

# Seasonal variation in population and community structure of shrews in a tropical forest of Gabon

Violaine Nicolas<sup>1</sup>, Patrick Barrière and Marc Colyn

Université de Rennes 1, Unité mixte de recherche n° 6552, Centre National de la Recherche Scientifique, Station Biologique, 35380 PAIMPONT, France  
(Accepted 23 July 2004)

**Abstract:** The composition, structure and reproductive phenology of a shrew community were investigated for 1 y at two neighbouring sites in an undisturbed African forest of south-western Gabon. We captured 717 shrews, belonging to four genera and 10 species. The data were analysed to answer three main questions: (1) to what extent does the shrew abundance vary seasonally? (2) is there a shift in species dominance over time? and (3) does the intensity of breeding activity vary seasonally? The number of species captured varied seasonally and tended to be least during the period of minimal trap success. Trap success for the four most abundant species (*Sylvisorex johnstoni*, *Crocidura batesi*, *Paracrocidura schoutedeni* and *Sylvisorex ollula*) varied seasonally with a minimum around the long dry season. *Sylvisorex johnstoni* remained the dominant species throughout the year. Seasonal variation in trap success of shrews might be related, at least partly, to their reproductive characteristics. Litter size, based on embryo counts, ranged from 1–4 among the species. Breeding occurred throughout the year, but its intensity was lower during the long dry season corresponding with the period of higher ecological constraints for shrews.

**Key Words:** Africa, community, dynamics, Gabon, reproduction, small mammals, tropical forest

## INTRODUCTION

Rain forests are characterized by seasonal variation in several ecological parameters, including rainfall, relative humidity, leaf and fruit fall and leaf litter depth (Happold 1977). Correlated with these variations, many animals (insects, reptiles, birds, mammals) show a seasonal variation in abundance and breeding activity (Nicolas & Colyn 2003, Vazquez *et al.* 2000, Wolda 1983, Woodman *et al.* 1995). Seasonal variation in abundance is not always synchronized between species, even for phylogenetically close ones (Vasquez *et al.* 2000, Wolda 1983). Consequently, community composition and structure can also vary seasonally (Malizia 2001, Rabinowitz & Nottingham 1989, Willig & Gannon 1986). A precise knowledge of the patterns of these variations and of their causality is necessary to define appropriate temporal scales when conducting biodiversity surveys.

Since the end of the 1980s, shrews have been sampled at several central African localities (Barrière & Nicolas 2000, Brosset 1988, Colyn *et al.* unpubl. data, Goodman

*et al.* 2001, Goodman & Hutterer 2004, Hutterer & Schlitter 1996, Hutterer *et al.* 1992, Lasso *et al.* 1996, O'Brien *et al.* in press). These studies gave information on species richness and composition and showed that shrews represent an important part of the mammal species richness in tropical Africa, with 6–18 species per locality. To date, there is little published information about seasonal pattern in population dynamics and community structure of Afro-tropical shrews. Trap success of shrews was shown to vary seasonally in two west Central African rain forests (Barrière & Nicolas 2000, Lasso *et al.* 1996), with a minimum around the dry season, but the causality of this variation was not investigated. It could be due to a seasonal variation in population size, resulting from the net effects of recruitment and survival, or in the probability of capture of individuals, correlated to movement activity (Slade & Blair 2000). According to the literature, breeding could occur throughout the year in several crocidurine populations inhabiting tropical regions and its intensity could reach a peak at certain periods of the year, usually coinciding with environmental conditions (Churchfield 1990, Yu *et al.* 2001). But this has not been tested for tropical Africa. In the course of a World Wildlife Fund project conducted in

<sup>1</sup>Corresponding author. Email: violaine.nicolas@laposte.net

the Monts Doudou forest (Gabon) to assess the biodiversity of this region, shrews were surveyed for 1 y at two neighbouring study sites. Data were analysed to answer three main questions: (1) to what extent does shrew abundance vary seasonally? (2) is there a shift in species dominance over time? and (3) does the intensity of breeding activity vary seasonally? Finally, we also present data on population structure (age class, sex ratio).

## METHODS

Our study was conducted in the eastern part of the Aire d'Exploitation Rationnelle de Faune (AERF) des Monts Doudou (02°09'S, 10°30'E), south-western Gabon, in an undisturbed lowland forest (110 m asl).

We sampled both murid rodents and shrews, and results obtained for rodents have been previously published (Nicolas & Colyn 2003). Study area characteristics, sampling periods, trapping methods and methods of analysis are the same as in Nicolas & Colyn (2003) and only brief notes are given here. Most of the study area was covered by dryland forest (87% of the surface), but small patches of flooded forest (riparian or swamp forests) were also surveyed. The forest canopy was approximately 35–45 m high and dominated by trees of the families Caesalpiniaceae and Mimosaceae. The understorey was open and *Dichostemma glaucescens* (Euphorbiaceae), *Meiocarpidium lepidotum* (Annonaceae) and a large variety of *Diospyros* species (Ebenaceae) were frequently encountered (Sossef *et al.* 2004).

The average annual rainfall recorded near this area (at Mouila) is about 2300 mm (Saint-Aubin 1963), with a short rainy season from March to May and a long one from October to December. The long dry season occurs from June to September and the short one in January–February. Temperature is more or less uniform throughout the year, with mean monthly minima between 19° and 23°, and maxima between 24° and 29 °C.

### Trapping methods

We trapped in two 875 × 1000-m study sites (sites A and B), 2500 m apart, which were located at the same altitude (110 m asl) and subject to similar climatic conditions. Rainfall was measured each trapping day with a standard rain gauge. At both sites, small mammals were surveyed monthly, from April 2000 to March 2001, with (1) three traplines (each 1 km long) of 200 traps baited with manioc (*Manihot esculenta*, Euphorbiaceae), a widely cultivated plant in tropical Africa. Each trapline was composed of 100 Sherman live traps (7.5 × 9 × 23 cm) and 100 metal snap traps (10 × 15 cm) spaced at 5-m intervals (one Sherman and one snap trap alternatively). Traplines were

set 25 m apart and each trapline was set for 7 d per month; (2) one pitfall line (300 m long) with plastic drift fences, comprising 30 10-litre plastic buckets placed at 5-m intervals. Trapping sessions lasted 21 d consecutively per pitfall line. All traps were checked daily.

Although pitfall-trapping is known to be the most effective protocol to collect shrews (Kalko & Handley 1992, Kirkland & Sheppard 1994, Maddock 1992, Williams & Braun 1983), some individuals were also captured in Sherman and snap traps. In this study, results obtained for the two types of device (pitfall lines and traplines) are presented.

Owing to the existence of sibling species, all animals captured were euthanased, by cervical dislocation, for cranial preparation and species identification. All collected samples were deposited at the Station Biologique de Paimpont (France). A previous study showed that removal trapping, with similar conditions as those employed in our study, did not adversely affect local population numbers and shrew species richness (Nicolas *et al.* 2003). Since all animals were removed from the study area, traplines were relocated monthly at a distance of 300 m for neighbouring pitfall lines and 25 m for neighbouring traplines.

### Species identification

Species identification, performed by PB, was based on external morphology and cranio-dental characteristics, and confirmed for several specimens by molecular analyses (16S rRNA sequencing). Identification was based on the most recent advances in the knowledge of shrew taxonomy, but several complexes of species are still in need of revision (Quérroul *et al.* in press).

### Methods of analysis

Because community structure and monthly trapping effort differed between dryland and flooded forest (Nicolas & Colyn 2003), in this paper we only took into account results obtained in dryland forest. We pooled results obtained at both sites when no significant difference between sites was apparent.

Trap success ( $T = \text{number of individuals caught per 100 trap-nights, TN}$ ), coefficient of variation ( $CV = [SD/m] \times 100$ , where SD is the standard deviation and m is the mean monthly trap success) and species relative abundance ( $p_i = \text{number of individuals of the } i\text{th species caught per 100 individuals}$ ) were calculated. The Renkonen index of similarity ( $P_R$ ) was calculated for all possible combinations of communities:  $P_R = \Sigma \text{minimum}(p_{1i}, p_{2i})$ , where  $p_{1i}$  is the relative abundance of species i in community 1 and  $p_{2i}$  is the relative abundance of species i

in community 2. This index ranges from 0 (no similarity) to 100 (complete similarity).

Results obtained using Sherman traps, snap traps and pitfall traps were used for the estimation of species richness, but only the results obtained with pitfall traps were used in trap success and species abundance calculations because trap success of shrews using other types of traps was low. Tooth-wear patterns, based primarily on the amount of wear on the fourth premolar and the two first molars of the left upper maxillary, were employed as a coarse estimation of relative age. Tooth-wear classes were determined using a six-state scale, adapted from Dippenaar (1977), from which classes 2 and 3 were subdivided in two (TW2A–2B, TW3A–3B). The specimens of the first two classes were considered as subadults (TW1–TW2A) and those of higher class (TW2B–TW4) as adults. Females were considered as breeding when they were pregnant or lactating.

Chi-square tests on contingency tables were used for trap success comparisons and to study the interactions between sex ratio and age (because of the small sample size, tooth-wear classes 4 and 5 were combined in the statistical analysis). Chi-square tests also were used to investigate seasonal variation in the proportion of young individuals and sex ratio. We used seasons rather than months in the analysis of population dynamics to ensure the large sample sizes needed for statistical analysis.

## RESULTS

### Community composition and structure

**Global results.** In total, 717 shrews belonging to four genera and 10 species were captured: *Crocidura batesi* Dollman, 1915 ( $n=86$  in pitfall lines;  $n=13$  in traplines), *C. crenata* Brosset, Dubost & Heim de Balsac, 1965 (51; 1), *C. dolichura* Peters, 1876 (22; 0), *C. goliath* Thomas, 1906 (15; 19), *C. grassei* Brosset, Dubost & Heim de Balsac, 1965 (31; 2), *C. cf. nigrofuscus* Matschie, 1895 (1; 0), *Paracrocidura schoutedeni* Heim de Balsac, 1956 (81; 3), *Suncus remyi* Brosset, Dubost & Heim de Balsac, 1965 (7; 0), *Sylvisorex johnstoni* (Dobson, 1988) (300; 1), *S. ollula* Thomas, 1913 (79; 5). Trap success was 4.61 individuals per 100 TN for the whole sampling period. *Sylvisorex johnstoni*, one of the smallest species of the shrew community, was the most abundant one ( $p_i=45\%$ ), followed by *Crocidura batesi* (13%), *Paracrocidura schoutedeni* (12%), *Sylvisorex ollula* (12%) and *C. crenata* (8%). Other species were rare (< 5%) and a single specimen of *C. cf. nigrofuscus* was captured. Three species were collected only by pitfalls traps (*C. dolichura*, *C. cf. nigrofuscus* and *S. remyi*) and six species were predominantly collected by this type of trap (more than 86% of individuals collected by pitfall). In contrast,

the largest species of the community (*C. goliath*) was the only one equally captured by pitfall and Sherman traps (55.9% collected in Sherman and none in snap traps).

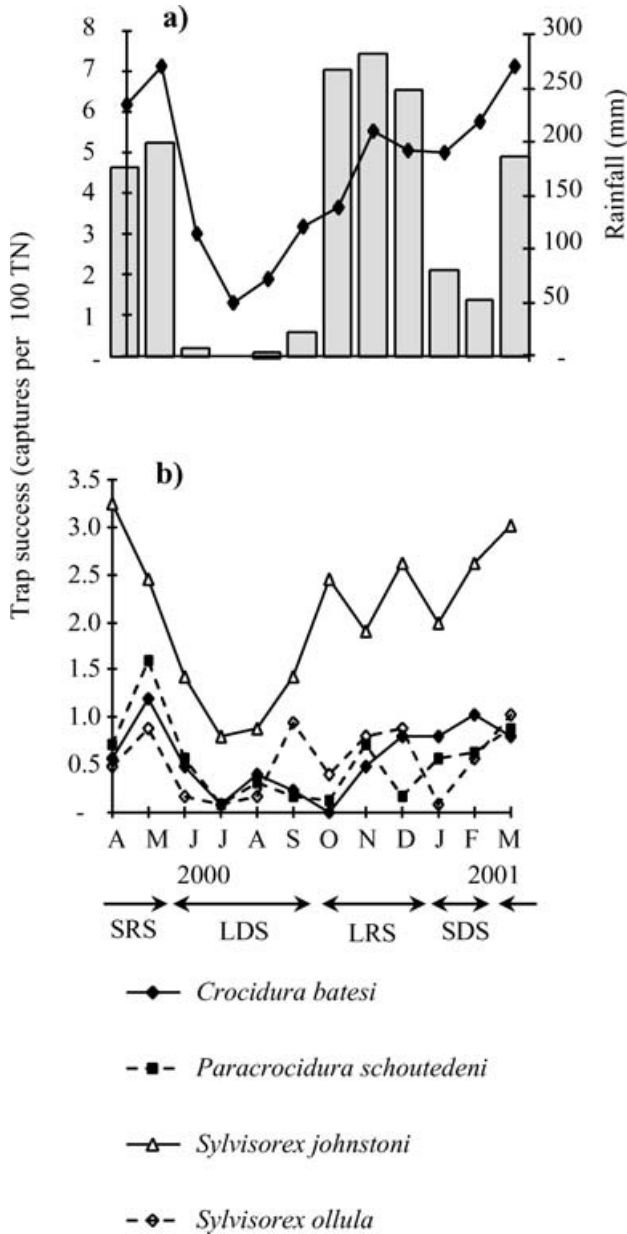
**Seasonal variation.** The number of species captured varied monthly from three to nine at site A and from four to nine at site B. Minima were mainly observed from July–October, i.e. during the long dry season and at the beginning of the long rainy season.

Shrew trap success varied significantly throughout the year ( $\chi^2 = 109$ ,  $P < 0.001$ ; Figure 1a), with a minimum in the middle of the long dry season (July) and a maximum in the short rainy season (March–May). This was mainly due to the population dynamics of the dominant species (*S. johnstoni*;  $\chi^2 = 42.4$ ,  $P < 0.001$ ; Figure 1b). Trap success of the three other most abundant species (*C. batesi*, *P. schoutedeni* and *S. ollula*) also varied significantly during the year ( $\chi^2 = 28.3$ , 43.3 and 33.0 respectively,  $P < 0.01$ ), with a minimum around the long dry season. Monthly fluctuations in trap success seemed greater for *C. batesi*, *P. schoutedeni* and *S. ollula* ( $CV = 64$ , 79 and 68% respectively) than for *S. johnstoni* ( $CV = 39\%$ ) even if the low monthly number of captures for the first three species may explain this result.

Even if the temporal variation in shrew trap success was rather synchronized between the two sites (cross correlation: 0.593), some differences were recorded: trap success significantly increased at site A from April to May 2000 and from February to March 2001; whereas, it decreased at site B, and the opposite was true from January to February 2001. Consequently, in May 2000, shrew trap success was significantly higher at site A than at site B ( $\chi^2 = 10.6$ ,  $P = 0.001$ ), while the reverse was true in February 2001 ( $\chi^2 = 5.71$ ,  $P = 0.017$ ). These differences were mainly due to differences in trap success of *S. ollula*, *C. batesi* and *P. schoutedeni*. The seasonal variation in trap success of *S. johnstoni* observed at the two sites was synchronized (cross correlation: 0.650) and whatever the month, no significant difference in its trap success was recorded between the two sites.

The four most abundant species were captured in nearly all months and their relative abundance varied during the year (Figure 2). However, *S. johnstoni* remained the dominant species throughout the year. Four species (*C. crenata*, *C. dolichura*, *C. goliath* and *C. grassei*) were trapped in most of the months but were never abundant ( $p_i$  mostly < 10%), and two others (*C. cf. nigrofuscus* and *S. remyi*) were trapped only in a few months and were always rare ( $p_i < 5\%$ ).

Even if the monthly variation in species relative abundance was not always synchronized between sites, the overall community structure was similar between sites A and B throughout the year ( $70\% < P_R < 88\%$ ), except in May ( $P_R = 40\%$ ), July ( $P_R = 67\%$ ), August ( $P_R = 55\%$ ) and October ( $P_R = 67\%$ ) 2000. Differences

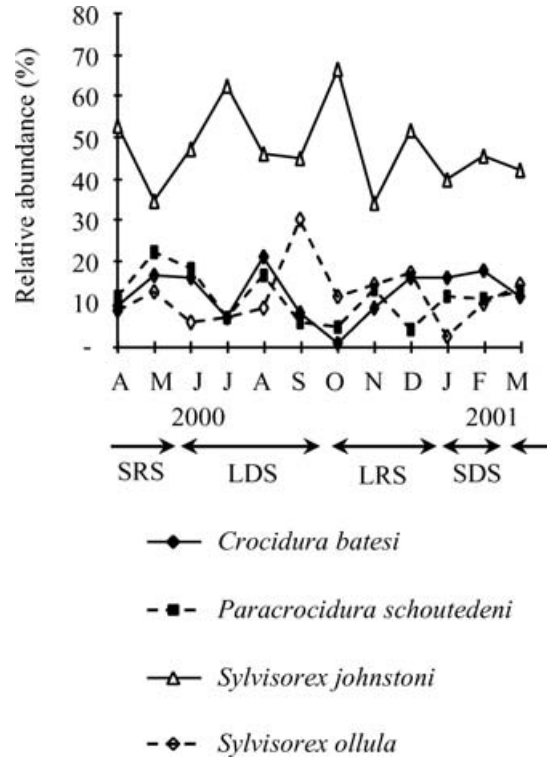


**Figure 1.** Rainfall recorded from April 2000–March 2001, during the 21 d of each trapping session (histograms), and monthly trap success (line) of all species combined (a) and of the four most abundant species (b). Results of the two sites (A and B) are combined. SRS: short rainy season, LDS: long dry season, LRS: long rainy season, SDS: short dry season.

observed in July and August could have resulted from the low monthly number of captures (less than 14 per site), and those observed in October could be due to the low pitfall-trapping effort at site A during this month.

**Reproduction**

Mean litter size, based on embryo counts, varied between species: it was  $1.71 \pm 0.5$  (range 1–2) for *P. schoutedeni*



**Figure 2.** Relative abundance of the four most abundant species, from April 2000–March 2001. Results of the two sites (A and B) are combined. For an explanation of abbreviations see legend to Figure 1.

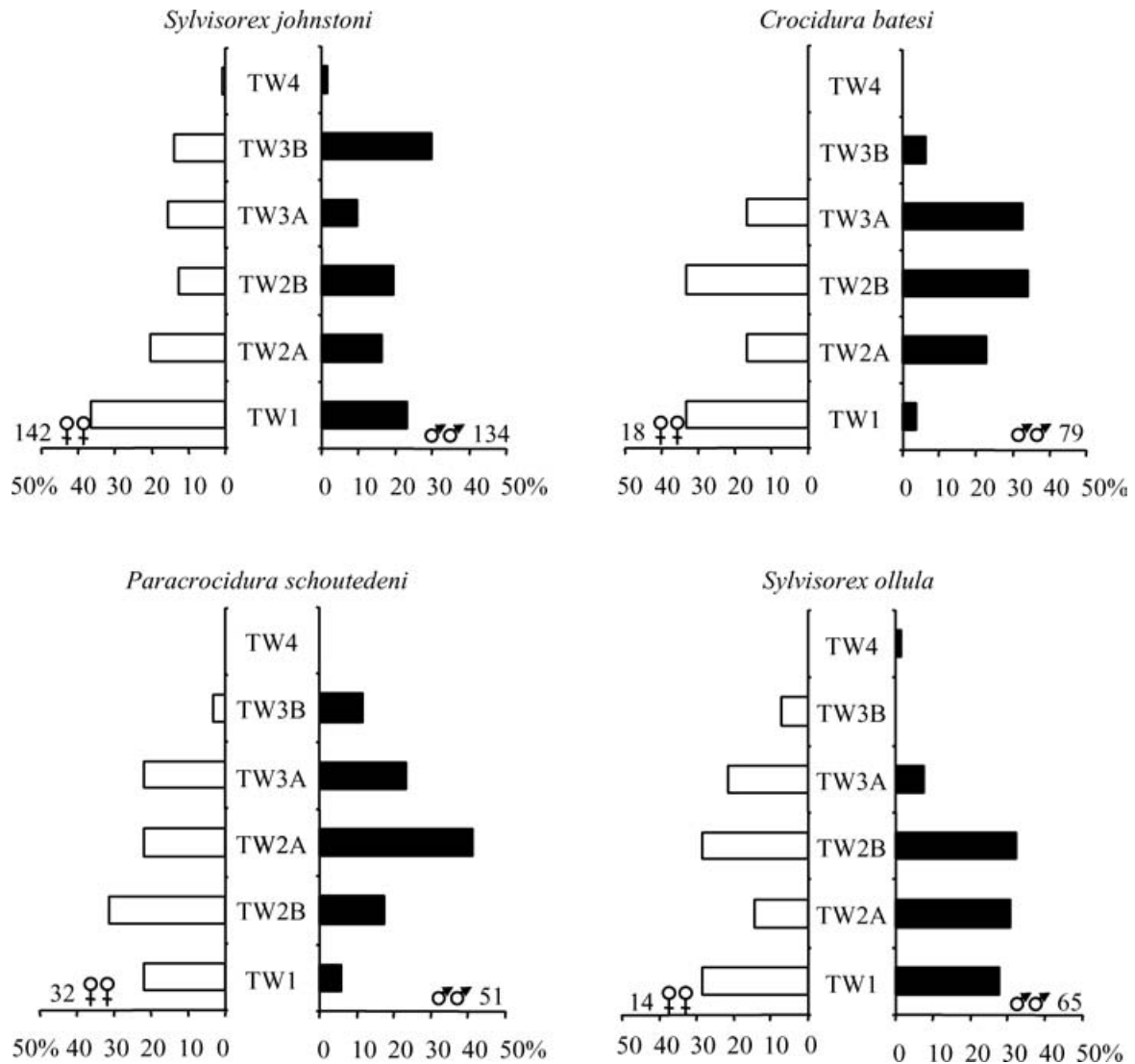
( $n = 7$ ),  $1.68 \pm 0.8$  (range 1–3) for *S. johnstoni* ( $n = 22$ ) and  $3.5 \pm 1.05$  (range 2–4) for *S. ollula* ( $n = 4$ ). Only three pregnant females of *C. batesi* (with 1, 2 and 4 embryos respectively), *C. crenata* (3, 3, 3) and *C. goliath* (2, 2, 3) were sampled.

Breeding females of *S. johnstoni* were recorded in all months, except in October when only three females were collected, and their proportion (25% of females) did not vary significantly across seasons ( $\chi^2 = 3.3$ ,  $P = 0.348$ ).

Only the numerically dominant species, *S. johnstoni*, was captured in high enough numbers to permit analyses of breeding condition as a function of relative age. Females in breeding condition were found for the first five tooth-wear classes (TW1–TW3B). A single female of the last tooth-wear class (TW4) was captured and was not in a breeding condition.

**Population structure**

**Sex ratio.** Sex ratios (Male/Female) of *C. dolichura* (13/9), *C. grassei* (17/16) and *S. johnstoni* (140/148) were not significantly different from 1/1 ( $\chi^2 = 0.727$ , 0.030 and 0.222 respectively,  $P > 0.05$ ), but those of *C. batesi* (79/19), *C. crenata* (35/16), *C. goliath* (24/10), *P. schoutedeni* (51/32) and *S. ollula* (67/16) were male biased ( $\chi^2 = 36.7$ , 7.0, 5.7, 4.3 and 31.3 respectively,  $P < 0.05$ ).



**Figure 3.** Age structure related to tooth-wear classes of the four most abundant species in the forest of Monts Doudou. The individuals are grouped in tooth-wear classes and the relative share (%) of each tooth-wear class is represented by horizontal bars. Animals belonging to one tooth-wear class are divided into females (open horizontal bars) and males (black horizontal bars).

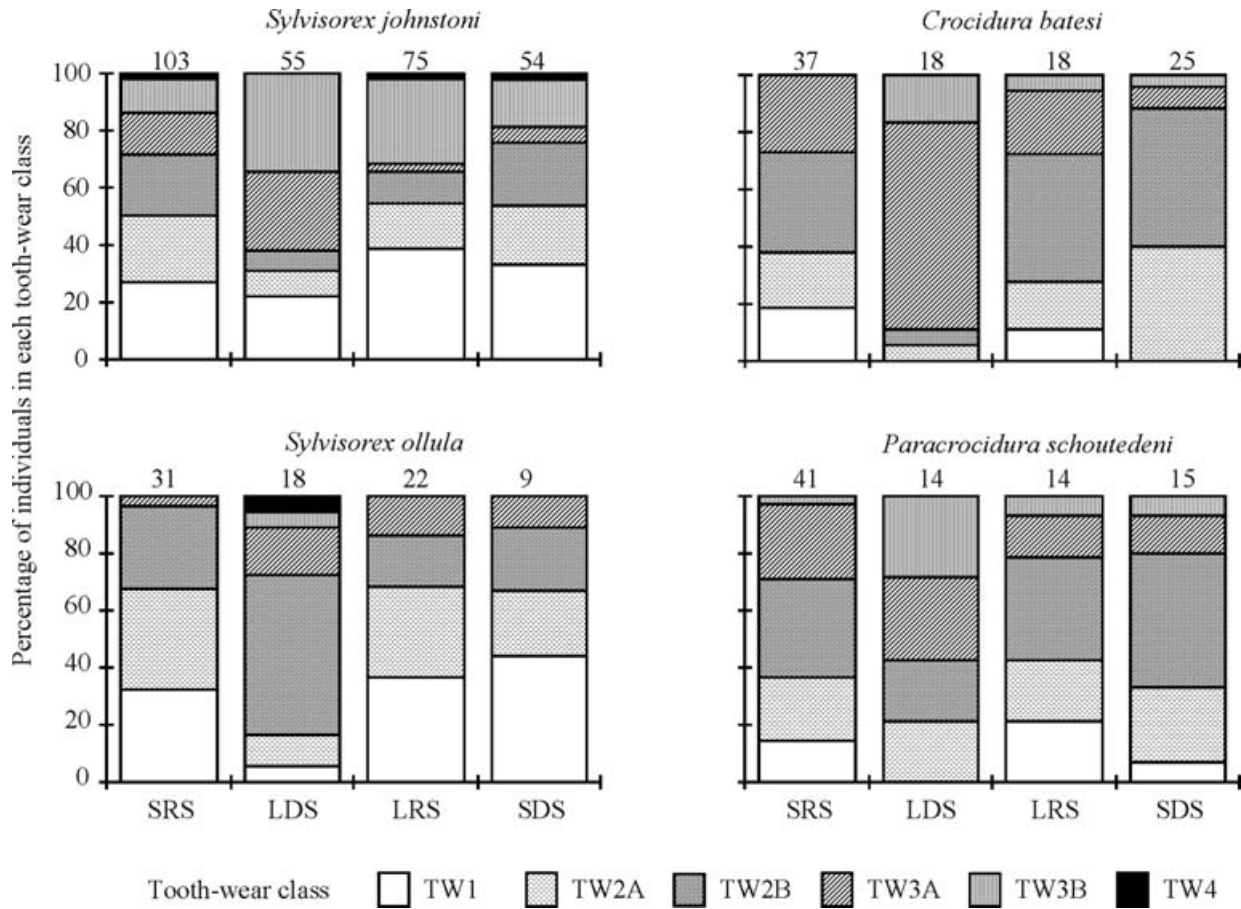
We found a significant interaction between sex ratio of *S. johnstoni* and tooth-wear classes ( $\chi^2 = 16.8$ ,  $P = 0.002$ ): sex ratio was female biased (31/52) for individuals of the first tooth-wear class (TW1), while it was male biased (42/21) for individuals of the last two tooth-wear classes (TW3A and TW4). For other species, the number of specimens captured per sex and tooth-wear class was too low for analysis.

Sex ratio of the four most abundant species did not vary with season ( $1.4 < \chi^2 < 6.3$ ,  $P > 0.05$ ).

**Tooth-wear composition.** Amongst the males of *C. batesi* and *P. schoutedeni*, the youngest subadults (TW1) represented a relatively low proportion of the population (< 6%,

Figure 3). In contrast, among the females of *S. johnstoni*, *S. ollula* and *C. batesi*, the proportion of the youngest subadults was high (> 28%). For both sexes, old adults (TW3B and TW4) represented a low proportion of the population, except for the males of *S. johnstoni* for which the specimens of the fifth tooth-wear class were dominant in the male population.

Tooth-wear composition of the four most abundant species varied throughout the year (Figure 4). In the long dry season, the proportion of middle-aged to old adults (TW3A to TW4) increased for all species ( $P < 0.05$ ). At the same time, the proportion of the youngest subadults (TW1) of *C. batesi*, *P. schoutedeni* and *S. ollula* decreased ( $P < 0.05$ ): no TW1 specimen of *C. batesi* and *P. schoutedeni* was captured and the only one *S. ollula*



**Figure 4.** Percentage of individuals of both sexes in each tooth-wear class, from April 2000–March 2001. The number above each bar is the sample size for each season. For an explanation of abbreviations see legend to Figure 2.

was captured in June, at the early beginning of the long dry season. No significant difference in the proportion of TW1 individuals was recorded for *S. johnstoni* during the long dry season ( $\chi^2 = 0.5$ ,  $P = 0.460$ ), even if none was captured in May and June.

**DISCUSSION**

**Seasonal variation in community structure**

In the forest of Monts Doudou, we recorded 10 species of shrew. In this faunal region (South Ogooué; Deleporte & Colyn 1999) shrew species richness is known to vary between 6 and 14 from one locality to another (Colyn *et al.* unpubl. data, O'Brien *et al.* in press). Differences in species richness and species composition between localities could be mainly due to (1) the existence of species complexes still in need of taxonomic revision and (2) differences between studies, in the types of habitats surveyed or in trapping methods and trapping effort developed. In our two study sites, the number of species varied throughout the year

and tended to be minimal during the period of minimal trap-success.

In agreement with the results obtained in other long-term surveys in west Central African rain forests (Barrière & Nicolas 2000, Lasso *et al.* 1996), trap success of shrews varied seasonally in Monts Doudou and was minimal around the dry season. In previous studies carried out in African rain forest, the causality of this variation was not investigated. It could be due to seasonal variation in population size or in the probability of capture of individuals (Slade & Blair 2000). Even if our trapping protocol does not allow us to separate probability of capture from population size, the age-structure and reproductive data give clues to the annual population dynamics in the species concerned.

During the long dry season, we noticed an ageing of the four most abundant populations (increased proportion of old adults and decreased proportion of young individuals) together with a decrease in their trap success. However, we did not observe a significant decrease in the proportion of breeding females for the dominant *S. johnstoni*. Two hypotheses may explain these contradictory results: the

low number of females collected in the long dry season (5–9 per mo) could not give a reliable estimate of the proportion of breeding females; alternatively, there could be as many births in the long dry season as in other seasons but survival of young individuals could be reduced at that time. Periods of weaning and dispersal are often critical periods in the lives of European shrews because the young have low fat reserves and have to feed regularly to avoid starvation (Churchfield 1990). Arthropods constitute the main food resource for shrews in tropical Africa (Churchfield *et al.* 2004, Dudu *et al.* in press). Flying insects are known to be less abundant, in Gabon, during the long dry season (Charles-Dominique 1977). Thus, survival of shrews, especially young individuals, may be reduced at this season. Moreover, desiccation of leaf litter, at that time, can increase the visibility of shrews and may enhance their predation by small carnivores (Ray 1998, Ray & Hutterer 1996).

However, it is important to keep in mind that some of the observed variation in trap success could also be due to differences in probability of capture (Slade & Blair 2000), which are known to be influenced by weather (precipitation, temperature and moonlight; Kirkland & Sheppard 1994, Stokes *et al.* 2001), seasonality (Getz 1961, Shanker 2000, Stokes *et al.* 2001) or inherent characteristics of the individual such as sex, age and breeding status (Patric 1970, Schwarz & Seber 1999, Shanker 2000). Shrews have high metabolic rates resulting in high energy requirements and water loss (Churchfield 1990) and numerous studies have highlighted the capacity of crocidurine shrews to enter torpor, either spontaneously or during food shortages (Frey & Vogel 1979, Genoud 1981, 1988; Nagel 1994, Vogel 1978), to reduce energy requirement and water loss (Churchfield 1990, Nagel 1994). This phenomenon was mainly studied in temperate species but is also known to occur in several tropical ones (Vogel 1978) and was observed in the field for *S. ollula* (PB, pers. obs.). Thus, an increase of torpid behaviours during dry season, induced by low food or water resources, could explain low trap success at this period by reducing the movement activity of shrews. The male-biased sex ratio observed for most species, as well as the differences of sex ratio between tooth-wear classes for *S. johnstoni*, could reflect either real differences in the number of individuals of each sex or differences in their probability of capture, as mobility or ranging patterns are known to vary between sexes for several species (Churchfield 1990, Favre *et al.* 1997, Stockley & Searle 1994).

Seasonal variation in trap success was similar among species. Even if the magnitude of variation differed between species, specific relative abundance did not vary greatly throughout the year. Thus, *S. johnstoni* remained the dominant species during the whole survey period. This result contrasts with what was observed for murid

rodents at the same locality (Nicolas & Colyn 2003), and for shrews and rodents in Ngotto forest (Barrière & Nicolas 2000), where shift in species dominance over time were recorded.

## Reproduction

In tropical regions, breeding could occur throughout the year in several crocidurine populations and its intensity could reach a peak at certain periods of the year, usually coinciding with environmental conditions (Churchfield 1990, Yu *et al.* 2001). In this study, the seasonal proportion of breeding females of the dominant *S. johnstoni* confirmed the general pattern of a continuous reproduction. A lower breeding intensity around the long dry season, could also be possible, as indicated by the lower proportion of young individuals of the four most abundant species.

Females of *S. johnstoni* in breeding condition were found for the first five tooth-wear classes, indicating that, in agreement with previous studies on crocidurine shrews (Churchfield 1990, Innes 1994), this species could mature within a few months after weaning and then could breed throughout its life span.

Litter size varied from one species to another and between females of a given species. Mean litter size obtained for *P. schoutedeni* and *S. johnstoni* in this study is congruent with what was recorded for these two species at Makokou–Belinga in north-eastern Gabon (Brosset 1988, Dubost 1968). In contrast, mean litter size differed between the two localities for *S. ollula* (3.5 and 2.0 in Monts Doudou and Makokou–Belinga, respectively) as well as for *C. batesi* (2.3 and 3.0). As litter size could differ, for a given shrew species, between habitats (Dubost 1968), the observed differences could either be due to the low number of pregnant females available, or to the fact that they were collected in distinct habitats (primary forest in Monts Doudou; primary forest, secondary forest, crops and human settlements in Makokou–Belinga). Gestation period of crocidurine shrews is usually 22–31 d and females of several genera and species can undergo a postpartum oestrus (Innes 1994).

Altogether, these data on reproduction characteristics suggest that shrews have the ability to produce many young during their life span and that they can adjust their breeding intensity to changes in environmental conditions.

Regardless of the seasonal variation in the number of species of shrews captured and their variations in term of trap success, it seems obvious that surveys of small mammals restricted to a short sampling period could inaccurately estimate species richness and abundance. It is advisable to use data which cover an entire year

when comparing shrew communities of different sites or habitats.

## ACKNOWLEDGEMENTS

Field studies were supported by the World Wildlife Fund (WWF) Gabon – Programme Régional de L'Information Environnementale. V. Nicolas and P. Barrière received a fellowship from the Ministère de l'Education Nationale, de l'Enseignement Supérieur et de la Recherche (France). We are particularly grateful to MM. O. Lengrand, A. Kandem and P. Obame Ondo (WWF) for logistic support in the field and to the local team of Monts Doudou (particularly, S. Guimondou, J. N. Assoume Ondo and A. Essono Bigang). We thank Mr Manfoumbi Kombila from the “Direction de la Faune et de la Chasse” in Libreville, and Ms Koumba from Moukalaba Reserve. We are grateful to E. Verheyen, S. Quérroul and M. Dillen (IRSNB, Belgium) for molecular analyses and to R. Hutterer (A. Koenig Museum, Germany) for his valuable help in the systematics of African Soricidae.

## LITERATURE CITED

- BARRIÈRE, P. & NICOLAS, V. 2000. *Rapport d'expertise sur la biodiversité animale en forêt de Ngotto (République Centrafricaine): écologie et structuration des peuplements de micro-mammifères musaraignes et rongeurs*. Programme ECOFAC (Forêt de Ngotto – République Centrafricaine). 46 pp.
- BROSSET, A. 1988. Le peuplement de mammifères insectivores des forêts du nord-est du Gabon. *Revue d'Ecologie Terre Vie* 43:23–46.
- CHARLES-DOMINIQUE, P. 1977. *Ecology and behaviour of nocturnal primates, prosimians of equatorial West Africa*. Duckworth, Liverpool. 277 pp.
- CHURCHFIELD, S. 1990. *The natural history of shrews*. Christopher Helm, London. 175 pp.
- CHURCHFIELD, S., BARRIÈRE, P., HUTTERER, R. & COLYN, M. 2004. First results on the feeding ecology of sympatric shrews (Insectivora: Soricidae) in the Taï National Park, Ivory Coast. *Acta Theriologica* 49:1–15.
- DELEPORTE, P. & COLYN, M. 1999. Biogéographie et dynamique de la biodiversité: application de la “PAE” aux forêts planitiaies d'Afrique centrale. *Biosystema* 17:37–43.
- DIPPENAAR, N. J. 1977. Variation in *Crociodura mariquensis* (A. Smith, 1844) in Southern Africa, Part 1 (Mammalia: soricidae). *Annals of Transvaal Museum* 30:163–206.
- DUBOST, G. 1968. Aperçu sur le rythme annuel de reproduction des muridés du nord-est du Gabon. *Biologica Gabonica* 4:227–239.
- DUDU, A., CHURCHFIELD, S. & HUTTERER, R. Community structure and food niche relationships of coexisting rain-forest shrews in the Masako Forest, north-eastern Congo. In Meritt, J. F., Churchfield, S., Hutterer, R. & Sheftel, R. (eds). *The biology of the Soricidae*. Carnegie Museum of Natural History Special Publication. In press.
- FAVRE, L., BALLOUX, F., GOUDET, J. & PERRIN, N. 1997. Female-biased dispersal in the monogamous mammal *Crociodura russula*. Evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London Series B* 264:127–132.
- FREY, H. & VOGEL, P. 1979. Etude de la torpeur chez *Suncus etruscus* (Savi, 1822) (Soricidae, Insectivora) en captivité. *Revue Suisse de Zoologie* 86:23–36.
- GENOUD, M. 1981. *Contribution à l'étude de la stratégie énergétique et de la distribution écologique de Crociodura russula (Soricidae, Insectivora) en zone tempérée*. Thèse de doctorat, Université de Lausanne. 167 pp.
- GENOUD, M. 1988. Energetic strategies of shrews: ecological constraints and evolutionary implications. *Mammal Review* 18:173–193.
- GETZ, L. L. 1961. Responses of small mammals to live-traps and weather conditions. *American Midland Naturalist* 66:160–170.
- GOODMAN, S. M. & HUTTERER, R. 2004. A report on the shrews (Mammalia: Soricidae) of Mts Doudou, Gabon: elevational distribution and preliminary insights into their ecology. Pp. 93–106 in Fisher, B. (ed.). *Monts Doudou, Gabon: a floral and faunal inventory, with reference to elevational variation*. Memoirs of the California Academy of Sciences, 28, San Francisco.
- GOODMAN, S. M., HUTTERER, R. & NGNEGUEU, P. R. 2001. A report on the community of shrews (Mammalia: Soricidae) occurring in the Minkébé Forest, north-eastern Gabon. *Mammalian Biology* 66:22–34.
- HAPPOLD, D. C. D. 1977. A population study on small rodents in the tropical rain forest in Nigeria. *Revue d'Ecologie – Terre et Vie* 31:385–455.
- HUTTERER, R. & SCHLITZER, D. A. 1996. Shrews of Korup National Park, Cameroon, with the description of a new *Sylvisorex* (Mammalia: Soricidae). Pp. 57–66 in *Contributions in Mammalogy: a memorial volume honouring Dr. J. Knox Jones, Jr.* Special publication of the Museum of Texas Tech University.
- HUTTERER, R., DIETERLEN, F. & NIKOLAUS, G. 1992. Small mammals from forest islands of eastern Nigeria and adjacent Cameroon, with systematical and biogeographical notes. *Bonner Zoologische Beiträge* 43:393–414.
- INNES, D. G. L. 1994. Life histories of the Soricidae: a review. Pp. 111–136 in Meritt, J. F., Kirkland, G. L. & Rose, R. K. (eds). *Advances in the biology of shrews*. Special publication of the Carnegie Museum of Natural History n° 18, Pittsburgh.
- KALKO, E. K. V. & HANDLEY, C. O. 1992. Comparative studies of small mammal populations with transects of snap traps and pitfall arrays in southwest Virginia. *Virginia Journal of Science* 44:3–18.
- KIRKLAND, G. L. & SHEPPARD, P. 1994. Proposed standard protocol for sampling small mammal communities. *Bulletin of the Carnegie Museum of Natural History* 18:277–283.
- LISSO, C., HUTTERER, R. & RIAL, A. 1996. Records of shrews (Soricidae) from Equatorial Guinea, especially from Monte Alen National Park. *Mammalia* 60:69–76.
- MADDOCK, A. H. 1992. Comparison of two methods for trapping rodents and shrews. *Israel Journal of Zoology* 38:333–340.
- MALIZIA, L. 2001. Seasonal fluctuations of birds, fruits and flowers in a subtropical forest of Argentina. *The Condor* 103:45–61.
- NAGEL, A. 1994. Metabolic rates and regulation of cardiac and respiratory function in European shrews. Pp. 421–434 in Meritt, J. F., Kirkland, G. L. & Rose, R. K. (eds). *Advances in the biology of shrews*.



- Carnegie Museum of Natural History, special publication n° 18, Pittsburgh.
- NICOLAS, V. & COLYN, M. 2003. Seasonal variations in population and community structure of small rodents in a tropical forest of Gabon. *Canadian Journal of Zoology* 81:1–13.
- NICOLAS, V., BARRIÈRE, P. & COLYN, M. 2003. Impact of removal pitfall-trapping on the community of shrews (Mammalia: Soricidae) in two African tropical forest sites. *Mammalia* 67:133–138.
- O'BRIEN, C. J., MCSHEA, W. J., GUIMONDOU, S., BARRIÈRE, P. & CARLETON, M. D. Terrestrial small mammals (Soricidae and Muridae) from the Gamba Complex in Gabon: species composition and comparison of sampling techniques. In Alonso, A., Campbell, P., Lee, M. Pauwels, O. & Dallmeier, F. (eds). *Gabon: biodiversity of a tropical African rainforest*. SIMAB Series 10, Smithsonian Institution, Washington DC. In press.
- PATRIC, E. F. 1970. Bait preferences of small mammals. *Journal of Mammalogy* 51:179–182.
- QUÉROUIL, S., BARRIÈRE, P., COLYN, M., HUTTERER, R., DUDU, A., DILLEN, M. & VERHEYEN, E. A molecular insight into the systematics of African *Crocidura* (Crocidurinae, Soricidae) using 16s rRNA sequences. In Meritt, J. F., Churchfield, R., Hutterer, S. & Sheftel, N. (eds). *The biology of the Soricidae II*. Special Publication of the Carnegie Museum of Natural History, Pittsburgh. In Press.
- RABINOWITZ, A. & NOTTINGHAM, B. G. 1989. Mammal species richness and relative abundance of small mammals in a subtropical wet forest of Central America. *Mammalia* 53:217–225.
- RAY, J. C. 1998. Temporal variation of predation on rodents and shrews by small African forest carnivores. *Journal of Zoology London* 244:363–370.
- RAY, J. C. & HUTTERER, R. 1996. Structure of a shrew community in the Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia: soricidae). *Ecotropica* 1:85–97.
- SAINT AUBIN, G. 1963. *La forêt du Gabon*. CIRAD, Montpellier. 208 pp.
- SCHWARZ, C. J. & SEBER, G. A. 1999. Estimating animal abundance: review III. *Statistical Science* 14:427–456.
- SHANKER, K. 2000. Small mammals trapping in tropical montane forests of the Upper Nilgris, southern India: an evaluation of capture-recapture models in estimating abundance. *Journal of Bioscience* 25:99–111.
- SLADE, N. A. & BLAIR, S. M. 2000. An empirical test of using counts of individuals captured as indices of population size. *Journal of Mammalogy* 81:1035–1045.
- SOSSEF, M. S. M., ISSEMBE, Y., BOUROBOU, H. P. & KOOPMAN, W. J. M. 2004. Botanical diversity of the Pleistocene forest refuge Monts Doudou. Pp. 17–92 in Fisher B. (ed.). *Monts Doudou, Gabon: a floral and faunal inventory, with reference to elevational variation*. Memoirs of the California Academy of Sciences, 28, San Francisco.
- STOCKLEY, P. & SEARLE, J. B. 1994. Characteristics of the breeding season in the common shrew (*Sorex araneus*): male sexual maturation, morphology and mobility. Pp. 181–188 in Meritt, J. F., Kirkland, G. L. & Rose, R. K. (eds). *Advances in the biology of shrews*. Carnegie Museum of Natural History, special publication n° 18, Pittsburgh.
- STOKES, M. K., SLADE, N. A. & BLAIR, S. M. 2001. Influences of weather and moonlight on activity patterns of small mammals: a biogeographical perspective. *Canadian Journal of Zoology* 79:966–972.
- VASQUEZ, L. B., MEDELLIN, R. A. & CAMERON, G. N. 2000. Population and community ecology of small rodents in montane forest of western Mexico. *Journal of Mammalogy* 81:77–85.
- VOGEL, P. 1978. Metabolic levels and biological strategies in shrews. Pp. 170–181 in Schmidt-Nielsen, K., Bolis, L. & Taylor, C. R. (eds). *Comparative physiology: primitive mammals*. Cambridge University Press, Cambridge.
- WILLIAMS, D. F. & BRAUN, S. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. *Journal of Wildlife Management* 47:841–845.
- WILLIG, M. R. & GANNON, M. R. 1986. Mammals. Pp. 399–432 in Reagan, D. P. & Waide R. B. (eds). *The food web of a tropical rain forest*. The University of Chicago Press, Chicago and London.
- WOLDA, H. 1983. Spatial and temporal variation in abundance in tropical animals. Pp. 93–105 in Sutton, S. L., Whitmore, T. C. & Chadwick, A. C. (eds). *Tropical rain forest: ecology and management*. Blackwell Scientific Publications, Oxford.
- WOODMAN, N., SLADE, N. A. & TIMM, R. M. 1995. Mammalian community structure in lowland tropical Peru, as determined by removal trapping. *Zoological Journal of the Linnaean Society* 113:1–20.
- YU, H. T., CHENG, T. W. & CHOU, W. H. 2001. Seasonal activity and reproduction of two syntopic white-toothed shrews (*Crocidura attenuata* and *C. kurodai*) from a subtropical montane forest in central Taiwan. *Zoological Studies* 40:163–169.