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Horns positive allometry in a Mexican population of *Strategus aloeus* (L.) (Coleoptera: Scarabaeoidea: Dynastinae)

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Abstract

Álvarez HA, Carrillo-Ruiz H, Morón MA. 2013. Horns positive allometry in a Mexican population of *Strategus aloeus* (L.) (Coleoptera: Scarabaeoidea: Dynastinae). Entomotropica 28(2): 87-94.

The scaling relationships between horns and body size in a Mexican population of males of the rhinoceros beetle *Strategus aloeus* are analysed. We performed an allometric analysis using a sample of 94 specimens from many localities in Mexico. Our results suggest that median horn frequency in *Strategus aloeus* has a non-linear bimodal distribution and adjacent horns frequency has a non-linear distribution, however, residual and logarithmic transformation suggest linearity. Therefore we analysed data of horns using MA (model II) regression between log horns length and log body length; results of MA regression show strong positive allometry. These results suggest that bigger males possess larger disproportioned horns than small males, and that males could be investing more in developing the principal horn than in adjacent horns, possibly reflecting strong sexual pressures. This supports the idea that positive static allometry in horn and adjacent horns in *S. aloeus* could be explained by an extreme reaction norm, suggested by the "positive allometry reaction norm model".

Additional key words: Positive allometry, rhinoceros beetles, sexual dimorphism.

Resumen

Álvarez HA, Carrillo-Ruiz H, Morón MA. 2013. Alometría positiva en una población mexicana de *Strategus aloeus* (L.) (Coleoptera: Scarabaeoidea: Dynastinae). Entomotropica 28(2): 87-94.

Se analizan las relaciones de escalamiento entre los cuernos y el tamaño corporal en una población Mexicana. de machos del escarabajo rinoceronte *Strategus aloeus*. Se realizó un análisis alométrico utilizando una muestra de 94 especímenes pertenecientes a diferentes localidades de México. Los resultados sugieren que la frecuencia del cuerno medio presenta una distribución bimodal no linear y la frecuencia de los cuernos adyacentes presenta una distribución no linear, sin embargo, la transformación a logaritmo y los residuales sugieren linealidad. Por consiguiente, analizamos los datos de los cuernos utilizando la regresión de ejes mayores (MA; modelo II) entre el logaritmo de la longitud de los cuernos y el logaritmo del tamaño corporal; los resultados de la regresión MA muestran una fuerte alometría positiva. Estos resultados sugieren, que los machos grandes poseen cuernos desproporcionadamente largos en comparación con los machos pequeños y que los machos en general podrían estar invirtiendo más en desarrollar el cuerno principal que los cuernos adyacentes, posiblemente reflejando fuertes presiones sexuales. Esto apoya la idea que, la alometría estática positiva en el cuerno principal y en los cuernos adyacentes puede ser explicada por una norma de reacción extrema, sugerida por el "modelo de norma de reacción alométrico positiva".

Palabras clave Adicionales: Alometría positiva, dimorfismo sexual, escarabajos rinoceronte.

Introduction

The study of shape variation of living forms and its evolution has been of great interest for researchers (Pomfret and Knell 2006, Bonduriansky 2007). One of these interests is the scaling relationship of certain structures showed by some groups of animals, called positive allometry. Allometry refers to the scaling relationship between one trait and body size (Huxley 1932, Gould 1974); thus, positive static allometry (hyperallometry; $\alpha > 1$) means that larger individuals have proportionally larger traits than smaller individuals, a scaling relationship among individuals, between one organ and total body size at one developmental stage (Stern and Emlen 1999, Shingleton et al. 2007).

Whereas the majority of traits in most organisms appear to be negatively allometric or isometric (Eberhard 2002, Bonduriansky and Day 2003, Bonduriansky 2007), sexually selected traits tend to show positive allometry (Alatalo et al. 1988, Petrie 1992, Green 1992, Simmons and Tomkins 1996, Knell et al. 1999, Emlen and Nijhout 2000, Baker and Wilkinson 2001, Gould 1974), and many of these are exaggerated or bizarre structures like the antlers of deer (Huxley 1932), the forceps of earwigs (Dermaptera) (Simmons and Tomkins 1996), the rubyspots of damselflies (Alvarez et al. 2013) and the eye stalks of diopsid flies (Wilkinson and Dodson 1997, Knell et al. 1999). Such sexually selected traits are employed in combat and courtship and shaped by sexual selection (Darwin 1871), like horn-like projections in horned beetles or enlarged mandibles in stag beetles (Kawano 2000).

Horned beetles present these types of exaggerated morphologies and have been used as a key model in this matter (Tomkins et al. 2005). In horned beetles the scaling relationship between horn and body size could be represented by a sigmoid curve; thus, sigmoid scaling relationships represent phenotypic variation in morphology and in behavioral strategies (Tomkins and Moczek 2009).

In this study we investigate the scaling relationships between horns and body size in males of a Mexican population of the rhinoceros beetle *Strategus aloeus* (L.) (Coleoptera: Scarabaeoidea: Dynastinae). *Strategus aloeus* present moderate sexual dimorphism, males have three projections in pronotum around a central cavity, one front horn-shape projection, (henceforth horn) and two below hill-shape lateral prominences (henceforth adjacent horns); females present bulges instead of horns (Figure 1A, 1C). Male horns show variation in shape and length among individuals in one population or between populations, bigger males show larger horns (Figure 1A, 1B). Into the genus *Strategus*, *S. aloeus* is the most widespread species occurring from the southern United States through Central America to central Brazil and Bolivia (Morón et al. 1997).

Material and methods

The *Strategus aloeus* specimens used for the analysis were a sample of 94 males, all of them held in the Entomological Collection of the Instituto de Ecología A.C., Xalapa, Mexico (IEXA); these specimens were collected in several localities from all over Mexico. We used a combined technique of measurement. First, each specimen was put on a grid plate, to make photographs with a digital camera (Kodak v550) and to make measurements with the image program tpsDig (version 2.12). Adjacent horns were measured from the base of the pronotum to the distal tip of the horn, as both adjacent horns have no normal distribution (see results and discussion) and the same size (Wilcoxon–test: $w = 4286$, $p = 0.7245$) we only used data from left adjacent horn; body length was measured from the anterior tip of the pronotum to the base of the pygidium (Figure 1E). Horn length was measured with calipers from the point of the head articulation to the distal tip of the horn

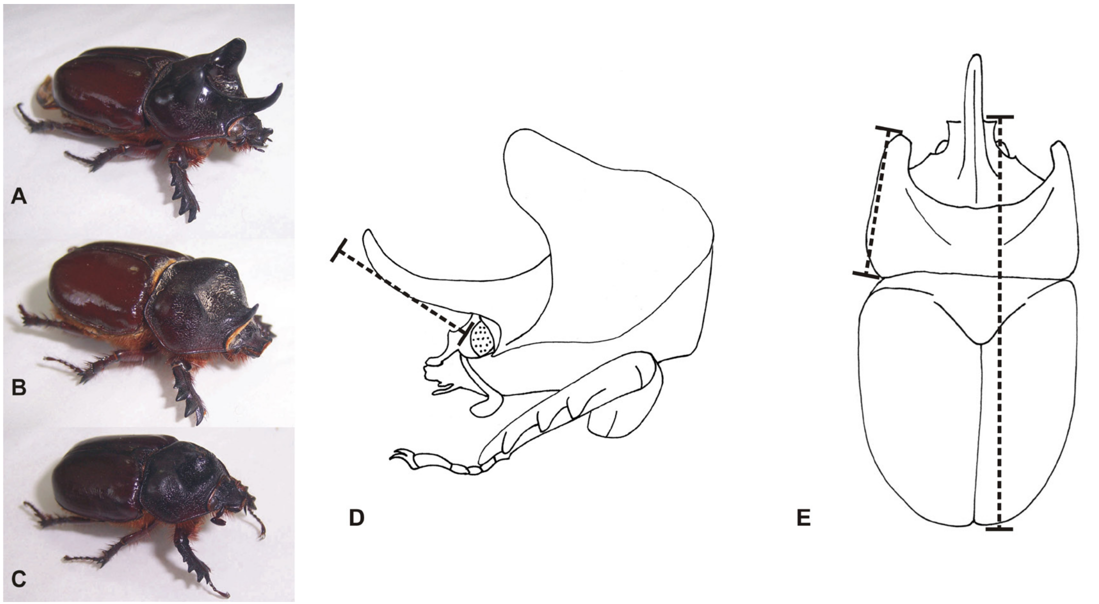

Figure 1. *Strategus aloeus*. Morphological variance of pronotum, large male (A), small male (B), female (C). Measurement of secondary sexual traits and body size of *Strategus aloeus* males. Lateral view of pronotum, principal horn measurement (D); upper view of *S. aloeus* male, adjacent horn and body length measurements (E).

(Figure 1D). We did not make measurement of horn with photographs because horn is projected, curved to the front over the head (Figure 1A) and we could not manipulate the specimens severely to make photographs.

To test the relation between horns and body size, we first investigated horn's distribution. Second, we investigated whether the proportion of horns was related to body length in a Pearson correlation. Third, we fitted a major axis (MA) regression (model II regression) (Sokal and Rohlf 2003) between log horns length and log body length. Forth, we compare MA slope values between horn and adjacent horn individuals; between major and minor horn (principal horn) individuals because of the nature of the trait development; finally we compare slope values between separated major and minor horn (principal horn) individuals and adjacent horn individuals.

We used MA regression instead of others types of regression methods because in example MA regression takes into account that both *x* and *y* are estimated with error when two variables are measured in the same units (variables have equal error variance) providing an accurate slope estimate, especially when logarithmic transformation is used. Although the link between ordinary least-squares (OLS) regression (model I regression) (Sokal and Rohlf 2003) and the allometric model is more clear than other methods (Pelabon et al. 2013); conversely to MA regression, OLS regression commonly underestimates the slope between two variables (and confidence intervals) because it assumes that *x* is measured with no error (Sokal and Rohlf 2003, Knell 2009). An MA slope significantly greater than one would suggest that large males have a higher horn. The MA slope and its 99 % confidence intervals (lower CI upper CI) are given (see results and discussion). Confidence intervals of the slope, *p*-values and slope values were calculated by using lmodel2 package and slope comparison were calculated by using smatr package, both with the log-transformed data in R program;

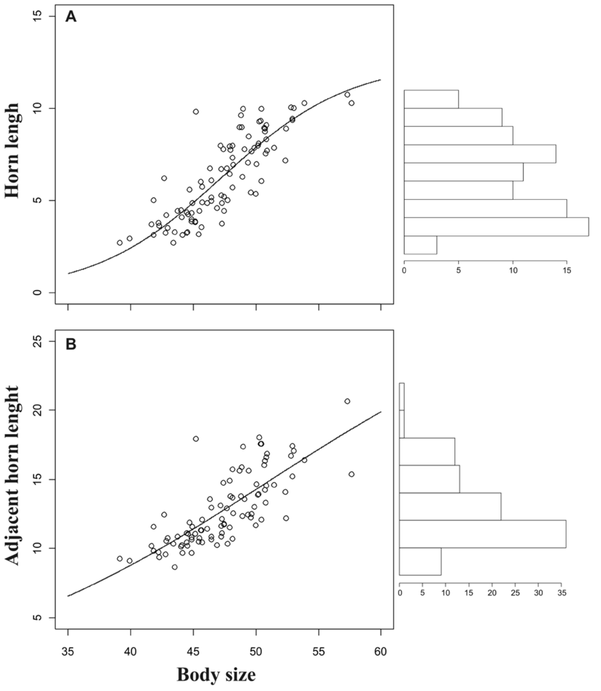

Figure 2. Scaling relationships of secondary sexual traits and body size. Plots and histograms of horn (A) and adjacent horn (B), it shows non-linear tendencies; data without log-transformation.

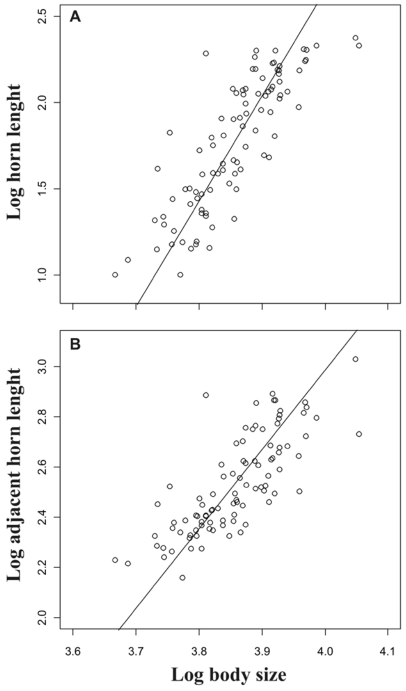

Figure 3. Scaling relationships of secondary sexual traits and body size. Plots of data in a logarithmic scale of horn (A) and adjacent horns (B), it shows the real tendency of the scaling relationship, linearity, positive allometry and certain limit in horns size.

procedure of MA slope values comparison is described in Wartoon et al. (2006).

Results

Frequency (non-transformed data) in *Strategus aloeus* shows a non-linear bimodal distribution in horn (Figure 2A) and adjacent horns frequency shows a non-linear distribution (Figure 2B), measurements of *S. aloeus* were no normal (Shapiro-Wilk test: horn, $W = 0.9442$, $p < 0.001$; adjacent horn, $W = 0.9246$, $p < 0.001$) (Figure 2A, 2C).

As suggested by Knell (2009) we examined non-log transformed data and log transformed data to see the tendencies of the relationship; log transformed data show a linear tendency for horn (Figure 3A) and residuals suggest linearity and normality; thus, Pearson´s test shows that correlation of horn and body size where positive and strong ($r = 14.438$, $p < 0.001$); therefore we performed MA regression, analysis shows strong positive allometry (CI = 5.181 - 7.467). For adjacent horns log transformed data and residuals suggest linearity and normality (Figure 3B), Pearson's test shows positive and strong correlation ($r = 11.477$, $p < 0.001$) and MA regression shows positive allometry (CI = 2.589 - 4.028). Table 1 summarizes the MA slope values and 99 % confidence intervals (lower CI upper CI) between log horns length and log body length. Also in table 1 is presented MA slope comparison values between horn and adjacent horn individuals; major and minor horn (principal horn) individuals. MA slope comparison values between separated major and minor horn (principal horn) individuals and adjacent horn individuals were different (slopes comparison P values: major horn, $P = 0.011$; minor horn, $P = 0.001$).

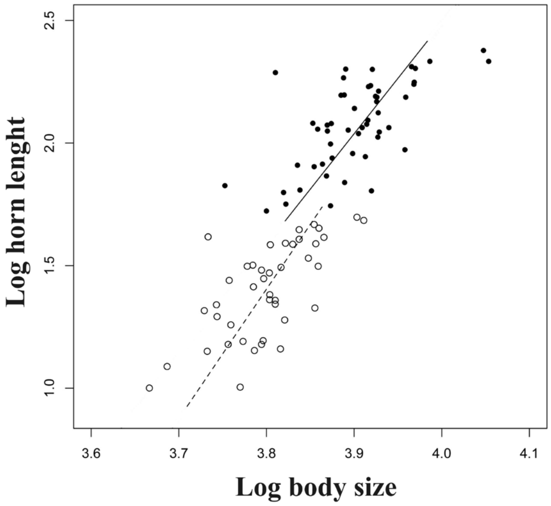

Figure 4. Scaling relationships of separated major (black dots) and minor (white dots) horn individuals and body size; data in a logarithmic scale, it shows the tendency of the allometric elevation been more variable than the allometric slope.

Discussion

MA regressions show positive static allometry in both horn and adjacent horns, these results suggest that males possess large disproportioned horns, however, due to the slope coefficients males might be investing more in develop the principal horn than adjacent horns (see results). Because horns in the genus *Strategus* are used in combat for access to mates as a secondary sexually selected trait (Morón 1976), positive allometry could be expressing strong sexual pressures for both sexual traits; however, allometric values are very different; assuming the suggestion that allometry reflects sexual pressures (Petrie 1992, Green 1992, Bonduriansky 2007), we can argue that pressures might be stronger in horn than adjacent horns. However, when we separate major and minor horn allometry we obtain slope values shallower (Figure 4) than the general principal horn slope value (Figure 3A) (Table 1). One explanation for this is that, as a result of the developmental nature of the trait, the general slope value of principal horn is a statistical-biological ensemble expressing higher allometric values (therefore higher sexual pressures) different to adjacent horn values. Furthermore, separated values of horn suggest that the allometric slope is less variable than the allometric elevation (slope comparison analysis, see results). According to this, different research have shown that the allometric slope might act as an evolutionary constrain, suggesting that the allometric elevation is more evolvable than the allometric slope (Egset et al. 2011, 2012). Nevertheless, in our study whereas major and minor horn allometries are equal, comparison analysis shows that both major and minor still have strong positive slope values; furthermore, both slope values are different comparing with adjacent horns, arguing with the idea that sexual pressures are different in horn and adjacent horns.

Boduriansky and Day (2003) presented a model that suggests that in nature, traits are expensive and resources are limited to generate extreme morphologies, hence, allometry evolves when net advantage of developed a large trait is great for bigger individuals. Bigger males invest more in traits than smaller males and when traits are devoted to its purpose, great sexual pressures will be expected; but the model also suggest that different types of allometries result from different fitness functions, one example is given by Pomfret and Knell (2006) in the dung beetle *Euoniticellus intermedius* (Reiche) that presents different types of allometry in the same trait; positive allometry in horn is shown by small males and large males show isometry, however, horn size is the most important factor in resolution contest between bigger males, conversely the positive allometric horns of small males are not. Horn in this specie shows a log-log scaling relationship that declines extremely as males been bigger.

In our study log transformed data show a linear tendency; presented in Figure 3A and 3B. Non-transformed data show certain non-linear

Table 1. Summarized MA slope values and 99 % confidence intervals (lower CI upper CI) between both log horn length and log adjacent horns length and log body length. MA slope comparison values between horn and adjacent horns individuals and between major and minor horn (principal horn) individuals.

y	*x*	Status	Slope	Lower CI – upper CI	*P*	Slopes comparison *P*
Horn	Body size	Total	6.12	5.385 - 7.086	0.001	0.001
Adjacent horn	Body size	Total	3.16	2.713 - 3.778	0.001	
Horn	Body size	Major	4.52	3.404 - 6.661	0.001	0.379
		Minor	5.28	3.929 - 7.949	0.001	

tendency (Figure 2A, 2B), which is not present in logarithmic scale. This agrees with the proposal of Tomkins et al. (2005) that is, the way that presents data tendencies will be the way that the possible outcomes be perceived, generating matters of scale, regarding to developmental models of trait evolution. Thus, in this case log transformed data is showing the continuity of a reaction norm; the explanation of how horns are developed will be providing by the "positive allometry reaction norm model" (Tomkins et al. 2005, Tomkins and Moczek 2009); which suggest that, to generate polyphenic plasticity and dimorphic patterns in the expression of traits, only a continuous extreme reaction norm is necessary, instead a developmental reprograming switch. The model also suggest that sigmoid tendencies showed in plots with non-transformed data arise because of an extreme allometric exponents across individuals, followed by a limit in elaboration of horn growth, that produces such asymptotic form (Knell et al. 2004, Tomkins et al. 2005, Tomkins and Moczek 2009).

Interestingly in other horned beetle species whose males have sexually selected traits used as weapons, is often observed that horn frequency presents a bimodal tendency, which suggests the existence of an alternative reproductive tactic (Moczek 2005). Several horned species in Dynastinae, mainly members of Oryctini and Pentodontini, dig borrows and tunnels into the soil or rotten wood where the male and female mate and lay their eggs. These beetles have alternative reproductive tactics, large males guard females and nests and small males sneak for mates, like in the genus *Onthophagus* (Emlen 2001, Emlen et al. 2007, Moczek 2005). However, within the genus *Strategus* the presence of alternative reproductive tactics are unknown, despite the presence of bimodal distribution in horn, the tendency of the scaling relationship between horn and body size (a sigmoid-like shape, figure 2A) and the behavioral observations in *S. aloeus* (cited as *Strategus julianus*, Morón 1976) similar to the reproductive behavior of *Onthophagus* beetles (in where males fight for the access to mates).

Conclusions

Horned beetles are important for their history as models in allometry research. Here, scaling relationships between horns and body size of mexican *S. aloeus* population suggest positive strong allometry and differential development of principal horn and adjacent horns that might reflect strong sexual pressures, this explained by an extreme reaction norm, suggested by the "positive allometry reaction norm model" and male sexual pressures for competing for the access to mates. *S. aloeus* shows non-linear tendencies that do not represent alternative tactics, contrasting with other horned beetle species. This species is very widespread in the

Americas, it is possible that horns allometry vary between populations from North and South America due to sensitivity that allometry has to environmental conditions; comparing such three populations could lead us to better understanding of the allometry of sexual traits and sexual pressures in this species. However, the details on the evolution and development of sexual traits in the genus *Strategus* remain for research.

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