Living in Atlantic forest fragments: life habits, behaviour, and colony structure of the cockroach *Monastria biguttata* (Dictyoptera, Blaberidae, Blaberinae) in Espirito Santo, Brazil

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Abstract: The life habits, behaviour, and colony structure of the cockroach *Monastria biguttata* were studied during 2 years in remnants of the Brazilian Atlantic forest. *Monastria biguttata* was abundant, conspicuous, and ubiquitous in the semideciduous forest in the north of Espirito Santo, Brazil. It was found in forest fragments of various sizes and disturbance levels, but never in the surrounding plantations. Adults and nymphs were found in colonies of 2.8–11.6 cockroaches, grasping the bark of the underside of dead trunks that were clumped on the ground, in the forest understory. The cockroaches were very sedentary, moved extremely slowly, and immediately froze when disturbed. Based on their brooding behaviour and aggregated distribution on trunks, they appeared to be gregarious with only a slow spread during nymphal development. Brood birth took place during the rainy period, and nymphs developed into adults in a minimum of 2 years. Brood size and egg number in oothecae were not very high (23.0 ± 1.5 and 31.1 ± 1.7 (mean ± SE), respectively). All these traits were analysed to understand the survival of species in forest fragments.

Résumé : Les traits de vie, le comportement et la structure des colonies de *Monastria biguttata* ont été étudiés pendant deux ans dans des fragments de la forêt atlantique du Brésil. *Monastria biguttata* est une espèce de blatte abondante et visible, ubiquiste dans le forêt semi-décidue du nord de l'état d'Espirito Santo au Brésil. Elle a été échantillonnée dans des fragments forestiers de taille et d'état de conservation variés, mais n'a jamais été trouvée dans les plantations entourant ces fragments. Les adultes et les larves forment des colonies de 2.8 à 11.6 blattes et vivent aggripés à l'écorce sur la face inférieure des troncs morts gisant sur le sol du sous-bois. Ils sont très sédentaires, se déplacent extrêmement lentement et s'immobilisent immédiatement en cas de perturbation. Du fait de leur comportement de soins aux jeunes et de leur répartition agrégée sur les troncs, ils peuvent être qualifiés de grégaires avec une lente dispersion pendant leur développement larvaire. Les naissances des portées sont observées pendant la saison des pluies et le développement jusqu'à l'âge adulte se fait en deux ans minimum. La taille des portées et des oothèques n'est pas très importante (23.0 ± 1.5 et 31.1 ± 1.7, moyenne ± erreur type). L'ensemble des ces traits ont été analysés dans la perspective d'une meilleure compréhension de la survie de l'espèce dans les fragments forestiers.

Introduction

The Brazilian Atlantic forest is presently reduced to less than 10% of its original surface and is divided into thousands of small remnants (SOS Mata Atlântica/INPE/ISA 1998). These remnants face the problems of ecosystem fragmentation, decreasing population sizes or migration rates, and changing environments, microclimates, and food webs (Saunders et al. 1991; Turner 1996).

The species endemic to the Atlantic forest in Brazil are thus fated to live in forest fragments, which are mostly small and often disturbed (Viana et al. 1997; Chiarello 1999). Whether these species remain present or disappear in the different forest remnants and what preexisting traits can make them preadapted to the present-day situation are matters of great concern (Brooks and Balmford 1996). For example, trophic specialization of animals could either expose them to or protect them against ecosystem fragmentation (Didham et al. 1996, 1998*a*).

Arthropods, particularly insects, living in the forest understory are the most abundant and diverse group in neotropical forests. However, the effect of forest fragmentation on communities and populations is still poorly known, and the available results show that responses to forest fragmentation can be very complex, particularly because of the high diversity of life habits in this group (Klein 1989; Margules et al. 1994; Didham et al. 1996, 1998*b*). In this context, one nec-

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essary advance is to study the population ecology and life strategies of insect species that could typify model organisms to better understand the way certain groups of organisms may or may not be affected by forest fragmentation (Chiarello 2000). In particular, saprophagous insects could be studied to analyse why they seem to better resist forest fragmentation (Didham et al. 1996). Generally, however, selection of organisms that fit the requirements of long-term field research is a challenge.

Based on research in the Brazilian Atlantic forest (Grandcolas and Pellens 2002; Pellens 2002; Pellens and Grandcolas 2002; Pellens et al. 2002), *Monastria biguttata* (Thunberg, 1826) was identified as an interesting organism with which to evaluate the effect of forest fragmentation on saprophagous insects. This species was described very early (Thunberg 1826) and then reported only a few times (Roth and Willis 1960). The genus is distributed throughout the Atlantic region of Brazil (Princis 1963) and belongs to a neotropical group, the ovoviviparous subfamily Blaberinae. This subfamily is reasonably well known in the laboratory and in the field, with representatives in central America and Amazonia (Grandcolas 1993*a*, 1998). *Monastria biguttata* is conspicuous, large (adult body is 4 cm long), and slow-moving, thus permitting comparative field population studies to be easily carried out as for some other biota (Grandcolas 1995*b*).

The present paper is aimed at providing a first general but carefully documented study of the biology of *M. biguttata* in the field. Populations of this cockroach in varied forest fragments in the state of Espirito Santo, Brazil, were studied to assess their habitat use, population and colony structure, and presence or absence in large forest reserves, in forest fragments, and in the surrounding matrix. This knowledge will be immediately instrumental as a basis for evaluating the effect of forest fragmentation on populations according to a 2-year-long sampling program (Pellens 2002).

Materials and methods

This study was carried out during a total of 7 months of field sampling between October 1999 and October 2001 at 12 study sites in the semideciduous Atlantic forest in the north of the state of Espirito Santo, Brazil. Of these study sites, five are part of a 46 000-ha forest remnant preserved mainly in two forest reserves. The remaining sites are forest fragments varying from 2.4 to 66.7 ha (Appendix A). The matrix surrounding the forest fragments consists mainly of coffee plantations and has also been systematically sampled (see Pellens and Grandcolas 2002). Deforestation of the region between 1950 and 1970 led to the isolation of the present fragments (Agarez 2002; Pellens 2002).

The climate of this region is hot and humid (AW in the Köppen classification) with the heaviest rainfall outside the winter period. Mean annual rainfall is around 1130 mm, with peak rainfall between November and March and minimum rainfall between May and August (the dry period of the region). One important feature of the climate of the region is the marked variation in rainfall among years: during some 2- or 3-year periods, total rainfall may be less than 900 mm. In these periods, the dry season can be very stressful, with precipitation indexes close to zero during three or four consecutive months (Garay et al. 1995; Pellens 2002).

In October 1999, a preliminary study of the habitat of the cockroach was conducted in the forest understory and in the plantations in the matrix according to the methodology employed by Schal and Bell (1986), Grandcolas (1994*a*, 1994*b*), and Pellens et al. (2002). Clumps of dead wood where *M. biguttata* was first found were studied along a transect perpendicular to existing tracks in each forest site. When a clump was found, the trunks were carefully rolled and searched for *M. biguttata*. Each cockroach found was put immediately in a 100-mL plastic bottle and left in the place where it was captured while the remainder of the dead wood in the same clump was searched. Every piece of dead wood was measured (length and diameter) and marked with labels attached to the trunks with wires. The size of each clump was evaluated by measuring its perimeter, and the distance to the nearest clump of dead wood was also measured.

After searching every piece of dead wood in a clump, the cockroaches left in the plastic bottles were measured (pronotum width) and sexed. For each cockroach, the position on the trunk and the distance to the nearest neighbour were recorded. The digestive tract was also observed through the pale ventral cuticle to determine whether it was full (indicated by a dark greenish color) or empty. Every cockroach captured was marked with a label (offset print on 120-g paper affixed with Neoprene® glue) or with a combination of cuts in the pronotum and the tergites and then released in the same place (see Fig. 6). When one cockroach was recaptured, the distance from the place it had been released was also recorded. Female reproductive status was assessed by examination of the brood sac in the field. The ootheca size was estimated from adult voucher specimens outside of the sampled colonies collected from October 1999 to October 2001. The age of nymphs was estimated by measurement of the pronotum width, similar to previous studies (e.g., Pellens et al. 2002).

The clumps of dead wood where at least one cockroach was found in August 2000 were searched for *M. biguttata* every 3 months from August 2000 to October 2001. The data obtained in August 2000 and the data from the biggest clump of dead wood, where the largest number of cockroaches was registered (RL-MA 4), were chosen to provide representative but reasonably sized examples of some populational trends studied by Pellens (2002). Population parameters and any measurements are given as means with standard errors. Statistical tests were performed with MINITAB® 13.20 (Minitab Inc. 2000).

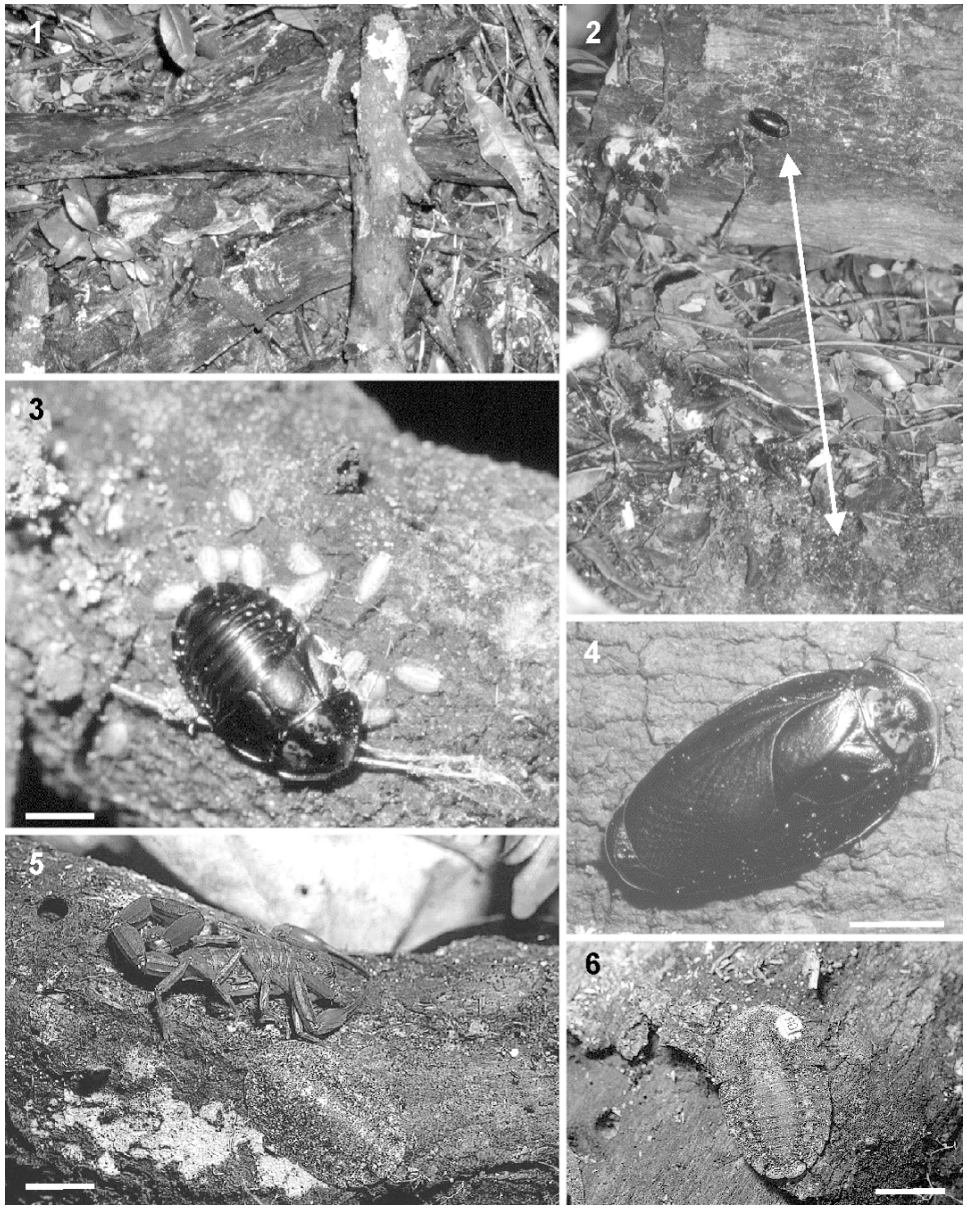
Results

Distribution, habitat, and behaviour

Monastria biguttata was easily found in every forest remnant visited, and it seemed ubiquitous in the semideciduous Atlantic forest in both big forest reserves and varied forest fragments (Appendix A). It was never captured in plantations, even when a few large pieces of dead wood from the preexisting forest remained on the bare ground, or more than 50 m beyond the edge of fragments.

Often, several *M. biguttata* were found together on the same piece of dead wood or on several pieces of wood close

Fig. 1. A small clump of pieces of dead wood with *Monastria biguttata* in the Bioparque Bionativa fragment. **Fig. 2**. An adult female at the underside of a dead trunk rolled up in the Linhares Forest Reserve, Tower. **Fig. 3**. Adult female with a brood recently born, from the São Pedro fragment. **Fig. 4**. Adult male in the Pasto Novo fragment. **Fig. 5**. A nymph motionless at the side of a predatorial scorpion, captured in colony 4 from the Linhares Forest Reserve, Mata Alta. **Fig. 6**. A nymph recaptured in the Bioparque Bionativa fragment in October 2000 with the label placed 3 months before (August 2000). Scale bars = 1 cm.

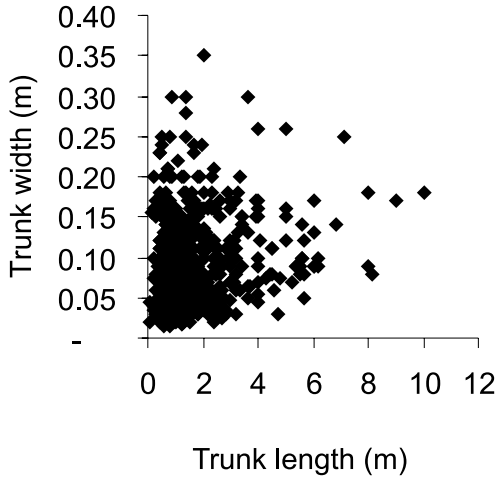


to each other (Figs. 1 and 2). They were not found in any other potential habitat where cockroaches are known to live (e.g., ground litter, loose bark, hollowed trunks, aerial litter, epiphytes, palms, leaves of understory plants, etc.). Nymphs and adults always grasped the bark or wood on the underside of dead trunks (Figs. 1–6) and could thus be seen only when the trunks were rolled up during day and night sampling sessions. Nymphs had tawny-brownish cuticles that were dorsally rough and often covered with dust, which gave the nymphs the appearance of the bark, contrary to the strikingly coloured adults with shiny cuticles (Figs. 3–6). The cockroaches usually moved extremely slowly and immediately froze when disturbed, grasping the substratum even more closely, with antennae hidden beneath the pronotum. If, however, the trunk remained underside up for a very long period, some of the cockroaches moved to the downside of the trunk.

Although the digestive tract of *M. biguttata* was full in 90% of the specimens examined (i.e., all cockroaches except neonates), feeding was not observed in the field. Dissections of *M. biguttata* revealed a diet of diverse microorganisms, fungi, and dead organic matter, most likely from the bark where *M. biguttata* was always found during the day or at night.

The only observation of predation was the seizure of one nymph by a small spider when the nymph exhibited unusual

Fig. 7. Relationship between length and width of pieces of dead wood from clumps harbouring 35 colonies of *M. biguttata* studied in the Sooretama Biological Reserve, the Linhares Forest Reserve, the Bioparque Bionativa fragment, and the São Pedro fragment (N = 685).



movement after the dead trunk was rolled underside up. Otherwise, cockroaches remained motionless when a potential predator was nearby (Fig. 5). A large swarm of army ants (subfamily Ecitoniinae) observed in Fragment Pasto Novo in October 1999 brought back no *M. biguttata* but did bring back many other cockroach species.

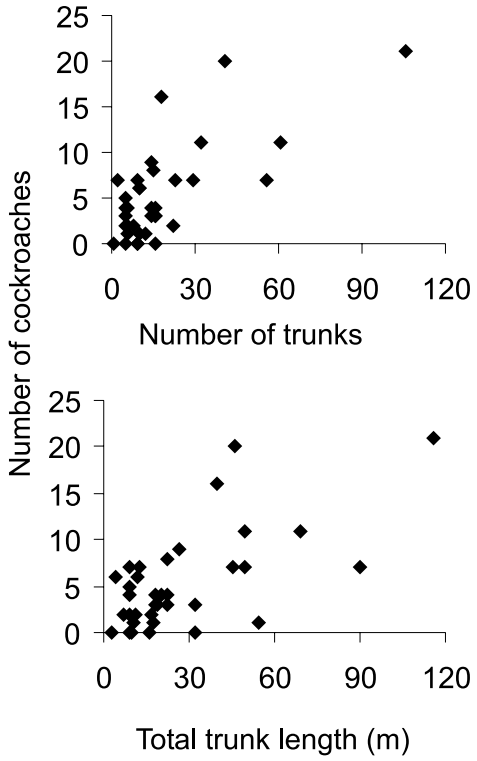
Colony size

Monastria biguttata occur in colonies; a colony can be defined as a group of cockroaches found in a piece or a set of dead wood, each member of the group being closer to each other than to the cockroaches in a neighbouring clump of dead wood. Thirty-five colonies were identified and sampled at four sites: Mata Alta in the Linhares Forest Reserve, the Sooretama Biological Reserve, the Bioparque Bionativa fragment, and the São Pedro fragment. All colonies were found in closed-canopy forest, except one in a treefall gap. Cockroaches were always found under pieces of dead wood that were shaded most of the time.

The mean number of cockroaches per colony varied from 11.6 in November 2000 to 2.8 in October 2001. The clumps of dead wood where cockroach colonies were found had perimeters no greater than 53 m (thus about 8.4 m in diameter), and the distance to the nearest clump of dead wood (always found unoccupied) was, on average, 4.8 ± 0.51 m. Colonies, therefore, were not found close to each other even if clumps of dead wood were found close together.

Within the perimeters of the 35 colonies studied, 685 pieces of dead wood were searched. The pieces of wood were very diverse, ranging from small branches of a few centimetres to large pieces several metres long. The mean length and width of these pieces were 1.56 ± 0.05 m and 8.8 ± 2.0 cm, respectively, the two measurements being correlated (R_S = 0.2466, P < 0.01, N = 685; Fig. 7). The mean number of pieces of dead wood in a clump where a colony occurred was 17.3 (±3.5), but the number varied from 1 to 106.

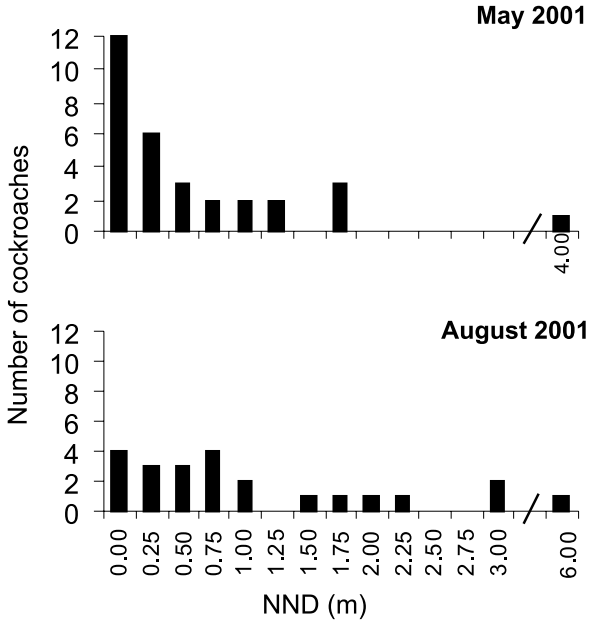
Fig. 8. Size of colonies of *M. biguttata* in August 2000 in relation to the number of pieces of dead wood in the colonies and to the total length of the pieces of dead wood (N = 35).



Monastria biguttata were not found to shelter on trunks of a particular species or morphology (kinds of bark, trunk diameter, etc.) There was a positive correlation between number of cockroaches and number of trunks in each colony (R_S = 0.581, P < 0.01, N = 35; Fig. 8), as well as between number of cockroaches and total length of trunks in each colony (R_S = 0.515, P < 0.01, N = 35; Fig. 8). The latter relationship (Fig. 8) was nonlinear, indicating that colonies were bigger on larger clumps of trunks but that there was a limit to the number of cockroaches in a colony after a certain clump size.

Cockroaches within the colonies were always relatively close to each other and aggregated, as shown by low nearest neighbour distances, although the relative closeness of cockroaches within a colony varied according to the season and the population age structure (Fig. 9). Cockroaches were found closer to each other when they were in the first nymphal stages (i.e., the first 6 months of the life cycle) and were moderately distributed during the following months (compare distances in May and August, Fig. 9). To document this pattern more precisely, 14 broods were more intensely studied, with a repeated sampling within each general session of observations after each brood was found (brood birth, Fig. 3) or first expected (from a heavily pregnant female). The brood size was estimated to be 23.0 ± 1.5 (N = 14), significantly less than the number of oothecae in brood sacs (31.1 ± 1.7, N = 11) (Wilcoxon two-sample test, W = 198.5, P < 0.01). When broods were laid, just-born nymphs clustered together with the female, sometimes even beneath the lateral expansions of tergites and pronotum (Fig. 3). The females remained with the brood from 3 to

Fig. 9. Distribution of nearest neighbour distances (NND) in colony MA-4 (Linhares Forest Reserve, Mata Alta) of *M. biguttata* in May 2001 (N = 31) and August 2001 (N = 24).



more than 23 days. In three of these cases, the females were observed to stay with the brood after the nymphs had first moulted, a process which took more than 8 days (Table 1). After the nymphs spread, some remained less than 0.25 m from their nearest neighbour for about 6 months (May, Fig. 9).

To verify the relationship between distribution and age of *M. biguttata*, the number of cockroaches in each nearest neighbour distance class was correlated with the number of cockroaches in each age class (see Colony structure and its seasonal variation). In the example given in Fig. 9, 48.4% of the cockroaches in the colony were from the broods born in November, and the pronotum was no wider than 1.0 cm. Thus, in May, there was a correlation between the nearest neighbour distances and the number of cockroaches in each age class (R_S = 0.374, $P < 0.05$, N = 31). In August, when cockroaches in the first age class represented only 8.3% of the colony, cockroaches were not as close together (Fig. 9), and the correlation between nearest neighbour distance and number of cockroaches in each age class was no longer observed (R_S = –0.102, $P > 0.05$, N = 24).

Except for this slow spread from the female after their birth, many cockroaches were very sedentary, even over the long term. For instance, of 34 cockroaches marked in the colony RL-MA 4 in May 2001, 13 (38.2%) were recaptured 3 months later (August 2001) when they represented 54.2% of the total number of cockroaches in the colony. Seven (20.6%) of these cockroaches were recaptured less than 2.5 m from the place they were first captured. Two (6.0%) were recaptured between 2.5 and 5.0 m from the place they were first found.

Colony structure and its seasonal variation

Most of the colonies consisted of small to large groups of nymphs, sometimes with a few adult females. In some cases, nymphs were found with adult females and neonates. Males were rare, as were male and female adults together (Table 2). It was common to find cockroaches from several age classes in the same colony, and the number of age classes was highly correlated with the number of cockroaches in each colony (R_S = 0.919, $P < 0.01$). Most colonies, therefore, consisted of several cohorts or broods, and colony size was bigger than brood size. The sex ratio of colonies was not significantly biased (χ^2 = 613.3, $P < 0.01$).

The seasonal variation in number of cockroaches in each age class is presented in Fig. 10. The highest number of cockroaches was found in November 2000, the month during which the highest number of broods was recorded. Although it was common to find nymphs of several age classes (along with adult females) in the population throughout the year, brood birth was registered only in November and February. In May, adult females were found close to males, but none of the females had oothecae in her brood sac. In August, 47% of adult females had oothecae. In November, fewer females (only 13%) had oothecae, but 69% of females were found with their brood. In February, 50% of adult females were with a brood (Fig. 10).

Table 1. Brood care and dispersal of 14 *Monastria biguttata* females and their broods during several time intervals.

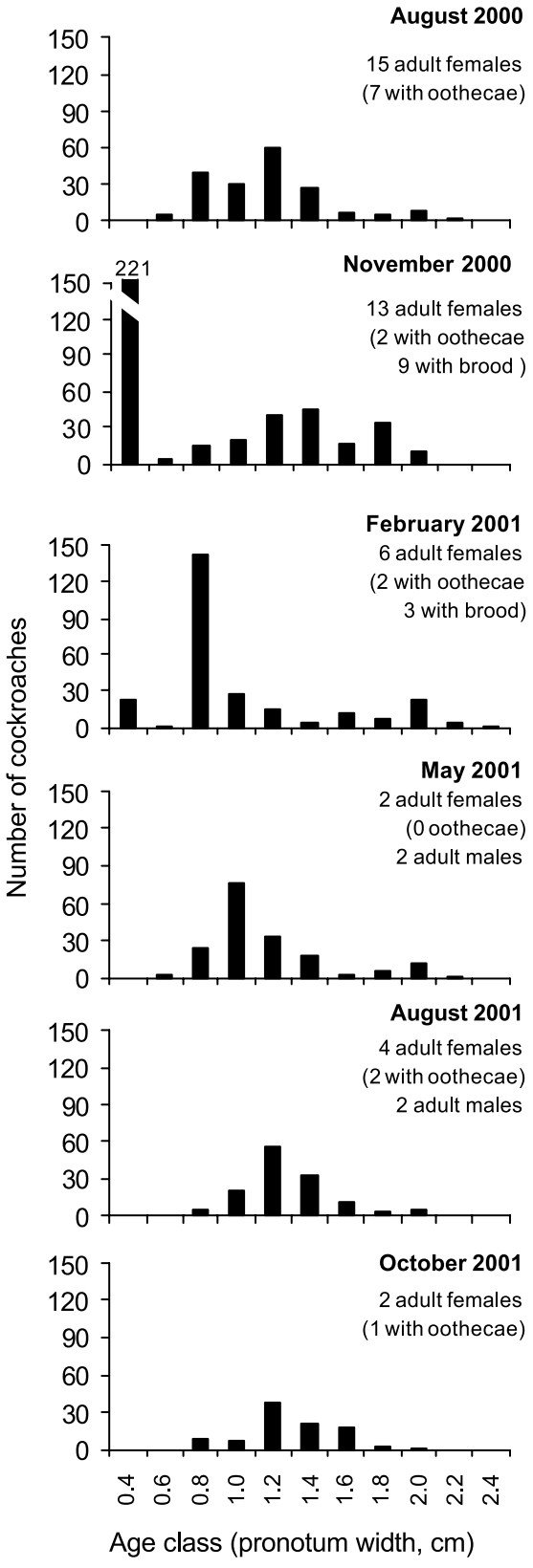
Number of days since brood birth	Number of females remaining with brood	Number of broods dispersing in the period
More than 3	1	
More than 5	2	
More than 8	3	2
More than 14		2
More than 23	1	
Between 2 and 8	1	1
Between 2 and 14	1	
Between 2 and 16	2	2

Table 2. Sex and age class structure of 35 *M. biguttata* colonies observed from August 2000 to October 2001.

	2000		2001			
	Aug.	Nov.	Feb.	May	Aug.	Oct.
Adult males	1					
Adult females	2				1	
Adult males and nymphs					1	
Adult females and nymphs	4	1	2		1	1
Adult females, neonates, and other nymphs		6	1			
Nymphs	27	21	24	26	23	24
Adult males and adult females					1	
Adult females and neonates		1				

Note: Except where noted, nymphs are not neonates.

Fig. 10. Seasonal variation in the age structure of the studied *M. biguttata* population (N = 35 colonies) between August 2000 and October 2001. Neonate nymphs are in the first class (0.4). The numbers of adults, oothecae, and broods refer to all cockroaches sampled (35 colonies and separate voucher specimens).



Two other important aspects of the development of the population can be seen from the analysis of the number of cockroaches in each age class at each of the six sampling dates. The first aspect is the important reduction of population size as cockroaches born in November 2000 pass from one age class to another. The number of cockroaches in October 2001 corresponded to only 24% of the total number registered in November 2000. The second aspect is that the cohort born in November 2000 reached half of the maximum pronotum size (1.2 cm) in August or October of the following year, which indicates that the entire nymphal development takes at least 2 years.

Discussion

According to our sampling, *M. biguttata* appears to be an ubiquitous and very common species in the remnants of the semideciduous Atlantic forest of the north of Espirito Santo, present both in big forest reserves and in very small and very disturbed fragments. *Monastria biguttata* is a forest-dwelling species not usually found in forest gaps or edges, even if it can occur in such habitats. Since adult females are wingless and unable to fly, and cockroaches were never found under the rare dead trunks or in any other kind of habitat searched in the matrix outside the forest fragments, it seems that the populations of this cockroach have been isolated and maintained in these forest fragments for several decades.

The ecological specialization of *M. biguttata* on the underside of dead trunks in the forest understory is completely original and has no equivalent in its group in any Amazonian or central American species or even in related African species (Grandcolas 1993*b*, 1993*c*, 1997*a*, 1998). In Amazonian clades, some taxa also inhabit dead trunks, but they always shelter under loose bark, not necessarily on the underside of the trunks (e.g., genus *Lanxoblatta*, subfamily Zetoborinae). This habitat specialization is thus peculiar to the Atlantic forest region and strongly characterizes *M. biguttata* as belonging to the saprophagous trophic group because this cockroach both feeds and shelters on dead trunks. Dead trunks are not only common and abundant resources in the understory, and conversely rare or absent in non-forested matrixes, but they are also long-lasting (several years for the most short-lived) (R. Pellens and P. Grandcolas, unpublished data) and microclimatically buffered (Nalepa et al. 1997). All these features make dead trunks a very valuable habitat and resource in this region that is characterized by high daily, monthly, and interannual variations in temperature and humidity (Garay et al. 1995; Pellens 2002), which are increased further by forest fragmentation and associated edge effects (Camargo and Kapos 1995; Murcia 1995; Didham et al. 1998*b*; Didham and Lawton 1999).

Monastria biguttata had an aggregated distribution fitting its habitat — the clumps of pieces of dead wood, which were themselves aggregated on the forest floor. *Monastria biguttata* nymphs displayed the most common, gregarious pattern of distribution, with closely aggregated nymphs in the brood spreading late after the brood birth and remaining aggregated until adulthood (Gautier et al. 1988; Grandcolas 1993*b*, 1998; Van Baaren and Deleporte 2001; Van Baaren et al. 2002). *Monastria biguttata* displayed the classical

brood care of gregarious species, care which is assumed to protect nymphs remaining with the female in gregarious Blaberinae (e.g., *Byrsotria fumigata*, Liechti and Bell 1975). This contrasts with solitary cockroaches whose nymphs disperse no later than 1 day after their birth (Grandcolas 1993*b*). Being gregarious, the nymphs of *M. biguttata* were able to stay together on the same clump of dead wood where their brood was born without taking the risk of early or continuous dispersal to the nearest clump of dead wood. Nymphal gregariousness, commonly found in Blaberinae, was already inferred to be an ancestral attribute that facilitated the evolutionary shift from inhabiting leaf litter toward the use of more scattered resources such as clumps of pieces of dead wood used by *M. biguttata* (Grandcolas 1993*c*, 1997*b*, 1998).

According to the developmental and reproductive traits observed in the study, *M. biguttata* displayed the same kind of "submergent behaviour" (Maiorana 1976) observed in *Thanatophyllum akinetum* (Grandcolas, 1991) (subfamily Zetoborinae, Grandcolas 1993*b*) in French Guiana: it was relatively inactive, moved very slowly, fed moderately, and easily displayed a strong antipredator freezing posture. This kind of behaviour is expected to maximize escape from predation, even if it increases the duration of development and does not increase fecundity (Maiorana 1976). These related advantages and disadvantages are again in accordance with the results of our long-term sampling, which showed that *M. biguttata* took more than 2 years to develop. This developmental period is much longer than that in many related Blaberinae cockroaches; for example, cockroaches belonging to the genera *Blaberus*, *Byrsotria*, or *Hyporhicnoda* develop in less than 1 year in the laboratory (Lefeuvre 1969). *Monastria biguttata* presented broods smaller (31.1 nymphs) than those of many Blaberidae (often more than 40 nymphs; Grandcolas and Deleporte 1998). Escape from predation was exemplified by strong freezing postures that permitted *M. biguttata*, like some Zetoborinae cockroaches (Grandcolas and Deleporte 1994), to escape many important predators including army ants, scorpions (Fig. 5), or spiders. Seven months of day and night fieldwork with no observed strong cases of predation showed that the submergent behaviour protected *M. biguttata* from attack by most predators, including those that could possibly be favoured by forest fragmentation (e.g., Margules et al. 1994; Didham et al. 1998*a*; Laurance et al. 2002).

The important cost of such an escape from predation was slower development, which could be either detrimental (e.g., in terms of low intrinsic rates of population increase) or beneficial. For example, developing over more than 1 year permits the cockroach to withstand adverse seasonal climatic conditions (because only one good season could be insufficient to develop and reproduce). This idea is substantiated by the case of tropical wood-eating cockroaches (*Parasphaeria* spp.), which develop slowly because of their nutrient-poor wood diet but are able to spread to areas with cold temperate climates because their development lasts much more than 1 year (Grandcolas 1995*a*; Park et al. 2002). The same was true for *M. biguttata* facing a severe summer season in dry fragments of the semideciduous Atlantic forest. In that case, the submergent behaviour seemed to be beneficial as a conservative bet-hedging strategy (Philippi and Seger 1989), permitting both escape from predation and survival in dry forests and forest fragments. By the same line of reasoning, the prevalence of brood births in the rainy season permitted *M. biguttata* to take advantage of the less dry period for the early development of their young nymphs and thus maximize the survival of their medium-sized broods. The same trend was observed for *Parasphaeria boleiriana* (Grandcolas and Pellens 2002), a related wood-eating cockroach belonging to the subfamily Zetoborinae also studied at the sites of the present work (Grandcolas and Pellens 2002; Pellens et al. 2002).

In conclusion, *M. biguttata* can be an invaluable insect organism for the development of long-term studies in the field because of its large body size, common habitat, and slow-moving behaviour, traits that are uncommon in many insects in tropical forests. In addition, the wide distribution and ubiquity of *M. biguttata* in any kind of forest remnant make possible comparative studies between sites. Study of this species may, therefore, improve understanding of the effects of forest fragmentation on saprophagous insects. This subject could bring very interesting insights to conservation efforts, since saprophagous insects do not seem to be affected by forest fragmentation (Didham et al. 1996, 1998*a*; Holt 1996).

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References

Agarez, F.V. 2002. Contribuição para a gestão de fragmentos florestais com vista à conservação da biodiversidade em Floresta Atlântica de Tabuleiros. Doctoral Science thesis, Programa de Pós-Graduação em Geografia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil.

Brooks, T., and Balmford, A. 1996. Atlantic forest extinctions. Nature (Lond.), **380**: 115.

Camargo, J.L.C., and Kapos, V. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. J. Trop. Ecol. **11**: 205–211.

Chiarello, A.G. 1999. Effects of fragmentation of the Atlantic forest on mammal communities in south-eastern Brazil. Biol. Conserv. **89**: 71–82.

Chiarello, A.G. 2000. Density and population size of mammals in remnants of Brazilian Atlantic forest. Conserv. Biol. **14**: 1649–1657.

Didham, R., and Lawton, J.H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. Biotropica, **31**: 17–30.

Didham, R., Ghazoul, J., Stork, N.E., and Davis, A.J. 1996. Insects in fragmented forests: a functional approach. Trends Ecol. Evol. **11**: 255–259.

Didham, R., Lawton, J.H., Hammond, P.M., and Eggleton, P. 1998*a*. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philos. Trans. R. Soc. Lond. B Biol. Sci. No. 353. pp. 437–451.

Didham, R., Hammond, P.M., Lawton, J.H., Eggleton, P., and Stork, N.E. 1998*b*. Beetles species responses to tropical forest fragmentation. Ecol. Monogr. **68**: 295–323.

Garay, I., Kindel, A., and Jesus, R.M. 1995. Diversity of humus forms in the Atlantic Forest ecosystems (Brazil): the table-land Atlantic forest. Acta Ecol. **16**:553–570.

Gautier, J.Y., Deleporte, P., and Rivault, C. 1988. Relationships between ecology and social behavior in cockroaches. *In* The ecology of social behavior. *Edited by* C.N. Schlobodchikoff. Academic Press, San Diego, Calif. pp. 335–351.

Grandcolas, P. 1993*a*. Monophylie et structure phylogénétique des (Blaberinae + Zetoborinae + Gyninae + Diplopterinae) (Dictyoptera : Blaberidae). Ann. Soc. Entomol. Fr. **29**: 195–222.

Grandcolas, P. 1993*b*. Habitats of solitary and gregarious species in the neotropical Zetoborinae (Insecta, Blattaria). Stud. Neotrop. Fauna Environ. **28**: 179–190.

Grandcolas, P. 1993*c*. The origin of biological diversity in a tropical cockroach lineage: a phylogenetic analysis of habitat choice and biome occupancy. Acta Ecol. **14**: 259–270.

Grandcolas, P. 1994*a*. Les Blattes de la forêt tropicale de Guyane Française: structure du peuplement (Insecta, Dictyoptera, Blattaria). Bull. Soc. Zool. Fr. **119**: 59–67.

Grandcolas, P. 1994*b*. La richesse spécifique des communautés de Blattes du sous-bois en forêt tropicale de Guyane Française. Rev. Ecol. Terre Vie, **49**: 139–150.

Grandcolas, P. 1995*a*. The appearance of xylophagy in cockroaches: two case studies with reference to phylogeny. J. Orthoptera Res. **4**: 177–184.

Grandcolas, P. 1995*b*. Bionomics of a desert cockroach, *Heterogamisca chopardi* Uvarov, 1936 after the spring rainfalls in Saudi Arabia (Insecta, Blattaria, Polyphaginae). J. Arid Environ. **31**: 325–334.

Grandcolas, P. 1997*a*. *Gyna gloriosa*, a scavenger cockroach dependent on driver ants in Gabon. Afr. J. Ecol. **35**: 167–171.

Grandcolas, P. 1997*b*. Is presocial behaviour evolutionarily reversible in cockroaches? Ethol. Ecol. Evol. **9**: 69–76.

Grandcolas, P. 1998. The evolutionary interplay of social behavior, resource use and anti-predator behavior in Zetoborinae + Blaberinae + Gyninae + Diplopterinae cockroaches: a phylogenetic analysis. Cladistics, **14**: 117–127.

Grandcolas, P., and Deleporte, P. 1994. Escape from predation by army ants in *Lanxoblatta* cockroach larvae (Insecta, Blattaria, Zetoborinae). Biotropica, **26**: 469–472.

Grandcolas, P., and Deleporte, P. 1998. Incubation of zigzag-shaped oothecae in some ovoviviparous cockroaches *Gyna capucina* and *G. henrardi* (Blattaria: Blaberidae). Int. J. Insect Morphol. Embryol. **27**: 269–271.

Grandcolas, P., and Pellens, R. 2002. A new species of the cockroach genus *Parasphaeria* (Dictyoptera: Blattaria: Blaberidae) from the Atlantic forest in Brazil. Trans. Am. Entomol. Soc. (Phila.) **128**: 23–29.

Holt, R.D. 1996. Food webs in space: an island biogeographic perspective. *In* Food webs: integration of patterns and dynamics. *Edited by* G.A. Polis and K.O. Winemiller. Chapman & Hall, New York. pp. 313–323.

Klein, B.C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology, **70**: 1715–1725.

Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G., and Sampaio, E. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. **16**: 605–618.

Lefeuvre, J.C. 1969. Recherches sur les organes alaires des Blattaria. Thèse de doctorat, Université de Rennes, Rennes, France.

Liechti, P.M., and Bell, W.J. 1975. Brooding behavior of the Cuban burrowing cockroach *Byrsotria fumigata*. Insectes Soc. **22**: 35–46.

Maiorana, V.C. 1976. Predation, submergent behavior and tropical diversity. Evol. Theory, **1**: 157–177.

Margules, C.R., Milkovits, G.A., and Smith, G.T. 1994. Contrasting effects of habitat fragmentation on the scorpion *Cercophonius squama* and an amphipod. Ecology, **75**: 2033–2042.

Minitab Inc. 2000. MINITAB. Version 13.20 [computer program]. Minitab Inc., State College, Pa.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. **10**: 58–62.

Nalepa, C.A., Byers, G.W., Bandi, C., and Sironi, M. 1997. Description of *Cryptocercus clevelandi* (Dictyoptera: Cryptocercidae) from the Northwestern United States, molecular analysis of bacterial symbionts in its fat body, and notes on biology, distribution and biogeography. Ann. Entomol. Soc. Am. **90**: 416–424.

Park, Y.C., Grandcolas, P., and Choe, J.C. 2002. Colony composition, social behavior and some ecological characteristics of the Korean wood-feeding cockroach (*Cryptocercus kyebangensis*). Zool. Sci. (Tokyo), **19**: 1133–1139.

Pellens, R. 2002. Fragmentação florestal em Mata Atlântica de Tabuleiros: os efeitos da heterogeneidade da paisagem sobre a diversidade de artrópodos edáficos. Doctoral Science thesis, Programa de Pós-Graduação em Geografia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil.

Pellens, R., and Grandcolas, P. 2002. Are successful colonizers necessarily invasive species? The case of the so-called invading parthenogenetic cockroach, *Pycnoscelus surinamensis*, in the Brazilian Atlantic forest. Rev. Ecol. Terre Vie, **57**: 253–261.

Pellens, R., Grandcolas, P., and Silva-Neto, I.D. 2002. A new and independently evolved case of xylophagy and the presence of intestinal flagellates in cockroaches: *Parasphaeria boleiriana* (Dictyoptera, Blaberidae, Zetoborinae) from the remnants of Brazilian Atlantic Forest. Can. J. Zool. **80**: 350–359.

Philippi, T., and Seger, J. 1989. Hedging one's evolutionary bets, revisited. Trends Ecol. Evol. **4**: 41–44.

Princis, K. 1963. Pars 4: Blattariae: Subordo Polyphagoidea: Fam.: Homoeogamiidae, Euthyrrhaphidae, Latindiidae, Anacompsidae, Atticolidae, Attaphilidae. Subordo Blaberoidea: Fam. Blaberidae. *In* Orthopterorum catalogus. *Edited by* M. Beier. Uitgeverij Dr. W. Junk, 's-Gravenhage. pp. 75–172.

Roth, L.M., and Willis, E.R. 1960. The biotic associations of cockroaches. Smithson. Misc. Collect. **141**: 1–470.

Saunders, D.A., Hobbs, R.J., and Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. **5**: 18–32.

Schal, C., and Bell, W.J. 1986. Vertical community structure and resource utilization in neotropical forest cockroaches. Ecol. Entomol. **11**: 411–423.

SOS Mata Atlântica/INPE/ISA. 1998. Atlas da evolução dos remanescentes florestais e ecossistemas associados no domínio da mata atlântica no período de 1990–1995. São Paulo [online]. Available from http://www.sosmatatlantica.org.br/ [accessed March 2003].

Thunberg, C.P. 1826. Blattarum novae species descriptae. Mem. Acad. Sci. Saint-Petersbourg, **10**: 275–293, pl. 14.

Turner, I.M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. J. Appl. Ecol. **33**: 200–209.

Van Baaren, J., and Deleporte, P. 2001. Comparison of gregariousness in larvae and adults of four species of zetoborine cockroaches. Entomol. Exp. Appl. **99**: 113–119.

Van Baaren, J., Deleporte, P., Grandcolas, P., Biquand, V., and Pierre, J.-S. 2002. Measurement for solitariness and gregarism: analysing spacing, attraction and interactions in four species of Zetoborinae (Blattaria). Ethology, **108**: 697–712.

Viana, V.M., Tabanez, A.A.J., and Batista, J.L.F. 1997. Dynamics and restoration of forest fragments in the Brazilian Atlantic moist forest. *In* Tropical forest remnants. Ecology, management, and conservation of fragmented communities. *Edited by* W.F. Laurance and R.O. Bierregaard. Chicago University Press, Chicago. pp. 351–365.

Appendix A

Table A1. Location, geographic coordinates, size and distance to nuclear area (big reserves) of forest fragments sampled in this study, as well as the main land use adjacent to these sites (also sampled).

Study site	Municipality	Geographic coordinates	Forest size (ha)	Distance to the big reserves (km)	Adjacent land use
Linhares Forest Reserve, Mata Alta	Linhares	19°08′32.5″S, 40°03′37″W	46 000*	*	Coffee and *Eucalyptus grandis* plantations
Linhares Forest Reserve, Tower	Linhares	19°09′10.2″S, 40°01′07″W	46 000*	*	Coffee and *Eucalyptus grandis* plantations
Linhares Forest Reserve, Mussununga	Linhares	19°09′47.1″S, 40°01′16.6″W	46 000*	*	Coffee and *Eucalyptus grandis* plantations
Linhares Forest Reserve, Mata Ciliar	Linhares	19°11′94″S, 39°57′24″W	46 000*	*	Coffee and *Eucalyptus grandis* plantations
Sooretama Biological Reserve	Sooretama	19°03′20.7″S, 40°08′49.0″W	46 000*	*	Coffee plantations
São Pedro fragment	Sooretama	19°09′14.9″S, 40°11′34.3″W	2.4	7.1	Coffee plantations
Pasto Novo fragment	Sooretama	19°05′04.2″S, 40°10′39.8″W	66.7	3.5	Coffee plantations
Bioparque Bionativa fragment	Sooretama	19°11′20.2″S, 40°06′54.3″W	32.7	4.0	*Eucalyptus grandis* plantations
MEME fragment	Linhares	19°08′15.8″S, 40°05′04.4″W	30	0.05	Fast-growing tree plantations (*Eucalyptus grandis*, *Joannesia princeps*, *Acacia mangium*, *Hevea brasiliensis*)
José Pinto fragment	Sooretama	19°10′10″S, 40°09′05″W	25	6.0	Coffee plantations
São Mateus fragment 1	76 km from São Mateus	18°47′27.2″S, 39°52′57.6″W	32	50.0	Coffee plantations
São Mateus fragment 2	91 km from São Mateus	18°31′09″S, 39°55′44.1″W	32	65.0	Coffee plantations

*Part of the big forest remnant preserved in the Linhares Forest Reserve, the Sooretama Biological Reserve, and some private properties between the two reserves.