

## Microhabitat shifts of lizards under different contexts of sympatry: a case study with South American *Liolaemus*

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**Summary.** The Iguanid lizard *Liolaemus tenuis* is shown to be a rock and trunk dweller (apparently preferring perches between 0–30 cm height) in a central Chilean locality where it coexists with a single ground-dwelling congener. In its southern distributional ranges *L. tenuis* is sympatric with another tree-dweller, *L. pictus*. Habitat shift is demonstrated in this latter case by *L. tenuis* concentrating on tree trunks, and at modal heights 30–60 cm. *Liolaemus pictus* occupies lower (apparently more favorable) perches, actively interfering with its congener.

**Key words:** South America – Chile – Iguanidae – *Liolaemus* – Habitat shift – Interference competition

Lizards are known to shift their patterns of habitat use according to the context of sympatry they encounter in different parts of their distributional range. All else being equal, interspecific competition is the process generally thought to underlie habitat shifts among lizards, either of the type exploitation (Schoener 1977; Roughgarden et al. 1983), or interference (Jenssen 1973; Carothers and Jaksic 1984). Although the actual occurrence of the competition phenomenon is most often not rigorously tested (see Schoener 1975; Dunham 1980; Smith 1981; Pacala and Roughgarden 1982; Tinkle 1982; M'Closkey and Baia 1987; for exceptions), detection and documentation of an interesting pattern is a first necessary step to set the stage for experimental testing.

Among *Liolaemus* lizards, habitat has been shown to be partitioned along geographical gradients (Fuentes and Jaksic 1980), along elevational transects (Fuentes and Jaksic 1979), and at the microhabitat level (Fuentes and Cancino 1979; Jaksic and Núñez 1979). Interestingly, vertical partitioning of microhabitat, say, along tree trunks, has not been previously reported. Jaksic et al. (1980) documented that only one among thirteen central Chilean *Liolaemus* was arboricolous, and that trees were occupied exclusively by *L. tenuis*. This species does not seem particularly suited for an arboricolous life: its body proportions are very similar to those of sympatric rock- and ground-dwellers (Jaksic et al. 1980). This fact opens the questions why have not other central Chilean *Liolaemus* occupied trees, or why is *L. tenuis* so restricted to this habitat type in said region.

We detected an interesting situation: in its southern distributional ranges *L. tenuis* becomes sympatric with another arboricolous lizard, *L. pictus*. Here we document a comparative study of habitat occupation by *L. tenuis* in central Chile (solitary on trees) and in southern Chile (sympatric with another tree-dweller), to determine the presence, extent and form of habitat shift in this little known species.

### Material and methods

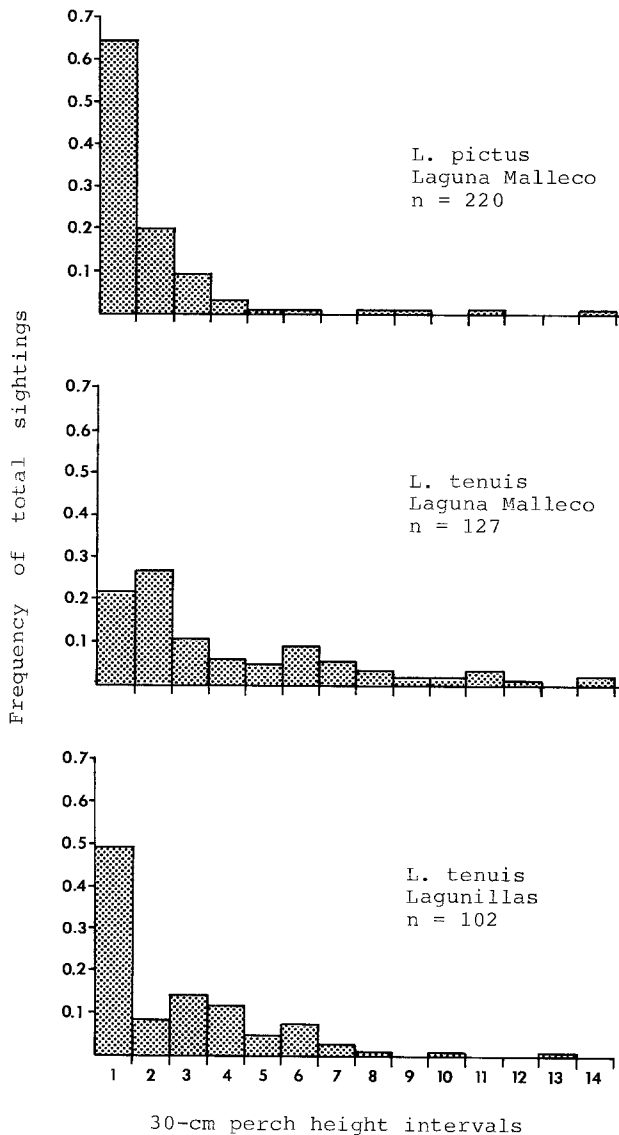
Through February and March 1987 we conducted a concomitant study of habitat use by *L. tenuis* in two localities with a different complement of lizard species. In Lagunillas (33°37' S, 70°18' W), *L. tenuis* coexisted with ground-dwelling *L. lemmiscatus*, whereas in Laguna Malleco (Parque Nacional Tolhuaca, 38°13' S, 71°49' W), it coexisted with tree-dwelling *L. pictus*. The study site in Lagunillas was a ravine populated by the trees *Maytenus boaria*, *Cryptocarya alba*, *Quillaja saponaria* and *Salix chilensis*, and by the shrubs *Escallonia myrtoidea* and *Muehlenbeckia hastulata*. The study site in Laguna Malleco was a premontane forest dominated by the trees *Nothofagus dombeyi*, *Nothofagus obliqua* and *Persea lingue*, with a dense underscrub of *Chusquea quila*.

Habitat use by the lizards was assessed along randomly placed transects. Location of first sighting was recorded only for undisturbed individuals. Perch height of tree-dwelling lizards was taken as the vertical distance between the perch and the ground. Microhabitat niche breadth for each species was computed with Levins' (1968) formula:  $B = 1/\sum p_i^2$ , where  $p_i$  was the proportional use of microhabitat category  $i$ . Four state resources were considered for the horizontal component of microhabitat use: rock, trunk, ground, and shrub, and fourteen states (height intervals of 30 cm) were considered for the vertical component. Levins' index renders values from 1 (only one resource state used) to  $n$  ( $n$  resource states evenly used).

Some lizards were also collected for measurement with callipers (precision 0.1 mm). Measurements taken were: 1) snout-vent length, from tip of snout to anterior lip of the cloaca; 2) length of forelimb, from axilla to tip of the longest finger; 3) length of hindlimb, from groin to tip of the longest toe; 4) tail length, from posterior lip of cloaca to the distal end of the appendage, only if intact. The three latter measurements were standardized by snout-vent length, and t-tests were performed previous angular trans-

**Table 1.** Horizontal microhabitat use (expressed as percentage of total sightings= $n$ ) by *Liolaemus* lizards in two Chilean localities.  $B$  = Horizontal microhabitat niche breadth

Microhabitats	Lagunillas		Laguna Malleco	
	<i>L. tenuis</i>	<i>L. lemniscatus</i>	<i>L. tenuis</i>	<i>L. pictus</i>
Trunk	52.0	0.0	86.6	56.8
Shrub	3.9	1.2	0.8	1.0
Rock	42.1	32.5	4.0	7.7
Ground	2.0	66.3	8.6	34.5
$n$	102	83	127	220
$B$	2.2	1.8	1.3	2.2



**Fig. 1.** Vertical microhabitat use (height of perches on trunks) by *Liolaemus* lizards in two Chilean localities. The ordinate is expressed as proportion of total sightings (same sample sizes as in Table 1); the abscissa is expressed as perch height intervals of 30 cm each. Vertical microhabitat niche breadths are: 2.2 for *L. pictus*; 6.5 and 3.5 for *L. tenuis* in Laguna Malleco and Lagunillas, respectively

formation of the proportions so computed (Sokal and Rohlf 1981).

## Results

Horizontal microhabitat niche breadth was broader for *L. tenuis* in Lagunillas than in Laguna Malleco, where it coexisted with tree-dwelling *L. pictus* (Table 1). Whereas in Lagunillas *L. tenuis* occupied a variety of microhabitat categories, in Laguna Malleco it concentrated on tree trunks. The frequency distributions of perch heights for *L. tenuis* in Lagunillas and Laguna Malleco differed significantly (Smirnov test,  $P < 0.001$ ; Conover 1980). Modal perch height was 0–30 cm in Lagunillas and 30–60 cm in Laguna Malleco (Fig. 1). The displacement of *L. tenuis* toward higher perches in this latter locality is consistent with the presence of tree-dwelling *L. pictus*, whose modal perch height was 0–30 cm.

The two populations of *L. tenuis* compared did not differ in body proportions (Table 2), despite their different patterns of horizontal and vertical microhabitat use. Lack of morphometric differentiation between conspecific *Liolaemus* with different microhabitat use patterns had been previously documented by Núñez et al. (1981) for *L. lemniscatus*. At a broader level, Jaksić et al. (1980) demonstrated that out of 13 central Chilean *Liolaemus*, ten species did not differ in body proportions despite using such disparate microhabitats as rocks, boulders, bare ground, and trees.

## Discussion

The case here reported falls within what Schoener (1974) described as “niche shift” in microhabitat, provided that *L. tenuis* in the absence of another arboricolous lizard expands its microhabitat use to occupy rocks and ground (Lagunillas). But in the presence of another tree-dweller (*L. pictus* in Laguna Malleco), *L. tenuis* restricts its microhabitat use to trees only, and to higher perches.

*Liolaemus tenuis* usually perches head-down, apparently watching for moving prey on tree trunks and on the surrounding ground. Lower perches may facilitate prey detection, and minimize the time needed to capture prey on ground, and thus may be preferred to higher perches. In this context, the displacement of *L. tenuis* toward higher perches in Laguna Malleco, where *L. pictus* uses the lower ones, may be interpreted as a competition-mediated microhabitat displacement. The likely mechanism is interference, as we watched numerous agonistic interactions between *L. tenuis* and *L. pictus* in Laguna Malleco. The victor always was *L. pictus*, an outcome that may be related to its larger body size in comparison to *L. tenuis* ( $63.4 \pm 2$  SE 1.4 mm versus  $53.4 \pm 1.8$  mm, respectively). Given that *L. pictus* dominated the lower perches, this may also explain why *L. tenuis* in Laguna Malleco was more arboreal than its conspecifics in Lagunillas: it simply was not permitted to make excursions to the ground.

It is interesting that Fuentes (1976), working in a physiognomically and climatically similar area to Lagunillas (in Fundo Santa Laura) documented that *L. tenuis* was strictly arboreal, despite no other tree-dwelling lizard was present at that locality. Instead, a higher diversity of ground dwellers was present: four species versus a single one in Lagunillas. Diffuse competition (Pianka 1973) from the

**Table 2.** Body proportions of *L. tenuis* in two Chilean localities. Figures are mean  $\pm$  twice standard error; SVL = snout-vent length (mm); FL/SVL = relative forelimb length (%); HL/SVL = relative hindlimb length (%);  $n_1$  = sample size for preceding measurements; TL/SVL = relative tail length (%);  $n_2$  = sample size for tail length;  $P$  = significance of the difference between proportions as evaluated by means of a t-test

Locality	SVL (mm)	FL/SVL (%)	HL/SVL (%)	$n_1$	TL/SVL (%)	$n_2$
Lagunillas	54.8 $\pm$ 1.0	39.7 $\pm$ 0.6	53.5 $\pm$ 0.8	30	189.0 $\pm$ 9.8	12
Laguna Malleco	53.4 $\pm$ 1.8	40.3 $\pm$ 0.6	54.0 $\pm$ 0.8	41	184.0 $\pm$ 3.2	24
$P$	>0.20	>0.10	>0.40		>0.20	

ground dwellers might be invoked to explain this phenomenon.

Jaksić et al. (1980) proposed that *L. tenuis* was the first (and so far only) central Chilean lizard to invade tree trunks, and that time has since allowed the evolution of its interesting social system (Manzur and Fuentes 1979) but not of an "arboricolous" morphology (say, longer limbs and tail than ground-dwelling congeners). The observations reported here provide an alternative explanation for the lack of morphological differentiation in *L. tenuis*: this species has retained an all-purpose morphology that allows it to use a variety of microhabitats, and the competitive milieu (interference or diffuse competition from congeners) determines how it actually uses the microhabitats available.

The scenario here depicted begs for the application of an experimental protocol such as that used by Tinkle (1982) and M'Closkey and Baia (1987) on other arboricolous lizards. For example, removal of dominant *L. pictus* might result in the expansion of microhabitat use by subordinate *L. tenuis* in Laguna Malleco. This species demonstrates high potential for the exploration of competition effects through field manipulations.

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