ECOTROPICA

EFFECT OF REDUCED-IMPACT AND CONVENTIONAL LOGGING TECHNIQUES ON THE LIZARD *KENTROPYX CALCARATA* (TEIIDAE) IN THE EASTERN AMAZON

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Abstract. Conventional logging (CL) in Amazonia is usually done without planning, resulting in a marked increase in canopy gaps, while reduced-impact logging (RIL) techniques can reduce the number of gaps by 50%. The lizard *Kentropyx calcarata* is known to be relatively common in those canopy gaps. We made a comparative evaluation of how the structural damage caused by CL and RIL affects *K. calcarata*. The study was carried out at Cauaxi Ranch, Paragominas district, Pará state, and used data from monthly samples between August and December 2000. We compared ecological and behavioral aspects of lizard populations in RIL (100 ha) and CL (100 ha), with unlogged forest (UF = 100 ha). For each area and sampling period the lizards were observed within five replicate 500-m transects, and time of day, behavior, macrohabitat (forest, gap, border), microhabitat (litter, fallen trunks, branches, leaves) and microclimate (sun, filtered sun, shade) recorded. Forest structure variables (canopy openness, understory density, and litter depth) were recorded at 50-m intervals along each transect. More lizards were observed in CL than in UF or RIL; 88 lizards were collected to record cloacal temperature and perform stomach content analyses. CL contained the largest gaps, exhibited a higher understory density, and a lower litter depth. RIL exhibited intermediate values between UF and CL. Lizards showed longer activity periods in CL, while thermoregulatory and foraging behaviors were similar in UF and RIL, and both were different from CL. The diversity of prey items taken by the lizards captured in RIL and CL were similar, but were distinct from UF, although Orthoptera, Blattodea, and Araneae were the most common prey items in all areas. Lizards captured in CL took significantly more prey items than those captured in UF and RIL. These results suggest that reduced-impact logging maintains a physical structure more similar to intact forests than conventional logging techniques. *Accepted 16 July 2009.*

Keywords: behavior, Brazil, disturbance, heliotherms.

INTRODUCTION

The annual rate of deforestation in the Brazilian Amazon, which does not include logging operations, is approximately 20,000 km² (INPE 2008). If logging activities were included, the extension of impacted land could increase by 50% (Asner *et al.* 2005). The currently used conventional logging practices cause major structural modification in the forest.

Such practices can increase canopy openness by 50% and damage c. 27 trees for each commercial tree harvested in average in some regions (Veríssimo *et al.* 1992). The impact of increased light on microclimate (sun light exposure, heat, humidity) has already been reported elsewhere (Uhl & Vieira 1989, Holdsworth & Uhl 1997).

Better logging practices can reduce negative impacts on forest structure (e.g. Johns *et al.* 1996, Feldpausch *et al.* 2005). Reduced-impact logging

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(RIL) techniques include 100% tree inventory, cutting of lianas, planning of tree-felling direction in order to minimize damage, and narrower roads and skidding trails (see also Feldpausch *et al.* 2006). RIL is being promoted as it is considered less damaging and can result in shorter cycles of exploitation when compared with conventional logging (Valle *et al.* 2006, 2007). However, the effects of RIL for Amazon biodiversity conservation are still poorly known (but see Vitt & Caldwell 2001, Azevedo-Ramos *et al.* 2006, and Peters *et al.* 2006).

Although logged forests conserve more biodiversity than other land uses such as agriculture and pasture (e.g. Dunn 2004), the response of animals to selective logging is variable. For example, selective logging has reduced the abundance of arboreal mammals in Guyana (Ochoa 1997), increased the abundance of frugivorous and nectarivorous bats in the southeastern Amazon (Peters *et al.* 2006), changed the functional diversity and composition of amphibians in Ivory Coast and central Guyana (Ernst *et al.* 2006), reduced the density of one termite species in central Amazon (Lima *et al.* 2000 b), and ant species composition was modified in the eastern Amazon (Kalif *et al.* 2001). The contrasting results from these studies indicate that the intensity of logging, time since logging, forest structure, and the taxa concerned must be considered when evaluating logging impacts (Putz *et al.* 2001, Azevedo-Ramos *et al.* 2005). Moreover, these results suggest it would be useful to adopt a more mechanistic approach for understanding the observed changes to the forest fauna.

This study aims to achieve this by examining the effects of conventional and RIL logging on the lizard *Kentropyx calcarata*, comparing their behavior and ecology in three different areas: an unlogged forest (UF), a conventionally logged forest (CL), and a reduced-impact logged forest (RIL). We specifically compared: (1) activity patterns, (2) thermoregulation and foraging behavior, (3) habitat use, and (4) diet. Since *Kentropyx calcarata* is a heliothermic lizard commonly found in open and sunny places in the forest (Martins 1991, Ávila-Pires 1995, Vitt *et al.* 1997) it should be favored by the large canopy gaps that characterize conventionally logged areas. Previous study at the same study site demonstrated that heliothermic lizards were largely responsible for changes in lizard species composition (Azevedo-Ramos *et al.* 1999). We chose *K. calcarata* to represent this group of lizards because of its abundance, aiming to under-

stand if logging techniques with varying impacts are reflected in different changes in the behavior and ecology of the species.

MATERIALS AND METHODS

Study site. The field work was carried out at Cauaxi ranch (3°45'32''S, 48°10'06''W), a *terra firme* forest located in the district of Paragominas in southeast Pará, Brazil. At this ranch, the Tropical Forest Institute (TFI) established demonstration management plots. Each of the three forest plots (UF, RIL, and CL) was 100 ha in size, intersected by transects 1 m in width every 100 m in N-S direction. Each plot was surrounded by a narrow road (4 m), and we avoided the edges of each plot by restricting the number of transects per plot to five. The maximum distance between plots (CL-UF) was 3 km. From both logged plots 25 m³ of timber per ha were harvested in 1996, one employing conventional logging and the other a reduced-impact technique. This study was conducted in 2000 (four years after logging).

Forest structure. All plots were sampled during 12-day periods in each month, during a 5-month period of the dry season (five field expeditions from August to December). The same transects used for lizard observations (see below) were sampled to record forest structure data (litter depth, understory vegetation density, and canopy openness). These variables were recorded in 2 x 2-m quadrats at 50-m intervals along the 500-m long transects (n = 11 quadrats in each transect, hence 55 quadrats in each plot, Fig. 1). Litter depth was measured with a ruler at two opposing corners of each quadrat. Understory density was indexed by counting how many times live vegetation touched a pole that was 2.5 m in height and 3.5 cm in diameter, placed upright at the four corners of each quadrat. Canopy openness was quantified by a spherical densiometer in the four corners of each quadrat. For each of these measurements, the average score was used to characterize each quadrat, and the average across all representative quadrats was used to characterize each transect.

Activity period, behavior, macrohabitat, microhabitat, and microclimate use by lizards. In order to determine lizard habitat use, activity patterns, thermoregulation, and foraging behaviors, we randomly selected the plot that would be sampled each day. We started at 08:30 h, walked each 500-m transect for one hour and randomly selected the next one. This process of
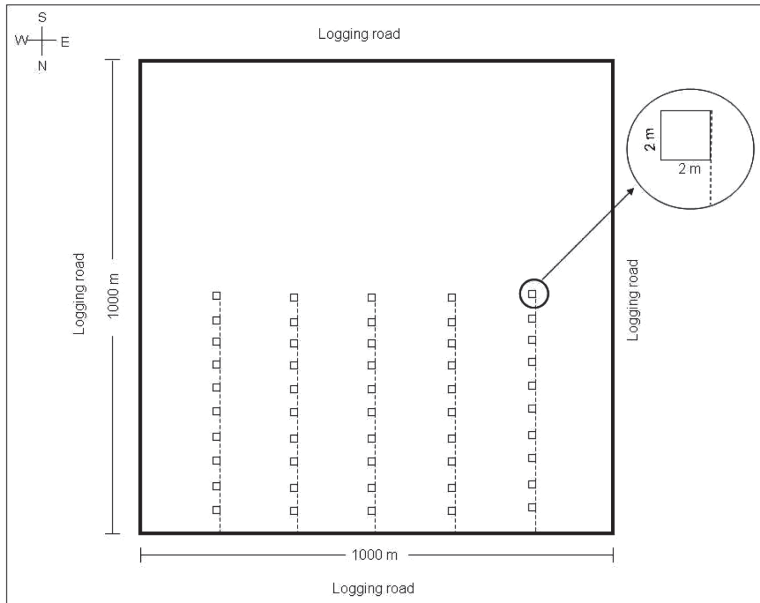
FIG. 1. Sample design of field data collection represented by five 500-m transects and 2 x 2-m quadrats at each 50 m along the transects. The logging roads were surrounded by non-explored forests.

selecting and walking transects continued until dusk, or until no further lizards were sighted along the 500-m transect, when it was assumed that *K. calcarata* activity had ceased. By randomly alternating the sequence in which transects were sampled we avoided any systematic bias in each plot. This also minimized the effects of the presence of one observer in the area, which could represent a possible disturbance to the lizards. Lizard activity in RIL and UF had generally ceased by 14:00 h, and transects were walked only once in these plots. In the CL plot, lizards were active for longer periods, and a few transects were walked more than once in the same day to capture the full diurnal activity range of *K. calcarata*. Total observational effort of the lizard activity period was similar for each area (33 hours for UF, 36 hours for RIL, and 35 hours for CL).

Ambient temperature (°C) and relative humidity (%) were recorded at the beginning, middle, and end of each transect sampled. For each sighting, we recorded the behavior, macro- and microhabitat, and microclimate type in the location where the lizards were first observed. Behavior was divided between (1) foraging and (2) basking. Active foragers were defined as individuals that were moving around and actively searching on and under substrates, whereas basking individuals remained motionless pressed against the substrate in direct or filtered sunlight.

Macrohabitat types included (1) forest, (2) border (i.e. a 3-m transition zone between closed canopy forest and a clearing created by logging), and (3) gap. Microhabitats included (1) leaf litter, (2) felled trunk, (3) fallen branches and (4) leaves. Microclimate included (1) full sun, (2) filtered sun (sunlight that reaches the floor after passing through leaves and branches, resulting in a mosaic of sun and shade), and (3) shade.

Lizard diet and body temperature. After recording behavior, macro- and microhabitat, and microclimate, lizards were killed with an air rifle and cloacal, air, and substrate temperatures were immediately measured using Miller and Weber® rapid-registering mercury thermometers. Lizards were returned to our field laboratory, individually tagged, preserved in 10% formalin temporarily before being transferred to 70% ethanol for permanent storage. All specimens were deposited at the Museu Paraense Emilio Goeldi, Belém, Pará, Brazil. Stomach contents were identified to the level of order, and the length and width of the food items were measured with a MaxCal® electronic caliper. The volume of each prey item was calculated based on the spheroid-ovoid formula (Pianka 1986): $V = 3/4\pi \cdot (\text{length}/2) \cdot (\text{width}/2)^2$. We constructed species accumulation curves to compare the diversity of prey items consumed by the lizards.
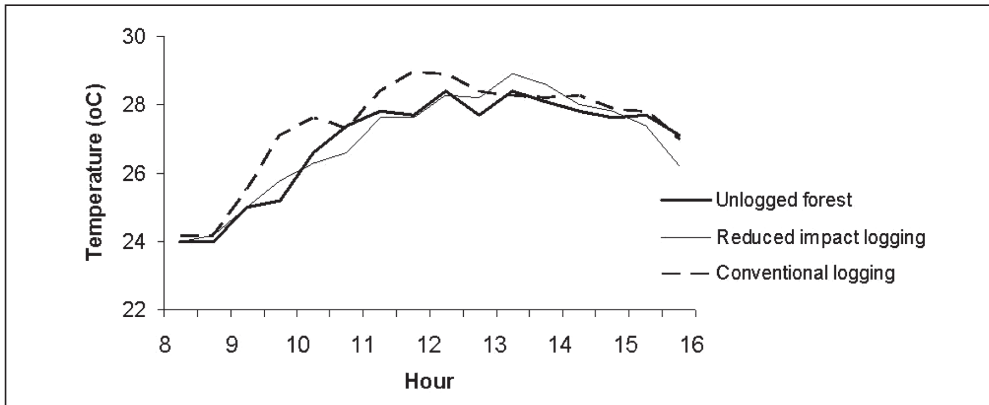
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FIG. 2. Transect temperatures of the three treatments: unlogged forest, reduced impact logging, and conventional logging.

Although we did not mark the lizards we sighted, we consider it unlikely that we sighted the same lizard more than once, or that repeated sightings influenced our data. Because *K. calcarata* is an active forager and walks through the forest during the day in search of prey items (Vitt *et al.* 1997), we kept a >160-m distance between transects to minimize the chance that the same individual could be sighted in another transect in the same day. Repeated sightings over time in the same transect are an inevitable component of transect surveys (*cf.* Buckland *et al.* 2001) and are unlikely to have affected our results.

Data Analysis. We tested the differences in forest structure, air temperature, lizard abundance (the number of lizards sighted in each transect), relative humidity, microhabitat, and the mean prey volume in the stomach of the lizards as well as number of prey items consumed using ANOVA, after checking data for normality, with pairwise comparisons using a Bonferroni post-hoc test for significant results. As Kruskall-Wallis and ANOVA were different for

macrohabitat data, we used the results of the former. The relationship between lizard body temperature and substrate and air temperature were tested using linear regression. For each hour in which lizards were recorded, we separated the observations into activity period and behavior patterns. Within each plot, the difference between the thermoregulatory and foraging behavior of the lizards were tested using *t*-tests after checking data for normality. We used a species accumulation curve for each plot to check the diversity of prey items consumed by the lizards.

RESULTS

Forest structure. As shown in Table 1, there were statistically significant differences in environmental characteristics between the three different plots. Canopy openness was significantly higher in CL than in other plots, and was four times more open than in UF. The RIL had intermediate canopy openness. The understory density reflected the pattern of canopy openness and was three times greater in CL than in

TABLE 1. Differences (mean ± SD) between environmental characteristics in the three areas: unlogged forest (UF), reduced impact logging (RIL), and conventional logging (CL). Different superscript letters mean significant differences in pairwise comparisons (Bonferroni).

Environmental characteristic	UF	RIL	CL	ANOVA
Canopy openness	0.04 ± 0.05[a]	0.10 ± 0.07[b]	0.17 ± 0.17[c]	$F_{2,660} = 81.94$, $P < 0.001$
Understory density	1.4 ± 0.85[a]	2.0 ± 1.17[b]	3.2 ± 1.353[c]	$F_{2,660} = 140.50$, $P < 0.001$
Litter depth	2.9 ± 1.45[a]	3.0 ± 1.78[b]	2.6 ± 1.28[c]	$F_{2,660} = 32.00$, $P < 0.001$

TABLE 2. Differences between macrohabitat use (mean ± SD) by lizards/transect (forest, border, and gap) in the three areas: unlogged forest (UF, *n* = 42), reduced impact logging (RIL, *n* = 45), and conventional logging (CL, *n* = 84). Different superscript letters mean significant differences in pairwise comparisons (Bonferroni).

Macrohabitat	UF	RIL	CL
Forest	1.50 ± 1.51	0.80 ± 0.79[a]	1.00 ± 1.25[a]
Border	1.10 ± 1.11	1.00 ± 1.703[a]	2.20 ± 1.81[a]
Gap	1.60 ± 1.17	2.70 ± 2.00[b]	5.20 ± 3.12[b]
ANOVA	$F_{2,42} = 0.43$, $P > 0.05$	$F_{2,45} = 4.36$, $P < 0.05$	$F_{2,84} = 9.63$, $P < 0.001$

RIL, which had an intermediate understory density (between CL and UF). Litter depth was also significantly different between plots, with RIL once again showing intermediate values (between CL-highest and UF-lowest) (Table 1).

Temperature and humidity. There were no significant differences between air temperatures in the three plots (mean ± SD: 27.8 ± 1.28°C in UF, 27.9 ± 1.07°C in RIL and 27.9 ± 1.15°C in CL; ANOVA: $F_{2,103} = 0.17$, $P > 0.05$). Although air temperature in

CL tended to be higher in the early morning than in the other plots (Fig. 2), this difference was not significant (ANOVA: $F_{2,30} = 0.10$, $P > 0.05$). There was no significant difference in humidity between the three plots (mean ± SD: 85.2 ± 6.61% in UF, 85.0 ± 5.57% in RIL and 86.0 ± 5.66% in CL; ANOVA: $F_{2,103} = 0.26$, $P > 0.05$).

Macrohabitat, microhabitat, microclimate use, and patterns of lizard abundance. Lizards used the forest, border, and gap macrohabitats to a similar extent in
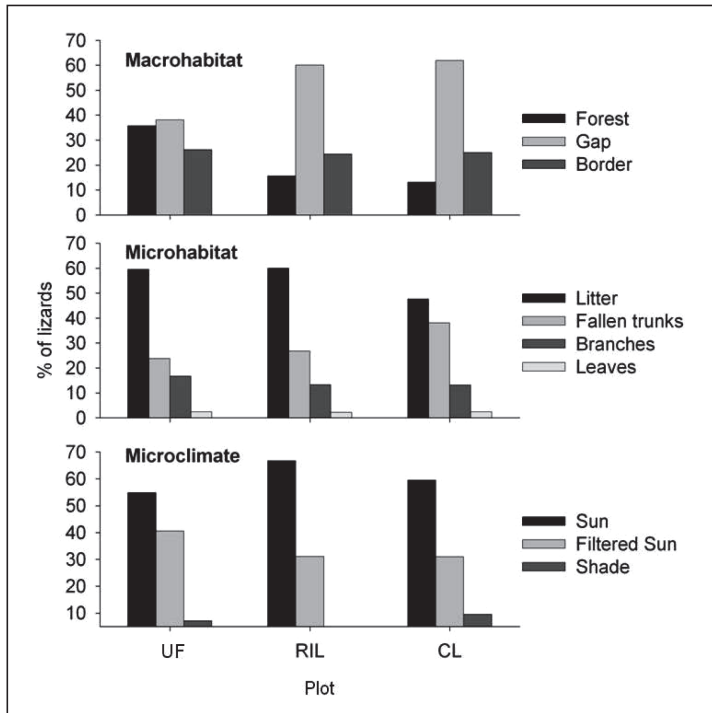

FIG. 3. Macrohabitat, microhabitat, and microclimate percentages of *Kentropyx calcarata* in the three treatments: unlogged forest (UF, *n* = 42), reduced impact logging (RIL, *n* = 45), and conventional logging (CL, *n* = 84).
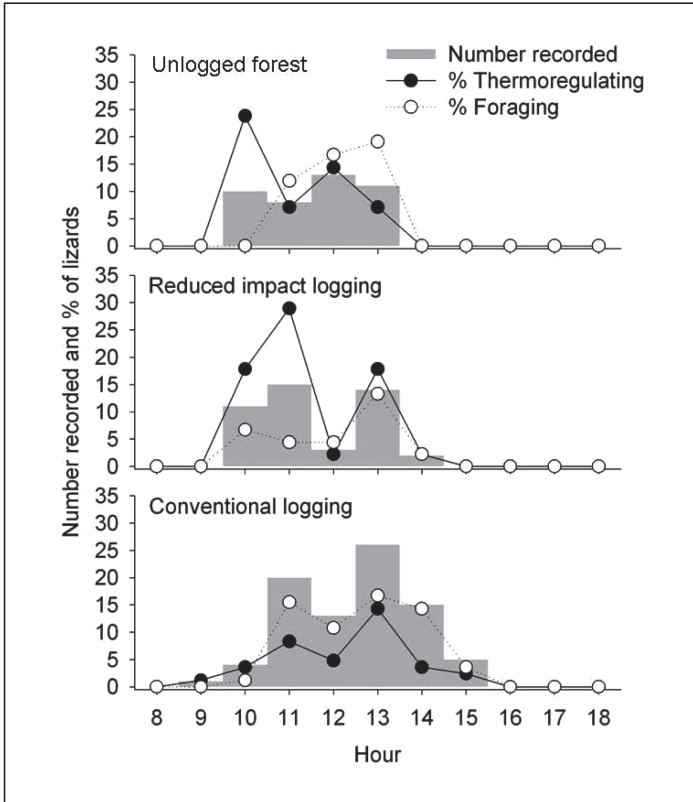
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FIG. 4. Activity period and behavior of *Kentropyx calca-rata* in the three treatments: unlogged forest (*n* = 42), reduced impact logging (*n* = 45), and conventional logging (*n* = 84).

the UF (*n* = 42). In RIL (*n* = 45) and CL (*n* = 84) we recorded more lizards in canopy gaps than in the forest and border macrohabitats (Table 2, Fig. 3). The use of the litter microhabitat in the three plots was similar (Fig. 3). However in CL there was an increase in the number of lizards recorded on fallen trunks (1.00 ± 1.02) when compared with UF (0.48 ± 0.75) and RIL (0.65 ± 1.00), although these differences were not significant (ANOVA: $F_{2,64}$ = 1.93, *P* > 0.05). Across all plots, more lizards were observed in

patches of full sunlight than in other categories of microclimate (filtered sun and shade) (Fig. 3).

The mean abundance of lizards per transect was significantly higher in CL than in UF and RIL (mean ± SD: 2.40 ± 2.53, 1.26 ± 1.62, 1.29 ±1.37 respectively; ANOVA: $F_{2,100}$ = 3.99, *P* < 0.01; post-hoc Bonferroni, *P* < 0.05).

Lizard activity period and behavior. Lizards were active for longer periods in the structurally most dis-

TABLE 3. Differences (mean ± SD) between the number of lizards/transect observed in the two categories of behavior: thermoregulation and foraging in the three treatments: unlogged forest (UF), reduced impact logging (RIL), and conventional logging (CL).

Behavior	UF	RIL	CL
Foraging	1.10 ± 1.29	0.76 ± 1.03	2.08 ± 1.96
Thermoregulation	1.00 ± 0.86	1.88 ± 1.45	1.15 ± 1.29
t-Test	t_{42} = 0.29, *P* > 0.05	t_{45} = 2.59, *P* < 0.05	t_{84} = 2.00, *P* = 0.05

TABLE 4. Number of lizards/transect (median ± kurtosis) observed foraging in the three categories of macrohabitats: forest, border, and gap in the three treatments: unlogged forest (UF, *n* = 42), reduced impact logging (RIL, *n* = 45), and conventional logging (CL, *n* = 84).

Macrohabitat	UF	RIL	CL	Kruskal-Wallis
Forest	1.80 + 1.92	1.00 + 0.71	1.20 + 1.64	H(2) > 0.05
Border	1.00 + 1.00	0.20 + 0.48	3.20 + 1.79	H(2) > 0.05
Gap	1.60 + 0.65	1.40 + 1.14	5.80 + 4.21	H(2) = 0.05

turbed plots (from 08:30 h to 15:30 h in the CL). The shortest activity period was in UF (from 09:30 h to 13:30 h). The activity period in RIL was intermediate (from 09:30 h to 14:30 h; Fig. 4).

The thermoregulation period in the three plots extended throughout the period in which the lizards were active (Fig. 4), indicating that *K. calcarata* alternates periods of thermoregulation with foraging. In the UF the lizard spent the first hour of activity thermoregulating, but there was no significant difference in time allocated to foraging and thermoregulation activity. However, marked behavioral differences were observed in the other two logging plots: there were significantly more lizards thermoregulating in the RIL, while there were significantly more lizards foraging in the CL (Table 3).

In CL we recorded a large number of lizards foraging at the border and in gaps, in contrast to UF and RIL where the lizards predominantly foraged in the forest habitat (Table 4).

Lizard diet. We collected 25 lizards in UF, 25 lizards in RIL and 38 lizards in CL. We believe that the number of lizards killed was not high enough to make a significant difference to population abundances. In the three study plots the prey items most frequently taken were orthopterans, blattodeans, and spiders (Table 5). Lizards captured in logged forests (RIL and CL) preyed on some invertebrate categories that were absent from the diet of lizards in the UF, including dipterans, lepidopterans, hemipterans, isopterans and hymenopterans (Table 5). The species accumulation curve indicated that the diet of lizards in both logged plots was more diverse than that in unlogged forest (Fig. 5). The mean volume of prey items in the lizards' stomachs was not significantly different between plots (mm³ ± SE: 99.69 ± 95.61

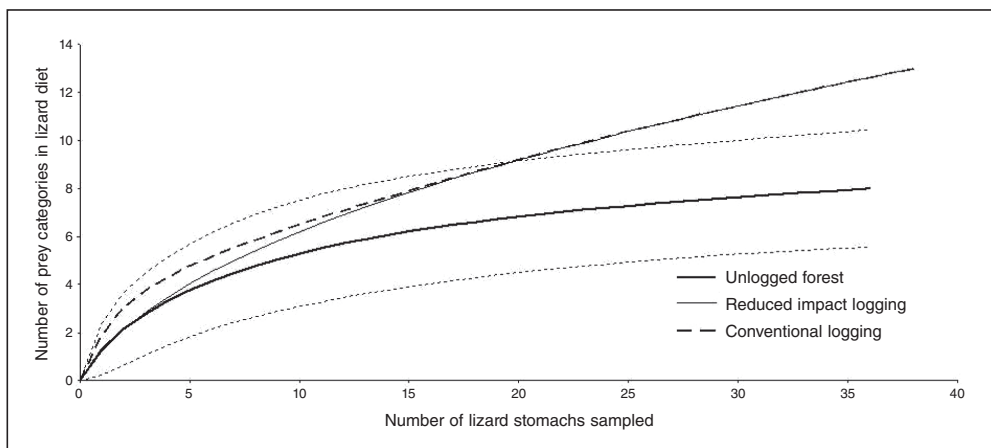FIG. 5. Species accumulation curve of the diet of *Kentropyx calcarata* in the three treatments: unlogged forest (*n* = 36), reduced impact logging (*n* = 36), and conventional logging (*n* = 38).

TABLE 5. Spectrum, frequency, and volume of prey items recorded in stomach contents of *Kentropyx calcarata* captured in unlogged forest (UF, *n* = 25), reduced-impact logging (RIL, *n* = 25), and conventional logging (CL, *n* = 38) areas. P is the number of prey items ingested, L the number of stomachs with that prey category, and V the total volume of each prey category (mm³).

| Prey categories	UF						RIL						CL					
	P	%	L	%	V	%	P	%	L	%	V	%	P	%	L	%	V	%
Orthoptera	35	55.38	22	88	4694.48	54.94	41	56.16	19	41.30	4381.16	51.8	45	36.59	24	31.58	2898.21	26.42
Blattodea	8	10.77	7	14.89	1627.07	19.04	10	13.70	7	15.22	1516.38	17.93	34	27.64	17		5964.75	54.37
Araneae	8	12.31	5	10.64	318.83	3.37	5	6.85	4	8.70	1766.48	20.89	21	17.07	16		994.83	9.07
Mollusca	7	10.77	6	12.77	544.71	6.37	6	8.22	5	10.70	255.15	3.02	5	4.07	4		54.18	0.49
Homoptera	3	4.62	3	6.38	218.69	2.56	2	2.74	2	4.35	151.09	1.79	4	3.25	2		165.44	1.51
Scorpiones	1	3.08	2	4.26	370.87	4.34	-	-	-	-	-	-	1	0.81	1		1.8	0.02
Odonata	1	1.54	1	2.13	232.65	2.72	-	-	-	-	-	-	-	-	-	-	-	-
Diptera	-	-	-	-	-	-	1	1.36	1	2.17	14.55	0.17	3	2.43	3	3,0	22.4	0.20
Hemiptera	-	-	-	-	-	-	1	1.36	1	2.17	32.15	0.38	1	0.81	1	1	0.2	0.002
Isoptera	-	-	-	-	-	-	1	1.36	1	2.17	2.80	0.03	-	-	-	-	-	-
Chilopoda	-	-	-	-	-	-	1	1.36	1	2.17	6.60	0.08	-	-	-	-	-	-
Lepidoptera	-	-	-	-	-	-	1	1.36	1	2.17	139.80	1.65	-	-	-	-	-	-
Isopoda	-	-	-	-	-	-	1	1.36	1	2.17	63.00	0.74	-	-	-	-	-	-
Hymenoptera	-	-	-	-	-	-	1	1.36	1	2.17	5.10	0.06	2	1.63	2	2	70.2	0.64
Coleoptera	-	-	-	-	-	-	-	-	-	-	-	-	1	0.81	1	1	0.1	0.001
Thysanura	-	-	-	-	-	-	-	-	-	-	-	-	1	0.81	1	1	37.2	0.34
Psocoptera	-	-	-	-	-	-	-	-	-	-	-	-	1	0.81	1	1	0.8	0.007
Mantodea	-	-	-	-	-	-	-	-	-	-	-	-	1	0.81	1	1	23.9	0.22
Eruciform larvae	-	-	-	-	-	-	-	-	-	-	-	-	2	1.63	1	1	279.6	2.55
Vermiform larvae	-	-	-	-	-	-	2	2.74	2	4.34	123.08	1.46	-	-	-	-	-	-
Anolis	1	1.54	1	2.13	537.74	6.29	-	-	-	-	-	-	1		1	1	456.8	4.16
Total	65	100.0	47	100.0	8545.04	100.0	73	100.0	46	100.0	8457.36	100.0	123	100.0	76	100.0	10970.5	100.0
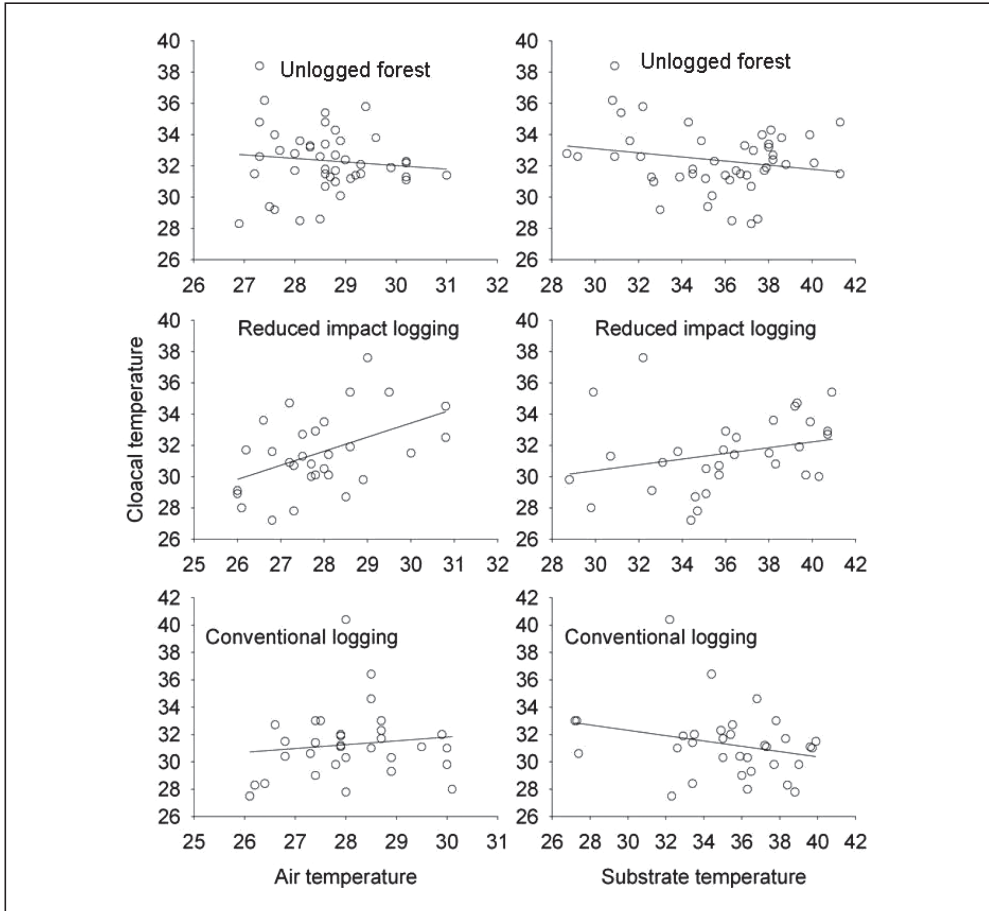
FIG. 6. Relationship between cloacal temperature of *Kentropyx calcarata* and ambient temperatures (air and substrate) in the three treatments: unlogged forest ($n = 36$), reduced impact logging ($n = 36$), and conventional logging ($n = 38$).

in UF, 113.73 ± 138.89 in RIL, 132.12 ± 161.33 in CL; ANOVA: $F_{2,248} = 0.01$, $P > 0.05$). However, the mean number of prey items in the stomachs was significantly different between plots (1.84 ± 1.66 in UF, 2.39 ± 2.17 in RIL, 3.04 ± 2.23 in CL; ANOVA: $F_{2,144} = 3.75$, $P < 0.05$). Pairwise comparisons (Bonferroni post-test) revealed that in CL the lizards consumed more prey items than the lizards of RIL and UF ($P < 0.05$).

Lizards and ambient temperatures. None of the between-plot comparisons of temperature (°C) was significant: lizard cloacal temperature (mean ± SD: 30.8 ± 1.73°C in UF; 31.2 ± 2.06 in RIL 32, 4 ± 2.03°C in CL; ANOVA: $F_{2,51} = 0.07$, $P > 0.05$); substrate temperature (means ± SD: 35.4 ± 3.43°C in UF; 36.4 ± 3.30°C in RIL; 35.7 ± 3.11°C in CL; ANOVA: $F_{2,51} = 0.09$, $P > 0.05$); air temperature (means 28.1 ± 1.13°C in UF; 27.8 ± 1.25°C in RIL; 28.6 ± 0.95°C in CL; ANOVA: $F_{2,51} = 1.43$, $P > 0.05$). However, we did observe some significant effects within habitats. For example, in the RIL there was a positive relationship between cloacal temperature and substrate temperature ($r^2 = 0.47$; $F_{1,23} = 18.8$, $P < 0.05$), and between cloacal temperature and air temperature ($r^2 = 0.28$; $F_{1,23} = 6.89$, $P < 0.05$). However, these positive correlations were not observed in the UF or CL (Fig. 6).

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DISCUSSION

Forest structure. Our data lend support to the evidence suggesting that RIL timber harvests can reduce structural changes within logged forests. For example, in the study plot where logging was not planned (CL) the increase in canopy openness was much greater than that observed in the RIL. This increase was accompanied by an increase in the understory density due to the effect of sunlight on pioneer trees (Webb 1998, Liu & Ashton 1999). The more open environment created by logging can favor heliothermic lizard species (Vitt *et al*. 1998). Furthermore, as lizards represent key predators of many smaller vertebrates and invertebrates, as well as a prey base for large predators such as snakes, birds and mammals, changes in the species-abundance distribution of lizard populations may have marked consequences for system-wide species interactions (Sartorius *et al*. 1999; see also Vitt *et al*. 1998).

Closed canopy forest does not provide sufficiently elevated temperatures for heliothermic species to maintain active behavior (Vitt *et al*. 1997), and the greater structural changes and canopy openness in the CL could have contributed to the higher abundance of *K. calcarata* in this plot. This result is similar to another study in a logged forest near Manaus, central Amazon, where populations of heliothermic lizards such as *Mabuya nigropunctata* increased, and the species *Kentropyx calcarata* and *Ameiva ameiva* showed the same tendency, although not significantly (Lima *et al*. 2000 a). The abundance of individuals in the RIL plot was similar to the UF plot, indicating that the gaps created by RIL operations may not be sufficient to cause a major change in the forest microclimate as perceived by *K. calcarata*. In another study site close to ours, where the size of gaps in a logged area was compared, maximum temperatures were higher in large gaps (>1500 m²) than in medium and small gaps (500-800 m² and 30-100 m² respectively) (Pinto & Azevedo-Ramos unpubl. data). These results reinforce the fact that temperature must be one of the main factors in the increase of heliothermic lizard populations. As large gaps are very common in conventional logging areas, this is likely to be the reason why lizard population in the CL plot in this study was higher. Vitt *et al*. (1998) also compared temperature and habitat use by heliothermic lizards between natural and man-made (similar to RIL) treefall gaps in a lowland rain forest in Acre, Brazil.

Their results showed that man-made treefall gaps were warmer than both natural treefall gaps and the forest interior, and therefore favored heliothermic lizards (including *Kentropyx pelviceps*).

Macrohabitat, microhabitat, and microclimate use by lizards. Lizards in logged plots (RIL and CL) tended to use open areas, whereas lizards of the UF plot used the three macrohabitats (forest, border and gap) to a similar extent. These results suggest that when a greater number of gaps are available this species is more able to actively thermoregulates, thereby conferring advantages in daily energy maintenance (see Vitt *et al*. 1998), and allowing a greater rate of overall energy transfer. In terms of choice of microhabitat and microclimate, *K. calcarata* was most frequently sighted within the litter and in areas directly exposed to the sun in all three study plots, in accordance with the known behavior of other Teiidae lizard species (e.g. Vitt & Colli 1994, Vitt & Zani 1996, Sartorius *et al*. 1999).

Lizards activity period and behavior. Our results indicate that lizards can extend their activity period in open areas with the increased sunlight. For example, the activity period of the lizards in UF (4 h) was similar to the activity period of the lizards in RIL (5 h), but these were both different from the activity period of the lizards in CL (7 h). The results for UF and RIL are similar to the activity periods observed in another non-explored area in Brazilian Amazon (Rondônia), where *K. calcarata* was active for approximately 5 h (Vitt 1991), and in another site in Pará, where the study was carried out eight years after selective logging (therefore resulting in a greater level of forest regeneration), where *K. calcarata* was active for approximately 6 h (Vitt *et al*. 1997). Apparently lizards of the genus *Kentropyx* have a similar pattern of activity in unlogged forests, since *K. pelviceps* and *K. altamazonica* were active for 5 h (Vitt *et al*. 2000) and *K. striata* was active for 4 h (Vitt & Carvalho 1992, 1995). However, as is shown by this study, this active period can increase if there is a greater availability of thermoregulation sites. However, extremely high temperatures can also alter the activity of *K. calcarata*. For example in this study, the lizards in the logged plots (RIL and CL) showed a bimodal activity pattern, and we saw fewer active lizards at exactly the time when the temperature was highest (around 12:00 h). Thus, although a hotter environment can increase the activity period of *K. calcarata*, excessive

temperatures appear to lead to reduced foraging activity.

The behavior of the lizards in the UF plot showed that *K. calcarata* invests in thermoregulation and foraging to a similar extent when there are a limited number of gaps in the forest. In RIL they invested in thermoregulation more than in foraging. On the other hand, logged areas with a greater modification of the forest structure (CL) and a warmer overall microclimate allowed *K. calcarata* to spend more time foraging than thermoregulating. The higher number of observations of lizards investing in thermoregulation more than foraging in UF and RIL plots suggests that they (and probably all heliothermic lizards) need to invest more time in thermoregulation when they are in habitats with little available sunlight (Vitt & Colli 1994). Increased thermoregulation time has costs beyond the obvious reduction in foraging activity, including increased risk of predation (see Huey *et al*. 1974, Huey & Slatkin 1976), since thermoregulating lizards directly exposed to the sunlight become more visible to predators (Vitt & Carvalho 1995).

In this study the lizards in the CL plot used the gaps to forage more, indicating that in opened-up forests *K. calcarata* uses gaps to look for food and not just for basking. This result contradicts the conclusions from numerous other studies (Rand & Humphrey 1968, Hoogmoed 1973, Magnusson & Lima 1984, Gallagher *et al*. 1986, Vitt 1991, Ávila-Pires 1995, Vitt *et al*. 1997), and indicates that *K. calcarata* may be more closely associated with gap environments than was previous believed.

Lizard diet. Across the three logged plots the prey categories most frequently consumed by lizards were Orthoptera, Blattodea, and Araneae. These are also the prey categories most frequently found in the diet of the genus *Kentropyx* by other researchers (e.g. *K. calcarata*, Vitt 1991, Gasnier *et al*. 1994; *K. striatus*, Vitt & Carvalho 1992; *K. pelviceps*, Vitt *et al*. 1995, 2000; *K. altamazonica*, Vitt *et al*. 2001). The greater diversity of items consumed by the lizards in the logged plots (RIL and CL) lead us to develop two non-exclusive hypotheses: (1) logging modifies the arthropod fauna in the litter, and (2) there was a change in lizard behavior (if they are active for longer in the logged plots perhaps they can be more selective of their favored prey types, e.g. those that are more nutritious but require a greater investment to catch). For the first hypothesis we have some evidence that logging modifies the arthropod composition in litter,

since at this same study site Kalif *et al*. (2001) observed changes in ant species composition in the conventional logging plot. Thus, with the exception of some genera that are specialists in catching ants and termites (see Huey *et al*. 1974, Pianka & Parker 1975), which can represent up to three-quarters of the total arthropod biomass in leaf litter (Fittkau & Klinge 1973), the preference for larger prey items is likely associated with the fact that they represent a greater energetic gain (Pough & Andrews 1985).

The greater number of items consumed by lizards in CL may be due to an increase in the overall activity period, allowing the lizards to invest more effort into foraging. The increase in the number of prey items consumed may support a greater energetic reserve, thus contributing to the reproductive success of the species, and the increase in local population size that was observed in this area (Ballinger 1977). In contrast to observations from CL the numbers of *K. calcarata* observed in UF was similar to RIL, possibly because their activity period was constrained by the limited sunlight in both plots, and they have to invest more time in thermoregulation.

Patterns of cloacal, air, and substrate temperatures. Previous research has reported that both overall ambient temperature and body temperature of heliothermic lizards are higher within conventionally logged areas (Vitt *et al*. 1998). More specifically, the body temperature of lizards that live on the forest floor has been related to both air (e.g. *Cnemidophorus depii*, Vitt *et al*. 1993) and substrate temperature (e.g. *Kentropyx pelviceps*, Vitt *et al*. 1995; *Kentropyx calcarata* and *Mabuya nigropunctata*, Vitt *et al*. 1997; *Ameiva festiva*, Vitt & Zani 1996). Despite our finding of a strong correlation between environmental (air and substrate) temperature and lizard body temperature across habitats, this pattern does not hold within habitats. This is not necessarily surprising because (1) the environment within habitats is more homogeneous than between habitats, and (2) we were catching and measuring lizards whose body temperature is a combined function of their activity patterns during the period immediately prior to capture, and is therefore influenced by all the microhabitats that were recently visited within the neighboring area. Hence if they live in a generally warmer or cooler habitat, the temperature of the exact place where an individual is encountered is unlikely to be a sufficient determinant of their body temperature. This suggests that the average environmental tem-

peratures of a habitat are what determine the likely patterns of body temperature in these lizards. Given this, it is surprising that we found a significant relationship between body and environmental temperatures in the RIL. However, this finding could be attributed to the fact that the RIL forest had the greatest range of environmental temperatures in comparison with other plots (temperatures were consistently higher in the CL and consistently lower in the UF), making it the most likely habitat to demonstrate significant within-habitat relationships between lizard temperature and local ambient temperatures.

CONCLUSIONS

Conventional logging benefits the lizards through increasing the number of sites suitable for thermoregulation, thus allowing them to extend their activity period and invest more time in foraging than in thermoregulation. This, presumably, allows them to increase their energetic reserves, enabling *K. calcarata* to colonize the area more efficiently than other non-heliothermic species. At the same time, its population increase could also be related to migration from neighboring sites, since logged areas (especially conventionally logged) are more open and have more gaps. The increase in population size of heliothermic lizards (e.g. Lima *et al.* 2000 a; this study) caused by conventional logging techniques may lead to increased competition pressure on other species, and cascading effects on local biodiversity (Vitt *et al.* 1998). We did not observe these patterns in the plot where the harvest was planned to reduce the impacts on forest structure, indicating that reduced-impact logging techniques can be more effective in preserving the overall forest structure and thermal environment. Overall, our results provide a strong indication that reduced-impact logging techniques can offer a more ecologically sustainable alternative to conventional methods of timber extraction. Nevertheless, a more comprehensive evaluation of the ecological impacts of reduced-impact techniques will require longer-term studies, including research on other groups of native fauna and flora.

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