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Food niche segregation between the Malachite Kingfisher, *Alcedo cristata*, and the Pied Kingfisher, *Ceryle rudis*, at Lake Nokoué, Bénin

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Several species of kingfisher occur on Lake Nokoué, southern Bénin, including Malachite (*Alcedo cristata*) and Pied Kingfishers (*Ceryle rudis*). Here, we compare their diet and estimate the degree of overlap in food niche by analysing contents of regurgitated pellets collected near nesting sites of Pied Kingfishers or inside the nest chambers of Malachite Kingfishers. Characteristic fish skull bones were identified using a reference collection of local fish skeletons. Malachite Kingfishers feed most frequently on fish that occur around floating vegetation, mainly *Kribia* sp. (56%), *Hemichromis fasciatus* (28%) and *Sarotherodon melanotheron* (8%). Important differences were found between different pairs, and between adults and nestlings, the latter being fed almost exclusively on *Kribia sp*. Larger fish are fed to nestlings than are eaten by the adults. Pied Kingfishers prey upon 14 different fish species, some of them being caught in the pelagic region of the lake, particularly clupeids taken by hovering. By comparison with Malachite Kingfishers, Pied Kingfishers feed on a wider diversity of prey, and take larger fish, so that the dietary overlap between the species is relatively low (O = 0.181).

Introduction

The Malachite Kingfisher (*Alcedo cristata*) is one of the most common kingfishers in Africa, and is abundant in lowland equatorial and subtropical savannas, where it inhabits reeds or papyrus fringes and the bank vegetation of ponds, lakes and rivers (Bannerman 1953, Fry *et al*. 1992). Throughout its large distribution area — almost the largest among African kingfishers — it is easily observed, hunting for prey from a low perch on small branches or emergent rocks. However, its feeding habits have been rarely studied. Bannerman (1953) and Bouet (1961) mention small fish and freshwater crustaceans (crabs and prawns) as its main food. Van Someren (1956) and Newman (1974) found the diet dominated by aquatic insects, mainly damselflies and dragonflies (nymphs and adults) as well as water beetles (Dytiscidae) and water boatmen (Notonectidae) but also including small fish (e.g. *Barbus* sp*. Tilapia* sp.), frogs, tadpoles and occasionally small lizards and terrestrial insects such as grasshoppers and mantises. On a polluted river where there were no fish, Meadows (1977) observed an individual feeding exclusively on insects (water beetles, water boatmen and adult Odonata) during a period of at least 47 days. Reyer (in Fry *et al.* 1988) reported an exclusive consumption of fish (*Tilapia grahami*) and estimated the daily requirements at 15–20 small fish, 30–40 when nesting, and 60 or more fed daily to five nestlings.

Many fish-eating birds occur on the lagoons and associated swamps of southern Benin, including cormorants, egrets, herons, terns and five kingfishers; Pied (*Ceryle rudis*), Woodland (*Halcyon senegalensis*), Giant (*Megaceryle maxima*), Malachite and African Pygmy-kingfisher (*Ispidina picta*) (Schockert 1998). Among these potential competitors, the Pied Kingfisher is probably the most numerous, the most widespread and the most likely to compete with the Malachite Kingfisher, as observed by Reyer *et al*. (1988). It therefore seems of interest to compare the composition of the diet of both species in the same habitat and to analyse the extent of overlap in their respective food niches.

In this paper we report on variations in the food of Malachite Kingfishers in relation to localities of nest sites and the age of nestlings. Detailed results of analyses of the food of Pied Kingfishers are discussed elsewhere (Laudelout and Libois 2003).

Study area

Southern Benin is in a subequatorial climate zone (Figure 1), with a high relative humidity (77–93%) and a high mean monthly temperature, ranging from 22.4–32.9°C. Annual rainfall is about 1 000mm distributed over a long rainy season from March/April to July and a short rainy season from September to mid-October (Pliya 1980).

Lake Nokoué (6°23'–28'N, 2°22'–33'E) is a shallow lagoon not exceeding 2.50m in depth. In 1990 and 1991, its mean depth ranged from 1.07m at the end of the dry season (April) to 1.72m during the floods (September). Its waters are relatively turbid, especially during the floods: Secchi depth varies between 50 and 120cm in Vêki, in the vicinity of the study sites. Salinity also fluctuates widely: from 25–30mg l^{-1} in April–June to 0–5mg l^{-1} in August–November (Laleye 1995). Its north-western edges correspond to the delta of the River Sô, occupied by villages built on piles, cultivated fields and *Paspalum vaginatum* meadows.

The fish community comprises at least 78 species from

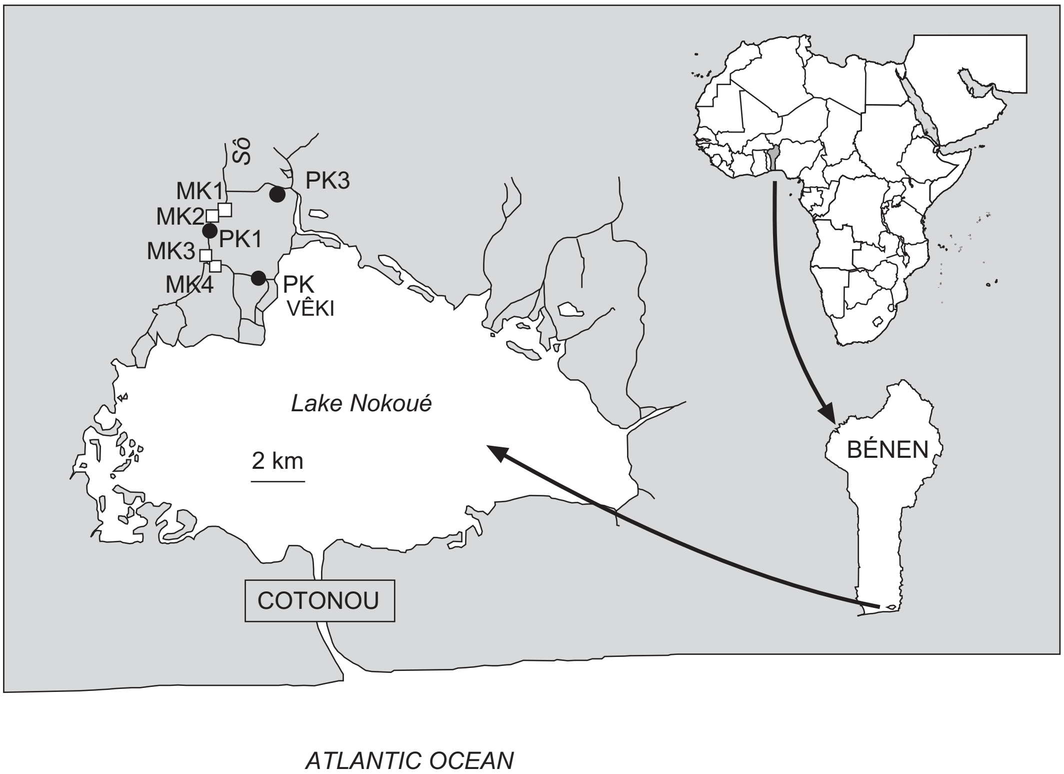

Figure 1: Schematic map of Lake Nokoué indicating the study sites

freshwater, brackish or marine origin, but is dominated throughout the year by three families: clupeids (*Ethmalosa fimbriata* (Bowdich)*, Pellonula leonensis* Boulenger*, P. vorax* Günther), cichlids (*Sarotherodon melanotheron* Rüppell, *Tilapia guineensis* (Günther)) and bagrids (*Chrysichtys auratus* Geoffroy St. Hilaire, *C. nigrodigitatus* (Lacépède)) (Laleye 1995). Fish is an important economic resource for the local peoples, who catch fish by various types of nets, long lines and especially in privately owned brush park enclosures called 'akadjas'. In the rivers, surfaces of akadjas are covered with tree branches that stop the floating vegetation, providing shelter to the fish and allowing the development of a rich zooplankton.

Material and Methods

The present study was based on an analysis of regurgitated pellets (Doucet 1969, Douthwaite 1976, Whithfield and Blaber 1978, Hallet-Libois 1985). The bony remains in pellets were identified by using a reference collection of the skull bones of the main fish species present in the area made from fish bought on the local markets and identified by P Laleye. Diagnostic bones were chosen in this collection to make the specific or generic identification of the fishes possible. These were right and left skull bones (dentaries, maxillaries, praemaxillaries, operculars, praeoperculars), chosen for being easily recognisable by their shape and strong enough to prevent deterioration either in the digestive tract of the birds or by trampling in the nest chamber (Laudelout and Libois 2003).

For both kingfisher species, the material was collected in the delta of the River Sô, north-west of Lake Nokoué (Figure 1) from the beginning of April to mid-May 1999. Most material was found on the nest site banks as individual pellets or (mainly) excavated in bulk from nest brood chambers. When recovered from the banks, the pellets were analysed without further treatment, but material recovered from the brood chambers was cleaned by immersion in water for a few days. Soaked pellets were then sieved under a weak water jet and dried before the characteristic skull bones were sorted, counted and some measured. In each sample, right and left bones were counted separately and the minimum number of prey belonging to a taxonomic category was considered as the maximum value of either count for this category. Exoskeleton remains of arthropods were recovered and identified to the order when possible.

For *Sarotheridon melanotheron* and *Hemichromis fasciatus* Peters, the standard length (SL) of the fish prey was determined from the length of the praeopercular bones (BL), using fish length-bone length relationships developed for local fishes. In *S. melanotheron*, SL = 5.731*BL + 10.132 (r = 0.981; n = 32) and in *H. fasciatus*, SL = 7.638*BL + 3.600 (r = 0.987; n = 27). (Laudelout and Libois, 2003). As some species have no economic interest and, for this reason, are not sold on the markets, and as we failed to catch a significant number of specimens, such a calculation was not possible in the case of *Hyporhamphus picarti* (Valenciennes) and of *Kribia* sp. Since the taxonomy of the genus *Kribia* is not well known (Teugels, pers. comm.), specific identification using skull bones is questionable.

The G test was used to compare the differences between the diets of different groups of birds, i.e. by time, location and species. The number of degrees of freedom is indicated by the value x in the expression $G_{x,corr}$. where the meaning of $_{corr}$ is 'value corrected for small sample size'. Student t-tests were performed to compare means and Kolmogorov-Smirnov tests to compare frequency distributions. Similarity between the diet of both kingfisher species was made using Pianka's equation: $O = 1 - (\Sigma|p_{im} - p_{ip}|)/2$, where p_{im} is the proportion (in numbers) of species i in the diet of Malachite Kingfisher and p_{ip} its proportion in the diet of Pied Kingfisher.

Results

Four fish taxons were found in Malachite Kingfisher pellets: *Kribia* sp. was the most important prey (56%), *Hemichromis fasciatus* (28%), *Sarotherodon melanotheron* and an undetermined species in low numbers. There were also some frogs, crustaceans, termites and undetermined insects. By comparison, the diet of Pied Kingfishers was much richer in fish species (n = 14) and also more diverse (H' = 2.66 vs 1.63) (Table 1), but the standardised food niche breadth of both species was similar.

The specific composition of the kingfishers diet is significantly different ($G_{4,corr}$ = 378.8, P < 0.0001). Nevertheless, the difference is less obvious when comparing nests 1–3 of the Malachite Kingfisher and the single nest of the Pied Kingfisher in the same vicinity, i.e. sharing similar ecological conditions (nest 1 in Laudelout and Libois, 2003) ($G_{4,corr}$ = 45.1, P < 0.001)

Therefore, the overall food niche overlap is not very important (O = 0.407). Two prey taxa are responsible of this overlap, *Kribia* sp. and *H. fasciatus*. However, considering the size distribution of the latter, it is evident that this value is overestimated because Pied Kingfishers eat larger cichlids (*H. fasciatus* and *S. melanotheron*) compared to those preyed upon by Malachite Kingfishers (Figure 2, Table 2). When these size differences are taken into account, the food niche overlap drops to 0.181, less than one-half the previously estimated value. This indicates that the food niche segregation between both kingfishers is not only the consequence of a fishing behaviour directed towards different prey species, but also towards different size classes.

Important differences between pairs were observed (Table 3) ($G_{9,corr.}$ = 46.3, P < 0.001). Three pairs ate a large proportion of *Kribia sp*. and very few *S. melanotheron* (G_6 = 10.6, n.s.), whereas the fourth pair had a much more diversified diet.

At nest 4, strong variations were also noted in the diet of the nestlings compared to their parents (Table 4) ($G_{9,corr.}$ = 54.7, P < 0.001). Once the young were 8 days old, they were fed almost exclusively on *Kribia sp*, compared with their food at 4–8 days old, when they were fed a more diverse diet with an intermediate composition, not significantly different from either the diet of the previous period ($G_{3,corr.}$ = 7.11, n.s.) or of the next two periods ($G_{6,corr.}$ = 7.6, n.s.). Other changes observed during this period include the mean standard

Table 1: Numbers of prey identified in the diet of Malachite and Pied Kingfishers in the western part of Lake Nokoué. The types of bone used to identify and estimate numbers of prey species is indicated *

	Bones*	Malachite Kingfisher (*Alcedo cristata*)	Pied Kingfisher (*Ceryle rudis*)**
Ethmalosa fimbriata	Po, De		313
Clupeidae unident.	Po, De		13
Gerres melanopterus	Po, De		10
Hyporhamphus picartii	De, Po		88
Hemichromis fasciatus	Po, Pmx	127	248
Sarotherodon melanotheron	Po, Pmx	37	260
Tilapia guineensis	Po, Pmx		6
Kribia sp.	Po, O	251	106
Yongeichtys thomasi	Po		21
Elops sp.	Po, O		4
Clarias sp.	De, spines		6
Chrysichtys sp.	Spines		5
Mugil sp.	Po		17
Unidentified fish, sp. 1			1
Unidentified fish, sp. 2***		2	
Amphibians		3	
Beetles (Coleoptera)			2
Termites		22	1
Other insects		2	1
Crustaceans		1	4
TOTAL		445	1 106
Diversity index (H')		1.63	2.66
Standardised food niche breadth		0.21	0.23

* De = dentary; O = otolith, Po = praeopercular, Pmx = praemaxillary
** After Laudelout and Libois 2003
*** Comparitive material was not available in our collection to identify some bones (praeopercular for sp. 1 and opercular for sp. 1 and 2)

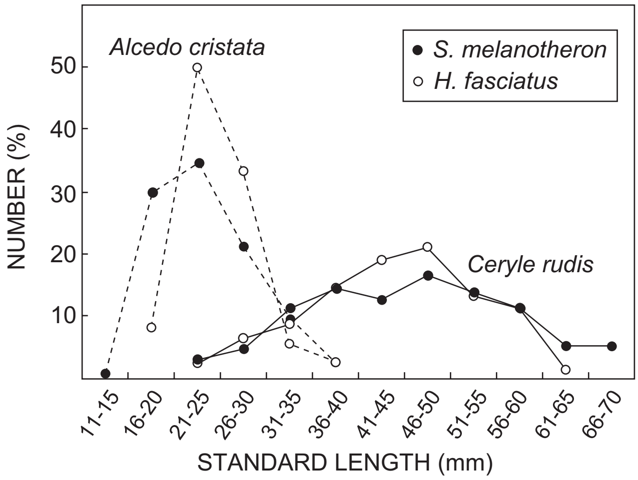

Figure 2: Size frequency distributions of two fish species in the diet of Pied and Malachite Kingfishers. For *S. melanotheron*, n = 36 and 256 respectively in the Malachite Kingfisher and in the Pied Kingfisher diet. Corresponding numbers for *H. fasciatus* are 112 and 229

length of *Hemichromis fasciatus* fed to the young (26.7 ± 6.0mm; n = 9), which were significantly larger (P = 0.037, Student t-test) than those eaten by the adults (23.1 ± 5.0mm; n = 39). Similarly, young also received larger *Kribia* fishes than eaten by adults (POL = 3.79 ± 0.61mm, n = 73 vs 2.92 ± 0.38, n = 20; P < 0.0001) (Figure 3), assuming that the length of the praeopercular (POL) bone of *Kribia* sp. is correlated to fish length.

Discussion and conclusions

As stated in the introduction, the diet of the Malachite Kingfisher is not well known, so it is difficult to compare our semi-quantitative results with the exclusively qualitative information reported in a few lines in short notes (Newman 1974, Meadows 1977) or in general reference books (Bannerman 1953, Van Someren 1956, Bouet 1961, Fry *et al.* 1988, 1992, Woodall 2001). However, the present findings underline the importance of small fish in the diet of the species. In Lake Nokoué, the main prey of Malachite Kingfisher is *Kribia* sp. These are small demersal freshwater fish, measuring less than 6cm in total length (Maugé 1986), occasionally found on the sandy bottom of streamlets or among aquatic vegetation of running waters (Roman 1975). These conditions may be met in the delta of the River Sô,

Table 2: Comparison of the standard length (SL) of *Hemichromis fasciatus* and *Sarotherodon melanotheron* preyed on by Malachite and Pied Kingfishers at Lake Nokoué

	Malachite Kingfisher	Pied Kingfisher	Statistical tests	
			Student	Kolmogorov-Smirnov
H. fasciatus				
Mean SL	24.1mm	46.4mm	t = 19.5, P < 0.001	P < 0.0001
Standard deviation	4.9mm	11.6mm		
Range	13–38mm	22–73mm		
Number	112	229		
S. melanotheron				
Mean SL	25.4mm	44.0mm	t = 12.0, P < 0.001	P < 0.0001
Standard deviation	3.9mm	9.2mm		
Range	15–39mm	24-65mm		
Number	36	256		
Student t-test	t = 1.45, n.s.	t = 2.53, P ≈ 0.02		
Kolmogorov-Smirnov test	P > 0.1, n.s.	P > 0.1, n.s.		

Table 3: Local variations in the diet of Malachite Kingfishers in western part of Lake Nokoué (numbers of prey recovered in each nest)

	Nest 1 Adults Late April–early May	Nest 2 Adults April	Nest 3 Adults mid April–mid May	Nest 4 Adults + Nestlings April
Hemichromis fasciatus	15	15	33	48
Sarotherodon melanotheron	2	1	2	22
Kribia sp.	14	25	93	22
Unidentified fish	1	1		
Amphibians	1		1	
Crustaceans		1		
Termites	2		11	5
Other				2
TOTAL	35	43	140	99
Diversity index (H’)	1.82	1.36	1.31	1.80
Standardised food niche breadth	0.37	0.29	0.25	0.49

Table 4: Number of prey eaten by Malachite Kingfisher adults compared to nestlings at Nest 4 in western part of Lake Nokoué

	Adults + nestlings 0–3 days old <28 April	nestlings 4–8 days old 28 April to 2 May	Nestlings 8–12 days old 2 May to 6 May	nestlings 12–16 days old 6 May to 10 May
Hemichromis fasciatus	48	10	2	4
Sarotherodon melanotheron	22	6	4	
Kribia sp.	22	24	37	36
Amphibian				1
Termites	5	4		
Other	2			
TOTAL	99	44	43	41
Diversity index (H')	1.80	1.67	0.71	0.62
Standardised food niche breadth	0.39	0.33	0.07	0.06

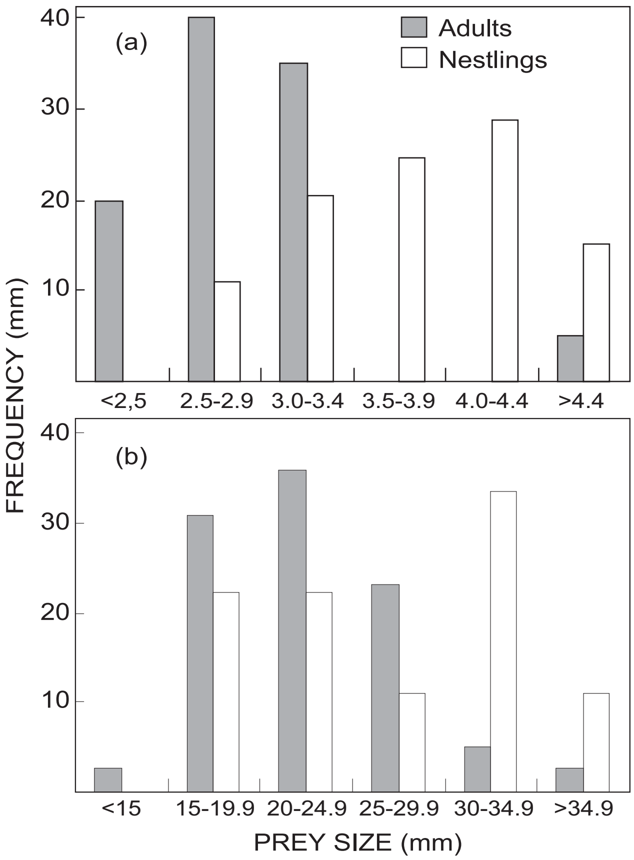

Figure 3: Differences in prey size between adult and nestlings Malachite Kingfishers at nest 4. Frequency distributions of A: the praeopercular bone length of *Kribia* sp. and B: of the standard length of *H. fasciatus*. For *Kribia* sp., the numbers are 20 and 73 for the adult birds and for the nestlings, respectively, whereas for *H. fasciatus*, the corresponding numbers are 39 and 9. The distributions are significantly ($P < 0.01$) different in both cases (Kolmogorov-Smirnov test).

particularly where the akadjas are located. The second main prey is cichlid fish. Both *H. fasciatus* and *S. melanotheron* are demersal and theoretically would not be available to Malachite Kingfishers. However, small sized individuals of both fish species are often found in shallow waters near the banks (Gosse 1963) where they are more vulnerable to predation by kingfishers. Other prey, including crustaceans and terrestrial insects, are quite infrequent at Lake Nokoué, unlike the findings of most other observers.

Cichlids are the main prey of Pied Kingfisher around Lake Nokoué, as in other areas (Tjomlid 1973, Douthwaite 1976, Whitfield and Blaber 1978). The second most important prey is Clupeidae, especially *Ethmalosa fimbriata*. This pelagic species lives in dense shoals and its availability is therefore limited to birds fishing offshore and hunting by hovering. Other pelagic species of minor importance in the diet are *Elops* sp. and mullets. The third important group is *Kribia* followed by *Hyporhamphus picartii,* a benthic species, feeding on algae and organic debris. However, its eggs are attached to the aquatic vegetation (Collette and Parin 1990) and the young fish are vulnerable to kingfishers after hatching. Other fish species are poorly represented in the diet of the Pied Kingfisher. In general, the diet reflects not only the different hunting modes (hovering vs sit and wait) of the Pied Kingfisher, but also the diversity of habitats it exploits, from freshwater (indicated by the presence of *Kribia*) to brackish areas (see Laudelout and Libois 2003). Indeed, the Pied Kingfisher appears highly adaptive in its feeding habits (Junor 1972, Cooper 1981, Jackson 1984, Wanink and Goudswaard 1994).

Important dietary differences were observed between Malachite and Pied Kingfishers nesting in same area. Such differences are not only between prey species and their respective proportions, but also the size of the fish taken by the birds. Malachite Kingfishers usually hunt from perches 50–90cm above the water surface, searching for small fish living in shallow waters or in the riparian subaquatic vegetation. Pied Kingfishers can use the same habitat type, though they perch higher (30–230cm). They can exploit deeper waters (Reyer *et al*. 1988) and, due to their ability to hover, are able to catch pelagic fish far from river banks or lake shores. Furthermore, in Lake Nokoué, Pied Kingfishers regularly hunt inside the nets designed to catch clupeids. The akadja poles can also be used for resting between fishing sessions, which also enables Pied Kingfishers to remain in the centre of the lake. The important proportion of clupeid fish (*Ethmalosa fimbriata*) in their diet is certainly a consequence of such behavioural traits. Being larger and stronger than Malachite Kingfishers means that Pied Kingfishers are able to swallow larger prey. Moreover, the size range of their prey is much wider, indicating a less strong size selection than in Malachite Kingfishers, as shown by Reyer *et al.* (1988). The overlap in food between both kingfishers is therefore reduced as a consequence of their different morphology and of their different fishing habits.

Local variations in Malachite Kingfisher diet are not as conspicuous as those in the Pied Kingfisher (Laudelout and Libois 2003). The regurgitated prey remains were collected at the same period of the year in a very restricted area, and their composition was therefore not very likely to change from one site to the next. However, the food eaten by the pair at nest 4 was very different from the pairs at the other three nests. This difference could be related to the vicinity of fish breeding ponds (presence of *S. melanotheron*) or to the peculiar status of this sample (presence of nestlings). As observed in other kingfishers, the nestlings are closely brooded for several days after hatching by one of the adults (Hallet-Libois 1985, Fry *et al*. 1992, Woodall 2001). It is likely that the brooding adult regurgitates pellets when present in the nest chamber, and the pellet samples from early in the breeding cycle may be a mixture of food remains from adults and nestlings. The first samples of pellets from nest 4 was taken when the nestlings were about three days old and probably contained such a mixture.

Nestlings and adults have diets that are markedly different. Adult birds have a more diverse food intake and rely upon two main prey species, *Kribia* sp. and *H. fasciatus*, whereas the young are fed mostly with *Kribia sp.* Moreover, the fish eaten by the adults are significantly smaller than those fed to the young, which was also shown to be the case in the Common Kingfisher *Alcedo atthis* (Hallet-Libois 1985) and in the Pied Kingfisher (Laudelout and Libois 2003).

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Résumé

Dans les lagunes du sud du Bénin, notamment sur le lac Nokoué, plusieurs espèces de martins-pêcheurs cohabitent. Les espèces les plus fréquentes sont le petit martin-pêcheur huppé (*Alcedo cristata*) et le martin-pêcheur pie (*Ceryle rudis*). Leur régime alimentaire a été comparé et le recouvrement de leur niche alimentaire a été estimé. Des pelotes de réjection ont été récoltées à proximité des sites de nidification (*C. rudis*) ou à l'intérieur des nids (*A. cristata*). Des os crâniens caractéristiques des différentes espèces de poissons ont été recherchés et identifiés au moyen d'une collection de référence constituée de squelettes de poissons pêchés sur place. Le petit martin-pêcheur huppé chasse huit catégories de proies. Ce sont les poissons qui vivent au voisinage ou à l'intérieur de la végétation flottante qui sont les plus nombreux dans son régime : *Kribia sp*. (56%), *Hemichromis fasciatus* (28%), *Sarotherodon melanotheron* (8%). D'importantes différences ont été mises en évidence entre le régime de couples voisins ou entre le régime d'adultes et d'oisillons. Ces derniers sont quasi exclusivement nourris de *Kribia sp*. En outre, ils consomment des poissons de plus grande taille que leurs parents. Le martin-pêcheur pie, pour sa part, se nourrit aux dépens de 14 espèces de poissons dont certaines sont capturées dans la zone pélagique du lac (clupéidés capturés à partir d'un vol stationnaire). Son régime est plus diversifié et il capture aussi des poissons de plus grande taille, en conséquence de quoi, le chevauchement alimentaire entre les deux espèces est assez faible (O = 0.181).

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