

Nestling development and post-juvenile moult of the African Swallow-tailed Kite *Chelictinia riocourii*

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Summary

We provide the first description of the growth and development of African Swallow-tailed Kite *Chelictinia riocourii* and information on its post-juvenile moult, based on observations at nest and roost sites in Cameroon and Senegal. The morphological development of 23 nestlings at 12 nests in Cameroon was studied from the first day after hatching to fledging in 2010. Photographs of live birds and of museum specimens were used to describe moult patterns. We show a lack of difference between the sexes in nestling growth patterns. Differences in pre-fledging body mass related to hatching order were not significant for first and second hatchlings, but third hatchlings were noticeably smaller than older siblings and none survived to fledging. Wing length was independent of sex and hatching order, and was useful for assigning nestling age. In the first 3–6 months after fledging, Swallow-tailed Kites appear to undergo a partial post-juvenile moult, which is more extensive than in the majority of raptors but comparable to that of *Elanus* kites for which moult patterns have been described. We provide an aging formula and photographic records to facilitate further studies of nestling development and breeding biology.

Résumé

Le développement au nid et la mue post-juvénile de l'Élanion naucier *Chelictinia riocourii*. Nous présentons la première description de la croissance et du développement de l'Élanion naucier *Chelictinia riocourii* et les premiers

renseignements sur sa mue post-juvénile, basés sur des observations de nids et de dortoirs au Cameroun et au Sénégal. Le développement morphologique de 23 oisillons dans 12 nids au Cameroun a été étudié du premier jour après l'éclosion jusqu'à l'acquisition des plumes en 2010. Des photographies d'oiseaux vivants et de spécimens de musée ont été utilisées pour décrire les caractéristiques de la mue. Nous montrons l'absence de différence entre les sexes dans leur croissance au nid. Il n'a pas été noté de différences significatives de masse corporelle avant de l'envol en relation avec le rang d'éclosion pour le premier et le second oisillon, mais les troisièmes sont notablement plus petits que les plus âgés du même nid et aucun n'a survécu jusqu'à l'envol. La longueur de l'aile était indépendante du sexe et du rang d'éclosion, et a été utile pour fixer l'âge de l'oisillon. Dans les premiers 3–6 mois après l'envol, il apparaît que les Élanions naucleur subissent une mue partielle post-juvénile, qui est plus étendue que chez la majorité des rapaces mais comparable à celle des espèces d'*Elanus* dont les mues ont été décrites. Nous proposons une formule pour évaluer leur âge et des photos pour faciliter des études ultérieures sur le développement des oisillons et la biologie de la reproduction.

Introduction

Little quantitative information exists on the growth and development of nestlings of the majority of raptors in tropical Africa (Virani & Watson 1998), despite the importance of such information for conservation management of threatened species. Measures of nestling growth permit the assessment of the impact of environmental factors on growth and development (Donazar & Ceballos 1989, Dawson & Bortolotti 2000), while morphometric guides and nestling aging formulae are important tools for scheduling nest visits and ringing when only a limited number of nest visits are possible or advisable (Steenhof & Newton 2007). Nestling growth measures can also be used for examining the effect of life-history parameters on development, such as hatching asynchrony (Mock 1984, Donazar & Ceballos 1989, Wiebe & Bortolotti 1995) or nestling sex (Ricklefs 1968, Richter 1983, Bortolotti 1986), while growth rates of different body parts have been useful in investigations of adaptive modifications of growth (O'Connor 1977, Ricklefs 1979, Bortolotti 1984).

The African Swallow-tailed Kite *Chelictinia riocourii* (hereafter: Swallow-tailed Kite) has an extensive breeding range throughout the Sahel zone from Senegal to Sudan, with scattered breeding reported east to Somalia and Kenya. Although adult plumages have been fairly well-described (Ferguson-Lees & Christie 2001), only anecdotal descriptions exist for nestlings (Davey & Davey 1980, Sutton *et al.* 1984) and none that cover post-fledging plumage development. Various field guides and handbooks (*e.g.* Hoyo *et al.* 1994) do not mention the absence of a black carpal patch

as a diagnostic feature for juvenile birds. Kemp & Kemp (1998), Borrow & Demey (2001) and Ferguson-Lees & Christie (2001) do illustrate a juvenile without black carpal patch, but Mackworth-Praed & Grant (1970) specifically state that presence or absence of this feature has no relation to age or sex. Therefore it was necessary to consult images and specimens to elucidate age-related diagnostic features of this species. Here, we describe for the first time the nestling growth, development, juvenile plumage, and post-juvenile (or preformative: see Howell *et al.* 2003) moult of the Swallow-tailed Kite, which will aid further studies on breeding biology, population demographics, and reproductive performance. Another aim was to examine sex-specific growth patterns and potential sexual differences related to the reversed sexual dimorphism usually found in raptors.

Methods

Study area and nest surveys

The study area in Senegal (14°12'–14°13'N, 16°16'–16°18'W) is an uninhabited island in the River Saloum called Kousmar, which covers 23 km² and is located 10 km west of Kaolack. The island harbours a massive winter roost of Swallow-tailed Kites (20,000–36,000 individuals in January 2008–12: Pilard *et al.* 2011) and Lesser Kestrels *Falco naumanni* (21,000–29,000 individuals), which has been present at least since the 1970s (Buij *et al.* 2013). The study area in the Far North Region of Cameroon (11°–11°40'N, 14°20'–15°E), c. 3400 km east of Kousmar, covers the Waza National Park (WNP) and the cultivated areas south of WNP. For a detailed description of both study areas, including maps, see Buij *et al.* (2013). In Cameroon, the breeding habitat was sampled by five census areas totalling 20 km² in WNP and five areas totalling 20 km² in cultivated habitat, from 3 to 16 May 2010. These areas were intensively searched on foot by a team of 4–8 researchers. The coordinates of all discovered nests were taken and the nest status (*e.g.* nest lining, attending adults, number of eggs) was recorded. In total, 12 nests were revisited at mean 5-day intervals during the incubation and nestling periods in Cameroon.

Nestling measurements and growth patterns

The morphological development of 23 nestlings at 12 nests in Cameroon was studied from the first day after hatching to fledging. Nestlings that were damp when first measured were classified as hatching on the day of the visit, while eggs that were opening on the day of the visit were noted as hatching the same day if the opening was substantial, or the day after the visit if merely cracked. 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, as well as comparison with known hatch dates of siblings. Fourteen nestlings were sexed by taking a small blood sample (0.01 ml) from the alar vein at c. 15

days and using the molecular primers described by Fridolfsson & Ellegren (1999). 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. Nestlings were marked on the right or left tarsus using a permanent black marker pen to distinguish between them during subsequent visits. During each nest visit, we measured the following: (1) body mass (g), with an electronic balance (EPB-10K) with a precision of 0.1 g and without correction for crop content; (2) flattened wing length (mm), with a ruler; (3) length of the 9th primary (the longest) from insertion (mm), with a ruler; and (4) tarsus length (mm), with callipers. The terminology for body parts follows Boal (1994). Photographic records were made of the development of juvenile plumage at each measurement. Wing measurements used to generate the age formula were restricted to those nestlings for which hatch dates were known to the nearest day ($n = 23$); hatch dates of nestlings of unknown age were calculated from the formula.

Post-juvenile moult

Digital images were taken of various plumages of sitting and flying birds at the roost in Senegal, between early November 2007 and late February 2012. Additional images of museum specimens under their care were obtained from W.S. Clark from the American Museum of Natural History, New York, and from a number of curators of European natural history museums (see Acknowledgments). Images were examined and commented upon by W.S. Clark, D. Forsman and P. Pyle.

Statistical analyses

Combined nestling growth curves were graphically fitted (Ricklefs 1967) to weight, tarsus and wing measurements for 23 hatchlings. In addition, we fitted individual growth curves to data for 12 nestlings which were measured until at least 22 days, enabling reliable estimation of growth parameters. Gompertz or logistic growth models were fitted to each individual bird's body mass, wing growth and tarsus growth data, by visual inspection and using the software CurveExpert Professional 1.2.3 to verify model selection. The hatching dates of first and second hatched nestlings were determined by linear regression analyses relating wing length to age for known-age nestlings. Mann-Whitney *U*-tests were used for investigating differences in growth parameters. Relationships between age and growth parameters were investigated using standard linear regression. Analyses were conducted in SPSS 19.0 (SPSS Inc., Chicago, USA).

Results

Nestling measurements and growth patterns

Nestlings were covered in pale grey down in the first 5–7 days after hatching ($n = 8$; Fig. 1). Thereafter, an orange-buff second down gradually replaced the first down until



Figure 1. Swallow-tailed Kite nestlings at various ages in days (photos: R. Buij).

14–18 days ($n = 5$), first on the upper-wing and subsequently on the back, head and chest. The pink skin was clearly visible through the developing second down, particularly on the back and breast. The remiges first emerged at age 4–9 days ($n = 7$) and body feathers first emerged on the scapulars at age 8–10 days ($n = 3$). The egg tooth was lost at 9–11 days ($n = 4$). At hatching, the legs were a yellowish pink colour, the cere yellow and the talons white. The legs gradually lost their pinkish tinge and turned a deeper yellow from 12–14 days ($n = 4$), whereas the talons remained white. The bill was dark grey and the pupils dark brown (Fig. 1, lower left). No differences were visible between nestlings of different sex. We did not find evidence of sexual dimorphism for growth rate or for body mass at day 30, despite a significant difference in body mass between first and second hatchlings at day 10 (Table 1).

Table 1. Body mass (mean $\pm$ SE) for nestling Swallow-tailed Kites according to sex and hatching order. W_{10-90} is the interval for growth from 10 to 90 % of the body mass asymptote. $*P < 0.05$.

Body mass day 10 (g)*		Body mass day 30 (g)	W_{10-90} (days)
male ($n = 7$)		123.9 $\pm$ 8.97	20.6 $\pm$ 1.46
female ($n = 3$)		125.2 $\pm$ 7.31	19.2 $\pm$ 1.56
first hatched ($n = 6$)	65.3 $\pm$ 2.65	122.6 $\pm$ 8.52	19.1 $\pm$ 1.51
second hatched ($n = 6$)	53.6 $\pm$ 3.62	118.2 $\pm$ 7.48	20.2 $\pm$ 1.73

Fig. 2 illustrates the growth curves for wing, tarsus and body mass for 23 nestling Swallow-tailed Kites of known age, including 12 first and 11 second hatchlings, with eight females and four males (11 nestlings of unknown sex). We did not include measurements of an additional seven third-hatched nestlings of known age, because six died after one or two measurements (mean age at final measurement = 6.0 $\pm$ 2.8 SD days; range 0–20 days) and the seventh, which survived to at least day 20, then weighed 50 g, *i.e.* well below the mean body mass for first and second hatchlings of that age (*cf.* Fig. 1e). Gompertz growth models fitted wing growth data better and logistic growth models fitted tarsus growth data better; in the case of body mass, different models fitted different individual birds’ growth curves best (Table 2). Average asymptotic body mass was 123 g for 12 nestlings measured from hatching to at least age 22 days (Table 2) and nestlings fledged with wing length at *c.* 75–80 % of adult wing length. For wing growth, the following equation was derived and can be used to predict the age of first and second hatchlings of age 7–30 days (the period when wing growth is linear, *i.e.* after emergence of the first primary feather):

$$\text{age (days)} = 0.162 \times \text{wing length (mm)} + 3.116$$

($F_{1, 56} = 580.7$, $r^2 = 0.91$, $P < 0.001$).

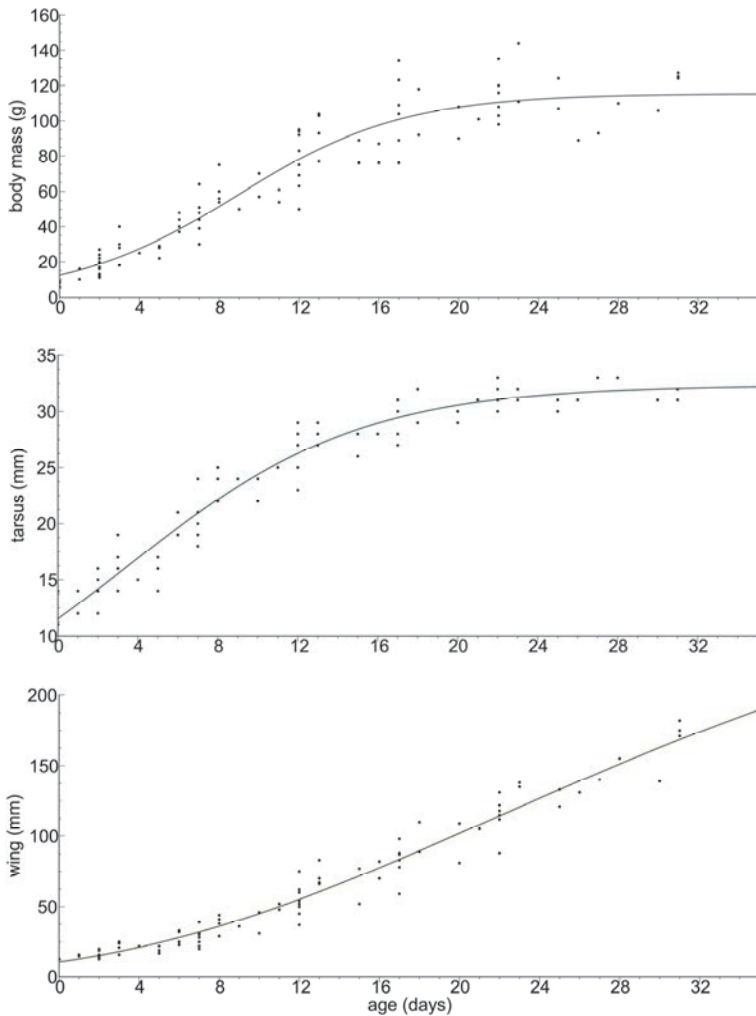


Figure 2. Growth curves of 23 nestling Swallow-tailed Kites: logistic growth model fitted to body mass and tarsus length, and Gompertz growth model to wing length. Sample includes 12 first and 11 second hatchlings.

Post-juvenile moult and age estimation

Newly-fledged juveniles already have a forked tail (Fig. 3a), though this is not always evident on specimens (B. Clark *in litt.*), and is not as deeply forked as that of first- years



Figure 3. (a) Recently fledged juvenile with *Agama agama* prey (photo: S. Cavaillès); (b) fledgling — note patagium bare of feathers and rufous wash on chest and cheek; (c) transitional first-year after partial moult — some or all rectrices and feathers on head, neck and breast have been replaced, but not under-wing coverts and remiges; (d) adult with characteristic black carpal patches (photos: W.C. Mullié, R. Buij).

after post-juvenile moult or adults (Fig. 3c, d). Fledglings have cinnamon-coloured tips to the upper-wing coverts, scapulars and the feathers of the mantle, back, crown, forehead, and nape, a brown iris (Fig. 1), and completely white under-wings, *i.e.* they lack the black carpal patch of adults (*cf.* Fig. 3b, d). In the first 3–6 months after fledging but possibly sooner, juveniles undergo a partial post-juvenile moult,

Table 2. Growth model parameters (mean ± SE) of nestling Swallow-tailed Kites (*n* = 12, including three males, seven females, two of unknown sex, six first and six second hatchlings). Gain is expressed as increase per day, *W*₁₀₋₉₀ is the interval (days) for growth from 10 to 90 % of the asymptote, *t* is the inflection point (days), *a* is the asymptote estimated by the growth curve. Data of individual nestlings fitted the growth models indicated.

	Body mass (g)	Tarsus length (mm)	Wing length (mm)
gain (0–10 days)	5.15 ± 0.28	1.27 ± 0.05	1.77 ± 0.09
gain (11–20 days)	4.84 ± 0.39	0.69 ± 0.02	5.23 ± 0.08
gain (21–30 days)	1.25 ± 0.21	0.20 ± 0.02	7.75 ± 0.11
<i>W</i> ₁₀₋₉₀	19.6 ± 1.11	26.6 ± 3.71	35.4 ± 2.45
<i>t</i>	9.58 ± 0.75	4.45 ± 0.99	25.6 ± 0.86
<i>a</i>	123.2 ± 5.53	33.1 ± 1.06	244.3 ± 8.62
Growth model	Gompertz (<i>n</i> = 3) or logistic (<i>n</i> = 9)	Logistic	Gompertz

characterised by the replacement of most or all of the body feathers, starting at the head and progressing down to the neck and upper body, as well as the upper-wing coverts. The black line of coverts at the base of the upper-wing, bordering the scapulars, becomes clearer after the partial moult (a few black coverts are present in fledglings: Fig. 1h). The rufous wash and shaft streaks to the body feathers fade during the first weeks after fledging and disappear completely with post-juvenile moult. Most or all remiges and under-wing coverts are not replaced during this partial moult, and thus the birds retain the white under-wing (Fig. 3c), or grow a few black feathers in the carpal area, until the first complete moult at the age of c. 12 months. The iris of one immature collected on 3 May 1968 at Lake Marguerite (= Abaya) in Ethiopia was orange according to the label information, as was the iris of several birds observed in Senegal between November and February. However, iris colour was red (as in adults) in most other birds in intermediate plumage observed in Senegal including one specimen collected at Dakar by Planchat on 28 Jan 1894 (MNHB, label information).

Discussion

In general, the development of Swallow-tailed Kite nestlings appears to be comparable to that described for closely related white-tailed kites (genera *Elanus* and *Gampsonyx*: ffrench 1982, Steyn 1982). As reported for other raptors (*e.g.* Red Kite *Milvus milvus*: Mougeot & Bretagnolle 2006), wing length was found to be independent of sex and hatching order, and useful for estimating nestling age. In line with the absent or weak reversed size dimorphism reported previously (Kemp & Kemp 1998), we recorded no differences in growth rate and body mass between nestlings of different sex. Similarly, differences in body mass related to hatching

order were absent just before hatching for first and second hatchlings. Third hatchlings were noticeably smaller, however, than older siblings and none survived to fledging, suggesting that brood reduction occurs (Newton 1979).

Already in the first 3–6 months after fledging, but possibly sooner, Swallow-tailed Kites undergo an early partial post-juvenile moult, similar to White-tailed Kite *Elanus leucurus* (Wheeler & Clark 1995) or Black-winged Kite *E. caeruleus* (Brown *et al.* 1982). During the same period, eye colour changes from brown to orange to red, the last typically attained within the first year. However, only during the first complete moult at about one year of age, individuals gain the full black carpal patch on the under-wing, which is typical for adult plumage (*contra* Mackworth-Praed & Grant 1970). Our results suggest that the Swallow-tailed Kite has a more extensive early post-juvenile moult than most raptors, which usually replace only a few body feathers at most, and sometimes none at all, before the first complete annual moult. White-tailed Kites undergo a comparable post-juvenile moult to that of Swallow-tailed Kites shortly after becoming independent, and become much more adult-like, retaining the remiges and a variable number of rectrices, and some greater and all primary upper-wing coverts (Wheeler & Clark 1995). Similarly, the majority of Black-winged Kites in South Africa have a pronounced early post-juvenile moult of body feathers and usually only retain juvenile remiges, rectrices and wing coverts thereafter, while 8 % of juveniles moult directly to adult plumage (Herremans 2000). The moult pattern of the monotypic Swallow-tailed Kite described here is therefore in general agreement with its proposed close relationship with the genus *Elanus* (*cf.* Hoyo *et al.* 1994).

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References

- BOAL, C.W. (1994) A photographic and behavioral guide to aging nestling Northern Goshawks. *Stud. avian Biol.* 16: 32–40.
- BORROW, N. & DEMEY, R. (2001) *Birds of Western Africa*. Christopher Helm, London.
- BORTOLOTTI, G.R. (1984) Physical development of nestling Bald Eagles with emphasis on the timing of growth events. *Wilson Bull.* 96: 524–542.
- BORTOLOTTI, G.R. (1986) Influence of sibling competition on nestling sex ratios of sexually dimorphic birds. *Am. Nat.* 127: 495–507.
- BROWN, L.H., URBAN, E. & NEWMAN, K. (1982) *Birds of Africa*. vol 1. Academic Press, London.
- BUII, R., CAVAILLÈS, S. & MULLIÉ, W.C. (2013) Breeding biology and diet of the African Swallow-tailed Kite *Chelictinia riocourii* in Senegal and Cameroon. *J. Raptor Res.* 47: 41–53.
- DAVEY, P. & DAVEY, G. (1980) Swallow-tailed Kites breeding at Porr, Lake Turkana. *Bull. E. Afr. Nat. Hist. Soc.* 1980: 47–49.
- DAWSON, R.D. & BORTOLOTTI, G.R. (2000) Reproductive success of American Kestrels: the role of prey abundance and weather. *Condor* 102: 814–822.
- DONAZAR, J.A. & CEBALLOS, O. (1989) Growth rate of nestling Egyptian Vultures *Neophron percnopterus* in relation to brood size, hatching order and environmental factors. *Ardea* 77: 217–226.
- FERGUSON-LEES, J. & CHRISTIE, D.A. (2001) *Raptors of the World*. Christopher Helm, London.
- FFRENCH, R.P. (1982) The breeding of the Pearl Kite in Trinidad. *Living Bird* 19: 121–131.
- FRIDOLFSSON, A.-K. & ELLEGREN, H. (1999) A simple and universal method for molecular sexing of non-ratite birds. *J. avian Biol.* 30: 116–121.
- HERREMANS, M. (2000) Cases of serial descendant primary moult (Staffelmauser) in the Black-shouldered Kite *Elanus caeruleus*. *Ringing Migr.* 20: 15–18.
- HOWELL, S.N.G., CORBEN, C., PYLE, P. & ROGERS, D.I. (2003) The first basic problem: a review of molt and plumage homologies. *Condor* 105: 635–653.
- HOYO, J. DEL, ELLIOTT, A. & SARGATAL, J. (eds) (1994) *Handbook of the Birds of the World*, vol. 2. Lynx, Barcelona.
- KEMP, A. & KEMP, M. (1998) *Birds of Prey of Africa and its Islands*. New Holland (UK), London.

- MACKWORTH-PRAED, C.W. & GRANT, C.H.B. (1970) *African Handbook of Birds*, ser. 3, vol. 1. *Birds of West Central and Western Africa*. Longmans, London.
- MOCK, D.W. (1984) Infanticide, siblicide, and avian nestling mortality. Pp 2–30 in HAUSFATER, G. & BLAFFER HRDY, S. (eds) *Infanticide: Comparative and Evolutionary Perspectives*. Aldine, New York.
- MOUGEOT, F. & BRETAGNOLLE, V. (2006) Breeding biology of the Red Kite *Milvus milvus* in Corsica. *Ibis* 148: 436–448.
- NEWTON, I. (1979) *Population Ecology of Raptors*. Poyser, Berkhamsted.
- O'CONNOR, R.J. (1977) Differential growth and body composition in altricial passerines. *Ibis* 119: 147–166.
- PILARD, P., LELONG, V., SONKO, A. & RIOLS, C. (2011) Suivi et conservation du dortoir de rapaces insectivores (Faucon crécerellette *Falco naumanni* et Elanion naucler *Chelictinia riocourii*) de l'île de Kousmar (Kaolack, Sénégal). *Alauda* 79: 295–312.
- RICHTER, W. (1983) Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Am. Nat.* 121: 158–171.
- RICKLEFS, R.E. (1967) A graphical method of fitting equations to growth curves. *Ecology* 48: 978–983.
- RICKLEFS, R.E. (1968) Patterns of growth in birds. *Ibis* 110: 419–451.
- RICKLEFS, R.E. (1979) Patterns of growth in birds. V. A comparative study of development in the Starling, Common Tern, and Japanese Quail. *Auk* 96: 10–30.
- STEENHOF, K. & NEWTON, I. (2007) Assessing raptor nest success and productivity. Pp 181–192 in BIRD, D.M. & BILDSTEIN, K.L. (eds) *Raptor Research and Management Techniques*. Hancock House, Surrey BC.
- STEYN, P. (1982) *Birds of Prey of Southern Africa. Their identification and life histories*. David Philip, Cape Town.
- SUTTON, J., SUTTON, A., DEWHURST, C.F. & DEWHURST, L.M. (1984) A confirmed breeding record for the Swallow-tailed Kite in the Rift Valley of Kenya. *Bull. E. Afr. Nat. Hist. Soc.* 1984: 12.
- VIRANI, M. & WATSON, R.T. (1998) Raptors in the East African tropics and Western Indian Ocean Islands: state of ecological knowledge and conservation status. *J. Raptor Res.* 32: 28–39.
- WHEELER, B.K. & CLARK, W.S. (1995) *A Photographic Guide to North American Raptors*. Academic Press, London.
- WIEBE, K.L. & BORTOLOTTI, G.R. (1995) Food-dependent benefits of hatching asynchrony in American Kestrels *Falco sparverius*. *Behav. Ecol. Sociobiol.* 36: 49–57.