# BIOENERGETICS OF THE CAMEL CRICKET
## *CEUTHOPHILUS STYGIUS*

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**Abstract**—1. In early summer, camel crickets in Mammoth Cave National Park exhibit a sex-specific relationship between crop-empty live weight and hind femur length.

2. They also exhibit curvilinear long-term weight loss patterns averaging 2.67 and 3.13 mg/hr for females and males, respectively, and caloric assimilation efficiencies of 65.6 and 70.5% for females and males, respectively.

## INTRODUCTION

Many caves, including the limestone caves in Mammoth Cave National Park (MCNP), are energy-poor. The major food base is finely triturated and larger organic debris washed into the cave ecosystem (Barr and Kuehne, 1971) augmented by cricket guano, eggs and carcasses (Poulson and Culver, 1969). These caves contrast markedly with the energy-rich caves occupied by large bat or bird colonies (see Howarth, 1983).

To provide initial baseline data necessary to quantify input of fixed energy by trogloxenes, we have begun studies of energetics of cave crickets (*Hadenoecus subterraneus*) (Studier *et al.*, 1986a) and water balance of cave and camel crickets (Studier *et al.*, 1986b). The present study concerns the energy budget of camel crickets (*Ceuthophilus stygius*).

## MATERIALS AND METHODS

Studies were conducted during the last week of June 1985 in Great Onyx Cave in MCNP, Ky. The potential relationship of hind femur length (HFL) to crop-free live weight (CFLW) was investigated as previously described (Studier *et al.*, 1986a). In addition to HFL and CFLW, data were obtained on fresh and dry weights of crop contents and enlarged reproductive tracts as well as crop-free dry weight for camel crickets of both sexes.

A long term weight loss study was begun at 0600 hr local time on 22 June 1985 (designated time = 6 hr). Sixteen (8 male and 8 female) large (HFL > 19.0 mm) camel crickets with apparently full crops were collected just inside the entrance to Great Onyx Cave. These camel crickets were all penultimate instars (T. H. Hubbell, personal communication). Weighings were then begun and periodically continued as previously described (Studier *et al.*, 1986a) until 1900 hr local time on 27 June 1985 (designated time = 139 hr). Temperature and relative humidity were recorded periodically throughout the study (Certified Hygrometer and Temperature Indicator, Model HTAB-176, Abbeon Cal. Inc., Santa Barbara, Calif.). After the last weighings, crickets were killed and processed as previously

described. All accumulated, combined wastes produced by these caged crickets throughout the entire experiment were collected, dried and weighed.

Crop contents, carcasses, and combined wastes were burned in a Parr Oxygen Bomb Calorimeter (Moline, Illinois) to determine energy content.

## RESULTS

The relationships of CFLW to HFL in female and male *C. stygius* are highly significant ($F = 36.77$; 1 and 24 d.f.; $P < 0.0001$; $r^2 = 0.605$; and, $F = 82.05$; 1 and 24 d.f.; $P < 0.0001$; $r^2 = 0.774$, respectively), are shown in Fig. 1 and are expressed by the equations:

$$\text{Female CFLW (g)} = 0.1040 \, \text{HFL (mm)} - 1.114$$
$$(\pm 0.0171) \quad (\pm 0.328)$$

and

$$\text{Male CFLW (g)} = 0.1151 \, \text{HFL (mm)} - 1.176$$
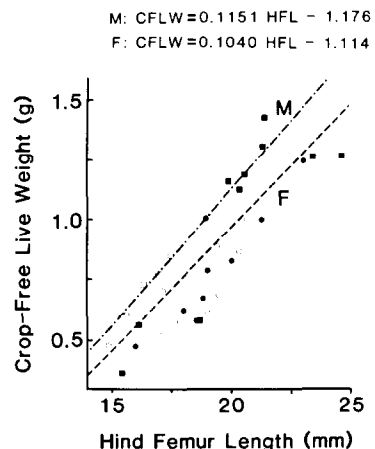$$(\pm 0.0127) \quad (\pm 0.247),$$



Fig. 1. The relationship of crop-free live weight (CFLW) to hind femur length (HFL) in *Ceuthophilus stygius*. Circles represent females and squares represent males. Filled symbols represent total weight of crickets with naturally empty crops. Open symbols represent carcass weight with crops dissected out.

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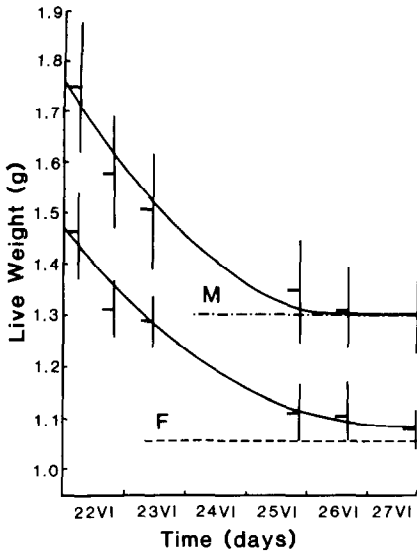
Fig. 2. Total live weight of caged large *C. stygius* over time, beginning with crop-full individuals. Symbols represent arithmetic mean and 95% confidence intervals. M = males, F = females. Dashed lines represent CFLW of male and female camel crickets

respectively, where values in parentheses are the standard errors of the means. These relationships are unaffected by whether CFLW is measured for crickets with naturally empty crops or with crop contents removed.

Long-term weight losses of aged camel crickets are curvilinear and are illustrated in Fig. 2. Weight loss as a function of time for large (average HFL = 20.5 mm) males ($F = 30.73$, 2 and 45 d.f., $P < 0.0001$, $r^2 = 0.577$) is expressed by:

Weight (mg) $= 0.03493 \pm 0.01377$ (time = hr)$^2$

$- 8.080 \pm 1.995$ (time = hr) $+ 1766 \pm 50$.

Weight loss over time for large (average HFL = 19.7 mm) females ($F = 102.26$, 2 and 45 d.f., $P < 0.0001$, $r^2 = 0.820$) is expressed by:

Weight (mg) $= 0.02350 \pm 0.00631$ (time = hr)$^2$

$- 6.000 \pm 0.914$ (time = hr) $+ 1472 \pm 23$.

Also shown in Fig. 2 are the average CFLW for the male (M) and female (F) camel crickets studied.

Table 1 gives caloric densities of camel cricket crop contents, and mixed wastes. In most cases it was necessary to pool crop contents from several individuals to obtain sufficient dry mass for bombing.

## DISCUSSION

In our previous study of cave crickets (Studier et al., 1986a), we found a highly predictive, curvilinear relationship between CFLW and HFL. The present data show a linear, predictive relationship between those variables (Fig. 1) for camel crickets. The linear equations for *C. stygius* predict a minimal HFL of about 10.5 mm (at CFLW projected to 0). That suggestion is not supported by observation, since camel crickets with HFL smaller than 10.5 mm are seen earlier in the year. The true relation of HFL and CFLW in *C. stygius* is almost certainly curved as in *H. subterraneus*. Although an attempt was made in June to collect camel crickets of wide range of HFL, only one individual was found with HFL less than 15.0 mm. Collections of *H. subterraneus* made in May, however, yielded relatively large numbers of individuals of HFL as short as 8.5 mm. The seasonally restricted size range of camel crickets suggests highly coherent, seasonal reproductive patterns, while the much broader range of available sizes of cave crickets indicate reproductive effort which is less seasonally restricted.

Unlike cave crickets (Studier et al., 1986a), camel crickets (penultimate instars) of similar HFL have differing gender-related mass, e.g. in large crickets of HFL = 20 mm, male CFLW weight averages 1126 mg while female CFLW average weight is 966 mg. This mass difference is also apparent in adult camel crickets. In October, the crops of roosting adult males are empty while adult female crops are not (Studier et al., 1986b). These cricket species and gender differences could relate to male territorial defense, courtship displays or polygynous reproductive habits among camel crickets. Camel crickets of either sex are much more massive than similarly sized cave crickets. Cave crickets of 20 mm HFL have an average CFLW of 352 mg, only about one-third of that of camel crickets of the same HFL (Studier et al., 1986a). This observation provides mild support to the generalization (see Culver, 1982) that highly cave-adapted animals have longer appendages and a gen-

Table 1. Caloric density of large (HFL >19.0 mm) camel cricket crop contents carcasses, and wastes. Values are mean and standard error of the mean; F = female; M = male; B = both

|  | n | cal/g total dry wt | cal/g total wet |
|---|---|---|---|
| crop (B) | 5 | 4475 ± 135 | 1342 ± 40 |
| wastes | 7 | 3760 ± 66 | ------- |
| carcass (F) | 7 | 5010 ± 74 | 1308 ± 19 |
| carcass (M) | 5 | 5388 ± 73 | 1407 ± 19 |

Table 2. Energetic parameters for large (HFL > 19.0 mm) camel crickets, *Ceuthophilus stygius*. Values shown are mean and standard error of the mean. Units are mg unless otherwise indicated; $N = 8$ for each sex; $* = P < 0.05$; $** = P < 0.01$

| Parameter | Females | Males | t |
|---|---|---|---|
| Hind femur length (mm) | 19.7 ± 0.2 | 20.5 ± 0.3 | 2.55* |
| Carcass wet wt; t=139 hrs | 1056. ± 51. | 1304. ± 55 | 3.34** |
| Carcass dry wt; t=139 hrs | 302.4 ± 11.6 | 384.5 ± 17.7 | 3.88** |
| Dry waste prod. (mg/hr) | 0.3191 ± 0.0434 | 0.2900 ± 0.0860 | NS |
| Wet crop wt; t=6 hrs | 409.6 ± 34.1 | 446.9 ± 67.9 | NS |
| Dry crop wt; t=6 hrs | 127.0 ± 10.6 | 129.6 ± 19.7 | NS |
| Dry crop wt used (mg/hr) | 0.8808 ± 0.0997 | 0.9740 ± 0.1480 | NS |
| Crop energy @t=6 hrs (cal) | 568.3 ± 47.4 | 579.8 ± 88.1 | NS |
| "Ingested" energy (cal/hr) | 3.942 ± 0.446 | 4.35 ± 0.662 | NS |
| Assimilated energy (cal/hr) | 2.742 ± 0.510 | 3.269 ± 0.486 | NS |
| Metabolic rate (cal/gm carcass wet wt·hr$^{-1}$) | 2.612 ± 0.490 | 2.636 ± 0.477 | NS |

erally more fragile appearance than less cave-adapted animals.

Unlike the data for cave crickets (Studier *et al.*, 1986a), average wet crop contents of large, fed female camel crickets (410 mg = 38.9% CFLW) at the start of the weight loss experiment are not different from values for males (447 mg = 34.4% CFLW) as seen in Table 2. Table 3 summarizes the potential individual fixed energy cave input by male and female cave and camel crickets. The absolute crop biomass and potential fixed calories introduced to caves per foraging bout, are similar in both sexes of both species except for somewhat lower values for male *H. subterraneus*. In terms of weight specific crop biomass (mg/mg CFLW) and calories (cal/mg CFLW), individual cave crickets bring considerably more fixed energy into cave ecosystems per foraging bout than do camel crickets. Since the latter are estimated to forage much more frequently than cave crickets, however, potential energy delivered daily to cave ecosystems by large camel crickets may markedly exceed input by individual cave crickets. Lack of significant data on seasonal

Table 3. Foraging parameters in large cave crickets (*H. subterraneus*) and large camel crickets (*C. stygius*). Data for cave crickets from Studier *et al.* (1986a). F = female; M = male

| Parameter | H. subterraneus | | C. stygius | |
|---|---|---|---|---|
| | E | M | E | M |
| Full crop (mg) | 428. | 284. | 410. | 447. |
| Full crop (cal) | 474.0 | 326.0 | 568.3 | 580.0 |
| CFLW (mg) | 422. | 390. | 1055. | 1304. |
| Full crop (mg/mg CFLW) | 1.004 | 0.720 | 0.389 | 0.343 |
| Full crop (cal/mg CFLW) | 1.123 | 0.836 | 0.539 | 0.445 |
| Foraging interval(days) | 11.5 | 9.9 | 3.0 | 2.3 |
| Forage rate (mg/day) | 37.2 | 28.4 | 136.7 | 194.3 |

population sizes or size distribution data preclude further quantitative projection of potential energy input by either cricket species.

As outlined earlier for cave crickets (Studier *et al.*, 1986a), long term weight loss in fed crickets can be used to estimate maximum foraging intervals if CFLW of crickets is also known. In cave crickets, the long term weight loss pattern was linear and projected to maximum foraging intervals of 11.5 and 9.9 days for females and males, respectively. The weight loss pattern of fed camel crickets is curvilinear (Fig. 2) and, therefore, does not lend itself to easy or accurate estimation of maximal foraging intervals. We interpret the rapid early weight loss to represent the rate of crop biomass usage during the first few days after feeding, while the much slower weight loss occurring on days 4–6 is interpreted to represent, not crop biomass usage, but utilization by camel crickets of stored energy in the form of fats or glycogen. Rate of weight loss during the first 2 days (5.69 mg/hr and 7.99 mg/hr, for females and males, respectively) was used to estimate time interval for crop emptying and foraging intervals (Table 3) of 3.0 and 2.3 days for females and males, respectively.

Energetic parameters for large camel crickets, given in Table 2, are based upon patterns over the entire long-term weight loss study. As just discussed, values in Table 2 underestimate actual energetic parameters during the first 2 days and overestimate those levels during the last 2 days. Calculation of entries in Table 2 requires data from Tables 1 and 4 and is explained in our previous paper (Studier *et al.*, 1986a). There are no gender related differences in energetic parameters in *C. stygius* except for carcass biomass differences already discussed. With the exception of estimated metabolic rates, there are also no differences in energetic parameters of *C. stygius* (Table 2) and cave crickets (Table 2, Studier *et al.*, 1986a) which cannot be readily attributed to biomass differences in the two species. Estimated metabolic rates (cal/gm CFLW/hr) of female ($2.61 \pm 0.49$) and male ($2.64 \pm 0.48$) camel crickets are not significantly different from expected rates for insects of similar

biomass (3.29 and 3.04, for females and males, respectively; Kayser and Heusner, 1964). Cave crickets, however, show metabolic rates which are markedly lower than expected (Studier *et al.*, 1986a). Low metabolic rates appear to be characteristic of cavernicolous as opposed to epigean species (Poulson and White, 1969; Culver, 1982). *C. stygius* may, therefore, not be as cave adapted as *H. subterraneus*.

Regarding measured caloric levels (Table 1) of large camel crickets, male carcass caloric density is significantly higher than in females ($t = 3.63$; d.f. = 10; $P < 0.01$). In comparing camel crickets (Table 1) with cave crickets (Studier *et al.*, 1986a), there are no differences in female carcass caloric density; however, carcass caloric density of male camel crickets exceeds that of male cave crickets ($t = 4.45$; d.f. = 10; $P < 0.01$). In general, differences in dry caloric density when values are near to or exceed 5.0 Kcal/g, are attributed to differences in lipid levels. Our data indicated a greater level of stored lipid in large male *C. stygius* compared to females of the same species or to cave crickets of either sex.

There is a great difference in caloric density of mixed wastes between the two species ($t = 11.11$; d.f. = 12; $P < 0.001$). The extremely low caloric density of mixed wastes of cave crickets has been previously discussed (Studier *et al.*, 1986a). The higher caloric density of camel crickets wastes may reflect a lesser contribution of microbial fermentation to digestive characteristics of camel crickets or reduced efficiency of assimilation.

The markedly lower mixed waste caloric content of cave crickets contributes significantly to the generally greater assimilation efficiencies of both dry matter and, especially, calories of cave crickets (Studier *et al.*, 1986a) in comparison to camel crickets (Table 4). Dry matter assimilition efficiency in camel crickets compares favorably with values for house crickets (Woodring *et al.*, 1979) as well as other insects (Slansky and Scriber, 1984).

Contributions of guano from each species to the energy base in the cave is affected by caloric value of wastes, amount of wastes, and frequency of feeding,

Table 4. Per cent water and per cent assimilation efficiency of large camel crickets, *Ceuthophilus stygius*. $N = 8$ for each sex

| Parameter | Female | Male |
|---|---|---|
| **Percent Water** | | |
| crop, day 0 | 69.0 | 71.0 |
| carcass, day 0 | 76.4 | 72.7 |
| carcass, day 5 | 71.4 | 70.5 |
| **Percent Assimilation Efficiency** | | |
| dry matter | 68.0 | 72.2 |
| calories | 65.6 | 70.5 |

suggesting that *C. stygius* may be an important source of imported detrital food compared to *H. subterraneus*. Seasonal differences in sizes of individuals making up the populations of *C. stygius* compared to the more consistent size distribution of *H. subterraneus*, however, may off-set some of the differences on a year-round basis. Distribution of the two species within a cave is also different, with camel crickets typically found close to cave entrances and cave crickets more widely distributed. Energy inputs from cave cricket guano, although low, are predictable, and are probably more important to the troglobitic animals deep within a cave than camel cricket guano.

## REFERENCES

Barr T. C. Jr. and Kuehne R. A. (1971) Ecological studies in the Mammoth Cave system of Kentucky, I. Biota. *Int. J. Speleol.* **3**, 147–204.

Culver D. C. (1982) *Cave Life; Evolution and Ecology*, Vol. IX. Harvard Univ. Press, Cambridge, Massachusetts.

Howarth F. G. (1983) Ecology of cave arthropods. *A. Rev. Ent.* **28**, 365–389.

Kayser C. and Heusner A. (1964) Etude comparative du metabolisme energetique dans la serie animale. *J. Physiol., Paris* **56**, 489–524.

Poulson T. L. and Culver D. C. (1969) Diversity in terrestrial cave communities. *Ecology* **50**, 153–158.

Poulson T. L. and White W. B. (1969) The cave environment. *Science* **165**, 971–981.

Slansky F. Jr. and Scriber J. M. (1984) Food consumption and utilization. In *Comprehensive Insect Physiology, Biochemistry, and Pharmacology* (Edited by Kerkut G. A. and Gilbert L. J.), Vol. 4, pp. 87–163. Pergamon Press, Oxford.

Studier E. H., Lavoie K. H., Wares W. D. II, and Linn J. A. M. (1986a) Bioenergetics of the cave cricket, *Hadenoecus subterraneus*. *Comp. Biochem. Physiol.* **A 84A**, 431–436.

Studier E. H., Wares W. D. II, Lavoie K. H. and Linn J. A. M. (1986b) Water budgets of cave crickets, *Hadenoecus subterraneus*, and camel crickets, *Ceuthophilus stygius*. *Comp. Biochem. Physiol.* **A 86A**, 97–102.

Woodring J. P., Clifford C. W. and Beckman B. R. (1979) Food utilization and metabolic efficiency in larval and adult house crickets. *J. Insect Physiol.* **25**, 903–912.