

BIOENERGETICS OF CAMEL CRICKETS (*CEUTHOPHILUS CARLSBADENSIS*, *C. LONGIPES* AND *C. CONICAUDUS*) FROM CARLSBAD CAVERNS NATIONAL PARK, NEW MEXICO

DIANA E. NORTHUP, KATHLEEN H. LAVOIE* and EUGENE H. STUDIER*

Museum of Southwestern Biology, Department of Biology, University of New Mexico, Albuquerque, NM 87131-1091, U.S.A. (Tel. 505-277-5232); *Department of Biology, University of Michigan-Flint, Flint, MI 48502-2186, U.S.A. (Tel. 313-762-3360)

(Received 14 December 1992; accepted 29 January 1993)

Abstract—1. Camel crickets in Carlsbad Caverns National Park exhibit linear long-term weight loss patterns for combined sexes of 1.05 mg/hr for *Ceuthophilus carlsbadensis*, 0.261 mg/hr for *C. conicaudus*, and 0.321 mg/hr for *C. longipes*.

2. From these patterns, maximal foraging intervals for females and males, respectively, of 5.1 and 4.4 days for *C. carlsbadensis*, 4.6 and 5.7 days for *C. longipes*, and 5.0 and 4.2 days for *C. conicaudus* were predicted.

3. Calculated metabolic rates (cal/hr) of 1.04 for *C. carlsbadensis* and 0.52 for *C. longipes* were half that predicted for epigeal species of similar size.

INTRODUCTION

Orthopterans show different levels of adaptation to life in caves. Guano, eggs and carcasses of these cavernicolous crickets may be important energy resources in caves, especially in areas which lack extensive guano inputs from birds or bats (Studier *et al.*, 1986). Carlsbad Cavern in Carlsbad Caverns National Park, Eddy County, New Mexico, is home to extensive cave swallow (*Hirundo fulva*) and Mexican free-tailed bat (*Tadarida brasiliensis*) populations which roost in defined areas in or near the entrance, respectively. Most of the extensive Cavern (approximately 33.8 km of passage) and smaller caves in the Park, including Spider Cave, have limited food resources due to the aridity of the surrounding region and lack of seasonal flooding.

Three species of "cave cricket" or "camel cricket" rhabdophorids inhabit these caves. Spider Cave is predominantly populated by *Ceuthophilus conicaudus* while *C. carlsbadensis* and *C. longipes* occur in Carlsbad Cavern. *C. carlsbadensis* occurs primarily on extensive guano deposits under the bat roosts and in areas visited by humans while *C. longipes* predominates in areas of the cave that are more food-limited. The biology of these three species is described by Bailey (1928), Campbell (1974, 1976) and Northup (1988), and the taxonomy by Caudell (1916, 1924) and Hubbell (1936). Based on morphological characteristics, extremes of cave adaptation are seen with the little adapted *C. carlsbadensis*, living in food-rich areas, and the smaller, more cave-adapted *C. longipes* found in food-poor areas. *C. conicaudus* is also found in food-poor areas, but shows fewer morphological adaptations than *C. longipes*. We present compara-

tive data on the energy budgets and water budgets of these three cavernicolous cricket species to provide information on their energy contribution to a cave ecosystem situated in an arid environment, and compare them to cavernicolous crickets from central Kentucky.

METHODS AND MATERIALS

Adult *C. carlsbadensis* (eight males, eight females) were hand-collected from Bat Cave in Carlsbad Cavern. Adult and juvenile *C. longipes* (eight males, six females) were collected in unbaited pit-fall traps from Sand Passage in Carlsbad Cavern. Adult *C. conicaudus* (seven males, eight females) were hand-collected from the entrance crawlway of Spider Cave.

A long-term weight loss study was set-up in Left Hand Tunnel, Carlsbad Cavern, from 14-18 May 1989 for *C. carlsbadensis* and *C. conicaudus*, and from 15 and 16-19 May 1989 for *C. longipes*. At the start of the study, crickets were weighed to the nearest 0.1 mg with an electronic balance (Fisher Scientific, Model 2100). Crickets were caged individually without food or water in pint canning jars. Each jar had a strip of plastic screencloth on the inside to provide a rough surface for climbing and roosting. Jars were sealed with plastic screencloth held in place by canning rings. The ambient temperature at the study site was the typical constant deep cave temperature of 15.2°C with a minimum relative humidity (r.h.) of 90.2%.

Crickets were weighed twice daily for the first 2 days and once daily for the remaining time. As the study of each group of crickets was terminated,

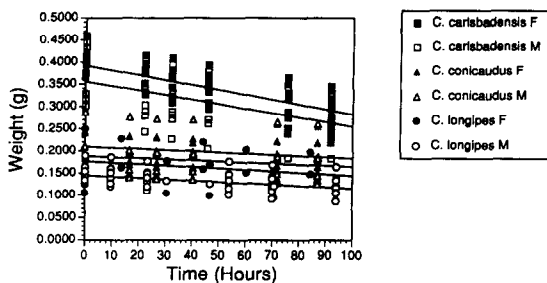


Fig. 1. Weight loss with time for female (F) and male (M) *C. carlsbadensis*, *C. conicaudus* and *C. longipes*. The regression for each is plotted.

crickets were frozen and dissected to separate carcasses, reproductive parts and crops and wet and dry weights were determined. Hind femur lengths (HFL) were measured to the nearest 0.1 mm using calipers. Guano produced during the study was collected, dried and weighed. Caloric density of samples were determined using a Parr oxygen bomb calorimeter. Carcasses were bombed individually while other samples were pooled to obtain a large enough sample. See Studier *et al.* (1986, 1987a,b) for details of the methodology.

RESULTS

Weight loss with time shows a linear decrease for all three cricket species with *C. carlsbadensis* losing weight most rapidly (Fig. 1). Regression equations are also plotted in Fig. 1, while significant and nearly significant regression equations are given in Table 1. Live weight loss with time for both female and male *C. carlsbadensis* is highly significant. Neither female nor male *C. conicaudus* weight loss with time was significant, however, combined male and female weight loss with time is nearly significant. Female *C. longipes* demonstrated a non-significant relationship of weight loss with time while males had a highly significant weight loss with time.

Energetic parameters for the three study species are presented in Table 2. [For calculations used to generate the data in Table 2, see Studier *et al.* (1986, 1987a,b)]. As evidenced by lowest carcass caloric density, *C. carlsbadensis*, from the most predictable food environment, has the least body fat reserves while *C. longipes* from the least predictable food

environment has the largest amount of body fat (Table 3). Female crickets may show lower carcass caloric density than males because of removal of lipid-rich ova from the carcass during analysis. Female *C. longipes* in this study were mostly sub-adults without mature ova, resulting in higher carcass caloric density. Data are incomplete for *C. conicaudus* and *C. longipes* because of small sample size. It is interesting to note that the food available to *C. carlsbadensis* in Bat Cave (bat guano) has nearly identical caloric value to its crop contents.

Water budget component levels are shown in Table 4 for *C. carlsbadensis* and *C. longipes* and compared with two cavernicolous crickets from Mammoth Cave, *Ceuthophilus stygius* and *Hadenoeocus subterraneus*.

Metabolic rates (MR) are compared (Table 5) as weight-specific MR, expected MR and actual MR for *C. carlsbadensis* and *C. longipes*, and compared with the two Mammoth Cave cricket species.

DISCUSSION

Weight loss in the three Carlsbad species of *Ceuthophilus* studied was linear (Fig. 1). Studies of cavernicolous rhabdophorids from Kentucky showed a curvilinear weight loss for *C. stygius* (Studier *et al.*, 1987a) and a linear weight loss for the more cave-adapted *Hadenoeocus subterraneus* (Studier *et al.*, 1986). The Carlsbad cricket with the least cave-adapted phenotype, *C. carlsbadensis*, showed the most rapid weight loss. An unexpected result is the similarity in rate of weight loss for the other two crickets. *C. conicaudus* shows some cave phenotypes in its pale coloration but has robust, relatively short femora in comparison to the more cave-adapted *C. longipes* (Studier and Lavoie, 1993). While *C. conicaudus* is mostly found in the twilight and entrance areas of caves, *C. longipes* is usually encountered deep in caves. Further investigation of the physiology and ecology of *C. conicaudus* is needed.

Weight loss over the short period of time of the study represents emptying of the crop and thus is useful in predicting when crickets should leave the cave to forage to avoid utilizing fat reserves (Studier *et al.*, 1986). The linear weight loss data can be extrapolated to intercept the crop empty live weight of each species to predict maximum foraging intervals. Predicted foraging intervals for females and

Table 1. Regression coefficients for weight loss with time

	a	SE	b	SE	F	d.f.	P	r ²
<i>C. carlsbadensis</i>								
Females	-1.07	±0.16	375	±51	47.1	46	<0.0001	0.506
Males	-1.02	±0.26	355	±57	14.9	46	0.00004	0.245
<i>C. conicaudus</i>								
Combined sexes	-2.61	±0.14	199	±43	3.31	94	0.072	0.034
<i>C. longipes</i>								
Females	—	—	—	—	2.034	26	0.166	0.072
Males	-0.321	±0.098	145	±22	9.05	44	0.0043	0.171

Weight in mg = a (time in hr) + b. SE is the standard error.

Table 2. Energetic parameters for camel crickets, *Ceuthophilus carlsbadensis*, *C. conicaudus* and *C. longipes*

Variable	Units	<i>C. carlsbadensis</i> 92 hr			<i>C. conicaudus</i> 87 hr			<i>C. longipes</i> 71-94 hr		
		<i>x</i>	\pm SE	<i>N</i>	<i>x</i>	\pm SE	<i>N</i>	<i>x</i>	\pm SE	<i>N</i>
HFL	mm	11.47	0.12	16	10.24	0.23	16	12.59	0.16	14
CELW	g	0.2836	0.0092	16	0.1660	0.0093	16	0.1202	0.0050	14
dry (t = 0) fraction	%	29.21	0.37	11	28.20	0.59	2	29.26	0.51	7
dry (t = end) fraction	%	32.51	0.83	16	28.97	0.50	15	33.96	2.41	14
crop wt. loss	mg/hr	1.071	0.163	96	0.261	0.143	96	0.321	0.115	74
avg. dry crop	mg/hr	0.3305		16	0.0746		16	0.1015		14
dry wastes produced	μ g/hr	66.80	7.0	16	15.17	2.34	16	7.76	1.37	14
dry assimil. efficiency	%	79.79		16	79.66		16	92.35		14
cal (in)	cal/hr	1.314		16			0.5511*		14	
cal (out)	cal/hr	0.2700		16			0.0314†		14	
caloric AE	%	79.46		16			94.30		14	
MR	cal/hr	1.044		16			0.520		14	
wt specific MR	cal/g/hr	3.681		16			4.324		14	

*at 5.430 Kcal/g dry; †at 4.042 Kcal/g dry.

Values shown are mean and standard error of the mean. HFL = Hind Femur Length. CELW = crop-empty live weight.

MR = metabolic rate.

males, respectively, of each species are; *C. carlsbadensis* 5.1 and 4.4 days, *C. conicaudus*, 5.0 and 4.2 days; and *C. longipes*, 4.6 and 5.7 days. These predictions are intermediate to those reported by Studier *et al.*, (1986, 1987a) for *C. stygius* (3.0 and 2.3 days) and *H. subterraneus* (11.5 and 9.9 days), although closer to *C. stygius* foraging intervals.

We note essentially no differences in foraging intervals for any of the Carlsbad *Ceuthophilus*, regardless of degree of cave adaptation or the food availability in each environment. *C. carlsbadensis*, the least cave-adapted species living in a food rich environment would not need to forage frequently, but we expected to find longer foraging intervals in the more cave adapted species.

Most of the *C. longipes* studied by Northup (1988) and those in this study had nearly empty crops, except those collected by Northup in Bat Cave, the food-rich bat roost area. Based on trapping data (Northup, unpublished data) these crickets seldom leave the cave to forage, and probably adopt a constant foraging strategy in the deep cave regions of low food availability. Foraging also influences body fat reserves, and *C. longipes* may maintain greater fat stores than the other two species (Table 3) to carry them through periods of starvation or low food input.

A study of *C. conicaudus* in Spider Cave, Carlsbad Caverns National Park (Campbell, 1976), showed that many *C. conicaudus* leave the cave to forage every third night. These crickets do not forage nightly, but do leave to forage before their crops would be completely empty.

Crickets in Carlsbad Caverns National Park may forage more frequently than expected because of poorer foraging opportunities in the arid environment surrounding the caves. The crickets studied by Studier and Lavoie (1990) forage only when epigeal humidity is high, which is less likely with the *Ceuthophilus* crickets in this study, as desert air is rarely saturated, although NPS weather station data from Carlsbad does show that nights of high maximum r.h. (>90%) do occur throughout the year. Alternatively, there may be physical restrictions on how much a crop can expand to accommodate forage. Further studies are required.

Studier *et al.* (1986, 1987) noted that male crickets in Mammoth Cave National Park foraged more frequently than females, since they were unable to consume as much food in a single feeding bout. The need to leave the refuge of the cave to forage more frequently, put males at greater risk of epigeal predation and probably accounted for the typically

Table 3. Caloric contents of carcasses, crop contents, ova and food of *Ceuthophilus carlsbadensis*, *C. conicaudus* and *C. longipes*

Variable	Caloric content (Kcal/gm dry wt)		
	<i>C. carlsbadensis</i>	<i>C. conicaudus</i>	<i>C. longipes</i>
Carcass, M	4.221 \pm 0.202(5)	4.509 \pm 0.222(4)	4.917 \pm 0.067(5)
Carcass, F	3.960 \pm 0.041(5)	4.389 \pm 0.126(4)	5.942 \pm 0.069(3)
Crop contents	3.982(1)	—	—
Mixed wastes	4.042(1)	—	—
Ova	5.838(1)	—	—
Food	3.977 \pm 0.111(10)	—	—

Values shown are mean and standard error of the mean: F = female; M = male.

Number in parentheses represent the number of samples bombed.

Table 4. Water budget components

	<i>H. subterraneus</i>	<i>C. stygius</i>	<i>C. carlsbadensis</i>	<i>C. longipes</i>
N	12	16	16	14
Temperature	13.6 C	13.6 C	15.2 C	15.2 C
CELW	0.408	1.180	0.284	0.120
TBW	0.300	0.836	0.1961	0.0822
Total loss	3.164	2.220	3.560	2.527
Wastes loss	0.927	0.896	0.528	0.140
EWL	2.283	1.351	3.032	2.387
Food gain	2.365	1.825	2.611	1.827
Metabolic gain	0.430	0.421	0.591	0.694

Units for CELW (crop-empty live weight) and TBW (total body water) are in g, while all other values are given in mg/g CELW/hr. Sexes combined in all species. Experiments were done in humid, still air. Data for *H. subterraneus* and *C. stygius* from Studier *et al.* (1987b). EWL = evaporative water loss.

female-skewed sex ratio observed in most Kentucky caves. No clear pattern of male-female foraging times is seen with the Carlsbad *Ceuthophilus*, and data on male:female distributions in the caves is limited and requires further study.

Water budget components from *C. carlsbadensis* and *C. longipes* are given in Table 4 with comparable data from the Kentucky crickets (Studier *et al.*, 1987b). The temperature in both studies was the ambient cave temperature in still, humid air. An inverse relationship between mass and weight specific values is expected for all surface-area to mass comparisons. The relationship is consistent in the Kentucky crickets but not with those from Carlsbad, although comparing data from all four species shows the three smaller species tightly clustered compared to the values for evaporative water loss in the large *C. stygius*. Some differences may be due to attenuation of limbs with increasing cave adaptation and associated effects of surface area.

Cave-adapted organisms are generally expected to have lower metabolic rates than epigeal species (Poulson and White, 1969; Culver, 1982); an expectation which is supported by our study. A comparison of metabolic rates (MR in cal/g/hr) in Table 5 shows the expected increase in weight-specific MR with decreasing size (Peters, 1983). All crickets showed MRs which were lower than expected when compared to predictions for epigeal species (Kayser and Heusner, 1964).

Cavernicolous crickets and their eggs and guano represent an important and relatively abundant food source for other cave organisms. Their importance in the food chain can be predicted based on knowledge

of the biology of the cricket and the caloric value of carcasses, crops, eggs and guano. In terms of weight specific crop calories, Studier *et al.* (1987) found that the more numerous *H. subterraneus* brings more fixed energy into Kentucky caves per foraging bout than does *C. stygius*. Caloric value of guano from both species was low, and markedly so for *H. subterraneus*, but importance to troglobitic species was offset by much greater numbers of *Hadenocetus* and its distribution away from entrance areas into deep cave areas. The only Carlsbad species we have comparable data for is *C. carlsbadensis*. The food for this cricket often consists of bat guano, which has a caloric value of 3.977 ± 0.111 kcal/g dry wt, essentially identical to the crickets' crop contents value of 3.982 kcal/g dry wt. This value is similar to crop values for *H. subterraneus* of 3.658 ± 0.0658 and 4.012 ± 0.159 Kcal/g dry wt for females and males, respectively (Studier *et al.*, 1986) and somewhat less than the 4.47 ± 1.35 Kcal/g dry wt for *C. stygius* females and males (Studier *et al.*, 1987a). The importance of *C. carlsbadensis* as a food resource for troglobites is limited by its occurrence on bat guano and in the highly disturbed area of the Big Room and its rare occurrence deeper into food-poor areas of the cave.

This study of comparative bioenergetics of camel crickets in Carlsbad Caverns National Park has demonstrated that cave-adaptation varies considerably among the three cricket species at Carlsbad and in comparison to the cave and camel crickets from Kentucky studied by Studier *et al.* (1986, 1987a,b) in foraging intervals, metabolic rates, and water budgets. Differences among the three Carlsbad

Table 5. Weight-specific metabolic rate, expected and actual metabolic rate (cal/gm/hr) of cave and camel crickets

Species	Sex	Weight Specific MR (cal/g/hr)	Expected MR (cal/hr)	Actual MR (cal/hr)	Percentage of Expected
<i>C. carlsbadensis</i>	B	3.681	1.8	1.044	58
<i>C. longipes</i>	B	4.324	1.1	0.520	47.3
<i>C. stygius</i>	F	2.612 ± 0.410	3.29	2.61 ± 0.49	79.3
	M	2.636 ± 0.477	3.04	2.64 ± 0.48	86.8
<i>H. subterraneus</i>	B	2.811 ± 0.579	1.93	1.08 ± 0.12	56.0

Expected rates are based on Kayser and Heusner (1964). Values shown are mean and standard error of the mean: F = female; M = male; B = both. Data for *C. stygius* and *H. subterraneus* from Studier *et al.* (1986, 1987a).

species are related to their level of cave adaptation. Further studies of population biology and the effects of temperature and humidity on metabolic rate of the Carlsbad species are indicated.

Acknowledgements—We appreciate assistance in the field by Ken Ingham, William "Ziggy" Ziegler, Ann Studier, Steve Sevick, Dennis Viele and David Barkley. We thank the Cave Research Foundation for use of their field buildings and National Park Service personnel at Carlsbad Caverns National Park, especially Ronal Kerbo and David Ek, for providing access to the study sites.

REFERENCES

- Bailey V. (1928) Animal life of the Carlsbad Cavern. *Monogr. Am. Soc. Mamm. No. 3*. Williams and Wilkins Co., Baltimore, MD.
- Campbell G. D. (1974) Activity rhythm of the cave cricket, *Ceuthophilus conicaudus* Hubbell. *Cave Research Foundation 1974 Annual Report*, p. 49.
- Campbell G. D. (1976) Activity rhythm in the cave cricket, *Ceuthophilus conicaudus* Hubbell. *Am. Midl. Nat.* **96**, 350–366.
- Caudell A. N. (1916) The genera of the tettiginid insects of the subfamily Rhabdiphorinae found in America north of Mexico. *Proc. U.S. Nat. Mus.* **49**, 655–690.
- Caudell A. N. (1924) Two new species of *Ceuthophilus* from the Carlsbad Cave in New Mexico (Orthoptera). *Proc. Entl. Soc. Wash.* **26**, 217–221.
- Culver D. C. (1982) *Cave Life; Evolution and Ecology*. Vol. IX. Harvard University Press, Cambridge, MA.
- Hubbell T. H. (1936) A monographic revision of the genus *Ceuthophilus* (Orthoptera, Gryllacrididae, Rhabdiphorinae). *Univ. Florida Publ. Biol.* **2**, University of Florida, Gainesville, FL.
- Kayser C. and A. Heusner A. (1964) Etude comparative du metabolisme energetique dans la serie animale. *J. Physiol.*, Paris **56**, 489–524.
- Northup D. E. (1988) Community structure of the arthropods of Carlsbad Cavern emphasizing Rhabdiphoridae of the genus *Ceuthophilus*. Unpublished Masters Thesis, Department of Biology, University of New Mexico, Albuquerque, NM.
- Peters R. H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge.
- Poulson T. L. and White W. B. (1969) The cave environment. *Science* **165**, 971–981.
- Studier E. H. and Lavoie K. H. (1990) Biology of cave crickets, *Hadenocerus subterraneus*, and camel crickets, *Ceuthophilus stygius* (Insecta: Orthoptera): metabolism and water economies related to size and temperature. *Comp. Biochem. Physiol.* **95A**, 157–161.
- Studier E. H. and Lavoie K. H. (1993) Attenuation and annual femur length: mass relationships in cavernicolous crickets (Insecta: Orthoptera). *J. Cave and Karst Sci. (Bull. natn. Speleol. Soc.)* (in press).
- Studier E. H., Lavoie K. H., Wares W. D. II and Linn J. A.-M. (1986) Bioenergetics of the cave cricket, *Hadenocerus subterraneus*. *Comp. Biochem. Physiol.* **84A**, 431–436.
- Studier E. H., Lavoie K. H., Wares W. D. II and Linn J. A.-M. (1987a) Bioenergetics of the camel cricket, *Ceuthophilus stygius*. *Comp. Biochem. Physiol.* **86A**, 289–293.
- Studier E. H., Wares W. D. II, Lavoie K. H. and Linn J. A.-M. (1987b) Water budgets of cave crickets, *Hadenocerus subterraneus* and camel crickets, *Ceuthophilus stygius*. *Comp. Biochem. Physiol.* **86A**, 295–300.