

# Lifetime Resource Utilization, Flight Physiology, and the Evolution of Contest Competition in Territorial Insects

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**ABSTRACT:** Adaptationist analyses of animal contests have contributed much to our understanding of behavioral evolution. One class of contest, however, the war of attrition, has proven difficult to interpret. In wars of attrition involving aerial displays, there is evidence that asymmetries in performance parameters such as flight energetics may be important determinants of contest resolution. This paradigm is not universal, however, and we presently lack a framework for understanding why certain biophysical parameters are important only in some cases. One possibility is that the relevance of these parameters is determined by evolutionarily conserved life-history-scale patterns of resource allocation and acquisition. We evaluated this hypothesis by investigating the correlates of competitive success in two territorial insects that exemplify markedly different lifetime patterns of resource utilization. We found that in the bot fly *Cuterebra austeni*, an extreme capital breeding species that depends entirely on energy acquired during its immature stages, territorial residency was most strongly correlated with a size-independent measure of energetic availability. In contrast, residency in the tarantula hawk wasp *Hemipepsis ustulata* was best predicted by variation in body size per se. Adult *H. ustulata* are able to supplement their larval-derived nutrient capital in the manner of an income breeder, and fuel reserves were independent of age and actually correlated negatively with residency in this species. These results underscore how the study of sexually selected phenomena may be enriched by an explicit consideration of life-history principles.

*Keywords:* life history, resource allocation, territoriality, war of attrition.

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Animal contest competition has intrigued behavioral ecologists for decades. The attraction of contests stems largely from the fact that they represent discrete behavioral events

with discrete outcomes in which the causal influences are often readily quantifiable and amenable to manipulation. This is particularly true of pairwise fights between males seeking reproductive opportunities (e.g., Marden and Waage 1990; Alcock and Bailey 1997). Male contest competition has therefore served as an important empirical model for the development and testing of evolutionary theories of animal behavior and cost-benefit decision making. Such theories, including evolutionary game theory (Maynard Smith 1982), have in turn contributed much to our general understanding of the processes of Darwinian natural selection and evolution.

Perhaps the most consistent finding with respect to animal contests is that fights are settled in favor of the individual with superior fighting ability. This parameter, also known as resource holding potential (RHP; Parker 1974), reflects a contestant's capacity for inflicting fitness costs on his opponent and/or minimizing his own rate of cost accrual. In physical battles, where contestants grapple, spar, or otherwise clash violently, RHP is routinely correlated with morphological traits such as large body size, strength, and weaponry (reviewed by Huntingford and Turner 1987). Contest resolution in these cases is often heavily influenced by obvious physical asymmetries. By contrast, many species compete less violently via protracted periods of display that demand high-endurance capability. The determinants of RHP in the context of these wars of attrition (Maynard Smith 1982) are obscure, and, indeed, it is often unclear whether RHP asymmetries are significant enough (in the face of asymmetries in other parameters such as resource value) to affect contest resolution. Species that engage in wars of attrition therefore present a special opportunity to test and refine present evolutionary contest theory.

Many male invertebrates compete for sole ownership of mating territories in wars of attrition involving elaborate, noncontact aerial interactions in which the determinants—and evolutionary significance—of RHP asymmetries are largely obscure. In many groups, such as butterflies, little evidence exists that physiological or morphological traits play a role in contest resolution, de-

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spite concerted attempts to identify the relevant attributes (reviewed in Kemp and Wiklund 2001). Even in cases when competitive success does co-vary with traits such as body size, it is rarely obvious how these traits contribute mechanistically to increased competitive ability (Tsubaki and Ono 1987; Hernández and Benson 1998). However, there are examples of situations in which physiological RHP asymmetries clearly are important. In several odonates, for instance, aerial contest endurance—and thus competitive ability—is mediated by internal resource asymmetries (i.e., abdominal lipid reserves; Marden and Waage 1990; Plaistow and Siva-Jothy 1996). Competitive ability also co-varies with age in these and other insect species (Pettersson 1989; Yuval et al. 1998), suggesting that lifetime patterns of resource acquisition and allocation have important consequences for the evolution of mating strategies.

Part of the puzzle with respect to aerial wars of attrition is that the candidate determinants of RHP differ markedly both within and between taxa that compete via superficially similar interactions (Kemp and Wiklund 2001). The intuitively appealing notion that these contests are mediated simply by flight energetics (Marden and Waage 1990; Plaistow and Siva-Jothy 1996) is apparently not a general paradigm (Strohm and Lechner 2000; Kemp 2002). One possibility is that the relative importance of this parameter is ultimately determined by broader-scale, evolutionarily conserved regimes of resource acquisition and allocation. Resource-use strategies can be placed along a continuum with two endpoints, termed capital breeding and income breeding (Stearns 1992; Jönsson 1997). By virtue of their compartmentalized life cycles, insects tend toward the capital breeding extremity; larval-derived energy resources and external structures such as wing membranes are irreversibly expended or degraded with age. Nevertheless, insects exhibit considerable variation in patterns of resource utilization; whereas species such as *Heliconius* butterflies have evolved the ability to feed on proteinaceous plant exudates and thus extend their adult life span considerably (Karlsson 1994), others such as mayflies subsist entirely on larval-derived nutrients (Sartori et al. 1992). This variation in the timing of resource acquisition/allocation could have consequences for the evolution of contest behavior because energetic costs should impinge more heavily on the extreme capital breeders. In other words, resource constraints may be more likely to emerge as an acute, ecologically significant cost—and thus serve as the basis of RHP asymmetries and contest settlement—in species that lack the ability to supplement or replenish their fuel reserves as adults.

In this article, we set out to evaluate the relevance of flight physiology to contest resolution in two unrelated territorial insects that are expected to differ with respect

to adult resource utilization: a cuterebrid bot fly, *Cuterebra austeni* Sabrosky, and the tarantula hawk wasp, *Hemipepsis ustulata* Dahlbom (Pompilidae). *Cuterebra austeni* is an obligate parasitoid of woodrats (*Neotoma* spp.), and adults do not feed, thus exemplifying the extreme capital breeding regime (Catts 1982; Baird 1997). *Hemipepsis ustulata* is a solitary hunting wasp that provisions its offspring with a variety of large burrowing spiders. Adult wasps, however, readily feed at nectar sources and thus have the ability to supplement their larval-derived resources (Williams 1956). In both species, males compete for the sole ownership of distinctive hilltop territories via conspicuous, noncontact aerial interactions. As with many wars of attrition, it is unclear how contestants may impose costs on rivals or whether these contests are ultimately resolved on the basis of physical or physiological cost asymmetries.

Although little is known about male competitive regimes in *C. austeni*, prior research on *H. ustulata* has indicated that territorial residents are larger on average than non-resident individuals as measured by head width (Alcock 1979; Alcock and Carey 1988). Adult body size co-varies with competitive ability in some related territorial wasps (e.g., *Sphecius grandis* and *Sphecius speciosus*; Hastings 1989; Coelho and Holliday 2001) but not others (e.g., *Philanthus triangulum*; Strohm and Lechner 2000). The relationship between body size and contest outcome within other insect groups, such as butterflies (Kemp 2000), is also inconsistent, and (as noted) it is not intuitively clear how a larger body could confer a mechanistic advantage in a war of attrition-type aerial duel. One possibility is that because of allometry, ontogeny, or other factors, variation in body size may co-vary with variation in other physiological variables that do directly affect flight performance. Size would then serve as an incidental correlate of competitive ability; its apparent importance across species would be determined by the subtleties of its relationship with the primary physical/physiological determinants of flight energetics and power output. We address this hypothesis, along with the hypothesis that physiological condition per se is important, by including body size parameters as predictor variables in our multivariate models of competitive ability for each species.

### Specific Physiological Predictions

The generalized physiological RHP hypothesis contends that some males possess a biomechanical advantage that endows them with increased endurance in an aerial war of attrition. The simplest potential application of this idea is that endurance is mediated by fuel reserves such that the male with the larger energy budget is willing or able to persist longer than his opponent (Marden and Waage 1990; Marden and Rollins 1994). The extended territorial

interactions of both *Hemipepsis ustulata* and *Cuterebra austeni* have the potential to be limited by energy reserves, although we expect that this cost currency may apply particularly in the extreme capital breeder, *C. austeni*. If energetic costs are ecologically relevant in either species, then individuals would be expected to evolve schedules of contest behavior that minimize energetic expenditure and/or that lead to accurate assessments of pairwise energy reserves (Parker 1974; Marden and Rollins 1994). Males in possession of greater energy reserves and thus greater RHP would then tend to win more contests and subsequently accumulate as residents at favored perching territories (Leimar and Enquist 1984).

Because of the logistical difficulties inherent in capturing the winners and losers of discrete contests over hilltop territories, we posed the specific, testable prediction that territorial residents should possess greater energy reserves (per unit flight load) than nonresident individuals. We focus primarily on lipid reserves as a measure of energetic status because many insects use abdominally stored lipids to fuel extended flight (beyond the first few seconds; Crabtree and Newsholme 1975), and this parameter has been implicated as a determinant of contest outcome in certain insect groups (Marden and Waage 1990). However, because adult *H. ustulata* feed at flowers (Williams 1956), it is also possible that this species uses nectar sugars to fuel flight activity. Nectar is composed mostly of water (Yuval et al. 1994) and is stored within the abdominal crop; thus, we use abdominal water content as a surrogate measure of nectar stores in this species.

The second specific application of the flight physiology hypothesis is that acceleration and maneuverability determine the outcome of male contests. As with energy reserves, these parameters have been implicated as determinants of RHP in male odonate contests (Convey 1989; Marden 1989; Plaistow and Tsubaki 2000) and are often discussed with respect to aerial contest ability in insects (Windig and Nylin 1999; Coelho and Holliday 2001; Berwaerts et al. 2002). More agile individuals could gain from an increased ability to avoid potentially damaging collisions or to evade predatory attempts during the contest. Because flying animals generate approximately constant force per unit flight muscle during high-intensity bursts of flight (Marden 1987), the most relevant physiological feature with respect to acceleration and maneuverability is the ratio of flight muscle mass to total body mass (hereafter FMR; Marden 1989; Berwaerts et al. 2002). Here, we specifically predicted that if maneuverability and/or acceleration are important determinants of contest ability, then territorial residents should exhibit higher FMR values than their nonresident counterparts.

## Material and Methods

### *Hilltop Territoriality and Contests in Cuterebra austeni and Hemipepsis ustulata*

The reproductive behavior of male *Cuterebra austeni* and *Hemipepsis ustulata* has been described in detail elsewhere (Alcock 1979, 1981, 2000; Alcock and Schaefer 1983; Alcock and O'Neill 1987; Alcock and Carey 1988; Alcock and Bailey 1997). Briefly, both species perch at and defend nonresource-based encounter sites at hilltops and along ridgelines during a 1.5–2.5-h (*C. austeni*) and 3–4-h morning period (*H. ustulata*) in the Sonoran Desert of central Arizona. Male *H. ustulata* select perches on conspicuous shrubs or small trees (e.g., *Larrea divaricata* and *Cercidium microphyllum*), whereas *C. austeni* prefer to perch on the ground in the center of small, gravelly clearings. At least some individuals of both species are site faithful within and between days and defend their perching sites against conspecific males via conspicuous, apparently stereotyped, noncontact aerial displays. Contests in *H. ustulata* generally consist of rapid (<20 s) chases, but in approximately 5% of cases (Alcock and O'Neill 1987), they escalate to ascending bouts in which the two combatants fly to heights of about 50 m before diving back to the perch territory, only to repeat the ascending flight a variable number of times. Like the wars of attrition exhibited by some territorial male odonates (e.g., *Calopteryx* spp.; Marden and Waage 1990), truly escalated contests in this species may last for more than an hour (Alcock and Bailey 1997). Male *C. austeni* contests are shorter in duration (maximum approximately 3 min) but consist of high-speed chases around the peaktop territory in which the two flies maintain close proximity to each other before one departs (Alcock and Schaefer 1983).

As with most territorial animals, resident male *C. austeni* and *H. ustulata* win most contests, but resident *C. austeni* at the most popular sites are typically defeated and replaced on their second or third day of territorial tenure (Alcock and Schaefer 1983). Territorial *H. ustulata* may retain residency of a site for up to 3 wk (Alcock 1981), although site tenure generally ranges from 7 to 10 d and may vary depending on territory quality (Alcock 2000). In both species, the losers of contests over preferred territories—including usurped residents—often subsequently perch in suboptimal sites at lower elevations around the peak or disperse to nearby peak tops in search of vacant territories.

### *Field Sampling Protocols*

We conducted the field component of this study at two hilltop sites in Maricopa County, Arizona, on 31 d between March 27 and May 26, 2002. The primary site (censused

on a total of 23 d) was Usery Mountain, an approximately 900-m-high peak that has been used extensively in previous studies of insect territoriality (e.g., Alcock and Carey 1988). We also sampled at the site used by Alcock and Schaefer (1983) in their initial study of hilltopping in *Cuterebra*, which is a slightly lower-elevation hilltop (approximately 700 m), approximately 1 km north of Usery Peak. Since both *C. austeni* and *H. ustulata* are active at hilltops for limited morning periods, we sampled for several hours beginning at about 8:00 A.M. but slightly earlier on warmer days.

Our core sampling methodology was the same for each species and consisted of identification and marking of perching residents, recapture of residents after a specified time interval, and capture of subsequent territorial replacement males. However, because of the more frenetic activity and higher population density of *C. austeni*, we used distinctive methods and criteria to classify territorial residents in this species. For *C. austeni*, we staked out either of the two popular hilltop territories (large patches of bare ground near prominent foothills palo verdes, *C. microphyllum*) immediately on arrival and proceeded to capture and mark flies as they moved in to perch at the site. Flies were marked with unique symbols on their dorsal thoracic surface using colored acrylic paints (Liquitex Concentrated Artist Colors) or white Liquid Paper Correction Fluid. We identified resident males as those individuals that were present at the site for at least 30 min (a substantial portion of this species' morning flight period), were observed as the sole returnee after two or more conspecific interactions, and were observed to fly up and chase all incoming flies, other insects, and thrown pebbles that passed overhead within about 0.3 m of their perching location. Once an individual satisfied these criteria, he was captured and placed immediately in an airtight vial within an ice-filled cooler. We then endeavored to capture and retain the next two males that moved in to perch at the site (capturing them as quickly as possible after their arrival). Over the course of this study, we successfully sampled 28 resident-replacement pairs, 21 of which contained two replacements and the remainder contained only one.

Because male *H. ustulata* were less densely distributed than *C. austeni*, we conducted transects at each site to survey a series of known, discrete perching sites (we used the previously established paths at the upper and lower sites, 175 m and 270 m long, respectively, which pass by certain trees that have been used as territorial perches by male wasps for more than 2 decades). Most of the males initially present along these transects were captured and marked, as were newcomers seen in subsequent censuses. We classified as a resident any male that was seen in sole attendance at his site of capture on a following day (usually the very next day). Identified residents were captured and

handled as in *C. austeni*. We then endeavored to capture the next male that flew in to perch at the site on that day; only those pairs ( $N = 31$ ) in which we managed to capture a same-day replacement male were retained for analysis.

#### Physiological Assessments

Individual flies and wasps captured from the hilltop were transported (still within the cooler) to the lab, where they were killed by freezing and immediately weighed (to the nearest  $1 \times 10^{-5}$  g) using a Mettler model H51AR balance. We then isolated and weighed each specimen's thorax and abdomen and measured maximum head width (*C. austeni* to the nearest 0.1 mm and *H. ustulata* to the nearest 0.05 mm) using a calibrated eyepiece micrometer fitted to a dissecting microscope. We scored wing wear in both species using a discrete three-point scale ([1] no visible wing wear, [2] wings with one or a very few nicks, and [3] wings with multiple nicks and fraying) as an index of age. Samples were then stored in a freezer in airtight plastic vials before the lipid analysis, which we initiated approximately 4 mo after the first samples were captured. Before extracting lipids, we dried each specimen at 65°C for 3 d and subsequently weighed whole body mass (the mass of all body parts except the wings), thorax mass, and abdomen mass. Lipid was extracted from both thoraces and abdomens using a microsoxhlet apparatus (see Marden 1989; Marden and Waage 1990). Samples were placed in a fat-free cellulose thimble (Whatman, 10 mm  $\times$  50 mm) plugged with cotton wool and exposed to refluxing petroleum ether for 8 h. This period of time is adequate for complete extraction of lipids from similarly sized insect body parts (Kemp 2002). Samples were dried for another day at 65°C before reweighing, with lipid mass calculated by subtracting postextraction dry mass (of both thorax and abdomen) from preextraction dry mass.

In light of the relatively very small amount of lipid extracted from *H. ustulata* abdomens (refer to table 1), we rechecked the extraction process for this species by placing eight randomly chosen abdomens in the apparatus for another 4 h. Fatless mass of these samples did not differ between 8- and 12-h extraction (paired *t*-test,  $d = 6.7 \times 10^{-5}$  g,  $t_7 = 1.58$ ,  $P = .159$ ), thus confirming the efficacy of the standard extraction method.

#### Statistical Analyses

Fly and wasp data were analyzed using the same general procedures. We used the standardized residuals from regressions of postextraction fresh thorax mass (dependent variable) against total fresh body mass and lipid mass (dependent variable) on fatless fresh body mass to determine the values of FMR and energetic status, respectively, for

**Table 1:** Summary of body composition parameters for each species

Parameter	<i>Cuterebra austeni</i>		<i>Hemipepsis ustulata</i>	
	Residents ( <i>N</i> = 28)	Replacements ( <i>N</i> = 49)	Residents ( <i>N</i> = 31)	Replacements ( <i>N</i> = 31)
Fresh body mass (mg)	267 ± 5.51	251 ± 5.22	343 ± 17.1	283 ± 20.1
Dry body mass (mg)	107 ± 3.46	96.3 ± 3.44	126 ± 6.69	99.9 ± 7.62
Head width (mm)	6.9 ± .1	7.0 ± .1	4.80 ± .05	4.55 ± .10
Fresh thorax mass (mg)	166 ± 2.30	162 ± 2.04	154 ± 7.69	124 ± 8.71
Fatless dry thorax mass (mg)	50.0 ± .630 (.468)	49.3 ± .530 (.511)	52.2 ± 2.71 (.415)	41.5 ± 3.05 (.415)
Thoracic lipid content (mg)	4.37 ± .380 (.041)	3.20 ± .340 (.033)	.830 ± .080 (.007)	.730 ± .100 (.007)
Fresh abdomen mass (mg)	55.1 ± 3.24	44.8 ± 3.09	83.7 ± 5.62	71.2 ± 6.27
Fatless dry abdomen mass (mg)	10.6 ± .300 (.099)	12.2 ± .214 (.126)	29.5 ± 2.22 (.235)	22.5 ± 2.09 (.225)
Abdominal lipid content (mg)	26.4 ± 2.54 (.247)	19.7 ± 2.50 (.204)	2.62 ± .300 (.021)	2.43 ± .460 (.024)
Abdominal water content (mg)			51.5 ± 3.52 (.410)	46.3 ± 4.21 (.464)
FMR	-.0925 ± .189	.0528 ± .143	.238 ± .211	-.238 ± .128
Energetic status	.202 ± .173	-.115 ± .147	-.120 ± .149	.120 ± .203
Abdominal water			-.270 ± .172	.270 ± .173

Note: Means are accompanied by standard errors, and parenthesized values represent proportions relative to total dry body mass. The composite variables FMR, energetic status, and abdominal water are explained in the text.

each specimen. This approach was used to yield size-independent measures of flight muscle and energy stores relative to flight load (body mass) and follows the methodology of Marden and Chai (1991), Marden and Rollins (1994), and Plaistow and Tsubaki (2000). These parameters are believed to offer the best surrogate measures of likely muscular power (thus, acceleration and maneuverability) and of the likely energetic expense of flight (Marden and Rollins 1994; Berwaerts et al. 2002; Kemp 2002). As a further size-independent measure of energetic status in *H. ustulata*, we calculated the residuals from a regression of abdominal water content (a surrogate measure of nectar) on total fresh body mass. We also regressed the total dry body mass, dry thoracic mass, and lipid mass against head width (all variables log-transformed) and used the residuals to estimate how the mass of these parameters changes in each species, relative to eclosion mass, with age (as estimated by wing wear). The use of head width to estimate eclosion mass is based on the premise that adult body size is fixed at maturity in these holometabolous insects (Kemp 2002 and references therein).

We tested the effects of morphological and physiological parameters, including FMR, energetic status (including abdominal water content in *H. ustulata*), total fresh body mass and head width, and the index of age (wing wear), on male territorial status using multivariate logistic regression. Absolute lipid mass was not included in these analyses because this parameter is redundant in the presence of measures of energetic status and total fresh body mass. Initial analyses of the *C. austeni* data, utilizing a within-subjects design, indicated no difference between first and second replacement males with respect to these

parameters (logistic model including all predictors:  $G_5 = 3.18$ ,  $N = 21$ ,  $P = .67$ ). We therefore averaged the parameter values across replacements within each sample group. Since resident flies and wasps were partly matched to replacements, we employed a modified, within-subjects analysis by randomly designating one individual of each pairing as the focal individual and subtracting his parameter values from those of his paired partner. The subsequent logistic regressions were carried out with the binary dependent variable coded as 0 or 1, indicating the focal male as either a replacement or resident. These analyses evaluated the ability of the predictor variables to explain the probability that the focal male was a resident. For comparison, we also conducted the conventional between-subjects logistic regression analysis in each case (the difference between within- and between-subjects analyses is analogous to the difference between a paired and independent *t*-test). In all regressions, we specified the maximum likelihood loss function and selected the most parsimonious model using the stepwise elimination procedure (Hardy and Field 1998). We based the order of elimination of parameters on their Wald values (a *z* score calculated as the regression coefficient divided by its standard error; Tabachnik and Fidell 1996).

Finally, there are some inconsistencies in the literature regarding the use of dry and fresh masses to estimate flight load (e.g., Marden and Waage 1990; Plaistow and Siva-Jothy 1996). Our results are qualitatively identical regardless of whether fresh or dry masses are used to derive the composite parameters (FMR, etc.); hence, only those obtained using fresh mass are presented here.

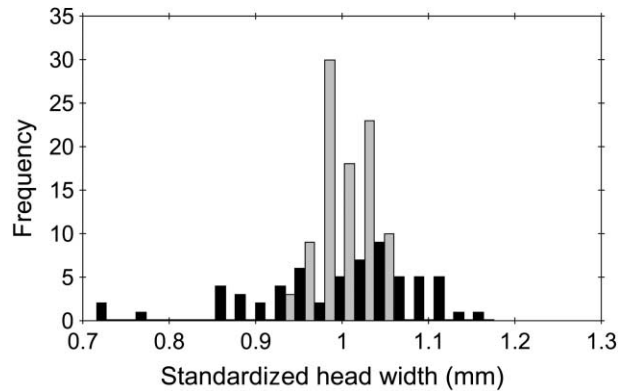
## Results

### General Morphological and Physiological Profiles

The mean parameter values for *Cuterebra austeni* and *Hemipepsis ustulata* (table 1) indicate superficial similarities between the two species with respect to most body composition parameters except lipid stores, which appear proportionately higher in *Cuterebra*. In addition, variation in head width—our measure of mature body size—was significantly greater in *H. ustulata* ( $F$ -test on variances in head width;  $F = 5.68$ ,  $df = 61, 92$ ,  $P < .00001$ ; fig. 1). Body mass parameters also co-varied tightly with head width in this species (table 2), suggesting that much of the intrapopulation variance in size and mass (of wasps of varying ages) relates to the size attained at maturity rather than changes that take place after maturity. By contrast, body mass parameters were almost perfectly independent of head width in *C. austeni* (table 2). Substantial mass changes therefore take place throughout the adult lifetime of *C. austeni* but not *H. ustulata*, which is the first line of support for the idea that these species exemplify capital and income breeding strategies, respectively.

Linear regressions conducted to yield size-standardized residuals of fatless thoracic mass, lipid content (the values of FMR and energetic status, respectively), and abdominal water content were highly significant in all cases (table 2). Regressions involving head width were also highly significant in *H. ustulata*; however, only fatless thorax mass co-varied significantly with this parameter in *C. austeni*. As previously noted, lipid mass was almost perfectly independent of head width in *C. austeni* (table 2). We nonetheless retained the residuals from all regressions (simply for convenience since the residual values from nonsignificant regressions were standardized to a mean of 0 yet were otherwise basically unchanged) and compared them across wing-wear classes to investigate age-specific patterns of resource use. We also examined the efficacy of our surrogates of energetic stores in *H. ustulata* by calculating the proportion of abdominal mass composed of lipids and water. These parameters accounted for approximately 85% of variation in fresh abdominal mass (once the variation due to size at eclosion was removed by regressing the relevant parameters against head width); hence, they were clearly the most significant constituents of this body region (regression:  $F = 367.5$ ,  $df = 1, 67$ ,  $P < .0001$ ,  $R^2 = 0.846$ ).

As expected, age-specific patterns of body composition and adult resource utilization differed markedly between species. In *C. austeni*, both body mass ( $F = 7.01$ ,  $df = 2, 90$ ,  $P < .005$ ) and lipid mass ( $F = 7.30$ ,  $df = 2, 90$ ,  $P < .005$ ) varied significantly with adult age and in a superficially similar manner (fig. 2), suggesting that body mass variation in adult *C. austeni* is age related and mostly



**Figure 1:** Distribution in body size at eclosion in *Cuterebra austeni* (gray columns) and *Hemipepsis ustulata* (black columns). Values for each species are standardized by their respective mean to facilitate interspecific comparison.

reflects the loss of lipids. This finding is consistent with an extreme capital breeding regime of resource use. Thoracic mass was constant across wing-wear classes ( $F = 0.0033$ ,  $df = 2, 90$ ,  $P = .997$ ); hence, flight musculature is not eroded with age in this species. By contrast, standardized body mass ( $F = 0.029$ ,  $df = 2, 66$ ,  $P = .97$ ), lipid mass ( $F = 1.62$ ,  $df = 2, 66$ ,  $P = .21$ ), thoracic mass ( $F = 1.22$ ,  $df = 2, 66$ ,  $P = .30$ ), and abdominal water mass ( $F = 1.35$ ,  $df = 2, 66$ ,  $P = .27$ ) did not vary significantly with age in *H. ustulata* (fig. 2). These patterns are consistent with a strategy of adult resource acquisition/allocation involving continued supplementation of larval-derived nutrients.

### Factors Associated with Territorial Status

*The Cuterebrid Fly, Cuterebra austeni.* The initial, within-subjects logistic model including all parameters (i.e., body mass, head width, age, energetic status, FMR) was significant ( $G_5 = 11.93$ ,  $N = 28$ ,  $P = .036$ ); however, we sequentially removed all parameters except energetic status because of their nonsignificant contributions ( $G_1 < 1.73$ ,  $P > .19$  in all cases). The final, highly significant model ( $G_1 = 9.10$ ,  $N = 28$ ,  $P = .0026$ ) included energetic status only and represented the probability of the focal male being a resident as  $y = (e^{0.075+1.042x})/(1 + e^{0.075+1.042x})$ , where  $x =$  energetic status. The positive regression coefficient ( $\beta = 1.042$ ) for energetic status indicates that residents typically possessed higher values of this parameter than did replacements (fig. 3). Hence, as expected, resource availability appears to have strong behavioral consequences in this extreme capital breeder. This result was near perfectly replicated in the between-subjects design, in which the most parsimonious model also included en-

**Table 2:** Summary of linear regression analyses performed to yield the values of FMR, energetic status, and abdominal water content and eclosion mass-corrected values of dry body mass, dry thorax mass, and lipid mass (using head width as a surrogate measure of eclosion mass) for each species

Species and parameter	Regression	ANOVA			
		<i>F</i>	df	<i>P</i>	<i>R</i> <sup>2</sup>
<i>Cuterebra austeni</i> :					
FMR	Fatless thoracic mass = .086 + .285 total body mass	130.7	1, 75	<.0001	.64
Energetic status	Lipid mass = -.126 + .651 fatless body mass	76.0	1, 75	<.0001	.50
Total body mass	Total body mass = 1.57 + 1.54 head width	3.1	1, 91	.079	.03
Thorax mass	Fatless thoracic mass = -.072 + .062 head width	26.8	1, 91	<.0001	.23
Lipid mass	Lipid mass = 1.57 + .634 head width	.023	1, 91	.88	.0002
<i>Hemipepsis ustulata</i> :					
FMR	Fatless thoracic mass = .0021 + .436 total body mass	1,828.2	1, 60	<.0001	.97
Energetic status	Lipid mass = -.00085 + .0134 fatless body mass	27.99	1, 60	<.0001	.31
Abdominal water	Abdominal water = -.0071 + .178 total body mass	226.1	1, 60	<.0001	.79
Total body mass	Total body mass = -1.93 + 4.27 head width	1,532.0	1, 67	<.0001	.96
Thorax mass	Fatless thoracic mass = -2.59 + 4.13 head width	1,716.0	1, 67	<.0001	.96
Lipid mass	Lipid mass = -6.46 + 4.81 head width	61.6	1, 67	<.0001	.48
Abdominal water	Abdominal water = -2.33 + 3.97 head width	234.3	1, 67	<.0001	.78

ergetic status only ( $G_1 = 8.68$ ,  $N = 56$ ,  $P = .0032$ ; energetic status  $\beta = 0.907$ ). The congruence between these two analyses reflects very little between-groups variation in mean parameter values; in other words, resident flies at different territories and different days were largely uniform with respect to morphology and physiology (relative to the differences between resident and replacement males).

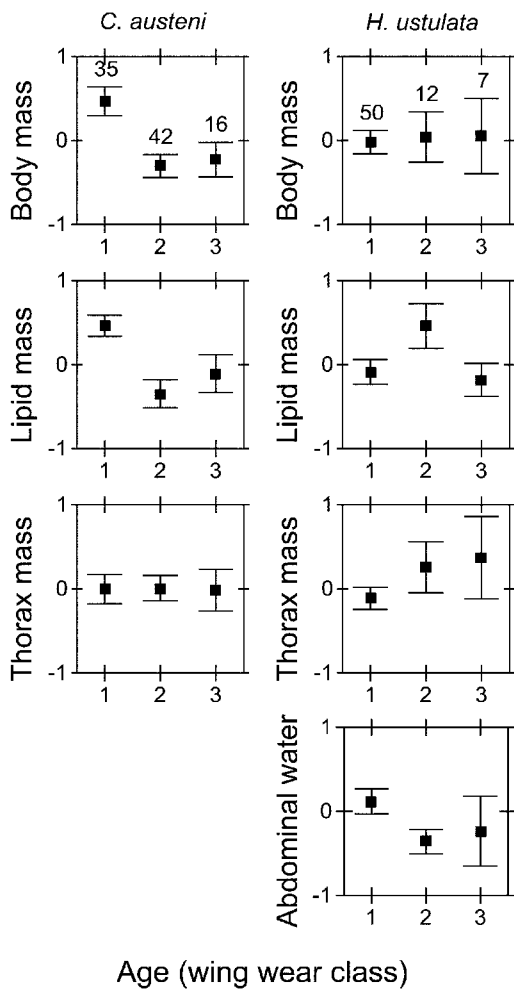
*The Pompilid Wasp*, *Hemipepsis ustulata*. The initial within-subjects model (which included all variables) was highly significant ( $G_6 = 21.25$ ,  $N = 31$ ,  $P = .0016$ ). We subsequently removed total fresh body mass ( $G_1 = 0.075$ ,  $P = .78$ ), FMR ( $G_1 = 0.51$ ,  $P = .48$ ), and age ( $G_1 = 2.81$ ,  $P = .094$ ) but retained energetic status ( $G_1 = 4.55$ ,  $P = .033$ ), abdominal water content ( $G_1 = 4.26$ ,  $P = .039$ ), and head width ( $G_1 = 10.64$ ,  $P = .0011$ ). Head width was the most powerful predictor (as indicated by the loss functions), but a model with this parameter removed remained significant ( $G_2 = 7.22$ ,  $P = .027$ ). Hence, the predictive usefulness of energetic status and abdominal water content extends beyond their ability to account for residual variance not explained by head width. The final model ( $G_3 = 17.86$ ,  $N = 31$ ,  $P = .00047$ ) represented the probability of the focal male being a resident as  $y = (e^{0.247+3.311x-1.012z-1.020w}) / (1 + e^{0.247+3.311x-1.012z-1.020w})$ , where  $x =$  head width,  $z =$  energetic status, and  $w =$  abdominal water content. The probability of residency thus co-varied positively with head width (fig. 4) but negatively with both energetic status and relative abdominal water content (fig. 5). These results show that residents were typically larger wasps, yet counter to the energetic constraint

hypothesis, they possessed relatively smaller amounts of total lipids and abdominal water than replacement males.

In additional contrast to the situation in *C. austeni*, we found some discordance between the within- and between-subjects analyses of *H. ustulata* data. The initial between-subjects model, including all variables (age, body mass, head width, FMR, energetic status, and abdominal water content) was only marginally significant ( $G_6 = 12.76$ ,  $N = 62$ ,  $P = .047$ ). Further investigation revealed that age, body mass, FMR, and energetic status described nonsignificant amounts of variance in this model ( $G_1 < 2.68$ ,  $P > .15$  in all cases). A model including only head width and abdominal water content was significant ( $G_2 = 10.46$ ,  $N = 62$ ,  $P = .0054$ ). As with the within-subjects case, these parameters co-varied with the probability of residency in opposite directions (regression coefficients = 1.494 and  $-0.620$ , respectively).

## Discussion

Animals that compete for resources via noncontact aerial wars of attrition present an interesting case because it is not immediately clear how persistence imposes fitness costs on the contestants. To the extent that territory ownership equates with mating success, these species also afford an opportunity to examine whether and how male fitness is mediated by life-history traits such as age, size at maturity, and lifetime regimes of resource utilization. In this study, we examined the relevance of morphological and physiological flight-related parameters to territorial residency status in two insect species, one of which was a suspected extreme capital breeder (*Cuterebra austeni*) and

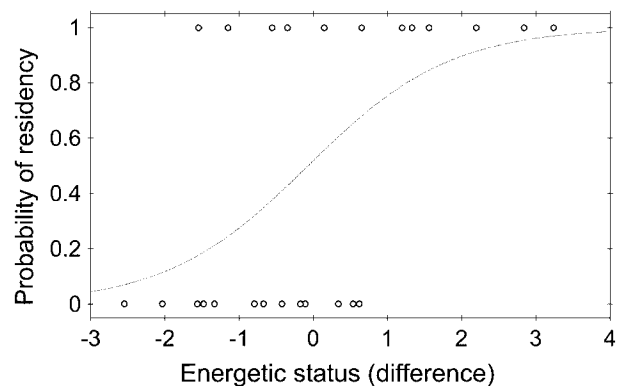


**Figure 2:** Mean body mass, thorax mass, and lipid mass of *Cuterebra austeni* (left plots) and *Hemipepsis ustulata* (right plots), grouped by age (wing wear). All values are standardized by eclosion mass (using head width as a surrogate of mass at eclosion; see table 2), and the common sample size is given in each species' body mass plot.

another that we anticipated would exemplify an income breeding strategy (*Hemipepsis ustulata*). Our initial physiological investigations confirmed these a priori resource-use classifications: lipid reserves (a measure of long-term energy stores) declined with a surrogate measure of age in *C. austeni*, whereas likely energy stores appeared unchanged with age in *H. ustulata*. Second—and more significantly—our multivariate analyses revealed striking differences between these species with respect to the physical correlates of territorial status. Residency in *C. austeni* covaried tightly with a size-independent measure of energetic availability, and this relationship operated in the anticipated direction of greater energy stores in resident males. Resource holding potential in this species therefore appears

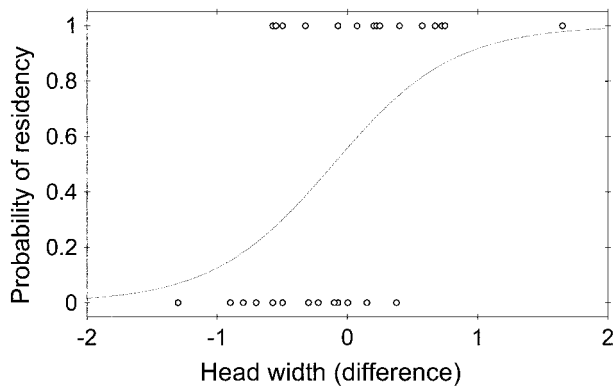
to be determined simply by energy stores. In contrast, the final multivariate model of residency in *H. ustulata* invoked no less than three independent predictors (primarily body size/mass per se). Potential measures of energy stores correlated negatively with residency status in this species, suggesting that residents may actually possess smaller energy stores than nonresident males. Our analysis therefore finds little evidence that competitive regimes are mediated by flight energetics in *H. ustulata*, unlike *C. austeni*. This is consistent with the notion that lifetime patterns of resource acquisition have important consequences for behavioral evolution in animals that compete for resources via “weaponless” persistence duels.

Only a handful of studies have revealed direct relationships between male flight physiology and contest outcome in species that engage in aerial contests (Convey 1989; Marden 1989; Marden and Waage 1990; Marden and Rollins 1994; Plaistow and Siva-Jothy 1996; Coelho and Holliday 2001). Of these, clearly the most compelling are investigations featuring damselflies in the genus *Calopteryx*, in which male contests equate to energetic wars of attrition (Marden and Waage 1990; Plaistow and Siva-Jothy 1996), and the dragonfly *Plathemis lydia*, in which aerial performance (FMR) appears more important (Marden 1989). The primary energetic currency in both *Calopteryx* and *Plathemis* is lipid reserves (Marden and Waage 1990; Plaistow and Siva-Jothy 1996); however, members of each genus differ with respect to how these reserves are utilized. Whereas individuals of the damselfly *Calopteryx maculata* (in which RHP is determined by energetics) accumulate lipid stores during a prereproductive “teneral” adult stage and expend them thereafter in the manner of a capital breeder (Marden and Waage 1990), *P. lydia* appear to re-



**Figure 3:** Logistic model of the probability of the focal male *Cuterebra austeni* being a resident as a function of energetic status. Energetic status is calculated as the residual from a regression of lipid mass on fat-free fresh body mass and is represented here as the difference between the values for focal and nonfocal individuals.





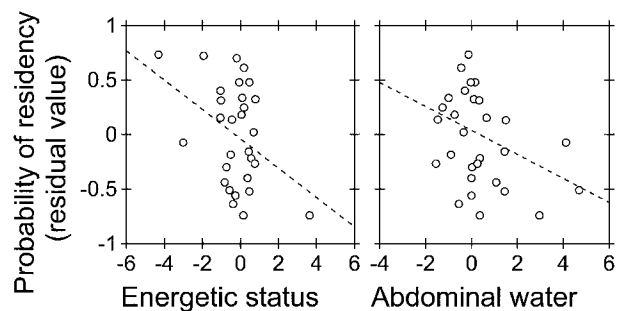
**Figure 4:** Logistic model of the probability of the focal male *Hemipepsis ustulata* being a resident as a function of the major predictor, head width. Head width is represented here as the difference between the values for focal and nonfocal individuals.

plenish their reserves throughout their territorial lifetime (J. H. Marden, unpublished data). These odonates therefore appear to support, at least superficially, the idea that lifetime strategies of resource utilization have consequences for behavioral evolution in species that compete via aerial persistence duels. Clearly, however, a more formal comparative analysis including appropriate phylogenetic controls will ultimately be required to assess the predictive capabilities of this hypothesis.

The data presented here strongly suggest that territoriality in the bot fly *C. austeni* is mediated by the same energetic constraints operating among capital breeding *Calopteryx* damselflies (Marden and Waage 1990; Plaistow and Siva-Jothy 1996). However, there are two caveats to this conclusion. First, our analysis suffers from a slight loss of resolution owing to the fact that we assayed regimes of territorial residency rather than the dynamics and outcome of discrete contests. This means that we cannot presently identify the precise mode of action of the energetic asymmetry, nor can we analyze specific phenomena such as the possibility of pairwise assessment during the flight interactions (*sensu* Parker 1974; Marden and Rollins 1994). Second, our analysis of residency status, although of a statistically controlled multivariate nature, is ultimately correlative. Thus, it remains possible that an unmeasured covariate of energetic status could instead operate to mediate competitive regimes in this system. We consider this possibility unlikely, however, given the specificity of the energetic status parameter and the consensus for this intuitively appealing result across other insect groups. Flight energetics is also invoked as an important determinant of reproductive success in lekking or swarming insects that compete primarily via scramble compe-

titition (e.g., Petersson 1989; Sartori et al. 1992; Otronen 1995; Yuval et al. 1998).

Whereas the *C. austeni* solution appears relatively clear-cut, the situation in *H. ustulata* exemplifies the general interpretive difficulties that surround war of attrition-type contest competition (Kemp and Wiklund 2001). Our primary finding that head width (i.e., body size) predicted regimes of territorial residency—although consistent with prior investigations (Alcock 1979, 1981; Alcock and Bailey 1997)—was weakened by the almost perfect covariance between this parameter and others such as total body mass and thoracic mass (table 2). Head width was thus statistically “chosen” as the key predictor because it best predicted residency, but it remains possible that one of the other covariates is more biologically significant (Kemp 2000). Nevertheless, all of the highly correlated variables in this instance are measures of body size or mass, and it is not intuitively obvious how these qualities could provide a competitive edge in aerial wars of attrition (Strohm and Lechner 2000; Kemp and Wiklund 2001). Empirical investigations have failed to reveal a consistent effect of size across and/or within the relevant insect groups (e.g., Hastings 1989; Strohm and Lechner 2000; Coelho and Holliday 2001; Kemp and Wiklund 2001). For example, consider the solitary sphecids wasps *Sphecius grandis*, *Sphecius speciosus*, and *Philanthus triangulum*, all of which are territorial and compete via elaborate aerial persistence duels. Although body size relates to contest outcome in the former two species (as do age and flight musculature, respectively; Hastings 1989; Coelho and Holliday 2001), this parameter appears independent of territorial success in *P. triangulum* (Strohm and Lechner 2000). One possibility for this discrepancy is that the aerial contests are ultimately settled on the basis of some other parameter (such as



**Figure 5:** The relationships between energetic status and abdominal water content (both calculated as focal male minus nonfocal male values) and the residual probability of territorial residency in *Hemipepsis ustulata*. The values of residency probability depicted here are residuals because the variance explained by the major predictor, head width, has been removed (using logistic regression).

maneuverability; Coelho and Holliday 2001), which itself varies sporadically with body size across species. However, our data provide no support for this idea. The most parsimonious multivariate model of residency in *H. ustulata* included body size as a primary predictor even in the presence of potentially more relevant and sophisticated flight performance parameters.

An alternate possibility for the phylogenetically inconsistent size effect is that the relevance of this parameter is ultimately determined by the dynamics of the contest itself. Larger individuals generally have greater ability to inflict injury costs on their opponent and/or minimize their own rate of cost accrual, as evidenced by the importance of body size as a determinant of RHP in animals that grapple or wrestle for mating opportunities (reviews in Huntingford and Turner 1987; Alcock and Houston 1996). If some apparent war of attrition-type contests carry injury risks or ultimately escalate to conventional grappling duels, then larger males would be expected to possess greater RHP and thus win more often. The sphecid wasp situation appears to support this idea because aerial contests in *P. triangulum* (in which body size is not important) never involve physical contact (Strohm and Lechner 2000), whereas *S. speciosus* contests escalate to butting, grappling, and falling to the ground, and larger males are competitively advantaged (Coelho and Holliday 2001). Hastings (1989) reported that in *S. grandis*, another species in which RHP is clearly related to body size, aerial contests involve intense physical contact and may ultimately result in injuries to wings and other bodily appendages. Also supportive is the apparent irrelevance of body size to competitive regimes in other insect groups that compete via truly noncontact displays—for example, butterflies (Kemp 2000). However, our results conflict with this general pattern because body size in *H. ustulata* correlates chiefly with territorial residency and yet even the most escalated contests in this species involve negligible physical contact (Alcock and Bailey 1997). One of us (J.A.) has charted the reproductive behavior of this species for more than 20 yr and never witnessed a single injury sustained as a result of a territorial male interaction. Thus, notwithstanding the intriguing question of why closely related wasps compete via different interactions, it appears that size-correlated asymmetries in something other than injury costs are operating to settle *H. ustulata* duels.

Another interesting finding was that likely energy stores in *H. ustulata* correlated negatively with residency status (fig. 5). This could indicate that like the males of other species that defend nonresource-based territories (e.g., butterflies; Kemp and Wiklund 2001), resident *H. ustulata* have relatively reduced foraging opportunities. In any event, this result mediates strongly against the energetic war of attrition hypothesis, especially when contrasted with

the apparently clear cases presented by *C. austeni* (this study) and *Calopteryx* damselflies (Marden and Waage 1990; Plaistow and Siva-Jothy 1996). Of course, it could always be argued that energy sources not assayed in this study, such as glycogen, glucose, or trehalose, are more ecologically relevant to *H. ustulata* and ultimately mediate contest persistence in this species (sensu Yuval et al. 1994). We cannot unequivocally reject this possibility, but there would be the problem of where these compounds are stored since lipids and water comprise almost 85% of total fresh abdominal mass. Furthermore, because escalated contests in this species may last longer than 1 h (Alcock and Bailey 1997), it is unlikely that muscular stores (i.e., thoracic stores of glycogen, arginine phosphate, and the like) could fuel such extended activity (Crabtree and Newsholme 1975). The other possibility is that body size scaling effects act in some way that grants larger animals a proportionately greater advantage with respect to energy utilization. However, this advantage would have to be significant enough to compensate for the relatively reduced energy stores apparently possessed by resident wasps encountered throughout this study.

In general terms, our investigation therefore finds no support for the idea that contest participation and success in *H. ustulata* is mediated simply by RHP asymmetries relating to flight performance. This suggests that either more complex solutions be sought in the future or that asymmetries in other factors, such as the likely payoff of residency (e.g., Johnsson and Forser 2002), differ between contestants of different body size and therefore settle these disputes. In this sense, *H. ustulata* offers a valuable model species in the study of war of attrition contest evolution and may even shed new light on those situations in which body size is presently thought to mediate aerial contest outcome simply and directly through its effects on physical fighting ability (e.g., Hastings 1989; Coelho and Holliday 2001). Owing to the highly intercorrelated nature of body size parameters, we suggest manipulative experiments (e.g., the addition of weights to manipulate FMR and the center of body mass; Srygley and Kingsolver 2000) may be ultimately required to resolve the matter. Nonetheless, the data presented here provide a mix of positive and negative support for the idea of intrinsic RHP differences in animals that compete via aerial wars of attrition. At least some of this disparity appears related—in the predicted direction—to interspecific differences in lifetime regimes of resource acquisition and utilization, a finding that underscores how the study of sexual selection may be enriched by an explicit consideration of life-history principles.

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