BIOLOGY OF CAVE CRICKETS, *HADENOECUS SUBTERRANEUS*, AND CAMEL CRICKETS, *CEUTHOPHILUS STYGIUS* (INSECTA: ORTHOPTERA): METABOLISM AND WATER ECONOMIES RELATED TO SIZE AND TEMPERATURE

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Abstract—1. Metabolic rate (MR) and water budget (WB) components of cave and camel crickets are directly related to size and temperature.
2. MR increases most rapidly with size for insects in general followed by cave crickets (females > males), and lastly, camel crickets (no sex differences).
3. Metabolic thermal sensitivity of cave crickets (males > females) is much greater than camel crickets.
4. WB components parallel MR relations.

INTRODUCTION

In karsted regions of Kentucky, cave crickets (*Hadenoecus subterraneus*) and camel crickets (*Ceuthophilus stygius*) represent the bulk of biomass present in many caves and through their wastes, eggs and carcasses represent the most dependable source of fixed energy for troglobites (Barr, 1967; Barr and Kuehne, 1971; Richards, 1971; Harris, 1973). With the exception of their taxonomic relations and geographic distributions (Hubbell, 1936; Hubbell and Norton, 1978), few aspects of the biology of these trogloxenes have been significantly investigated. The interrelations of *H. subterraneus* and their egg predator *Neaphenops tellkampfii*, have been studied extensively (Poulson, 1975; Norton *et al.*, 1975; Kane and Poulson, 1976). Our general interest in the physiological ecology of cavernicolous organisms, coupled with the biological importance of these insects to cave ecosystems, has stimulated our continuing examination of these insects (Studier *et al.*, 1986, 1987a, 1987b, 1989). This study reports metabolic rates and water budget components in these two species as functions of size and temperature.

MATERIALS AND METHODS

Metabolic rates (MR) and water budget (WB) components were calculated essentially as previously described (Studier *et al.*, 1986, 1987a, b). The relations of these variables to size in *C. stygius* (65 crickets tested) were done on 25–30 July 1986, 19–24 October 1986, 22–24 February 1987 and 26–30 April 1987, with individuals collected from entrance areas of Great Onyx, Frozen Niagara, and Crystal Caves and tested in Crystal Cave or Marion Avenue of Mammoth Cave. Relations of MR and WB components to size in *H. subterraneus* (62 crickets) were studied on 22–24 February 1987 with crickets collected from the entrance of Frozen Niagara and Sophys Avenue of Mammoth Cave and tested in Marion Avenue of Mammoth Cave. Ambient temperature (T_a) for all size studies was normal cave T_a of 13.0 ± 0.5°C. The only variations from previously described methods were that small size crickets were caged in pint

rather than quart jars and successive weights of crickets studied in Marion Avenue were taken with an electronic balance accurate to 0.1 mg (Fisher Scientific, Model 2100).

The relations of T_a to MR and WB components in 48 *C. stygius* were studied from 8–11 July 1987 on individuals collected from the entrance to Great Onyx Cave and in 48 *H. subterraneus* were studied from 27–30 April 1987 on crickets collected from the entrance area of Crystal Cave and Sophys Avenue of Mammoth Cave. These studies were done in Marion Avenue of Mammoth Cave using the previously mentioned electronic balance. Below cave T_a of 9.5°C was achieved in a Styrofoam cooler containing ice and T_as above cave temperature were obtained with incubators containing trays of water to insure water saturated air in the incubators. Cave crickets were tested at T_as above cave T_a at 16.0, 18.5, 22.0 and 25°C. Camel crickets were tested at T_as above cave T_a of 19.5, 23.5, 27.5 and 31.0°C. Weight loss was followed for 40–48 hr (14–18 hr at the highest two T_as) for both species.

Hind femur lengths (HFL) and sex were determined and recorded for all studied crickets. Crop empty live weight (CELW), termed crop-free live weight (CFLW) in our first study, for all crickets was determined by dissection or by use of a HFL to CELW relationship as previously described (Studier *et al.*, 1986). Percent water of crop contents and carcasses and dry caloric densities of crop contents were also calculated as previously described.

RESULTS

Exponential relations of MR to CELW for the crickets studied as well as insects in general are shown in Fig. 1. Table 1 gives the relations of MR and WB components to CELW for both species. Linear slopes of mass to MR relations of male and female *C. stygius* do not differ, while slopes for *H. subterraneus* differ significantly ($t = 2.846$; 56 df, $P < 0.01$).

Size-specific metabolic rates of studied crickets in relation to T_a are shown in Fig. 2 and enumerated in Table 2. Weight specific MR and WB components in relation to T_a for both species are given in Table 3. Percent water in crops and carcasses as well as caloric
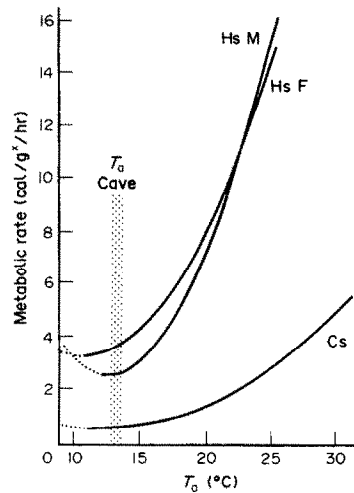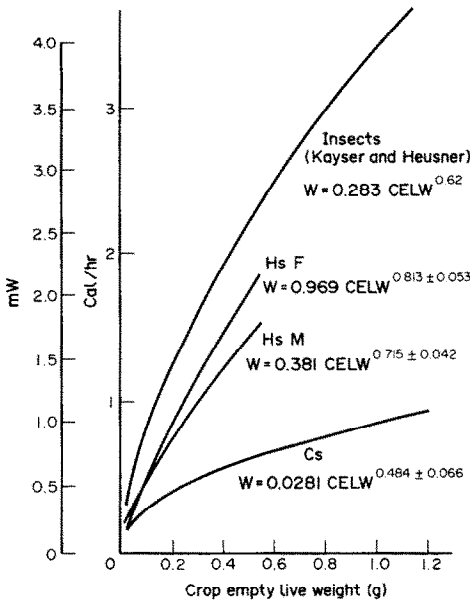
Fig. 1. Relation of metabolic rate (in Watts, W, or cal/hr) to mass (crop-empty live weight, CELW in kg) in insects in general (Kayser and Heusner, 1964), female *H. subterraneus* ($F = 230.47$; df = 1 and 32; $P < 0.0001$; $r^2 = 0.878$), male *H. subterraneus* ($F = 287.35$; df = 1 and 26; $P < 0.0001$; $r^2 = 0.917$) and combined sexes in *C. stygius* ($F = 54.105$; df = 1 and 63; $P < 0.0001$; $r^2 = 0.462$).

density of crop contents are given in previous papers (Studier *et al.*, 1986, 1987a, b).

DISCUSSION

The expected increase in absolute MR (power or energy/time) with increasing mass in animals

Fig. 2. Relation of metabolic size adjusted metabolic rate (cal/g/hr) of cave and camel crickets as functions of ambient temperature (T_a in °C). See legend of Table 2 for units of metabolic rate.

(whenever a broad enough range in mass is available) is seen in this study. In *H. subterraneus*, MR increases more rapidly with mass in females than in males; however, there are no gender related differences in *C. stygius*. Metabolic rates of cave crickets are greater than in camel crickets of similar size. Adult *H. subterraneus* in this study exhibited MR which were higher than in our previous study (Studier *et al.*, 1986), while the MR of *C. stygius* in this study are very much lower than in our previous study (Studier *et al.*, 1987a). These differences may reflect seasonal differences in MR which will be discussed in a later paper. MR of *H. subterraneus*, reported here in terms

Table 1. ANOVA results and regression coefficients for metabolic rate (cal/hr) and weight specific water budget components (mg/g/hr) as functions of size (g). Regression equations are of the form $y = bx + c$ or $y = ax^2 + bx + c$, where x is mass in grams. Dependent variables (DV) include metabolic rate (MR), crop water gain (CWG); metabolic water gain (MWG) and total water gain (TWG)

DV	a	b	c	df	F	r^2	P
H. subterraneus (males)							
MR		3.058	0.0886	1,26	147.06	0.8497	< 0.0001
		(0.252)	(0.0679)				
CWG	49.84	−30.75	6.077	2,25	27.545	0.6878	< 0.0001
	(14.65)	(6.75)	(0.467)				
MWG	6.641	−3.978	0.9404	2,25	13.419	0.5177	= 0.0001
	(2.558)	(1.179)	(0.0816)				
TWG	56.49	−34.73	7.017	2,25	25.747	0.6732	< 0.0001
	(17.00)	(7.84)	(0.542)				
H. subterraneus (females)							
MR		4.546	−0.0363	1,32	98.51	0.7548	< 0.0001
		0.458	(0.1183)				
CWG	39.60	−24.96	5.562	2,31	10.723	0.4089	= 0.0003
	(11.05)	(5.99)	(0.529)				
MWG	5.823	−3.423	0.9004	2,31	6.166	0.2846	= 0.0056
	(1.844)	(1.000)	(0.0883)				
TWG	45.52	−28.38	6.465	2,31	10.097	0.3945	= 0.0004
	(12.82)	(6.95)	(0.613)				
C. stygius (both sexes)							
MR		0.6590	3.263	1,63	43.996	0.4112	< 0.0001
		(0.993)	(0.076)				
CWG	1.669	−3.186	2.177	2,62	27.906	0.4737	< 0.0001
	(0.563)	(0.755)	(0.174)				
MWG	0.5665	−1.021	0.5484	2,62	37.500	0.5474	< 0.0001
	(0.1405)	(0.188)	(0.0435)				
TWG	2.236	−4.209	2.726	2,62	30.379	0.4949	< 0.0001
	(0.696)	(0.932)	(0.215)				

Table 2. ANOVA results and regression coefficients for metabolic size specific metabolic rates (MR) as functions of temperature. Regression equations are all of the form $MR = ax^2 + bx + c$, where x is T_a in °C. Units for MR are $cal/g^{0.813}/hr$ for female *H. subterraneus*, $cal/g^{0.715}/hr$ for male *H. subterraneus* and $cal/g^{0.484}/hr$ for *C. stygius*. Standard errors of the means are given in parentheses. In all cases, $P < 0.0001$

	a	b	c	df	F	r^2
H. subterraneus (females)						
	0.05692	−1.213	9.673	2,21	31.477	0.7477
	(0.02126)	(0.7444)	(6.111)			
H. subterraneus (males)						
	0.08794	−2.210	16.41	2,21	117.53	0.9180
	(0.01279)	(0.448)	(3.68)			
C. stygius (both sexes)						
	0.01386	−0.3243	2.343	2,44	50.609	0.6970
	(0.00394)	(0.1590)	(1.436)			

of CELW, are doubtless maximal when compared to insects in general where MR is normally expressed per gram live weight instead of CELW. Since crop content wet weight (CWW) may easily equal CELW, expression of MR per gram live weight for cave crickets would reduce reported MR by half. In *C. stygius*, CWW represents a much smaller fraction of live weight, and is often zero and, therefore, would have little effect on reported MR. The frequent occurrence of empty crops in the

C. stygius studied would, in fact, yield a marked understatement of MR if those crickets were metabolizing stored body fat instead of crop contents. Caloric density of fat, about 9.5 kcal/g, greatly exceeds the kcal/g dry weight of crop contents of camel crickets; thus, MR of *C. stygius* may be up to twice the reported level. Since cave crickets routinely contain significant crop contents, *H. subterraneus* routinely do not catabolize stored body fat as an energy source.

Table 3. ANOVA results and regression coefficients for weight specific metabolic rates and water budget components as functions of ambient temperature (T_a). Regression equations are of the form $y = ax^2 + bx + c$ or $y = bx + c$ where $x = T_a$ in °C. Dependent variables (DV) include metabolic rate (cal/g/hr), crop water gain (CWG), metabolic water gain (MWG), total water gain (TWG), mixed wastes water loss (WWL) and evaporative water loss (EWL), all in mg/g/hr. In all cases, $P < 0.0001$, except*, where $P = 0.0086$

DV	a	b	c	F	df	r^2
H. subterraneus (males)						
MR	0.1178	−2.971	22.08	121.73	2,21	0.9206
	(0.0167)	(0.584)	(4.80)			
CWG	0.07596	−1.784	13.35	177.54	2,21	0.9206
	(0.01025)	(0.359)	(2.94)			
MWG	0.01751	−0.4417	3.283	121.74	2,21	0.9206
	(0.00248)	(0.0868)	(0.713)			
TWG	0.09346	−2.225	16.63	172.54	2,21	0.9426
	(0.01248)	(0.437)	(3.59)			
WWL	NS					
EWL	0.1039	−2.658	19.65	100.38	2,21	0.9053
	(0.0157)	(0.551)	(4.53)			
H. subterraneus (females)						
MR	0.06445	−1.376	11.06	28.749	2,21	0.7325
	(0.02514)	(0.880)	(7.22)			
CWG	0.05154	−1.010	8.168	35.298	2,21	0.7707
	(0.02026)	(0.709)	(5.824)			
MWG	0.01178	−0.2808	2.219	27.186	2,21	0.7214
	(0.00395)	(0.1383)	(1.136)			
TWG	0.06124	−1.217	9.832	34.398	2,21	0.7661
	(0.02399)	(0.8398)	(6.896)			
WWL	—	0.1277	−0.9917	26.643	1,22	0.5477
		(0.0247)	(0.4493)			
EWL	0.06005	−1.303	10.50	26.761	2,21	0.7182
	(0.02370)	(0.830)	(6.81)			
C. stygius						
MR	0.01448	−0.3316	2.388	54.844	2,44	0.7137
	(0.00405)	(0.1636)	(1.477)			
CWG	0.01163	−0.2533	2.038	33.185	2,44	0.6013
	(0.00442)	(0.1787)	(1.614)			
MWG	0.001901	−0.04354	0.3135	54.847	2,44	0.7137
	(0.000532)	(0.2147)	(0.1939)			
TWG	0.01354	−0.2970	2.347	36.012	2,44	0.6208
	(0.00491)	(0.1983)	(1.790)			
WWL		0.04881	−0.1937	7.548*	1,45	0.1437
		(0.01777)	(0.3909)			
EWL	0.001193	−0.2816	1.996	58.472	2,44	0.7266
	(0.00311)	(0.1258)	(1.136)			

NS, not significant.

Since crop water gain (CWG), metabolic water gain (MWG), and, therefore, total water gain (TWG) are calculated directly from the rate of CWW and CDW loss, as are MR, water gains as functions of size generally parallel MR. Since the crop water fraction in male *H. subterraneus* is greater than in females (Studier *et al.*, 1986), however, WB components in both sexes are nearly identical. Weight specific water gains in cave crickets are curvilinear (Table 1), with minimal values reached in small adults (HFL = 20.0 mm) at CELW of about 0.30 g where values for females (CWG = 1.63 mg/g/hr, MWG = 0.398 mg/g/hr and TWG = 2.04 mg/g/hr) slightly exceed those of males (CWG = 1.33 mg/g/hr, MWG = 0.354 mg/g/hr and TWG = 1.68 mg/g/hr). These minimal WB components only slightly exceed values of similar sized (0.30 g) camel crickets of both sexes (Table 1) where CWG = 1.37 mg/g/hr, MWG = 0.293 mg/g/hr and TWG = 1.66 mg/g/hr. In both larger and smaller sized cave crickets, WB components greatly exceed values for camel crickets. In camel crickets, minimal values for WB components (Table 1) are also reached at small adult size (CELW = 0.90 g) where CWG = 0.661 mg/g/hr, MWG = 0.088 mg/g/hr and TWG = 0.749 mg/g/hr. The progressive decreases in weight specific WB components in both species below minimal adult size conforms to expectations based on surface area to mass relations. The increases in weight specific WB components in crickets which exceed minimal adult size present an enigma.

In ectothermic organisms such as these crickets, MR is expected to rise with increasing temperature, as shown in Fig. 1 and Table 2. Absolute increase in MR is much greater in cave than camel crickets. The fact that cave crickets died very quickly and, therefore, could not be tested in T_as exceeding 25°C indicates much greater thermal sensitivity of *H. subterraneus* in comparison to *C. stygius*. Relative thermal sensitivities are, however, normally discussed in terms of Q_{10}. These Q_{10} values in the range of 13° (normal cave temperature) to 23°C are 4.75 and 3.38 for male and female cave crickets, respectively, and 4.72 for camel crickets. Based on these Q_{10} values, metabolic thermal sensitivity of female *H. subterraneus* is less than that of males whose MR increases in comparable fashion with camel crickets. Values for Q_{10} in excess of 3 are relatively rare and indicate extreme thermal sensitivity of the system measured. These great thermal sensitivities indicate marked adaptation to the nearly constant cave temperatures, would greatly increase metabolic demands at higher temperatures, and would preclude voluntary epigean foraging activity in T_as much in excess of cave T_a, especially in cave crickets.

Equations for weight specific WB components, including evaporative water loss (EWL) and combined wastes water loss (WWL), given in Table 3, indicate direct relations to T_a. At cave T_a of 13°C, gains and losses in female cave crickets (CWG = 4.75 mg/g/hr, MWG = 0.559 mg/g/hr, TWG = 5.31 mg/g/hr and EWL = 3.71 mg/g/hr) exceed those of males (CWG = 3.00 mg/g/hr, MWG = 0.500 mg/g/hr, TWG = 3.50 mg/g/hr and EWL = 2.66 mg/g/hr) and both greatly exceed WB components of camel crickets (CWG = 0.711 mg/g/hr and MWG =

0.0687 mg/g/hr, TWG = 0.77 mg/g/hr and EWL = 0.351 mg/g/hr). At a T_a of 23°C, TWG in male and female cave crickets increase by factors of 4.25 and 2.86, respectively, while TWG in camel crickets increase 3.46 times. Increasing T_a, therefore, TWG (= total water loss, TWL) increases most profoundly in male *H. subterraneus*, least in female *H. subterraneus* and an intermediate level in *C. stygius*. At cave T_a, water turnover in female cave crickets (0.53 mg%/hr) exceeds that of males (0.35 mg%/hr) and both exceed water turnover in camel crickets (0.077 mg%/hr). At a T_a of 23°C, water turnover in female and male cave crickets is nearly identical (1.52 and 1.49 mg%/hr, respectively) and is much higher than in camel crickets (0.27 mg%/hr).

Reduced MR are characteristic of many cave-adapted animals; thus, it is not surprising that MRs of the studied crickets are less than for insects in general (Kayser and Heusner, 1986). Cave crickets are also extremely sensitive to temperatures above cave temperatures, and show markedly greater metabolic demands with modest increases in ambient temperature compared to camel crickets. Cave crickets exhibit more of the features expected in cavernicoles than camel crickets. Camel crickets spend extended periods of time in the Kentucky caves only as young nymphs in the Winter. From late spring to autumn, *C. stygius* roost just inside cave entrances or in forest shelters and leave the caves frequently, almost nightly, for epigean feeding. These camel crickets mate in late summer and autumn in cave entrances and, presumably, lay their eggs in the forest. Cave crickets, conversely, are found in many cave areas throughout the entire year, and copulate and lay eggs in caves. Metabolic adaptation to cave life by *H. subterraneus* is evidenced by a somewhat lowered MR coupled to the ability to store a very large amount of food in their crops, thus providing quite long intervals between required epigean foraging activity.

Epigean foraging activity at elevated T_as (23°C) by cave crickets is probably precluded more by increase in water losses than by increase in MR. Foraging by camel crickets at similar T_as is, however, not as stressful due to the lesser increase in water demand. The greater water turnover in cave crickets than camel crickets at cave T_a may be attributed to greater EWL in the former (76–80% of TWG) as opposed to the latter (45% of TWG). Furthermore, with increasing T_a, EWL of cave crickets increases more profoundly than in camel crickets. In cave crickets, rapidly rising EWL with increasing T_a indicates the presence of highly volatile cuticular surface lipids which evaporate readily at T_as slightly in excess of cave T_a. Preliminary histologic work suggests that these differences may also relate to structural differences in cuticles which allow greater water permeability in cave crickets than camel crickets.

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