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A scientometric analysis on pre- and post-copulatory traits in Odonata

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Abstract: In the last decades, studies on sexual selection in odonates have shown a relationship between mating success and costly sexual ornaments, mainly male characters. Here, we conducted a scientometric analysis to assess the state of art of studies on sexual selection in odonates, especially on the role of male ornamentation (pre-copulatory traits) and sperm competition (post-copulatory traits). We found 51 papers focused on sexual ornamentation and 34 on sperm competition. Only one study simultaneously addressed both pre- and post-copulatory traits, nevertheless without an integrative approach. Results show that calopterygids are extensively studied regarding pre-copulatory traits (*i.e.*, male wing pigmentation), while libellulids are mostly studied in post-copulatory traits (*e.g.*, sperm competition) focused research. These preferences seem to be related to characteristics like presence of ornamentation and territoriality, large body size, variation and complexity of sperm removal structures, respectively. For the post-copulatory traits, sperm removal is frequently addressed, but few other strategies, like the investment in sperm quality and quantity, are investigated. Finally, we demonstrate that it is necessary to conduct studies focused on addressing the relationship between pre- and post- mating sexual traits.

Keywords: sexual ornamentation, sperm competition, dragonfly, damselfly

Introduction

Since Darwin (1871), several studies on sexual selection theory have been carried out to understand how sexually selected traits favor individual fitness before and after mating (*i.e.,* pre- and post- copulatory traits). Odonates emerge as key-organisms for studies on sexual selection, mainly because of their sexual ornaments used in intra and intersexual contexts (*e.g.* Córdoba-Aguilar, 2002; Moore, 1990; Schultz & Fincke, 2009; Siva-Jothy, 1999) and their sperm competition strategies (*e.g.* Cordero-Rivera, 2016; Córdoba-Aguilar, 2003).

Sexual ornamentation is one of those traits, which can be found in many Odonata species where males exhibit colorful conspicuous traits that play a role in animal communication, acting as visual signals for mate attraction and intrasexual competition (Andersson, 1994; Osorio & Vorobyev, 2008). Male ornamentation may also function as honest signals and transmit information about morphological and physiological quality of the bearer (Zahavi, 1975). Because of the high costs of sexual ornament production, only those able to allocate the finite physiological resources to such ornaments will display a better quality to conspecifics (Webster *et al.*, 2018; Contreras-Garduño *et al.*, 2011). Hence, some studies have demonstrated a direct relationship of such elaborated ornaments of some odonates with mate attraction and mating success (Siva-Jothy, 1999; Pena-Firme & Guillermo-Ferreira, 2020).

Males of some Odonata species exhibit coloration patterns on body and wings that may operate in premating displays, which influence mate choice and contest resolution (Siva-Jothy, 1999; Vilela *et al.*, 2017). For instance, in territorial species, ornaments may be used to assess rivals during male-

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male aerial contests (Guillermo-Ferreira *et al*., 2015) and mediate dispute decisions (Pestana *et al*., 2018). These ornaments may also be related to contest outcome, *e.g.*, *Tigriagrion aurantinigrum* Calvert (Zygoptera: Coenagrionidae) and *Chalcopteryx scintillans* McLachlan (Zygoptera: Polythoridae), wherein winners usually have increased pigmentation of the visual signal (Guillermo-Ferreira *et al*., 2019; Vilela *et al*., 2017).

A previous study showed female mate preference based on male pigmentation in *Calopteryx xanthostoma* Charpentier 1825*,* in which females avoid mating with less pigmented males (Siva-Jothy, 1999). In some cases, males may use courtship displays wherein wing pigmentation is exhibited in a series of wing movements to attract females (Orr, 1996; Thompson, 1990). In both intra- and intersexual contexts, the use of odonate ornaments as visual signals may be related to a possible positive relationship with individual quality (Zahavi, 1975). In this sense, ornaments may act as honest signals of male physiological and morphological traits such as body size, parasite resistance, oxidative stress defenses and other traits (Martinez-Lendech *et al*., 2018; Sarfaty & Pruett-Jones, 2010; Siva–Jothy, 2000).

In species where females mate with more than one male, sperm from different males may compete for egg fertilization – known as sperm competition – and competitors need to evolve adaptations to avoid or reduce this conflict (Parker, 1970). In Odonata, sperm removal is considered in the context of sperm competition strategies (Waage, 1979; Cordero-Rivera, 2016;). Moreover, sperm repositioning, sperm displacement mechanisms and the investment in sperm quantity and quality were reported (Cordero-Rivera *et al*., 1995; Córdoba-Aguilar, 2003; Nakahara & Tsubaki, 2008; Siva-Jothy & Tsubaki, 1994). Previous studies suggest a relationship between pre- and post-mating sexual traits, such as ornaments and sperm quality, in which a positive correlation or a trade-off may be found (Parker *et al*., 2013; Sheldon, 1994). However, the evidence on the correlation between ornaments and sperm traits are scarce, thus, further studies are needed to include additional factors, such as life history, mating systems and ecological variables in order to understand how sexual selection act on sexual ornamentation and ejaculate traits (Simmons *et al*., 2017).

Therefore, here we aimed at conducting a scientometric analysis on the available literature on odonate sexual selection, focused on male ornamentation and sperm competition. This analysis was carried out to raise the accumulated knowledge and to reveal existing gaps in this field addressing the following: How many articles were published on the role of male ornamentation?; How many articles were published on sperm competition strategies?; What are the most relevant studies in this area?; How many articles had demonstrated the relationship between these pre- and post- copulatory traits?; What do we know about ornamentation function in males of Odonata?; What do we know about strategies of sperm competition in Odonata?; What are the most used Odonata families in these studies?.

Material and Methods

To analyze the available literature on sexual selection in Odonata, the data were collected from two databases: Web of Knowledge (Thomson-Reuters) and Scopus (Elsevier). To access data, the following terms were used, present in title, abstract and/or keywords: “sexual selection” OR “mating system*” OR “reproductive behavior” OR “mate choice” OR “female choice” OR “female preference” OR “territoriality” OR “male-male” OR agonistic OR contest* OR fight OR aggressive OR courtship AND “secondary sexual character*” OR “sexual ornamentation” OR ornament* OR pigmentation OR “sexually selected character*” OR coloration OR spot AND odonat* OR dragonfl* OR damselfl* OR Zygoptera OR Anisoptera, to the first step; “Sperm competition” OR “Sperm removal” OR “Sperm quality” OR “Sperm viability” AND odonat* OR dragonfl* OR damselfl* OR Zygoptera OR Anisoptera, to the second step. Only articles in English published until 2020 were considered and review studies were excluded.

We conducted a criteria analysis (Figure 1) that consisted in reading all the recovered articles to check the scope of each study and filtering the retrieved articles to select only those that had focused

on (i) the role of male ornamentation in different contexts and, (ii) adaptations to sperm competition. The studies that had investigated the impact of ecological variables and other possible sexually-selected traits were removed. After that, we compiled information about authors, name of journal, year of publication, number of citations, country where data was collected, and study species. The selected articles were organized according to their aims by interaction types (intrasexual, intersexual, physiological, and / or morphological) and sperm competition strategies (according to adaptation investigated in the article such as sperm removal, sperm quality or quantity). The interaction types were classified according to the following criteria: 1. Intersexual interaction: studies about the role of male ornamentation in male-female contexts; 2. Intrasexual interaction: studies about the role of male ornamentation in male-male contexts; 3. Physiological interaction: studies about the relationship between male ornamentation and physiological traits such as immunity, parasite resistance, survival, and hormones; and 4. Morphological interaction: studies about the relationship between male ornamentation and other morphological traits such as body mass, body size and fat reserve. Data were analyzed using the *Bibliometrix* package (Aria & Cuccurullo, 2017), in the R environment (R. Core Team, 2019)

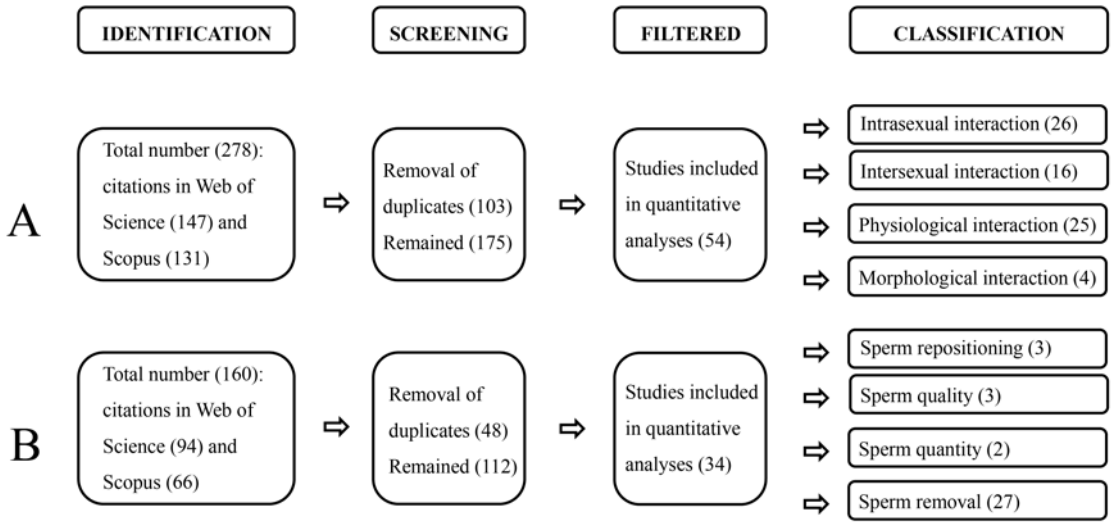

Figure 1: Fluxogram about methodology steps; a) The role of male ornamentation; b) sperm competition strategies.

Results

The search of studies concerning the role of male ornamentation on sexual selection of Odonata returned 175 articles, from these 54 articles (30.9%) were filtered through the criteria analysis to the final table. We also found 112 articles focused on sperm competition strategies, which were filtered into 34 studies (30.36%). The role of male ornamentation covered a shorter timespan if compared with sperm competition strategies (30 years versus 39 years), but the stronger research interest on this subject in the last two decades made it the most studied theme (Figure S1). The total citations show that studies on the role of male ornamentations presented a more equitable distribution of citations; while sperm competition strategies have their citations mostly concentrated in one article (Figure S1). Despite the great interest on these two themes, the role of interaction between them has not received much attention over the past decades, and only one article addresses both subjects (1.2%).

Concerning the publication efforts, Mexico has the most active research group focused on understanding the role of male ornamentation; names such as Alex Córdoba-Aguilar, Jorge Contreras-Garduño and Martin Serrano-Meneses are common in dozens of articles (Table S1) and the Country stands out when we look at studies done by researchers from one single country and in international partnerships (Figure S2). Another group whose work stands out is led by Rhainer Guillermo-Ferreira, who places Brazil among the most active countries in this study subject. In the opposite way, 'sperm competition strategies' is a subject greatly studied by Adolfo Cordero-Rivera's group, located in Spain (Table S1), while the most active group comes from Japan. Another different characteristic of this area of study is the low number of articles produced in international partnership (Figure S2). Finally, the United Kingdom and the United States emerge as countries that have a greater number of studies in both subjects (Figure S2).

The citations in both areas are mostly headed by classical studies. The 10 most cited articles in both subjects were produced before the 2010's (Table 1 and 2). A network analysis highlighted the distribution of citations in both themes; while the role of ornamentation presented a more complex structure and diverse articles as important nodes (Figure S3), the sperm competition showed a clear division between older articles, published in the 1980's and newer articles, published in the 1990's and 2000's linked by Waage (1979), the first published and most cited article from this subject area (Figure S4).

Table 1: The 10 most cited articles about the role of male ornamentation.

	Article Name	Reference	Journal	Citations	Citations per Year
1	A mechanistic link between parasite resistance and expression of a sexually selected trait in a damselfly	Siva-Jothy, 2000	Proceedings of The Royal Society B-Biological Sciences	189	9.0
2	The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection	Moore, 1990	Evolution	131	4.23
3	Intrasexual competition alone favors a sexually dimorphic ornament in the rubyspot damselfly *Hetaerina americana*	Grether, 1996	Evolution	124	4.96
4	Male wing pigmentation may affect reproductive success via female choice in a calopterygid damselfly (Zygoptera)	Siva-Jothy, 1999	Behaviour	115	5.23

	Article Name	Reference	Journal	Citations	Citations per Year
5	Wing pigmentation, immune ability, fat reserves and territorial status in males of the rubyspot damselfly, Hetaerina Americana	Contreras-Garduño *et al.*, 2006	Journal of Ethology	100	6.67
6	Wing pigmentation in territorial male damselflies, *Calopteryx haemorrhoidalis*: a possible relation to sexual selection	Córdoba-Aguilar, 2002	Animal Behaviour	81	4.26
7	The size of the red wing spot of the American rubyspot as a heightened condition-dependent ornament	Contreras-Garduño *et al.*, 2008	Behavioral Ecology	79	6.08
8	The expression of a sexually selected trait correlates with different immune defense components and survival. in males of the American rubyspot	Contreras-Garduño *et al.*, 2007	Journal of Insect Physiology	58	4.14
9	Structural colours create a flashing cue for sexual recognition and male quality in a Neotropical giant damselfly	Schultz *et al.*, 2009	Functional Ecology	49	4.08
10	Territorial behaviour and immunity are mediated by juvenile hormone: The physiological basis of honest signalling?	Contreras-Garduño *et al.*, 2009	Functional Ecology	41	3.42

Table 2: The 10 most cited articles about the sperm competition strategies.

	Article Name	Reference	Journal	Citations	Citations per Year
1	Dual function of the damselfly penis - sperm removal and transfer	Waage,1979	Science	396	9.429
2	Male copulatory sensory stimulation induces female ejection of rival sperm in a damselfly	Córdoba-Aguilar, 1999	Proceedings of The Royal Society B-Biological Sciences	91	4.136
3	Sperm competition in the damselfly *Enallagma hageni* Walsh (odonata, coenagrionidae) - benefits of multiple mating to males and females	Fincke, 1984	Behavioral Ecology and Sociobiology	84	2.270
4	Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence	Waage, 1986	Biological Journal of the Linnean Society	82	2.343
5	Variation in copulation duration and the resultant degree of sperm removal in *Orthetrumcancellatum* (L.) (Libellulidae, Odonata)	Siva-Jothy, 1987	Behavioral Ecology and Sociobiology	75	2.206
6	Postmating sexual selection: Allopatric evolution of sperm competition mechanisms and genital morphology in calopterygid damselflies (Insecta : Odonata)	Cordero-Rivera *et al.*, 2004	Evolution	37	2.176

	Article Name	Reference	Journal	Citations	Citations per Year
7	Male disturbance, repeated insemination and sperm competition in the damselfly coenagrion scitulum (zygoptera, coenagrionidae)	Cordero-Rivera *et al.*, 1995	Animal Behaviour	31	1.192
8	Sperm "repositioning" in *Crocothemis erythraea*, a Libellulid dragonfly with a brief copulation	Siva-Jothy, 1988	Journal of Insect Behavior	30	0.909
9	Sperm competition and sperm precedence in the dragonfly *Nanophya pygmaea*	Siva-Jothy & Tsubaki, 1994	Physiological Entomology	29	1.074
10	Direct and indirect estimates of sperm precedence and displacement in the dragonfly *Sympetrum danae* (Odonata: Libellulidae)	Michiels & Dhondt, 1988	Behavioral Ecology and Sociobiology	27	0.931

Both study subjects are broadly studied around the world. For the role of ornamentation, samples were taken from the Americas, Europe, Oceania, and Africa (Figure S5a), while sperm competition strategies were already tested in organisms from Americas, Europe, Asia, and Oceania (Figure S5b). It is important to highlight that all studies focused on the role of male ornamentation provided information about the study sampling location, while four articles focused on sperm competition strategies did not provide this information. Regarding the role of male ornamentation, the most studied organisms belong the Zygoptera, mainly the Calopterygidae family (45 times) and followed by Chlorocyphidae (12) and Coenagrionidae (8); Among the Anisoptera, Libellulidae (9) (Figure 2a) was the most studied family. For sperm competition strategies, organisms from the Anisoptera suborder, mainly Libellulidae family, were mostly studied (107 times), followed by the zygopteran families Coenagrionidae (26) and Calopterygidae (13) (Figure 2b). Concerning the interaction types, the most studied was related to intraspecific interaction (26 times), followed by physiological (25), interspecific interaction (16) and morphological (4) (Figure 3a), and, for sperm competition strategies, the most accessed strategies were sperm removal (27 times), sperm quantity (3), sperm repositioning (3) and sperm quality (2) (Figure 3b).

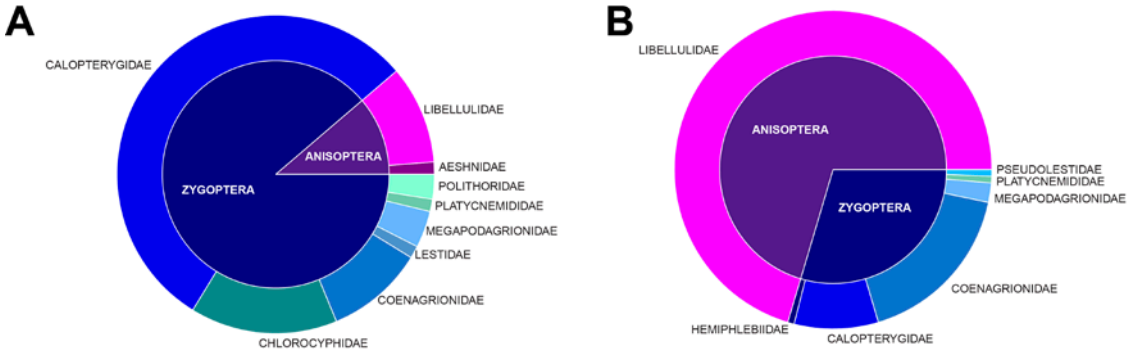

Figure 2: Odonate families used to access information about the role of male ornamentation (A) and the sperm competition strategies (B).

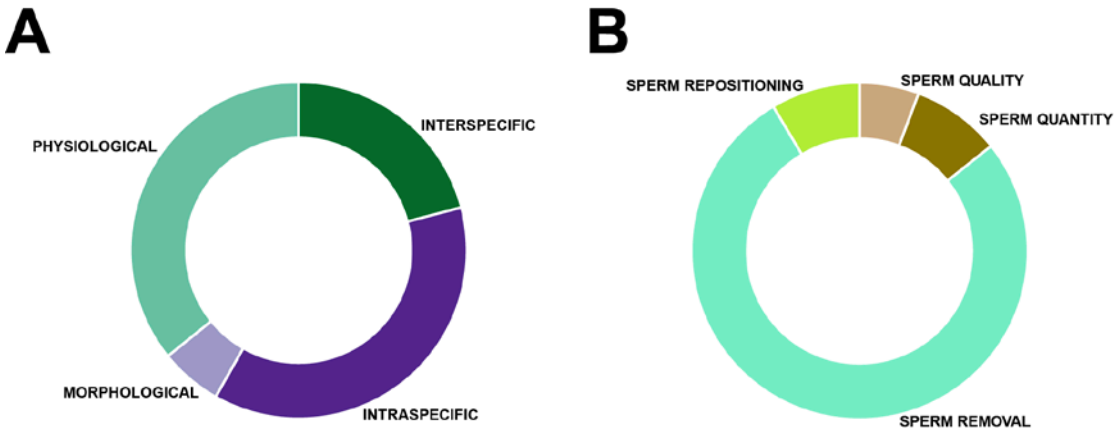

Figure 3: (A) Studied behavior strategies that are related to the role of male ornamentation; (B) Studied behavior strategies that are related to the sperm competition strategies.

Discussion

Studies on the role of male ornamentation and sperm competition strategies using dragonflies and damselflies as study models have been developed by several research groups around the word. In Mexico, there is a strong research group responsible for a higher number of studies on sexual ornamentation, authoring some of the most cited pre-mating traits studies in damselflies (*e.g.* Contreras-Garduño *et al*., 2006; Córdoba-Aguilar, 2002; Córdoba-Aguilar *et al*., 2009). The larger production of research on pre-copulatory traits is recent. Despite this, most cited articles are the classic ones (older studies) (*e.g.* Grether, 1996; Moore, 1990; Siva–Jothy, 2000). Studies on male ornamentation showed a wider international partnership network and all selected studies were interconnected in the co-citations network, which may occur due to a scientific globalization that makes it easier for researchers to contact each other and access the articles. Studies on sperm competition strategies are older, and consequently, with less international partnerships. These studies are interconnected by co-citations networks with a central article, which is the most important study on post-copulatory

traits: Waage's classical work with the first evidence of sperm removal in Odonata (Waage, 1979). Other studies were conducted on the mechanism of sperm removal in different species since then (Cordero-Rivera, 2016; Miller, 1990; Waage, 1986ab).

Odonata is a very speciose group with distinct characteristics according to suborder. Adults of Zygoptera are generally smaller, while anisopterans are more robust and larger (Garrison *et al*., 2006). Notwithstanding, our study also found differences in study categories for both groups. zygopterans are mostly used as models in studies on pre-copulatory traits, mainly territorial calopterygid damselflies (Córdoba-Aguilar & Cordero-Rivera, 2005), which usually exhibit ornamented wings used as visual signals to attract mates and to fight against rivals (Córdoba-Aguilar *et al*., 2009; Guillermo-Ferreira *et al*., 2015; Siva-Jothy, 1999). In contrast, anisopterans are the most used models in studies on post-copulatory traits, mainly libellulid dragonflies, what may occur due to their larger body size, and variation and complexity of structures linked to sperm removal (Artiss, 2001; Miller, 1991; Waage, 1986ab). A major part of studies on sperm competition in Odonata is focused on sperm removal, what we consider an evidence of the necessity of research focused on other strategies, such as investment in sperm traits (sperm quantity or quality) for a better understanding of these traits in a group that is considered one of the best models for studying sperm competition and sexual conflict (Cordero-Rivera & Rivas-Torres, 2019).

Our results also retrieved only one paper that addressed both pre- and post-copulatory traits together. The referred study showed the use of male wing pigmentation in courtship displays to attract females and the mechanism of sperm removal in a species of Protoneurinae, *Nososticta kulumburu* (Thompson, 1990). This is a complete study on reproductive behavior, but not in an integrative way, because the relationship between pre- and post-copulatory traits was not considered. Other studies also discussed these traits separately (*e.g. Hetaerina americana*; Córdoba-Aguilar, 2009; Córdoba-Aguilar *et al*., 2009).

Conclusion

Here, we presented a general view on the literature on sexual selection in Odonata. In conclusion, studies addressing the relationship between pre- and post-copulatory sexual traits are necessary in order to complement literature and understand how selection act on sexual ornamentation and ejaculate traits, using odonates as a study model with distinct pre- and post-copulatory behavior (Simmons *et al*., 2017).

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