

Long-term effect of forest fragmentation on the Amazonian gekkonid lizards, *Coleodactylus amazonicus* and *Gonatodes humeralis*

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Abstract We investigated the effect of forest fragmentation on the abundance of the gekkonid lizards *Coleodactylus amazonicus* and *Gonatodes humeralis* in fragments associated with Amazonian savanna near Alter do Chão, Pará, Brazil. These fragments have been isolated for at least 150 years and probably more. Abundance of lizards, tree density and food availability were estimated in 1000-m transects in eight sites in continuous forest and 21 forest fragments, ranging in size from 3.6 to 360 ha and distant from ~150–10 000 m from continuous forests. *Coleodactylus amazonicus* was at least an order of magnitude more abundant than *G. humeralis* in continuous forest, and both species were negatively affected by fragmentation. *Coleodactylus amazonicus* was encountered only in continuous forest, the largest fragment, and one fragment adjacent to continuous forest. *Gonatodes humeralis* occurred in the majority of fragments, but was more common in continuous forest, and occurred in lower densities in fragments more distant from continuous forest. The species with lowest recorded densities in continuous forest was the most resistant to fragmentation, contrary to what would be predicted from neutral models, such as island-biogeography theory, possibly because other factors are more important than initial population size in long-term fragmented landscapes.

Key words: Alter do Chão, Amazonian savanna, *Coleodactylus*, fragmentation, *Gonatodes*.

INTRODUCTION

Loss and fragmentation of tropical forests are among the major threats to biodiversity (Laurance *et al.* 1997). Most effects of fragmentation are negative and are related to fragment size (MacArthur & Wilson 1967), habitat quality (Fleishman *et al.* 2002), amount of edges (Murcia 1995), isolation (Gascon *et al.* 1999; Pires *et al.* 2002) and time since isolation (Turner & Corlett 1996). However, fragmentation effects are complex and species respond differently, depending on a range of traits, such as population dynamics and habitat requirements (Fleishman *et al.* 2002; Henle *et al.* 2004).

Island-biogeography theory, which is neutral in the sense that all species have the same requirements (Hubbell 2001), assumes that population size, and hence time to local extinction, is a simple function of island size and isolation from the source area. However,

even for species that are closely related, and that have similar diets, population size is likely to be related to body size (Lawton 1999). Smaller species are expected to maintain higher population densities, and hence be able to persist longer in smaller fragments.

A review of habitat fragmentation experiments indicates a lack of consistency across studies (Saunders *et al.* 1991; Debinski & Holt 2000; Fahrig 2003), and this has been attributed in part to the relatively short time of fragmentation. Most studies on Amazonian forest fragmentation come from the Biological Dynamics of Forest Fragments Project (BDFFP) in Manaus (Laurance *et al.* 1997, 2002), or from other recently fragmented areas (e.g. Michalski & Peres 2005). Studies on fragments that have been isolated for more than a few decades are rare. Short-term dynamics may not predict equilibrium states because forest fragments are subject to abrupt changes in ecosystem functioning in the first years after fragmentation (Laurance *et al.* 2002).

Many studies of fragmentation have been undertaken on mammals and birds, taxa with high metabolic rates that are unlikely to be able to maintain viable populations in the fragments of 1 ha to 100 ha that

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have frequently been studied. Studies on lizard responses to fragmentation are rare (Kitchener *et al.* 1980; Sarre *et al.* 1995; Hadden & Westbrooke 1996; Sumner *et al.* 1999; Driscoll 2004), particularly in the neotropics, where much global tropical deforestation occurs (but see Schlaepfer & Gavin 2001; Gainsbury & Colli 2003; Bell & Donnelly 2006; Urbina-Cardona *et al.* 2006).

We evaluated the effects of the size of fragments, isolation, food availability, and vegetation structure on abundance of two forest-dwelling sphaerodactyline geckos in forest fragments in the Alter do Chão region that have been isolated for over 150 years. *Coleodactylus amazonicus*, has a maximum snout-vent length (SVL) of about 24 mm, and occurs at much higher natural densities in continuous forest than *Gonatodes humeralis* (maximum SVL ~42 mm). Neither species has been reported from savanna vegetation in Amazonia, so savannas probably represent an inhospitable matrix for these species (Ávila-Pires 1995).

METHODS

The study was undertaken near the village of Alter do Chão, Pará, Brazil (2°31'S, 55°00'W). Mean annual temperature is 27.5°C and mean annual rainfall is 1950 mm (Miranda 1993). Rainfall in the area is seasonal, with most rain falling between December and May.

The region at the confluence between the Tapajós and Amazon rivers is characterized by a pronounced dry season and high incidence of fires (Nepstad *et al.* 1999). As a result, most of the region is covered by semideciduous forest and patches of savanna. Embedded in this savanna are numerous forest fragments that vary in size, shape and degree of isolation (Fig. 1). The landscape has been fragmented for at least 150 years (Bates 1892; pers. comm. 2000, from 113-year-old villager) and probably more, but there is evidence that the region was covered by continuous arboreal vegetation about 2000 years ago (Sanaiotti *et al.* 2002).

We sampled eight continuous-forest sites and 21 forest fragments, ranging in size from 3.6 to 360 ha (Table 1). The order of sampling was unrelated to fragment size ($r^2 = 0.042$, $P = 0.371$) and continuous forest sampling was interspersed with fragment sampling. Both continuous forest and fragments have been subject to localized slash and burn agriculture in the past, which may explain the lack of large differences in forest structure between fragments and continuous forest. We did not sample the savanna matrix, because geckos have never been recorded in this habitat, despite intensive lizard surveys in previous studies (e.g. Magnusson *et al.* 1985; Magnusson & Silva 1993; Magnusson 1993; Faria *et al.* 2004).

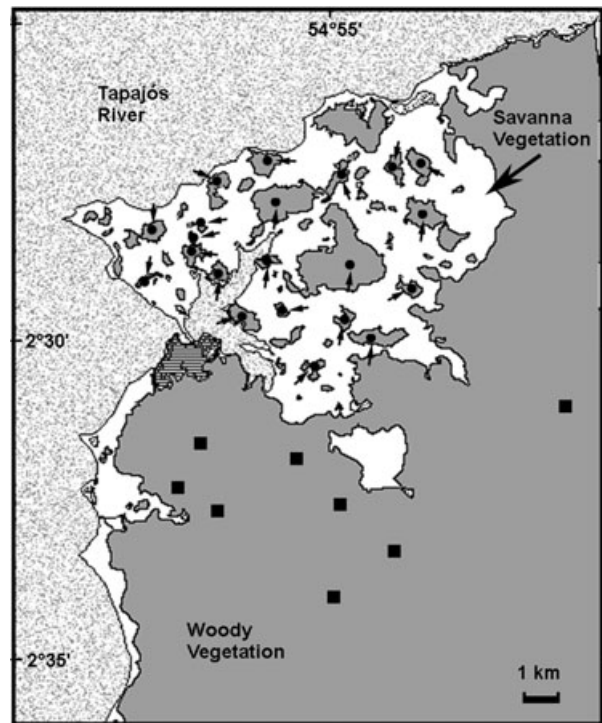


Fig. 1. Map of the study site, showing the vegetation types and the sampling sites (circles = fragments; squares = continuous forest).

We counted lizards at each site and collected data on vegetation structure and food availability. Data were collected in four 250-m long parallel transects, 50 m distant from each other. Data from the four transects at each site were combined for analyses. Transects started at the border and were orientated toward the centre of the fragments, so the ratio of border to interior sampled was similar, independent of the size of the fragment. The 360-ha fragment was sampled at two different locations, so we pooled data for the two sets of four transects and analysed mean values for that fragment.

Fieldwork was conducted from August to December 2001. We used two methods to survey lizards. For *G. humeralis*, two people walked in the centre of the transect searching for individuals in a 6-m wide strip (3 m each side) and up to 3 m height. For *C. amazonicus* the same two people overturned leaf litter in a 1-m wide strip along the transect line. The same people undertook all surveys between 09.00 and 16.00 hours.

Fourteen other species of lizards were encountered during surveys. However, they were not included in the study because they are not forest specialists, their densities were too low for analysis, or they were difficult to count and their counts could have depended on habitat structure as well as population density. The two species of sphaerodactyline geckos were easy to detect

Table 1. Untransformed data on fragment size in ha (size), distance (m) from continuous forest (isolation) (m), density of trees (D_trees), biomass of invertebrates eaten by *Coleodactylus amazonicus* (BI_Ca) and *Gonatodes humeralis* (BI_Gh), and number of *C. amazonicus* (#Ca) and *G. humeralis* (#Gh) counted at each sampling site

Site	Size	Isolation	D_trees	BI_Ca (g)	BI_Gh (g)	# Ca	# Gh
F-1	152	3600	871	0.393	0.538	0	2
F-2	31.5	8714	421	0.366	0.461	0	0
F-3	8.5	9135	1020	0.388	0.555	0	3
F-4	26.3	7779	923	0.053	0.068	0	2
F-5	22.4	7509	780	0.097	0.262	0	7
F-6	3.6	7766	523	0.085	0.128	0	4
F-7	41.3	6502	251	0.213	0.284	0	2
F-8	37.8	3024	216	0.222	0.436	0	9
F-9	46.7	4855	363	0.091	0.198	0	0
F-10	360.4	944.3	205	0.221	0.263	3	5
F-11	10.6	2162	169	0.059	0.073	0	4
F-12	14.7	3400	561	0.266	0.334	0	3
F-13	39.6	2806	341	0.070	0.116	0	13
F-14	21.4	683.9	266	0.144	0.207	0	6
F-15	14.1	647.8	165	0.141	0.260	0	2
F-16	59.7	162.4	151	0.255	0.354	49	21
F-17	23.2	146.1	163	0.324	0.460	0	19
F-18	66.4	1466	111	0.111	0.123	0	45
F-19	28.2	1262	172	0.312	0.521	0	7
F-20	42.8	560.8	147	0.335	0.397	0	4
F-21	7.5	7268	928	0.458	0.577	0	6
CF-1	–	–	143	0.322	0.478	31	12
CF-2	–	–	199	0.336	0.461	13	19
CF-3	–	–	157	0.242	0.417	77	12
CF-4	–	–	257	0.360	1.545	19	10
CF-5	–	–	259	0.127	1.412	22	14
CF-6	–	–	235	0.433	0.724	45	8
CF-7	–	–	204	0.129	0.347	61	2
CF-8	–	–	380	0.364	0.460	79	29

and we know of no differences in habitat associated with fragment size that might affect their probability of detection.

Fragment size and distance from continuous forest were digitized in the CAMRIS program (Ford 1993). Digitizing was based on a Landsat TM5 image, previously georeferenced with IDRISI 32 software (Eastman 1995). As a rough index of distance from probable source populations, we used the minimum distance between forest fragments and continuous forest (edge to edge, straight lines whenever possible, but in some cases curves to avoid large water bodies). Measurements were made in the ARC-VIEW 3.2 program (ESRI 1996). All fragments were entirely surrounded by savanna.

We collected data on forest structure at each site, counting trees in four classes of diameter at breast height (d.b.h.), in four 250 m × 2 m plots (total area = 0.2 ha) that coincided with the transects used to sample lizards. d.b.h. classes were 1.6–9.9 cm, 10–19.9 cm, 20–29.9 cm, and >29.9 cm. We used principal component analysis to construct a rough index of vegetation structure, using as attributes tree densities in the four d.b.h. classes. The first principal component

captured 46.5% of the variance in the original data, however, it was highly correlated with total tree density ($r = 0.85$). Therefore we used tree density as an index of vegetation structure because of its simpler interpretation.

We used invertebrate biomass (wet weight) as an index of food availability for *G. humeralis* and *C. amazonicus*. Invertebrates were sampled in the same transects used for the lizard surveys, with pitfall traps made from 2-L plastic bottles. A 23 × 15 cm opening was cut along one side, and the bottle was buried on its side in the soil, so that the long axis of the opening was parallel to, and flush with the soil. The bottles were filled with a 1% formalin solution mixed with detergent to reduce the surface tension. We placed five traps on each transect, at 50-m intervals (20 traps per site). Traps were installed after lizard surveys, to avoid accidental capture of lizards before surveys. We deployed the traps for 48 h and stored invertebrates collected in 70% alcohol. Wet weight (excess water removed with filter paper) of invertebrates was measured on an electronic balance with 0.0001 g precision. The size and type of prey included in food availability was based on Vitt *et al.* (1997) for *G. humeralis* and Vitt and

Caldwell (1994) and Ramos (1981) for *C. amazonicus*. *Gonatodes humeralis* has been recorded to eat Araneae, Collembola, Coleoptera, Hymenoptera, Isoptera, insect larvae and Mollusca. *C. amazonicus* has been recorded to eat mainly Acari and Collembola.

We used Kruskal–Wallis one-way ANOVA to evaluate the effect of forest condition (fragmented or continuous) on the number of *C. amazonicus* and *G. humeralis*, because of heterogeneous variances. We used hierarchical partitioning (HP) to evaluate the effect of fragment size, isolation, vegetation structure and food availability on the number of *G. humeralis*. HP compares the influence of independent variables over a hierarchy of all possible 2^N models for N predictors, instead of selecting a single best model (MacNally 2000, 2002). The analysis was carried out using the *hier.part* package (Walsh & MacNally 2004) in the statistical software R version 2.5.0. (Venables *et al.* 2007). The significance of independent contributions to variance (I) for the different independent variables was assessed using Z-scores from a comparison between observed I s and I s resulting from 500 permutations on randomized data. Data on patch size and lizard density were transformed ($\text{Log}(X + 1)$) prior to statistical analysis to homogenize variance.

RESULTS

These small delicate geckos are not suitable for large-scale mark-recapture studies, and the high variability among fragments meant that it was more important to sample more fragments than to obtain more precise or accurate estimates for individual fragments. However, the data indicated a large difference in mean density of the two species in continuous forest. *C. amazonicus* was sampled in a 1-m strip, and *G. humeralis*, which sits in exposed positions on the lower trunks of trees, was sampled in a 6-m wide strip. The very large difference in abundance in mean estimated density per 1-m-wide transect (*C. amazonicus* 43.3, SD = 26.3; *G. humeralis* 2.2, SD = 1.3) indicated that *C. amazonicus* was at least an order of magnitude more abundant in continuous forest than *G. humeralis*.

Coleodactylus amazonicus was found in eight continuous forests, usually in high numbers (mean = 43.4), but was found in only two fragments (Table 1, Fig. 2). One fragment had a low density (only three individuals recorded) and we recorded 49 individuals in one fragment close (162 m) to continuous forest. The number of *C. amazonicus* differed significantly between fragments and continuous forest (Mann–Whitney U -test statistic = 163, $P < 0.001$). There was no significant difference between fragments and continuous forests in food availability for *C. amazonicus* (ANOVA: $F_{1,29} = 1.8$, $P = 0.184$) or in density of trees (ANOVA:

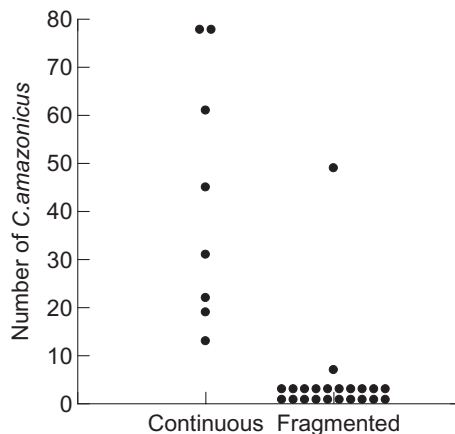


Fig. 2. Number of *Coleodactylus amazonicus* counted in continuous and fragmented forest.

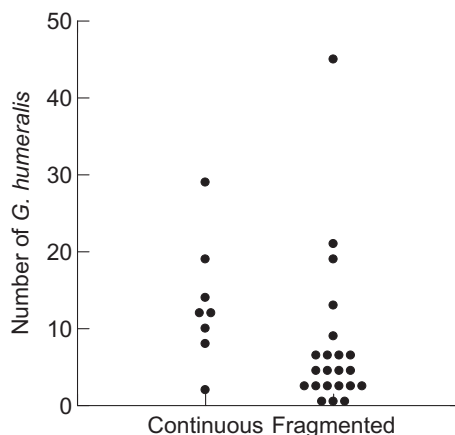


Fig. 3. Number of *Gonatodes humeralis* counted in continuous and fragmented forest.

$F_{1,29} = 2.8$, $P = 0.103$), suggesting that the lower density of *C. amazonicus* in fragments was unrelated to these factors.

The number of *G. humeralis* differed significantly between fragments and continuous forest (Mann–Whitney U -test statistic = 127.5, $P = 0.015$). The mean density of lizards was higher in continuous forest (Table 1), but the species was recorded in most fragments (Fig. 3). Hierarchical partitioning analysis (Fig. 4) indicated that fragment isolation explained most variation in density of *G. humeralis* in fragments (75.8%) and this was the only variable that contributed significantly ($P < 0.05$) to the model (Fig. 5).

DISCUSSION

In our study, both species were negatively affected by fragmentation. Previous studies have reported variable responses of lizards to fragmentation and other distur-

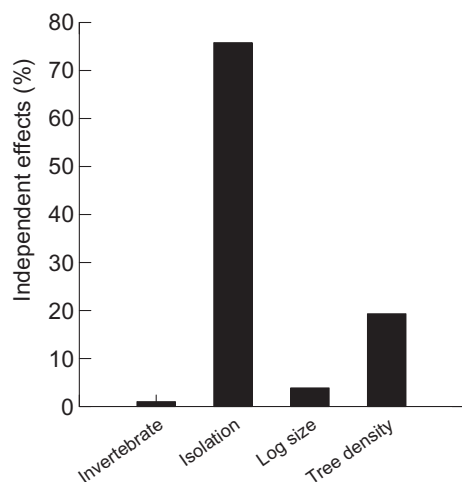


Fig. 4. Percentage contribution of independent effects calculated from hierarchical partitioning for explanatory variables on the number of *Gonatodes humeralis* counted in forest fragments.

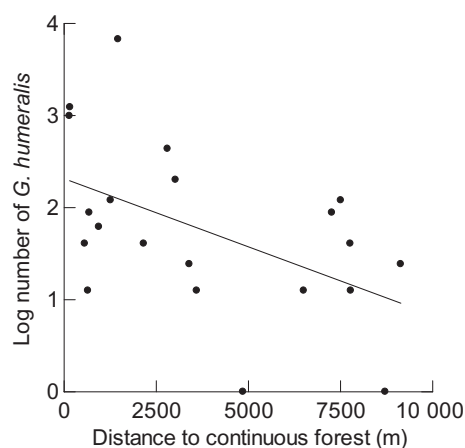


Fig. 5. Linear regression between the abundance of *Gonatodes humeralis* ($\log X + 1$) and distance from continuous forest.

bances, even among closely related taxa (Sarre *et al.* 1995; Vitt *et al.* 1998; Lima *et al.* 2001; Anderson & Burgin 2002; Driscoll 2004). In many cases, the kind of response was related to ecological attributes of the species, such as degree of habitat specialization (Case 1975; Tiebout & Anderson 2001) and dispersal ability (Sarre *et al.* 1995; Driscoll 2004). *Coleodactylus amazonicus* is more specialized than *G. humeralis*, both in microhabitat and diet (Vitt *et al.* 1999), being found primarily in shaded forest and avoiding gaps and edges (Cunha *et al.* 1985; Vitt *et al.* 1998). *Gonatodes humeralis* also inhabits shaded forest but, unlike *C. amazonicus*, is usually common in edge and secondary forest (Cunha *et al.* 1985; Vanzolini 1986; Vitt *et al.* 1997, 2000), and at least one population of this

species thrives around human habitation (Vitt *et al.* 1997). Fragmentation affects forest structure and microclimate (Young & Mitchell 1994; Camargo & Kapos 1995) and increases the amount of edges (Murcia 1995), even to the point that in small patches the forest interior microclimate is completely eliminated (Young & Mitchell 1994). The presence of *C. amazonicus* in one (59.7 ha) patch may be explained by the close proximity of that patch to continuous forest.

Neutral models have had great success in predicting community patterns in forest trees (Hubbell 2001) and neutral island-biogeography models are often used in conservation biology (Ferraz *et al.* 2003). However, habitat models may be more important for understanding organismal responses to deforestation (Chase 2005). Neutral models assume ecological equivalence among individuals or species (Hubbell 2001), and that the probability of extinction is a simple function of population density. In patches where they co-occurred, *C. amazonicus* was generally 12–18 times more abundant than *G. humeralis*, but *C. amazonicus* was almost completely restricted to continuous forest. Some vital resource for *C. amazonicus* is missing in fragments, and this resource does not appear to be directly related to food availability or tree density. Physical factors, such as ground fires that occasionally invade forest patches (Nepstad *et al.* 1999) may restrict this leaf-litter specialist to continuous forest. Furthermore, the sensitivity of *C. amazonicus* to edges and open areas may restrict dispersal through the savanna, and consequently reduce the chance of recolonizing fragments. Whatever the factor involved, it appears that niche models will be necessary to understand the response of this species to deforestation.

In contrast, *G. humeralis* occurred in most fragments, although usually in lower densities than in continuous forest, and was negatively affected by distance from continuous forest. For this species, demographic effects associated with low population sizes and reduced dispersal, are more likely candidates to explain its overall lower density in fragments than the lack of some vital resource. Most fragments are close together at Alter do Chão and the savannas have moderate densities of trees that could act as stepping stones for dispersing individuals. Although the negative effect of distance from continuous forest supports this hypothesis, *G. humeralis* has never been recorded in the savannas, despite intensive lizard surveys in this habitat (Magnusson *et al.* 1985; Magnusson 1993; Magnusson & Silva 1993; Faria *et al.* 2004).

Patterns of species occurrence in forest patches that have been isolated for long periods may be very different from the predictions based on studies of recently fragmented patches. Regions with a long history of human intervention, such as Alter do Chão, may provide insights into fragmentation that cannot be

obtained in other areas (Vasconcelos *et al.* 2006). Small gekkonids are extremely abundant vertebrates in Amazonian forest, and they undoubtedly provide food for many larger vertebrates and invertebrates. Our data indicate that more than 150 years of fragmentation have led to a much reduced abundance for these species in the forest ecosystem.

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