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Departamento de Genética, Ecologia e Evolução

PPG Ecologia, Conservação e Manejo da Vida Silvestre

João Gabriel Lacerda de Almeida

O QUE FORMA O MELHOR LUTADOR? ENTENDENDO AS ESTRATÉGIAS DE AVALIAÇÃO DURANTE INTERAÇÕES AGONÍSTICAS DA LIBÉLULA *PERITHEMIS TENERA*

Belo Horizonte

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Gabriel Estevão Nogueira Aguila

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"O que forma o melhor lutador? Entendendo as estratégias de avaliação durante interações agonísticas da libélula *Perithemis tenera*"

JOÃO GABRIEL LACERDA DE ALMEIDA

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(UFPR)

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(UFV)

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Resumo:

Estudos teóricos de conflito animais presumem que os indivíduos irão desistir dos conflitos utilizando informações sobre sua própria capacidade de briga, a capaciade de briga de seu oponente e o valor relativo do recurso. Contudo, estudos empíricos ignoram a possibilidade dos três fatores contribuirem simultaneamente para essa decisão. Além disso, essas contribuições podem variar entre as fases do conflitos. A grande variedade de comportamentos durante of conflitos entre machos da libélula *Perithemis tenera* pode representar diferentes fases com diferentes contribuições da capacidade de briga do indivíduo, do oponente e o valor do recurso para a decisão de desistir. Nesse estudo, investigamos se os conflitos de machos de *P. tenera* são estruturados em fases distintas e quais fatores determinam a decisão dos indivíduos de desistir de um conflito. Primeiro nós testamos se existia um conjunto de comportamentos que eram mais provaveis de transitar entre eles. Depois avaliamos a contribuição da massa de gordura do perdedor (medida de capacidade de briga própria), massa de gordura do vencedor (medida de capacidade de briga do oponente) e índice de qualidade do território (medidade de valor do recurso) para a duração do conflito. Nós encontramos que os comportamentos durante os conflitos transitam ao acaso, o que indica uma única fase. Além disso, nós encontramos que a massa de gordura dos vencedores e o índice de qualidade do território não esta relacionado a duração total do conflito. Contundo, nós encontramos que a massa de gordura dos perdedores foi positivamente relacionado a duração total do conflito, o que dá suporte para uma estratégia de avaliação própria. Enquanto muitos estudos empíricos encontram suporte parcial ou misto para mais de uma estratégia de avaliação durante o conflito, nossa nova abordagem forneceu evidência inequívoca que machos de *P. tenera* utilizam avaliação própria para decidir desistir de um conflito.

Palavras-chave: conflito animal, capacidade de briga, valor do recurso, estratégia de avaliação própria; estratégia de avaliação mútua.

Abstract

Animal contest theory presumes that rivals can withdraw from a contest based on both individual and opponent fighting capacity and relative resource value. However, empirical studies often overlook the possibility that these three factors simultaneously contribute to individuals' decision to withdraw. At the same time, these contributions can vary between contest phases, highlighting the need for efficient identification of potential contest phases. In contests for mating territories among males of the amberwing dragonfly (*Perithemis tenera*), rivals perform a wide range of behaviors that may represent distinct contest phases. If this is true, each phase may have a different contribution of both individual and opponent fighting capacity and resource value. Therefore, to understand the contest dynamic between *P. tenera* males, we evaluated if contests are structured in distinct phases and which factors determine individuals' decision to withdraw. We first tested if there were behavioral subsets that were more likely to transit among themselves rather than with other behaviors. After that, we tested whether male decisions to withdraw are based on a combination of loser's total fat mass (a surrogate for self-fighting capacity), winner's total fat mass (a surrogate for opponent fighting capacity), and territory quality index (a surrogate for resource value) or exclusively on one of these factors. We found that the behaviors adopted by males of *P. tenera* during contests can transit in any direction, which indicates that contests occur in a single phase. In addition, winners total fat mass and territory quality index were unrelated to the overall contest duration. However, loser's total fat mass was positively related to the overall contest duration, supporting self-assessment strategy. While many empirical studies provide mixed or partial support for various assessment strategies during contests, our novel approach offers clear evidence that *P. tenera* males primarily use self-assessment in their decision to withdraw.

Keywords: animal contest; fighting capacity; resource value; self-assessment strategy; mutual assessment strategy.

Sumário

What makes the ultimate fighter? Unpacking boxes in assessment strategies in contests of males of the dragonfly *Perithemis tenera*

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Introduction

When two rivals engage in a contest, the victory is typically determined in favor of the individual with higher fighting capacity or the one that considers the disputed resource more valuable (Arnott & Elwood, 2008; Vieira & Peixoto, 2013). The fighting capacity (also termed resource holding potential - Parker, 1974) is represented by morpho-physiological traits that grant individuals a greater capacity to inflict costs on the opponent or to accumulate more costs (in terms of injury received or energy depleted) during the contest (Parker & Stuart, 1976; Vieira & Peixoto, 2013). On the other hand, resource value is associated with characteristics that affect the potential benefits individuals can gain by monopolizing that resource (Arnott & Elwood, 2008). In some species, the resource value will be accessed only by individuals that already own the resource, which will give them more accurate information about the resource quality (Arnott & Elwood, 2008). This information can make owners more prone to bear greater costs during the contest, which increases their chances of winning (i.e. asymmetric contests - Kemp & Wiklund, 2004; Maynard-Smith & Parker, 1976; Parker, 1974; Parker & Stuart, 1976). On the other hand, when the characteristics of the resource can be accessed by any individual, both individuals will invest more in contests for more valuable resources (i.e. symmetric contests - Kemp & Wiklund, 2004). Therefore, both fighting capacity and resource value may affect how much each individual will be able to invest in each contest.

Because both fighting capacity and resource value affect individual chances of winning, a major puzzle to understand contest dynamics relies on determining the way these two factors contribute to each rival's decision regarding when to withdraw the interaction. Such decisions, in turn, depend on which assessment strategy is adopted by each individual (Maynard-Smith & Parker, 1976; Payne, 1998; Payne & Pagel, 1996; Enquist & Leimar, 1983; Arnott & Elwood, 2009). If individuals perform a self-assessment strategy, the decision to withdraw from a contest is made when the individual reaches its own cost threshold. The cost threshold may be solely dependent on the individual actions, as predicted by pure-self assessment models (War of attrition model, WOA and Energetic war of attrition model, E-WOA - Mesterton-Gibbons et al., 1996; Payne & Pagel, 1996) or may also be affected by costs imposed by the opponent as predicted by the cumulative assessment model (Cumulative assessment model, CAM - Payne, 1998). An alternative to self-assessment occurs when individuals are able to assess information about the fighting capacity of their rivals and make decisions based on a comparison with their own fighting capacity (mutual assessment strategy - Enquist & Leimar, 1983). If individuals perform a mutual assessment strategy, a greater asymmetry between fighting capacity increases the chance of the weaker individual withdrawing from the contest faster (Sequential assessment model, SAM - Enquist & Leimar, 1983). In addition, in species in which the individuals can access information about resource value, individuals fighting for a high-quality resource can be more prone to support a higher cost threshold or face opponents with a greater fighting capacity before withdrawing (Resource assessment strategy - Arnott & Elwood, 2008). Therefore, to determine which of these assessment strategies is adopted by an individual during a contest, it is essential to evaluate the contribution of self fighting capacity, opponent fighting capacity, and resource value to the individual decision to withdraw.

The most common approach used to evaluate the contribution of fighting capacity and resource value to the individual decisions to withdraw is testing how contest costs vary in response to morpho-physiological traits that indicate fighting capacity (e.g. body size, weapon size), or the characteristics of the disputed resource that may affect the individual motivation to fight (e.g. presence/absence of mating partners in the disputed resource) (Arnott & Elwood, 2008; Taylor & Elwood, 2003). The contest cost is frequently represented by the contest duration (Arnott & Elwood, 2008; Taylor & Elwood, 2003). If individuals decide to withdraw based on pure self-assessment, a positive relationship between contest duration and loser fighting capacity and a nonexistent relationship between contest duration and opponent fighting capacity are expected (Taylor & Elwood, 2003). If individuals decide to withdraw based on cumulative or mutual assessment models, the expected relationship between contest duration and loser fighting capacity should not change, but for winners, there should be a negative relationship between contest duration and individual fighting capacity (Payne, 1998; Taylor & Elwood, 2003). For resource value, a positive relationship between the value of the resource to each rival and contest duration is expected (Arnott & Elwood, 2008). Each of these models is usually tested as mutually exclusive explanations (Arnott & Elwood, 2009; Taylor & Elwood, 2003). However, despite these straightforward predictions and wide investigations of the relationship between contest duration and traits linked to fighting capacity or resource value, there has been a growing discussion that testing these assessment strategies as mutually exclusive explanations may represent an oversimplification of individuals decisions in actual contests (Briffa et al., 2020; Chapin et al., 2019; Parker, 2019; Pinto et al., 2019).

If individuals differ in the ability to gather information about their opponent and their own fighting capacity, this can generate an asymmetric contribution of individual and opponent fighting capacity to the decision to withdraw (Fawcett & Mowles, 2013; Prenter et al., 2006; Briffa & Elwood, 2002). In this way, self-assessment can be seen as an extreme possibility in which the opponent and resource value effects are negligible to individual decision, while mutual assessment can be seen as a situation in which both self and opponent, but not a resource, equally contribute to individual decision do withdraw (Briffa et al. 2020). Therefore, when studies consider the relationship between contest duration with loser fighting capacity, winner fighting capacity, and resource value separately, they may overlook nuances in the contribution of each one of these traits to individual decisions during contests (Briffa et al., 2020). One potential solution to this oversimplification is to simultaneously evaluate the proportional contributions of both self (i.e. loser) and opponent (i.e. winner) fighting capacities, as well as resource value to contest duration (Briffa et al., 2020). This approach considers that the relative contribution of different effects to the decision to withdraw may vary continuously across species, potentially leading to a more comprehensive understanding of the factors that determines an individual decision to withdraw from a contest (Briffa et al., 2020).

An important aspect of adopting the continuous approach is recognizing that animal contests may be structured in distinct behavioral phases (Hardy & Briffa, 2013). A contest phase is determined by changes in the predictable behavioral sequences adopted during the fight (Enquist et al., 1990; Green & Patek, 2018; Hardy & Briffa, 2013). For instance, in contests between male crickets of the species *Melanotes ornata*, the first phase involves mutual antennal touching by opponents, followed by a second phase where individuals move closer and engage in pushing and kicking with their hind legs (Lobregat et al., 2019). These phases represent different stages of the contest (Enquist & Leimar, 1983; Hardy & Briffa, 2013), and consequently individuals may perform different assessment strategies to decide to withdraw from each one. Therefore, to correctly understand contest dynamics, it is necessary to determine if the contest is structured in different phases (e.g. Dihn & Patek, 2023; Green & Patek, 2018) and then investigate the relative contribution of self, opponent, and resource value to decision to withdraw in separately for phases. However, identifying the occurrence of behavioral phases during a contest remains a challenge in empirical studies (e.g., Enquist et al., 1990; Dinh & Patek, 2022; Green & Patek, 2018). A potential approach to detect contest phases may be based on the theory of complex networks (Bascompte, 2007). Complex networks are commonly used in community ecology to identify modules of species that interact more frequently within the same subset of species than with those from different modules in a community (e.g., Donatti et al., 2011; Maruyama et al., 2015). By applying this approach to contest behaviors, we can identify groups of behaviors that are more likely to transit within the same module, thereby representing distinct contest phases.

One species that employs different behaviors during contests and may show distinct contest phases determined by different assessment rules is the eastern amberwing dragonfly, *Perithemis tenera* (Odonata, Libellulidae) (Say, 1840; Paulson, 2020). In this species, males fight for access to mating territories in the margin of ponds or streams (Switzer, 2002). In these territories, males defend areas usually formed by clumps of partially submerged grasses and tree branches, in which females oviposit (Jacobs, 1995; Switzer, 1997a; Switzer, 2002). Males can be selective when searching for territories, refusing margins with few or no emerging substrates on the water (Wildermuth, 1991). This selectivity indicates that the territories may vary in their quality (Wildermuth, 1991). Fight between males of *P. tenera* may show up to eight different aerial displays without (Switer, 2004; Jacobs, 1995) and with physical contact (Pers. obs). The sequence of non-contact behaviors transitioning to physical contact behaviors may indicate that contests in *P. tenera* have phases that may involve different assessment strategies (Taylor & Elwood, 2003). A previous study has suggested that *P. tenera* males' decision to withdraw from a contest is primarily based on their own fighting capacity (i.e., self-assessment strategy) (Switzer, 2004). However, the approach used for this conclusion did not correctly discriminate between self and mutual assessment strategies (Taylor & Elwood, 2003) and did not consider the simultaneous contribution of self, opponent, and resource value on the decisions made by rivals. Therefore, to fully understand the contest dynamics in *P. tenera*, we investigated if the contest is structured in phases, and which factors determine the male's decision to withdraw. We evaluated the hypothesis that the male's decision to withdraw is based on a partial contribution of their own fighting capacity, the opponent's fighting capacity, and the resource value. However, we could not rule out the possibility that males make decisions based on mutually excluded possibilities. Therefore, we also investigated an alternative hypothesis that the male decisions to withdraw are exclusively based on their own fighting capacity, on the opponent’s fighting capacity or on the resource value.

Methods

Study area and model organism

We collected the data from February to March, and from October to December 2023 in ponds located at the Florestal campus of the Federal University of Viçosa in the city of Florestal, Minas Gerais state, Brazil (19°52'56" S; 44°25'03" W). According to Köppen classification, the climate of Florestal is type Cwa (temperate humid with summer rains and dry winter - Fonseca et al., 2019; Kottek et al., 2006). The average annual rainfall is 1,393 mm and the average temperature during the year is 28.9 ºC. Mature males of *P. tenera* guard territories near pond margins between 10:00 a.m. and 04:00 p.m. (Personal observation). Resident males usually stay most of the time perched near the oviposition site or try to evict intruder males from the territory (Wildermuth, 1991). Residents males tend to be site-faithful, returning to the same site for up to 10 days (Pers. obs.).

Identification of males territories

To investigate which factors determine the decision of *P. tenera* males to withdraw from a contest, we recorded contests between males for territory ownership. To be able to record the territorial contests, we first identified the location of territories defended by males along the pond margin. For this, we made behavioral observations of *P. tenera* males during 10 min. During these observations, we recorded whether the male patrolled or perched in a fixed area and evicted other males from it. These aggressive behaviors indicate that males were guarding the site (Schultz & Switzer, 2001; Switzer, 1997a; Switzer, 2004; Wildermuth, 1992). After the observation, we captured each male with an entomological net and marked it by writing a number on its right hind wing with a non-toxic pen to be able to identify each individual on subsequent days with binoculars (Switzer, 2004). After marking the individuals, we also marked the pond margin in front of the perch mostly used by the males during the 10 min observation. To confirm the site as a territory, we returned for two consecutive days to observe if the former male, or another male, was established in the same area and performed aggressive behaviors against other males. If the area was defended during this period, we considered it as a suitable territory location.

After determining the location of each territory, we inserted at the center of each one (at about 1 m distance from the pond margin), a floating platform consisting of polystyrene covered by green-colored plastic foil with wood sticks inserted at the vertices (supplementary material - Fig. S1). Such platforms concentrated the perchers used by territorial males at the same point, increasing the predictability of the perch that individuals would use inside each territory (Switzer, 2005; Wildermuth, 1992). This increased predictability facilitated the location, observation, and identification of resident males inside the defended territories. However, it's important to note that although the platform provides an attractive place for perching, it does not function as an oviposition site. Consequently, it did not induce the formation of new territories or change the location of existing ones.

Recording of territorial contests

To gather information on contest duration and evaluate if the contest is structured in phases, we recorded contests between males for mating territories. Most contests between *P. tenera* males were between a resident (i.e. a male that was defending the same territory for at least two consecutive days) and an intruder (i.e.

a male that did not defend the territory previously) (Switzer, 2004; Personal Observations). To avoid bias from potential asymmetry in residency status (Maynard-Smith & Parker, 1976; Maynard Smith, 1982; Parker & Rubenstein, 1981), we only recorded contests in vacant territories where none of the males had previously established ownership (i.e., symmetric contests). We defined symmetric contests as those between a male that perched in a vacant territory and fought for it with an intruder on the same day, or contests between males that simultaneously entered a vacant territory. We recorded all the contests between males using a voice recorder (see the next paragraph for a detailed description of the behaviors we recorded). We defined the beginning of a contest as the moment when one male entered the territory and started touching the substrate in the water with his hind legs while flying and the rival male either mimicked this behavior or began circling the first male in a roundabout flight. In our initial recordings, we observed that the maximum time taken for an expelled individual to return and reinitiate a contest was 180 s. Therefore, we defined the end of a contest as the point when one male (the loser) flew away and did not return within the next 180 s. Consequently, we considered the male who remained in the perch as the winner (Switzer, 2004). In the end of the sample collection, we recorded 33 symmetric contests and were able to capture both rivals at the end in 20 of them (61%).

To categorize each behavior adopted by males during the contest, we followed the behavioral description of Switer (2004) and Jacobs (1995) but added two behaviors previously undescribed. According to this, we classified the behaviors into the following categories: I) “Oviposition site touching”, in which males use their hind legs to touch the substrate near water while the opponent hovers nearby; II) “Roundabout flight”, in which one individual flies around the rival while the opponent hovers in the air; III) “Hover”, in which both opponents remain relatively stationary in the air at a distance of 1 - 2 m from each other; IV) “Bounce”, in which one male flies above the other and then they changed their position recurrently while remaining in roughly the same high; V) “Circle chase”, in which males chase each other in a circular flight; VI) “Back-and-forth flight”, in which one male pursue the other around the territory boundary, taking turns between chaser and chased during the flight; VII) “Escalated back-and-forth flight” (previously undescribed) in which one male pursue the other beyond the territory boundaries, varying in distance, speed, and flying height and VIII) “Physical aggression” (previously undescribed), in which males briefly pushed one another or grabbed during the flight. For each contest, we described the behavioral transition sequence adopted during the contest, including the adoption of new behaviors and back changes to previously adopted ones.

Identification of fighting capacity proxies

To be able to determine the influence of self and opponent effects on the decision to withdraw from a contest, we needed to first identify the trait that better represents the fighting capacity of *P. tenera* males. For this, we measured surrogates of the most common traits that determine the fighting capacity in odonate contests: body size and energetic reserves (e.g. Kasuya et al. 1997; Plaistow & Siva-Jothy, 1996; Tsubaki & Ono, 1987). In addition to these traits, it is important to note that males of *P. tenera* exhibit a conspicuous orange coloration in both wings, a trait absent in females (Schultz & Switzer, 2001; Shiffer, 1968). Visual cues play an important role in some behaviors of *P. tenera* males, such as in territory selection, conspecific identification, and detection of territory intruders (Switzer, 1997a, 2000; Shultz & Switzer, 2001). Therefore, we also measured parameters of reflectance and transmittance spectra of male wings as potential cues of fighting capacity used by males of *P. tenera.*

As a surrogate of body size, we measured the wing length (mm), the fresh mass (mg), and the dry mass (mg) of each male. To measure the wing length, we took a photograph of the right frontal wing of each male on a graph paper background using a semi-professional camera (Canon EOS Rebel T5). We used these pictures to calculate the linear distance from the insertion point of the wing in the thorax until the wing apex, using the software ImageJ (Schneider et al., 2012). To measure fresh mass, we subtracted the weight of an empty entomological envelope from the weight of the same envelope with the individual using a 0.001 g accuracy scale during its capture in the field (e-Labshop BD50). To measure the dry mass of each individual, we first dried each male in an oven at 60 °C for 96 h. After drying, we weighed the thorax and abdomen separately using a digital scale with a precision of 0.01 mg (Auw220D Marte Shimadzu). Since we lacked prior information about the ideal duration for completely drying *P. tenera* mass, we repeated these procedures until the weight difference between successive dry weights became smaller than 0.001 g, indicating a stable weight. Specifically, we measure the mass again after 48 hours and then after an additional 24 hours (a total of 168 hours). We considered the last measure of abdomen and thorax weight after the last drying as our final measure of abdomen and thorax dry mass.

As a surrogate of energetic reserves, we measured the fat mass of each individual. For this, we inserted the thorax and abdomen of each individual in a sealed tube with 1.2 ml of chloroform for 72 h to extract lipids (Dos Santos & Peixoto, 2017; Junior & Peixoto, 2013; Marden, 1989; Marden & Waage, 1990). After lipid extraction, we dried the samples in the oven at 60 °C for 96 h and weighed them using the 0.01 mg precision digital scale. We repeated these procedures of chloroform immersion and drying until the weight difference between successive dry weights became smaller than 0.001 g, indicating a stable weight (Marden, 1989). We considered the difference between the abdomen and thorax dry mass and their respective masses after the final chloroform immersion (a total of 288 h in chloroform) as the amount of fat stored by each individual.

To estimate the wing coloration of *P. tenera* males, we measured spectra parameters from the reflectance and transmittance of male wings. We did not measure spectra parameters from absorbance since the previous analysis reviewed a low range of absorbance spectra on *P. tenera* male wings. For this, we used a spectrophotometer (HR-4000, Ocean Optics Inc, Dunedin, Florida, USA) with a deuterium/tungsten halogen light source guided through a 200-µm diameter optical glass fiber. We transmitted the light in a broad spectral range from ultraviolet to near-infrared (200 to 1100 nm) directly through the *P. tenera* wings. To measure the light spectra reflected by *P. tenera* wings, we positioned a spectrometer sensor attached to the light source. To measure the transmittance spectra parameters, we directly transmitted a light source through the wings and positioned the spectrometer sensor below the wing to capture the light spectra transmitted by *P. tenera* wings (Guillermo-Ferreira et al., 2015). To obtain the final spectra for each individual, we calculated the mean of three different measures on the wing: wing apex area (sensor positioned near the pterostigma), middle wing area (sensor positioned near the node), and wing basal area (sensor positioned near the wing insertion into the thorax). We measured these areas in both hind and forewings. We measured all the spectral parameters using the software “SpectraSuite” (Ocean Optics).

After measuring the spectra, we evaluated if *P. tenera* males are capable of distinguishing opponent colors. However, there is no photoreceptor sensitivity model for *P. tenera*. Therefore, we chose to model a conspecific visual system based on the available photoreceptor sensitives of a closely related species (*Sympetrum rubicundulum* - Meinertzhagen et al., 1983). We assumed that the tetra chromatic visual model of *P. tenera* was 340, 410, 490, 530, and 620 nm, and we used the cone proportions 2: 2.5:2.5:1 (UV : S : M : L) in the model (Meinertzhagen et al., 1983). We calculated the receptor quantum catches (Qi) for each photoreceptor (i) using the package pavo (Maia et al., 2019) in R (R Core Team 2024). We used a standard "bluesky" illuminant vector as fights between males of *P. tenera* occur in open areas in our study site. We measured the just notable differences (i.e. JND) of *P. tenera* rivals using values of chromatic contrast (Δs), which determine the threshold for discriminability between two stationary spectra. We considered values upper 1 as indicative of discriminability between two stationary color patches for the *P. tenera* visual system. As color patches that differ in 1 JND are barely discernible, and the value increases the color patches become less similar (e.g. Siddiqi et al. 2004; Langmore et al. 2011). If values were upper 1, we measured the hue, chroma, and brightness measures from transmittance and reflectance (Endler, 1990). For this, we used the chromatic contrast (Δs) as a surrogate of hue and chroma, and the achromatic contrast (Δl) of each individual as a surrogate of brightness (Maia et al., 2019).

Estimation of resource value

To estimate the resource value of each territory, we created a quality index based on female visitation and female behavior when arriving in each territory. When females of *P. tenera* arrive in a territory, they may fly away without adopting any specific behavior or may hover near the partly submerged substrate touching the tarsi and the abdomen tip in the substrate, the same movements of oviposition behavior (Wildermuth, 1991, 1992). After the female touches the substrate, she may copulate with the resident male or fly away to another territory (Wildermuth, 1991). Therefore, the initial touching behavior may serve as a mechanism to evaluate the quality of the oviposition site (Wildermuth, 1991, 1992). To calculate the quality score index, we scanned all territories every 10 min between 10:00 a.m. and 4:00 p.m. on the same days we recorded contests between males. For this, at least two people always conducted field observations, ensuring that if a contest for territory began, one observer could record it while the other continued the scanning. During the scans, we recorded whether females visited each territory and documented their behaviors. If we did not see any female during the scan or the female entered the territory but did not touch the substrate, we assigned a value of 0 in the score, indicating that the territory was unsuitable for that female. If the female entered the territory and touched the substrate, but flew away without mating with the resident male, we considered the territory as potentially suitable but not valuable enough for the female. Therefore, we recorded a value of 1 in the score. If the female touched the substrate and mated with the resident male subsequently, we considered the territory suitable for the female. Therefore, we recorded a value of 2 in the score. If more than one female entered a particular territory during the scan, we observed all of them and summed their behaviors to the final score of the territory for that scan. At the end of the field sampling, we summed the score of each territory and divided it by the number of total scans in all field sampling. The minimum index value expected for each territory would be 0 while the maximum value expected would be 2 (if we observed mating in all scan events).

Data analysis

To identify the trait that better represents the fighting capacity of *P. tenera* males, we tested which trait most effectively predicted the chance of victory in contests. For this, we built generalized linear mixed models (GLMM) with a binomial error distribution, using the focal individual’s status (winner or loser) as the response variable. Since most morpho-physiological variables we measured are correlated, we created separate models for each predictor variable: fresh mass, wing length, abdominal dry mass, thorax dry mass, total dry mass and the abdominal fat mass, thorax fat mass, total fat mass and spectra parameters from the reflectance and transmittance of male wings. We accounted for potential pseudoreplication among fights by including the identity of the pair of males who fought as a random variable in each model (Zuur et al., 2009). To make the models comparable, we standardized the values of each predictor variable (Schielzeth, 2010). To determine which trait best predicts the chance of victory, we compared the estimate of the predictor variable of each model as a measure of effect size (Schielzeth, 2010). To create and compare the models we used the package “lme4” (Bates, 2014) in the R software (R Core Team 2024).

To test if the *P. tenera* contests are structured in phases, we evaluated if subsets of behaviors adopted in the symmetric contests were more likely to transit among themselves rather than with other behaviors (Briffa et al., 2013). For this, we created a behavioral transition network and assessed the presence of behavioral modules using an approach based on ecological network theory. In community ecology, graph networks are commonly used to represent species (nodes) and their interactions (edges) (Maruyama, 2015; Vizentin-Bugoni, 2014). In our network, we represented nodes as the behaviors observed in the contest while edges represented the transitions for the subsequent behavior. To create this network, we first constructed an adjacency matrix summarizing all behavioral transitions, with each cell representing the number of times one behavior (rows) transitioned to another (columns) (similar to Green & Patek, 2018). To identify if a subset of behaviors interacts more frequently with behaviors of the same subset than other behaviors in our network, we calculated the modularity index of our network (Dicks et al., 2002; Dupont & Olesen 2009; Olesen et al. 2007). The modularity index ranges from 0 to 1, with values near 1 indicating the presence of modules in the network (Barber, 2007; Fortuna et al, 2010). To assess the significance of our modularity index, we generated 10,000 models that randomized the transitions in the adjacency matrix while maintaining the constant frequency of each behavior. This created a null distribution of modularity index values, which we compared to our observed modularity index using the Patefield algorithm (Patefield, 1981). We considered the existence of modules in our behavioral transition network if our observed modularity index was equal to or greater than the values in less than 5% of the null models. To create the network diagram, we considered only the transitions more frequently observed than their respective 95% quantile in the null distribution (Green & Patek, 2018). We used the "Igraph" package (Csardi & Nepusz, 2006) to create the adjacency matrix and the network diagram. In addition, we used the "bipartite" package (Dormann et al., 2008) in R (R Core Team, 2024) to calculate the modularity index of our matrix, the mean modularity index of the null models and the confidence interval.

To test whether loser fighting capacity, winner fight capacity, or resource value determine the male's decision to withdraw in each contest phase, we used a generalized least squares (GLS) model. In this model, we considered the contest duration as the response variable, and the loser fighting capacity trait (i.e. focal individual fighting capacity), winners fighting capacity trait (i.e. opponent fighting capacity), and the territory quality index (i.e. resource value) as predictor variables

(Briffa et al., 2020). To adjust the expected residual distribution, we used the VarPower function modeled according to loser fighting capacity (Pekar & Brabec, 2016; Pinheiro & Bates, 2000). We opted to use GLS models because the linear model did not provide a suitable fit to the data (based on visual inspection of residuals). It is important to note that in our data set, we had one winner male that participated in two contests against different losers contests and six territories in which we observed more than one contest. Due to the limited number of repetitions, we were unable to control for these factors using a Generalized Linear Mixed Model (GLMM) (Zuur et al., 2009). Instead, we performed GLS models with and without the pseudo-replicated observations (see Table 2 and S1). Since the qualitative results were similar (see Table 2 and S1), we proceeded with the model with all sample sizes.

If our hypothesis that the male's decision to withdraw is based on a partial contribution of their own fighting capacity, opponent’s fighting capacity, and resource value is correct, we expect to find the following relationships: 1) a positive relationship between contest duration and traits linked to losers fighting capacity; 2) a negative relationship between contest duration traits linked to winners fighting capacity and 3) a positive relationship between contest duration and territory quality index. On the other hand, if our hypothesis that male's decision to withdraw is exclusively based on their own fighting capacity, opponent’s fighting capacity, or resource value is true, we expect only one of the prior relationships with contest duration to be significant. To determine the contribution of the loser and winner fighting capacity and territory value to the individual decision to withdraw, we calculated the semi-partial coefficient of determination (partial R^2) for each predictor variable in the model. We selected the partial R^2_{lik} (likelihood) as a partial R^2 measure due to its efficiency in representing the real contribution of each predictor in GLS models (Ives, 2019). To represent the simultaneous contribution of individual fighting capacity, opponent’s fighting capacity, and resource value to the individual decision to withdraw we used a ternary diagram. This diagram is structured in an equilateral triangle, in which each predictor in the model represents one axis. Each axis is scaled from 0 to 100%, representing the proportional contribution of each predictor to the response variable variance (partial R^2_{lik}). To create the GLS model, we used the packages “nlme” (Pinheiro & Bates, 2023) and “car” (Fox & Weisberg, 2019). To calculate the partial R^2_{lik} we used the package “rr2” (Ives & Li, 2018), and to create the ternary plot we used the package “Ternary” (Smith, 2017) in the R software (R Core Team 2024).

Results

We identified a total of 55 locations repeatedly used as territories and marked a total of 281 individuals. Males returned to the same territory for a mean± SD of 2.8 ± 3.7 days. We recorded 136 visits of females in territories occupied by males, of which 39 resulted in copulation and oviposition events (28% of the visits). The territory quality score index varied between 0 to 0.67. The frequency of mating events per day ranged from 0 ± 0 in territories with a quality index of 0, to 0.24 ± 0.1 in territories with a quality index of 0.67. The contests occur between 11 a.m. and 2 p.m. The mean duration of contests was 847.6 ± 679.55 s (n=20), with a maximum duration of 2695 s. We never recorded any sneak or satellite alternative mating tactic performed by non-resident males, as is common in other dragonfly species (e.g. Irusta & Araujo, 2007; Tsubaki & Ono, 1986).

Recording of territorial contests

During the contest, the less frequent behavior was physical aggression, representing 7% of the total behaviors observed (Fig. 1). Bounce, circle chase, and oviposition site touching each represented 9% of the behaviors, while hover represented 11% of the behaviors observed (Fig. 1). Roundabout behavior represented 16% of all behaviors observed, while the escalated back-and-forth flight represented 17% (Fig. 1). The most common behavior we observed was back-and-forth flight, which represented 21% of the behaviors observed (Fig. 1). Additionally, there was a period when individuals fought out of sight, making up 1% of all behaviors observed. Despite its lower frequency, physical aggression occurred in 59% of the contests we observed (19 out of 32). However, this behavior did not lead to significant wing damage in any individual collected after contests. We defined significant wing damage as the loss of more than 10% of the wing area, determined through visual inspection (e.g. Rajabi et al., 2017).

In 28% of the contests, the male's initial behavior was oviposition site touching (9 out of 32), while roundabout flight also frequently initiated contests, being the initial behavior in 34% of the contests (11 out of 32). The most common behavior to finish the contest was escalated back-and-forth flight, occurring in 59% of contests (19 out of 32), followed by back-and-forth flight and physical aggression, which occurred in 12% of contests each (4 out of 32, each). Despite this wide variation of behaviors during contests, our modularity index value overlapped the 95% confidence interval of null values of modularity, which indicates the absence of modules (M = 0.25; Mnull= 0.066, P = 0.079; n = 32). Therefore, we considered *P. tenera* contests were not structured in phases.

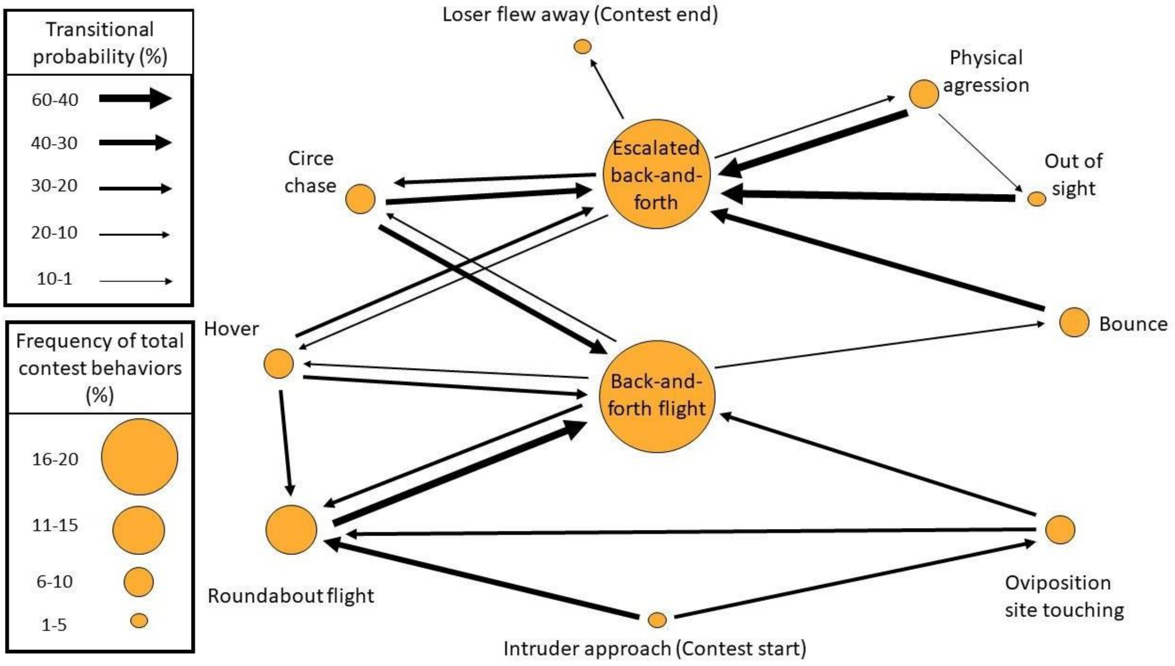


Figure 1: Depiction of the diagram representing the most frequently observed behavioral transitions and the overall frequency of behaviors during territorial contests in *Perithemis tenera* males. Black arrows indicate transitions that occurred more often than their respective 95% quantile in a null distribution, with arrow width scaled to reflect the observed transitional probabilities. Circle size corresponds to the total frequency of each behavior observed throughout the contests.

Identification of fighting capacity proxies

The model that better predicted the individual chance of victory in the contest included individual total fat mass as the predictor variable (b= 0.53, df= 45, n= 47, p= 0.003; Table 1). The overall mean total fat mass of individuals was 0.003 ± 0.002g. The mean total fat mass of the winners was 0.004 ± 0.002 g, while the mean total fat mass of the losers was 0.002 ± 0.0006 g. Therefore, we used the total fat mass as a surrogate of individual fighting capacity in the subsequent analyses.

Table 1: Results of generalized linear mixed models (GLMM) with a binomial error distribution using the focal individual status (winner or loser) as the response variable. We created separate models for each predictor variable. To make models comparable, we standardized the values of each predictor variable and compared the estimate of the predictor of each model. The last two columns indicate the mean ± sd values for winner and loser males of each predictor variable in the model. In all models, we inserted the identity of the pair of males who fought as a random variable. The difference between sample numbers from one model to another is explained due to the absence of some measurements for some individuals collected. The Δs and ΔI values represent chromatic contrast (hue and chroma) and achromatic contrast (brightness), respectively.

Predictor variable	Estimate (b)	df	Mean ± sd winner	Mean ± sd loser	n
Wing length	0.17	45	1.97 ± 0.09 cm	1.95 ± 0.09 cm	46
Fresh weight	0.20	47	0.08 ± 0.01 g	0.07 ± 0.01 g	48
Thorax dry weight	0.31	46	0.013 ± 0.001 g	0.012 ± 0.002 g	47
Abdominal dry weight	0.52	46	0.005 ± 0.001 g	0.004 ± 0.001 g	47
Total dry weight	0.52	46	0.018 ± 0.002 g	0.017 ± 0.003 g	47

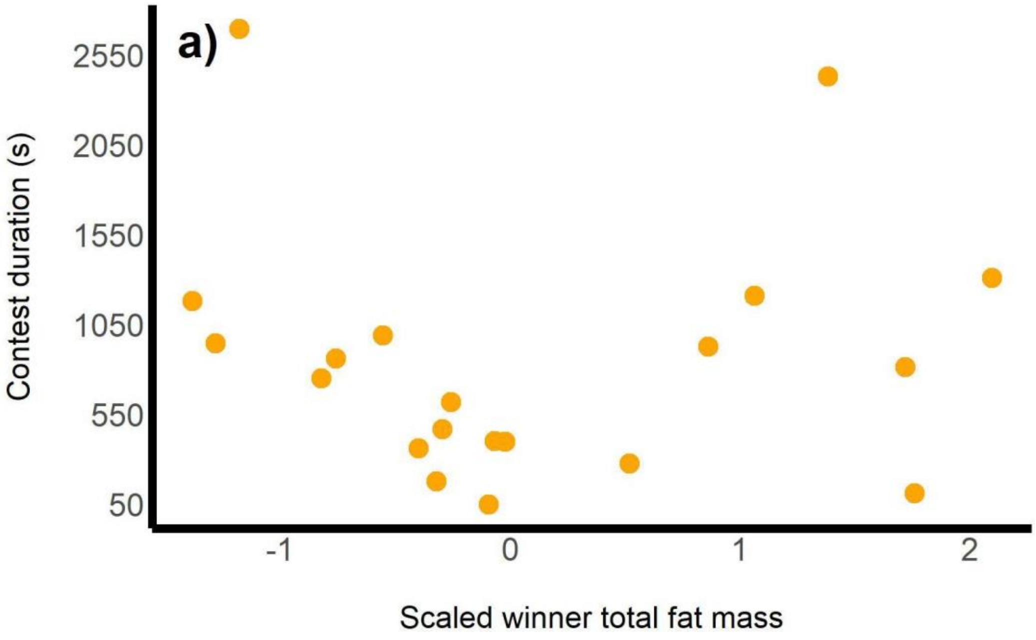
Thorax fat weight	0.15	46	0.002 ± 0.001 g	0.001 ± 0.0004 g	47
Abdominal fat weight	0.31	47	0.002 ± 0.001 g	0.001 ± 0.0008 g	48
Total fat weight	0.53	45	0.004 ± 0.002 g	0.002 ± 0.0006 g	46
Residual thorax fat weight	0.26	46	0.0001 ± 0.001 g	-0.0002 ± 0.0003 g	47
Δs of Reflectance	-0.11	40	2.974 ± 0.755 Δs	3.059 ± 0.845 Δs	41
Δs of Transmittance	-0.01	40	4.901 ± 1.318 Δs	4.914 ± 1.225 Δs	41
ΔI of Reflectance	-0.50	40	2.086 ± 0.556 ΔI	2.422 ± 0.851 ΔI	41
ΔI of Transmittance	-0.11	40	3.929 ± 0.255 ΔI	2.983 ± 0.669 ΔI	41
Residual abdomen fat weight	0.12	46	5.33^{e-05} ± 0.0005 g	- 4.02^{e-05} ± 0.0004 g	48

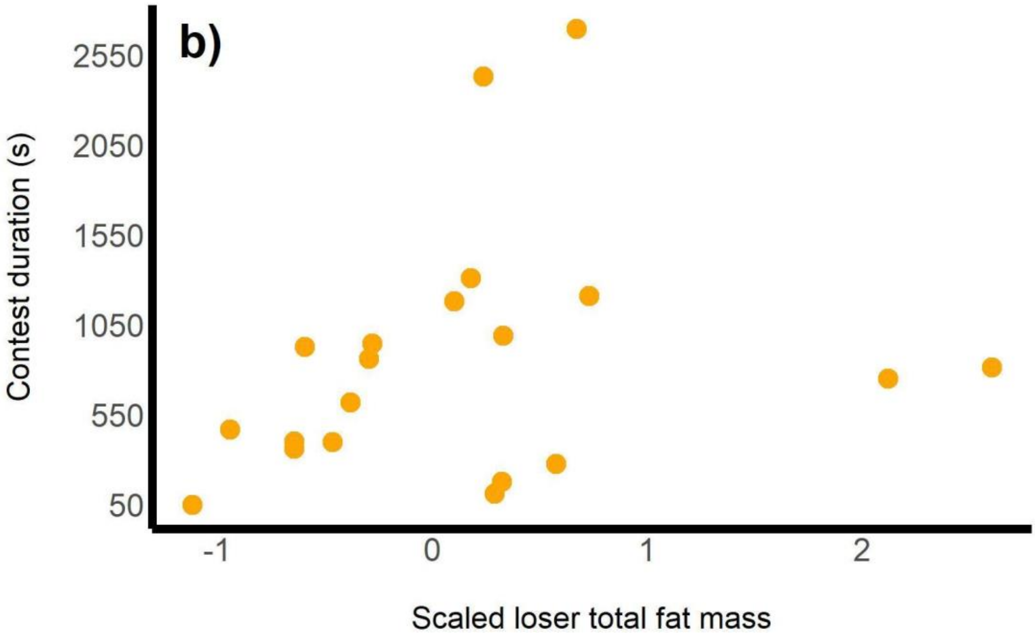
Contribution of each factor to males decision to withdraw

Using the overall contest duration as the response variable, we found a positive relationship between loser's total fat mass and the overall contest duration (Fig. 2a; Table 2). We did not find a relationship between winner's total fat mass and the overall contest duration (Fig. 2b; Table 2), and the territory quality index and the overall contest duration (Fig. 2c; Table 2). In relation to the contribution of loser and winner fighting capacity and territory value to the individual decision to withdraw, the loser's total fat mass had the greatest contribution to the contest duration variation (partial $R^2_{lik} = 0.36$; Fig. 3), followed by the winner total fat mass (partial $R^2_{lik} = 0.35$) and the territory quality index (partial $R^2_{lik} = 0.16$).

Table 2: Summary statistics for the generalized least squares model. We used the overall contest duration as the response variable, the loser's total fat mass (a proxy for focal individual fighting capacity) and winner's total fat mass (a proxy for opponent fighting capacity), and the territory quality index (a proxy for resource value) as predictor variables (n = 20). The analysis is illustrated in Figure 2.

Predictor variables	df	b	χ^2	p
Scaled winner total fat mass	1	-65.71	0.10	0.74
Scaled loser total fat mass	1	359.53	7.93	0.004
Territory quality index	1	-139.60	0.39	0.53
Residuals	17			


a)
Contest duration (s)
2550
2050
1550
1050
550
50
-1
0
1
2
Scaled winner total fat mass


b)
Contest duration (s)
2550
2050
1550
1050
550
50
-1
0
1
2
Scaled loser total fat mass

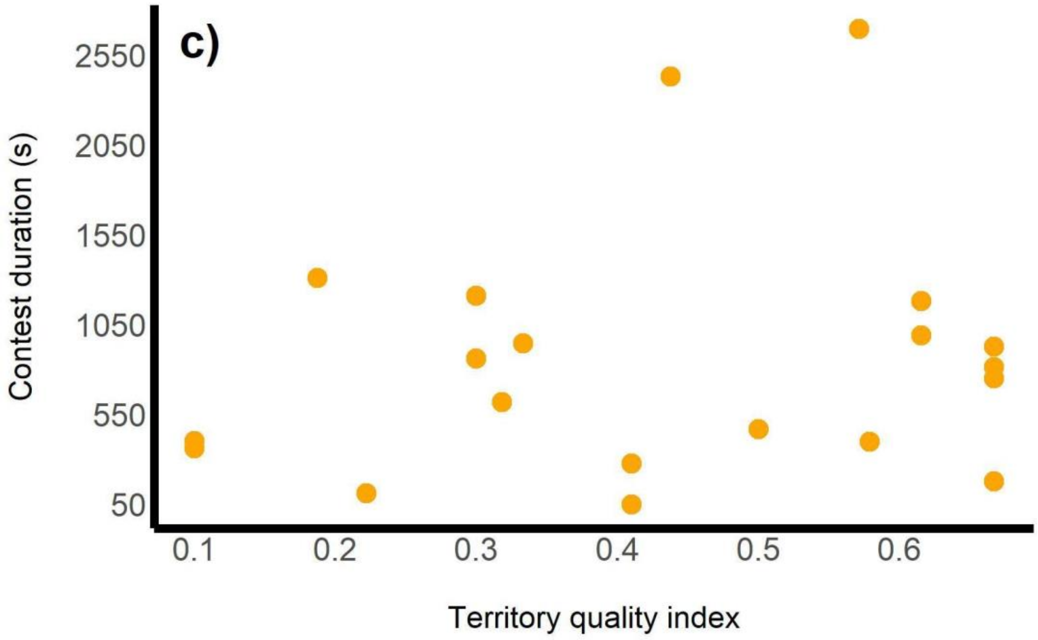


Figure 2: Relationship between the overall contest duration (s) between males of Amberwing dragonflies *Perithemis tenera* for access to mating territories and the winner's total fat mass (g) (a); the loser's total fat mass (b) and territory quality index (c). We defined the beginning of a contest as the moment when one male entered the territory and started touching the substrate in the water with his hind legs while flying and the rival male either mimicked this behavior or began circling the first male in a roundabout flight. We defined the end of a contest as the point when the loser male flew away and did not return within the next 180 s. We considered the male who remained in the perch as the winner.

Figure 3: Ternary plot illustrating the contribution of the significant predictor of our GLS model to the overall contest duration variation of Amberwing dragonfly *Perithemis tenera*. We calculated the contribution of each predictor using the R^2_{lik}. The circle represents only partial R^2 values that were statistically significant in the same model.

Discussion

In this study, we evaluated which factors determine *P. tenera* male's decision to withdraw from a territorial contest. However, first, we evaluated which trait is the better surrogate of fighting capacity in *P. tenera*. We found that total fat mass was the better predictor of individual chance of victory, which indicates that energetic reserve is a suitable surrogate for fighting capacity in this species. After that, to understand the contest dynamic, we investigated if these contests are structured in phases. For this, we evaluated if there were behavioral subsets that were more likely to transit among themselves rather than with other behaviors. We found that the behaviors adopted by males of *P. tenera* during contests can transit in any direction, ruling out the possibility that contests are structured in phases. This also excludes the possibility that males change assessment rules during the contest. In another Odonata species, *Calopteryx maculata*, males also withdraws from contests based on their energetic reserves and the contest is also structure in a transition between fast and slow behaviors (Marden & Waage, 1990). In *C. maculata*, this behavior transition is structured in a “follow-the-leader” dynamic, where one individual alternates between slow and fast behaviors, leading the rival to mirror these actions (Marden & Waage, 1990). If this dynamic is also present in *P. tenera* contests, the rival's mirroring of subsequent displays may serve to signal that they have not yet reached their threshold cost, allowing them to remain engaged in the contest rather than simply responding to the opponent's fighting capacity (e.g. Arnott et al., 2016; Balzarini et al., 2014; Elwood et al., 2014).

We found that the winner total fat mass and territory quality were both unrelated to the overall contest duration. Although R^2_{lik} values for the winner and loser total fat mass were similar, the slope for the winner's total fat mass was less steeper than that for the loser's total fat mass. This slope difference suggests that the winner's total fat mass has a minimal effect on contest duration. Consequently, we can rule out the hypothesis that the opponent's fighting capacity and the resource value contribute to an individual's decision to withdraw. However, we also found a positive relationship between loser total fat mass and the overall contest duration, which gives support for the hypothesis that males follow a pure self-assessment strategy during the contest (Arnott & Elwood, 2009; Payne & Pagel, 1996, Mesterton-Gibbons et al., 1996). The fact that total fat mass was the most suitable proxy for fighting capacity in *P. tenera* indicates that individuals decide to quit the contest when they reach their own energetic threshold as predicted by the energetic war of attrition model (E-WOA - Payne & Pagel, 1996, 97).

If *P. tenera* males indeed fight according to E-WOA, the physical contact we observed between males should not have an effect on cumulative individual costs during the contest (Taylor & Elwood, 2003). Despite pure self-assessment models predicting that there should be no physical contact during contests, empirical studies frequently find evidence of species engaging in physical contact while still employing pure self-assessment (e.g. Constant et al., 2011; Sun et al., 2019). In fact, a recent meta-analysis showed that among 36 species that exhibited pure self-assessment, only two species did not violate the “no physical contact” assumption (Pinto et al., 2019). In particular, for *P. tenera*, the duration of the physical contact behavior is relatively short compared to other contest behaviors (see results and Fig. 1). This suggests that the costs of physical contact may not be significant for individuals (e.g., Barlow et al., 1986), and thus may not affect each individual cost threshold. This would explain why we did not find males with significant wing damage during our observations (see results), despite the wing damage being a pattern commonly seen in dragonfly contests involving physical contact (Rajabi et al., 2020; Rüppell &

Hilfert-Rüppell, 2013).

We found that the territory quality index is unrelated to the overall contest duration for both losers and winners, discarding the possibility that the territory quality contributes to the decision of *P. tenera* males to withdraw from a contest. Previous studies showed evidence that males tends to be more site-faithful in territories where they have previously mated (Switzer, 1997a,b, 2002). Since females inspect territories before mating (Wildermuth, 1991, 1992), mating can serve as a reliable cue for males regarding territory quality. If this is true, males may only gain qualitative information about territories after establishing residency. As a result, males engaged in symmetric contests might evaluate a site as suitable for oviposition without utilizing quality information to decide to withdraw or not. However, we did not find in the literature and we did not observe during the field sample any male of *P. tenera* performing the satellite, sneak or other behavior that could indicate an alternative mating tactic. Therefore, we can expect that males will fight until they reach their threshold cost independently of the resource value.

We also found that winner 's total fat mass was unrelated to the overall contest duration, discarding the possibility that the opponent's fighting capacity contributes to *P. tenera* male decision to withdraw from a contest. A recent meta-analysis suggests that species engaging in high-cost contests often employ a self-assessment strategy (Massote et al., 2024, under review). These pattern can occurs because high-cost contests are more likely to evolve in systems where reproductive success depends strictly on winning a contest (Massote et al., 2024). If this is true, individuals will fight until they reach their maximum cost threshold when resources are scarce, regardless of their rival's fighting capacity (Massote et al., 2024). Contests among odonates can be energetically expensive, as seen with males of

Calopteryx maculata, that can lose up to 50% of their fat reserves after a single contest (Marden & Waage, 1990). In *P. tenera*, the cost may be even greater since males do not feed while guarding territories (Switzer, 2004; personal observation). In addition, since there is no alternative mating tactics, males must secure a territory to mate within a limited reproductive lifespan (on average five days, according to Switzer, 1997a,b). Therefore, this urgent need to establish a territory through a high-cost contest, can make a mutual assessment strategy unfeasible for *P. tenera* males.

Many empirical studies evaluating how individuals withdraw from contests find partial support for E-WOA or WOA model assumptions (e.g. Constant et al., 2011; Rink et al., 2019; Sun et al., 2019). This partial support can occurs due an overlook of empirical steps, such as identifying the suitable surrogate of fighting capacity, investigating the presence of contest phase, or simultaneously evaluating the contributions of both self and opponent fighting capacity and resource value to contest duration. In our study, we addressed these three steps and, contrary to our predictions, found support for a pure self-assessment strategy. However, it is important to highlight that correct evaluation of previous steps allowed us to unequivocally support this assessment strategy in *P. tenera* males. Therefore, we suggest future empirical studies integrate these three steps to improve the consensus on the assessment strategies animals use when withdrawing from contests.

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Apêndice (Supplementary Material)

Figure S1: One of the floating platforms was used to identify the territories of male *P. tenera*. The platform is made of polystyrene covered with green plastic foil, with wooden sticks inserted at the vertices. These platforms were designed to increase the predictability of the perches that individuals would use within each territory, without inducing the formation of new territories or altering the location of existing ones, as the territory sites were already established beforehand.

Table S1: Summary statistics for the generalized least squares model without repeated samples of males and territories. We used the overall contest duration as the response variable, and the loser total fat mass (proxy for focal individual fighting capacity) and winner total fat mass (proxy for opponent fighting capacity), and the territory quality index (proxy for resource value) as predictor variables (n = 15).

Predictor variables	df	b	χ^2	p
Scaled winner total fat mass	1	179.32	0.43	0.50
Scaled loser total fat mass	1	371.67	5.94	0.01
Territory quality index	1	-445.35	0.50	0.47
Residuals	12			

Table S2: Summary statistics for the generalized least squares model without territory quality index (proxy for resource value). We used the overall contest duration as the response variable, and the loser total fat mass (proxy for focal individual fighting capacity) and winner total fat mass (proxy for opponent fighting capacity) (n = 20).

Predictor variables	df	b	χ^2	p
Scaled winner total fat mass	1	-77.33	0.15	0.70
Scaled loser total fat mass	1	339.25	8.78	0.003
Residuals	18			