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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 6

Breeding biology and diet of the African Swallow-tailed Kite in Senegal and Cameroon

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Abstract

We report on 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 extent (Senegal) of the species' breeding range. With 110 nests in 2.8 km^2 suitable breeding habitat, Kousmar islet (23 km^2) in Senegal supports the largest documented colony of Swallow-tailed Kites to date, which was located nearby a massive winter roost. We recorded on average 7 pairs/colony in Cameroon, where nest density was 0.3 nests/km^2 in protected woodland and 0.9 nests/km^2 in cultivated habitat. In Senegal, breeding groups had on average 9 pairs. 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 days based on two nests, and the fledging period at 32-35 days (n = 3 fledglings). Mean clutch size was 2.5 (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 dominated by lizards (30-54% of items) and insects (27-49%), notably grasshoppers, whereas the diet at the winter roost in Senegal was dominated by Orthoptera (55%) and Solifugids (43%). African Swallow-tailed Kites appear to cope with moderate land transformation, but widespread loss of tree cover near floodplains leads to deteriorating roost and nest availability.

Left: adult African Swallow-tailed Kite above breeding colony in Cameroon.

6.1 Introduction

The African Swallow-tailed Kite *Chelictinia riocourii* (hereafter: Swallow-tailed 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. 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 1977a, 1978a), after which populations migrate to the north (14°-19°N). Areas south of 14°N are largely vacated during the rains, but between December and April, Swallow-tailed Kites descend to the southern Sahelian and Sudan savannas (from 10°N-15°N, but as far south as 8°N; Brown & Amadon 1968; Thiollay 1977a, 1978a), while records south of West Africa's Sudan savanna zone probably occur only in very dry years (Elgood 1981). During this period, they feed predominantly 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, such as 20,000-36,000 individuals in Senegal in January 2007-2012 (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 in litt.), 6000 in Cameroon (J. Thal pers. comm.) and 1300 in Niger in January 1993 (W. Mullié and J. Brouwer pers. obs.; Figure 1). Numbers are high year-round in large West African floodplain systems, such as the Inner Niger Delta in Mali (Thiollay 1978a), which constitute the principal habitat because of the high availability of grasshoppers and locusts. Duhart & Descamps (1963) found up to 30 individuals of *Locusta migratoria migratorioides* in the gizzard of a single Swallow-tailed Kite in the floodplains of the Inner Delta of the Niger.

In spite of locally high numbers, comparative road counts indicated significant population declines between 1969 and 2004 inside and outside protected areas in Burkina Faso, Mali and Niger (Thiollay 2006a), and a decreasing trend in Cameroon (Thiollay 2001). Breeding populations are threatened by 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, Swallow-tailed Kites are suspected to be in decline owing to locust control measures and the use of pesticides in general (Ferguson-Lees & 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 (1974-1989, summarized in Mullié 2009) and a desert locust plague (1986-1988, US Congress OTA 1990) swept the entire Sahel in the same period, suggesting that food supply, at least locally, was not limited within the kites' breeding range.

Although Swallow-tailed Kites occupy a huge breeding range of approximately 600,000 km^2, published accounts on the breeding biology were derived mostly from short-term observations at a few nests in Kenya (Brown 1970, Davey & Davey 1980, Dewhurst &

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 & Rodwell 1998, Brasseur 2000, King 2000). Systematic observations of their diet during the breeding cycle are even scarcer, but we know that kites feed skinks (Squamata; Scincidae) to their young (Bates 1930). The objectives of the present study are to quantify for the first time the nest site characteristics, breeding density, reproductive success, and diet of the Swallow-tailed Kite in the central (Cameroon) and western (Senegal) parts of the breeding range. We include a diet comparison of kites at nests and roost sites and examine how breeding performance varied between populations, including an assessment of causes of nest failure.

6.2 Materials and methods

Study area

The study area in the Far North Province of Cameroon (11°00'N-11°40'N, 14°20'E-15°00'E) covers 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 Before Present) and 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 in the Cameroon study area were comparable.

The study area in Senegal (14°07'N, 16°10'W) is 3400 km west of the Cameroonian site on an uninhabited islet (area of 23 km^2), 65 km from the Atlantic Ocean in the Saloum River estuary called Kousmar, 10 km west of the town of Kaolack (Figure 3). Its conservation status is protected forest. The islet harbors 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 (inhabitants of Ndiafate to S. Cavaillès pers. comm.) and is largely vacated from April to June each year. The habitat consists of intertidal mudflats (6.1 km^2) and degraded hypersaline areas ("tan" in Wolof, the main language in Senegal) partially covered with salt crusts at their lowest elevation, herbaceous vegetation on higher ground least exposed to spring tides (14.3 km^2), and, at the highest elevation, wooded savanna to closed woodland (2.8 km^2) in two blocks of which the largest measures 1.7 km^2. There are no permanent fresh water sources, but temporary pools form on the higher 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 pers. obs.). The soil of the islet consists mainly of silt.

The climate in the study areas in Cameroon and Senegal is semi-arid and characterized by a cold dry season (Nov-Feb) which precedes a hot dry season (March-May) with rains from April into October. Mean long-term annual precipitation in the Cameroon study area is 500 mm and in the Senegal study area is 610 mm.

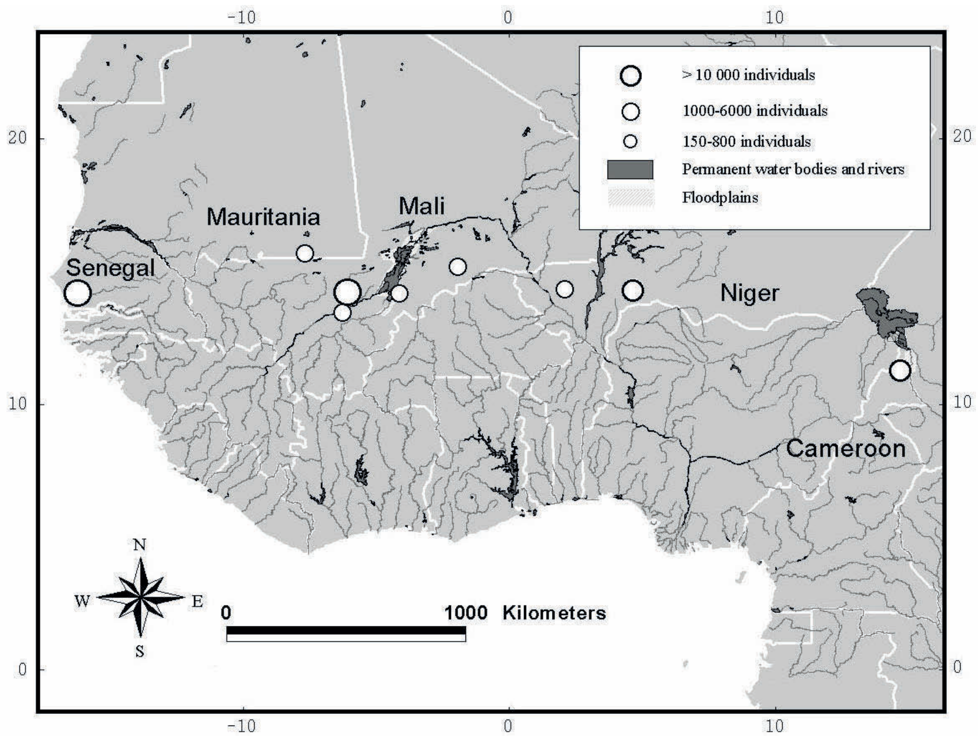

Figure 1. Locations of large Swallow-tailed Kite roosts in West Africa reported between 1980 and 2012, based on published literature and unpublished reports. Locations in Senegal and Cameroon correspond with study sites. Mali: Lamarche 1980, Strandberg & Olofsson 2007, J. Gremaud pers. obs., J. van der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

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 tarred 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 laying. All nests found were recorded with GPS coordinates and their status (e.g. nest lining, attending adults, number of eggs) noted. Nests within 2.5 km of one another were considered to be part of a single colony. The height of trees and nests was measured using extendable aluminium poles of known length. Occupied nests were defined as those nests with at least one adult present at the nest, or those nests containing one or more eggs or nestlings. A mirror on the end of an aluminium pole was used to check the contents of a nest throughout the breeding season to limit disturbance to a minimum.

In Cameroon, 20 nests were visited twice in 2009, during the incubation and nestling phases, and 29 nests were revisited at mean 5-day (3-7) intervals in 2010. In Senegal, 40 nests were visited at mean 4-day (1-9) intervals throughout the breeding cycle in 2010 and five nests were visited at mean 6-day (4-15) 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 re-nesting 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 (Mullié *et al.* in prep.); clutch size; hatching success (nestling number/egg laid); fledging success (fledgling number/nestling number); breeding success (fledgling number/egg laid); and productivity (fledgling number/nesting pair, fledgling number/successful pair). A nesting pair is defined here as pairs occupying nests, whereas laying pairs are defined as those pairs that lay eggs (Steenhof & Newton 2007). Fledgling number was the number of nestlings which reached 80% of the mean fledging age (cf. Steenhof and Newton 2007), i.e. 26 days (this study). The cause of egg or nestling loss was determined in Cameroon by intensively searching the area < 100 m around the nest and the nest cup for clues such as dead nestlings or adults, clipped or bitten-off remiges, carcasses, broken branches or claw marks on the nest tree, and pieces of egg shell. In Senegal the nest cup and the area immediately surrounding the nest (< 5 m) was searched each time a 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 (e.g. feathers, body parts) 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 in May-July 2010 in Cameroon and in April-May 2010 in Senegal. Pellets were also collected monthly at the Senegal roost from October till March (2007/08 and 2008/09; W.C. Mullié & C. Riols unpubl. data), but only data from March 2008 and 2009 were used to compare the diets of breeding and roosting (i.e. non-breeding) kites, as March coincides with the onset of the breeding season and therefore would provide the least biased data set 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. The frequency by number of prey was calculated by dividing the number of prey items by the total number of prey items identified from the combined pellet and prey remain sample. Prey numbers in each of the 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 & Guèye 2010) and calculated based on a locally obtained random sample of specimens for small mammals (15.3±7.5g; Rodentia, *n* = 12), birds (18.7±2.5g; Passeriformes, *n* = 3), frogs and toads (14.5±2.1g; Anura, *n* = 4), sunspiders (2.1±0.4g; Solifugae, *n* = 2), lizards (22.6±9.4g; Agamidae, *n* = 6; 13.8±8.3g; Scincidae, *n* = 6) and snakes (13.4±9.1g; Serpentes, *n* = 5). For other insect prey items identified to order, the average mass of the identified genera in the order was used based on the cumulative mass of 7-50 individuals of each order collected in the field divided by the number of individuals.

Statistical analyses

We used Program MARK (White & 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 & 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, IL, USA) 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 ±S.E.

6.3 Results

Nest site features and breeding density

A total of 151 occupied nest sites were described during the study from 2009-2010, 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 9 other nest-tree species recorded, most importantly *Mitragyna inermis* (9%), *Balanites aegyptiaca* (7%) and *Bombax costatum* (6%). In 2012 a single nest in Senegal was found in a *Borassus aethiopum* palm tree. Nests were averagely 7.4 m above the ground in Cameroon and 4.8 m in Senegal (Table 1). Nests in *Sclerocarya birrea* (Cameroon) were most often (82%) situated on side-branches < 10 cm diameter, 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 for lining of the nest, 16 (80%) contained cloth, and 5% feathers. A single nest in 2012 had white paper lining added at least four days after the clutch of two eggs had been completed. Outer twigs and surrounding branches became increasingly white from feces during the breeding season, conspicuously so from halfway 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 located < 200 m from cultivated fields, 30% < 400 m from a Fulbe nomad camp, and 26% in heavily exploited woodland (logging, tree pruning, heavily grazed). All nests in Senegal were in mixed woodland or wooded savanna exploited by villagers for wood and grasses, and most nests (64%; n = 56/88 nests in the largest woodland block) were at the periphery of the woodland habitat. Villagers regularly cut grass under and among the 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 Swallow-tailed Kites in Cameroon (96%; n = 50) nested in colonies of two or more nesting pairs, which had about 7 pairs on average, 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, while one colony had been re-established 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 and nest success

Nest building started in Senegal from 14 January in 2012 and first eggs were recorded on 14 and 18 February 2012 (n = 2 nests). Only a single clutch of four eggs was recorded (Cameroon), which was entirely lost. No immature birds were recorded among nesting pairs in Cameroon but at least three breeding individuals in Senegal in 2010 had not completed their first molt (Mullié *et al.* in prep.), indicating that immature birds were part of the breeding population. As in 2010 no special attention was given to the age of breeding birds in Senegal, on 11th April 2012 a random sample of 11 nests was more closely inspected. Of 14 birds that were observed attending these nests, five (35.7%) were in immature plumage, of which two formed a pair.

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 taken by a predator. Incubation lasted 27-31 days and nestlings hatched between April and June in both study sites in 2010 (Table 1), but from 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 days; 4-5 mm), but most pairs laid eggs after the first rains. In Senegal, all eggs under surveillance 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 days for three nestlings in Cameroon (n = 2 nests). Nestlings were observed returning to the nest where the adults delivered food until 12 days after fledging in Cameroon (n = 2 nests). In at least one nest in Senegal, after a clutch of three eggs had been predated, new eggs were laid and two young hatched, suggesting a potential for renesting.

Table 1. Nest site and reproductive characteristics (mean ±S.E.; range) of Swallow-tailed Kites in Senegal and Cameroon in 2009 and 2010.

Parameter	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 (days)	27-29 (n = 1)	29-31 (n = 1)

[1] Defined as a breeding aggregation with inter-nest distance < 200 m in Cameroon, and inter-nest distance < 100 m in Senegal.
[2] First-born nestlings in 2010.

The Daily Survival Rate (DSR) for nests containing eggs or nestlings in Cameroon and Senegal was 0.959±0.005 (n = 50), which raised to the number of days from initiation (first egg laid) to nest completion (first nestlings fledged; i.e. minimum of 59 days) leads to 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 (β = 0.59±0.27; ΔAICc = 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).

Table 2. Breeding parameters (mean ±S.E.) of Swallow-tailed Kite nests in Senegal and Cameroon in 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 (cf. Steenhof and Newton 2007); breeding success is the number of nestlings that attained 80% of the fledging age, per egg laid; and productivity is the number of nestlings that attained 80% of the fledging age, per nesting pair or per successful pair.

Parameter	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 for nesting pairs	0.33±0.11	0-2	45	0.19±0.07	0-2	48
Productivity for successful pairs‡	1.88±0.12	1-2	8	1.29±0.19	1-2	7

‡Differences between sites by means of Mann-Whitney U-tests $P < 0.05$.

Egg and nestling loss

Small carnivores were responsible for a third of nestling losses in Cameroon (Table 3). Based on the strength of branches holding the nests and their usual position at the end of the branches, 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 days at one colony. An African Harrier Hawk *Polyboroides typus* was seen eating a 6-day old nestling at a Swallow-tailed Kite nest while being attacked by four adult kites for 4 min. Two dead adults were recorded underneath nest trees in Cameroon, in one instance two nestlings survived at least 10 days after an adult was found dead at the base of the nest tree but died before fledging.

Circumstantial evidence indicated Pied Crow *Corvus alba* 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 at 320 m from the nearest nest of the largest Swallow-tailed Kite colony (13 pairs), and was observed foraging near (< 200 m) or over the colony on 38% of visits (n = 8). In two instances, when crows perched within 100-250 m of the colony, four to seven Swallow-tailed Kites positioned themselves in trees at the edge of the colony, facing the crows. A crow flying towards the colony was chased by a group of two to eight kites uttering alarm calls until 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.

Table 3. Cause of egg or nestling loss in 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

Predation in Senegal was presumed to be mainly from nocturnal carnivores and Verreaux's Eagle Owls *Bubo lacteus*. Three Verreaux's Eagle Owls, probably a nesting pair with juvenile, roosted in January-February at 6.5 km from the breeding colony. Another individual roosted at 2.5 km from the nearest kite nest in 2010, and a Verreaux's Eagle Owl pair nested at this location in April 2012. During two subsequent 30-min visits each of to the three roosting Verreaux's Eagle Owls, 4-5 Swallow-tailed Kites constantly mobbed the owls, but light grey or white feather remains in two out of 18 pellets, or pellet fragments, could not with absolute certainty be attributed to Swallow-tailed Kites. Dead Swallow-tailed Kites showing signs of mammalian predation were frequently found underneath roost trees in Senegal, but few visits were made at night and, except for African Wild Cat, no small carnivores were seen, although genets may have 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 where failure was recorded, 13 nests lost eggs or young without any trace, three showed signs of egg predation, two had young preyed upon, and a hatchling died shortly after hatching at one nest. Two nests were lost because the branch on which they were constructed was cut and one adult was found taken by a predator under the nest and a nestling had fallen from another nest.

Nestling diet and comparison with roost diet

In terms of biomass contribution, > 50% of nestling diets in Cameroon and Senegal consisted of reptiles whereas diets of roosting kites were dominated by Orthopterans and Solifugids (Figure 2). Dietary overlap according to Pianka's (1973) Index based on the percentage frequency of prey numbers in the diet for nine prey categories (micro-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 between roost site and nestling diets.

6.4 Discussion

With 110 nesting pairs in 2.8 km^2, Kousmar islet in Senegal supports the largest Swallow-tailed Kite breeding colony documented to date, compared with single colonies reported from Senegal (3, 5, > 15 nests; Brasseur 2000, King 2000, P. Pilard in litt.), Cameroon (2-13 nests; this study), and Kenya (two nests; Davey & Davey 1980). Based on our data and observations of inter-colony distances elsewhere (Davey & 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, Swallow-tailed Kites were known to breed on the mainland along the border of the Saloum River, 6 km east of Kousmar (Figure 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 the birds on islets, where tree diversity, density and height has been maintained to a certain extent. Other breeding nuclei in the Delta have also been recorded on islets, or relatively intact forests on peninsulas (Figure 3).

Our observations of immature birds among nesting pairs in Senegal is interesting in light of the foraging efficiency hypothesis (Beauchamp 1999), since coloniality delivers particularly strong advantages for less experienced breeding pairs (Muller *et al.* 1997, Sergio & Penteriani 2005). Possibly, these immature, inexperienced Swallow-tailed Kites cue opportunistically on the presence of successfully breeding conspecifics (Sergio & Penteriani 2005), as suggested by the settlement of new pairs in one Swallow-tailed Kite colony which already held nests with eggs or nestlings in Senegal (Brasseur 2000). The observed communal nest defense against diurnal predators suggests that Swallow-tailed Kites may also benefit from improved predator protection at colonies during the day, although the conspicuousness of a large colony to nocturnal predators might outweigh such benefits. Frequent small carnivore predation in Cameroon suggests, however, that nocturnal predators may depress reproductive output even in small, relatively inconspicuous colonies.

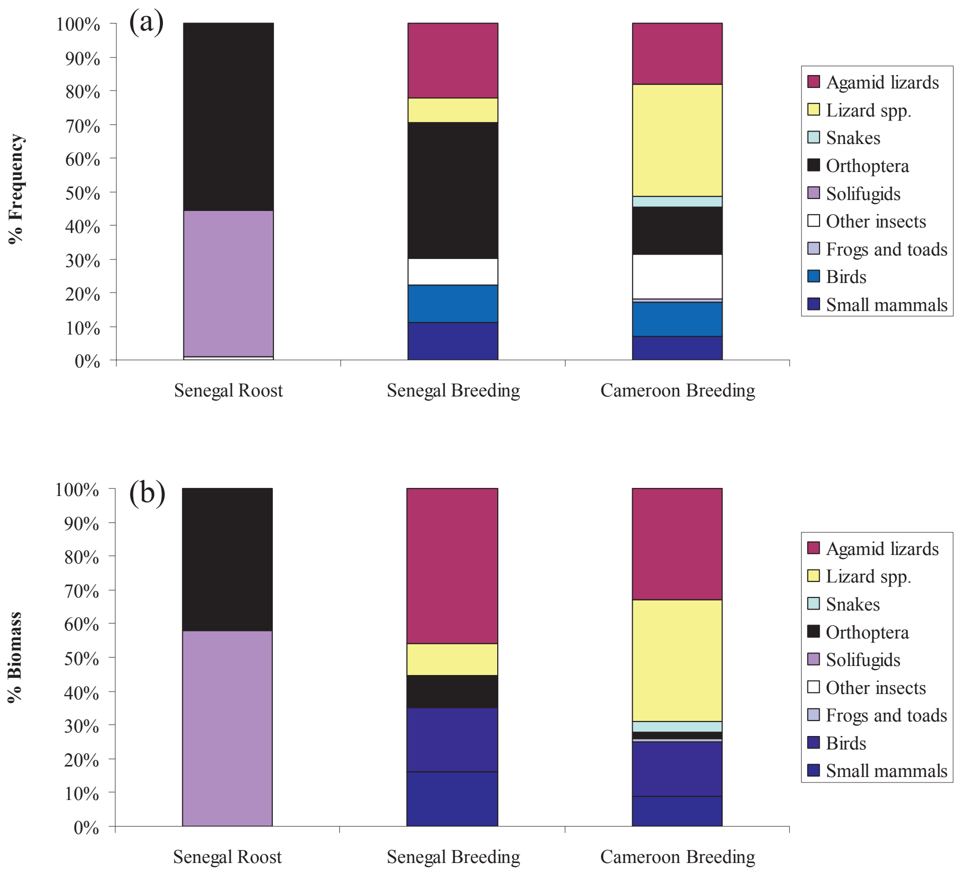

Figure 2. Diet composition based on prey remains and pellet contents of Swallow-tailed Kites in 2009-2010 at the Kousmar roost site in Senegal (n = 2660 prey items), at nests in Senegal (n = 27 prey items; five nests) and at nests in Cameroon (n = 98; 22 nests): (a) prey categories in pellets as percentage 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.

The proximity of breeding or roosting Verreaux's 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).

Timing of breeding and productivity

The laying dates of Swallow-tailed Kites in Cameroon were consistent with Thiollay's (1977a, 1978a) observations of breeding during the start of the rains from May-July in the southern Sahel, and 85% of pairs in Cameroon laid eggs after the first rains. Conversely, laying dates in Senegal have all been 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 in litt.). Laying thus appears to span at least four months (last week of December-first week of May) in Senegal, resembling a protracted breeding season comparable to sympatric Black-winged Kites *Elanus caeruleus* (Rodwell *et al.* 1996).

The very low frequency of clutches of four eggs (1.6%; n = 61), suggested to be the usual clutch size in this species (Brown & 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 norm, it seems likely that large clutches 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 in litt.), and another clutch of four collected by Bisseling at Sennar, Sudan on 16 May 1959 (M. Louette in litt.) coincided with massive Desert Locust swarms in the mentioned territories (cf. Waloff 1966, Mullié 2009). Similarly, Davey & Davey (1980) report 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 SW 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 might have constrained reproductive output, for example if younger. Suboptimal breeding conditions in the second half of the dry season, when we monitored nests, might also have contributed to the low reproductive success. Although this period is characterized by greatly reduced vegetation cover, facilitating capture of terrestrial prey (Thiollay &

Clobert 1990), grasshopper densities are known to decline during this time, mainly due to bird predation (Mullié & Guèye 2010). This may worsen the effect of food competition due to high numbers of conspecifics.

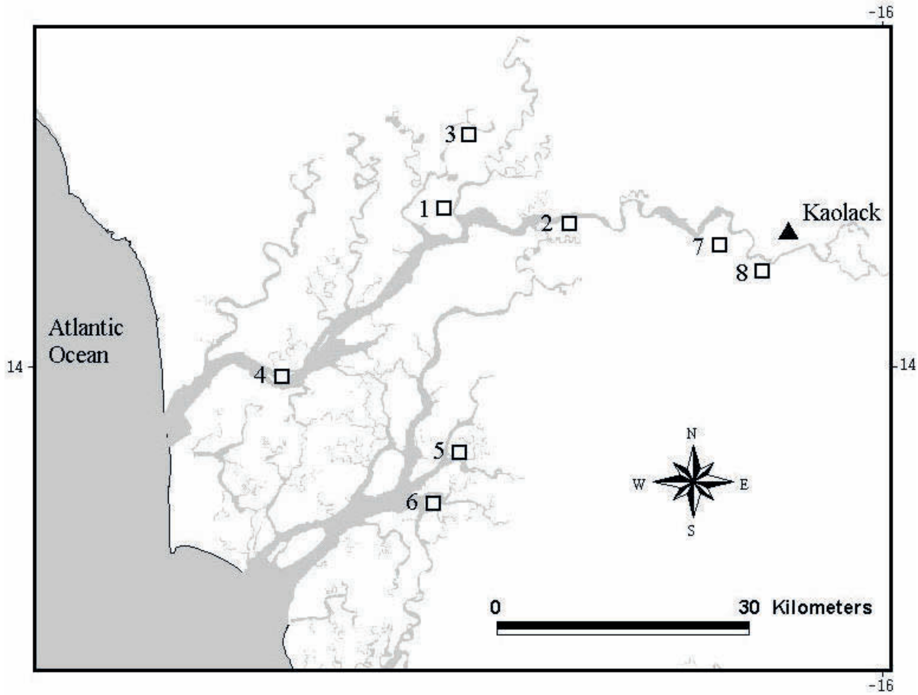

Figure 3. Breeding sites of Swallow-tailed Kites in 2000-2012 in the Saloum Delta of west Senegal. Numbers on the map correspond to 1: J. Peeters in litt. and in Brasseur 2000; 2: Petekele 2010, S. Cavaillès pers. comm.; 3: P. Pilard in litt.; 4: Il de Diable 2011, Manga pers. comm.; 5: R.E. Brasseur 2000 and in litt.; 6: Manga pers. comm.; 7: Kousmar 2010-2012 (this study); and 8: abandoned colony, S. Ndiaye pers. comm.

A prolonged breeding season and the possibility for re-nesting may allow Swallow-tailed Kites to compensate for losses incurred early in the season, as observed in various tropical raptors (Mader 1982, Delannoy & Cruz 1988, Thorstrom & Quixchán 2000), or raise multiple broods while opportunistically capitalizing on conditions of prolonged food abundance, as reported for *Elanus* kites (Mendelsohn 1984, Ey 1984). We recorded renesting at one nest in Senegal after nest predation, but follow-up studies will have to confirm the frequency at which this occurs and how it contributes to improving reproductive output.

Breeding in changing landscapes

Similar to other kites that breed in dense colonies (*Gampsonyx*, *Elanoides*, *Ictinia*; Newton 1979), Swallow-tailed Kites in Senegal and Cameroon opportunistically settled in food-rich floodplain habitats, accepting 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 Swallow-tailed Kites is in line with previous reports from western Africa (e.g. Thiollay 1978a, Pilard *et al.* 2011), which refer to congregations in or nearby floodplains, estuaries, or temporary wetlands. The ability of Swallow-tailed Kites to adapt to fluctuating resource conditions in these wetland systems may limit their vulnerability to human-induced land transformation. 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 appear to profit from reduced grass cover and height and improved prey catchability following moderate grazing or cultivation, even hunting alongside livestock to capture flushed insects (Gregory 1982; R. Buij pers. obs.), while transformation of woodland habitats into cropland mosaics may boost grasshopper prey (Mullié & 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% locally in the 1990s, leading to a strong increase in firewood extraction (Scholte 2003), e.g. estimated at 10 tonnes wet mass a day for Kalamaloué N.P. north of Waza N.P. Similarly, 20% of the trees at the roost site in Senegal were lost between 2007 and 2010 due to firewood extraction (Pilard *et al.* 2011). At present, the decline of woodland cover in the Saloum River estuary exposes the islets where the kites breed to an increasing exploitation of wood (Cavaillès 2010). Such loss of woodland cover may further influence dispersion patterns and possibly drive aggregations into larger breeding colonies, possibly contributing to lower breeding output.