

# Allometry of Male Grasping Apparatus in Odonates Does Not Suggest Physical Coercion of Females

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**Abstract** Male abdominal grasping apparatus that are used to secure a female prior, during and after mating, are widespread in arthropods. The scarce evidence regarding its selective regime suggests that they are male adaptations to circumvent female mating decisions, as predicted by the sexual conflict hypothesis. A recent discussion regarding this way of selection suggests that, similar to weapons and traits that have to do with physical endurance, grasping apparatus should show hyperallometry (proportionally larger compared to body size) as an indication of selection towards increased size. We have tested this idea by measuring the length, width and area of the grasping apparatus of five dragonfly species (*Anax junius*, *Rhionaeschna multicolor*, *Dythemis nigrescens*, *D. sterilis* and *Phyllogomphoides pacificus*). We used two proxies of body size (wing and body length). Our measures did not indicate any pattern of hyperallometry. Thus, the grasping apparatus in these animals does not seem to be positively selected for increased size as would be expected if they were forcing females to mate. Given this, we discuss three other explanations for the maintenance of the grasping apparatus in odonates: 1) a firm grip that secures the tandem and mating position; 2) courtship devices subject to female choice; and, 3) isolation structures that mechanically prevent interspecific matings. The first hypothesis, however, could not

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explain the highly elaborated and species specific morphology of grasping apparatus in these animals. Support for the second hypothesis comes from the fact that odonate females have mechanoreceptor sensilla embedded in their mesostigmal plates (the place grabbed by the grasping apparatus). For the third hypothesis, coevolutionary patterns in morphology in the grasping apparatus and mesostigmal plates in some Zygoptera can also be used as support.

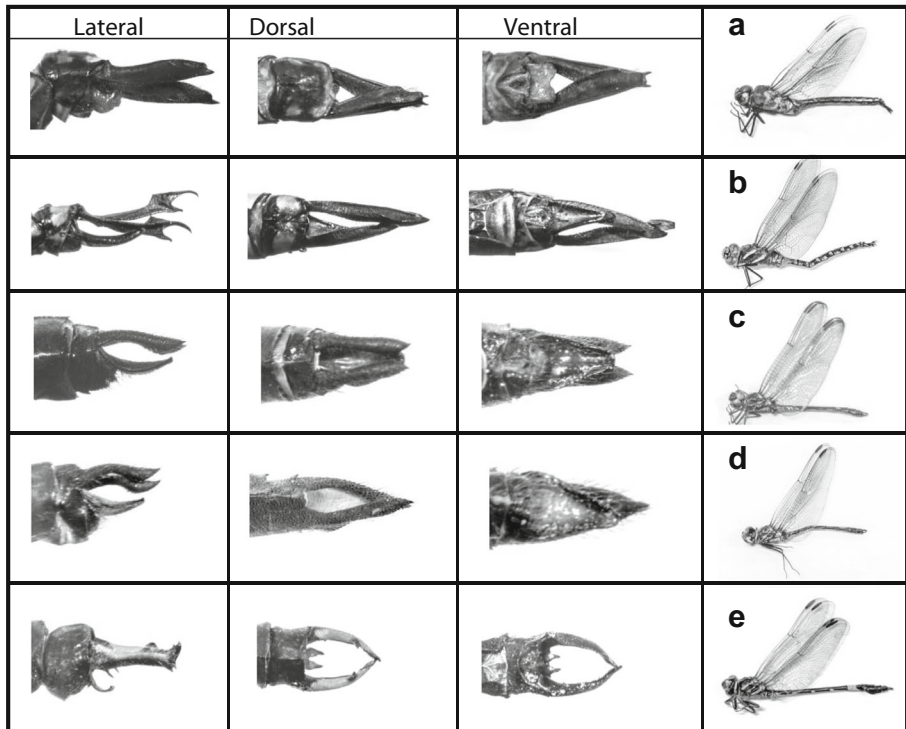
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## Introduction

Sexual selection has promoted the evolution of a number of morphological structures that are used either prior, during or after mating. In this respect, one particular set of traits are male grasping apparatus which are present in a number of arthropods (for example, mecopterans, Gao and Hua 2013; hemipterans, Khila et al. 2012; arachnids, Rodríguez-Márquez and Peretti 2010). Several sources of experimental evidence have indicated that such traits have evolved as a way to overcome female mating decisions (e.g. Rowe and Arnqvist 2002; Cothran 2008; Perry and Rowe 2012). For example, in water striders, male use their grasping apparatus to grab a female that resist mating so that she cannot “escape” and ends up using the grabbing male’s sperm (reviewed by Arnqvist 1997). This form of sexual selection has been coined sexual conflict as it reflects a difference of interests between the sexes (Parker 2006; Arnqvist and Rowe 2005) - in this case whether mating should take place or not. Sexual conflict is the opposite to the more traditional female choice idea where females could be choosing males on the basis of males’ expression of sexually selected traits (Arnqvist and Rowe 2005). Given the evidence around the grasping apparatus, the evolution of these traits in male arthropods has been interpreted as a male-win situation via sexual conflict with no role for female choice (Arnqvist and Rowe 2005).

Recently, the static allometry of a particular trait has been used as a proxy to understand whether a trait has been selected via sexual conflict or female choice (for example, genitalic traits; Eberhard et al. 1998; Eberhard 2009, 2010). Static allometry (from now on, allometry) refers to the proportional size of any structure with respect to body size in conspecific individuals of the same ontogenetic stage, and is the net result of different selective pressures acting on both the trait and body size. Allometry slope of a trait can be positive (hyperallometry,  $>1$ ), isometric ( $=1$ ), or negative (hypoallometry,  $<1$ ). The rationale of using allometry to deduce the form of sexual selection is that traits that can be used to physically constrain females’ mating decision should be hyperallometric (Eberhard 2009). This rationale is based on a theoretical basis (Clutton-Brock 1982; Green 1992) and the widespread nature of positive allometry shown by characters used as weapons (e.g. Kodrick-Brown et al. 2006). Weapons, in this case, are used to solve aggressive encounters and so a relatively large trait with respect to body size would be selected (Clutton-Brock 1982; Green 1992).

Grasping apparatus (i.e. abdominal appendages or cerci) are widespread in male odonates (Paulson 1974; Fig. 1). Prior to mating, a male has to translocate its sperm from the ninth abdominal segment to the second and third abdominal segments,



**Fig. 1** Different views of the male grasping apparatus according to study species: **a)** *Anax junius*; **b)** *Rhionaeschna multicolor*; **c)** *Dythemis nigrescens*; **d)** *D. sterilis*; and **e)** *Phyllogomphoides pacificus*

where the intromittent genitalia are located (Cordero Rivera and Córdoba-Aguilar 2010). Once the male has grabbed the female neck with his grasping apparatus, then the male genitalia are introduced to the female's last abdominal segments and sperm is transferred (Cordero Rivera and Córdoba-Aguilar 2010). This mode of copulation necessary implies that the male holds the female at least during mating. Although this may seem a natural selection explanation for the grasping apparatus, other pieces of information suggest that these structures may be selected via sexual conflict: a) males hold the female well before she accepts to mate and sperm is translocated (Wildermuth 1991; Cordero et al. 1995); b) males hold the female after mating has finished for extremely long periods in some species, to reduce the female's chances to remate (reviewed by Córdoba-Aguilar et al. 2009); c) male holding takes place with females that are not receptive (e.g. Fincke 1984; Cordero et al. 1992); and, d) sometimes males show signs of struggle with the female trying to disengage (Cordero 1999; Cordero Rivera and Andres 2002; Cham 2008). These behaviors are suggestive of physical coercion by the male and could be used as a "weapon" to subdue females that are reluctant to mate.

In this paper, we provide a test for whether male grasping structures in odonates are selected via sexual conflict using allometric estimates. For this, we have selected five species whose males are representative of extremely exaggerated grasping apparatus. Our prediction was that they should show positive allometry.

## Material and Methods

We used males of *Anax junius*, *Rhionaeschna multicolor*, *Dythemis nigrescens*, *D. sterilis* and *Phyllogomphoides pacificus* from the Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México. The upper pair of the grasping apparatus was photographed (using a camera Canon EOS 60D with a COMPACT-MACRO LENS EF 50 mm 1:2.5) having milimetric paper as a scale. The following traits of the upper grasping apparatus were measured: a) the length of the right apparatus from its basis to its distal site (that is, the most extreme points); b) the dorsal width of the widest site of the right apparatus; and, c) the dorsal area of the right apparatus (to locate these measuring sites see supp. mat. Fig. 1). These traits were measured using IMAGEJ software (version 3.00, National Institute of Health, MD, USA). Wing length (from the wing basis to its distal tip) and body length (head to distal grasping apparatus) were used as body size indicators. We used two body size indicators given current discussions as for what traits truly represent body size (e.g. Córdoba-Aguilar et al. 2010). All traits were measured by the same person four times, to keep a constant measurement error. However, this error was calculated. The average of the four measurements was used to estimate the allometric slopes for each body size indicator.

Data were log-transformed to linearize the relationship between the grasping apparatus and body size indicators. Model II regression was employed because the morphometric variables are random and not controlled by the researcher (Warton et al. 2006). There are different versions of model II regressions, such as major axis (MA), standardized major axis (SMA), and ranged major (RMA) regressions (Legendre and Legendre 1998; Warton et al. 2006). SMA regressions are preferred over MA for allometric studies when the morphometric traits are in different order of magnitude or differ in their measurement units (Warton et al. 2006). The disadvantage of SMA is that there is not a direct way to assess whether allometric coefficients are significantly different from zero (that is, if there is a relationship between the grasping apparatus and size; Quinn and Keough 2002). However, a correlation test between morphometric variables has been suggested as a proxy (Legendre and Legendre 1998; Quinn and Keough 2002). RMA analysis can be used with the advantage of being able to assess whether the allometric slope differs from zero but is sensitive to extreme values (Legendre and Legendre 1998). To solve all these controversies, we present both SMA and RMA allometric coefficients.

When the grasping apparatus was related to body size indicators (i.e., a non-zero slope), we determined whether there was support for isometry (slope =1), hypoallometry (slope <1), or hyperallometry (slope >1) by looking at the confidence intervals of the allometric slope using the SMA method. We used R software (R Core Development Team 2012) for statistical analysis.

## Results

With a few exceptions, error measurements indicated fairly repeatable measurements (Table 1). In general, most grasping apparatus traits were not significantly related to body size indicators for the five species (see correlations in Table 2). According to the

**Table 1** Measurement error, coefficient of variation and sample sizes for body size indicators and the grasping apparatus (GA) traits

Species	Trait	Measurement error	Coefficient of variation (%)	Number
<i>Anax junius</i>	Body length	6.994	2.784	18
	Wing length	4.325	3.514	18
	GA length	3.121	3.834	18
	GA width	1.689	0.078	15
	GA area	0.522	0.120	15
<i>Rhionaeschna multicolor</i>	Body length	3.374	3.362	15
	Wing length	2.295	3.179	15
	GA length	5.272	3.466	15
	GA width	3.729	0.070	15
	GA area	4.609	0.069	15
<i>Dythemis nigrescens</i>	Body length	3.803	3.610	51
	Wing length	6.681	3.847	51
	GA length	2.226	6.740	51
	GA width	9.264	0.086	15
	GA area	1.499	0.154	15
<i>D. sterilis</i>	Body length	2.054	3.976	21
	Wing length	1.643	4.125	21
	GA length	0.626	13.899	21
	GA width	6.450	0.077	15
	GA area	1.126	0.127	15
<i>Phyllogomphoides pacificus</i>	Body length	2.081	3.321	25
	Wing length	1.861	4.140	25
	GA length	2.435	8.590	25
	GA width	4.622	0.052	15
	GA area	0.674	0.132	15

slopes produced by SMA and RMA methods, isometry was detected for grasping apparatus length (using the two body size indicators) and width (for only wing length) in *A. junius*, while the grasping apparatus length (for the two body size indicators) of *D. nigrescens* and *D. sterilis* showed hyperallometry (Table 2). For the width and area of the grasping apparatus the relationship did not differ from zero, and so no allometric relationship was detected for the five species (Table 2).

## Discussion

Contrary to a sexual conflict expectation, there was not a general trend towards hyperallometry for the grasping apparatus. Unfortunately, there is not much information of our study species that can be used to explain the differences we found. However, the male grasping apparatus of odonates is in general associated to a physical control during male–female interactions. During tandem, odonate males seem to grasp females

**Table 2** Relationships between three grasping apparatus traits and two body size indicators in five odonate species

Species	Trait	r (p-value)	RMA slope	p value	SMA slope	SMA Slope CI	Number	Allometry relationship
<i>Anax junius</i>	GA length/body	0.684 (<0.001)	1.434	0.001	1.386	0.950/2.021	18	Isometry
	GA length/wing	0.724 (<0.001)	1.147	0.001	1.100	0.769/1.572	18	Isometry
	GA width/body	0.324 (0.119)	4.952	0.103	1.603	-0.934/2.751	15	No relationship
	GA width/wing	0.443 (0.049)	3.277	0.051	1.458	0.872/2.439	15	Isometry
	GA area/body	0.319 (0.123)	7.009	0.153	2.322	1.352/3.990	15	No relationship
	GA area/wing	0.250 (0.184)	7.972	0.202	2.113	1.217/3.669	15	No relationship
<i>Rhionaeschna multicolor</i>	GA length/body	0.197 (0.241)	2.303	0.269	1.023	0.586/1.787	15	No relationship
	GA length/wing	-0.311 (0.130)	-1.78	0.144	-1.092	-1.879/-0.634	15	No relationship
	GA width/body	0.310 (0.130)	1.723	0.122	1.853	1.007/3.189	15	No relationship
	GA width/wing	0.457 (0.043)	1.907	0.057	1.973	1.184/3.287	15	No relationship
	GA area/body	0.158 (0.286)	0.290	0.301	1.792	1.022/1.383	15	No relationship
	GA area/wing	0.235 (0.198)	7.770	0.203	1.908	1.097/3.319	15	No relationship
<i>Dythemis nigrescens</i>	GA length/body	0.560 (<0.001)	1.903	0.001	1.876	1.482/2.374	51	Hyperallometry
	GA length/wing	0.565 (<0.001)	1.903	0.001	1.781	1.409/2.253	51	Hyperallometry
	GA width/body	0.410 (0.064)	0.844	0.092	0.779	0.463/1.315	15	No relationship
	GA width/wing	0.478 (0.036)	0.923	0.070	0.851	0.513/1.409	15	No relationship
	GA area/body	0.410 (0.064)	0.844	0.104	0.779	0.462/1.314	15	No relationship
	GA area/wing	0.478 (0.036)	0.923	0.067	0.851	0.513/1.409	15	No relationship
<i>D. sterilis</i>	GA length/body	0.427 (0.027)	3.594	0.044	3.853	2.528/5.874	21	Hyperallometry
	GA length/wing	0.472 (0.015)	3.328	0.022	3.697	2.449/5.579	21	Hyperallometry
	GA width/body	-0.208 (0.228)	-1.874	0.224	-1.463	-2.554/-0.839	15	No relationship
	GA width/wing	-0.210 (0.226)	-1.232	0.212	-1.392	-2.430/-0.798	15	No relationship
	GA area/body	0.196 (0.241)	3.493	0.259	2.362	1.352/4.127	15	No relationship

**Table 2** (continued)

Species	Trait	r (p-value)	RMA slope	p value	SMA slope	SMA Slope CI	Number	Allometry relationship
<i>Phyllogomphoides pacificus</i>	GA area/wing	0.358 (0.095)	2.252	0.093	2.248	1.318/3.833	15	No relationship
	GA length/body	-0.079 (0.359)	-10.499	0.308	-2.770	-4.206/-1.823	25	No relationship
	GA length/wing	-0.026 (0.451)	-25.314	0.407	-2.237	-3.401/-1.471	25	No relationship
	GA width/body	0.012 (0.498)	27.421	0.498	1.095	0.621/1.933	15	No relationship
	GA width/wing	0.049 (0.431)	5.218	0.422	0.961	0.545/1.695	15	No relationship
	GA area/body	-0.371 (0.087)	-3.144	0.101	-3.006	-5.112/-1.77	15	No relationship
	GA area/wing	-0.305 (0.134)	-2.608	0.119	-2.636	-4.539/-1.530	15	No relationship

Pearson correlation coefficients (along with their p-value) are provided, the RMA allometric coefficients (p-values obtained from permutations to test if the allometric coefficients differed from zero), SMA allometric coefficients and their confidence intervals (CI). GA, grasping apparatus

against females' interests so one would expect there is some sort of brutal force applied by males. Some reports have actually indicated that females may end up with head damage as a possible consequence of being grasped (Dunkle 1984, 1991; Wildermuth 1984). Dunkle (1991), for example, documented that in 12 gomphid species, 88–100 % of females had from two to six holes in their head as a possible by-product of the male seizing with their grasping apparatus. Apparently and due to this, odonate females have evolved an arrester system (a series of adjusting organs located between the head and neck to immobilize the head during feeding and tandem) partly to prevent damage during tandem and still provide stabilization during flight (Gorb 1998a, 1998b, 1999). Despite this, our results do not support positive selection towards increased length, width or area of these male structures. A similar finding was found in a zygopteran, *Calopteryx virgo meridionalis*, where length of the grasping apparatus was not hyperallometric either (Outomuro and Cordero-Rivera 2012).

What other explanations can be laid out for the evolution of grasping apparatus in odonates? A first obvious explanation has to do with informing both sexes that a tandem is taking place. Indeed this was a necessary step in the evolution of odonate mating position given that the evolutionary transition in insect mating position was likely a female-above male followed by a male-above position (Huber 2010). This information reason may actually explain the presence of sensory terminals in both males (e.g. microtrichia) and females (sensilla) on the places involved in holding (Gorb 1998a, 1998b, 1999). However, although a well-secured tandem linkage is important in a number of difficult situations (e.g. flying, ovipositing, overcoming mating attempts by other males; Corbet 1999), this cannot explain the vast species-specific complexity in morphology (Paulson 1974). A second explanation could be related to sexual selection: males may use their grasping apparatus to stimulate females and the latter may use such stimulation to filter males. Supporting evidence for these male structures acting as courtship devices is practically non-existent. An indirect source is related to the sensory mechanism located in the female's grabbed area (female mesostigmal plates or the head, in Zygoptera and Anisoptera respectively; Gorb 1999). For example, females of some *Enallagma* species actually show embedded sensilla on their plates (e.g. Robertson and Paterson 1982). As Eberhard (1985) has already hypothesized, the sensilla presence seems coherent in *Enallagma* with the idea that females have evolved a mechanism to evaluate males prior, during and after mating. Whether sensilla are present in other species, needs to be corroborated, along with an experimental framework where either the grasping apparatus, sensilla or both are manipulated. If such manipulation is possible, one would need to assess female responses after manipulation. For example, if the grasping apparatus is manipulated in such a way that females cannot be properly stimulated, one would expect females to lay fewer eggs, eject more sperm after copulation (sperm ejection is a post-copulatory response for females to choose males in odonates; Córdoba-Aguilar 2006). Interestingly, males also show sensilla embedded in their grasping apparatus but their function has been only associated to inform the male whether he is holding a female only (Meurgey and Faucheu 2009). Since the sensilla of both sexes may make contact during tandem, it would be interesting to see whether a communication channel is established. A recent analogous case was documented in spiders in which such communication occurs: male squeezing of females and female stridulation responses during copulation allow "dialogues" by which females assess male performance (Peretti et al. 2006). Those males able to



sustain such “dialogue” by squeezing females according to certain female stridulation patterns, gain a higher paternity compared to males unable to sustain the “dialogue” (Peretti et al. 2006). A third explanation is a natural selection one. McPeck and collaborators (2008, 2009, 2011) have determined a punctuated rate of evolution at the time of speciation and a reduced variance in inter-population differentiation for the grasping apparatus and mesostigmal plates in several *Enallagma* species. These pieces of evidence are coherent with the idea that both the grasping apparatus and mesostigmal plates have evolved to prevent interspecific mating and thus serve as a species isolation mechanism (McPeck et al. 2008, 2009, 2011). This idea makes perfect sense for *Enallagma* and other species that show no precopulatory courtship, and where males simply chase females due to a poor ability to recognize conspecifics. That both male and female structures can determine the strength of species isolation has also found support in studies of interspecific crosses between *Ischnura graellsii* and *I. elegans* (Sánchez-Guillén et al. 2012). Paradoxically, the strength of these structures was not the same for the combination of interspecific crosses (*I. graellsii* females and *I. elegans* males mating were more successful than the opposite combination; Sánchez-Guillén et al. 2012). Furthermore, the species isolation mechanism would not seem convenient for species whose males court females, as such precopulatory courtship may actually serve as the mechanism to discriminate heterospecific males or females as has been shown in *Calopteryx* species (Waage 1979; Svensson et al. 2007). Thus, even if the species isolation hypothesis applied it would be limited to species with no precopulatory courtship.

As a summary, although the grasping apparatus in odonates does not support a male coercing function, further work should be done in terms of whether these structures are used as courtship devices or mechanical isolation barriers.

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