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Selection on weapon allometry in the wild

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Abstract

Allometry is the scaling relationship between a trait and body size. This relationship can often explain considerable morphological variation within and among species. Nevertheless, much remains unknown about the factors that underlie allometric patterns. For example, when different allometric relationships are observed amongst closely related species, these differences are regularly considered to be products of selection. However, directional selection on allometry (particularly the slope) has rarely been tested and observed in natural populations. Here, we investigate selection on the scaling relationship between weapon size and body size (i.e., weapon allometry) in a wild population of giant mesquite bugs, *Pachylis neocalifornicus* (previously *Thasus neocalifornicus*). Males in this species use their weapons (enlarged femurs) to compete with one another over access to resources and females. We found that large males with relatively large weapons successfully secured access to mates. However, we also found that small males with relatively small weapons could access mates as well. These two patterns together can increase the allometric slope of the sexually selected weapon, suggesting a straightforward process by which the allometric slope can evolve.

Keywords: allometry, body size, insects, sexual selection, weapons

Many morphological traits are highly correlated with an individual's size (Brown & West, 2000). Therefore, the scaling relationships between traits and body size (i.e., allometry) may explain considerable morphological diversity within and among species (Frankino et al., 2009; Gould, 1966; Thompson, 1942). Understanding the processes that promote and maintain morphological diversity is a fundamental aim of evolutionary biology, making it important to understand the factors that alter allometry.

Allometric relationships are often expressed by the equation $y = \alpha x^b$, given that most traits show a nonlinear relationship with body size (Huxley, 1924). In this equation, y is trait size, x is body size, and α and b are parameters describing the relationship between the two. This power law can also be expressed as a linear equation when the x and y variables are log-transformed. This results in the equation $\log(y) = (b*\log(x)) + \log(\alpha)$. Thus, $\log(\alpha)$ is the intercept and b is the slope of the linear regression. If body size and trait size are proportional to one another then the slope (b) will equal 1 (isometry). However, if the trait gets disproportionally larger as body size increases, then the slope will be >1 (hyperallometric scaling or positive allometry). Alternatively, if the trait gets disproportionally smaller as body size increases, then the slope will be <1 (hypoallometric scaling or negative allometry).

Allometry can be measured within individuals during growth (developmental/ontogenetic allometry), among conspecific individuals at the same developmental stage (e.g., adults; static allometry), and across species (evolutionary allometry). All three measures are of particular interest in the study of sexual selection because of the steep, positive allometric slopes that are often associated with sexually selected traits (i.e., hyperallometric scaling of weapons and ornaments; Eberhard et al., 2018; O'Brien et al., 2018; Rodríguez & Eberhard, 2019). The static allometries of sexually selected traits have arguably received the most attention, with numerous studies finding that traits have positive allometries within species. Examples include the horns of beetles (Kawano, 1997), claws of fiddler crabs (Rosenberg, 2002), and eyespans of stalk-eyed flies (Baker & Wilkinson, 2001). These findings originally led researchers to hypothesize that sexually selected traits almost universally exhibit positive static allometries (Kodric-Brown et al., 2006). However, subsequent studies have shown that this is not necessarily the case (Bonduriansky, 2007; Voje, 2016). Although static allometry patterns have repeatedly been quantified, much less is known about the evolutionary processes that underlie them.

There are various ways that the scaling relationships between a trait and body size (i.e., allometry) can evolve. Two of the most straightforward ways are by changing the slope and/or by changing the intercept (Figure 1). Artificial selection experiments have shown that the static allometry of a trait can be heritable and can evolve in response to selection (Bolstad et al., 2015; Egset et al., 2012; Frankino et al., 2005; Stillwell et al., 2016; Wilkinson 1993). These studies also suggest that the intercept can evolve more quickly than the slope (Bolstad et al., 2015; Egset et al., 2012).
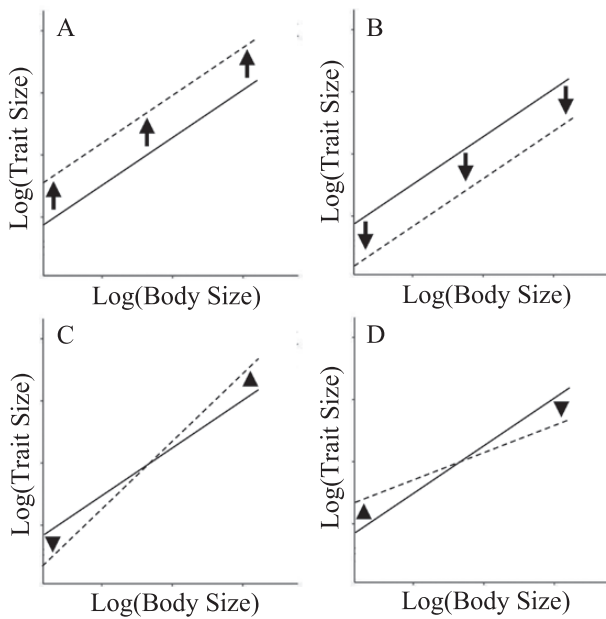
Figure 1. Hypothetical graphs illustrating different ways that static allometries can change in a population over time. One way that allometry can change (i.e., go from the solid line to the dashed line) is by altering the y-intercept. The y-intercept can increase (A) or decrease (B). In scenarios (A) and (B), body size stays the same while trait size proportionally increased (A) or proportionally decreased over time (B). Note that the length and direction of the arrows in (A) and (separately, B) are the same across the range of body sizes. In practical terms, positive selection on the y-intercept (A) results in the population now (dashed line) having larger traits than before (solid line), even when correcting for body size. Another way that allometry can change is by altering the slope. The slope can become steeper (C) or shallower (D). Again, in scenarios (C) and (D), body size stayed the same. In scenario (C), the population changes so that now (dashed line) the large males have larger traits, and the small males have smaller traits than before (solid line). This ultimately increases variation in trait size. Conversely, in scenario (D), variation in trait size decreases.

Despite these important studies of artificial selection on allometry in the lab, relatively few studies have quantified selection on allometry in the wild (O'Brien et al., 2017; Pélabon et al., 2014). Even fewer studies have explicitly tested for directional selection that may alter the allometric slope (Figure 1). When such studies have been conducted, stabilizing selection has been observed instead (O'Brien et al., 2017). Hypothetically, previous selection analyses that focused on particular traits (e.g., weapon size) rather than on allometry per se might have captured directional selection on the allometric slope. However, we have not seen this pattern explicitly described. Directional selection on allometric slopes could help explain a widespread pattern: the variation in the static allometric slopes of sexually selected traits among species (e.g., variation in allometric slopes in eyespans among stalk-eyed flies; Baker & Wilkinson, 2001; Voje & Hansen, 2013).

To test for selection on allometry in the wild we conducted analyses of phenotypic selection on a natural population of the giant mesquite bug, *Pachylis neocalifornicus* (Insecta: Hemiptera: Coreidae; previously *Thasus neocalifornicus*; Costa & Campos, 2022). Like several other coreids (Eberhard, 1998; Mitchell, 1980; Miyatake, 2002; Procter et al., 2012), males in this species have sexually dimorphic hind legs that they use in combat with other males over access to females and territories (Supplementary Figure S1; Emberts & Wiens, 2021; Graham et al., 2022). Specifically, males will place their tibial spines onto the wings of their rivals during fights and squeeze, which can result in injuries that have metabolic costs and that impair flight performance (Emberts & Wiens, 2021; Emberts et al., 2021b). Individuals with larger hind leg size can squeeze their rivals harder, likely increasing the amount of injury they can inflict (Graham et al., 2022). Although fights can generate injuries, death from a fight has not been reported in this species, presumably because the losing male flees (Emberts & Wiens, 2021). Thus, individuals may survive but lose a mating opportunity. For this study, we specifically investigated selection on weapon size (hind leg size), body size, and the scaling relationship between the two (i.e., weapon allometry). We were particularly interested in testing for directional selection on the allometric slope.

Methods

Data collection

We obtained three snapshots of selection from a single population of *Pachylis neocalifornicus* over 2 years. The population was located just north of the town of Rio Rico in Santa Cruz County, Arizona, USA (31.5294, –111.0218). Data for the first snapshot were collected on August 9, 2021, whereas data for second and third snapshots were collected on July 19 and 22, 2022, respectively. We sampled at three timepoints because selection patterns can vary over time (Punzalan et al., 2010; Siepielski et al., 2009). Thus, taking multiple temporal samples allowed a more dynamic perspective on how selection operates.

For each snapshot, all individuals observed in a ~2,500 m², easily accessible area were actively collected. This area was discrete because it contained a high density of velvet mesquite trees (*Prosopis velutina*). Individuals were collected by hand by two researchers for 1 hr for each snapshot. Most individuals were found in clusters on new foliage growth of velvet mesquite (Figure 2), but clusters were also sometimes found on the fruits (seed pods). Individuals were observed feeding on both new foliage and fruits. Growth sites with new foliage were frequent, and there generally appeared to be more new foliage growth sites than individuals of *Pachylis neocalifornicus* (Supplementary Figure S2). Thus, it seems unlikely that females clustered exclusively because feeding resources were limited. Nevertheless, some feeding sites may be preferable (e.g., have more nutrients) and an uneven resource distribution might explain why females cluster.

Clusters ranged from two to four individuals, and generally consisted of one male and one to three females. Only individuals that were touching were considered part of a cluster. These clusters were discrete and obvious (Figure 2); multiple clusters were never found on the same feeding resource. Most pairs/groups had individuals that were actively mating during collections, but since we prioritized collecting all individuals before they escaped for the first snapshot, it was not always possible to record which specific individuals were actively mating. However, for the second and third snapshots, we were able to note which males were actively mating at the time of collection. Each individual and group was assigned a unique identification number. Some individuals were found alone.

All individuals were preserved and morphological measurements of males were taken in the lab (Supplementary Figure S3). First, each individual was photographed next to

a scale bar with a Canon EOS 7D camera. Maximum pronotal width and maximum femur width of the right hind leg (excluding spines) were then measured to the nearest micrometer in ImageJ. Pronotal width is a widely used proxy for body size in this clade (Emberts et al., 2020; Procter et al., 2012) and hind femur width is a good proxy for weapon size (Emberts et al., 2021a). In *P. neocalifornicus*, hind femur width is sexually dimorphic (Graham et al., 2022). Moreover, most of the muscle that males utilize during combat resides in the femur; thus, the amount of force that males can exert can be explained by maximum femur width (Graham et al., 2022). Finally, femur width seems to be more important than spine length for explaining variation in the severity of fighting-related damage observed among species of Coreidae (i.e., the family to which *P. neocalifornicus* belongs; Emberts et al., 2021a).

Several coreid species can autotomize (drop) their legs, including *P. neocalifornicus* (Emberts et al., 2016, 2020). Among 245 males collected, seven were missing one hind leg (2.9%). For the males that autotomized their right hind leg, the left was measured instead. Femur widths in *P. neocalifornicus* are generally symmetrical (Supplementary Figure S4), so this change should have no impact.

Measures of fitness

We used three measures of fitness in this study. We first examined selection on males that were found with at least one female (coded as "1") relative to those found without any females (coded as "0"). In *P. neocalifornicus*, our observations indicate that mating can be protracted (lasting for at least several minutes) and that a male can only mate with one female at a time, even if a male is found with multiple females. This is because genitalia remain attached during mating. Thus, this binomial partitioning of males provides a conservative estimate of mating success, with the assumption that a male would have mated with at least one of the females in his cluster. This assumption is supported by our observation that a majority of males (65.4%, 51/78) found in contact with a female were actively in copula in our second and third snapshot (Supplementary Dataset S1; Emberts et al., 2023).

For our second fitness measure, we used actual mating events. This is our most direct fitness proxy, but we were only able to collect active mating data for our second and third snapshots. An additional benefit of this proxy is that it takes into consideration the role that females have in the mating process. For example, female *Narnia femorata* (a closely related species) can refuse to mate by keeping their genital plates closed (Gillespie et al., 2014; Cirino & Miller, 2017). Thus, using actual mating events takes into consideration the possibility that some females may reject males.

As a final fitness proxy, we examined the number of females that a male was in contact with (i.e., 0, 1, 2, or 3). This proxy assumes that the male (if not collected) would eventually mate with all the females in his cluster. This measure was potentially important in that the other proxies do not reflect whether a male gained access to multiple females (in a cluster). Overall, all three fitness proxies had distinct advantages and disadvantages, and so we considered all three.

We used mating events and access to females as proxies for male fitness in this study, as opposed to more direct fitness proxies (e.g., number of offspring). Although we do not know each individual's fitness contribution to the next generation, we know which males were able to secure potential mates (a necessary step towards producing offspring). Moreover, we were able to collect actual mating data (i.e., males in copula) for our second and third snapshots; we confirmed that the results were largely congruent using both potential mates and actual mating events (see Results).

We used relative fitness of individuals because selection and its evolutionary consequences are dependent on an individual's fitness in relation to other competing individuals, as opposed to an individual's absolute fitness. Relative fitness
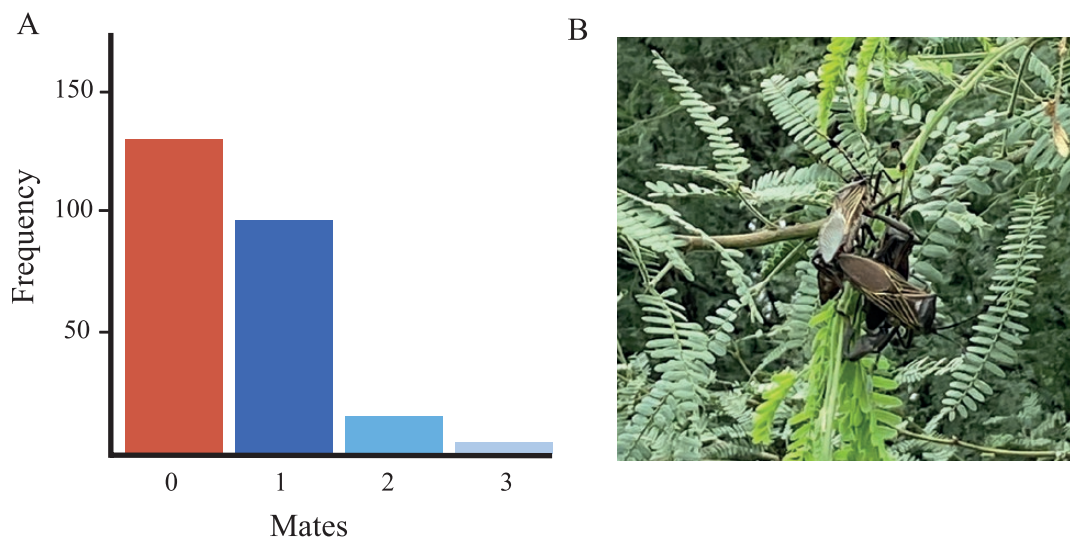

Figure 2. (A) Number of females (mates) found with each of the 245 male *Pachylis neocalifornicus* measured in this study. Most groups of individuals consisted of one male and one female. One group consisted of two males and two females. For our analyses we considered each male in this latter group to be with one female. (B) A representative group, including one male and three females on new foliage growth of the velvet mesquite tree (*Prosopis velutina*). The male (i.e., the bottom right individual) is mating with the female in the foreground (i.e., the top left individual). Note how tightly clustered these four individuals are.

was calculated by dividing an individual's mating success by the average mating success of all the sampled males in the population. For example, when we used actual mating events for our fitness proxy, 51 of the 185 males (snapshots 2 and 3 combined) were found mating. Thus, the average mating success was 27.56%. A fitness of 1 (i.e., an individual was mating when captured) divided by 0.2756 equals 3.63. A fitness of 0 (i.e., an individual was not mating when captured) divided by 0.2756 equals 0. Therefore, using this fitness proxy, mating males had a relative fitness of 3.63 and nonmating males had a relative fitness of 0. This data conversion prevented us from conducting logistic regressions with our binary data. Thus, we used linear regressions instead (all models assumed a Gaussian distribution and an identity link function).

Statistical analyses

We used two main statistical approaches to investigate selection on weapon size, body size, and weapon allometry. The first was a model-comparison approach. Specifically, we compared several generalized linear models (GLMs) to determine the factors that best explain a male's relative fitness (i.e., our dependent variable; similar to O'Brien et al., 2017). The second approach involved an analysis of covariance that directly compared static allometry between males with and without access to females.

Model-selection approach

Below, we detail the 15 GLMs compared to determine which factors best explain a male's relative fitness (i.e., the dependent variable). The specific model number, the independent variables in the model, and the hypothesis that we are testing with each model are outlined in Table 1 and are described in detail in the next several paragraphs.

To determine whether weapon size and/or body size (i.e., independent variables) could best explain relative fitness we conducted four generalized linear models (GLMs). Before conducting our analyses, we z-standardized trait values (mean = 0, SD = 1) using the built-in "scale" function in R (version 4.0.3; R Core Team, 2020). This standardization allowed for easy comparison of selection measures. Our first model only included body size as an explanatory variable (model 1). Support for this model would indicate directional selection on body size. The second model included body size as both a linear and a quadratic term (i.e., body size squared; model 2). Support for this model would indicate either stabilizing or disruptive selection on body size, depending on the sign of the coefficient. The third model only included weapon size, to test for directional selection on weapon size (model 3). The fourth included weapon size as both a linear and a quadratic term (model 4), to test for stabilizing or disruptive selection on weapon size.

Next, we conducted three additional GLMs (one GLM is described in each of the three paragraphs following this one) to determine if individuals that gained a mating opportunity differed in the relative proportionality of weapon size to body size, in comparison to individuals that did not. These differences can allow us to infer selection on static allometry. Static allometry is a population-level parameter and not a property of an individual. However, each individual's weapon size (relative to body size) collectively contributes to the population's static allometry. This relationship is captured by Huxley's (1924) model of relative growth (see also

Table 1. Overview of the 15 GLMs that we compared to determine which factors could best explain a male's relative fitness.

Model number	Model specification	Model hypothesis
1	Relative fitness ~ log(body size)	Directional selection on body size
2	Relative fitness ~ log(body size) + log(body size)^2	Stabilizing (or disruptive) selection on body size
3	Relative fitness ~ log(weapon size)	Directional selection on weapon size
4	Relative fitness ~ log(weapon size) + log(weapon size)^2	Stabilizing (or disruptive) selection on weapon size
5	Relative fitness ~ residuals	Directional selection on the allometric intercept
6	Relative fitness ~ selection index	Directional selection on the allometric slope
7	Relative fitness ~ |residuals|	Stabilizing selection on the allometric slope
8	Relative fitness ~ log(body size) + snapshot	Directional selection on body size, takes snapshot into consideration
9	Relative fitness ~ log(body size) + log(body size)^2 + snapshot	Stabilizing (or disruptive) selection on body size, takes snapshot into consideration
10	Relative fitness ~ log(weapon size) + snapshot	Directional selection on weapon size, takes snapshot into consideration
11	Relative fitness ~ log(weapon size) + log(weapon size)^2 + snapshot	Stabilizing (or disruptive) selection on weapon size, takes snapshot into consideration
12	Relative fitness ~ residuals + snapshot	Directional selection on the allometric intercept, takes snapshot into consideration
13	Relative fitness ~ selection index + snapshot	Directional selection on the allometric slope, takes snapshot into consideration
14	Relative fitness ~ |residuals| + snapshot	Stabilizing selection on the allometric slope, takes snapshot into consideration
15	Relative fitness ~ 1	The models are not informative

Bolstad et al., 2015; Egset et al., 2012; Voje et al., 2013). Thus, following Huxley (1924), we assumed that body size and weapon size follow a linear relationship with the function $\log(y) = (b*\log(x)) + \log(\alpha)$. In this equation, y is trait size, x is body size, and α and b describe the relationship between the two.

To test for selection on the allometric intercept, we first calculated each individuals' residual (R) from Huxley's (1924) equation. Thus, we regressed log-transformed weapon size on log-transformed body size and calculated the residuals. Individuals with a relatively large weapon for their body size would have a positive residual, while individuals with a relatively small weapon for their body size would have a negative residual. Therefore, if there is selection to increase the allometric intercept, mating access should be explained by individuals with positive residuals. Thus, our fifth model only included residuals (R) as an explanatory variable (model 5).

We then used a selection index (SI; e.g., Egset et al., 2012; Mitchell-Olds & Shaw 1987) to test for directional selection on the allometric slope. The SI has two components. The first includes the individuals' residual deviation (R). The second incorporates an individual's body size relative to the rest of the population (B). To calculate B we took the difference between the population's mean pronotal width (body size) and each individual's pronotal width. Using these two components, the SI for each individual was calculated as SI = B/std(B)*R/std(R). In this equation, each component (B, R) is divided by its *SD* to equalize their contributions to the selection index (Egset et al., 2012; Mitchell-Olds & Shaw, 1987). This selection index attributes a positive value to large individuals that have disproportionately large femurs (i.e., individuals that have a pronotum larger than the population mean and with residual weapon size that is positive). Similarly, individuals smaller than the population mean and with negative residuals for relative weapon size will also have positive values for SI (since multiplication of two negative values results in a positive value). Both scenarios (individually and/or collectively) could drive the allometric slope to become steeper (Figure 1; Egset et al., 2012; Pélabon et al., 2014). Thus, if there is selection to increase the allometric slope, mating success should be a function of the SI value, with positive values associated with higher mating success. Therefore, our sixth model only included the selection index (SI) as an explanatory variable (model 6).

To test for stabilizing selection on the allometry, we took the absolute value of the residuals (R; following O'Brien et al., 2017). Thus, individuals close to the current static allometric regression would have smaller values, while individuals further away would have larger values. If there is stabilizing selection on the allometric relationship between weapons size and body size, mating access should be explained by individuals whose weapon size (relative to body size) is close to the current allometric slope of the sampled population. Therefore, our seventh model only included the absolute value of the residuals (|residuals|) as an explanatory variable (model 7).

Since we conducted three separate snapshots (i.e., data were collected on three different days), we also examined the effects of including snapshot as an explanatory variable. Thus, in addition to the first seven models above, we compared seven equivalent models that also included snapshot as an additional explanatory variable (models 8–14).

Finally, we also included a null model (model 15). This model simply tested whether relative fitness could be explained by a constant (i.e., an intercept-only model). All 15 of these GLMs were compared using the Akaike (1974) information criterion (AIC). Models differing by ∆AIC < 2 were considered equivalent (Burnham & Anderson, 2002).

Analysis of covariance approach

As a complementary approach to the model-selection analysis above, we also conducted an analysis of covariance that directly compared static allometries between males with and without access to females. Here, our dependent variable was log-transformed weapon size (femur width). Thus, our dependent variable differed between our first and second statistical approaches. Our independent variables were log-transformed body size (pronotal width), mating status of individual (with or without a female), snapshot day, and the two-way interaction between log-transformed body size and mating status.

Amongst these independent variables, we were particularly interested in knowing whether the interaction term between log-transformed body size and mating status was statistically significant, which would indicate selection on the allometric slope. We assumed a Gaussian distribution and an identity link function for this model.

All calculations were performed in R version 4.0.3 (R Core Team, 2020). All results can be recreated using the data (Supplementary Dataset S1) and code (Supplementary Dataset S2) provided on Dryad (Emberts et al., 2023).

Results

We quantified morphology and the number of potential mating partners for 245 males. A total of 60 males were collected on August 9, 2021 (snapshot 1), 73 on July 19, 2022 (snapshot 2), and 112 on July 22, 2022 (snapshot 3). Combining all three snapshots (Figure 2), a total of 129 males were found alone (53%), 94 were with a single female (38%), 15 were each with two females (6%), 5 were with 3 females (2%), and 2 were in a single group with 2 females (1%). We considered females in a group with a male to be potential mating partners. However, in the one group consisting of two males and two females (potentially indicating an imminent fight), each male was considered to be with one female (Supplementary Table S1). The frequency distributions of females associated with each male were similar across the three snapshots (Supplementary Table S1).

To test for selection on body size, weapon size, and weapon allometry, we first took a model-comparison approach (Tables 1–4). Regardless of our proxy for relative fitness (i.e., actual mating events, males touching at least one female, or the number of females per cluster), selection to increase the allometric slope was always among the best-fitting models (Tables 2–4, Supplementary Tables S2–S4). When we used actual mating events (possibly the most direct fitness proxy; Table 2, Supplementary Table S2), we found that the model of directional selection on the allometric slope had the best fit (with or without snapshot in the model). When we used a male's access to one or more females as the fitness proxy (Table 3, Supplementary Table S3), the model with directional selection on the allometric slope (including snapshot) again had the best fit. The results were largely congruent when we used the total number of females in a cluster as our proxy for relative fitness (Table 4, Supplementary Table S4). Again, the model of direction selection on the allometric slope (including snapshot) had the best fit. However, two additional models had similar support (∆AIC < 2), those for stabilizing selection on weapon size and directional selection on body size (Table 4, Supplementary Table S4).

To investigate selection on the allometric slope more thoroughly, we also conducted an analysis of covariance that directly compared static allometry between males with and without access to females (Figure 3; Supplementary Figure S5), using log-transformed weapon size as the dependent variable. For this analysis we focused on whether the interaction term between body size and mating status was statistically significant, which would indicate differences in the allometric (regression) slopes between groups. We found a significant interaction between body size and mating status when using actual mating events as the fitness proxy (estimated coefficient = 0.326, SE = 0.135, t = 2.416, p = .017, r^2 = 0.798; Supplementary Table S5). Mated males had an allometric

Table 2. Models comparing selection on weapon size, body size, and weapon allometry when using actual mating events as the proxy for relative fitness. The best-fitting model and those with similar AIC values (ΔAIC < 2) are boldfaced. Additional information about the model parameters can be found in Supplementary Table S2.

Model	k	LL	AIC	ΔAIC
Directional selection on the allometric slope	**3**	**−348.65**	**703.30**	**0.00**
Directional selection on allometric slope (includes snapshot in model)	**4**	**−348.64**	**705.29**	**1.99**
Null model (constant)	2	−351.86	707.72	4.42
Directional selection on weapon size	3	−351.14	708.28	4.98
Directional selection on allometric intercept	3	−351.17	708.34	5.04
Directional selection on body size	3	−351.59	709.17	5.87
Stabilizing selection on the allometric slope	3	−351.79	709.57	6.27
Stabilizing selection on weapon size	4	−350.85	709.71	6.41
Directional selection on weapon size (includes snapshot in model)	4	−351.14	710.28	6.98
Directional selection on allometric intercept (includes snapshot in model)	4	−351.17	710.34	7.04
Stabilizing selection on body size	4	−351.44	710.88	7.58
Directional selection on body size (includes snapshot in model)	4	−351.59	711.17	7.87
Stabilizing selection on allometric slope (includes snapshot in model)	4	−351.78	711.57	8.27
Stabilizing selection on weapon size (includes snapshot in model)	5	−350.85	711.70	8.40
Stabilizing selection on body size (includes snapshot in model)	5	−351.44	712.88	9.58

Note. k = number of parameters in the model; LL = log likelihood; AIC = Akaike information criterion; ΔAIC = difference in AIC from the best-fitting model.

slope of 1.787, whereas nonmated males had an allometric slope of 1.461. Our results were similar when using males with access to (touching) at least one female as the fitness proxy (estimated coefficient = 0.270, *SE* = 0.085, *t* = 3.170, *p* = .002, r^2 = .830; Supplementary Table S6). Males with access to females had an allometric slope of 1.660, whereas solo males had an allometric slope of 1.390. Finally, when using the total number of females in a cluster as the fitness proxy, we also found that there was a significant interaction between body size and mating status (estimated coefficient = 0.142, *SE* = .062, *t* = 2.281, *p* = .023, r^2 = .827; Supplementary Table S7). Thus, these results were concordant regardless of our proxy for fitness.

Discussion

The scaling relationships between traits and body size (i.e., allometry) may help explain a large amount of the morphological diversity observed within and among species because many morphological traits are highly correlated with an individual's size (Frankino et al., 2009; Gould, 1966; Thompson, 1942). Despite the potential of allometry to help explain morphological diversity, much remains unknown about the factors that underlie allometric patterns, particularly the allometric slope. For example, why do static allometric slopes of sexually selected traits often vary among species within a clade? One obvious explanation is that there is directional selection within species to alter their allometric slopes, but this has rarely been tested in wild populations. Here, we provide evidence for selection favoring an increase in the allometric slope of a sexually selected weapon in a wild insect population.

We performed two different statistical approaches, and both provided evidence for directional selection on the allometric slope (Tables 2–4, Supplementary Tables S5–S7). The only ambiguity was that under the model-selection approach,

there was also some support for two alternative models when using one of the three fitness proxies (Table 4). Nevertheless, the model of directional selection on the allometric slope had the best fit (i.e., the lowest AIC) for all three proxies (Tables 2–4), including the most conservative one (actual mating events; Table 2).

Multiple mechanisms can potentially lead to selection on the allometric slope (Pélabon et al., 2014). Here, it appears that the mechanism involves an adaptive ridge (Pélabon et al., 2014). Thus, individuals that successfully secured access to mates had a different scaling relationship between trait size and body size, relative to the population's overall scaling relationship (Figure 3). Under this mechanism, a male with an average weapon size and body size (relative to the rest of the population) can still access mates. However, relative weapon size becomes important if a male has a small or large body size. Therefore, both large males with relatively large weapons and small males with relatively small weapons can more successfully secure access to mates.

Our finding that large males with relatively large weapons can successfully secure access to mates is unsurprising. Males use their weapons to compete with other males over access to mates and resources (Emberts & Wiens, 2021; Graham et al., 2022). Specifically, it appears that males with large weapons can prevent other males (with smaller weapons) from accessing females by fighting them off (Figure 3; Graham & Emberts, 2023).

Our finding that small body sizes with relatively small weapons can be advantageous for mating success is more counterintuitive. One potential explanation is that small males that possess small weapons may have increased mobility. Increased male mobility is often associated with scramble competition (e.g., Herberstein et al., 2017; Kelly et al., 2008). However, increased mobility may also influence an individual's ability to use alternative mating tactics to secure mating opportunities (e.g., Moczek & Emlen, 2000). For example,

Table 3. Models comparing selection on weapon size, body size, and weapon allometry when using a male's access to at least one mate as the proxy for relative fitness. The best-fitting model and those with similar AIC values (ΔAIC < 2) are boldfaced. Additional information about the model parameters can be found in Supplementary Table S3.

Model	k	LL	AIC	ΔAIC
Directional selection on allometric slope (includes snapshot in model)	**5**	**−350.72**	**711.44**	**0.00**
Stabilizing selection on weapon size	4	−355.41	718.83	7.38
Directional selection on body size	3	−356.47	718.93	7.49
Directional selection on the allometric slope	3	−357.36	720.71	9.27
Stabilizing selection on weapon size (includes snapshot in model)	6	−354.36	720.73	9.28
Directional selection on weapon size	3	−357.43	720.87	9.42
Stabilizing selection on body size	4	−356.47	720.93	9.49
Directional selection on body size (includes snapshot in model)	5	−355.50	721.01	9.56
Directional selection on weapon size (includes snapshot in model)	5	−355.65	721.30	9.86
Stabilizing selection on allometric slope (includes snapshot in model)	5	−356.03	722.06	10.62
Stabilizing selection on body size (includes snapshot in model)	6	−355.32	722.64	11.19
Directional selection on allometric intercept (includes snapshot in model)	5	−356.45	722.91	11.46
Null model (constant)	2	−360.65	725.30	13.86
Stabilizing selection on the allometric slope	3	−360.01	726.01	14.57
Directional selection on allometric intercept	3	−360.64	727.28	15.84

Note. k = number of parameters in the model; LL = log likelihood; AIC = Akaike information criterion; ΔAIC = difference in AIC from the best-fitting model.

Table 4. Models comparing selection on weapon size, body size, and weapon allometry when using the total number of mates a male had access to as the proxy for relative fitness. The best-fitting model and those with similar AIC values (ΔAIC < 2) are boldfaced. Additional information about the model parameters can be found in Supplementary Table S4.

Model	k	LL	AIC	ΔAIC
Directional selection on allometric slope (includes snapshot in model)	**5**	**−385.31**	**780.63**	**0.00**
Stabilizing selection on weapon size	**4**	**−386.82**	**781.63**	**1.00**
Directional selection on body size	**3**	**−388.18**	**782.36**	**1.73**
Stabilizing selection on weapon size (includes snapshot in model)	6	−385.47	782.94	2.31
Directional selection on weapon size (includes snapshot in model)	5	−386.89	783.77	3.14
Directional selection on body size (includes snapshot in model)	5	−387.01	784.01	3.38
Stabilizing selection on body size	4	−388.04	784.07	3.44
Directional selection on weapon size	3	−389.10	784.19	3.57
Stabilizing selection on body size (includes snapshot in model)	6	−387.00	786.00	5.37
Stabilizing selection on allometric slope (includes snapshot in model)	5	−388.25	786.49	5.86
Directional selection on allometric intercept (includes snapshot in model)	5	−388.71	787.43	6.80
Directional selection on the allometric slope	3	−393.81	793.62	12.99
Stabilizing selection on the allometric slope	3	−394.26	794.53	13.90
Null model (constant)	2	−395.42	794.83	14.20
Directional selection on allometric intercept	3	−395.37	796.74	16.11

Note. k = number of parameters in the model; LL = log likelihood; AIC = Akaike information criterion; ΔAIC = difference in AIC from the best-fitting model.

we found numerous unaccompanied females. Thus, an alternative mating strategy to guarding a territory might involve flying around to find unaccompanied females: being small and having relatively small weapons may reduce the energetic cost of this strategy. Moreover, previous work in other coreids has shown that sexually selected weapons are energetically expensive to develop and maintain (Miller et al., 2016; Sasson et al., 2016; Somjee et al., 2018a, 2018b). Thus, by investing less in weaponry, individuals may be able to invest more energy in mate searching and/or postcopulatory traits (i.e., a

resource allocation tradeoff; DeJong, 1993; e.g., Joseph et al., 2018; Somjee et al., 2015). These potential explanations (and others) should be explored in future studies.

A potential limitation of our study is that we focused on sexual selection (as opposed to net selection). Thus, we found that there is sexual selection to increase the allometric slope of weaponry. Large-scale reviews have shown that selection on traits that influence mating success (e.g., sexually selected traits) is generally stronger than on traits that influence survival (Hoekstra et al., 2001; Kingsolver et al., 2001).
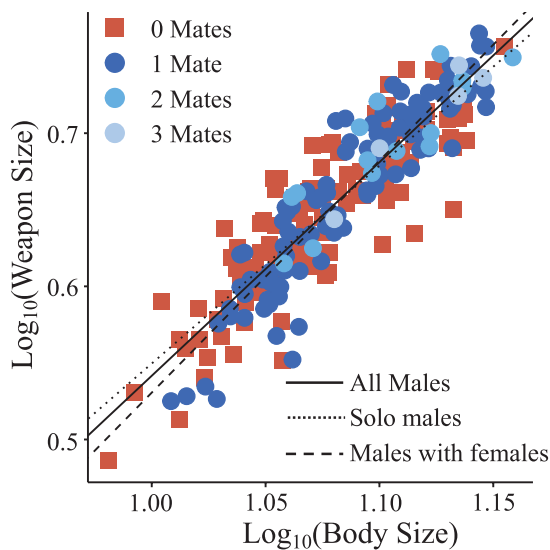
Figure 3. Selection on weapon allometry in a wild population of *Pachylis neocalifornicus.* The scaling relationship between weapon size and body size (i.e., allometry) is steeper for mating males (dashed regression line) compared to nonmating males (dotted regression line). Note that these regressions are not parallel across the range of body sizes, indicating a difference in their slopes. This pattern seems to occur because having a relatively large weapon is important for securing mates for large individuals. However, for small individuals, having a relatively small weapon also seems to be important for securing mates.

Nonetheless, it is possible that other selection pressures acting on the scaling of weapon size may differ in strength, form, or direction relative to sexual selection. For example, it is feasible that body size and/or weapon size can also influence an individual's ability to evade predators (e.g., Metz et al., 2018). Future work should continue to investigate how other factors (in addition to sexual selection) may influence selection on weapon size, body size, and the scaling relationship between the two (i.e., weapon allometry).

Another limitation of this study is that we do not know which of the three fitness proxies used here is the most accurate at describing the nature of sexual selection in this system (i.e., actual mating events, males touching at least one female, or the number of females per cluster). This uncertainty should not be problematic here, because all three fitness proxies provided evidence for directional selection on the allometric slope (Tables 2–4, Supplementary Tables S5–S7). Still, it would be advantageous to know which proxy is the most appropriate, and this should be explored in future studies (e.g., does a male typically mate with all the females in his cluster?). Overall, despite these limitations, studies of selection on allometry in the wild are rare (O'Brien et al., 2017; Pélabon et al., 2014) and quantifying this aspect of selection (i.e., sexual selection on allometric slope) is an important first step. Moreover, future studies should investigate the degree to which such selection results in evolutionary changes to weapon allometry in *P. neocalifornicus* (e.g., is heritability low? Miller et al., 2016; is there a genetic constraint? Voje et al., 2014).

In summary, we provide evidence that there is directional selection to increase the allometric slope of a sexually selected weapon in a wild population. Given that the static allometry of a trait can be heritable (Bolstad et al., 2015; Egset et al., 2012; Frankino et al., 2005; Stillwell et al., 2016; Wilkinson, 1993), this finding suggests a straightforward process by which the allometric slope can evolve among species. Thus, our finding may help explain why sexually selected traits commonly have positive static allometries (Voje, 2016) and why different allometric relationships of sexually selected traits are frequently observed amongst closely related species (e.g., Baker & Wilkinson, 2001).

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data and code needed to replicate our analyses can be found on the Dryad Digital Repository: https://doi.org/10.5061/dryad.r4xgxd2k4.

Author contributions

Z.E., U.S., and J.J.W. designed the study, Z.E. collected the data, Z.E. and U.S. performed statistical analyses, Z.E. wrote the first draft, and all authors provided critical feedback during the writing process and gave final approval.

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