Breeding Biology and Diet of the African Swallow-Tailed Kite (Chelictinia riocourii) in Senegal and Cameroon

Author: Buij, Ralph

Source: Journal of Raptor Research, 47(1) : 41-53

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-12-36.1

J. Raptor Res. 47(1):41–53

BREEDING BIOLOGY AND DIET OF THE AFRICAN SWALLOW-TAILED KITE (*CHELICTINIA RIOCOURII*) IN SENEGAL AND CAMEROON

RALPH BUIJ[1]
Institute of Environmental Sciences, Leiden University, P.O. Box 9518, 2300 RA Leiden, The Netherlands
and
Behavioural Ecology and Self-organization, Centre for Ecological and Evolutionary Studies, University of Groningen, Centre for Life Sciences, Nijenborgh 7, 9747 AG Groningen, The Netherlands

SIMON CAVAILLÈS
Les Fontaines, 72650 Aigné, France

WIM C. MULLIÉ[2]
Project Biological Management of Locusts and Grasshoppers, Agriculture Directorate, Ministry of Agriculture, Dakar, Senegal

ABSTRACT.—We studied the breeding biology of the African Swallow-tailed Kite (*Chelictinia riocourii*) in two study areas located 3400 km apart in the central (Cameroon) and western (Senegal) portions of the species' breeding range. With 110 nests in 2.8 km² of suitable breeding habitat, Kousmar islet (23 km²) in Senegal supports the largest documented colony of African Swallow-tailed Kites known to date. Breeding kites in Senegal nested in a single large colony near a massive winter roost. In Cameroon, breeding colonies averaged seven pairs/colony, with nest densities of 0.3 nests/km² in protected woodland and 0.9 nests/km² in cultivated habitat. Egg-laying coincided with the end of the dry season in Cameroon, but eggs were recorded from the middle of the dry season in Senegal. Eggs hatched between April and June in both study sites in 2010, but from March 2012 in Senegal. The incubation period was estimated at 27–31 d based on two nests, and the fledging period was 32–35 d ($n = 3$ fledglings). Mean clutch size was 2.5 eggs ($n = 32$) in Cameroon and 2.1 in Senegal ($n = 29$); one clutch of four eggs was recorded in Cameroon. Nest success estimated with the Mayfield method was low at 17% in Cameroon and exceptionally low at 4% in Senegal, possibly related to a combination of suboptimal food conditions, high predation pressure, intraspecific aggression, and lack of experience among breeding pairs. Prey items at nests were made up primarily of lizards (30–54% of items) and insects (27–49%), notably grasshoppers, whereas the diet at the winter roost in Senegal was predominantly Orthoptera (55%) and Solifugids (43%). Our study suggested that African Swallow-tailed Kites were able to adapt to moderate land transformation near floodplains.

KEY WORDS: *African Swallow-tailed Kite*; Chelictinia riocourii; *breeding biology*; *diet*; *night roosts*; *reproduction*; *West Africa.*

BIOLOGÍA REPRODUCTIVA Y DIETA DE *CHELICTINIA RIOCOURII* EN SENEGAL Y CAMERÚN

RESUMEN.—Estudiamos la biología reproductiva de *Chelictinia riocourii* en dos áreas de estudio ubicadas a 3400 km una de otra, en las porciones central (Camerún) y oeste (Senegal) del área de reproducción de la especie. Con 110 nidos en 2.8 km² de hábitat reproductivo adecuado, el islote de Kousmar (23 km²) en Senegal alberga la mayor colonia de *C. riocourii* documentada a la fecha. Los individuos reproductivos en Senegal anidaron en una colonia individual grande cerca de un dormidero masivo de invierno. En Camerún, las colonias reproductivas promediaron siete pares/colonia, con densidades de nido de 0.3 nidos/km² en bosques protegidos y 0.9 nidos/km² en hábitats cultivados. La puesta de huevos coincidió con el final de la época seca en Camerún, pero en Senegal se registraron huevos a partir de la mitad de la época seca. Los huevos eclosionaron entre abril y junio en ambos sitios de estudio en 2010 y en Senegal a partir de

[1] Email address: ralph.buij@gmail.com
[2] Present address: BP 45590, Dakar-Fann, Senegal.

marzo. El período de incubación se estimó en 27–31 días basado en dos nidos, y el período de emplumamiento fue de 32–35 días (n = 3 volantones). El tamaño medio de nidada fue de 2.5 huevos (n = 32) en Camerún y de 2.1 en Senegal (n = 29); una nidada de cuatro huevos se registró en Camerún. El éxito del nido estimado con el método Mayfield fue bajo con 17% en Camerún y excepcionalmente bajo con 4% en Senegal, posiblemente relacionado a la combinación de condiciones alimenticias sub-óptimas, alta presión de depredadores, agresión intra-específica y la falta de experiencia entre los pares reproductivos. Las piezas de presa en los nidos se compusieron principalmente de lagartos (30–54% de las presas) e insectos (27–49%), notablemente saltamontes, mientras que la dieta en los dormideros de invierno en Senegal estuvo compuesta principalmente por Orthoptera (55%) y Solífugos (43%). Nuestro estudio sugiere que los individuos de *C. riocourii* pudieron adaptarse a una transformación moderada del suelo cerca de las planicies aluviales.

[Traducción del equipo editorial]

The African Swallow-tailed Kite (*Chelictinia riocourii*; hereafter ''kite'') is a small, gregarious raptor endemic to sub-Saharan Africa largely north of the equator, from Senegambia in the west to Ethiopia and Somalia in the east, and south to Kenya. It is a slim, tern-like kite, with long pointed wings and a deeply forked tail, often recorded in groups on the wing and occasionally hovering to scan for terrestrial prey. African Swallow-tailed Kites reportedly breed in the Sahelian parts of the range (between 13°N and 16°N) at the start of the rains between May and July (Thiollay 1977, 1978), after which populations migrate northward (14°–19°N). Areas south of 14°N are largely vacated during the rains, but between December and April, African Swallow-tailed Kites descend to the southern Sahelian and Sudan savannas (from 10°N–15°N, but as far south as 8°N; Brown and Amadon 1968; Thiollay 1977, 1978). Reports of this species south of West Africa's Sudan savanna zone probably occur only in very dry years (Elgood 1981). During this period, they feed primarily on grasshoppers (Pilard et al. 2009, 2011, Mullié 2009), occasionally in large foraging groups (Mullié et al. 1992). These gather in large congregations at night roosts, with as many as 20 000–36 000 individuals in Senegal in January 2007–12 (Pilard et al. 2011), 2480–4500 in the Office du Niger in Mali in December 2003 and January and December 2006 (Zwarts et al. 2005, Strandberg and Olofsson 2007, Guitard and Reynaud 2008) and >10 000 there in February 2012 (J. Gremaud pers. comm.), 6000 in Cameroon (J. Thal pers. comm.) and 1300 in Niger in January 1993 (W. Mullié and J. Brouwer unpubl. data; Fig. 1). Numbers are high year-round in large West African floodplain systems, such as the Inner Niger Delta in Mali (Thiollay 1978), which constitute the principal habitat of this species because of the high availability of grasshoppers and locusts. Duhart and Descamps (1963) found up to 30 individuals of *Locusta migratoria migratorioides* in the gizzard of a single kite in the floodplains of the Inner Delta of the Niger.

Despite locally high numbers, repeated road transects indicated significant population declines between 1969 and 2004 inside and outside protected areas in Burkina Faso, Mali, and Niger (Thiollay 2006), and a decreasing trend in Cameroon (Thiollay 2001). Breeding populations are threatened by the unprecedented degradation of the fragile arid Sahelian ecosystems, resulting from expanding cultivation, woodcutting, and overgrazing by livestock associated with increasing human populations (Wardell et al. 2003, Wood et al. 2004). Further, kites are believed to be declining due to locust control measures and the use of pesticides in general (Ferguson-Lees and Christie 2001). Drought conditions in the Sahel from the late 1960s may have modified the principal habitats of the kites' insect prey resources, reducing the geographical distribution and duration of locust plagues (Mullié 2009). However, unprecedented grasshopper outbreaks (1974–89; summarized in Mullié 2009) and a desert locust plague (1986–88; U.S. Congress-OTA 1990) swept the entire Sahel during the same period, suggesting that food supply, at least locally, was not limited within the kite's breeding range.

Although African Swallow-tailed Kites occupy a huge breeding range of approximately 600 000 km^2, published accounts of the breeding biology were derived mostly from short-term observations at a few nests in Kenya (Brown 1970, Davey and Davey 1980, Dewhurst and Fishpool 1984, Sutton et al. 1984, Demey 2011). Reports from the much more extensive West to Central African breeding range are scarce (Bannerman 1951, Barlow et al. 1997, Sauvage and Rodwell 1998, Brasseur 2000, King 2000). Systematic observations of their diet during the breeding cycle are even scarcer, although there is one report of kites feeding skinks (Squamata; Scincidae) to their young (Bates 1930). The objectives of the present study

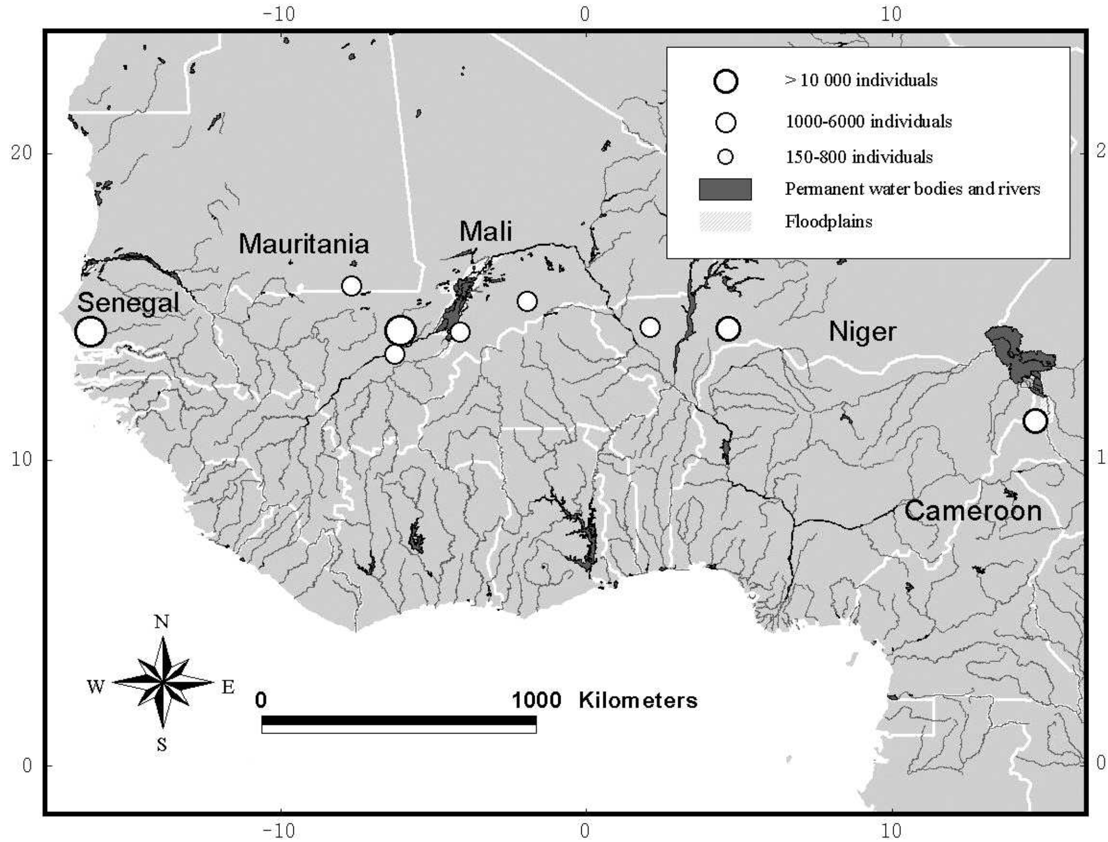


Figure 1. Locations of large African Swallow-tailed Kite roosts in West Africa reported between 1980 and 2012, based on published literature and unpublished reports. Locations in Senegal and Cameroon correspond with study sites. Sources of local data: Mali: Lamarche 1980, Strandberg and Olofsson 2007, J. Gremaud unpubl. data, J. van der Kamp unpubl. data; Mauritania: Lamarche 1987; Niger: Mullié et al. 1992, NiBDaB; Cameroon: J. Thal unpubl. data; Senegal: Pilard et al. 2011, W.C. Mullié unpubl. data.

were to quantify for the first time the nest-site characteristics, breeding density, reproductive success, and diet of the African Swallow-tailed Kite in the central (Cameroon) and western (Senegal) parts of the breeding range. We include a comparison of kite diets at nests and roost sites and a preliminary assessment of causes of nest failure.

METHODS

Study Areas. *Cameroon.* The study area in the far northern region of Cameroon (11°00′–11°40′N, 14°20′–15°00′E) included the Waza National Park (WNP) and the cultivated areas south of WNP. The area is located on sandy deposits forming the southern ridge of the former Lake Chad (6000 B.P.) and is bordered to the north by *Acacia* woodlands and the seasonally inundated grasslands of the Waza–Logone floodplains. Vegetation in the study area is characterized by open woodland dominated by *Sclerocarya birrea*, *Anogeissus leiocarpus*, and *Balanites aegyptiaca.* The habitat outside WNP is characterized by a mosaic of cultivated fields (sorghum, millet), settlements, and fragments of heavily exploited woodland. Soil type and general topography of protected and cultivated land within the Cameroon study area were comparable.

Senegal. The study area in Senegal (14°07′N, 16°10′W) was 3400 km west of the Cameroon site, on an uninhabited islet called Kousmar (area of 23 km^2), 65 km from the Atlantic Ocean in the Saloum River estuary, 10 km west of the town of Kaolack (Fig. 2). Its conservation status is protected forest. The islet harbors a massive winter roost of African Swallow-tailed Kites (20 000–36 000

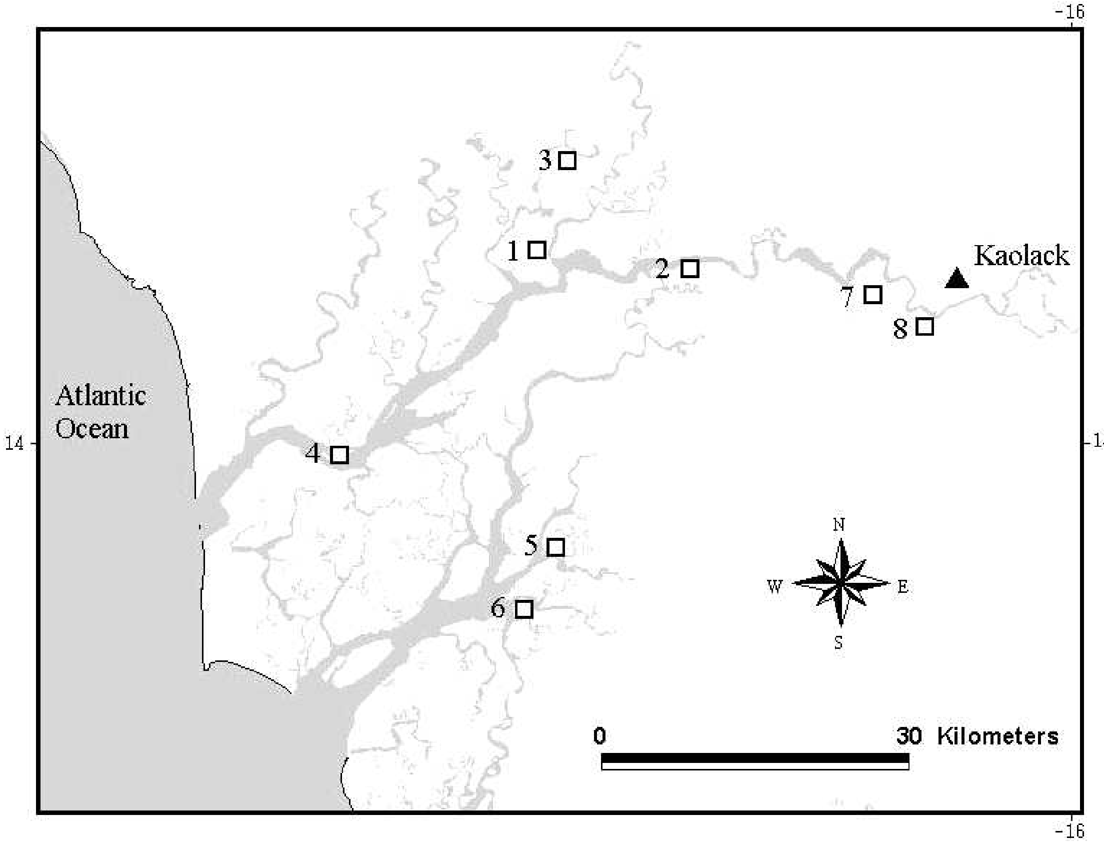


Figure 2. Breeding sites of African Swallow-tailed Kites in 2000–12 in the Saloum Delta of west Senegal. Numbers on the map correspond to 1: J. Peeters pers. comm. and in Brasseur 2000; 2: Petekele 2010, Cavaillès pers. comm.; 3: P. Pilard pers. comm.; 4: Il de Diable 2011, Manga pers. comm.; 5: R.E. Brasseur 2000 and pers. comm.; 6: Manga pers. comm.; 7: Kousmar 2010–12 (this study); and 8: abandoned colony, S. Ndiaye pers. comm.

individuals in January 2008–12; Pilard et al. 2011) and Lesser Kestrels *Falco naumanni* (21 000–29 000 individuals), which has been present since at least the 1970s, according to local residents (S. Cavaillès unpubl. data) and is largely vacated from April to June each year. The habitat consists of intertidal mudflats (6.1 km^2) and degraded hypersaline areas (''tans'' in Wolof, the primary language in Senegal) partially covered with salt crusts at their lowest elevation, with herbaceous vegetation on higher ground (14.3 km^2), and, at the highest elevation, wooded savanna to closed woodland (2.8 km^2) in two patches, the largest of which measures 1.7 km^2. There are no permanent fresh water sources, but temporary pools form on the higher-elevation vegetated parts of the ''tans'' during the rainy season. There are small villages north and south of the islet. Their inhabitants exploit wood and grasses on Kousmar during the dry season. They do not graze livestock because of the lack of permanent fresh water sources, the difficulty in accessing the islet and the presence of approximately 20 spotted hyenas (*Crocuta crocuta*) and a dozen jackals (*Canis aureus*; S. Cavaillès unpubl. data). The soil of the islet consists mainly of silt.

Climate. The climate in the study areas in Cameroon and Senegal is semiarid and characterized by a cold dry season (November–February) which precedes a hot dry season (March–May) with rains from April (Cameroon) or June (Senegal) into October. Mean long-term annual precipitation in the Cameroon study area is 650 mm and in the Senegal study area is 610 mm.

Nest Surveys and Breeding Performance. The breeding habitat in Cameroon was sampled in seven rectangular census areas totalling 14 km^2 in 2009 and 20 km^2 in 2010 in WNP, and seven rectangular areas totaling 32 km^2 in 2009 and 20 km^2 in 2010 in cultivated habitat, from 2–18 May 2009 and from 3–16 May 2010. We selected census areas based on wet-season accessibility (<13 km from a paved road). A team of four to eight researchers searched these areas intensively on foot. In Senegal, S. Cavaillès conducted nest searches along the southern and eastern border of the forest and in the western part of the islet, where open woodland prevails, from 26 March–19 June 2010. Additional nest searches were conducted from 14 January–18 February 2012 to assess the start of nest construction and egg-laying. Locations of all nests found were recorded with GPS coordinates. Nests within 2.5 km of one another were considered to be part of a single colony. Nest status (e.g., presence of nest lining, attending adults, number of eggs) was noted. The heights of trees and nests were measured using extendable aluminum poles of known length. Occupied nests were defined as nests with at least one adult present at the nest, or containing one or more eggs or nestlings. We used a mirror on the end of an aluminum pole to check the contents of nests throughout the breeding season to limit disturbance.

In Cameroon, 20 nests were visited twice in 2009, during the incubation and nestling phases, and 29 nests were revisited at mean 5-d (3–7 d) intervals in 2010. In Senegal, 40 nests were visited at mean 4-d (1–9 d) intervals throughout the breeding cycle in 2010, and five nests were visited at mean 6-d (4–15 d) intervals during early breeding and egg-laying in 2012. Intervals between visits in 2010 were sufficient to determine nest success without violating the assumptions of the Mayfield method (Johnson 1979). Nests that failed were revisited to verify whether renesting occurred. We recorded the following breeding parameters: the proportion of laying pairs among nesting pairs; hatching date, which was assessed when nests were visited during hatching or by backdating nestling age from body measurements (W. Mullié unpubl. data); clutch size; hatching success (number of nestlings/number of eggs laid); fledging success (number of fledglings/number of nestlings); breeding success (number of fledglings/number of eggs laid); and productivity (number of fledglings/nesting pair; number of fledglings/successful pair). A nesting pair was defined as a pair occupying a nest, and a laying pair was defined as a pair that laid eggs (Steenhof and Newton 2007). Number of fledglings was the number of nestlings which reached 80% of the mean fledging age (Steenhof and Newton 2007; i.e., 26 d in this case). The presumptive cause of egg or nestling loss was determined in Cameroon by intensively searching the nest cup and the area <100 m around the nest for dead nestlings or adults or signs such as pieces of egg shell, clipped or bitten-off remiges, or broken branches or claw marks on the nest tree. In Senegal, the nest cup and the area immediately surrounding the nest (<5 m) was searched each time the nest was visited. When evidence of predation was found, the number and age of the eggs or nestlings, the date, the type of evidence, and a description of the remains were recorded. Losses were recorded as ''unknown cause'' when we found no remains or clues to the disappearance of eggs or nestlings.

Diet. We investigated nestling diet using prey remains and analyses of pellets collected at nests from May–July 2010 in Cameroon and from April–May 2010 in Senegal. Pellets also were collected monthly at the Senegal roost from October until March (2007/08 and 2008/09; W. Mullié and C. Riols unpubl. data). We only used data from March 2008 and 2009 to compare diets of breeding and roosting (i.e., nonbreeding) kites, because March coincides with the onset of the breeding season and therefore would provide the least biased dataset for comparison. We collected pellets and prey remains at each nest during each nest visit; remains were either discarded (insect wings, legs, etc.) or returned to the nest (fresh remains). Items (e.g., mandibles, legs, jaw bones) were identified to class or order, or if possible to family, genus, or species level using regional reference collections. We calculated the prey frequency by dividing the number of prey items by the total number of prey items identified from the combined pellet and prey remains sample. Prey numbers in each of five prey categories were multiplied by the average mass of the prey to calculate the proportion of total biomass for each prey category. Average adult mass was available for individual Orthoptera species (Mullié and Guèye 2010) and calculated based on a locally obtained random sample of specimens for small mammals (15.3 ± 7.5 g; Rodentia, n = 12), birds (18.7 ± 2.5 g; Passeriformes, n = 3), frogs and toads (14.5 ± 2.1 g; Anura, n = 4), sunspiders (2.1 ± 0.4 g; Solifugae, n = 2), lizards (22.6 ± 9.4 g; Agamidae, n = 6; 13.8 ± 8.3 g; Scincidae, n = 6), and snakes (13.4 ± 9.1 g; Serpentes, n = 5). For other insect prey items identified to order, we used the average mass of the identified genera in the order based on the cumulative mass of 7–50

Table 1. Nest site and reproductive characteristics (mean ± SE; range) of African Swallow-tailed Kites in Senegal and Cameroon, 2009–10.

	CAMEROON	SENEGAL
Nest tree height (m)	8.96 ± 0.31 (5–13; n = 50)	6.47 ± 0.13 (4.5–10.5; n = 94)
Nest height (m)	7.35 ± 0.27 (4–12; n = 50)	4.80 ± 0.12 (3–9.5; n = 94)
Nearest nest distance (m)	63.4 ± 11.2 (4–456; n = 50)	11.3 ± 1.6 (4.5–16.3; n = 10)
Colony size[1] (nests)	6.6 ± 1.4 (2–13; n = 6)	110 (n = 1)
Hatching date[2]	28 May (± 13.6; 26 April–19 June, n = 13)	27 April (± 20.4; 05 April–31 May, n = 12)
Incubation period (d)	27–29 (n = 1)	29–31 (n = 1)

[1] Defined as a breeding aggregation with inter-nest distance <2.5 km.
[2] First-hatched nestlings in 2010.

individuals of each order collected in the field divided by the number of individuals.

Statistical Analyses. We used Program MARK (White and Burnham 1999) to estimate nest survival rate for nests of laying pairs, assuming a constant Daily Survival Rate (DSR; Dinsmore et al. 2002). Fail dates were assumed to be the midpoint between the last visit in which eggs or young were recorded at the nest and the next visit when the nest was empty. We used the Akaike Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002) to evaluate models, with the lowest AICc values being selected as the best model. We used Mann-Whitney U-tests (SPSS 19.0, SPSS Inc., Chicago, Illinois, U.S.A.) to investigate differences in reproductive parameters. We used Pianka's (1973) Index to calculate diet overlap using the percentage frequency of the main prey categories in the diet. Data are expressed as means ± SE.

RESULTS

Nest-site Features and Breeding Density. We found a total of 151 occupied nest sites during the study from 2009–10, 50 in Cameroon and 101 in Senegal. An additional 13 nests were discovered in 2012 in Senegal. In Cameroon, 98% of nests were in *Sclerocarya birrea* and 2% in *Balanites aegyptiaca*. We recorded up to three occupied nests in one *Sclerocarya birrea* in Cameroon. In Senegal, 32% of nests were built in *Lannea acida*, 21% in *Commiphora africana*, and 11% in *Sterculia setigera*, with nine other nest-tree species recorded, most importantly *Mitragyna inermis* (9%), *Balanites aegyptiaca* (7%) and *Bombax costatum* (6%). In 2012 we found a single nest in Senegal in a *Borassus aethiopum* palm tree. Nests were an average of 7.4 m above the ground in Cameroon and 4.8 m in Senegal (Table 1). Nests in *Sclerocarya birrea* (Cameroon) were most often situated on side-branches <10 cm diameter (82%), occasionally against a larger side-branch (10–20 cm diameter; 15%), or in the tree top (3%), and usually exposed to the sky. Nests were small (18–25 cm diameter) structures of twigs and grasses, lined with feathers, pieces of white plastic, paper and/or cloth (Cameroon and Senegal). Of 20 nests in Senegal inspected throughout the breeding cycle, 16 (80%) contained cloth, and 5% feathers as nest lining. A single nest in 2012 had white paper lining added at least 4 d after the clutch of two eggs had been completed. Outer twigs and surrounding branches became increasingly white from excreta during the breeding season, conspicuously so from halfway through the nestling period. Although nests may have been reused, most were newly built in Cameroon.

Seventy-six percent of nests in Cameroon were in cultivated habitat, of which 44% were <200 m from cultivated fields, 30% <400 m from a Fulbe nomad camp, and 26% in heavily exploited woodland (logging, tree pruning, heavy grazing). All nests in Senegal were in mixed woodland or wooded savanna exploited by villagers for wood and grasses, and most nests (64%; n = 56 of 88 nests in the largest woodland patch) were at the periphery of the woodland habitat. Villagers regularly cut grass under and among nest trees and they occasionally cut branches of trees holding occupied nests.

Nesting density in nest census areas in protected, intact habitat in Cameroon was 0.34 ± 0.19 nests/km^2 and 0.90 ± 0.47 nests/km^2 in cultivated habitat ($U_{7,7}$ = 22.0, Z = −1.10, P = 0.27). In Senegal, nesting density in the 2.8-km^2 study area was 39.3 nests/km^2. Nearest nest distances in Cameroon and in Senegal reflected the higher nest density in the latter site (Table 1). Most kites in Cameroon (96%; n = 50) nested in colonies of two or more nesting pairs, which had about seven pairs on average,

Table 2. Breeding parameters (mean ± SE) of African Swallow-tailed Kite nests in Senegal and Cameroon, 2010. Clutch size is the number of eggs laid in a nest (only for laying pairs); nesting pairs are pairs that occupied a nest; hatching success is the number of nestlings per egg laid; fledging success is the proportion of nestlings that attained 80% of the mean fledging age (Steenhof and Newton 2007); breeding success is the proportion of eggs that hatched and attained 80% of the fledging age; and productivity is the number of nestlings that attained 80% of the fledging age, per nesting pair or per successful pair.

	Cameroon	Range	n	Senegal	Range	n
Clutch size*	2.50 ± 0.14	1–4	32	2.10 ± 0.13	1–3	29
Nestlings/nesting pair*	1.14 ± 0.19	0–3	44	0.64 ± 0.14	0–3	47
Hatching success*	0.60 ± 0.09	0–1	25	0.34 ± 0.08	0–1	29
Fledging success	0.38 ± 0.11	0–1	18	0.22 ± 0.10	0–1	16
Breeding success	0.21 ± 0.05	0–1	31	0.06 ± 0.03	0–0.7	29
Productivity per nesting pair	0.33 ± 0.11	0–2	45	0.19 ± 0.07	0–2	48
Productivity per successful pair*	1.88 ± 0.12	1–2	8	1.29 ± 0.19	1–2	7

* Significant difference between sites (Mann-Whitney U-test, $P < 0.05$).

much smaller than the colony in Senegal (Table 1). We discovered one breeding colony in 2009 in Cameroon which was no longer present in 2010, and one colony which had been relocated 1.5 km from a breeding location used in 2009. The nest trees and immediate surroundings of the abandoned breeding site had apparently remained relatively unchanged between 2009 and 2010.

Reproductive Parameters. Nest building started in Senegal on 14 January in 2012, and the first eggs were recorded on 14 and 18 February 2012 ($n = 2$ nests). No immature birds were recorded among nesting pairs in Cameroon. However, at least three breeding individuals in Senegal in 2010 had not completed their first molt (W.C. Mullié unpubl. data), indicating that immature birds were part of the breeding population. Because in 2010 we did not quantify the age of breeding birds in Senegal, on 11 April 2012, we carefully observed a random sample of 11 nests. Of 14 birds observed attending these nests, five (35.7%) were in immature plumage, of which two formed a pair.

Mean clutch size was 2.5 eggs ($n = 32$) in Cameroon and 2.1 in Senegal ($n = 29$). Only a single clutch of four eggs was recorded (Cameroon), which was entirely lost. We did not record eggs at 28% of occupied nests ($n = 50$) in Cameroon and at 32% of nests ($n = 53$) in Senegal, although we could not determine whether these nests had failed prematurely; i.e., before egg-laying, or whether eggs had been laid and subsequently lost. Incubation lasted 27–31 d and nestlings hatched between April and June in both study sites in 2010 (Table 1), but as early as March 2012 in Senegal. A small proportion of pairs (15%; $n = 13$) in Cameroon laid eggs before the first rains on 22 April in 2010 (total April rainfall: 3 d; 4–5 mm), but most pairs laid eggs after the first rains. In Senegal, all eggs we monitored hatched well before the first rains on 4 June 2010. However, some laying might have continued after that date, because nests discovered after 19 June (when observations ceased) were only mapped and contents were not inspected. The nestling period (time from hatching to first flight from the nest) was estimated at 32–35 d for three nestlings in Cameroon ($n = 2$ nests). Nestlings were observed returning to the nest where the adults delivered food until 12 d after fledging in Cameroon ($n = 2$ nests). After a clutch of three eggs had been predated at one nest in Senegal, new eggs were laid and two young hatched, suggesting a potential for renesting.

The Daily Survival Rate (DSR) for nests containing eggs or nestlings in Cameroon and Senegal was 0.959 ± 0.005 ($n = 50$), which extrapolated to the number of exposure days from initiation (first egg laid) to nest completion (first nestlings fledged; i.e., minimum of 59 d) resulted in an estimated maximum nest success of 0.085 ± 0.002. Compared with the intercept-only model, model fit improved with country (Senegal = 1, Cameroon = 2) added as a covariate ($\beta = 0.59 \pm 0.27$; $\Delta AICc = 2.91$), and indicated that DSR was higher in Cameroon (0.970 ± 0.006; $n = 21$) compared to Senegal (0.948 ± 0.008; $n = 29$). Nest success thus estimated was 0.166 ± 0.05 for Cameroon and 0.043 ± 0.02 for Senegal, reflecting the higher productivity in Cameroon (Table 2).

Egg and Nestling Losses. *Cameroon.* Small carnivores were apparently responsible for a third of nestling losses in Cameroon (Table 3). Based on the

Table 3. Causes of egg or nestling loss in African Swallow-tailed Kite nests, Cameroon.

Stage	Cause	Number of Eggs or Nestlings Lost	Percentage of Total
Egg	Pied Crow	2	11
	Unknown	17	89
Nestling	Mammalian carnivore	9	33
	Starvation	6	22
	Pied Crow	3	11
	Wind	3	11
	Tick infestation	2	7
	African Harrier-Hawk	1	4
	Unknown	3	11

strength of branches holding the nests and the usual position of nests at the end of the branches, we believed that genets (*Genetta* spp.) were the most likely mammalian predators of nestlings. African wild cats (*Felis silvestris lybica*), which were frequently observed in the study area, might have been responsible for a portion of losses. Three nests holding six nestlings were preyed upon by a mammalian carnivore in a period of 4 d at one colony. An African Harrier-Hawk (*Polyboroides typus*) was seen eating a 6-d-old nestling at a kite nest while being attacked by four adult kites for 4 min. Two dead adults were found underneath nest trees in Cameroon; in one instance two nestlings survived at least 10 d after an adult was found dead at the base of the nest tree but died before fledging.

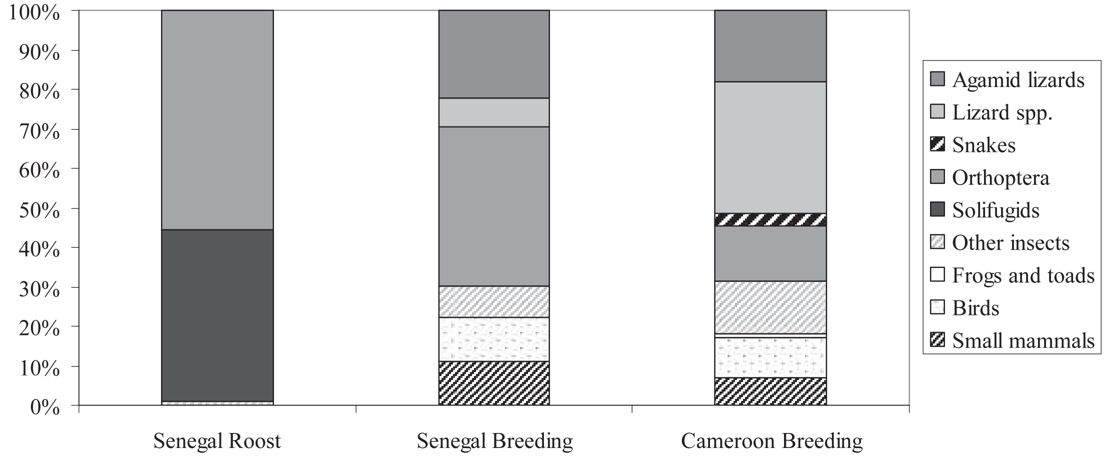
Circumstantial evidence indicated Pied Crow (*Corvus albus*) predation at one nest in Cameroon (a Pied Crow was recorded perching 3 m from the nest while being attacked by two adults). One Pied Crow pair nested 320 m from the nearest nest of the largest kite colony (13 pairs), and was observed foraging near (<200 m) or over the colony on 38% of our visits to the site (n = 8). In two instances, when crows perched within 100–250 m of the colony, we observed that four to seven kites positioned themselves in trees at the edge of the colony, facing the crows. On another day, a crow flying toward the colony was chased by a group of two to eight kites uttering alarm calls as far as 300 m from the edge of the colony. Of the nests in this colony, 23.1% were empty at our first visit, 43.5% of eggs (n = 23) were lost before hatching, and only a single nest produced fledglings.

Senegal. Predation in Senegal was presumed to be mainly from nocturnal carnivores and Giant Eagle-Owls (*Bubo lacteus*). Three Giant Eagle-Owls, probably a nesting pair with juvenile, roosted in January–February 6.5 km from the breeding colony. Another individual roosted 2.5 km from the nearest kite nest in 2010, and a Giant Eagle-Owl pair nested at this location in April 2012. During two subsequent 30-min visits to each of the three roosting eagle-owls, 4–5 kites constantly mobbed the owls; we found light grey or white feather remains in two of 18 owl pellets or pellet fragments, but we could not with absolute certainty confirm these as kite remains. Dead kites showing signs of mammalian predation were found frequently under roost trees in Senegal, but we made few visits at night and, except for African wild cats, we saw no small carnivores. Presumably other small carnivores such as genets occurred in the area. Pied Crows and other potential avian predators were only rarely observed, mostly crossing the islet and never near the nests. An African Harrier-Hawk was seen once, leaving the islet. Of 23 nests that failed, 13 nests lost eggs or young without any trace, three showed signs of egg predation, two had predation upon young, and a hatchling died shortly after hatching at one nest. Two nests were lost because the branch on which they were built was cut. One adult carcass was found, apparently predated, under a nest, and one nestling fell from another nest.

Diets of Nestling and Roosting Kites. By biomass, >50% of nestling diets in Cameroon and Senegal consisted of reptiles, whereas diets of roosting kites were dominated by Orthopterans and Solifugids (Fig. 3). Dietary overlap according to Pianka's (1973) Index based on the percentage frequency of prey numbers in the diet for nine prey categories (small mammals, birds, Agamid lizards, other lizards, serpents, orthopterans, solifugids, other insects, amphibians) was 0.68 for nestling diets from Senegal (n = 27 prey items) and Cameroon (n = 98 prey items). Using the same prey categories and the combined prey sample from nests (n = 125 prey items) and the Kousmar roost (n = 2660), overlap was 0.37 for diets of kites from the roost site and nestlings.

DISCUSSION

With 110 nesting pairs in 2.8 km^2, Kousmar islet in Senegal supports the largest African Swallow-tailed Kite breeding colony documented to date, much larger than colonies reported from Senegal (3, 5, and ca. 15 nests; Brasseur 2000, King 2000, P. Pilard pers. comm.), Cameroon (2–13 nests; this study), and



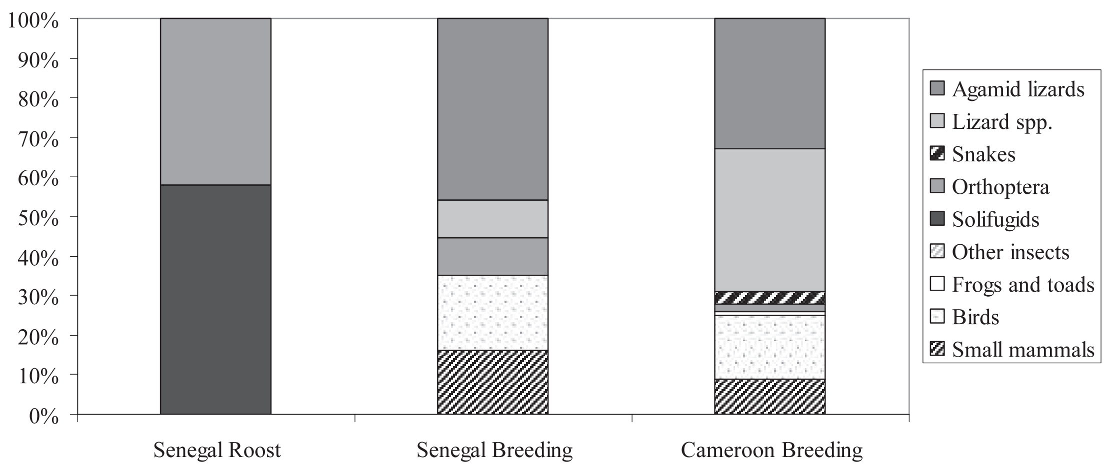


Figure 3. Diet composition based on prey remains and pellet contents of African Swallow-tailed Kites in 2009–10 at the Kousmar roost site in Senegal (n = 2660 prey items), at nests in Senegal (n = 27 prey items; five nests) and at nests in Cameroon (n = 98; 22 nests): (A) prey categories in pellets as percentage of total prey number and (B) as percentage of total prey biomass. Lizard spp. were dominated by Skinks in Cameroon (81%; n = 32), also *Trachylepis quinquetaeniatus*, *Latastia longicaudata*. Orthoptera identified at species level: *Ornithacris cavroisi*. Birds: *Oenanthe heuglini* (one juvenile). ''Other insects'' included: Mantidae, Termitidae, Forficulidae, Heteroptera, Lepidoptera, Hymenoptera, Coleoptera, Scolopendridae.

Kenya (two nests; Davey and Davey 1980). Based on our data and observations of inter-colony distances elsewhere (Davey and Davey 1980, Brasseur 2000), we suspect that the nest-dispersion pattern in Cameroon and away from Kousmar in Senegal is probably most common. It is likely that the huge roost and breeding congregation in Senegal resulted from habitat suitability, possibly in combination with good food conditions as reported for Palearctic migratory raptors (e.g., Sánchez-Zapata et al. 2007). Until the 1980s, African Swallow-tailed Kites were known to breed on the mainland along the border of the Saloum River, 6 km east of Kousmar (cf. Fig. 3). However, fairly recent and extensive loss of woodland in the Saloum River estuary, mainly to allow for groundnut production (Cavaillès 2010), seems to have concentrated kites on islets, where tree diversity, density and height has been maintained to a certain extent. Other breeding nuclei in the Delta also have been recorded on islets, or relatively intact forests on peninsulas (Fig. 2).

Our observations of immature birds among nesting pairs in Senegal is interesting in light of the foraging efficiency hypothesis (Beauchamp 1999), because coloniality delivers particularly important advantages for less-experienced breeding pairs (Muller et al. 1997, Sergio and Penteriani 2005). These immature, inexperienced kites may cue opportunistically on the presence of successfully breeding conspecifics (Sergio and Penteriani 2005), as suggested by the settlement of new pairs in one African Swallow-tailed Kite colony that already had nests with eggs or nestlings in Senegal (Brasseur 2000).

The observed communal nest defense against diurnal predators suggests that kites also may benefit from improved predator protection at colonies during the day, but the conspicuousness of a large colony to nocturnal predators might outweigh such benefits. Frequent predation by small carnivores in Cameroon suggests, however, that nocturnal predators may depress reproductive output even in small, relatively inconspicuous colonies. The proximity of breeding or roosting eagle-owls, which are known to regularly prey upon raptor nestlings (Steyn 1982), might have been another important cause of nestling loss in Senegal, given the impact of large owl predation on raptor colonies elsewhere (Sergio et al. 2003, Coulson et al. 2008).

Reproductive Rates and Phenology. The laying dates of African Swallow-tailed Kites in Cameroon were consistent with Thiollay's (1977, 1978) observations of breeding during the start of the rains from May–July in the southern Sahel; 85% of pairs in Cameroon laid eggs after the first rains. Conversely, laying dates in Senegal were all from the dry season. Although the earliest recorded laying dates during our surveys were in early March in 2010 and in mid-February in 2012, eggs and nestlings have been observed as early as 20 January at nests 38 km southwest of Kousmar (Brasseur 2000, King 2000), and eggs were recorded in two nests on 24 January 2011, 32 km northwest of Kousmar (P. Pilard pers. comm.). Laying thus appears to span at least 4 mo (last week of December–first week of May) in Senegal, resembling a protracted breeding season similar to that of the sympatric Black-winged Kite (*Elanus caeruleus*; Rodwell et al. 1996).

The very low frequency of clutches of four eggs (1.6%; $n = 61$), suggested as the usual clutch size in this species (Brown and Amadon 1968), might reflect suboptimal breeding conditions in our study areas. We suspect, however, that Brown and Amadon's assessment of clutch size may have been based on a very low and unrepresentative sample size. Rather than reflecting the mean, it seems likely that large clutches (i.e., clutches of four) occur mainly when feeding conditions prior to breeding are very good, as is the case in the related Black-winged Kite (Mendelsohn 1984), Letter-winged Kite (*E. scriptus*; Ey 1984) and various other raptors (Dijkstra et al. 1982). Indeed, one clutch of four previously recorded by Bannerman (1951) and collected by Bates on 18 June 1931 north of Taoua in Niger (D. Russell pers. comm.) and another clutch of four collected by Bisseling at Sennar, Sudan, on 16 May 1959 (M. Louette pers. comm.) coincided with massive Desert Locust swarms (Waloff 1966, Mullié 2009). Similarly, Davey and Davey (1980) reported three nests containing respectively one egg, two and four fledglings at Lake Turkana in Kenya, between 12 and 19 April 1979, when a Desert Locust upsurge occurred in southwestern Ethiopia (FAO 1978, 1979), immediately north of the area where the kites were nesting.

Our estimate of nest success using the Mayfield method was low at 17% for Cameroon and exceptionally low at 4% for Senegal, even in light of the generally low reproductive output of tropical raptors (Newton 1979). The extremely low reproductive output in Senegal might have resulted from frequent intraspecific interactions (Newton 1979), due to the presence of thousands of conspecifics using the breeding area and its immediate surroundings (Pilard et al. 2011). Additionally, high predation levels and the presence of younger, less-experienced birds in the nesting population might have depressed reproductive output. Suboptimal breeding conditions in the second half of the dry season, when we monitored nests, also might have contributed to low reproductive success. Although this period is characterized by greatly reduced vegetative cover, facilitating capture of terrestrial prey (Thiollay and Clobert 1990), grasshopper densities decline during this time, mainly due to bird predation (Mullié and Guèye 2010). This may worsen the effect of food competition due to high numbers of conspecifics.

A prolonged breeding season and the possibility for renesting may allow African Swallow-tailed Kites to compensate for losses incurred early in the season, as observed in various tropical raptors (Mader 1982, Delannoy and Cruz 1988, Thorstrom and Quixchán 2000), or raise multiple broods while opportunistically capitalizing on conditions of prolonged food abundance, as reported for *Elanus* kites (Ey 1984, Mendelsohn 1984). We recorded renesting at one nest in

Senegal after nest predation, but follow-up studies will be needed to determine the frequency at which this occurs and how it contributes to reproductive output.

Breeding in Changing Landscapes. Like other kites that breed in dense colonies (*Gampsonyx*, *Elanoides*, *Ictinia*; Newton 1979), African Swallow-tailed Kites in Senegal and Cameroon opportunistically settled in food-rich floodplain habitats, using various common tree species for breeding, including relatively small trees and occasionally those stunted from frequent pruning. The importance of floodplains for nesting and roosting kites is consistent with previous reports from western Africa (e.g., Thiollay 1978, Pilard et al. 2011), which note congregations of kites in or near floodplains, estuaries, or temporary wetlands. The ability of kites to adapt to fluctuating resource conditions in these wetland systems may limit their vulnerability to human-induced land changes. Colonies in Senegal relocated to islets when breeding habitats on the mainland were destroyed, and frequently settled close to cultivated fields and human habitation in Cameroon, as previously reported from Kenya (Britton 1980). Foraging kites appeared to profit from reduced grass cover and height and improved prey vulnerability to capture following moderate grazing or cultivation, even hunting alongside livestock to capture flushed insects (Gregory 1982; R. Buij unpubl. data), whereas transformation of woodland habitats into cropland mosaics may boost grasshopper prey (Mullié and Guèye 2010). Still, extensive loss of tree cover around floodplains, which are a restricted and little-protected habitat in West Africa (Zwarts et al. 2009), reduces availability of roost and breeding sites. The Waza–Logone floodplains experienced annual human population growth up to 5% in the 1990s, leading to an increase in firewood extraction (Scholte 2003), estimated at 10 tons wet mass a day for Kalamaloué National Park (north of Waza National Park). Similarly, 20% of the trees at the roost site in Senegal were lost between 2007 and 2010 due to cutting for firewood (Pilard et al. 2011). At present, the decline of woodland cover in the Saloum River estuary exposes the islets where the kites breed to increasing exploitation of wood (Cavaillès 2010). Such loss of woodland cover may further influence dispersion patterns and could drive aggregations into larger breeding colonies, possibly contributing to lower reproductive output.

ACKNOWLEDGMENTS

R. Buij was financially and logistically supported by the Institute of Environmental Sciences (CML) of the University of Leiden, the Netherlands, through its collaborative program with the University of the Dschang, Cameroon, at the Centre for Environment and Development Studies in Cameroon (CEDC). W.C. Mullié received partial funding from KR2 funds through the Japanese Embassy in Senegal to the Agriculture Directorate, Dakar, to execute a study of avian predation on grasshoppers in the framework of a project to investigate the use of reduced dosages of *Metarhizium acridum* for grasshopper control and from LPO, France, for pellet analysis. Amadé Ali, Abba Boukar, Barbara Croes, Kim Kortekaas, Ingrid Folkertsma, Ralph van Krimpen, Saskia van der Zanden, Rien van Wijk, and Hamidou Hamadou are acknowledged for their important contribution to data collection in Cameroon; Sama Gagare of Agrhymet Regional Centre, Niger, Franck Noël and Christian Riols, France, for analyzing the pellets. For providing information on clutch-sizes we are greatly indebted to Michel Louette (RMCA, Tervuren) and Douglas Russell (BMNH, Tring). We thank Karen Steenhof, Rick Watson, and an anonymous referee for their valuable comments which improved this manuscript.

LITERATURE CITED

BANNERMAN, D.A. 1951. The birds of tropical west Africa. Vol. 8. The Crown Agents for the Colonies, London, U.K.

BARLOW, C., T. DISLEY, AND T. WACHER. 1997. A field guide to the birds of the Gambia and Senegal. Christopher Helm, London, U.K.

BATES, G.L. 1930. Handbook of the birds of west Africa. John Bale, Sons and Danielsson, Ltd., London, U.K.

BEAUCHAMP, G. 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behavioral Ecology* 10:675–687.

BRASSEUR, R.E. 2000. African Swallow-tailed Kite *Chelictinia riocourii* breeding in the Saloum Delta, Sénegal. *Bulletin of the African Bird Club* 7:134.

BRITTON, P.L. 1980. Birds of east Africa: their habitat, status and distribution. East Africa Natural History Society, Nairobi, Kenya.

BROWN, L.H. 1970. African birds of prey: a study of Africa's 89 diurnal raptors and 31 owls. Houghton Mifflin, Boston, MA U.S.A.

——— AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Vol. 1. McGraw-Hill Book Company, New York, NY U.S.A.

BURNHAM, K.P. AND D.R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach, Second Ed. Springer, New York, NY U.S.A.

CAVAILLÈS, S. 2010. Caractérisation de la faune vertébrée et état écologique de l'île de Kousmar, Sénégal. M.Sc. thesis, Muséum National d'Histoire Naturelle de Paris, Paris, France.

COULSON, J.O., T.D. COULSON, S.A. DEFRANCESCH, AND T.W. SHERRY. 2008. Predators of the Swallow-tailed Kite in southern Louisiana and Mississippi. *Journal of Raptor Research* 42:1–12.

DAVEY, P. AND G. DAVEY. 1980. Swallow-tailed Kites breeding at Porr, Lake Turkana. *EANHS Bulletin* 1980:47–49.

DELANNOY, C.A. AND A. CRUZ. 1988. Breeding biology of the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*). *Auk* 105:649–662.

DEMEY, R. 2011. Recent reports. *Bulletin of the African Bird Club* 18:93–109.

DEWHURST, C.F. AND L.D.C. FISHPOOL. 1984. The Swallow-tailed Kite *Chelictinia riocourii* breeding in the Kedong Valley, Kenya. *Scopus* 8:25–26.

DIJKSTRA, C., L. VUURSTEEN, S. DAAN, AND D. MASMAN. 1982. Clutch size and laying date in the kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis* 124: 210–213.

DINSMORE, S.J., G.C. WHITE, AND F.L. KNOPE. 2002. Advanced techniques for modelling avian nest survival. *Ecology* 83:3476–3488.

DUHART, F. AND M. DESCAMPS. 1963. Notes sur l'avifaune du Delta Central Nigérien et régions avoisinantes. *L'Oiseau et la Revue Française d'Ornithologie.* Numéro spécial 1–106.

ELGOOD, J.H. 1981. The birds of Nigeria. BOU Checklist No. 4. British Ornithologists' Union, London, U.K.

EY, A. 1984. Notes on Letter-winged Kites breeding in western Queensland, 1972–83. *Australian Bird Watcher* 10:243–247.

FERGUSON-LEES, J. AND D.A. CHRISTIE. 2001. Raptors of the world. Christopher Helm, London, U.K.

GREGORY, P.A. 1982. Swallow-tailed Kite associating with cattle. *Ostrich* 53:221.

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS. 1978. Desert Locust situation, summary and forecast. No. 1–4. FAO-AGP, Locusts, Other Migratory Pests and Emergency Operations Group, Rome, Italy.

———. 1979. Desert Locust situation, summary and forecast. No. 5–16. FAO-AGP, Locusts, Other Migratory Pests and Emergency Operations Group, Rome, Italy.

GUITARD, J.J. AND P.A. REYNAUD. 2008. Concentration de Nauclers d'Afrique *Chelictinia riocourii* près de Niono, Mali. *Malimbus* 30:170–172.

JOHNSON, D.J. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk* 96:651–661.

KING, M. 2000. Breeding of Swallow-tailed Kite *Chelictinia riocourii* in Senegal. *Malimbus* 2:90–91.

LAMARCHE, B. 1980. Liste commentée des oiseaux du Mali. *Malimbus* 2:121–158.

———. 1987. Liste commentée des oiseaux de Mauritanie. Unpubl. report, Nouakchott, Mauritania.

MADER, W.J. 1982. Ecology and breeding habits of the Savanna Hawk in the llanos of Venezuela. *Condor* 84: 261–271.

MENDELSOHN, J. 1984. The timing of breeding in Black-shouldered Kites in southern Africa. *Proceedings Pan-African Ornithological Congress* 5:799–808.

MULLER, K.L., J.A. STAMPS, V.V. KRISHNAN, AND N.H. WILLITS. 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *American Naturalist* 150:650–661.

MULLIÉ, W.C. 2009. Birds, locusts and grasshoppers. Pages 202–221 *in* L. Zwarts, R.G. Bijlsma, J. van der Kamp, and E. Wymenga [EDS.], Living on the edge: wetlands and birds in a changing Sahel. KNNV Publishing, Zeist, The Netherlands.

———, J. BROUWER, AND C. ALBERT. 1992. Gregarious behaviour of African Swallow-tailed Kite *Chelictinia riocourii* in repsonse to high grasshopper densities near Ouallam, western Niger. *Malimbus* 14:19–21.

——— AND Y. GUÈYE. 2010. Does bird predation enhance the impact of green muscle (*Metarhizium acridum*) used for grasshopper control? *Journal of Orthoptera Research* 19:139–155.

NEWTON, I. 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, U.K.

PIANKA, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74.

PILARD, P., G. JARRY, AND V. LELONG. 2009. Suivi et conservation du dortoir de Faucons crécerellettes et d'Elanions naucler de la région de Kaolack (Sénégal). Pages 159–161 *in* P. Pilard [ED.], Actes du VII Congrès International sur le Faucon crécerellette. LPO Service Edition, Almendralejo, Spain.

———, V. LELONG, A. SONKO, AND C. RIOLS. 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.

RODWELL, S.P., A. SAUVAGE, S.J.R. RUMSEY, AND A. BRÄUNLICH. 1996. An annotated check-list of birds occurring at the Parc National des Oiseaux du Djoudj in Senegal, 1984–94. *Malimbus* 18:74–111.

SÁNCHEZ-ZAPATA, J.A., J.A. DONÁZAR, A. DELGADO, M. FORERO, O. CEBALLOS, AND F. HIRALDO. 2007. Desert locust outbreaks in the Sahel: resource competition predation and ecological effects of pest control. *Journal of Applied Ecology* 44:323–329.

SAUVAGE, A. AND S.P. RODWELL. 1998. Notable observations of birds in Senegal (excluding Parc National des Oiseaux du Djoudj), 1984–94. *Malimbus* 20:75–122.

SCHOLTE, P.T. 2003. Immigration: a potential time bomb under the integration of conservation and development. *Ambio* 32:58–64.

SERGIO, F., L. MARCHESI, AND P. PEDRINI. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *Journal of Animal Ecology* 72: 232–245.

——— AND V. PENTERIANI. 2005. Public information and territory establishment in a loosely colonial raptor. *Ecology* 86:340–346.

STEENHOF, K. AND I. NEWTON. 2007. Assessing raptor nest success and productivity. Pages 181–192 *in* D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Hancock House, Surrey, BC, Canada.

STEYN, P. 1982. Birds of prey of southern Africa: their identification and life histories. David Philip, Cape Town, South Africa.

STRANDBERG, R. AND P. OLOFSSON. 2007. Bird observations in Mali. *Malimbus* 29:123–125.

SUTTON, J., A. SUTTON, C.F. DEWHURST, AND L.M. DEWHURST. 1984. A confirmed breeding record for the Swallow-tailed Kite in the Rift Valley of Kenya. *East Africa Natural History Society Bulletin* 1984:12.

THIOLLAY, J.-M. 1977. Distribution saisonnière des rapaces diurnes en Afrique occidentale. *L'Oiseau et la Revue Française d'Ornithologie* 47:253–285.

———. 1978. Les migrations de rapaces en Afrique occidentale: adaptations écologiques aux fluctuations saisonnières de production des écosystèmes. *La Terre et la Vie* 32:89–133.

———. 2001. Long-term changes of raptor populations in northern Cameroon. *Journal of Raptor Research* 35:173–186.

———. 2006. The decline of raptors in west Africa: long-term assessment and the role of protected areas. *Ibis* 148:240–254.

——— AND J. CLOBERT. 1990. Comparative foraging adaptations of small raptors in a dense African savanna. *Ibis* 132:42–57.

THORSTROM, R. AND A. QUIXCHÁN. 2000. Breeding biology and nest site characteristics of the Bicolored Hawk in Guatemala. *Wilson Bulletin* 112:195–202.

U.S. CONGRESS, OFFICE OF TECHNOLOGY ASSESSMENT. 1990. A plague of locusts–Special Report. OTA-F-450. U.S. Government Printing Office, Washington, DC U.S.A.

WALOFF, Z. 1966. The upsurges and recessions of the desert locust plague, an historical survey. Anti-Locust Memoirs No. 8., London, U.K.

WARDELL, D.A., A. REENBERG, AND C. TØTTRUP. 2003. Historical footprints in contemporary land use systems: forest cover changes in savanna woodlands in the Sudano-Sahelian zone. *Global Environmental Change–Human and Policy Dimensions* 13:235–254.

WHITE, G.C. AND K.P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.

WOOD, E.C., G.G. TAPPAN, AND A. HADJ. 2004. Understanding the drivers of agricultural land use change in south-central Senegal. *Journal of Arid Environments* 59:565–582.

ZWARTS, L., R.G. BIJLSMA, J. VAN DER KAMP, AND E. WYMENGA. 2009. Living on the edge: wetlands and birds in a changing Sahel. KNNV Uitgeverij, Utrecht, The Netherlands.

———, P. VAN BEUKERING, B. KONE, AND E. WYMENGA. 2005. Le Niger, une artère vitale. Gestion efficace de l'eau dans le Bassin du Haut Niger. RIZA/Wetlands International/Institute for Environmental Studies (IVM)/A&W conseillers écologiques. Lelystad/Sévaré/Amsterdam/Veenwouden, Mali/The Netherlands.

Received 17 May 2012; accepted 24 October 2012
Associate Editor: Karen Steenhof