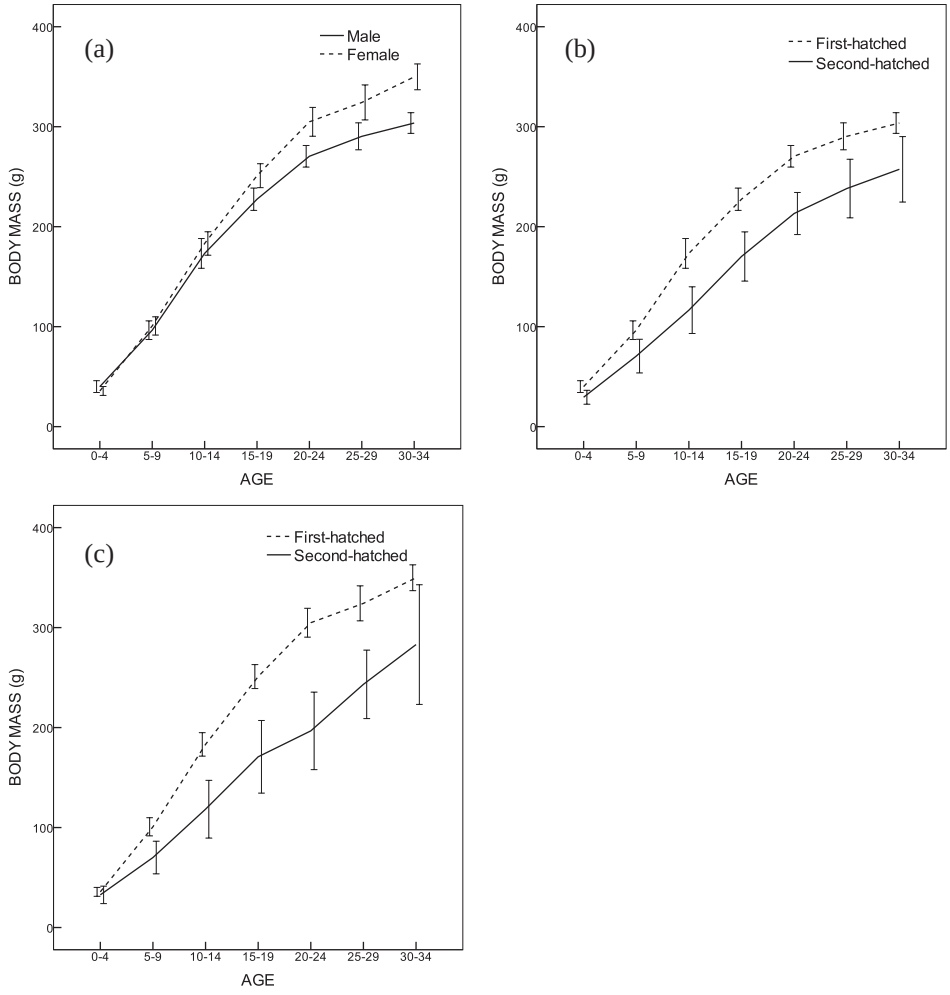

Figure 2. (a) Mean body mass for first hatchlings/singles of known age (n = 68 males, n = 50 females); (b) for first hatchling/single (n = 64) and second hatched (n = 20) male nestlings; and (c) for first hatchling/single (n = 48) and second hatched (n = 13) female nestlings. Error bars indicate 95% confidence intervals of the means.

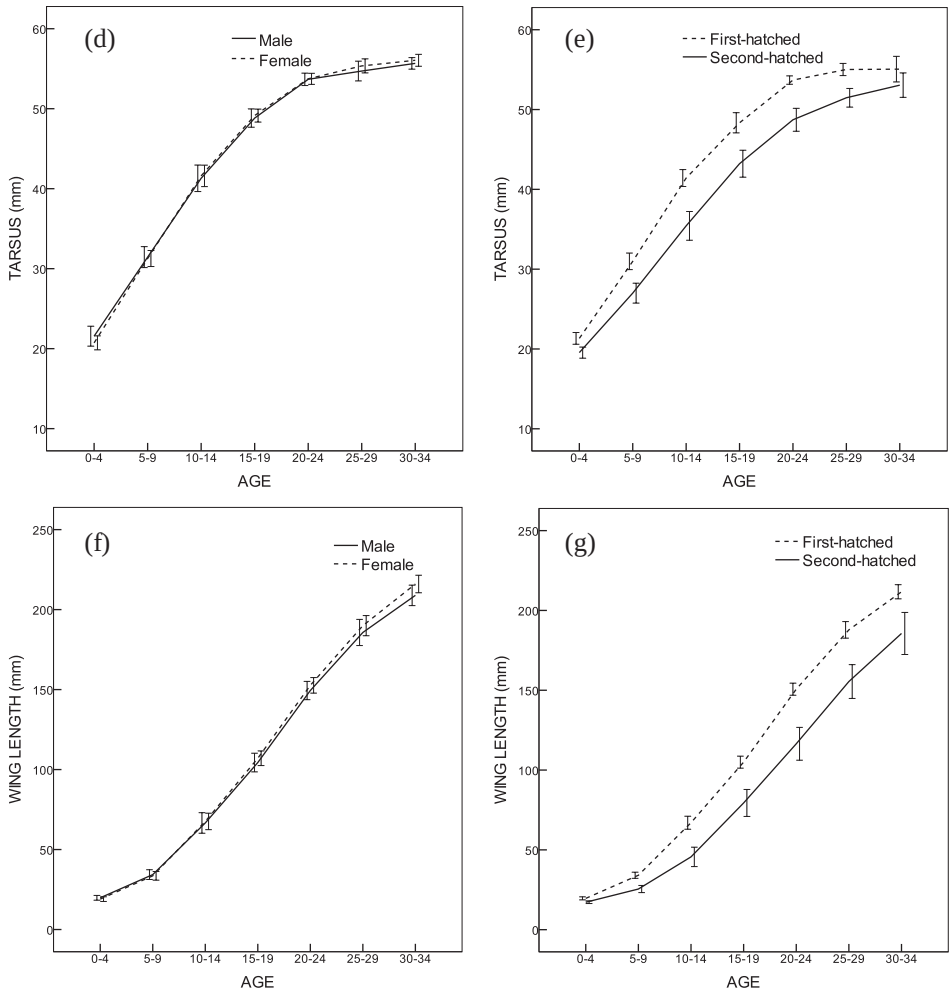

Figure 2. (d) Mean tarsus length for first hatchlings/singles (n = 68 males, n = 50 females); and (e) for first hatchlings/singles (n = 139) and second hatchlings (n = 68) of known age; (f) mean wing length for first hatchlings and singles (n = 68 males, n = 50 females); and (g) for the first hatchlings/singles (n = 139) and second hatchlings (n = 68) of known age. Data for first and single hatchlings were grouped since brood size had no significant effect on these parameters. Error bars indicate 95% confidence intervals of the means.

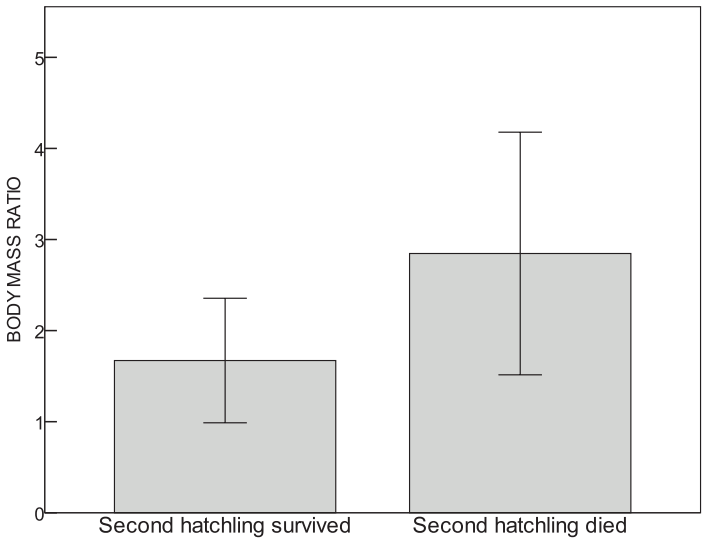

Figure 3. Mean body mass ratio for similarly-aged Grasshopper Buzzard nestlings (body mass first hatchling /body mass second hatchling), for second hatchlings surviving to fledging (n = 22) or dying prematurely (n = 22), at 44 nests in 2009 and 2010 where circumstantial evidence suggested starvation and/or siblicide caused the death of the second hatchling.

3.4 Discussion

Timing of breeding and rainfall

The period from the start of incubation to fledging was shorter in Grasshopper Buzzards (66 days) than in the *c*. 28% heavier Grey-faced Buzzard *B. indicus* breeding in China (71 days; Deng *et al.* 2004), as were values for the time interval for growth from 10 to 90% of the body mass asymptote (22 vs. 25-27 days). Whereas predation rates were rather low at Grey-faced Buzzard nests (Deng *et al.* 2004), high predation risk for small and medium-sized raptors in savannas (Thiollay 1976) is likely to be a strong selective pressure favoring short incubation and nestling periods. The pronounced seasonal variability in vegetation cover further constrains the length of the breeding season for Grasshopper Buzzards, whose hunting success decreases with increasing grass cover and height (Thiollay & Clobert 1990). The importance of low herbaceous cover for optimal prey accessibility, and rainfall as an apparent timing mechanism for laying, is underlined by the synchronous breeding periods between and within years, and the fact that breeding is initiated progressively later with increasing latitude (Brouwer *et al.* 2000), corresponding with a latitudinal shift in the start of the rainy season.

Our observations suggested a postfledging dependence period of approximately three weeks, which is comparable to migratory Palearctic harriers and kites (Newton 1979), but rather short compared to smaller and similarly-sized tropical raptors (Delannoy & Cruz

1988, Thorstrom & Quixchán 2000). Rapid postfledging independence appears to be driven by the northward migration soon after fledging, which generally shortens post-fledging dependence in raptors (Newton 1979, Bustamante & Hiraldo 1989), and facilitated by the dependence on easily caught insect prey, rather than more agile prey (e.g. birds; Delannoy & Cruz 1988, Griffin *et al.* 1998). Insects reach peak abundance in the study area in July (Njiforti 1997), when juveniles disperse from the nest territories, and decreases again from August when the majority of the population has moved into the Sahel where they feed on grasshoppers (Jensen *et al.* 2007).

Nestling growth and sex

Early development in both sexes was characterized by rapid body growth, wing growth, tarsus growth, early inflection points, and early emergence of primaries, which is the general growth pattern of raptors (Ricklefs 1968). Whereas growth rate is inversely related to body size at species level (Ricklefs 1968), we did not find a relationship between growth rate and asymptotic body mass of nestlings, although later inflection points in females were associated with greater asymptotic body mass. The moderate sexual size dimorphism (fledged females averaged 10-15% heavier than males depending on hatch order) is expected for raptors feeding predominantly on reptiles and insects (Newton 1979) and offering generally small, monopolizeable food items to nestlings, which would otherwise lead to excessive mortality in the smaller males (Anderson *et al.* 1993). Growth rate of body mass, tarsus, wing and primary feathers were similar between sexes, contrasting growth patterns in more strongly sexually dimorphic raptors, which are characterized by earlier development of feathers and younger fledging age by males than females (e.g. Richter 1983, Bortolotti 1984).

The significantly male-biased sex ratio (61%) at fledging was in accordance with Fisher's (1930) hypothesis, which predicts biased population sex ratios at the end of parental care in favor of the smaller, less costly males (in terms of energy requirements; Riedstra *et al.* 1998), assuming that the benefits associated with raising either sex are equal (Frank 1990). However, male-biased sex ratios have only rarely been observed in raptors (Rosenfield *et al.* 1996, Brommer *et al.* 2003), possibly because body size is generally a poor indicator of potential parental costs (Boulet *et al.* 2001). Although sex ratio did not differ significantly from parity for nestlings ≤ 18 days, it was already male-biased (57%), and greater female mortality compared to males before the age at which nestlings were sexed (*c.* 15 days) might have caused a sex ratio shift. Alternatively, clutches might have already been sex-biased, although the unpredictable food conditions during the nestling phase limit options for adaptive modification of clutch sex ratio (Appleby *et al.* 1997, Komdeur *et al.* 1997). We also did not record a male bias among second hatchlings, which would suggest parents favoring second-hatched males over second-hatched females for greater returns in the former (McDonald *et al.* 2005), nor did we find evidence that sex influenced the mortality odds of second hatchlings at nests with two nestlings. We suspect, therefore, that other factors leading to increased starvation risk of female nestlings compared to males, such as averagely poor food conditions and/or poor condition of the parents prior to egg laying

(Wiebe & Bortolotti 1992, Aparicio & Cordero 2001; but see Hipkiss *et al.* 2002), might have contributed to the male-biased sex ratio at fledging.

Nestling growth and hatch order

Irrespective of gender differences, second-hatched Grasshopper Buzzards were consistently smaller in body mass and structural dimensions compared to first hatchlings and singles, suggesting an age difference far in excess of the actual difference (cf. Figure 1). The same was true for third hatchlings, although death of the majority of third hatchlings at a young age precluded examination of their growth parameters. In contrast to other raptors (McDonald 2003, Mougeut & Bretagnolle 2006), wing length was dependent on hatch order, necessitating different ageing formulae for broods with multiple nestlings. Second-hatched Grasshopper Buzzards were also characterized by retarded development of body plumage, contrary to other birds (Boag 1987, Donazar & Ceballos 1989), and primary development. However, primaries showed little variance in growth rates, confirming a frequently observed pattern in raptors that primaries are less likely to be influenced by food shortages than body mass (Picozzi 1980, Bortolotti 1984; but see Negro *et al.* 1994).

The significantly greater body mass (males), wing, and tarsus length of first hatchlings compared to second hatchlings shortly after hatching suggested that the inferiority of the latter already existed at hatching, as reported for other raptors (Dijkstra *et al.* 1990). Such a developmental deficit may be reinforced when smaller siblings are outcompeted by larger siblings (Edwards & Collopy 1983, Bortolotti 1986), and aggravated by hypothermia experienced by smaller siblings (Ricklefs 1983). According to Lack's (1947, 1954) brood reduction hypothesis, the feeding hierarchy resulting from asynchronous hatching allows the youngest nestling to be rapidly eliminated if food supply is short, which might be adaptive when food supply during brood-rearing is unpredictable. Indeed, we found that death of second hatchlings depended on their body mass ratio with first siblings, irrespective of differences in sex and age of nestlings, indicating that brood reduction was facilitated by a more pronounced intrabrood mass hierarchy and a difference in competitive ability between nestlings (Wiebe & Bortolotti 1995). The young age at which second-hatched nestlings died (9 days) might be especially beneficial for survivors, because fewer resources are wasted (Husby 1986). We observed several cases where the elder sibling frequently attacked the smaller sibling, suggesting that brood reduction in Grasshopper Buzzards was also achieved through siblicide, as commonly reported in large raptors (e.g. Meyburg 1974, Brown 1976, Edwards & Collopy 1983), but less often in smaller species (Bortolotti *et al.* 1991, Gerhardt *et al.* 1997, Viñuela 1999). Often, siblicide goes hand in hand with monopolizeable food items delivered at nests (Mock 1985, Mock *et al.* 1987), which favors aggressive dominance of the larger nestling to guarantee their access to food at the expense of smaller siblings. Indeed, the majority of prey items fed to nestling Grasshopper Buzzards was small and swallowed whole, and prey was often claimed by larger nestlings which generally appeared to be in the most favorable position, also during parental feeding sessions. Although we found some evidence that siblicide was driven by suboptimal food supply, follow-up studies should clarify what role it has in regulating brood reduction under different food conditions.