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Do territorial butterflies show a macroecological fighting pattern in response to environmental stability?

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ABSTRACT

The territorial defense of mating sites by males should be favored when female monopolization is possible. Such monopolization should occur in species in which females emerge asynchronously, since males may have time to copulate with one female before the arrival of other. However, regions with smaller reproductive windows should promote higher synchronicity of female emergence, generating a predictable macroecological pattern associated to the rewards from territorial defense. In this study we evaluated the hypothesis that territorial male butterflies should invest more in fighting in species that occur in areas with stable climatic conditions that should present longer reproductive windows. We compiled studies reporting mean butterfly fighting times, mean trait differences among winners and losers and local Köppen climatic classification (a surrogate for climatic stability). We found that males from butterfly species located in areas with stable climatic conditions fight for longer times. However, although winners were stronger than intruders only in areas with intermediate climatic conditions, there was a marked variation among winner–loser comparisons in species in areas with stable climatic conditions. We conclude that males from butterfly species that occur in areas with stable climatic regimes invest more in fighting due to the higher payoffs accrued with territorial defense, but that such investment does not change the effect of trait asymmetries in settling territorial conflicts. This article is part of a Special Issue entitled: Special Issue:Neotropical Behaviour.

1. Introduction

Territorial defense as a strategy to increase mating opportunities is common in males of many animal species (Andersson, 1994). In such mating systems, males can defend a wide range of places, such as areas containing resources required by females (e.g. oviposition or feeding resources), specific environmental places located in non-resource areas with high female encounter rates or directly defend females (Alcock, 1987; Fischer and Fiedler, 2001; Takeuchi and Imafuku, 2005; Thornhill and Alcock, 1983). Whichever is the resource used for territorial establishment by males, it is expected that a reduction in its availability will be inversely related with the intensity of conflicts in which males must incur (e.g. contest, struggle, physical fight) in order to ensure exclusive access to the mating rewards associated with such places (Baker, 1983; Fitzpatrick and Wellington, 1983).

The conditions favoring the evolution of territoriality have been widely discussed (Emlen and Oring, 1977; Rutowski, 1991b; Shuster and Wade, 2003). Since territorial fights are assumed to be costly and often represented by energy depletion (mainly for non-contact fights—Briffa and Sneddon, 2010) or injuries (Briffa and Elwood, 2005; Decarvalho et al., 2004; Prenter et al., 2006; Vieira and Peixoto, 2013), it may be adaptive for males to optimize the duration or intensity of such contests in order to maximize the number of mating partners achieved during the period that they are able to maintain a territory (e.g. Alcock and Carey, 1988; Bergman et al., 2007). Such optimization is highly dependent upon the spatial and temporal distribution of receptive females (or the resources used by them) and the distribution and abundance of competitor males in relation to female dispersion (Shuster and Wade, 2003; Wacker and Amundsen, 2014).

Despite the great consensus about the key role that environmental factors plays in the distribution of receptive females as well as in the decision made by contestants to establish territories

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(Emlen and Oring, 1977; Shuster and Wade, 2003; Thornhill and Alcock, 1983), a comprehensive review at broad ecological scales still remains poorly explored. In particular, the variation in environmental conditions (i.e. temperature and humidity) associated to biogeographic patterns, has been shown to affect growth and development in insects (Chown and Gaston, 1999), and they may also determine variations in factors important to the cost-benefit payoffs of territorial defense by males such as resource availability, resource allocation, female predictability and operational sex ratio (Gibbs et al., 2011; Peixoto and Mendoza-Cuenca, 2013). In a macroecological perspective, climatic zones with marked seasonality or low climatic predictability may restrict species reproductive opportunities to short periods in which climatic conditions or resource availability are suitable for reproduction. In this case, low reproductive periods should increase the synchrony in the availability of sexually receptive females, which in turn, may reduce male opportunity to monopolize sexual partners through territorial strategy (Emlen and Oring, 1977; Klug et al., 2010; Peixoto and Mendoza-Cuenca, 2013). On the opposite, in areas with higher climate stability, feeding and oviposition resources are available most of the year, increasing males and females energy budgets, generation overlap and asynchrony in female emergence. This pattern should increase the opportunity of female monopolization by males in permanent territories and also promote more pronounced combat asymmetries once that territorial fights could be held between males of different ages, RHP and experiences. All above should generate a macroecological pattern in male contest behavior: areas with higher climatic stability should present species in which male mating success is positively related with their territorial investment and where traits that increase male RHP (e.g. endurance, size) are favored by selection.

Perhaps, butterflies represent the most diverse insect group in which territorial behavior is widely widespread (Kemp, 2013; Kemp and Wiklund, 2001). Males of many species can be found defending territories in a wide range of sites like sunspots, hilltops, forest margins or even in walls (Peixoto and Mendoza-Cuenca, 2013). The typical and remarkably similar agonistic encounters across butterfly species consist of a brief interaction mainly characterized by non-contact spiral or circular flights that ends when one rival fly off the territory (but see Chaves et al., 2006; Eff, 1962; Lehnert et al., 2013 for fights with physical contact and possibly injuries). There is no consensus on how conflicts are settled (Bergman et al., 2010; Kemp and Wiklund, 2001; Peixoto and Benson, 2008, 2011b; Takeuchi, 2011). However, since most of the energy budget of territorial males is invested on expensive surveillance flights or aerial fights (Vande Velde and Van Dyck, 2013), contest structure, duration and outcome are reliable estimators of their physiological phenotype and territorial investment.

Territorial butterfly species can be found in areas with contrasting environmental conditions, ranging from “stable sites” that are hot (>18 °C in the coldest month) and humid during all year long (e.g. Alcock, 1988; Macías-Ordóñez et al., 2013; Peel et al., 2007; Sinclair et al., 2003) to “highly seasonal or unpredictable sites” with long periods of low temperature or precipitation in which suitable periods for emergence, development time and reproduction are short and unpredictable (e.g. Brown and Alcock, 1990; Macías-Ordóñez et al., 2013). In particular, temperature variation modifies almost all aspects of butterfly ecology as for example, distribution and abundance (Hill et al., 2001), habitat and oviposition selection (Davies et al., 2006; Dennis and Sparks, 2006), fecundity (Karlsson and Van Dyck, 2005) and even mating behavior (Gibbs et al., 2011). In this sense, due to the highly sensitivity of butterflies on climate conditions (Dennis and Sparks 2006; Ide 2002; Nylin and Gotthard, 1998), we predict that the intensity of territorial fights in butterflies follow a macroecological pattern associated to variations in environmental stability. For this reason, here we conducted a meta-analytical approach of studies of territoriality in butterfly species to evaluate the hypothesis that the augment in environmental stability will promote a greater fighting investment and a higher asymmetry between winners and losers in territorial contests.

2. Methods

2.1. Male investment in fighting

To evaluate if butterfly species differ in the effort invested in male-male contests according to local climatic stability we searched for articles that provided information about butterfly territorial behavior in the ISI Web of Science and Google Scholar websites and also in our particular data sets. To perform this search we used the keywords “Fight”, “Agonistic interaction”, “Territorial*” and “Mating system”, all in conjunction with “Lepidoptera”. We included articles that provided information about butterfly fighting behavior and mean fight duration (with an associated measure of variation). We did not include studies which included experimental manipulations that could modify butterfly fighting times since they are frequently designed to increase mean fight duration due to other factors unrelated to climatic conditions (e.g. Bergman et al., 2010; Takeuchi, 2006; Takeuchi and Honda, 2009).

We also gathered local climatic information, according to the Köppen classification, for each butterfly study included in our dataset. When such information was absent in the original article, we estimated it based on the study location. To perform this estimation we assessed the information available in http://koeppen-geiger.vu-wien.ac.at/present.htm (Kottek et al., 2006). However, it is important to note that such classification can lead to some discrepancies between the climatic subdivision and the real features at local climate habitat due to the usage of a rigid boundary criterion and also due to data interpolation in areas with low availability of temperature stations (Kottek et al., 2006; Peel et al., 2007). For this reason, we also performed a detailed search for local weather conditions, altitude and vegetation types in each study site reported in the literature in order to corroborate the assignation of Köppen climatic classification or to re-assign a most precise climatic classification prior to statistical analysis (see Table 1 for details of species that we re-assigned the Köppen climatic classification according to this last criterion).

The Köppen climatic classification has been a widespread and accurate model to classify world climates for more than a century, and is based on monthly precipitation and temperature time series throughout the year (Peel et al., 2007). Since both immature and adult stages of butterflies depend on the availability of feeding resources and suitable temperatures to develop, which in turn, are higher during rainy and warm periods, the Köppen climatic classification represents an accurate estimator of environmental stability and reproductive windows for these insects (Macías-Ordóñez et al., 2013; Peixoto and Mendoza-Cuenca, 2013). In this sense, areas with Köppen classifications Af (tropical rainforest) and Am (tropical monsoon) should present the highest climatic stability for butterflies because both climates describe areas with rains during all year long (with no month with less than 60 mm of rain) and mean temperature of the coldest month greater than 18 °C. Climates classified as Aw (tropical savannah), C (temperate) and D (cold) on the other hand, show a marked, but predictable, environmental variation during the year related to temperature and rainy period (C and D climates present temperature of the hottest month greater than 10 °C. The mean temperature of the coldest month in category C lies between 0 and 18 °C, while mean temperature of the coldest month is smaller than 0 °C in category D. Aw climates presents some months with marked reduction or