Record breeding densities of Frances's Sparrowhawk *Accipiter francesiae*, and effects on bird communities in the Comoros

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Abstract. - In two study plots on Mayotte Island, the territorial, neotenic-endemic race *brutus* of the Frances's Sparrowhawk occurred at world-record breeding densities for a small raptor of 2.0-2.6 ha/pair, with average inter-nest distances of 140-159 m in the breeding season of 1997. Measured in nine transects, the abundance of birds of potential prey-size correlated negatively with sparrowhawk abundance on Mayotte, while numbers of birds larger than sparrowhawks varied in parallel with sparrowhawk abundance, both corresponding to rainfall and lushness of the vegetation. Throughout the Comoro archipelago, there is a negative relationship at island level between sparrowhawk abundance and the proportion of small birds in the community. Several species of small birds are lacking from islands with sparrowhawks compared to islands without sparrowhawks; anomalies that cannot be explained by island size, distance to source or habitat. More species are lacking from islands with high sparrowhawk abundance. We suspect that the chances of survival for colonizing birds may have been affected historically by the abundance of Frances's Sparrowhawks on some of the Comoro Islands.

Introduction

Several Falconiforms breed colonially, and many other raptors form loose breeding associations with high densities of nests under exceptional conditions of food abundance (Cramp and Simmons 1980, del Hoyo *et al.* 1994). Although the immediate vicinity of the nest is usually defended against conspecifics also under colonial conditions, hunting grounds are communal. Truly territorial raptors, i.e. species which obtain most of their requirements from within the boundaries of an exclusive territory which is defended against intrusions by conspecifics other than the breeding mate or offspring, have their nests regularly spaced at intervals which reflect the space requirements of the species in relation to the quality of the habitat (Newton 1979, 1986, Marquiss and Newton 1982, Newton *et al.* 1986): e.g. densities on the European continent are 2-62 pairs/100 km^2 in the small, territorial Eurasian Sparrowhawk *Accipiter nisus* (Forsman and Solonen 1984, Newton 1986, Blondel *et al.* 1988, Bühler 1991, Bijlsma 1993, Tomialojc and Wesolowski 1996), while densities are slightly higher 14-96 pairs/100 km^2 in Great Britain, where inter-nest distances are typically 0.5-2.1 km (Newton *et al.* 1986, Newton 1986). In the genus *Accipiter*, territorial raptors, particularly "high densities" are reported from such islands as Taveuni (Fiji) (Clunie 1981), New Caledonia (Thiollay 1993) and (particular) Solomon islands (Webb 1997).

Indeed, animal densities are in general higher on islands than on the adjacent mainland (MacArthur *et al.* 1972, Williamson 1981, Crowell 1983, Blondel 1986), which has sometimes been ascribed to lower levels of predation (Faeth 1984, George 1987). The principle of density inflation on islands does also hold for raptors (Thibault *et al.* 1992, Thiollay 1993, Pérez del Val *et al.* 1994), and consequently, adjacent islands which have or lack a raptor species can be subject to very different levels of predation.

Frances's Sparrowhawk *Accipiter francesiae* is a small sparrowhawk (males 100 g, females 150 g: Herremans *et al.* 2001) endemic to the Malagasy region (del Hoyo *et al.* 1994), with distinct subspecies on Madagascar and on each of three Comoro Islands, while it is absent from the fourth island, Moheli (Mwali). Sexes on Madagascar have well differentiated plumages, but on each Comoro island, sexes are similar. In the race *brutus* on Mayotte (Maore), birds have brown upperparts and are heavily barred brown underneath, closely resembling the female and juvenile plumage from Madagascar; on Grand Comoro (Ngazidja) and Anjouan (Ndzuani), both sexes have a masculine plumage (Benson 1960, Louette 1988, Langrand 1990, Louette 2000). Compared to the nominate form in Madagascar, *brutus* on Mayotte is partially neotenic (Herremans 1990). A relationship between neotenic evolution, e.g. in plumages and reduced territoriality (Herremans 1990), and increased densities has been shown on the Comoros as one of the 'insular syndromes' shared by several species (Louette *et al.* 1993a). From point-transect counts of birds in October 1992 (Louette *et al.* 1993b), 1993 and 1994 (Stevens and Louette 1999), we became aware that this sparrowhawk is particularly abundant on Mayotte. We observed several successful attempts to prey on reptiles, and we witnessed that the sparrowhawk readily responds to traps baited with small birds. Mizuta (2007) mentions the direct observation of predation of this sparrowhawk on a small bird.

Predator populations typically follow prey dynamics (e.g. Newton 1991), but experimental predator control did only in about half the studies result in an increase of prey populations, indicating that other factors than predation were limiting (Newton 1991). All cases where predator removal resulted in an increase of bird breeding populations refer to vulnerable ground nesting species which were secondary or alternative prey for predators with population levels supported by a staple food (other than birds) that failed occasionally or cyclic (Newton 1991). During the comprehensive studies of the Eurasian Sparrowhawk, a systematic effects of the predator on the population sizes of a prey species, the House Sparrow *Passer domesticus,* was detected in Britain (Bell *et al.* 2010), and also an impact on Grey Partridge *Perdix perdix,* where the prey numbers were at low levels (Park *et al.* 2008). Sometimes severe temporal or local impact on some species or age categories was found (Newton 1986, Whitfield *et al.* 1988, Newton *et al.* 1997). Frances's Sparrowhawks are the only important avian predator on small forest birds in the Comoros: numbers of Peregrine Falcon *Falco peregrinus*, Sooty Falcon *F. concolor,* Eleonora's Falcon *F. eleonorae*, and Yellow-billed Kite *Milvus parasitus* are small, and the first species preys mainly on waders, the second and third on insects and the fourth is not specialized on birds; Madagascar Harrier *Circus maillardi*, which is nowadays absent from Mayotte feeds largely on rodents (Benson 1960, Louette 1988). Barn Owl *Tyto alba* occasionally preys on birds, but its staple food on Mayotte is the Black Rat *Rattus rattus*, itself a nest predator of small birds (Louette 1996b, 1998).

The present paper reports world-record breeding densities for a sparrowhawk from the Comoros, and investigates whether and how these might have affected the bird communities on the islands.

Material and Methods

Densities. — During bird studies on the Comoros (1981-2001), we kept annotated daily lists of species observed. From these lists, we calculated the daily reporting rate of sparrowhawks (fraction of lists in which sparrowhawks were seen) to compare abundance on Grand Comoro and Anjouan. During nine point-transect counts on Mayotte in October 1993, the distance between bird and observer was estimated. This enabled the calculation of densities in concentric bands around the observer (Bibby *et al.* 1992).

In August 1995, at the onset of the breeding season, Frances's Sparrowhawks were inventoried in the western quarter of the Coconi study-plot (Fig. 1A) by a method called "trefclus" in use for passerines occurring at high density (Bult 1995). After familiarization, each morning from 27 August till 1 September between 7-8h two observers (M. Louette and an assistant) walked in opposite directions along a 2.25 km path. All sparrowhawk contacts were plotted on a map. This yielded a 6-day position map of (supposed) individuals. This procedure was repeated during 5 days in August 1996.

Breeding densities. — We studied breeding densities of Frances's Sparrowhawks at two sites in the wet western sector of Mayotte between 13 December 1997 and 14 January 1998: (A) 75 ha of small-scale plantations and crop farming with remnants of indigenous forest, accessible via a multitude of tracks, situated immediately NE of the Coconi forestry station; this site encompassed the study site of 1995 and 1996 (Fig. 1A); (B) 61 ha 10 km further north, between the villages of Tsingoni and Mrowalé. This was less accessible and we made inventories from tracks along two small river valleys, and in a coconut plantation on the adjacent plateau; a central part of this site was too far from the tracks and is excluded (Fig. 1B). We visited the study area at Coconi during 65 hours on 21 days, and Mrowalé during 29 hours on 8 days.

While walking study plots slowly, M. Herremans called up Frances's Sparrowhawks by imitating the territorial call ("vhit vhit vhit"), or the higher pitched and huskier begging call of juveniles ("whiest whiest whiest"). Dependent on topography, birds could be heard up to 100 m away, and where response was received, we searched the area systematically for the nest. Nests were plotted on a detailed map, and once a pattern of regular spacing of nests emerged, gaps were particularly carefully searched for nests or presence of territorial birds. Where nests had not yet been found, we watched adults for signs of breeding behavior. Where territorial boundaries were not resolved, we released caught and ringed sparrowhawks 100-200 m from the place of capture, to provoke response from neighboring territories. We also used resightings of ringed birds to differentiate territories. We recorded nest positions with an MX8600-pc GPS and GPS-Leica 2.40 groundstation software, resulting in an accuracy of <5 m. Boundaries of the study areas were determined in a GIS environment, using distance from the inventory tracks and topography as the main features.

Bird communities. — We sampled bird communities (mostly in forests) on the Comoros during 1985-1995 by point-transect counts. Each transect consisted of 20 points, where birds were counted for 15 minutes. We only use in this study counts from the breeding season (October-December). We used 31 transect counts from Grand Comoro, of which eight were repeats in two different years (Louette *et al.* 1988a, Stevens *et al.* 1995). We counted three transects on Moheli (Louette *et al.* 1989). We repeated nine transects during three years on Mayotte (Louette *et al.* 1993b, Stevens and Louette 1999). Repeated counts were averaged. We use the number of birds observed in transects as a measure of relative abundance. Assuming that abundance of a species was similar for repeated counts, detectability of the species can be deduced from the year to year variation; we define detectability as the fraction of the minimum to the maximum count in a transect.

Based on our own data on body mass of Comoro birds, we allocated species to weight classes: (1) likely prey <20g, (2) possible prey 20-<70g, (3) 70-<150g, (4) >=150g. We consider categories (1) and (2) as 'potential prey', while (3) and (4) are no regular prey of Frances's sparrowhawks (although Clément *et al.* 2008 show a picture of a Frances' Sparrowhawk grabbing such an unlikely prey as a Dabchick *Tachybaptus ruficollis*). We excluded aerial foragers that are not directly part of the forest bird-community interacting with sparrowhawks (e.g. the Black Swift *Apus barbatus*) from these analyses. However, the Spinetail Swift *Zoonavena grandidieri*, which forages extensively below the canopy and might be taken by sparrowhawks, was included.

The forest patch on La Grille, the northern volcano on Grand Comoro is isolated by inhospitable recent lava flows from the Karthala, the southern volcano. La Grille lacks several bird species present on the Karthala (Louette *et al*. 2008). For inter-island comparisons, La Grille is given the status of a separate 'zoogeographical island'. On Anjouan, Moheli and Mayotte, forest species occur down to sea level, but on Grand Comoro there is a dry coastal zone where habitat for forest species is lacking (except on the wettest southwestern flank of the Karthala). We include only estimated surfaces of potential habitat, and exclude for Grand Comoro the dry coastal zone, the large areas of inhospitable recent lava fields and the montane zone (absent on the other islands). To compare forest species numbers between islands, the following areas were used to compensate for island size: Moheli=250 km^2, Mayotte=374 km^2, Anjouan=425 km^2, Grand Comoro (Karthala)=450 km^2, Grand Comoro (Grille)=225 km^2.

Results

Density. — Except for their conspicuous behavior near nests and responsiveness to calls, Frances' Sparrowhawks were unobtrusive and remarkably infrequently encountered on Mayotte. Our data demonstrate this as follows: (1) variability of numbers encountered in transect counts was high, with a mean detectability of 0.36 (range 0.13-0.64), Frances's Sparrowhawk was the second least stable species (after Madagascar Turtle Dove *Streptopelia picturata*); (2) while undoubtedly the same number of birds is present during counts in the morning and in the afternoon, 45% fewer were detected in the afternoon ($\boldsymbol{X}^2_{df=1}$=34.8, P<0.00001); (3) during the standardized census work in

August 1995 and 1996 at Coconi, the average number of encounters with sparrowhawks during an hour in the morning varied between 0-15 birds (average 5.6), while 'trefclus' and subsequent data on the number of nests normally present in this area indicate that in fact there were about 12-14 adults and possibly some unpaired floaters present; (4) during the 6-day census at Coconi in August 1995, the probability to detect one member of a pair in a single morning was 52% (assuming seven pairs and no floaters in part of the Coconi plot).

Daily reporting rates in the years 1983 - 1992 were 0.2 on Anjouan (sparrowhawks seen on three days out of 14) and 0.3 on the Karthala (16 days out of 49). In 2005, the reporting rate on Anjouan was higher: 0.47 – seven days out of 15 - C. Marsh in Louette *et al.* 2008). Density estimates on concentric bands from point-transect counts indicated a rapidly declining detectability of sparrowhawks beyond 50 m, and an average density of >1 bird/ha throughout the densely vegetated wet sector of Mayotte in October 1993 (Table 1).

Non-nesting adults were difficult to inventory, and immature floaters were observed only on three occasions during 1997-98. Several factors greatly facilitated the inventarisation of Frances's Sparrowhawk nests on Mayotte during December-January: details on the synchronization and phenology of breeding, the exposed nest positions, the conspicuous behavior around the nest and the extreme tameness are reported elsewhere (Herremans *et al.* 2001). With the full inventory at hand, with hindsight, 70% of females called back within minutes in response to imitations and were discovered in the first visit, while during a single visit of a few minutes, on average 63% of known sites were re-confirmed by calling young when less than one month fledged.

In the study plot at Coconi, we found 29 pairs in an area of 75 ha; 20 pairs fledged young, two were still incubating by the end of the study in January 1998 and seven failed, in four of which the empty nest was found. No evidence of breeding could be found for three pairs (Fig. 1A). At Mrowalé, we found 30 pairs in 61 ha; 19 fledged young, eight nests failed and for three pairs no evidence of breeding could be found (Fig. 1B). We investigated particularly the nests closest to each other for signs of polygyny by catching the adults, but no cases of polygyny were recorded.

Table 1. Density estimates of Frances's Sparrowhawk *Accipiter francesiae brutus* in concentric zones (Bibby *et al.* 1992) around 180 points in transect-counts on Mayotte in October 1993 (unpubl. data JS).

Radius of zone (m)	Number of sparrowhawks observed	Density (birds/ha)
<25	45	1.27
25-<50	93	0.98
50-<75	15	0.48
75-<100	28	0.32
100-150	24	0.16

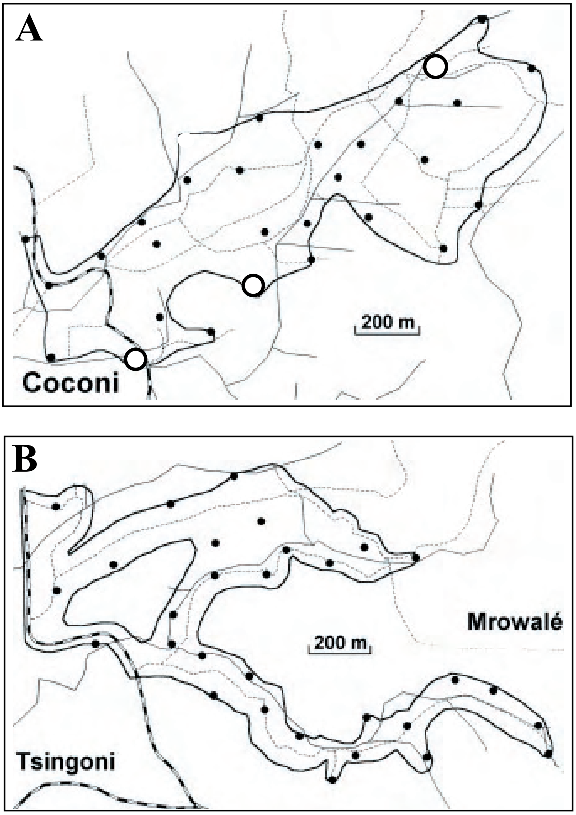

Figure 1. Spacing of Frances's Sparrowhawk *Accipiter francesiae brutus* nests and territories at two study sites on Mayotte (Comoro Islands) during December 1997-January 1998: 1A. Coconi; 1B. Mrowalé.

Average nearest-neighbor distances between nests (or territory centers) were 158.5 m (SE 7.0, range 87-234 m, n=29) at Coconi and 140.2 m (SE 7.9, range 101-274 m) at Mrowalé (Fig. 2). Second-nearest neighbor analyses showed that 63% of all occupied nests were within 200 m of two other occupied nests.

Sparrowhawks and bird communities on Mayotte. — The numbers of small, 'likely prey' birds (<20g) correlated negatively with sparrowhawk abundance on Mayotte, while those of birds in the category 20-70g showed a weak similar tendency (Fig. 3). In contrast, numbers of 'larger' birds (>70g) other than sparrowhawks were higher in places with more sparrowhawks (Fig. 3); the difference between both trendlines of potential prey and non-prey species is significant ($P<0.01$; $P<0.05$). There was also a significant negative trend on Mayotte between the number of sparrowhawks recorded in transects and the proportion of potential prey species in the overall number of birds other than sparrowhawks ($r_s=-0.62$, $P<0.05$; Fig. 4 inset).

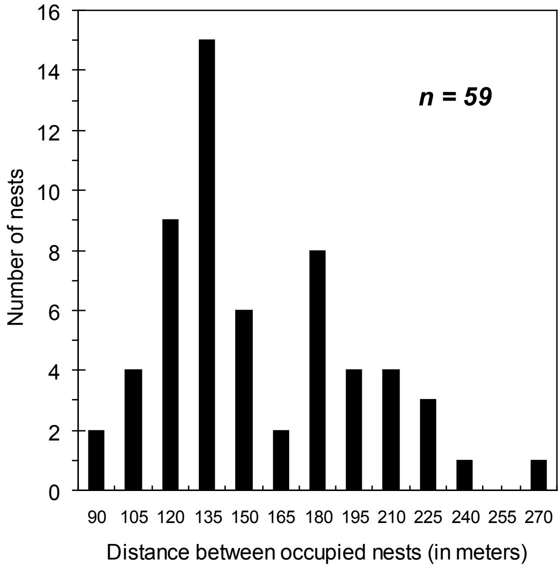

Figure 2. Nearest-neighbor distances of Frances's Sparrowhawk *Accipiter francesiae brutus* nests and territory centers on Mayotte Island.

In a stepwise multiple regression, sparrowhawk numbers were not significantly explained by a model containing only 'environmental' variables (rainfall, altitude and seven vegetation parameters), though rainfall (positive) and altitude (negative) accounted for 52% of the variation in sparrowhawk numbers (Table 2). Potential prey species had 47% of variation in numbers explained by altitude (negative) and a further 9% by rainfall (negative). When bird numbers were included in the regressions, they became significant. Sparrowhawk numbers varied in parallel to the variation in numbers of other larger birds (excluding sparrowhawks), and correlated with parameters of more lush vegetation (Table 2); abundance of potential prey species did not contribute to this model. On the other hand, sparrowhawk numbers alone explained 33% of the variation in the abundance of potential prey species (negative correlation) (Table 2). Small birds were furthermore concentrated at lower altitude and in lower vegetation (Table 2).

Sparrowhawks and Comoro bird faunas — The Comoro bird fauna's show a number of anomalies: some abundant, widespread and good colonizing species are inexplicably absent from some islands. We constructed a presence/absence table for not introduced, terrestrial species to investigate whether there would be a predictable sequence of species loss merely related to island size. If the relation was purely and predictably island-size related, we would expect only 0's in the top left of Table 3, and only 1's in the right bottom corner (Simberloff and Levin 1985). Any deviation from that pattern needs permutations of the data to obtain a sequence with exclusively 0's followed by

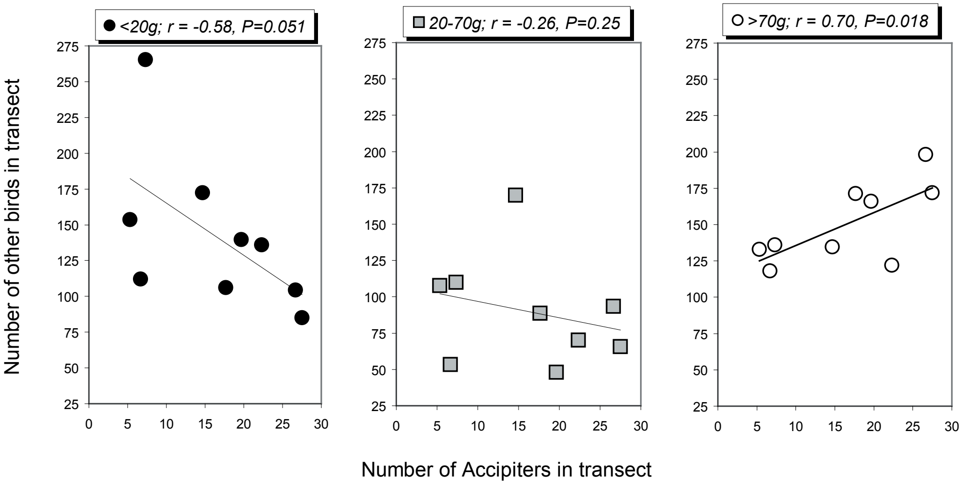

Figure 3. Relationship between Frances's Sparrowhawk *Accipiter francesiae brutus* numbers and numbers of other birds in the weight categories of likely prey (<20g), possible prey (20-70g) and no prey (>70g) in transect-counts on Mayotte Island.

Table 2. Main factors in stepwise multiple regressions on bird community and environmental variables on Mayotte Island.

VARIABLES					
Dependent	Step	Independent	Significant	Contribution to R^2	Significance
Models including only environmental variables:					
Accipiters	1	Rainfall (+)	no	27%	*P* = 0.15
	2	Altitude (-)	no	25%	
	3	% shrubs (+)	no	15%	
Potential prey	1	Altitude (-)	no	47%	*P* = 0.08
	2	Rainfall (-)	no	9%	
Models including environmental and bird population variables:					
Accipiters	1	Larger birds (+)	yes	46%	*P* = 0.002
	2	% shrubs (-)	yes	10%	
	3	% bare ground (-)	yes	24%	
	4	% small trees (+)	yes	10%	
	5	% dead trees (-)	yes	8%	
Potential prey	1	Altitude (-)	no	47%	*P* = 0.026
	2	Accipiters (-)	yes	33%	
	3	Vegetation height (-)	yes	9%	
	4	% dead trees (+)	no	3%	
	5	% bare ground (-)	no	4%	

Table 3. Presence/absence table of landbirds breeding on the Comoros as a function of island size; birds in order of increasing number of islands occupied and increasing number of permutations needed, islands in order of increasing size. Permutations are the number of steps necessary to convert the observed sequence for a species to one fitting the 'island-size model' whereby a series of absences (0) on the smaller islands is followed by a series of presence (1) on the larger islands.
LG - La Grille, Mh - Moheli, My - Mayotte, A - Anjouan, K - Karthala, Is - number of islands occupied P - permutations, W - weight class

	LG	Mh	My	A	K	Is	P	W
Area (km^2)	225	250	374	425	450			
Endemic taxa								
Accipiter francesiae griveaudi	0	0	0	0	1	1	0	3
Otus pauliani	0	0	0	0	1	1	0	3
Leptosomus discolor gracilis	0	0	0	0	1	1	0	4
Cyanolanius madagascarinus bensoni	0	0	0	0	1	1	0	2
Humblotia flavirostris	0	0	0	0	1	1	0	1
Zosterops mouroniensis	0	0	0	0	1	1	0	1
Dicrurus fuscipennis	0	0	0	0	1	1	0	3
Accipiter francesiae pusillus	0	0	0	1	0	1	1	3
Otus capnodes	0	0	0	1	0	1	1	3
Leptosomus discolor intermedius	0	0	0	1	0	1	1	4
Turdus bewsheri bewsheri	0	0	0	1	0	1	1	2
Nesillas typica longicaudata	0	0	0	1	0	1	1	1
Terpsiphone mutata vulpina	0	0	0	1	0	1	1	1
Nectarinia souimanga comorensis	0	0	0	1	0	1	1	1
Zosterops maderaspatana anjouanensis	0	0	0	1	0	1	1	1
Foudia eminentissima anjouanensis	0	0	0	1	0	1	1	2
Dicrurus forficatus potior	0	0	0	1	0	1	1	3
Accipiter francesiae brutus	0	0	1	0	0	1	2	3
Otus rutilus mayottensis	0	0	1	0	0	1	2	3
Terpsiphone mutata pretiosa	0	0	1	0	0	1	2	1
Nectarinia coquereli	0	0	1	0	0	1	2	1
Zosterops maderaspatana mayottensis	0	0	1	0	0	1	2	1
Foudia eminentissima algondae	0	0	1	0	0	1	2	2
Dicrurus waldenii	0	0	1	0	0	1	2	3
Treron australis griveaudi	0	1	0	0	0	1	3	4
Otus moheliensis	0	1	0	0	0	1	3	3
Coracina cinerea moheliensis	0	1	0	0	0	1	3	2
Hypsipetes parvirostris moheliensis	0	1	0	0	0	1	3	2
Cyanolanius madagascarinus comorensis	0	1	0	0	0	1	3	2
Turdus bewsheri moheliensis	0	1	0	0	0	1	3	2
Nesillas mariae	0	1	0	0	0	1	3	1
Nesillas typica moheliensis	0	1	0	0	0	1	3	1
Terpsiphone mutata voeltzkowiana	0	1	0	0	0	1	3	1
Nectarinia humbloti mohelica	0	1	0	0	0	1	3	1
Nectarinia notata voeltzkowi	0	1	0	0	0	1	3	1
Foudia eminentissima eminentissima	0	1	0	0	0	1	3	2
Zosterops maderaspatana comorensis	0	1	0	0	0	1	3	1
Coracopsis nigra sibilans	0	0	0	1	1	2	0	4

Table 3. continued

	LG	Mh	My	A	K	Is	P	W
Area (km^2)	225	250	374	425	450			
Zoonavena grandidieri mariae	1	0	0	0	1	2	3	1
Coracina cinerea cucullata	1	0	0	0	1	2	3	2
Hypsipetes parvirostris parvirostris	1	0	0	0	1	2	3	2
Saxicola torquata voeltzkowi	1	0	0	0	1	2	3	1
Turdus bewsheri comorensis	1	0	0	0	1	2	3	2
Nesillas brevicaudata	1	0	0	0	1	2	3	1
Terpsiphone mutata comorensis	1	0	0	0	1	2	3	1
Zosterops maderaspatana kirki	1	0	0	0	1	2	3	1
Nectarinia humbloti humbloti	1	0	0	0	1	2	3	1
Nectarinia notata moebii	1	0	0	0	1	2	3	1
Foudia eminentissima consobrina	1	0	0	0	1	2	3	2
Coracopsis vasa comorensis	1	1	0	1	1	4	2	4
Columba polleni	1	1	1	1	1	5	0	4
Alectroenas sganzini	1	1	1	1	1	5	0	4
Cypsiurus parvus griveaudi	1	1	1	1	1	5	0	1
Apus barbatus mayottensis	1	1	1	1	1	5	0	2
Streptopelia picturata comorensis	1	1	1	1	1	5	0	4
Not endemic taxa								
Leptosomus discolor discolor	0	1	1	0	0	2	4	4
Circus maillardi macrosceles	1	1	1	1	1	5	0	4
Falco peregrinus radama/perconfusus	1	1	1	1	1	5	0	4
Coturnix coturnix erlangeri	1	1	1	1	1	5	0	3
Turtur tympanistria	1	1	1	1	1	5	0	2
Streptopelia capicola tropica	1	1	1	1	1	5	0	3
Tyto alba affinis	1	1	1	1	1	5	0	4
Agapornis cana cana	1	1	1	1	1	5	0	2
Merops superciliosus superciliosus	1	1	1	1	1	5	0	2
Hypsipetes m. madagascariensis	1	1	1	1	1	5	0	2
Lonchura cucullata scutata	1	1	1	1	1	5	0	1
Foudia madagascariensis	1	1	1	1	1	5	0	1
Corvus albus	1	1	1	1	1	5	0	4

Recently introduced *Passer domesticus*, *Acridotheres tristis* and *Pycnonotus jocosus* omitted from list. Historical records included (e.g. *Circus maillardi* on Mayotte); *Milvus parasitus* considered not breeding.

1's; the number of such permutations per species is a measure of how much the species deviates from the 'island-size model'. The majority of endemic taxa, most of which are forest species, need several permutations to fit the 'island-size model', while the recent colonizers, most of which prefer open habitat, occur throughout the archipelago (Table 3). In general, small endemic birds (<70g) need significantly more permutations to fit the 'island-size model' than large birds (Table 4; 2-tailed Fisher exact, $P = 0.0011$), meaning that more small birds are absent from larger islands than expected, which is contrary to expectations of island biogeography and viable population concepts.

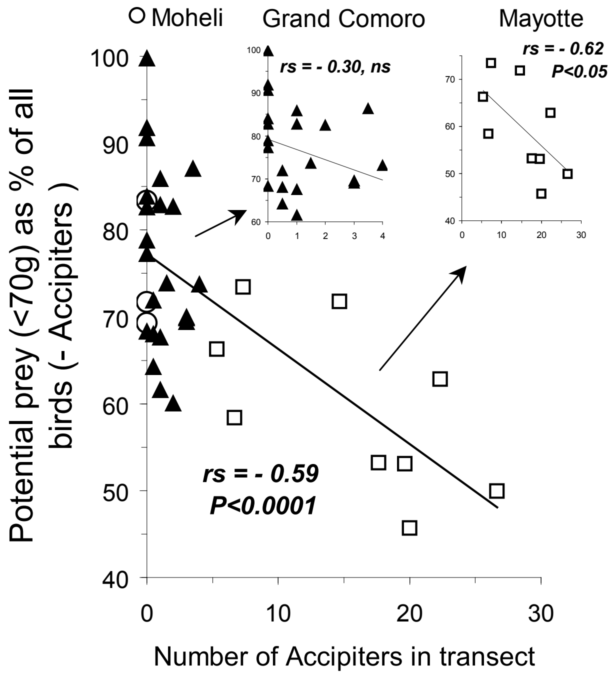

Figure 4. Relationship between Frances's Sparrowhawk *Accipiter francesiae* numbers and the proportion of potential prey in the bird communities in transect-counts on Mayotte, Grande Comoro and Moheli Islands (Comoros).

Table 4. Frequency distribution (number of bird taxa) of the number of permutations needed to fit the 'island-size model' (cf. Table 3) for small (<70g) and large (>=70g) endemic birds on the Comoros.

	Number of permutations needed	
Weight class	0-2	>2
small (<70g)	15	22
large (>=70g)	16	2

1's; the number of such permutations per species is a measure of how much the species deviates from the 'island-size model'. The majority of endemic taxa, most of which are forest species, need several permutations to fit the 'island-size model', while the recent colonizers, most of which prefer open habitat, occur throughout the archipelago (Table 3). In general, small endemic birds (<70g) need significantly more permutations to fit the 'island-size model' than large birds (Table 4; 2-tailed Fisher exact, $P = 0.0011$), meaning that more small birds are absent from larger islands than expected, which is contrary to expectations of island biogeography and viable population concepts.

We quantified 'deficiencies' at the generic level for not introduced, terrestrial species, under the assumption that every genus could be expected to be represented by a similar number of species on each island, except that the Karthala does have a montane zone, lacking on the other islands; Grand Comoro White-Eye *Zosterops mouroniensis*, the single exclusively montane species on the Karthala has been excluded from this comparison. There are e.g. two *Coracopsis* parrot species on the Karthala and Anjouan, one on La Grille and Moheli, and none on Mayotte; consequently, the deficiency is -1 for La Grille and Moheli, and -2 for Mayotte. There are more deficiencies of large birds on small islands which also lack sparrowhawks (La Grille; Moheli), while more prey-size species are lacking on Mayotte (Table 5; Fisher exact test, $P = 0.018$). Anjouan also lacks many small bird species, but historical sparrowhawk abundance is less certain here (see discussion).

The previous analysis does not take into account the important effect of island size and isolation, which affects the probability of colonization by any species. When the number of species in the weight-category of potential prey which currently survive on each island is compensated for island size and isolation, a clear negative relationship with sparrowhawk abundance emerges (Fig.5).

Discussion

Sparrowhawk densities. — Benson (1960) gave an appreciation of Frances's Sparrowhawk densities on the different Comoro Islands: he found it 'unrepresented' on Moheli, 'not at all common' on Grand Comoro, 'far from uncommon' on Mayotte, and 'formerly common, but now practically extinct' on Anjouan (this appreciation was based undoubtedly on the fact that many 19th century specimens are present in collections, see e.g. Knox and Walters 1994). The average density estimate from the point-transect counts in 1993 on Mayotte was 1.25 bird/ha, which, taking into account the low detectability of the species, must still have been an underestimation. The interpretation of the exclusive position of individuals (of each sex) in the mapping and the "trefclus" analysis in 1995 and 1996 indicated (correctly as it turned out later) six or seven pairs in a quarter of the Coconi study plot. However, at the time we were suspicious about the results of such a

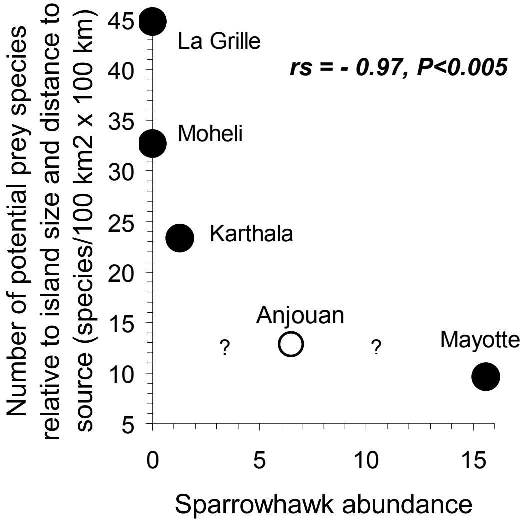

Figure 5. Relationship between Frances's Sparrowhawk *Accipiter francesiae* abundance (number of birds in transect) and the number of potential bird prey species on the Comoro Islands, re-scaled for island size and distance to source population (sparrowhawk abundance on Anjouan is historically uncertain and varied between years, see results and discussion sections).

Table 5. Species deficiencies at the generic level for terrestrial, not introduced birds on the Comoro Islands (excluding montane species).

Genus	Weight class	Grand Comoro (Karthala)	Grand Comoro (La Grille)	Moheli	Anjouan	Mayotte
Accipiter	3		-1	-1		
Treron	4	-1	-1		-1	-1
Otus	3		-1			
Coracopsis	3,4		-1	-1		-2
Zoonavena	1			-1	-1	-1
Coracina	2				-1	-1
Hypsipetes	2				-1	-1
Cyanolanius	2		-1		-1	-1
Saxicola	1			-1	-1	-1
Turdus	2					-1
Nesillas	1	-1	-1		-1	-2
Humblotia	1		-1	-1	-1	-1
Nectarinia	1				-1	-1
Dicrurus	3		-1	-1		
Total likely prey	1	-1	-2	-3	-5	-6
Total possible prey	2	0	-1	0	-3	-4
Total no prey	3,4	-1	-5	-3	-1	-3
Class 1&2 as % of all		50	38	50	89	77

high density. The subsequent data from nest counts showed an average territory size of 2.3 ha/pair in the study plots in the wet northwestern sector of Mayotte. The study plot at Mrowalé where nests were counted in 1997/98 was also part of a transect count in 1992-94; we encountered only 'average' numbers of sparrowhawks here, and less than half the numbers found in the two highest transects (Stevens and Louette 1999). This suggests that there might be places on Mayotte (e.g. Ochoungui and Pic Combani) with breeding densities of Frances's Sparrowhawks approach 1 pair/ha.

Like in the Eurasian Sparrowhawk (Newton 1986), the finding of nests is the best method to study the population and spacing of the Frances's Sparrowhawk, and it is surprising how easily the birds are overlooked, even in this exceptionally confiding species; this aspect, and the consequent underestimation may apply to other studies which have not used comprehensive nest counts for density estimations. The regular spacing of nests (Fig. 1) suggests that the species is strictly territorial (Marquiss and Newton 1982, Newton 1989); occasional observations of a marginal overlap in individual hunting ranges (Herremans *et al.* 2001), would not invalidate this concept, because it is also found in other truly territorial accipiters (Newton 1986, Bijlsma 1993). Difficulties in locating adult pairs which showed no breeding activity (either not breeding or having suffered nest-loss early in the breeding season) suggest that the densities presented in Fig. 1 may still be a slight underestimation. The positive skew and tendency for a secondary peak in the graph of the nearest-neighbor distances at about twice the minimal inter-nest distance also suggests that some pairs or nests may still have been overlooked (Fig. 2: skewness=1.48, SE=0.62). With an average fledging success of 1.5 young per initiated nest (Herremans *et al.* 2001), the density in the humid sector of Mayotte is minimally 150 sparrowhawks/km^2 by the end of the breeding season. Immature birds can be recognized by plumage up to two years after hatching (Herremans *et al.* 2001), but no such birds were observed attending nests. This indicates that the high densities were not due to exceptionally favorable conditions with a rapidly expanding population, which is normally based on increased recruitment with high percentages of young birds taking part in breeding (Reese and Kadlec 1985, Newton 1986, Bijlsma 1993). Using mortality rates as in the Eurasian Sparrowhawk (55% during the first year, 40% in the second and 30% yearly thereafter in adults: Newton *et al.* 1983, Bijlsma 1993), 26 recruits would be needed per km^2 in the Frances's Sparrowhawk to keep the population stable on Mayotte, but from our studies only 17 would be available by the end of the second year. Clearly, either mortality is lower on Mayotte than assumed from the example of the Eurasian sparrowhawk, or more young fledge on average than noted during our study. With mortality rates at 45% in the first year, 30% in the second year and 20% in adults, and no recruitment in the first two years, there would be a surplus and the number of floaters would become about 80 birds/km^2, which would bring the total population to 230 birds/km^2 (0.43 ha/bird) by the end of the breeding season. There are, however, indications that birds may disperse from the high-density breeding areas to the drier parts of the island, and part of the floating population might spend time outside the main breeding areas (Herremans *et al.* 2001).

As far as we could establish from quantitative or qualitative information in the literature, the presently documented breeding densities of Frances's Sparrowhawks on

Mayotte Island are by far the highest documented for any Accipiter in the world, and possibly for any strictly territorial raptor (compare Thiollay 1975, 1993, Cramp and Simmons 1980, Blakers *et al.* 1984, Forsman and Solonen 1984, Newton 1986, 1989, Patrimonio 1987, Aumann 1989, Brazil and Hanawa 1991, Bühler 1991, Bijlsma 1993, van Balen 1994, Galushin *et al.* 1996, Tomialojc and Wesolowski 1996). However, a valid ecological comparison for the Frances's Sparrowhawk on a Comoro Island is difficult to find. There appear to be only seven *Accipiter* species in the world in its size class <250g with reptiles as a major part of the diet: *francesiae*, *butleri*, *imitator*, *badius*, *brevipes, soloensis* and *trinotatus* (del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001). Frances's Sparrowhawks are qualified as "very common" on Madagascar (Rene de Roland & Thorstrom 2003), but no comparable quantitative data are available (Rands 1936, Wattel 1973, Langrand and Meyburg 1984, Langrand 1990, Thorstrom and Watson 1997), other than the statement that the distance between nests of the same pair in successive years was on average 105 m (range 0-250 m) (Rene De Roland 2000). *A. badius* occurred at 1-2 pairs/100 km^2 and at nearest-neighbor distances of 4.7 km in study areas in South Africa, where it co-occurs with six other Accipiters (Tarboton 1978, Tarboton and Allan 1984). In woodland areas of West Africa, where it is the only species in the genus, 26 pairs/100 km^2 were found in the Ivory Coast (Thiollay 1975), and 1 pair/1.2 km^2 in Nigeria (Smeenk and Smeenk-Enserink 1977). It is the commonest *Accipiter* in Guinea (Rondeau *et al.* 2008). This species however does not occur on any of the circum-African islands, but is qualified as 'the commonest small hawk, found almost everywhere' on Sri Lanka (Henry 1955). Two of these seven *Accipiter* species are migrants: *brevipes* has been recorded to breed at 17.3 pairs/100 km^2 (Galushin *et al.* 1996), but no density estimates of *soloensis* in its breeding quarters were found (Choi *et al.* 2008 say it used to be common in Korea). The sixth species, *trinotatus*, is said to be common on Sulawesi (del Hoyo *et al.* 1994). On other Indian Ocean Islands, two endemic Kestrels became specialists of reptiles: Seychelles Kestrel *Falco araea* on Mahé (Seychelles) occurs with 7 pairs/km^2 (recalculated from Feare *et al.* 1974) at an unusually high density for a kestrel, while Mauritius Kestrel *F. punctatus* on Mauritius is now recovering after having been at the brink of extinction, with the densities in historical times unknown (Jones 1987).

At comparable densities to its ecological counterparts, there would be place for 4-312 pairs of Frances's Sparrowhawks on Mayotte only. The breeding population on Mayotte can at present preliminary be estimated in the order of magnitude of 7,225-10,960 pairs, using figures of 35-50 pairs/km^2 in 175 km^2 of the wettest northwestern section of the island (but assigning the coastal strip to the next category), 10-20 pairs/km^2 in 110 km^2 of a drier zone in the east including the Choungui massif (assigning the coastal strip to the next category), and 0-0.1 pairs/km^2 in 89 km^2 of the dry southern part (excluding the Choungui massif), along the coast in the east, and in habitat rendered unsuitable by too extensive clearing (delimitations of abundance-zones based on Louette *et al.* 1993b, Stevens and Louette 1999).

On Grand Comoro, Frances's Sparrowhawks are about ten times less frequently encountered in suitable habitat than on Mayotte (Louette *et al.* 1993b), and breeding densities may therefore be in the order of magnitude of 20 ha/pair in suitable areas. We did no standardized transect-count on Anjouan ourselves, but the daily reporting rates (including the data from C. Marsh from 2005) indicate that the abundance on Anjouan is at present of the same order of magnitude or slightly lower than in suitable habitat on Grand Comoro. Anjouan has the highest human population density of the Comoros, with the longest period of settlements in the interior, where people are dependent on the terrestrial system for all their requirements. The island has been severely transformed in recent times, leaving little original forest vegetation and with substantial areas cleared of tall vegetation, which has probably also fundamentally affected birdlife. Both sexes of the subspecies *pusillus* from Anjouan have masculine plumage (Benson 1960, Louette 2000) and in view of the generally positive relationship between neoteny and density (Louette *et al.* 1993a), it is unlikely that sparrowhawk densities would historically have been as high on Anjouan as those of the neotenic form *brutus* on Mayotte. We use therefore for the following discussions a historical sparrowhawk abundance on Anjouan greater than that on Grand Comoro but smaller than on Mayotte.

Sparrowhawk numbers may fluctuate; contemporary abundance does furthermore not necessarily reflect abundance in historical times. In stable environments, however, raptor populations tend to be remarkably stable (Newton and Marquiss 1986, Newton 1991). In general, forest bird numbers did not fluctuate greatly on Mayotte (Louette *et al.* 1993b, Stevens and Louette 1999). We believe that the order of magnitude of contemporary abundance was appropriately captured by the transect counts, most of which represent the average of up to three repeats. Historical abundance will inevitably remain undocumented, but because Frances's Sparrowhawks co-evolved with the lush indigenous forest vegetation on the Comoro Islands, contemporary density estimates in this vegetation may be the best approximation one can make about the order of magnitude of the historical density. Only if significant niche expansion would have taken place, to which insular forest birds may be particularly partial (Blondel *et al.* 1988, Thibault *et al.* 1992), would densities in forest edge or in open landscapes be higher than in the primary habitat. Our data from Mayotte show similar sparrowhawk densities in forest and forest-edge habitat (Stevens and Louette 1999). Anjouan is more problematic in judging historical densities, and Benson's appreciation based on the number of early specimens is the best available.

Do sparrowhawks affect the bird communities on Mayotte ?— With Mayotte holding the highest breeding density of a sparrowhawk in the world, would there be any impact on the bird communities ? Generally, predator numbers follow those of prey populations. In the Eurasian Sparrowhawk, higher densities correlated with higher prey indices (Newton *et al.* 1986) and there was inconclusive evidence for effects of changing sparrowhawk populations on prey abundance (Newton *et al.* 1997), except in the immediate vicinity of the nest (<60 m), where prey-bird populations were depressed (Newton 1986). With the presently documented high densities on Mayotte, the entire sparrowhawk territory becomes the 'immediate vicinity of the nest' and impact on prey populations may be expected over most of the island, except the drier parts, where sparrowhawks are sparse (Herremans *et al.* 2001).

The choice of weight-categories of prey species was based on data from: (1) the

Eurasian Sparrowhawk which takes 92% of all prey smaller than 55% of its own body weight in the British Isles (Newton 1986), while about 90% of its prey items weigh <50 g in Europe (Bühler 1991, Bijlsma 1993), and (2) the Sharp-shinned Hawk *Accipiter striatus* in which >90% of prey is <50% of its body weight (Storer 1966, Reynolds 1972). The cut-off of 70g we used for Frances's Sparrowhawk is 56% of its average body weight. However, the previous two sparrowhawk species are specialized bird hunters, while the mainly reptilivorous Shikra seems to take only small birds (Smeenk and Smeenk-Enserink 1977, Tarboton 1978). Birds below 20 g therefore are the most likely to fall victim to Frances's Sparrowhawk, while class 2 (20-70g) is still considered to be within the potential prey range. Class 3 (70-<150g) may only exceptionally be taken as prey, and birds over 150g are unlikely to be taken (see also Herremans *et al.* 2001). Potential-prey size birds (<70g) were expressed as a percent of all birds, excluding Accipiters (ignoring the possibility of cannibalism) for comparisons of prey abundance between islands. This measure is better buffered against stochastic effects than the numbers of birds observed (see e.g. the effects of an encounter with a bird party). It facilitates comparisons between islands because differences in conspicuousness could affect numbers counted, e.g. because different species, habitats and maybe shifts in breeding seasons could interfere with inter-island comparisons.

Frances's Sparrowhawks are catholic in their food choice and take a variety of small vertebrates (reptiles, birds, rodents), large insects and occasionally carrion, though sparrowhawks on Mayotte have a much larger proportion of reptiles in the diet than on Madagascar (Herremans *et al.* 2001). The central toe is short in the Frances's Sparrowhawk, which therefore belongs to the *brevipes*-type, indicating that it is not a specialized bird hunter, but potentially omnivorous, capturing most prey by pouncing, not aerial pursuit (Wattel 1973, Herremans *et al.* 2001). Reptiles, most particularly skinks *Mabuya comorensis* and green gecko's *Phelsuma sp*., are the staple food on Mayotte. Green geckos have radiated on Mayotte into three endemic species, and two more species became established in recent history (Losos 1986, Meirte 1994). With five species, niche partitioning and specialization of the *Phelsuma's* on Mayotte can be expected to have resulted in a high overall density and biomass in the wet sector. Anecdotal information seems to confirm this: several tens of gecko's were found when a single tree was felled, and it is not uncommon to observe up to ten *Phelsuma*'s from a single vantage point (D.Meirte unpubl. data). The only indication that sparrowhawk numbers follow biomass of gecko's on Mayotte may come from the preference of both for the wettest zone of the island, while both are uncommon in the drier parts, and absent from the small islets around Mayotte (Herremans *et al.* 2001, D. Meirte unpubl. data). On Praslin Island in the Seychelles, the highest lizard biomass was also found in native forest on higher ground (Evans and Evans 1980). The inverse relationship between the abundance of prey-size birds and sparrowhawk numbers (Figs. 2-3, Table 2) is compatible with the proposition that the exceptionally high abundance of Frances's Sparrowhawks limits the numbers of small birds on Mayotte. Bird counts on Mayotte were aimed at studying forest bird communities (Louette *et al.* 1993b), and there were no transects in the dry eastern and southern coastal areas, nor on the eastern islet Pamandzi (Petite Terre), where sparrowhawks are only observed occasionally (Herremans *et* *al.* 2001), but where small birds are strikingly abundant. Including the results from transects from areas on Mayotte with few sparrowhawks is expected to strengthen the relationships in Figs. 3-4. There is no evidence at all from hunting behavior, territorial pressure, time allocation or breeding success for any food shortage for sparrowhawks on Mayotte (Herremans *et al.* 2001). Although hunting is opportunistic, reptiles are the staple food of Frances's Sparrowhawks on Mayotte, similar to specialization in other endemic small raptors on Indian Ocean Islands (e.g. Seychelles Kestrel (Watson 1992) and Mauritius Kestrel (Jones 1987)). It is, however, possible that birds, if available, would be preferred as prey, possibly because hunting the generally heavier bird is more profitable for a similar energy expenditure; furthermore, although by far less common compared to reptiles, a bird may simply be more conspicuous to an opportunistic hunter than the more cryptic reptiles and the proportional impact on the numbers of birds may thus be higher, even though they do not figure very high in a study of prey numbers (Herremans *et al.* 2001). There are examples from New Zealand, where predators with mammalian staple food had severe impact on bird numbers only when the predator population became high as a consequence of changes in the staple food (Taylor 1979, Griffin *et al.* 1988). Lizard populations seem generally to be rather stable (Schoener 1985), including *Mabuya and Anolis* species, the latter being ecologically similar to *Phelsuma*. There is nevertheless some evidence from the Seychelles, that numbers of green gecko's, or at least their apparent availability to a predator, may fluctuate considerably (Watson 1992), in which case sparrowhawks could temporarily become more dependent on alternative prey. A depressing effect by predators on the population levels of alternative prey is not uncommon, particularly in simplified ecosystems, such as small oceanic islands with depaupered faunas. Where population levels of predators are maintained by an abundant staple food, any decline of this prey basis forces the predators to switch to alternative prey: classical examples are the lemming-fox-wader cycles in the arctic (Summers 1986, Summers and Underhill 1987, Syrouchkovskiy *et al.* 1991), the hare-goshawk-grouse cycles in North America (Keith and Rusch 1988) and the studies where experimental removal of predators made population levels of secondary prey to increase (Newton 1991). Whether it is a seasonal fluctuation in the staple food, a preference for birds or merely their conspicuousness that makes bird numbers depressed in parallel to sparrowhawk numbers on Mayotte remains unknown. Direct suppressive predation remains a possibility (Kenward and Marcström 1988), but with the present data, effects of direct predation can not be distinguished from an effect of predation risk avoidance and prey refuge use (Mittelbach and Chesson 1987, Sih *et al.* 1988, Meese and Fuller 1989, Sodhi *et al.* 1990), which could be an alternative explanation for the higher abundance of small bird species in areas with fewer sparrowhawks. In any case, 'prey refuges' in an insular situation inevitably also reduce effective island and population size, and therefore probably increases the risk of extinction. A direct relationship between low survival rate and high extinction risk was demonstrated for insular birds on Barro Colorado Island (Karr 1990), and the effects of introduced predators on island birds are well known (Griffin *et al.* 1988). Reduced survival rates under increased predation pressure by high numbers of sparrowhawks may also be the mechanism that has driven to extinction (or prevented establishment) on Mayotte some species common elsewhere in the region. A situation with a rather similar outcome has been documented for an intermediate trophic level in the Bahamas, where abundant predatory lizards limited the numbers of individuals and species of spiders (Schoener and Toft 1983, Toft and Schoener 1983, Schoener and Spiller 1987, Spiller and Schoener 1988). The negative effects of lizards on the establishment of invading spiders have been experimentally demonstrated in this case (Schoener and Spiller 1995).

There are only limited data on density for bird communities from mainland Madagascar (e.g. O'Dea *et al.* 2004, Watson *et al.* 2004, Scott *et al.* 2006) at hand, and therefore it remains impossible to assess whether the sparrowhawks on Mayotte depress bird populations below the densities found on the adjacent "mainland", or whether even these high sparrowhawk densities can not undo the density inflation effect which is part of the insular syndromes affecting small insular birds. Several small birds are certainly less common on Mayotte than on other Comoro islands (Stevens and Louette 1999). However, if the densities of small birds on Mayotte were still higher than on the mainland, despite the sparrowhawks, the 'low predation' theory which has been invoked to explain higher densities of insular populations (Faeth 1984, George 1987), may need modification.

May sparrowhawks have shaped Comoro bird faunas in evolutionary terms ? — Three distinctly different subspecies of the Frances's Sparrowhawk have evolved on the Comoro Islands, and their presence on the islands is therefore certainly historic. Colonization of an island by any bird is dependent on the success of a fragile founder population, most probably arriving in very low numbers and being dependent on long survival in order to find the right habitat and improving the chances to encounter a mate. Under such conditions where the presence and survival of an individual is fundamental, the impact of a high sparrowhawk population on the island can be decisive. Newton (1986) e.g. predicted from the high elimination rate of escaped budgerigars by Eurasian Sparrowhawks in Scotland that the latter would be efficient at preventing the former from becoming established, and generalized that rare and easily caught species may be eliminated by sparrowhawks that thrive on an alternative staple food.

The Comoro bird faunas have a number of as yet unexplained anomalies (Louette *et al.* 1989, 1993b, 2008). Particularly Mayotte and Anjouan have too few species, especially small birds (Louette 1988, Fig.5, Tables 3-5). Small birds deviate more from the 'island-size model' than large birds, meaning that, at odds with expectations, more small birds had difficulties either to colonize or to maintain viable populations on larger islands. The anomalies are particularly striking on islands with sparrowhawks (Tables 3,5). Some species which are absent or have only one species on Mayotte and Anjouan, but sometimes two on other islands (including on the smallest islands), are widespread in the region and common in a variety of habitats (*Nesillas*, *Nectarinia*, *Turdus, Hypsipetes*: Louette and Herremans 1985, Louette *et al.* 1988b), indicating that they are good colonizers and opportunists. The absence of several species from Mayotte and Anjouan is even more remarkable in zoogeographical terms because these islands are larger and closer to Madagascar, the main source area than is the small island of Moheli, which is richer in species, but lacks a sparrowhawk (we do not take into account here the possibility that Grand Comoro itself may have acted as a source for some species: Louette 1996a). The position of Anjouan in Fig. 5 is uncertain, both in terms of historical sparrowhawk abundance (see above), and maybe also in terms of the number of small bird species presently remaining: if any species became extinct recently because of habitat destruction by humans, Anjouan would shift upwards in Fig. 5. There are furthermore anomalies of distribution and inexplicable scarcity on Mayotte, whereby species (e.g. Forest Fody *Foudia eminentissima,* Mayotte Sunbird *Nectarinia coquereli,* Madagascar White-Eye *Zosterops maderaspatana*) in genera that prefer altitudinal forest vegetation on other islands are more abundant at lower altitude, and in the drier and less lushly vegetated parts of Mayotte (Louette *et al.* 1989, 1993b, Stevens *et al.* 1995, Stevens and Louette 1999, Table 5), where Frances's Sparrowhawks occur only marginally (Herremans *et al.* 2001). The House Sparrow *Passer domesticus* occurs all over Moheli, where there is no *Accipiter*, but is restricted to towns in the drier, coastal areas of Mayotte and Grand Comoro (Louette 1988), which are not frequented by sparrowhawks.

In conclusion, past evolutionary processes remain inevitably speculative and can not be confirmed by experimentation, yet contemporary evidence from bird distribution and abundance, and historical evidence from the lower rate of successful colonization are all compatible with the hypothesis that the record abundance of Frances's Sparrowhawks on Mayotte (and possibly also on Anjouan) have substantially affected the prey-bird communities, either directly by predation or indirectly through predation avoidance on an island with insufficient prey refuges. The sparrowhawk predator effect hypothesis can account for a number of the too many as yet unexplained zoogeographical anomalies on the Comoros. Theoretically, the ultimate test could be to translocate neotenic sparrowhawks from Mayotte to Moheli, but in view of the high level of endemism among potential prey species on Moheli and the predicted impact by sparrowhawks, such would not be a good idea for conservation. More in general, we would like to argue against the translocation of insular predators (in fact of any trophic level) with a clear potential for density inflation to places with endemism.

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