

Survival is predicted by territorial status but not wing pigmentation in males of a polythorid damselfly, *Euthore fasciata* (Odonata: Zygoptera: Polythoridae)

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(Received 5 April 2016; final version received 29 June 2016)

Robust male condition must be favored and should be signaled to conspecifics via enhanced aggression and more highly expressed ornamental traits. One way that such robust condition, and thereby the expression of aggression and ornamental traits, can be assessed is via survival. In odonate adults, condition (in the form of lipid reserves, muscle mass and immune ability) has been correlated with the expression of: (a) territorial behavior (as opposed to nonterritorial, satellite behavior), and (b) larger wing pigmentation patterns. In the present work, we investigated these two patterns using adult males of *Euthore fasciata* in a field study. Males bear black and white pigmented wing patterns and express territorial and nonterritorial behaviors to secure matings. We predicted that, due to their better condition, territorial males should have higher survival and larger pigmented patterns than nonterritorial males, and that larger pigmented patterns would correlate positively with survival. We marked–recaptured males, measured their pigmented patterns and recorded their behavior. Our results indicated that territorial males ($n = 12$) had a higher survival, but not larger pigmented areas, than nonterritorial males ($n = 39$), and that there was no significant relationship between wing pigmentation and survival. This result confirms that territorial males are in better condition than nonterritorial males. However, wing pigmentation does not seem to signal such condition to conspecifics although the reduced number of animals may have affected our analysis. Tentatively, the assumed relationship pigmentation/condition cannot be generalized in odonates.

Keywords: condition; survival; territorial behavior; wing pigmentation

Introduction

Sexual selection theory predicts that males with a better condition are more likely to assume more aggressive roles during male–male competition or produce more exaggerated ornamental traits (Roulin, 2015). This assumption implies that only such condition can offset the energetic costs of

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both producing and maintaining the aggressive behavior and/or the ornamental trait, and entering into a physical contest during male competition. Several studies have provided evidence for these relationships across the diversity of animal taxa (for aggression see, for example, Fujimoto, Miyake, & Yamahira, 2015; Girard-Buttoz et al., 2015; White & Rundle, 2015; for ornaments see, for example, Hill, 2015; Izzo & Tibbetts, 2015; Whittingham, Freeman-Gallant, Taff, & Dunn, 2015). Although condition can be assessed in many different ways, one key proxy is survival where animals in higher condition (and thus, showing higher aggression and more elaborated ornamental traits) can survive for longer (e.g. Cotton, Fowler, & Pomiankowski, 2004). In damselflies, for example, after condition was manipulated, males in better condition survived for longer (González-Santoyo, González-Tokman, Munguía-Steyer, & Córdoba-Aguilar, 2014). Indeed, the condition–survival relationship is extended across taxa (e.g. mammals, McFarland & Majolo, 2013; birds, Blums, Nichols, Hines, Lindberg, & Mednis, 2005; reptiles, Wikelski & Trillmich, 1997; fish, Kuparinen, Hardie, & Hutchings, 2011).

One insect group where studies of male condition have been carried out extensively is order Odonata (dragonflies and damselflies). In a number of odonate species, males usually engage in energetically demanding flying contests for places where encountering a female is more likely. Males dispute these places and those better able to secure such sites (i.e. territorial) obtain a significantly higher number of matings compared to males unable to secure such places (i.e. nonterritorial; reviewed by Suhonen et al. 2008). During these different roles, territorial males are far more aggressive than nonterritorial males, with the latter assuming satellite behaviors, and intercepting females on their way to mating and/or oviposition areas (reviewed by Suhonen, Rantala, & Honkavaara, 2008). In different odonate species, it has been found that physiological condition is a key factor to secure a territory (e.g. Córdoba-Aguilar & González-Tokman, 2014; Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996). This condition aspect has to do with both muscle lipid content and thoracic muscle mass, both of which are intimately related with the above referred flying contests (Contreras-Garduño, Buzatto, Serrano-Meneses, Nájera-Cordero, & Córdoba-Aguilar, 2008; Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996). According to this, males with larger lipid contents and muscle mass are more likely to defend a territory. During territorial competition, males assess such physiological condition (and resource holding potential) using the opponent's wing pigmentation patterns (e.g. Guillermo-Ferreira, Gorb, Appel, Kovalev, & Bispo, 2015; Xu & Fincke, 2015; however, see Ramírez-Delgado, López-García, Lara, & Serrano-Meneses, 2015). In addition, males with a better condition (and also larger wing pigmentation areas), are also those with a higher survival (Córdoba-Aguilar, 2002; Grether, 1996; Munguía-Steyer, Córdoba-Aguilar, & Romo-Beltrán, 2010). Paradoxically, and contrary to the aggression–survival relationship indicated above, the only study that tested whether territorial males in odonates exhibited a higher survival when compared with nonterritorial males found no difference (Munguía-Steyer et al., 2010).

To expand the test of whether a more aggressive behavior during male competition and larger wing pigmentation patterns correlate positively with survival, we have used males of the polythorid damselfly, *Euthore fasciata* (Hagen in Selys, 1853). Males of these species engage in territorial and nonterritorial behaviors and both bear wing pigmentation patterns (De Marmels, 1982). We have marked–recaptured a population subset in the field, and have analyzed whether survival is higher in territorial males versus nonterritorial males, and in males with larger pigmentation patterns. This analysis is based on the assumption that only males in better condition can hold a territory and have lower mortality rates. Finally, we have compared pigmentation areas between territorial males and nonterritorial males. We first predict that survival and pigmentation areas should be higher in territorial males than in nonterritorial males. And second, the larger the pigmentation, the higher the survival.

Materials and methods

Species description and study area

Euthore fasciata is a South American damselfly whose adults live in streams where males defend riverine vegetation areas which females use for mating and oviposition (De Marmels, 1982). Adult male damselflies of this species show pigmented wing areas in the form of one dark spot on the wing base and a white-pearly spot on the distal wing area (Supplemental Figure S1a). Females do not show these wing patterns. We studied a population located in Santa Maria mountains, in Boyacá department in Colombia (04°51'48'' N, 73°16'04'' W). This location is 850 m above sea level and has an annual precipitation of 4694 mm (Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia [IDEAM], 2005). The work was done at three patches of 100 m length each of the same river, separated by 1 km each patch (Supplemental Figure S1b).

Data collection

We carried out our investigation over 36 days, from 31 October to 5 December 2011. During this time, we marked each male on their abdominal segments 7–10, with a unique combination of colors. For this, we used permanent Sharpie® markers of the following colors: yellow, orange, light blue, dark blue, brown, purple, black, red, pink and green. Additionally, we measured the length (in mm) of the dark and white wing spots using a Stainless® digital caliper. Marking and body measurements took less than a minute for each individual. Two observers checked the field site for marked males everyday from 09.00–16.00 hours (the hours of maximum activity for this species; all authors' unpublished data), for marked males, so that an encounter history was made for each individual, composed of 0 s (i.e. not-detected males) and 1 s (i.e. detected males). These two observers walked along each riverine site once during this time. To distinguish territorial from nonterritorial males, each marked male was observed for 15 min during our daily censuses. During this period, we recorded whether it remained in the same site after facing or being faced by conspecific males. This, along with our daily recordings, which allowed detection of whether a male remained in the same riverine area, led us to differentiate territorial males as those individuals that occupied the same place, from nonterritorial males as those individuals that did not occupy the same place.

Statistical analyses – survival

We used Cormack–Jolly–Seber capture–recapture models to estimate survival and recapture probabilities of males in the field. These models dissociate survival from recapture probabilities (Lebreton, Burnham, Clobert, & Anderson, 1992). The predictor variables contained in the models for survival and recapture probabilities were: tactic (territorial, nonterritorial), wing length, and black and white wing spot length (mm). We tested 19 models that included the different combinations of predictors of survival and recapture probabilities. Fifty-one males were individually marked and 28 were recaptured at least once. Twelve males were classified as territorials and 39 as nonterritorials. To check and correct the possible overdispersion we employed the median \hat{c} -hat approach in the global model to estimate the variance inflation factor. Overdispersion factors greater than 3.0 may indicate structural deficiencies in the model. Our global model had minimal overdispersion (\hat{c} -hat = 1.02). For this reason, we employed the Akaike information criteria for overdispersed data (QAIC; Burnham & Anderson, 2002) to select the best of the competing models (i.e. the model with the lowest QAIC value). As the most supported models presented similar degree of support we performed model averaging for survival and recapture probabilities

(Burnham & Anderson, 2002). Additionally we performed a likelihood ratio test between the most supported model that included tactic as a predictor, and another that only differed because it did not include tactic as a predictor variable. We employed MARK 6.1 software to estimate these capture–recapture models (White & Burnham, 1999).

Statistical analyses – comparison of pigmentation areas according to mating tactic

We fitted a multivariate analysis of variance (MANOVA) to assess if male tactics differed in their wing pigmentation (both black and white spots) lengths. The response variables were: black and white pigmented wing length, and as predictor variable the tactic each male adopted. We employed a Pillai test to assess the significance of the predictor variable. Analyses were carried out using R v.3.02 (R Core Development Team, 2013).

Results

The most supported models included male tactic (territorial, nonterritorial) as a relevant predictor variable for survival (Table 1). However, the importance of both black and white wing spots to explain systematic differences in survival is not evident, because the degree of support of the models that contain both wing spots as predictor variables is similar to those that do not include them. Survival differs according to tactic after we compared a model that included Φ (black wing spot + tactic) p (constant) to Φ (black wing spot) p (constant) models, $LRT = 5.213$, $df = 1$, $p = 0.022$. Additionally, we model averaged survival probabilities of territorial males and non-territorial males since the top models have similar degree of support (Table 1). Territorial males showed a higher daily survival probability ($\Phi = 0.933$, $CI\ 95\% = 0.851–0.971$) than nonterritorial males ($\Phi = 0.847$, $CI\ 95\% = 0.764–0.904$ (Figure 1). Black and white wing spot lengths did not differ according to male reproductive tactics ($F = 1.297$, $df = 1.49$, $p = 0.26$).

Table 1. Model selection of capture–recapture CJS models for *Euthore fasciata* males.

Survival (Φ)	Recapture (p)	QAICc	Delta QAICc	QAICc weight	Model likelihood	#par	QDeviance
T + BW	C	432.455	0.00	0.14558	1.0000	4.0000	424.124
T + WW	WW	432.533	0.08	0.14001	0.9617	5.0000	422.033
T + BW	WW	432.849	0.39	0.11956	0.8213	5.0000	422.349
T + WW	C	433.057	0.60	0.10773	0.7400	4.0000	424.727
T	C	433.910	1.46	0.07032	0.4830	3.0000	427.714
T + WL	C	434.082	1.63	0.06454	0.4433	4.0000	425.751
T + BW	T	434.314	1.86	0.05748	0.3948	5.0000	423.814
T + BW	WL	434.606	2.15	0.04965	0.3410	5.0000	424.106
T + BW	BW	434.624	2.17	0.04923	0.3382	5.0000	424.124
T + WW	WL	435.222	2.77	0.03650	0.2507	5.0000	424.722
BW	C	435.534	3.08	0.03123	0.2145	3.0000	429.337
T	T	435.725	3.27	0.02838	0.1949	4.0000	427.394
WW + BW	C	435.807	3.35	0.02725	0.1872	4.0000	427.476
WW	C	436.084	3.63	0.02371	0.1629	3.0000	429.888
BW	WW	436.263	3.81	0.02169	0.1490	4.0000	427.932
T + BW)	T + BW	436.466	4.01	0.01960	0.1346	6.0000	423.760
WL	C	440.057	7.60	0.00325	0.0223	3.0000	433.860
C	C	440.724	8.27	0.00233	0.0160	2.0000	436.626
C	T	441.086	8.63	0.00195	0.0134	3.0000	434.889

T, tactic; BW, black wingspot; WW, white wingspot; WL, wing length; C, constant.

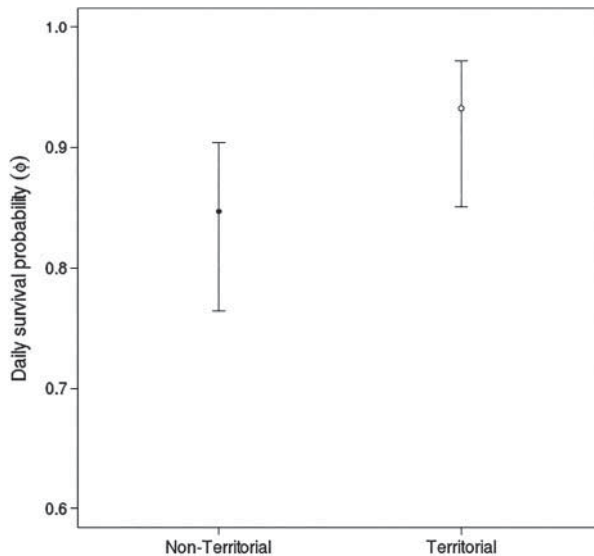


Figure 1. Daily survival probabilities of *Euthore fasciata* males according to their mating tactic.

Discussion

Despite our reduced sample size, our results indicated that territorial males survived longer than non-territorial males, which differs from another study in damselflies using the tropical species *Paraphlebia zoe* Hagen, 1861 (Munguía-Steyer et al., 2010). Our results are entirely coherent with the idea that territorial male individuals are in better condition than nonterritorial males, which is the case for odonates (e.g. Contreras-Garduño, Lanz-Mendoza, & Córdoba-Aguilar, 2007; Grether, 1996) and other animals (Brockmann & Taborsky, 2008). In odonates, such better condition has been observed at the levels of physiological traits and morphological traits. For example, in damselflies, territorial males usually have higher lipid reserves and muscle mass than nonterritorial males (Contreras-Garduño et al., 2008; Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996) while in dragonflies the former have a larger body size than the latter (McCauley, 2010; Tsubaki & Ono, 1987). These differences may, in the long term, enable territorial males to survive for longer than nonterritorial males perhaps due to being better able to survive after mate competition or pathogenic attacks. In fact, territorial males survive better after an experimental bacterial challenge (Contreras-Garduño, Canales-Lazcano, & Córdoba-Aguilar, 2006; Contreras-Garduño, Lanz-Mendoza, et al., 2007), which supports this notion. On the other hand, differences in survival probabilities may be confused by dispersal differences across tactics (nonterritorial males dispersing more than territorial males) or differential predation events which are not necessarily related to male condition or competition (e.g. larger wing pigmented areas; Kuchta & Svensson, 2014). Related to predation, since nonterritorial males should have to move more among territories, this may expose them more to predators. Although a recent study detected that nonterritorial males survived better during bird predation compared to territorial males in a calopterygid (Toivanen, Rantala, & Suhonen, 2009), the higher exposure to predators by nonterritorial males may come in the form of being trapped and eaten by spiders. In the exploration of new sites, nonterritorial males may be less familiar with several sites where such sit-and-wait predators are present. Although a study, also with a calopterygid, found that spider predation can affect males when these are engaged in territorial fights (Rehfeldt, 1992), this was not made to compare predation events for territorial and nonterritorial males. Unfortunately, we were not

aware of predation events in our study species. Thus, it remains to be seen what explains survival differences according to mating tactic in *E. fasciata*.

Contrary to what we expected, we did not find that pigmentation area was related to survival. A key issue here is that our reduced sample size may obscure this result. Supposing that this situation is not a problem, our result is counterintuitive given that previous studies have found support for a positive relationship (Córdoba-Aguilar, 2002; Contreras-Garduño et al., 2007; Grether, 1996). These studies also indicated that pigmentation area is positively related to different aspects of condition, using observational and experimental data. For example, some of the most robust pieces of evidence showed that a reduced provision of food (Álvarez, Serrano-Meneses, Reyes-Márquez, Jiménez-Cortés, & Córdoba-Aguilar, 2013) and an immune challenge (Contreras-Garduño et al., 2008) can both induce a reduction in wing pigmentation area from teneral to sexually mature ages. Furthermore, investment in wing pigmentation comes in the form of a trade-off with survival where both variables covary negatively (Contreras-Garduño, Córdoba-Aguilar, Azpilicueta-Amorín, & Cordero-Rivera, 2011; Kuchta & Svensson, 2014). These studies have provided support for the condition-dependent nature of pigmentation and resource allocation conflicts between pigmentation and survival. These studies also imply that pigmentation and survival cannot be maximized, and that even when switching between mating tactics can increase mating success (for example, when becoming territorial), there will be a survival cost (Córdoba-Aguilar & Munguía-Steyer, 2015). Thus, our results do not corroborate these sources and may imply that pigmentation does not indicate male quality in the form of a trade-off in our study species. In fact, and in partial support of this, pigmentation area did not differ according to tactic in our study species. This null difference implies that wing pigmentation may not communicate condition, which is ultimately related to tactic and survival. This is similar in at least one calopterygid, *Hetaerina titia* (Drury, 1773). In this species, males carry black and red pigmentation spots, but black pigmentation did not correlate with the ability to respond to a challenge (González-Santoyo, Córdoba-Aguilar, González-Tokman, & Lanz-Mendoza, 2010; González-Tokman & Córdoba-Aguilar, 2010). Thus, the relationship between pigmentation and male condition in calopterygids cannot be generalized. In the case of our study species, it remains to be seen whether pigmentation is related to other aspects of sexual selection. For example, it would be interesting to see if more pigmented males spend more time on territories and/or gain more matings, as survival and mating success do not necessarily correlate with each other (e.g. Brooks, 2000). Finally, wing pigmentation may be involved in other natural selection functions such as signaling mate recognition to avoid intra- (e.g. Guillermo-Ferreira, Therézio, Gehlen, Bispo, & Marletta, 2014) or inter-specific (e.g. Anderson & Grether, 2010a, 2010b) mistakes. According to these explanations, pigmentation should not vary among males, which is coherent with the lack of difference between male tactics. Further tests that manipulate pigmentation presence/absence in our study species should clarify this.

Acknowledgements

We are grateful to Hernando Mesa, Aura Blanco, Eibar Algarra, Nidia Buitrago, and Angel Arturo Ciro for key assistance. Thanks also to the AES Chivor & Cia SCA ESP, Grupo de Investigación en Odonatos de Colombia, Laboratorio de Artrópodos – Universidad Nacional de Colombia, and Grupo de Investigación en Biología, Universidad El Bosque (Bogotá, Colombia) for support. Two anonymous reviewers provided key, enriching comments to a previous version.

Funding

This work was supported by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica – Universidad Nacional Autónoma de México [grant IN203115 (AC-A); IA204315 (RM-S)].

Supplemental data

Supplemental data for this article can be accessed at <http://dx.doi.org/10.1080/13887890.2016.1209137>.

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