

Is the major-minor male dimorphism of the stag beetle (*Lucanus cervus*) explained by a weaponry and wing investment trade off?

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Abstract

The size variation and male dimorphism of stag beetles (Lucanidae) have often been subject of studies but an ecological explanation for this male dimorphism has rarely been given or proven. As the major male clearly invests in weaponry which helps with competing with other males, we especially wonder what is the advantage of the minor morph. We hypothesized that minor males predominantly invest in wings and therefore can fly better and actively look for females. In order to test this 147 live and 164 dead specimens (including 235 males) were measured. We found a positive allometry for mandible length in major males, indicating that large major males relatively invest more in weaponry. Nevertheless, major males also exhibit the largest wings. However, minor males had a lower wing load due to their smaller body size and consequently they can probably fly better. They furthermore invest less in mandibles, giving them even a better mobility when flying on when on ground. Consequently, minor males might be of special importance in fragmented populations for exchange of genetic material.

Keywords: allometric equation, dimorphic, sexual selection, Lucanidae.

Introduction

The size variation and male dimorphism of stag beetles (Lucanidae) have often been subject of studies but an ecological explanation for this male dimorphism has rarely been given or proven. This size variation within stag beetles is by most authors believed to be explained by the length of the larval stage and differences in temperature, quality and quantity of the larval food source (e.g. TOCHTERMANN, 1992; VAN HELSDINGEN *et al.*, 1995; ROMITI *et al.*, 2015). These findings have already been proven for some species. For the dung beetle, *Onthophagus taurus*, the size variation and accompanied male dimorphism was related with larval feeding conditions (MOCZEK & EMLÉN, 2000) and the size of the parasitic carabid beetle, *Brachinus lateralis*, is dependent on its host size (JULIANO, 1985). For plant feeding beetles it is even assumed as a general rule that larval diet is instrumental in affecting the size of adult insects (SCHOONHOVEN *et al.*, 2005).

However, the male dimorphism should be explained by a rivaling reproduction strategy of the adult males (e.g. EMLÉN *et al.*, 2005). Based on earlier research on Asian Lucanidae (KANWANO, 1997; 2000), we hypothesize that the male dimorphism is explained by a tradeoff between weaponry and wing investment. In this case, major males are believed to relatively invest more in large mandibles and heads. The head of males mainly contains mandible muscles and therefore, the size (length and width) of the head is a good estimator for the investment in mandible muscles (GOYENS *et al.*, 2014). Consequently, we use these measurements as mandibles associated measurements. Better weaponry gives them an advantage in competing with other males. Adult stag beetles feed on sap runs of trees or rotten fruit. Major males are often found competing for such food sources where they can mate with females that are attracted to it. In contrast, minor males that result from lesser larval habitat quality are believed to relatively invest more in flight performance by increasing their wing surface. Consequently, minor males more actively look for females by flying. Lower investments in mandible

size also helps them to enhance their flying capacity (GOYENS *et al.*, 2015b) and on ground mobility (GOYENS *et al.*, 2015a).

Allometry studies the relationships between changes in the size of a certain body part compared to the overall size. This relationship is in general log-linear (KAWANO, 1997, 2000) and described as $Y = a.X^b$, where Y is the length of a given body part, X: total body weight and b the allometric coefficient. This allometric coefficient describes the scale of investment in a certain body part. If $b > 1$ (called positive allometry), larger individuals have a disproportionately larger body part. When $b < 1$ (negative allometry), larger individuals have a relatively smaller body part and when $b \sim 1$ (isometry) the given body part remains in proportion with the total body weight. However, in polymorphic species the allometric relations of the body parts associated with the polymorphism are discontinuous (clearly defining the different morphs) or nonlinear (resulting in a different b for each morph), e.g. KNELL (2009) and NIJHOUT & WHEELER (1996).

Material and methods

Data was collected from living and dead material. Living animals were caught in Overijse (Belgium, 50.7738°N, 4.5348°E) at three sites from 29 June to 11 July 2016 from about 20 to 23 hours. Beetles were measured with a calliper when they lied on their back on a flat surface. The live beetles were also weighted with a kitchen scale (with 0,1gr precision) by placing them in a plastic container to remain on the scale. Captured individuals were marked to prevent double measuring.

Secondly, we used dead specimens from the genetic collection that is stored at the Research Institute for Nature and Forest. Samples used for this research, either came from Northwestern Europe (Belgium and France) or Eastern Europe (Slovenia, Czech republic, Hungary, Romania, Greece, Ukraine and Russia). One wing was removed and soaked in water for one hour. Then the wing could be folded open and stuck on paper. Wings were scanned and size of the wing calculated based on number of pixels multiplied by the surface of a single pixel. In the genetic

collection, specimens are stored either dried or on ethanol depending on how we receive them, this to obtain the best storage of the genetic material. Due to this different storage and the fact that many samples are incomplete, we did not obtained a dry weight of these specimens.

The main body parts (Fig. 1) of the live and dead specimen were measurements with a calliper. All measurements were taken at the largest distance. For the dead specimens only, also wing length (Lw) and width (Ww) was measured. In the results, we will focus on the wings and mandibles measurements of male specimens only.

For statistical analysis, we used the allometric equation, transformed to $\log Y = \log a + b.\log X$. First, the measured weight of living specimens was modelled based on elytra length with linear regression (of the log transformed data) for males and females separately. Elytra length was selected as this measurement provided the best fit (highest R^2) for weight of both sexes compared to all other body measurements. This equation was then used to estimate the weight of the dead specimens. Wing surface and wing load (weight / wing surface) were computed the dead specimens. Finally, the allometric equation were recalculated for data of dead and live beetles. If this relation was bilinear the species is dimorphic and two equations were fitted for each morph separated. Statistics were performed using SPSS (IBM CORP., 2013).

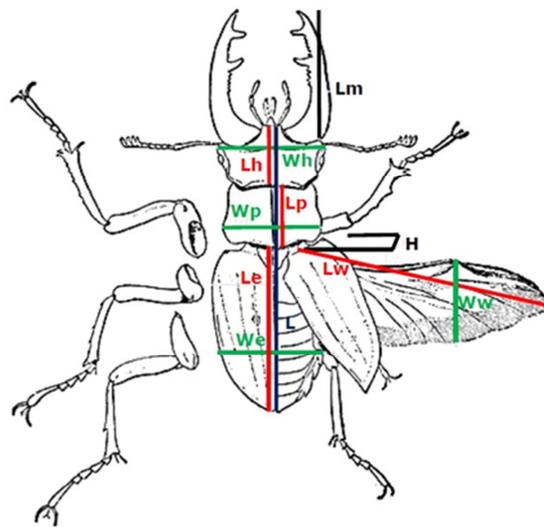


Fig. 1. Measurements taken from stag beetle (*Lucanus cervus*). Le: Length elytra, Lp: length pronotum, Lh: length head, Lm: length mandible, We: width abdomen, Wp: width pronotum, Wh: width head and H: height (thickness of the beetles body).

Table 1. Number of individuals used in this study separated by country, gender and alive and dead status.

	Alive		Dead	
	Male	Female	Male	Female
Northwestern Europe:				
Belgium	126	21	71	35
France	-	-	1	5
Eastern Europe:				
Slovenia	-	-	2	2
Czech republic	-	-	1	0
Hungary	-	-	2	3
Romania	-	-	4	0
Greece	-	-	18	10
Ukraine	-	-	8	0
Russia	-	-	2	0
Total	126	21	109	55

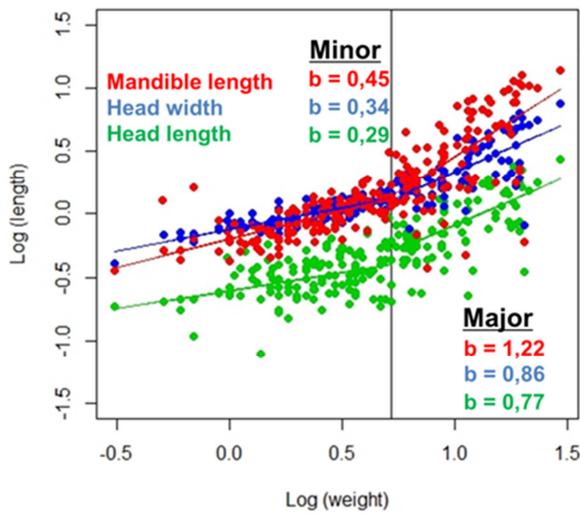


Fig. 2. Graph with log of mandible length (red), head width (blue) and head length (green) of minor and major males plotted against log of body weight. Allometric coefficients (b) are given.

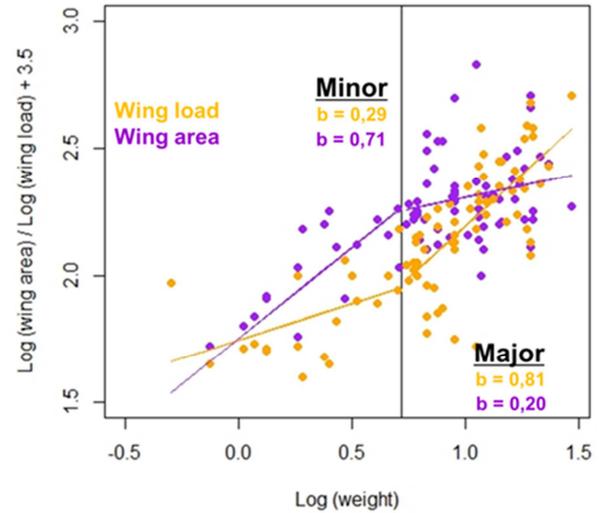


Fig. 3. Graph with log of wing load (orange, plotted as $\log(\text{wing load}) + 3,5$) and wing area (purple) of minor and major males plotted against body weight. Allometric coefficients (b) are given.

Results

In total 311 beetles were measured including 235 males and 76 females, 147 live and 164 dead specimens (Table 1).

Within the males, both the investment in mandibles and wings were clearly dimorphic while this was not the case for females or for other measurements of males. The transition point between minor and major males was visually estimated, at 2,05 gr. Consequently, allometric coefficients for females, minor males and major males for these measurements were estimated separately (Figs 2- 3).

The only positive allometry ($b > 1$) was found for the mandible length of the major males meaning that the log length of the mandibles increases more than proportionally of the log weight increase when comparing major males. In other words, if males would be scaled to the same weight (or same elytra length), the biggest males would still exhibit the largest mandibles. Despite the fact that head length and width did not display positive allometry among major males, the allometric coefficient was still clearly larger than these of minor males (Fig. 2).

However, the largest wings were found among the biggest major males (Fig. 3). Nevertheless the relative investment (allometric coefficient) of majors was smaller than this of minor males. But if we look at the wing load, we see a reverse pattern. The wing load of minor males is much smaller (meaning they have a higher capacity to fly) than major males. Furthermore, the relative investment reveals a stronger increase in wing load of major males compared to minor males.

Discussion

From our results, it is clear that major males clearly invest in mandible length and associated body parts but they still have bigger wings than minor males despite their investment in larger wings is fairly low. Minor males seem to benefit from their lower body mass and relatively higher wing area investment, resulting in a lower wing load (higher capacity to fly) and likely they fly better.

These results fit with our hypothesis and the ecology of both morphs as we have described in the introduction. However, these results contrast with the findings of KAWANO (1997), who find positive wing area allometry within minor males for the stag beetle *Dorcus antaeus*.

Furthermore, we might assume that the increased investment in mandibles further reduces their flight performance (GOYENS *et al.*, 2015b). They found that size rather than weight or shape of mandibles negatively effects flight performance. Consequently, major males fly even worse than estimated from their wing load. This is probably why, minor males have a negative allometric coefficient for mandible length, in other words they actively invest in smaller mandibles.

Furthermore, smaller mandibles gives them a higher stability when walking on the ground (GOYENS *et al.*, 2015a) and allows them to better search actively for females at the ground level were they have to manoeuvre between branches and in galleries underground.

The results remain similar when studied for the separated regions (Northwestern and Eastern Europe) and for the tree sites within Overijse, which indicates that the results are rather stable and identical between populations.

For the conservation of the stag beetle in fragmented urban habitat, minor males might be very important for genetic exchange as they are better capable of flying. This might be of especial importance as these kind of habitat are often of lower quality and consequently have more minor males.

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