

LEG ATTENUATION AND SEASONAL FEMUR LENGTH: MASS RELATIONSHIPS IN CAVERNICOLOUS CRICKETS (ORTHOPTERA: GRYLLIDAE AND RHAPHIDOPHORIDAE)

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*We report here some factors that affect the relationship between hind femur length (HFL) to crop-empty live weight (CELW) and propose a quantitative, non-lethal measurement ratio that has potential as an index of extent of adaptation to a cavernicolous existence in "crickets". Curvilinear relationships exist between HFL and CELW for camel crickets (*Ceuthophilus stygius*) and cave crickets (*Hadenocoelus subterraneus*). The relationships differ significantly between the species and also by gender within both species and, in cave crickets, by season as well. In *C. stygius*, females of small HFL are slightly lighter, and those of large HFL slightly heavier than males. In *H. subterraneus*, females have progressively greater CELW than males as HFL increases. In adult *H. subterraneus* of identical HFLs, CELW is greatest in fall and least in spring, i.e., individuals are most robust in the fall in these long-lived crickets, probably due to seasonal constraints on surface feeding. An attenuation index of $CELW/HFL^3$ yields a ratio that ranks the extent of adaptation to cave life in these two and eight other species of variously adapted cavernicolous and epigeal "crickets". Lower values of the attenuation index indicate greater adaptation to cavernicolous existence. The three gryllid species from Hawaii Island are closely related and include the blind, obligate cave cricket, *Caconemobius varius*, and two surface species, the lava flow cricket, *Caconemobius fori*, and the marine littoral cricket, *Caconemobius sandwichensis*. The latter two species are nocturnal scavengers on barren rock habitats. The lower $CELW/HFL^3$ ratio in lava flow crickets suggest they use caves more frequently for daytime roosts than does the marine littoral species.*

Rhaphidophorids and Gryllids are found in a wide range of environments, including caves, and those that occupy deep cave habitats are often known as cave crickets. The deep cave environment is quite stable, with high humidity and nearly constant year-round temperature, although both of these conditions are more variable near entrances (Poulson & White 1969; Howarth 1982). Beyond the twilight zone, caves are characterized by complete darkness and are perceived as being food-poor, or where food is difficult to locate and exploit. Culver (1982) and Howarth (1983) summarize expected adaptations to cave life into four areas: metabolic economy, increased senses, adaptations to high moisture and humidity, and development of neoteny. These features, commonly associated with reduced eyes and bodily pigment, are collectively known as troglomorphic characteristics (Christiansen 1995) and are discussed further in Culver *et al.* (1995).

The general perception of elongated appendages and fragile appearance is widely regarded as being characteristic of cave animals, but few studies compare cave-limited species with surface relatives and ancestral species (Culver 1982). Elongated appendages, particularly antennae, could increase sensory perception, while elongated legs may be an adaptation for walking on irregular surfaces in total darkness, i.e., in a 3D dark maze where stepping across gaps may be safer than jumping or walking around. Elongated appendages also could be an

adaptation for metabolic economy-with longer legs, the animal could move farther with each step.

Vandel (1965) generalizes very broadly that cavernicolous raphidophorids show extreme appendage elongation, even within a group that tends to have long appendages, although he states that cavernicolous *Ceuthophilus* have limbs of normal dimensions. Culver (1982) criticizes many of Vandel's conclusions, citing use of inappropriate comparisons of cave and surface species.

Holsinger and Culver (1970), in an allometric study of populations of the amphipod *Gammarus minus* in springs and caves, show that significantly longer first antennae in cave populations is not due to positive allometric effects. They also point out that the genetic basis and the role of selection in these differences is unclear. Recent studies have begun to examine the genetic basis of adaptation to cave life by North American (Caccone & Sbordoni 1987) and European cave crickets (Allegracci *et al.* 1991) and biogeography (Caccone & Sbordoni 2001)

Cave crickets that feed outside and roost in caves are important in the food budgets of cave ecosystems. When bats or seasonal flooding in upper-level passages are absent, cricket guano, eggs and carcasses are a major food resource for obligate cavernicoles (Poulson & White 1969). As part of our studies of many aspects of raphidophorid biology (Studier *et*

al. 1986; 1987a; 1987b; 1991; Northup *et al.* 1993; Studier 1996), we have collected data on hind femur length (HFL, a measure of attenuation) and crop empty live weight (CELW, a measure of mass) in several species that are variously adapted to a cavernicolous existence. We use crop-empty live mass to minimize the effects of foraging on the relationship. Some cave crickets are known to consume 100% or more of their body weight in a single night of foraging (Studier *et al.* 1986).

Species examined in this study include epigeal gryllids: the house cricket (*Acheta domestica*) and field cricket (*Gryllus pennsylvanicus*), neither of which is adapted for cave life, as well as other species of both gryllids and raphidophorids that are variously adapted to cave life from Kentucky, New Mexico, and Hawaii.

Kentucky species include the cave cricket, *Hadenocoelus subterraneus*, and camel cricket, *Ceuthophilus stygius*. Studies indicate that *H. subterraneus* is a long-lived (at least 1.5 years as an adult) species (Studier *et al.* 1988), which possesses highly attenuated appendages (Christiansen 1995), copulates and lays large eggs in caves, reproduces in all seasons (Cyr *et al.* 1991), and forages outside caves at irregular, long intervals when epigeal conditions are favorable (Studier *et al.* 1986; Poulson *et al.* 1995). *Ceuthophilus stygius* completes its life cycle in a year, copulates in cave entrances in the fall, is found deeper in caves only as young instars in the winter, leaves caves nightly to forage and appears to be very robust with few adaptations to cave life (Studier *et al.* 1988).

Raphidophorids studied from New Mexico are *Ceuthophilus longipes*, *Ceuthophilus conicaudus*, and *Ceuthophilus carlsbadensis*. Of these, *C. longipes* appears to be the most highly adapted to cave life while *C. conicaudus* seems to be the functional equivalent of *C. stygius*. *C. carlsbadensis*, which feeds on surface material in the massively abundant guano deposited by the Mexican free-tailed bat, *Tadarida brasiliensis*, appears to be the least cave adapted. Details of their behavioral, morphological, and physiological adaptation to cave life are given in Northup (1988) and Northup *et al.* (1993).

The gryllids studied from Hawaii are the rock crickets, *Caconemobius sandwichensis*, *Caconemobius fori*, and *Caconemobius varius*. The genus *Caconemobius* is found only in Hawaii and all known species are specialized to live only in barren wet rock habitats (Howarth 1987; Otte 1994). The presumed ancestor of the island terrestrial species is *C. sandwichensis*, a nocturnal marine littoral species living in the wave splash zone of boulder beaches on all the main Hawaiian Islands (Otte 1994). This species shows no cave adaptation but will roost in deep crevices and caves if available and moistened by salt spray. On Hawaii Island, several species have evolved to live inland on similar barren wet rock habitats. *Caconemobius fori*, a nocturnal scavenger of wind-borne debris on young, unvegetated lava flows on Kilauea Volcano (Howarth 1979), colonizes new flows within a month of eruption and disappears when plants begin to colonize the flow. During the day, these crickets hide deep in fumaroles, moist

cracks, and caves within the flow but exhibit no troglomorphy. In contrast, the closely related *C. varius* is troglomorphic and obligately adapted to live only in caves and associated medium-sized subterranean voids in young basaltic lava. Although *C. varius* occasionally forage among wet rocks in the twilight zone of caves, they do not occur on the surface and display no activity rhythm, being minimally active throughout each 24-hour cycle (Ahearn & Howarth 1982).

This paper examines seasonal changes in the extent of attenuation in *H. subterraneus* and explores the possibility of using relative HFL attenuation as a simple, non-lethal index of degree of cave adaptation in cavernicolous and epigeal orthoptera.

MATERIALS AND METHODS

Techniques used to determine HFL and CELW follow Studier *et al.* (1986). HFL is measured using calipers and a metric ruler. CELW is determined by dissection and removal of the distensible crop to create a baseline curve that can then be used non-lethally to predict mass using HFL and, by difference, the amount of material in the crop. Approximately 100 *H. subterraneus* of both sexes and varying ages were collected seasonally (spring - 29 April 1986; summer - 26 July 1986; fall - 20 October 1986; and winter - 24 January 1987) from Walnut Hill Cave near Park City, Kentucky (KY). Smaller total numbers (n=247) of *C. stygius* were collected during the same time span, at nearly monthly intervals (9-36 individuals/month), from the entrances of Great Onyx and White caves, and the Frozen Niagara, Floyd Collins Crystal, and Austin entrances to Mammoth Cave in Mammoth Cave National Park, KY. In May 1989, *C. carlsbadensis* (n=29), *C. longipes* (n=21) and *C. conicaudus* (n=20) were taken from the Bat Cave and Sand Passage portions of Carlsbad Cavern and Spider Cave, respectively, in Carlsbad Caverns National Park, New Mexico (NM). In September 1989, house crickets, *A. domestica*, were purchased from a local pet store and field crickets, *G. pennsylvanicus*, were collected in Iosco Co., Michigan. In May 1988, individuals of both sexes of *C. varius* (n=19) were collected from Kaumana Cave, *C. fori* (n=19) from the 1974 Mauna Ulu and the 1987 Pu'u 'O'o lava flows, and *C. sandwichensis* (n=14) from a rocky slope leading to the sea on the north side of Wailuku River mouth, on the island of Hawaii, (HI). Examples of the Kentucky and New Mexico crickets studied have been deposited in the insect collection, Museum of Zoology, University of Michigan-Ann Arbor. Voucher specimens of Hawaiian crickets are housed in the Bishop Museum, Honolulu, HI.

The possible relationship between CELW, HFL, HFL², HFL³, sex and season was analyzed in a multiple regression (backward elimination) model using SPSSX where sex and season were included as dummy (categorical) variables (SPSS 1993). Dummy variables were assigned as follows: males = 0, females = 1; winter = 0, spring = 1, summer = 2, fall = 3. Variables were tested for normal distributions and transformed

if necessary. The critical probability value for multiple regression analyses was set at 0.10. Critical values for all other analyses were set at 0.05. Descriptive statistics and polynomial regression equations were generated with SYSTAT (Wilkinson 1988) for relationships between CELW and HFL, done separately by sex and season for *H. subterraneus*. Reproduction occurs only once on an annual cycle in *C. stygius* (Studier *et al.* 1988), thus regression analysis was done separately only by sex in this species.

RESULTS AND DISCUSSION

Multiple regression analysis of log CELW as a function of HFL, HFL², sex, and season for *H. subterraneus* (F = 3201.4, d.f. = 6 and 421, P < 0.0001, r² = 0.98) is summarized in Table 1. Neither HFL³ nor interactions between sex and season were significant and both were excluded from the model. The dummy variables for gender and season exhibit significance in the overall analysis for *H. subterraneus*, therefore separate polynomial regression analyses of the relation of CELW to HFL and HFL² were performed (Table 2). The analyses indicate that female *H. subterraneus* are larger than males in all seasons, that individuals of identical HFL are lightest in the spring and heaviest in the fall, and that the aforementioned differences are progressively greater as HFL increases.

Gonad mass is markedly greater in female than male *H. subterraneus* (Studier *et al.* 1986), thus mature females would be expected to have greater CELW than males of similar HFL. The observed seasonal differences may relate to the epigeal foraging frequency and reproductive effort of *H. subterraneus*, because it exhibits extreme metabolic and water budget sensitivities to ambient relative humidity and temperature (Studier & Lavoie 1990). Epigeal feeding in *H. subterraneus* appears limited to nights when above-ground relative humidity is at or near saturation and is near cave temperatures of 12-14°C (Studier & Lavoie 1990; Poulson *et al.* 1995). Such conditions occur most frequently in late summer and fall in Kentucky; therefore, we expect that these cave crickets exhibit positive energy budgets, greatest secondary productivity, and greatest

mass in the fall. Although *H. subterraneus* are reproductively active throughout the year, they exhibit a peak in occurrence of mature gonads and rates of egg laying in winter months (Hubbell & Norton 1978; Cyr *et al.* 1991). These activities, coupled with infrequent appropriate conditions for epigeal feeding, account for the individual loss of biomass through the winter and extending into spring. The combined stress of infrequent foraging and great energy expenditure for reproductive effort, explain the loss of individual biomass and may account for the apparent marked mortality of adults that occurs in the

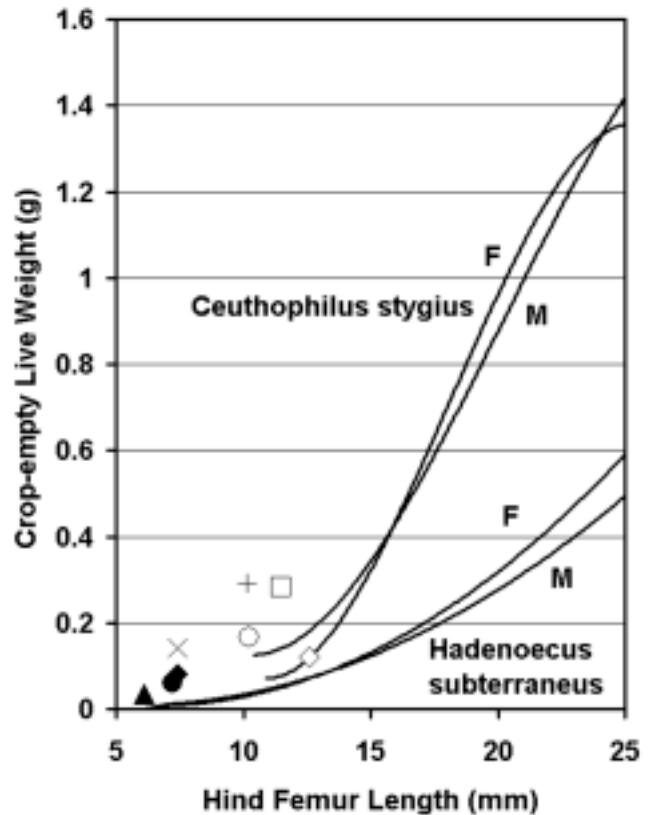


Figure 1. Relationship between hind femur length (HFL in mm) and crop-empty live weight (CELW in g) in various aged male (M), female (F) and immature cave crickets, *Hadenoeocus subterraneus*, (solid lines; equations for spring – see Table 2) and camel crickets, *Ceuthophilus stygius* (dashed lines; equation for males: $CELW = -0.0004101 HFL^3 + 0.02481 HFL^2 - 0.3824 HFL + 1.881$; and, for females: $CELW = -0.0008709 HFL^3 + 0.04734 HFL^2 - 0.7233 HFL + 3.459$). Both species can be separated reliably by gender at $HFL \geq 15$ mm. Other species and symbols are *Ceuthophilus longipes* (open diamond), *Ceuthophilus carlsbadensis* (open square), *Ceuthophilus conicaudus* (open circle), *Caconemobius varius* (closed triangle), *Caconemobius fori* (closed circle), *Caconemobius sandwichensis* (closed diamond), *Gryllus pennsylvanicus* (+), and *Acheta domestica* (x). Data for these species are from Table 3.

Table 1. Multiple regression analysis of log CELW as a function of HFL, HFL², and the categorical variables, sex, and season of *Hadenoeocus subterraneus*. Values in parentheses are standard errors (SE). Variable interactions and HFL³ were not significant and not retained in the model.

Variables	Coefficient (SE)	Probability
HFL	0.1369 (0.0039)	<0.0001
HFL ²	-0.001700 (0.000135)	<0.0001
Female	0.01336 (0.00810)	0.0999
Spring	-0.03381 (0.01127)	0.0029
Summer	0.02396 (0.01091)	0.0287
Fall	0.03810 (0.01112)	0.0007
Constant	-2.6084 (0.0263)	<0.0001

Table 2. Polynomial regression analysis of CELW (gm) to HFL and HFL² (both in mm) for *Hadenoecus subterraneus* by sex and season. All equations are of the form $CELW = a(HFL^2) + b(HFL) + c$, where a and b are regressions coefficients and c is the intercept. Numbers in parentheses are standard errors. $P < 0.0001$ in all cases.

Sex	Season	a	b	c	r ²	df	F
Males	Spring	0.001283 (0.000143)	-0.01426 (0.00402)	0.04856 (0.02320)	0.970	2, 33	542.1
	Summer	0.001225 (0.000146)	-0.01238 (0.00414)	0.04430 (0.02543)	0.960	2, 48	570.9
	Fall	0.001662 (0.000268)	-0.02174 (0.00726)	0.08807 (0.04118)	0.933	2, 39	271.2
	Winter	0.001482 (0.000133)	-0.01948 (0.00394)	0.08157 (0.02609)	0.959	2, 66	772.3
Females	Spring	0.001699 (0.000188)	-0.02202 (0.00565)	0.07896 (0.03681)	0.942	2, 59	475.8
	Summer	0.001740 (0.000174)	-0.02302 (0.00510)	0.08722 (0.03318)	0.955	2, 48	505.6
	Fall	0.001856 (0.000193)	-0.02739 (0.00230)	0.01178 (0.03420)	0.940	2, 54	423.7
	Winter	0.001590 (0.000117)	-0.02120 (0.00355)	0.08791 (0.02333)	0.980	2, 54	1323.1

winter to spring time span (Studier *et al.* 1988).

Relationships between HFL and CELW are curvilinear in those species where a range of sizes of individuals were studied (Fig. 1). In both *H. subterraneus* and *C. stygius*, the ratio of CELW to HFL changes greatly with size and, therefore, does not provide a useful index of attenuation. These species reach sexual maturity when $HFL \geq 20$ mm. Because mass and volume are related to linear measures cubed, we compared the ratio of CELW to HFL^3 as a potential attenuation index. In *H. subterraneus*, the ratio of $CELW/HFL^3$ averages 0.0334, is essentially constant with a total range of 0.0296-0.0380, and is independent of size. While slightly more variable in *C. stygius* (0.0508-0.1214; average=0.0996), this ratio is proposed as an index of the extent of attenuation, which is useful in species comparison.

This attenuation index ($CELW/HFL^3$) ranks the cricket species with respect to their level of adaptation to a cavernicolous existence, with low values indicating a high degree of cave adaptation (Table 3). Comparison of the attenuation index within genera (*Hadenoecus*, *Ceuthophilus*, and *Caconemobius*) demonstrates agreement with the degree of adaptation of each group to life in caves. *Ceuthophilus* crickets from New Mexico and Kentucky cover a wide range of levels of cave adaptation and show increased attenuation indices with increased adaptation to life in caves.

The situation with the gryllids from Hawaii is particularly striking considering that the 3 closely related *Caconemobius* species studied represent an appropriate comparison between a cave-adapted species and its 2 closely related surface congeners. All 3 diverged from each other within a relatively short evolutionary time since the island of Hawaii emerged from the sea and became available for colonization between 700,000

and 1,000,000 years ago (Howarth 1982, 1991; Otte 1994). Although both surface species have similar behavior and morphology, the attenuation index data suggest that *C. fori* is more troglonec than *C. sandwichensis*. Because of the difficulty of sampling in their solid rock habitats, precise daytime roosting and egg-laying sites cannot be determined except indirectly by behavioral, morphological, and ecological studies. *Caconemobius sandwichensis* does not need to descend very far into its boulder habitat to roost in a permanently moist environment, whereas *C. fori* lives in a much more variable and diverse habitat and may, at times, need to descend into caves to find moisture. Ahearn and Howarth (1982) studied water balance physiology and metabolic rate of these same species and, as expected, their ability to conserve water is strongly correlated with their environment. *Caconemobius sandwichensis*, the marine littoral ancestor, is rarely, if ever, subjected to extremes in temperature or to an ambient relative humidity different from 98%, the equilibrium humidity of seawater. *Caconemobius fori*, the lava flow species, is exposed to extreme daily temperature and relative humidity fluctuations as well as to geothermal heat. The cave species, *C. varius*, lives in a constant temperature environment and is extremely sensitive to and avoids relative humidity below saturation. After 12 hours in a desiccating environment near their normal ambient temperature (19°C), the cave species lost significantly more water ($14.7 \pm 0.7\%$ of body mass) than did either surface species, *C. fori* ($8.8 \pm 0.7\%$) and *C. sandwichensis* ($11.5 \pm 0.6\%$) (Ahearn & Howarth 1982).

In summary, a relationship exists between body mass (CELW) and a linear body measurement (HFL) in those species of cavernicolous crickets where a wide range of sizes has been measured—*H. subterraneus* and *C. stygius*. In both

Table 3. Averages or ranges [in brackets] of hind femur lengths (HFL), crop-empty live weight (CELW) and attenuation indices (CELW/HFL³) for “cricket” species, Rhaphidophoridae and Gryllidae, variously adapted to a cavernicolous or epigean environment. Values in parentheses are standard errors. Crickets are ranked specifically by attenuation index and broadly by status of cave adaptation in decreasing order indicated as TB = troglobite, TP = troglophile, TX = troglonexe, EP = epigean.

Species	Status in caves	Number location	CELW (mg)	HFL (mm)	CELW/HFL ³
Rhaphidophoridae					
<i>Hadenoecus subterraneus</i>	TP	425 KY	[11.3-556.8]	[7-25]	0.0334 [0.0296-0.0380]
<i>Ceuthophilus longipes</i>	TP	21 NM	120.2 (0.1)	12.6 (0.1)	0.0602
<i>Ceuthophilus stygius</i>	EP/TX	247 KY	[108.5-1338]	[10-25]	0.0996 [0.0508-0.1214]
<i>Ceuthophilus conicaudus</i>	EP/TX	20 NM	166.0 (9.3)	10.2 (0.2)	0.1546
<i>Ceuthophilus carlsbadensis</i>	EP/TX	29 NM	283.6 (0.1)	11.5 (0.1)	0.1879
Gryllidae					
<i>Caconemobius varius</i>	TB	19 HI	34.0 (2.4)	6.1 (0.1)	0.1474
<i>Caconemobius fori</i>	EP/TX	19 HI	59.4 (0.1)	7.2 (0.2)	0.1571
<i>Caconemobius sandwichensis</i>	EP	14 HI	80.9 (4.0)	7.4 (0.2)	0.1998
<i>Gryllus pennsylvanicus</i>	EP	20 MI	291.7 (0.1)	10.1 (0.1)	0.2831
<i>Acheta domestica</i>	EP	20 —	142.2 (4.0)	7.4 (0.2)	0.3543

species, the relationships differ between sexes with adult females routinely being heavier than adult males of similar HFL. In *H. subterraneus*, relationships additionally differ with season where individuals of similar HFL are lightest in the spring and heaviest in the fall. An attenuation index (CELW/HFL³) inversely ranks the studied cricket species to their level of adaptation to a cavernicolous existence and is proposed as a potentially useful non-lethal quantitative indicator of extent of cave adaptation in orthopterans.

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