Frequency of missing legs in the cave cricket, *Hadenoecus subterraneus*

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ABSTRACT

The cave cricket (*Hadenoecus subterraneus*) is a keystone species in maintaining biological diversity in cave communities in Mammoth Cave National Park. Crickets must leave the cave to forage on nights when conditions are favorable, which puts them at considerable risk of predation. Invertebrates have developed defenses for predation, including autotomy (voluntary loss of a limb). We hypothesize that missing legs are a sign of predation pressure on the crickets, and may be vary in different environments. We used a visual census to record the sex-specific frequency of missing legs among adult cave crickets at eight different cave entrances. We expected males to be missing legs more than females because they must leave the cave refuge to forage more frequently than females; however, we found that males and females were missing legs in equal numbers. The hind leg was missing with greater frequency than other limbs, likely the result of cricket predator avoidance behavior (jumping), which puts the larger hind limb closest to the predator. The frequency of crickets with missing limbs varied among cave entrances from a low of 6.6% to a high of nearly 40%, with abundance varying yearly. In Frozen Niagara, which consistently had a high proportion of crickets missing legs, the percentage missing legs was highest in crickets roosting closer to the entrance (30.8%) than deeper (18.7%) into the cave. The goal of this survey was to study the pattern and implications of limb loss on foraging and predator avoidance.
Key words: Cave cricket, Hadenoecus subterraneus, autotomy, predation, missing limbs

INTRODUCTION

Hadenoecus subterraneus cave crickets are habitual trogloxenes and are often abundant adjacent to cave entrances in the American Southeast (Lavoie *et al.*, 2007). *H. subterraneus* crickets leave the cave to forage on nights when temperature and humidity conditions are favorable, returning to the cave as a daytime refuge. The crickets serve as keystone species by maintaining communities of specialized egg predators (Poulson 2002), establishing a diverse guano community under roosts (Poulson, 1992; Poulson *et al*, 1995), and providing energy for obligate troglobites.

Cave crickets are vulnerable to a wide range of predators. Inside the cave, *H. subterraneus* are preyed upon by spiders, particularly *Meta ovalis*, and cave salamanders, *Eurycea lucifuga*. Outside the cave, crickets are frequently consumed by *Peromyscus leucopus*, white footed mice. Viele and Studier (1990) showed that *Peromyscus* preferentially overlapped feeding ranges around a cave entrance in Mammoth Cave National Park. Helf (2003) found more than four times the number of *P. leucopus* within 50 m of a cave entrance compared to a control area without a cave entrance.

The three sets of paired insect legs, including those of crickets, are attached to the three thoracic segments. Insects walk using a characteristic pattern that is described as an alternating triangle gait. The front and rear legs on one side of the body move together with the middle leg on the other side of the body, creating a supportive triangle. The next step switches sides, maintaining the triangle. The movement

is highly stereotyped and controlled by neurons. In some insects, the need for coordination decreases at faster speeds. The attachment point of the leg at the coxa is very weak, and legs can be easily lost. In many insects, voluntary loss of legs (autotomy) is a strategy used to reduce predation (Bateman and Fleming, 2005). Cave crickets primary response to a threat is to jump. Insects typically adapt rapidly to the loss of one or more legs.

Field crickets (*Gryllus bimaculatus*), with one missing hind limb, experienced a reduced escape speed and decreased jumping ability (Fleming and Bateman, 2007). They were also slower, moved shorter distances, and used more energy than those with hind limbs (Fleming and Bateman, 2007). The same pattern was found among house crickets (*Acheta domestica*), such that they experienced a reduced escape response to actively foraging lizards and mice (Bateman and Fleming, 2006).

We hypothesized that male cave crickets would be missing limbs more frequently than females since males must leave the cave to forage more frequently than do females (Studier *et al*., 1986). We expected the hind leg to be missing most often, since it would be in close proximity to the predator and it is largest. Variability in the proportion of crickets missing legs might be higher in caves with more human impact (visitors) or in caves with sink *vs*. source populations (Helf *et al*., 1995).

METHODS

The study was performed in May 2007 and 2008 at eight different sites (entrances to the Mammoth Cave system and isolated caves) within Mammoth Cave National Park, KY, USA. Cave crickets were censused from the entrance until population density dropped off, which ranged from 20 m to 150 m into the cave. We performed a visual census of adult crickets, noting gender as well as the particular limb lost and associated side of body. Adult crickets have a hind femur length of ≥ 20 mm (Studier *et al*. 1986) with highly sclerotized (brown) legs and ovipositors and do not molt, such that they cannot regenerate a lost leg.

Leg loss was analyzed for gender and limb location (front, middle, and hind limb) differences by Univariate Analysis of Variance (ANOVA) and a *post-hoc* Bonferroni test, respectively.

RESULTS and DISCUSSION

Some individual crickets were missing more than one leg, but the proportion was very variable and averaged 2.2% in 2008 (Tables 1, 2). Crickets missing multiple legs were included in the total reported (Table 1). A *post-hoc* Bonferroni test for position of missing leg, using multiple comparisons showed that the hind leg was missing significantly more than other legs. The dependent variable was the number of crickets missing a leg at each position.

Table 1. Crickets missing legs (May 2007).

Location (cave or entrance)	Sex	Total	Number Intact	Number Missing Legs	Missing Hind Leg	Missing Middle Leg	Missing Front Leg	Percent Missing Legs (M&F)
New Discovery	M	113	91	22	17	1	4	22.6%
	F	126	104	22	17	2	3	
Carmichael	M	59	54	5	5	0	0	6.6%
	F	87	93	4	2	2	0	
Frozen Niagara	M	168	146	22	18	1	2	17.0%
	F	218	184	34	30	1	2	
Floyd Collins Crystal Cave	M	25	19	6	6	0	0	23.6%
	F	45	36	7	6	0	1	
Sophy's Avenue	M	30	25	5	1	1	3	20%
	F	12	10	2	2	0	0	
Violet City	M	12	11	1	1	0	0	20%
	F	17	16	1	1	0	0	
Great Onyx Cave	M	45	42	3	3	0	0	7.4%
	F	47	43	4	4	1	1	
Little Beauty Cave	M	34	27	7	7	0	2	38.9%
	F	41	27	14	14	2	3	
TOTALS		1077	918	159	159	11	21	17.3%

As we censused in 2008, the students noted that there was a higher proportion of "broken crickets" closer to the entrance than deeper into the cave at the Frozen Niagara entrance (Table 2). The proportion of crickets missing legs in Frozen Niagara was greater in the first 10-30 m into the cave (Males 31.9%, Females 30.4%) as compared to crickets deeper into the cave 60-80 m (Males 14.6%, Females 20.4%).

Table 2. Crickets missing multiple legs (May 2008).

Location	Gender	Total	Total Intact	Number Missing Legs	Multiple Missing Legs	Multiples as % of Total Crickets
New Discovery 1	M	48	38	10	0	0%
	F	67	56	11	2	2.9%
New Discovery 2	M	51	40	11	2	3.9%
	F	132	111	21	2	1.5%
Frozen Niagara 1	M	105	82	23	0	0
	F	213	178	35	7	3.3%
Frozen Niagara (Front)	M	62	47	15	0	0
	F	133	102	31	6	4.5%
Frozen Niagara (Deep)	M	47	41	6	1	2.1%
	F	118	98	20	2	1.7%
Violet City	M	53	46	7	1	1.9%
	F	115	108	7	0	0
Carmichael	M	103	91	12	0	0
	F	129	109	20	2	1.5%
	TOTALS	1376	1147	229	25	2.20%

There was no difference in the proportion of males and females missing legs (ANOVA F=0.817). Hind legs were autotomized significantly more often than other legs (F=34.069, p>0.001). The proportion of crickets missing legs in 2007 varied from a low of 6.6% in Carmichael to a high of 38.9% in Little Beauty Cave (Table 1). The proportion of crickets missing legs varied annually (Figure 1), and was consistently higher in 2008. Sites vary by amount of human impact and source vs. sink populations, but there were no consistent patterns to explain this variability. New Discovery was the least visited area, Frozen Niagara the most visited.

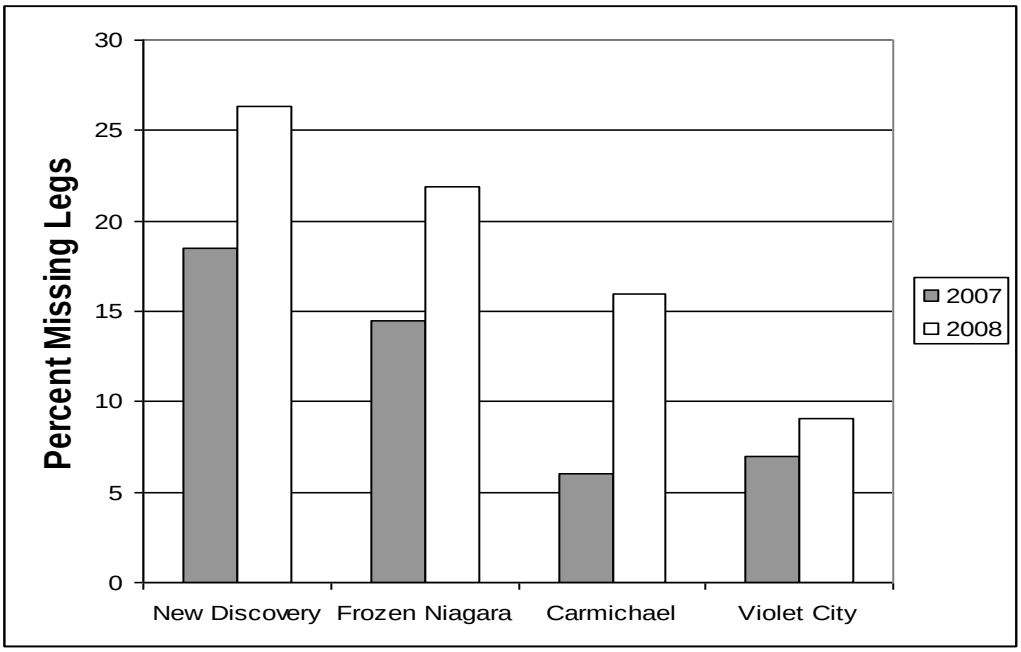

Figure 1. The percent of the censused population of adult crickets missing legs in 2007 and 2008 among four entrances and caves in Mammoth Cave National Park.

Future Research:

Crickets missing hind legs were more likely to be found closer to a cave entrance, suggesting these crickets were less capable of movement or needed to leave the cave more frequently to forage. Crickets with missing legs may not be as effective at foraging. We plan on extending this study by comparing the jumping ability of crickets missing one or both hind legs as compared to intact crickets. A comparison of crop contents will further show how effective the crickets missing legs are at foraging. Future studies will include repeating the census of crickets missing legs from all of the study sites. We will collect and weigh all collected crickets from proximal and distal cave regions to assess population-level foraging effectiveness. Additionally, the effect of missing legs on cricket endurance (see Fleming and Bates, 2007) will be evaluated in future sampling events. We have also noted anecdotally that crickets lose their legs more in winter when handled. The same vulnerability may be true for predation risk in winter.

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