

The effects of fire on behaviour and relative abundance of three lizard species in an Amazonian savanna

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Most savanna areas are affected by fire (San José & Fariñas 1983, Scholes & Archer 1997), and presumably all of the fauna that normally occurs in them have characteristics that allow them to maintain populations despite regular fires. Fires are frequent in Amazonian savannas and the vegetation is fire adapted. The Amazonian savanna at Alter do Chão suffers regular fires that affect vegetation structure (Sanaiotti & Magnusson 1995). Fires pass quickly in this area, the vegetation recovers most of the pre-fire cover within 6 mo, and there appears to be no long-term effect on soil structure. Trees are generally little affected by fires and they retain most of their foliage after the fire passes.

As there are no rock outcrops, and large logs are rare, the only refuges available to terrestrial lizards after the fire are holes in the ground, or small patches of bushes that were not burned because they were surrounded by bare ground. The general biology of lizards in this savanna has been studied extensively (Magnusson 1993, Magnusson *et al.* 1985, 1986, 2001), but nothing is known of their responses to fire.

In the first part of this study, we investigated the small-scale (days to weeks, hundreds of metres) effects of fire on activity in direct sunlight, activity period, and number of individuals of *Cnemidophorus lemniscatus* and *Anolis auratus* encountered in burned and unburned areas. In the second part, we investigated the medium scale (4 mo, kilometres) effects of the fire on relative abundance of *Kentropyx striata*, *Cnemidophorus lemniscatus* and *Anolis auratus*.

Kentropyx striata and *Cnemidophorus lemniscatus* (Teiidae) are diurnal heliotherms that forage actively. *Cnemidophorus lemniscatus* is frequently abundant in open areas next to shrubs on sandy substrates in savannas and river beaches, and uses holes to escape predators,

unfavourable environmental conditions, and when not active (Magnusson *et al.* 1985). *Anolis auratus* (Polychrotidae) forages over relatively small areas (<10 m²) during the activity period, and lizards may be found on the ground or perched on vegetation (Magnusson *et al.* 1985).

The study area is located approximately 40 km southwest of Santarém, Pará, Brazil, (2°31'S, 55°00'W) on the right bank of the Tapajós River. This region is covered by a mosaic of vegetation types, with savanna fragments interdigitated among isolated forest fragments and gallery forest. The savanna in this region is heterogeneous, with the proportions of grasses, sedges, shrubs and trees varying among sites (Magnusson *et al.* 2001). The climate is strongly seasonal. The rainy season lasts from January to June, and the dry season from July to December.

Over 90% of the area of each of 29 savanna plots in the area was burned at least once in the 4 y for which we have data between 1997 and 2001. In 1997, an 'El Niño' year, the dry season was severe between August and December. In this period widespread fires occurred in the region (Nepstad *et al.* 1999), affecting almost 90% of the savanna area. The fires removed over 90% of the grass, sedge and shrub cover in many areas, leaving large areas of exposed soil.

To evaluate short-term effects of fire, data on the activity and the amount of time exposed to direct sunlight by *C. lemniscatus* and *A. auratus* were collected in January 1998, at the beginning of the rainy season, immediately after the fires in the region. Because of the low density of *K. striata*, short-term effects were not studied in this species.

We used 66 transects of 300 m × 5 m in an area with a mosaic of burned and unburned patches. Thirty-three of the transects were in burned patches and 33 in unburned patches. Only one transect was placed in each burned patch and transects in unburned areas were paired with transects in burned areas. Although some transects in

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unburned areas were close (≥ 100 m) to transects in unburned areas, no two transects in burned areas, or in unburned areas, were less than 500 m apart. Most burned patches were separated by several km. Each transect was surveyed only once.

ASF and an assistant walked along the boundaries of the transects searching for lizards in open areas, and kicking grasses and shrubs to flush lizards. Species identity, the time of sighting, and whether the lizard was in the sun or in shade were recorded. At the beginning and end of each transect, temperatures of the air, soil in the shade, and soil exposed to sun were measured. Transects were surveyed at hourly intervals between 07h00 and 18h00. Several transects were surveyed per day, but surveys in burned and unburned transects were alternated.

To estimate the medium-term effects of fire on relative abundance of the three lizard species we collected data in two independent time periods. The first sampling period was between July and October of 1997 (the dry season) before the fires in the region, and the second, after fire, between March and June of 1998 (the rainy season) when the vegetation had regenerated to original composition and stature.

The medium-term study was undertaken in 29 (3.75-ha) plots, distributed as uniformly as possible in the savanna fragments (Magnusson *et al.* 2001). In each plot, four 250-m transect lines separated by 50 m were surveyed, giving a total of 1000 m of transect per plot. Since the sampled area and survey protocol were the same in all plots, we used the number of individuals seen as an index of relative abundance.

Based on preliminary surveys, the lizards were counted only when air temperature was ≥ 30 °C. In each of the 29 plots, ASF and an assistant walked transects using the same methods as described for the short-term study.

To determine the extent of burns that had occurred in the dry season (September to November) of 1997, we noted the presence or absence of burned vegetation at 2-m intervals along survey lines in each plot in March 1998. The presence or absence of burned vegetation in each of 500 point quadrats distributed evenly along the transect lines was used to estimate the proportion of the plot that had burned.

Parametric regression, correlation and Analysis of Variance (ANOVA) were undertaken using the SYSTAT program (Wilkinson 1990). Proportions were arcsine-transformed before analysis. Parametric ANOVA is sensitive to outliers and heterogeneity of variances (Anderson & Legendre 1999, Manly 1997). We tested for heterogeneity of variances using Levene's test before applying ANOVA and, when outliers were present, conducted a Randomization Analysis of Variance (RANOVA) in the RT statistical package, using 1000 permutations of residuals. As time of day may have complex non-linear relationships with activity, it was treated as a categorical variable.

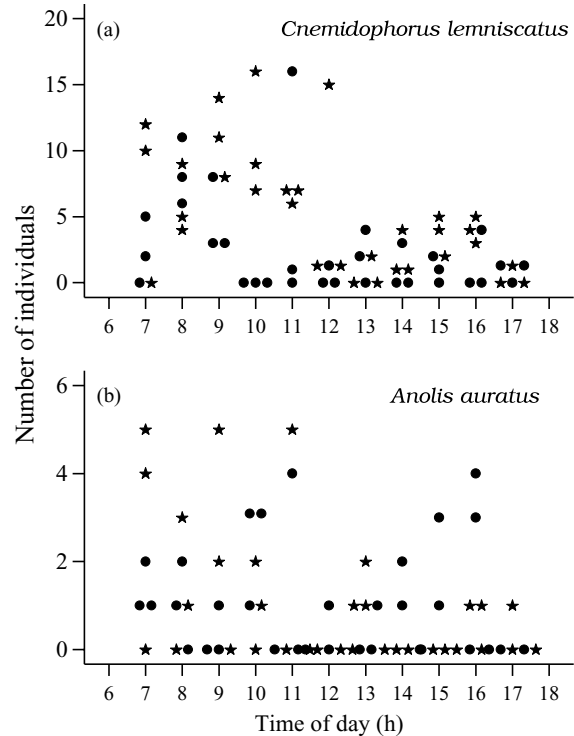


Figure 1. Number of (a) *Cnemidophorus lemniscatus* and (b) *Anolis auratus* counted at different times of day in unburned (stars) and in burned areas (circles).

In the short-term study, more individuals of *C. lemniscatus* were sighted in unburned than in burned places (Figure 1a). However, one survey, undertaken in a burned area on an overcast day, was an extreme outlier (Studentized residual = 3.98). Therefore, we analysed the data with RANOVA. Excluding all data collected on that day (two unburned and one burned plot) and analysing with parametric ANOVA gave qualitatively identical results. The mean number of *C. lemniscatus* sighted differed significantly (RANOVA, $P = 0.004$; ANOVA, $F_{1,63} = 5.4$, $P = 0.02$) between burned (mean = 2.5, SE = 0.6) and unburned (mean = 5.2, SE = 0.8) areas and with time of day (RANOVA, $P = 0.003$). However, there was no interaction between time of day and fire history (RANOVA, $P = 0.11$), indicating that the activity period did not differ between burned and unburned areas.

There was a significant interaction between time of day and fire on the number of active *A. auratus* (ANOVA: $F_{1,62} = 4.0$, $P = 0.05$), indicating that fire affected the activity period of this species in the short term. The simple effect of time of day was significant (ANOVA: $F_{1,62} = 5.4$, $P = 0.023$) and the probability of no effect of fire on the overall density of *A. auratus* was low (ANOVA: $F_{1,62} = 3.7$, $P = 0.06$). More individuals tended to be active in the morning (mean = 1.6, SE = 0.5) in unburned areas than in the burned areas (mean = 1.1, SE = 0.3),

and more individuals were active in the afternoon (mean = 1.0, SE = 0.3) in burned areas than in the unburned (mean = 0.5, SE = 0.2) areas (Figure 1b).

The percentage of *C. lemniscatus* individuals exposed to direct sunlight, did not differ between burned (mean = 55.1, SE = 7.0) and unburned (mean = 46.5, SE = 9.0) areas (ANOVA: $F_{1,41} = 0.08$, $P = 0.77$). However, time of day affected this percentage (ANOVA: $F_{1,41} = 9.8$, $P = 0.003$). There was no interaction between time of day and fire (ANOVA: $F_{1,41} = 0.3$, $P = 0.6$), indicating that the activity period did not differ between burned and unburned areas. More individuals of this species were found in the sun between 07h00 and 11h00 (mean = 66.5, SE = 6.1) than between 12h00 and 17h00 (mean = 34.3, SE = 8.4), in both burned and unburned areas.

For *A. auratus*, the proportion of individuals exposed to the sun did not vary significantly (ANOVA: $F_{1,29} = 0.69$, $P = 0.41$) between burned (mean = 52.7, SE = 11.1) and unburned (mean = 43.5, SE = 10.7) places, but varied with time of day (ANOVA: $F_{1,29} = 7.2$, $P = 0.01$). There was no interaction between time of day and fire (ANOVA $F_{1,29} = 0.45$, $P = 0.50$), indicating that the activity period did not differ between burned and unburned areas. There were more individuals in the sun between 07h00 and 13h00 (mean = 63.3, SE = 8.6) than between 14h00 and 17h00 (mean = 11.6, SE = 7.8).

The differences in numbers of individuals of *A. auratus* and *C. lemniscatus* between burned and unburned areas were not due to changes in extremes of habitat temperature. There were no significant differences in temperatures of the air or soil exposed to the sun between burned and unburned areas (ANOVA: $F_{1,64} = 0.72$, $P = 0.40$ and $F_{1,64} = 0.32$, $P = 0.57$, respectively), though burned areas had less shade.

To estimate the medium-term effects of fire on relative abundance of lizards we recorded the lizards before and after fires in the region. The proportion of the plot burned varied from 0–100%, and 12 plots burned only partially. Plots also had different initial relative abundance of lizards. Multiple regression ($A2 = 1.42 + 0.20A1 - 0.001FI$; $F_{2,26} = 4.1$, $P = 0.02$) relating abundance of *A. auratus* after the fire in 1998 (A2) to pre-fire abundance (A1) and the proportion of the area burnt during the fire (FI) indicated a significant effect of A1 ($P = 0.03$) but not FI ($P = 0.52$). Multiple regression ($C2 = 4.3 + 0.44C1 - 0.002FI$; $F_{2,26} = 18.0$, $P < 0.001$) indicated that the abundance of *C. lemniscatus* (C2) was significantly related to pre-fire densities C1 ($P < 0.001$), but not to extent of fire in the plot ($P = 0.97$). Multiple regression ($K2 = 1.7 - 0.19K1 - 0.001FI$; $F_{2,26} = 1.4$, $P = 0.26$) indicated no significant effect of initial abundance (K1) ($P = 0.13$) or fire ($P = 0.19$) for *K. striata*.

In this study, relative abundances of *C. lemniscatus*, *A. auratus* and *K. striata* were lower at the beginning of the rainy season, after fires had affected many plots, than

in the first survey at the beginning of the dry season, but this decrease occurred in both burned and unburned plots. In a savanna area in the same region, Magnusson (1987) showed that the teiids *C. lemniscatus*, *K. striata* and *A. ameiva* have seasonal reproduction. This is the most probable cause of the seasonal variation in densities, though long-term fluctuations cannot be discounted. Densities of *A. auratus* and *C. lemniscatus* in the second survey were significantly positively related to densities in the first survey, indicating consistent differences between plots. However, there was no effect of the extent of fire in the preceding dry season on densities at the end of the wet season for any of the species. Therefore any changes in apparent density due to fires in the short term had no discernable effect in the medium term.

In this study, the fire affected the three lizard species in different ways. In the short term, just after the fire passed, and before the vegetation regenerated, *C. lemniscatus* had apparently lower densities in burned area, than in unburned areas, indicating that individuals were less active above ground in burned places, they migrated from the burned to unburned areas, or they died. As there was no evidence of an effect of fire on this species in the medium term, after the vegetation regenerated, mortality is the least likely of these hypotheses.

The difference in apparent density of *C. lemniscatus* between burned and unburned places could have occurred because of the reduction in shade availability. However, soil and air temperatures were not significantly different between burned and unburned areas. That the diel activity pattern of this species was not different between burned and unburned areas suggests that inability to thermoregulate was not the cause of differences in behaviour. Air and soil temperatures generally have little influence on body temperatures of *Cnemidophorus* (Magnusson 1993). Trees are common in the savannas and provided patches of shade in areas where the grass and shrub layer had been removed by fire, and this may explain why lizards did not have to change their daily activity patterns in the absence of shade from shrubs and grasses. However, *C. lemniscatus* at Alter do Chão is generally more common in areas with an open-area/shrub interface (Magnusson *et al.* 1986). The reduction in the apparent density may have been because the lizards avoided, or reduced above-ground activity in areas in which the fire had removed shrub cover.

Fire apparently affected some aspects of the behaviour of *A. auratus* in the short term; most individuals were observed in the morning in the unburned areas, but individuals were recorded throughout the day in the burned areas. There was a trend for more lizards to be recorded shortly after fires, before the vegetation had regenerated, and a likely explanation is that the fire removed bushes and grass clumps used as refuges by the lizards in the afternoon, making them more visible during

surveys. Although behaviour may have changed in the short term, there was no evidence of fire-induced changes in population density in the medium term. However, *A. auratus* is dependent on food chains originating in C_4 grasses, and repeated fires could affect the species in the long term by altering the proportions of grasses and C_3 plants in the savanna (Magnusson *et al.* 2001).

Many species of lizards survive the passage of fire, and some species may even prefer recently burned areas (Cunningham *et al.* 2002). *Cnemidophorus lemniscatus* digs holes for shelter. *Kentropyx striata* and *Anolis auratus* normally use the vegetation for refuge, although *K. striata* sometimes use holes dug by other animals. During fires, lizards that live in holes generally have an advantage over lizards that depend on the leaf litter or the vegetation for shelter (Caughley 1985). However, the fire had little effect on either *A. auratus* or *K. striata*, both of which shelter in the vegetation. Fires are so frequent in Amazonian savannas that it is likely that only species little affected by fire occur in them.

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