UNIVERSITY OF CALIFORNIA

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Microhabitat selection and interspecific aggression in rubyspot damselflies (*Hetaerina*)

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Shawn Christopher McEachin

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ABSTRACT OF THE DISSERTATION

Microhabitat selection and interspecific aggression in rubyspot damselflies (*Hetaerina*)

by

Shawn Christopher McEachin

Doctor of Philosophy in Biology

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Professor Gregory F. Grether, Chair

Interspecific aggression is a complex interaction with important evolutionary and ecological implications. While it can be an adaptive response to reproductive interference, it bears costs including energy expenditure, loss of territory, and missed mating opportunities. Consequently, species may diverge in habitat preferences or exhibit spatial partitioning, which reduce the costs of fighting. However, empirical evidence of such shifts is lacking. I studied the relationship between interspecific aggression, habitat partitioning, and spatial segregation in interspecifically aggressive species of rubyspot (*Hetaerina*) damselflies.

In Chapter 1, I explored whether species differences in microhabitat use reduce the frequency of interspecific fighting in 25 sympatric population pairs. I found that almost all population pairs had lower observed rates of interspecific fighting relative to chance expectations. Reduced rates of interspecific fighting were explained by competitor recognition, species differences in microhabitat use, and spatial segregation. I also found strong positive

correlations between heterospecific aggression and species differences in microhabitat use, likely explained by competitive displacement and/or agonistic character displacement, and between heterospecific aggression and spatial segregation. These correlations were explored further in Chapters 2 and 3.

In Chapter 2, I tested the competitive displacement hypothesis using removal experiments. If competitive displacement occurs, territory holders of the subordinate species should shift their microhabitat use to that of the dominant species in the absence of the dominant species. However, I found no evidence of such shifts. I therefore reject the competitive displacement hypothesis and conclude that species have likely evolved divergent microhabitat preferences through agonistic character displacement.

In Chapter 3, I examined the correlation between heterospecific aggression and spatial segregation. Spatial partitioning is common among competing species, but there are numerous mechanisms that can cause species to be spatially segregated. Conspecific attraction is a widespread habitat selection mechanism, but the potential for it to cause spatial partitioning between interspecifically aggressive species is unknown. I explored this question by comparing the clustering of territories to a model that simulates territory settlement from microhabitat availability. I found that both conspecific attraction and microhabitat preferences contribute to the spatial partitioning between interspecifically aggressive species.

The dissertation of Shawn Christopher McEachin is approved.

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University of California, Los Angeles

2021

D,
And the future won't just be great, it'll be… fantastic.

"Nothing in biology makes sense except in the light of evolution"
Theodosius Dobzhansky 1973

TABLE OF CONTENTS

Chapter 3: Conspecific attraction and microhabitat preferences drive spatial partitioning between interspecifically aggressive rubyspot damselflies (*Hetaerina*)………………..86

LIST OF TABLES

LIST OF FIGURES

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The Acknowledgements section of many dissertations begins with thanking academic advisors and committee members, and for good reason. But I find it necessary to begin mine a little differently. I want to express my eternal gratitude to my wife Deanna for her unconditional love and support. In this journey through graduate school, I have experienced some of the most difficult challenges of my life. There were times where that light at the end of the tunnel seemed to be sucked in to a supermassive blackhole and I just wanted to give up, but there was one constant in my life the whole time. D has been my rock, the perch to my territory, the submerged root to my egg, the rubyspot to my wings, she puts the dam in damselfly because, damn, she's fly! From letting me escape to work in my cave, to getting ready to call the National Guard when I didn't have phone service in Costa Rica for a couple days, I literally would not have been able to get through this journey without her. She never let me give up, pushed me to do more, gave me the confidence I needed to keep going, and loved me even when I was a sleep-deprived grump. Everyone needs a Deanna in their life, and I'm lucky to have mine.

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I got a late start to the field of ecology and evolution; I didn't even take an ecology class until my senior year of college. But Drs. Steve Gliessman and Chris Wilmers were truly inspiring teachers and researchers who made me want to continue to pursue ecology. After graduating, my lack of experience made it difficult to make headway, but luckily Donald Solick took a chance and gave me my first wildlife job. He not only allowed me to get my foot in the door, but made the job fun and cemented my interest in jumping headlong into the field. From there, I needed another lucky break because I was still a novice figuring things out. Enter Bryan Kleuver, who, like Donald before him and Greg after him, took a chance on me, despite my lack of experience, and supported my professional development in a way that spurred the rest of my career. Later, at Irvine Ranch Conservancy, where there are too many people to thank, I am especially grateful for Matt Major who was the first one to really encourage my interest in research by giving me the latitude and confidence to manage various experimental sites. Fast forward six years to Kahung Lee mentoring me in my first foray into teaching at a community college. I am truly humbled to have so many people who took a risk by taking me on, both professionally and academically, and look forward to the days I can pay it forward and support a burgeoning ecologist as they start on their own path, however long and windy it may be.

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Grether, GF, JP Drury, KW Okamoto, **S McEachin**, CN Anderson. 2020. Predicting evolutionary responses to interspecific interference in the wild. *Ecology Letters* 23(2): 221-230.

Drury, JP, CN Anderson, MB Cabezas Castillo, J Fisher, **S McEachin**, and GF Grether. 2019. A general explanation for the persistence of reproductive interference. *The American Naturalist* 194(2): 268-275.

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Chapter 1: Mechanisms of reduced interspecific interference between territorial species

ABSTRACT

Interspecific territoriality has complex ecological and evolutionary consequences. Species that

interact aggressively often exhibit spatial or temporal shifts in activity that reduce the frequency

of costly encounters. We analyzed data collected over a 13-year period on 50 populations of

rubyspot damselflies (*Hetaerina* spp.) to examine how rates of interspecific fighting covary with

fine-scale habitat partitioning and to test for agonistic character displacement in microhabitat

preferences. In most sympatric species, interspecific fights occur less frequently than expected

based on the species' relative densities. Incorporating measurements of spatial segregation and

species discrimination into the calculation of expected frequencies accounted for most of the

reduction in interspecific fighting (subtle differences in microhabitat preferences could account

for the rest). In 23 of 25 sympatric population pairs, we found multivariate differences between

species in territory microhabitat (perch height, stream width, current speed, and canopy cover).

As predicted by the agonistic character displacement hypothesis, sympatric species that respond

more aggressively to each other in direct encounters differ more in microhabitat use and have

higher levels of spatial segregation. Previous work established that species with the lowest levels

of interspecific fighting have diverged in territory signals and competitor recognition through

agonistic character displacement. In the other species pairs, interspecific aggression appears to be

maintained as an adaptive response to reproductive interference, but interspecific fighting is still

costly. We now have robust evidence that evolved shifts in microhabitat preferences also reduce the frequency of interspecific fighting.

INTRODUCTION

Competition between animal taxa is widespread and often involves aggression. Interspecific aggression may initially arise from misdirected intraspecific aggression (Murray 1971; Nishikawa 1987; Singer 1989; Schultz and Switzer 2001; Korner et al. 2010; Cowen et al. 2020). However, in the absence of a contested resource, species are expected to diverge in ways that reduce the frequency and costs of interspecific aggression, a process known as divergent agonistic character displacement (ACD). Most documented cases of divergent ACD involve evolutionary shifts in agonistic signals and competitor recognition (Grether et al. 2009; Grether et al. 2013; Grether et al. 2017; Latour and Ganem 2017; Moran and Fuller 2018a; Moran and Fuller 2018b; Zambre et al. 2020). Conversely, species with a contested resource in common may converge in agonistic signals and competitor recognition to facilitate resource defense and partitioning, i.e., convergent ACD (Cody 1973; Grether et al. 2009; Reif et al. 2015; Pasch et al. 2017; Souriau et al. 2018; Kirschel et al. 2019). Interspecific mate competition arising from reproductive interference has also been shown to cause convergent ACD (Drury, Okamoto, et al. 2015; Grether et al. 2020).

In addition to convergence or divergence in traits related to competitor recognition, interspecific aggression can also cause drastic changes in species' spatial and temporal niches (Melville 2002; Gotelli et al. 2010; Pigot and Tobias 2013; Edgehouse et al. 2014; Ulrich et al. 2017; Eurich et al. 2018). One common result of interspecific territoriality is competitive displacement where a dominant or more aggressive species forces a subordinate species into a

different habitat or to be active during different periods (Garcia 1983, Reitz and Trumble 2002, Langkilde and Shine 2004, Jankowski et al. 2010, Pasch et al. 2013, Kajtoch et al. 2015). In other cases, both species may shift in habitat use or temporal activity (Bay et al. 2001; Eurich et al. 2018; Reif et al. 2018). Whether the shift in activity occurs in one or both species, interspecific competition is reduced, although one species may be forced into suboptimal habitat (Randall 1978; Robinson and Terborgh 1995; Grether et al. 2013). Habitat partitioning can occur at various spatial and temporal scales, such as elevational or latitudinal gradients on a macroscale (Connell 1983; Schoener 1983; Lewin 1989; Hawkins 1999; Mark et al. 2001) as well as across small scale variation in microhabitat (Eurich et al. 2018; Reif et al. 2018).

Habitat partitioning could also arise from species differences in habitat preferences that evolved in response to selection against interspecific fighting in the past, which would be a form of divergent ACD (Grether et al. 2009). As yet, however, there are few if any well documented cases of ACD in habitat preferences (for a possible example, see Vallin et al. 2012). Species can diverge in habitat use for many reasons, and determining whether these differences are products of past or ongoing interspecific interactions is challenging (Connell 1978; Ross 1986; Wisheu 1998; Pinter-Wollman et al. 2006).

Rubyspot damselflies (*Hetaerina*) are a good system for examining the relationship between interspecific aggression and niche partitioning because levels of interspecific aggression vary widely among sympatric species. Male rubyspots defend mating territories along streams and rivers (Johnson 1963; Córdoba-Aguilar et al. 2009; Anderson and Grether 2011; but see Guillermo-Ferreira and Del-Claro 2011). Mature males of all species in the genus have red pigmentation at the base of their wings, whereas the lack of red or other conspicuous pigmentation in female wings makes them more cryptic (Garrison 1990). Simulated territory

3

intrusion and wing color manipulation experiments have shown that the responses of territory holders to intruders is largely based on wing coloration and that species with more similar wing coloration respond more aggressively to each other (Anderson and Grether 2010a; Drury and Grether 2014; Grether et al. 2015).

Interspecific aggression in *Hetaerina* appears to largely be an adaptive response to interspecific mate competition (Drury, Okamoto, et al. 2015; Drury, Anderson, et al. 2019; Grether et al. 2020), but selection should still favor adaptations that reduce the frequency of interspecific fighting. Territorial fights are costly, primarily because they can result in males losing their territories and priority of access to ovipositing females (territory possession confers a three-fold mating advantage; Grether 1996; Drury & Grether 2014). Damselfly fights also have energetic and physiological costs (reviewed in Suhonen et al. 2008; Vieira and Peixoto 2013; Córdoba-Aguilar and González-Tokman 2014; Kemp 2018; Grether 2019), and fights that do not immediately result in territory turnover likely reduce the ability of the residents to win future fights. Thus, selection may favor divergence in microhabitat use because this reduces the probability of interspecific encounters and therefore the frequency of interspecific fights.

Species differences in microhabitat use have been documented in *Hetaerina* (Johnson 1973; Anderson and Grether 2011), but it is unknown whether these differences are products of past or ongoing interspecific aggression. Sympatric species could differ in microhabitat use for reasons unrelated to interspecific aggression, or because one species actively displaces the other from preferred microhabitat, or because of selection against interspecific fighting, i.e., divergent ACD (Grether et al. 2009).

In this paper, we analyze data collected in the field over a 13-year period on 14 species pairs of rubyspot damselflies to examine whether current levels of interspecific fighting can be

4

explained by species pair differences in spatial segregation and species discrimination, and to test the ACD prediction that species that respond more aggressively to each other in direct encounters show higher levels of divergence in microhabitat use. To the best of our knowledge, this is the first study, on any taxon, to approach either of these questions with an adequate level of replication at the species level.

METHODS

Sympatric populations

We studied 14 sympatric species pairs (10 different species) across 15 sites in the southwestern United States, Mexico, and Costa Rica from 2005 to 2017 (see Supplementary Methods S1 for criteria for inclusion of study sites). Some sites were visited multiple times in different years. Because of interannual variation in microhabitat availability and species densities, pooling the data across visits could have obscured patterns of interest. We therefore kept visits to the same sites in different years separate for the analyses presented in this paper, for a total of 25 species-pair-site-years, which we refer to henceforth as sympatric population pairs (Table S1.1).

Behavioral sampling

At the beginning of each study period, we established a 200-300 m transect by fastening a rope with numbered flags in 1-m increments along one or both banks of the river. Males within the transect were captured with aerial nets, marked on the abdomen with unique color codes using paint pens (200-S Fine Point, MarvyDecocolor Paint Marker; Uchida of America, Torrance, CA, USA; Anderson et al. 2011), photographed (Figure S1.1), and released where they were captured. Each day, 2-5 observers continuously walked along the transect during periods of

territorial activity (~0800-1800) recording the ID and locations of males (as [x, y, z] coordinates where x is the flag number, y is the distance from the bank of the stream, and z is the height) to the nearest 0.1 m on hand-held computers (Psion PLC, London). In total, we marked 7,483 males and made 34,614 observations. A male was considered a territory holder if he was observed in the same location ($\pm$ 2 m) and perching close to the water, as males do when they are defending a site, on at least two consecutive days (Anderson and Grether 2010a).

When fights were observed, we recorded the species involved, the males' IDs (if marked), and the location. Fights between the same two marked males on the same day, and fights involving unmarked males at the same location on the same day, were collapsed into a single fight for the purpose of calculating intra- and interspecific fighting frequencies (Anderson and Grether 2011; Drury and Grether 2014).

Microhabitat sampling

To quantify the microhabitat use of the damselflies at each site, we measured canopy cover, stream width, stream current speed, and the perch height of territory holders. We measured canopy cover, an especially important axis of microhabitat variation for ectothermic insects (Shelly 1982; Huey 1991; Tsubaki et al. 2010; Okuyama et al. 2013), every 5-10 m along the stream using a concave spherical densiometer (Forestry Suppliers, Inc.). We made one measurement in the middle of the stream where the stream was $\leq$3 m wide, two measurements (one on each side of the stream) where the stream was 3-10 m wide, and three measurements (one on each side of the stream and another in the middle) where the stream was $\geq$10 m wide. Canopy cover ranges from 0 to 100% and higher values indicate shadier habitat. We measured stream width every 2 m along the transect with a measuring tape and visually assessed current

speed every 2 m near both banks and the middle of the stream using a 0 to 4 scale, where 0 is still water and 4 is rapidly moving white water. To characterize the microhabitat of each male's territory, we interpolated between the two nearest canopy cover, stream width, and current speed readings, and averaged the male's recorded perch heights.

Expected frequencies of interspecific fighting

We considered interspecific fighting to be reduced relative to intraspecific fighting if the observed frequency of interspecific fights was lower than expected based on a simple null model (Anderson and Grether 2011). The null model assumes that males encounter and fight with conspecific and heterospecific males in direct proportion to the species' relative densities. The null expectation for the frequency of interspecific fights is simply the observed total number of fights multiplied by $2d_i d_j$ where d_i and d_j are the species' relative densities (Supplementary Methods S2a). All previous comparisons of observed and expected rates of interspecific fighting in *Hetaerina* were based on this null model (Anderson and Grether 2011; Drury et al. 2015).

Factors that could cause the observed frequency of interspecific fights to be lower than the null expectation include: (1) spatial segregation between the species, which would reduce the frequency of interspecific encounters; and (2) species discrimination, which would reduce the probability of interspecific encounters resulting in territorial fights. To evaluate whether spatial segregation alone accounts for the reduction in interspecific fighting, we constructed lists of all males of each species observed within 4 m of the center of each established territory. From these lists, we calculated the average proportion of heterospecific "neighbors" from each species' perspective and multiplied the average of these two estimates by the total number of observed fights to obtain the expected frequency of interspecific fights (Supplementary Methods S2b). The

7

4 m-criterion is based on the observation that males respond to conspecific males up to ~2 m away from their perch and in doing so could enter the reaction zone of a male perched 4 m away; beyond a distance of 4 m males are unlikely to interact (Anderson and Grether 2011 used the same criterion for similar reasons).

To evaluate whether species discrimination alone accounts for the reduction in interspecific fighting, we calculated the expected interspecific fighting rate by multiplying the null expectation by the probability of males chasing a heterospecific intruder. Heterospecific chase probabilities were calculated from the results of simulated territory intrusion tests in which territory holders were presented with live, tethered males in timed trials (Anderson and Grether 2010a; Supplementary Methods S2c).

Finally, we combined the methods above to calculate the expected frequency of interspecific fighting based on observed levels of spatial segregation and species discrimination (Supplementary Methods S2d).

Heterospecific aggression ratio

The ACD hypothesis predicts that species pairs with high heterospecific aggression (HA) will differ more in microhabitat use than those with low HA. We obtained a relative measure of HA for each species in each sympatric population pair by dividing the average proportion of time heterospecifics were chased by the average proportion of time conspecifics were chased in the simulated territory intrusion trials, and refer to this as the HA ratio (Grether et al. 2020; Table S1.2).

Statistical methods

We used chi-squared tests to determine whether observed frequencies of interspecific fighting differed from expected frequencies, the Monte Carlo simulation method to calculate p-values in cases with expected frequencies < 5, and Holm's sequential Bonferroni procedure (Holm 1979) to correct for multiple comparisons. Wilcoxon matched pairs signed ranks tests were used to compare the alternative methods of calculating expected frequencies to the null model.

To examine the causes of variation in interspecific fighting rates, we constructed a linear multiple regression model where the dependent variable was the log of the ratio of the observed number of interspecific fights to the expected number of fights under the null model. The predictors were the mean proportion of heterospecific neighbors, the species difference in microhabitat use, and the heterospecific chase probability ($n = 25$; Supplementary Methods S2c Equation S2b).

We used principal component analysis (PCA) to find the principal axes of variation in microhabitat use across all territory holders in the study ($n = 1974$). To obtain an overall measure of the species difference in microhabitat use at each site, we calculated the Euclidean distance between the species' PC centroids ($n = 25$).

To more fully characterize species differences in microhabitat use at each site, we used linear discriminant analysis (LDA) and mixed-effects multivariate regression. The microhabitat variables were transformed to a mean of 0 and variance of 1 to make the LDA coefficients comparable and to weight the microhabitat variables equally in the regression models. The predictor variables in the regression models were species (1 or 2), an index identifying the microhabitat variable (1-4), the species by microhabitat variable interaction, and a random-effects term for male ID ($n = 1974$). To make the sign of the mean difference between species

the same for all four microhabitat variables, we assigned the species with the smaller mean an index of 1 and the species with the larger mean an index of 2 (Table S1.3).

The ACD hypothesis predicts that species that respond more aggressively when interspecific encounters occur should differ more in microhabitat use and exhibit higher levels of spatial segregation. To test the first part of this prediction, we constructed linear mixed-effects regression models with all sympatric population pairs included ($n = 25$) and nested random-effects terms for population pair and male ID. The full, multivariate model included indices to identify the species (1 or 2) and microhabitat variables (1-4), the mean HA ratio, and all interactions between these terms. We also constructed separate models for each microhabitat variable, with species index, mean HA ratio, the 2-way interaction, and a random-effects term for sympatric population pair, and used the Akaike information criterion (AIC) to evaluate whether adding quadratic terms improved the model fit. We used a similar approach to test for effects of heterospecific aggression on the proportion of heterospecifics in a male's territory neighborhood but coded the species index based on the relative density of territory holders (1 = low, 2 = high).

Mixed-effects regression models were implemented with `mixed` in STATA 16.1 (StataCorp 2019). Other analyses were carried out in R 4.0.3 – 4.0.5 (R Core Team 2020, 2021); LDA was implemented with the `lda` default in R package `MASS` 7.3-53.1 (Venables and Ripley 2002).

RESULTS

Species differences in microhabitat use

The first three principal components (PCs) accounted for 83.4% of the variance in microhabitat use (Table 1.1). PC1 explained 33.8% of the variance and had a large positive loading for canopy

cover and negative loadings for the other variables (Table 1.1; Figure S1.2). PC2 explained

26.3% of the variance and had a large negative loading for current speed and a positive loading

for perch height, while PC3 explained 23.3% of the variance and had a large positive loading for

stream width and a negative loading for current speed (Table 1.1; Figure S1.2). PC1 likely

represents variation in stream size (smaller streams tend to be slower and make smaller gaps in

the forest canopy) while the other axes represent variation in stream gradient and size

independent of canopy cover (males tend to perch low on emergent rocks in fast current and

higher in the bank vegetation in slower sections).

Twenty three of the 25 sympatric populations differ significantly in microhabitat use

(Table 1.2). Overall, the LDA correctly classified 79.7% of territory holders to species based on

microhabitat use, and for many populations the species classifications were 80-100% correct

(Table 1.2). As shown by the species means and LDA coefficients, all four microhabitat

variables proved useful for differentiating between sympatric species (Tables 2, S3).

Interspecific fighting

Across the 25 pairs of sympatric populations, we collected data on 1,974 territory holders and

1,793 fights, of which 346 (19.3%) were between heterospecific males. The observed frequency

of interspecific fights was significantly lower than the null expectation in 21 out of 25 cases

(Table 1.3). There was considerable variation in this relationship across species, as reflected by

the wide range of chi-square values (Table 1.3). The multiple regression analysis with species

differences in neighborhood composition, microhabitat, and chase probabilities as predictors

accounted for 54% of the variation in the ratio of observed to expected interspecific fights (Table

1.4). The greater the proportion of heterospecifics in a territory holder's neighborhood and the

greater the species difference in microhabitat use, the lower the ratio of observed to expected interspecific fights.

We were also able to explain much of the reduction in the frequency of observed interspecific fights compared to the null expectation. In some sympatric population pairs, the reduction in the frequency of interspecific fights was explained by spatial segregation (Figure 1.1a), while in others the reduction was explained by species discrimination (Figure 1.1b) or both spatial segregation and species discrimination (Figure 1.1c). Yet there were some sympatric populations for which these factors could not fully explain the reduction in observed interspecific fights (Figure 1.1d). The mean difference between the number of observed and expected interspecific fights decreased by 32.4% when the expected rate was calculated using only neighborhood composition, 19.1% using only chase probabilities, and 50% with neighborhood composition and chase probabilities combined (Table 1.5).

Effects of interspecific aggression on microhabitat and spatial partitioning

Overall, we found striking support for the hypothesis that interspecific aggression drives species apart in microhabitat use. In the full multivariate model, the 3-way interaction was highly significant ($\chi^2 = 85.70$, df = 3, $p < 0.0001$), which indicates that the effect of heterospecific aggression on the species difference in microhabitat use varies strongly among microhabitat variables. We therefore analyzed the microhabitat variables separately. Adding quadratic terms substantially improved the fit of the perch height (ΔAIC = -15.55) and stream width (ΔAIC = -14.58) models but worsened the fit of the current speed (ΔAIC = 3.25) and canopy cover models (ΔAIC = 0.26). The species difference in perch height was greater between sympatric populations with low and high HA compared to those with intermediate HA (Figure 1.2;

species×HA: -0.68 ± 0.14, $z = -4.91$, $p < 0.0001$; species×HA^2: 0.43 ± 0.11, $z = 3.96$, $p = 0.001$).

The species difference in the other three microhabitat variables increased with the HA ratio

(Figure 1.2; stream width, species×HA: -4.64 ± 1.88, $z = -2.47$, $p = 0.013$; species×HA^2: $5.95 \pm$

1.45, $z = 4.11$, $p < 0.0001$; current speed, species×HA: 0.16 ± 0.074, $z = 2.20$, $p = 0.028$; canopy

cover, species×HA: 15.31 ± 2.28, $z = 6.70$, $p < 0.0001$). Also as predicted by the ACD

hypothesis, the proportion of heterospecific neighbors decreased, and thus spatial segregation

increased, with the level of heterospecific aggression (Figure 1.3; HA: -0.20 ± 0.06, $z = -3.22$, p

$= 0.001$), particularly for species with a low relative density of territory holders, as indicated by a

positive interaction between the relative density of territory holders and the HA ratio ($0.095 \pm$

0.035, $z = 2.72$, $p = 0.0066$).

To evaluate whether the results were affected by males at site GO contributing data to

two different sympatric population pairs, we ran the mixed-effects regression models on subsets

of the data and found that dropping any two GO pairs had no qualitative effect on the results

(Table S1.4).

DISCUSSION

This 13-year investigation of 14 species pairs provides an unprecedented level of support for the

general hypothesis that interspecific aggression increases spatial habitat partitioning between

sympatric species. Specifically, we found that sympatric species that are more aggressive to each

other in simulated intruder tests differ more in microhabitat use (Figure 1.2) and are more

spatially segregated (Figure 1.3). In principle, three non-mutually exclusive mechanisms could

have produced this pattern: species sorting, competitive displacement, and agonistic character

displacement (ACD). We discuss each of these potential mechanisms in turn and explain why we consider ACD to be the most likely mechanism.

In this context, species sorting refers to effects of interspecific interactions on the probability of species occurring in sympatry (Pfennig and Pfennig 2012). If interspecific fighting reduces the probability of co-occurrence, the positive relationship between microhabitat partitioning and heterospecific aggression could be a byproduct of variation in the level of microhabitat divergence prior to secondary contact. It has yet to be shown, however, that interspecific fighting affects the probability of co-occurrence in damselflies. Most research on coexistence mechanisms in Odonata has focused on resource competition and predation at the larval stage (e.g., McPeek 2004; Siepielski et al. 2010; Siepielski et al. 2011; Bried and Siepielski 2019); it is not yet clear whether behavioral interference at the adult stage affects coexistence in this taxon (reviewed in Grether et al. 2022).

Competitive displacement has been shown, or strongly inferred, to be the primary cause of species differences in habitat use in other territorial animals, including insects and arachnids (Reitz and Trumble 2002), barnacles (Connell 1961), mammals (Brown 1971; Pasch et al. 2013), birds (Garcia 1983; Jankowski et al. 2010; Kajtoch et al. 2015; Martin and Bonier 2018), and reptiles (Langkilde and Shine 2004; Edgehouse et al. 2014). A common feature of systems in which competitive displacement occurs is that one species is competitively superior and displaces the other species from the preferred habitat (Reitz and Trumble 2002). In general, there are several ways that one species could be competitively superior, but in the case of damselflies competing for mating territories, competitive superiority would entail behavioral dominance or superior aerial fighting ability. We are not aware of any rubyspot damselfly species pairs in which one species is dominant or consistently wins territorial fights, but further research is

14

warranted. Whether competitive displacement occurs, and the extent to which it explains the effects of heterospecific aggression on microhabitat use, could be tested with removal experiments or microhabitat manipulations.

While species sorting and competitive displacement are both plausible post-hoc explanations, neither of those hypotheses could have been used to predict that microhabitat partitioning would correlate positively with heterospecific aggression without making unsupported assumptions about the study system. By contrast this was a well-founded prediction of the agonistic character displacement hypothesis. Previous research showed that some sympatric rubyspot damselfly species have diverged substantially in male wing coloration and competitor recognition, and that the territories of these species often overlap extensively (Anderson and Grether 2010a; Anderson and Grether 2010b; Anderson and Grether 2011). In most rubyspot damselfly species pairs, however, interspecific territorial aggression is adaptive because females of these species are too similar in coloration for males to distinguish between them; a territory holder that tolerated heterospecific males on his territory would risk losing mating opportunities (Drury, Okamoto, et al. 2015; Drury et al. 2019; Grether et al. 2020). In this situation, divergence in microhabitat preferences might be the only way for selection to reduce the costs of interspecific aggression. Our initial evidence that microhabitat divergence has evolved in response to interspecific aggression was based on four sympatric species pairs (Anderson and Grether 2011). Now with data on 14 sympatric species pairs, across multiple sites and years, we can confirm that microhabitat divergence is strongly associated with interspecific aggression (Figure 1.2).

We expect positive relationships between habitat partitioning and heterospecific aggression to be found in other taxa as well. Our other findings are rather damselfly specific, but

parallels might be found in other taxa. For example, interspecifically territorial birds are expected to vertically stratify in habitats with a large height dimension, such as woodlands (Murray 1971). Indeed lunulated and Salvin's antbirds (*Gymnopithys lunulate* and *G. salvini*) forage from taller perches in the presence of larger, behaviorally dominant antbirds and woodcreepers (Willis 1968). Similarly, the iguanid lizard *Liolaemus tenuis* perches higher when sympatric with the aggressively dominant *L. pictus* (Medel et al. 1988). Rubyspot damselfly species with both low and high levels of heterospecific aggression differ more in mean perch height than those with intermediate levels of heterospecific aggression (Figure 1.2). Considering that species with low levels of heterospecific aggression have overlapping territories (Anderson & Grether 2011), the species differences in perch height probably function to reduce accidental interspecific interference.

We found a negative relationship, at the population level, between the mean proportion of heterospecific neighbors and the ratio of observed to expected frequencies of interspecific fights (Table 1.4). Logically, territory holders with more heterospecific neighbors should be observed in more, not fewer, interspecific fights. The counterintuitive population-level result is probably an artifact of the mathematical constraint that males in populations with lower relative densities have more heterospecific neighbors. What this population-level analysis did show, however, is that species differences in microhabitat use reduce interspecific fighting (Table 1.4).

When we based expected frequencies on the proportion of heterospecific neighbors and the probability of males responding aggressively to heterospecifics, the mean difference between the observed and expected numbers of interspecific fights was 50% less than under the null model (Table 1.5). However, the observed number of interspecific fights was still significantly below the expected number in many populations (Figures 1, S3). Species differences in

16

microhabitat use, which were found in all but two sympatric population pairs (Table 1.2), likely reduce the frequency of interspecific fights below what would be expected based on the composition of territorial neighborhoods and heterospecific aggression. For example, species that perch at different heights tend to fight at different heights (authors, pers. obs.), and therefore may be less likely to fight with heterospecific neighbors than expected based on the spatial arrangement of territories. Additionally, differences between species in stream current speed preferences might also reduce the frequency of interspecific fighting because current speed can vary among neighboring territories.

Studies on other taxa have also revealed adaptive connections between interspecific aggression and microhabitat use. For example, fine-scale microhabitat partitioning has been reported in interspecifically territorial damselfish (Eurich et al. 2018). Territorial neotropical cichlid fish (*Amphilophilous* spp.) are more likely to tolerate heterospecific neighbors with divergent coloration (Lehtonen et al. 2010; Lehtonen et al. 2015). Interspecifically aggressive nightingales (*Luscinia megarhynchos* and *L. luscinia*) "escape" to allotopic sites in the sympatric region of their geographic ranges and occupy habitat avoided by the congener (Reif et al. 2018).

Selection against interspecific interference is only one of many possible reasons that closely related species might differ in microhabitat preferences. For example, microhabitat preferences could have diverged in allopatry before secondary contact (Berner and Thibert-Plante 2015; Dufour et al. 2015). Conspecific attraction might also reduce spatial overlap between sympatric species (Scott and Lee 2013; Stodola and Ward 2017) and result in chance differences in microhabitat use (Buxton et al. 2020). Nevertheless, the results presented here provide compelling evidence that interspecific aggression has played an important role in microhabitat divergence.

Table 1.1 Microhabitat principal component loadings (% variance explained)

	PC1 (33.8%)	PC2 (26.3%)	PC3 (23.3%)	PC4 (16.6%)
Perch height	-0.579	0.522	-0.014	-0.626
Stream width	-0.345	-0.380	0.858	-0.017
Current speed	-0.284	-0.760	-0.459	-0.361
Canopy cover	0.682	-0.066	0.231	-0.691

Table 1.2 Results of linear discriminant analyses (LDA) and multivariate regression analyses (MVA) of species differences in microhabitat use

Pop. pair	Spp. code	LDA species classif. # correct	# wrong	% correct	LDA coefficients (standardized) Perch ht.	Width	Cur. speed	Can. cov.	MVA z
1	c	41	9	82	-0.31	-0.07	-1.40	0.50	7.62***
	o	33	5	87					
2	o	45	10	82	0.77	0.10	-0.30	0.23	4.83***
	t	17	12	59					
3	o	11	27	29	0.66	-0.02	-0.94	-0.30	2.23*
	t	44	10	81					
4	a	15	14	52	0.79	-0.20	-1.10	0.70	5.70***
	t	68	3	96					
5	a	38	9	81	0.78	-0.19	-1.17	0.66	4.82***
	t	18	16	53					
6	a	14	4	78	0.98	-0.03	0.06	-0.18	2.64**
	t	24	3	89					
7	a	48	8	86	-0.10	-0.01	0.65	1.06	5.85***
	c	23	4	85					
8	c	54	0	100	0.75	0.64	0.87	2.48	1.20
	v	0	15	0					
9	a	92	5	95	1.36	-0.04	-0.11	0.87	4.88***
	v	8	19	30					
10	o	120	19	86	2.17	-0.15	-0.09	0.32	5.61***
	t	38	38	50					
11	o	190	12	94	2.36	-0.11	-0.18	0.39	6.37***
	t	27	31	47					
12	o	46	3	94	1.73	-0.03	0.23	2.82	4.07***
	s	12	10	55					
13	o	16	3	84	-0.14	-0.95	0.17	6.15	2.22*
	p	9	3	75					
14	n	6	0	100	-1.03	0.20	-0.16	-0.85	14.65***
	o	80	2	98					
15	c	10	18	36	1.13	0.59	-0.76	-1.16	3.21**
	m	64	4	94					
16	c	28	8	78	0.83	0.35	0.53	2.14	6.32***
	p	34	0	100					

17	o	29	18	62	2.29	0.01	0.10	4.98	2.45*
	p	42	10	81					
18	n	8	8	50	2.32	0.03	-0.45	-1.48	2.35*
	t	48	2	96					
19	n	19	3	86	-0.28	0.11	-0.03	-0.61	6.34***
	o	41	12	77					
20	f	6	1	86	-2.25	0.39	1.79	-0.83	3.11*
	o	10	0	100					
21	f	4	3	57	0.51	-0.20	-0.50	-0.85	3.81***
	t	19	1	95					
22	o	8	2	80	0.80	-0.42	-1.02	-0.29	3.98***
	t	20	0	100					
23	f	16	2	89	-1.50	0.06	0.30	-2.19	2.38*
	o	11	6	65					
24	f	18	0	100	0.45	-0.24	-0.03	-2.48	1.27
	t	4	6	40					
25	o	13	4	76	1.87	-0.23	-0.49	0.66	2.35*
	t	6	4	60					

See Table S1.1 for site info and species names.

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

Table 1.3 Comparison of the observed frequencies of interspecific fights to those expected under the null model

Pop. pair	Spp.	Observed freq. Intrasp. fights	Intersp. fights	Expected freq. Intrasp. fights	Intersp. fights	Chi-sq. test
1	c	8	2	2.8	9.0	15.78**
	o	9		7.3		
2	o	13	6	19.4	25.3	88.18***
	t	34		8.3		
3	o	8	4	8.6	26.3	42.00***
	t	43		20.1		
4	a	6	8	2.4	18.6	12.63*
	t	43		36.0		
5	a	25	18	19.1	30.1	9.44*
	t	18		11.9		
6	a	3	3	3.5	18.7	23.86**
	t	41		24.8		
7	a	37	7	31.0	19.0	17.91*
	c	9		2.9		
8	c	38	23	39.9	23.5	4.46
	v	7		3.4		
9	a	31	12	28.5	16.2	2.57
	v	4		2.3		
10	o	16	11	15.6	21.2	17.47**
	t	17		7.2		
11	o	30	14	19.2	41.0	35.55***
	t	38		21.8		
12	o	26	12	17.5	26.5	15.61***
	s	16		10.0		
13	o	25	5	15.4	19.5	20.57***
	p	11		6.2		
14	n	2	2	2.2	25.5	29.25**
	o	98		74.3		
15	c	29	26	12.6	60.2	45.36***
	m	90		72.2		
16	c	27	15	4.5	33.8	123.95**
	p	60		63.7		
17	o	42	24	32.8	69.9	69.05***

	p	74		37.2		
18	n	7	33	13.2	75.8	49.12***
	t	158		109.0		
19	n	4	6	4.2	19.2	17.36**
	o	35		21.6		
20	f	13	7	10.2	10.2	1.85
	o	3		2.6		
21	f	13	18	10.1	36.7	17.81**
	t	49		33.2		
22	o	3	4	15.4	27.9	134.86***
	t	49		12.7		
23	f	145	53	125.5	100.4	64.22***
	o	48		20.1		
24	f	145	18	132.7	35.0	18.94*
	t	7		2.3		
25	o	48	15	39.6	26.1	8.20
	t	7		4.3		

See Table S1.1 for site info.

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$ after sequential Bonferroni correction

Table 1.4 Predictors of variation in the ratio of observed to expected interspecific fights under

the null model

Predictor	B	SE	p
Intercept	0.01	0.24	0.98
Neighborhood composition	-1.08	0.39	0.011
Microhabitat differences	-0.30	0.058	<0.001
Chase probabilities	0.29	0.15	0.078

Linear multiple regression, $n = 25$, model adjusted $R^2 = 0.54$, $F(3, 21) = 10.4$, $p < 0.001$.

Table 1.5 Comparison of three alternative methods of calculating expected frequencies of interspecific fighting to the null model, with Wilcoxon matched pairs signed ranks tests

| Model | Obs. – Exp. | | V | p |
	Mean	SE		
Relative density (null)	-18.8	2.52	-	-
Spatial segregation	-12.7	2.33	57	0.0034
Species discrimination	-15.2	2.37	57	0.0065
Spatial segregation and species discrimination combined	-9.4	2.04	30	<0.001

$n = 25$ population pairs

Figure 1.1 Observed and expected numbers of interspecific fights, based on different methods of calculating the expectation, for selected sympatric population pairs (see Fig. S3 for the remaining populations). An example of the reduction in the number of observed interspecific fights that can be explained by (a) spatial segregation of territory holders based on the proportion of heterospecific males in territory holders' neighborhoods (*H. occisa-H. miniata* at LH03 2016), (b) competitor recognition based on the aggressive response of territory holders to heterospecific intruders relative to conspecific intruders in simulated territory intrusions (*H. occisa-H. titia* at OT 2007), (c) both spatial segregation and competitor recognition (*H. fuscoguttata-H. titia* at GO01 2016), and (d) a population pair in which neither spatial distribution nor competitor recognition can account for the reduction in observed interspecific fights (*H. cruentata-H. majuscula* at MV04 2016). Combined refers to the model that calculates expected fighting rates based on both spatial segregation and competitor recognition. See Table 1.3 for statistical results comparing all 25 sympatric population pairs.
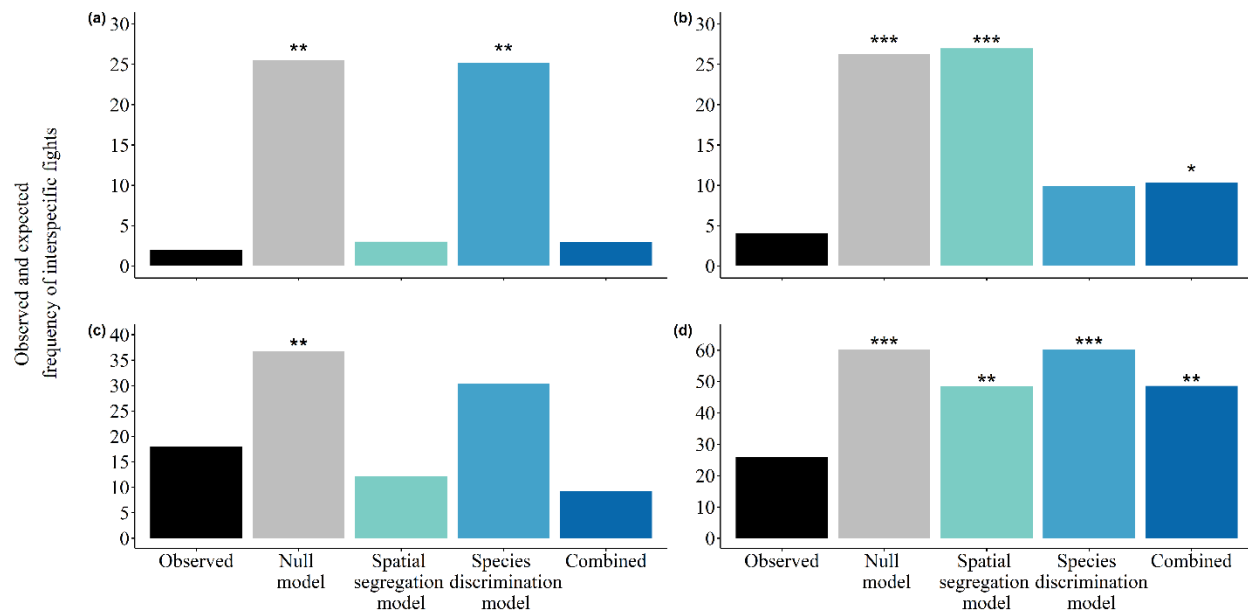
Figure 1.2 Evidence that interspecific aggression causes species to diverge in microhabitat preferences. As heterospecific aggression increases, so do species differences in territory microhabitat. The exception is perch height, which differs the least between sympatric species at intermediate levels of heterospecific aggression. Points and bars represent population means and standard errors. Triangles (circles) represent the population with higher (lower) relative density in each pair. Colors uniquely identify the paired populations. Lower (upper) black lines represent predicted values for the populations with lower (higher) means of the corresponding microhabitat variable, and gray areas are 95% confidence intervals, from the mixed-effects regression model described in **Statistical methods**.
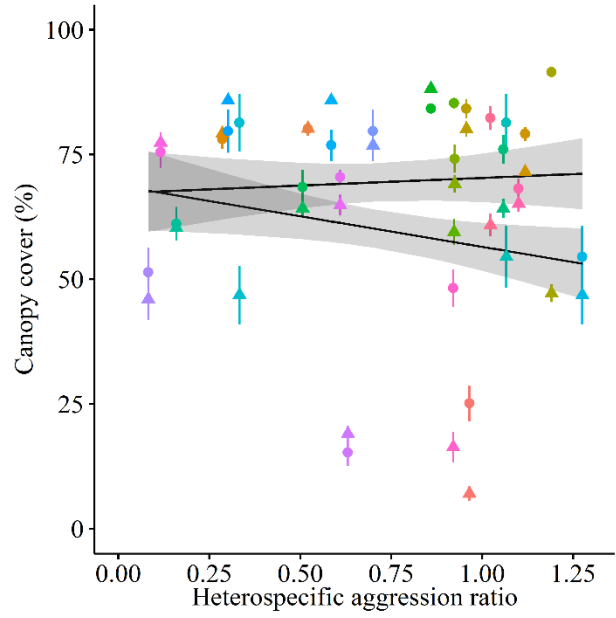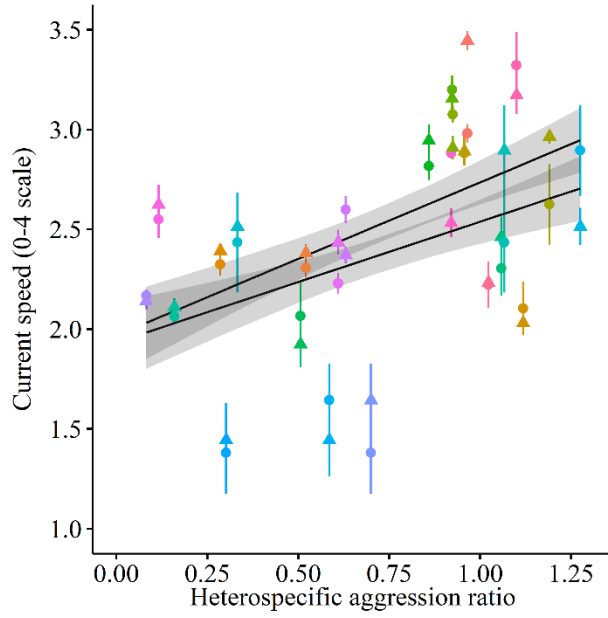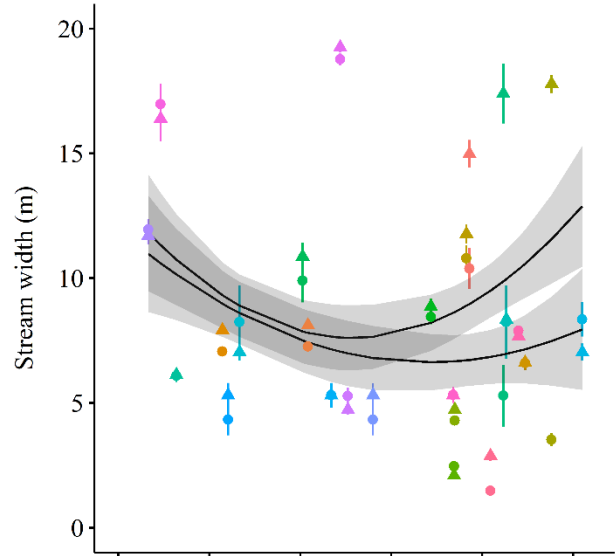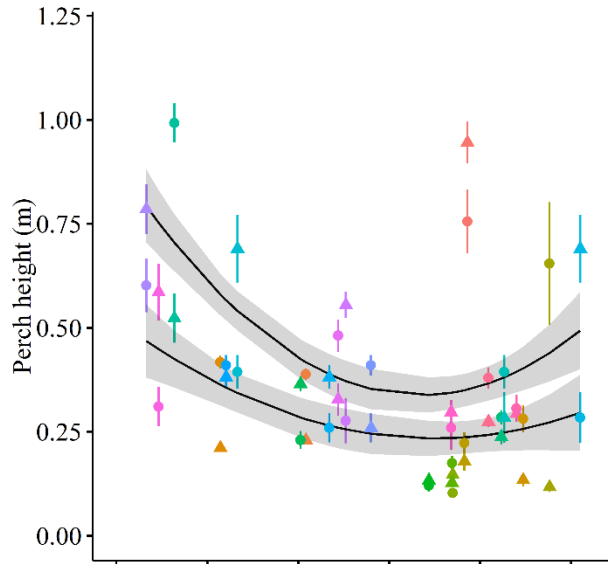
Figure 1.3. Evidence that interspecific aggression increases spatial separation between species. The proportion of heterospecific neighbors decreases as heterospecific aggression increases. The slope of the relationship is steeper for populations with low relative density compared to those with high relative density. Lower (upper) black lines represent predicted values for the populations with lower (higher) relative density in each pair. All other symbols and codes follow Figure 1.2.
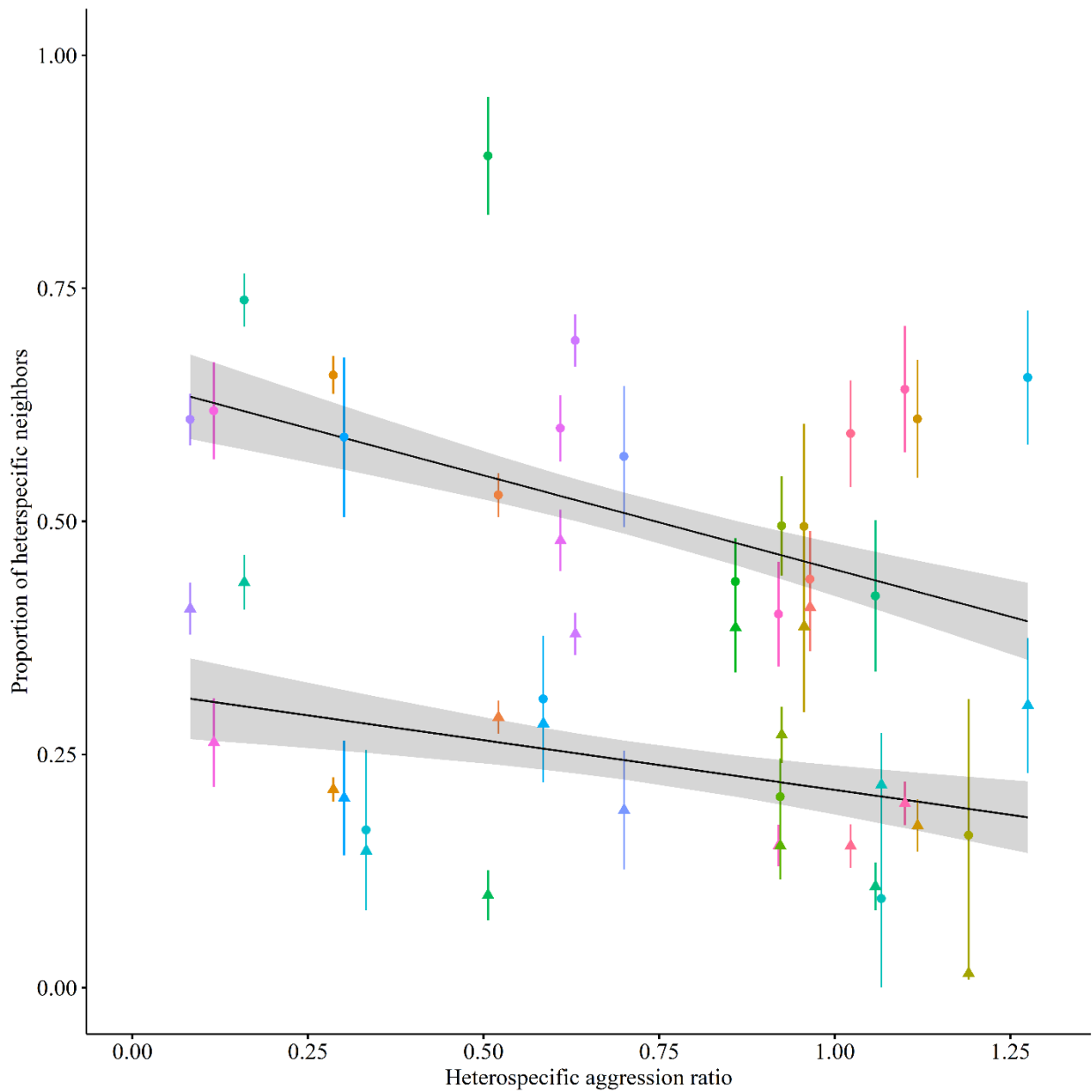
Chapter 1 Supplementary Materials

S1. Criteria for including study sites in this study

During the period of 2005-2017 we visited several sites that were not included in this study (see

Anderson and Grether 2010b; Anderson and Grether 2010a; Anderson et al. 2011; Anderson and

Grether 2011; Drury and Grether 2014; Drury et al. 2015a; Drury et al. 2015b). Some sites were

visited for carrying out specific experiments that were not appropriate for the current analysis.

For example, in some cases, the simulated intruder tests were only carried out on territory

holders of one of the species present. Results from the simulated intruder tests were used to

calculate the probability of chasing a heterospecific, the heterospecific attack ratio, and the

expected rate of observed interspecific fights, all of which required data from both species in a

species pair. For this study, we included only the sites where simulated intruder tests were

carried out on both species in a species pair, microhabitat features were measured, and observed

fights and territory locations were recorded.

S2. Methods for calculating the expected frequency of interspecific fighting

We examined the extent to which interspecific fighting was reduced relative to intraspecific

fighting and the mechanisms that drove this reduction. To do so, we compared the observed

frequency of interspecific fighting to the expected frequency of interspecific fighting, and we

calculated the expected frequency in four ways. We started with the null expectation, which

assumes that males are just as likely to encounter and attack a conspecific as they are a

heterospecific. Then, we calculated the expected frequency of interspecific fighting in three ways

to determine whether the spatial segregation of territory holders, differential aggressive

responses to heterospecifics, or the interaction of these mechanisms reduce the frequency of interspecific fighting. We discuss the null expectation and three mechanisms in greater detail and explain our calculations in the following subsections (S2a-d).

S2a. Expected frequency of interspecific fighting under the null model

The null expectation assumes encounters between males are random and that each encounter is equally likely to result in a fight. This expectation is calculated from the binomial expansion of the relative density of each species (Anderson and Grether 2011):

Equation S1a. Proportion of fights involving two males of species i: $\quad d_i^2$

S1b. Proportion of fights involving heterospecifics: $\qquad 2d_i d_j$

S1c. Proportion of fights involving two males of species j: $\quad d_j^2$

where d_i is the relative density of species i and d_j is the relative density of species j. We multiplied the total number of observed fights by $2d_i d_j$ to obtain the expected number of interspecific fights under the null model.

S2b. Calculating the expected frequency of interspecific fighting under the spatial segregation model

To evaluate whether spatial segregation accounts for reduced interspecific fighting, we examined each territory holder's neighborhood and calculated the proportion of neighbors that were conspecific and heterospecific.

We used the variables n_{ij} and n_{ji} to represent the proportion of territory holders' neighbors that were heterospecific for species i and j, respectively. Then, we calculated $\bar{n}$, the average of n_{ij} and n_{ji}, as an estimate for the average proportion of heterospecific neighbors

30

across both species in a species pair. We multiplied $\bar{n}$ by the total number of observed fights to calculate the expected number of interspecific fights based on the spatial segregation of males in each pair of sympatric populations.

S2c. Calculating the expected frequency of interspecific fighting under the competitor recognition model

To determine whether the aggressive response to heterospecifics relative to conspecifics explains the reduction in the frequency of interspecific fighting, we calculated the expected rate of interspecific fights by multiplying the null expectation by the probability of chasing a heterospecific intruder, calculated from simulated intruder tests.

The simulated intruder test is composed of two trials (or three at sites where three species were present), where each trial involves a conspecific or heterospecific intruder presented to a territory holder for two minutes, with at least five minutes between trials. We systematically alternated the presentation of conspecifics and heterospecifics to territory holders to minimize any effect presentation order may have on a territory holder's response. A test was considered successful and included in the analysis if the territory holder chased an intruder for a minimum of 20 seconds in at least one of the trials (otherwise it is unlikely that the male was actively defending the territory).

We considered a response to be aggressive if the territory holder chased the tethered male for at least 20 seconds. We used this definition of an aggressive response to calculate the probability that territory holders engage in a territorial dispute using the following equations:

Equation S2a. $p_{con_i} = p_{ii} * p_{ii} + 2p_{ii}(1 - p_{ii})$

S2b. $p_{het} = p_{ij} * p_{ji} + p_{ij}(1 - p_{ji}) + p_{ji}(1 - p_{ij})$

31

$$\text{S2c. } p_{con_j} = p_{jj} * p_{jj} + 2p_{jj}(1 - p_{jj})$$

where p_{con} is the probability of two conspecific males chasing each other, p_{ii} is the probability of a territory holder of species i chasing a conspecific tethered intruder, p_{jj} is the probability of a territory holder of species j chasing a conspecific tethered intruder, p_{het} is the probability of two heterospecific males chasing each other, p_{ij} and p_{ji} are the probabilities that a territory holder of species i and species j chase a tethered intruder of species j and species i, respectively, for at least 20s.

The probabilities of two conspecific and heterospecific males chasing each other were multiplied by the null expectation using the following equations:

$$\text{Equation S3a. } e_{con_i} = (p_{con_i})(d_i^2)$$

$$\text{S3b. } e_{het} = (p_{het})(2d_i d_j)$$

$$\text{S3c. } e_{con_j} = (p_{con_j})(d_j^2)$$

where e_{con} and e_{het} refer to the expected proportions of fights between conspecifics and heterospecifics, respectively. These proportions were scaled by dividing each proportion by the sum of the proportions, then multiplied by the total number of observed fights to calculate the expected number of fights for each pair of sympatric populations.

S2d. Calculating the expected frequency of interspecific fighting under the combined spatial segregation and competitor recognition model

We tested whether there is an interaction between spatial segregation and differential aggressive responses to heterospecifics on the frequency of interspecific fighting. For each territory holder, we multiplied the proportion of heterospecific neighbors (n_{ij} and n_{ji}) by the probability that

heterospecific males chase each other (p_{het}) and calculated the average across all territory holders at each site. For this analysis, we essentially replaced the null expectation (d) in Equation 3 with the proportion of heterospecific neighbors (n_{ij} and n_{ji}) to calculate the expectation based on space use and competitor recognition data. The average probabilities were multiplied by the total number of observed interspecific fights to calculate the expected number of interspecific fights for each pair of sympatric populations.

Table S1.1 Sites, study periods, and species

Pop. pair	Site	Study period	Species	Marked males	Rel. dens.	Latitude	Longitude
1	CT	Jul-06	*H. cruentata* (c)	147	0.42	18.371	-95.00148
			H. occisa (o)	207	0.58		
2	PA	Jul-07	*H. occisa* (o)	137	0.54	18.5501	-95.06671
			H. titia (t)	115	0.46		
3	OT	Jun-07	*H. occisa* (o)	132	0.40	18.6834	-96.3835
			H. titia (t)	198	0.60		
4	AR	Apr – May 2008	*H. americana* (a)	56	0.17	18.664	-103.098
			H. titia (t)	271	0.83		
5	CV	Apr-08	*H. americana* (a)	144	0.50	29.3335	-98.8669
			H. titia (t)	145	0.50		
6	CV-L	Aug-08	*H. americana* (a)	32	0.21	29.3335	-98.8669
			H. titia (t)	119	0.79		
7	EL	May-08	*H. cruentata* (c)	55	0.25	21.261	-104.24
			H. americana (a)	163	0.75		
8	PX	Aug-10	*H. cruentata* (c)	164	0.78	19.4668	-96.95018
			H. vulnerata (v)	47	0.22		
9	BC	Jul-12	*H. americana* (a)	220	0.78	32.9163	-109.4928
			H. vulnerata (v)	63	0.22		
10	PA1	Apr-12	*H. occisa* (o)	764	0.67	18.5501	-95.06671
			H. titia (t)	375	0.33		
11	PA2	May – Jun 2012	*H. occisa* (o)	203	0.49	18.5501	-95.06671
			H. titia (t)	209	0.51		
12	ES	Apr-13	*H. occisa* (o)	135	0.44	18.5925	-95.0839
			H. sempronia (s)	173	0.56		
13	RT	Aug-15	*H. occisa* (o)	98	0.61	10.949	-85.51163
			H. capitalis (p)	62	0.39		
14	LH	Jun-16	*H. occisa* (o)	332	0.85	10.9893	-85.37769
			H. miniata (n)	57	0.15		
15	SL	Apr-16	*H. cruentata* (c)	98	0.29	10.278	-84.78627
			H. majuscula (m)	235	0.71		
16	RS	Mar – Apr 2016	*H. cruentata* (c)	110	0.21	10.2783	-84.81893
			H. capitalis (p)	415	0.79		
17	RT	May-16	*H. occisa* (o)	263	0.48	10.949	-85.51163
			H. capitalis (p)	280	0.52		
18	RB	Apr - May 2017	*H. titia* (t)	345	0.74	9.71961	-82.9657
			H. miniata (n)	120	0.26		
19	LH	Jul-17	*H. occisa* (o)	194	0.69	10.9893	-85.37769

			H. miniata (n)	86	0.31		
20 (o-f)	GO	Jul-16	*H. occisa* (o)	32	0.33	8.643	-83.19527
21 (f-t)			*H. fuscoguttata* (f)	64	0.52		
22 (o-t)			*H. titia* (t)	58	0.64		
23 (o-f)	GO	Mar - Apr 2017	*H. occisa* (o)	94	0.29	8.643	-83.19527
24 (f-t)			*H. fuscoguttata* (f)	235	0.88		
25 (o-t)			*H. titia* (t)	31	0.25		

Study sites visited, data collection periods, species present (species code in parentheses),

numbers of males individually marked, relative species densities, and study site coordinates.

Table S1.2 Heterospecific aggression (HA) ratios for each sympatric population pair

Pop. pair	Sp 1	HA ratio	Sp 2	HA ratio
1	c	1.007152	o	0.922462
2	o	0.146678	t	0.171897
3	o	0.047819	t	0.116647
4	a	0.791838	t	0.469500
5	a	0.730603	t	0.488256
6	a	0.048568	t	0.183541
7	c	0.841807	a	0.998206
8	c	1.048868	v	1.150855
9	a	1.010918	v	1.034357
10	o	0.676993	t	0.365272
11	o	0.256602	t	0.315398
12	o	0.872043	s	1.363800
13	o	0.970986	p	0.941966
14	o	0.828017	n	1.553047
15	c	0.988046	m	0.860774
16	c	0.943418	p	0.901474
17	o	0.800637	p	0.916745
18	n	0.885097	t	0.127374
19	o	0.765533	n	1.350216
20	o	1.049237	f	1.083322
21	f	0.469985	t	0.195842
22	o	2.121072	t	0.428723
23	o	0.508395	f	0.661769
24	f	0.391339	t	0.211661
25	o	1.104847	t	0.295119

HA ratios were calculated from simulated intruder tests as the average proportion of time

territory holders spent chasing heterospecific intruders divided by the average proportion of time

spent chasing conspecific intruders. See Table S1.1 for population pair and species codes.

Table S1.3 Mean value (species index) for each microhabitat variable and for spatial segregation

Pop. Pair	Species	Perch height (m)	Stream width (m)	Current speed (0-4)	Canopy cover (%)	Spatial segregation
1	c	0.95 (1)	14.98 (1)	3.45 (1)	7.02 (2)	0.41 (2)
1	o	0.76 (2)	10.39 (2)	2.98 (2)	25.13 (1)	0.44 (1)
2	o	0.52 (2)	6.13 (1)	2.11 (1)	60.25 (2)	0.43 (2)
2	t	0.99 (1)	6.09 (2)	2.06 (2)	61.11 (1)	0.74 (1)
3	o	0.60 (2)	11.95 (1)	2.17 (1)	51.40 (1)	0.61 (1)
3	t	0.79 (1)	11.70 (2)	2.14 (2)	46.03 (2)	0.41 (2)
4	a	0.28 (2)	5.27 (1)	2.60 (1)	15.25 (2)	0.69 (1)
4	t	0.55 (1)	4.73 (2)	2.37 (2)	19.05 (1)	0.38 (2)
5	a	0.33 (2)	19.26 (1)	2.44 (1)	64.85 (2)	0.48 (2)
5	t	0.48 (1)	18.78 (2)	2.23 (2)	70.46 (1)	0.60 (1)
6	a	0.31 (2)	16.98 (1)	2.55 (2)	75.48 (2)	0.62 (1)
6	t	0.59 (1)	16.4 (2)	2.62 (1)	77.39 (1)	0.26 (2)
7	a	0.30 (1)	5.31 (2)	2.53 (2)	16.36 (2)	0.15 (2)
7	c	0.26 (2)	5.32 (1)	2.88 (1)	48.20 (1)	0.40 (1)
8	c	0.29 (2)	7.68 (2)	3.17 (2)	65.16 (2)	0.20 (2)
8	v	0.31 (1)	7.89 (1)	3.32 (1)	68.15 (1)	0.64 (1)
9	a	0.27 (2)	2.88 (1)	2.23 (1)	60.88 (2)	0.15 (2)
9	v	0.38 (1)	1.48 (2)	2.22 (2)	82.32 (1)	0.59 (1)
10	o	0.23 (2)	8.11 (1)	2.38 (1)	80.20 (1)	0.29 (2)
10	t	0.39 (1)	7.26 (2)	2.31 (2)	80.16 (2)	0.53 (1)
11	o	0.21 (2)	7.92 (1)	2.39 (1)	79.20 (1)	0.21 (2)
11	t	0.42 (1)	7.06 (2)	2.32 (2)	78.07 (2)	0.66 (1)
12	o	0.13 (2)	6.62 (1)	2.03 (2)	71.50 (2)	0.17 (2)
12	s	0.28 (1)	6.60 (2)	2.10 (1)	79.12 (1)	0.61 (1)
13	o	0.18 (2)	11.77 (1)	2.89 (1)	80.12 (2)	0.39 (2)
13	p	0.22 (1)	10.8 (2)	2.88 (2)	84.17 (1)	0.49 (1)
14	n	0.65 (1)	3.52 (2)	2.63 (2)	91.51 (1)	0.16 (1)
14	o	0.12 (2)	17.79 (1)	2.96 (1)	47.20 (2)	0.02 (2)
15	c	0.10 (2)	4.30 (2)	3.08 (1)	74.13 (1)	0.50 (1)
15	m	0.15 (1)	4.73 (1)	2.91 (2)	69.12 (2)	0.27 (2)
16	c	0.13 (2)	2.09 (2)	3.15 (2)	59.45 (2)	0.15 (2)
16	p	0.17 (1)	2.46 (1)	3.20 (1)	85.28 (1)	0.20 (1)
17	o	0.12 (2)	8.44 (2)	2.82 (2)	84.17 (2)	0.44 (1)
17	p	0.13 (1)	8.87 (1)	2.94 (1)	88.21 (1)	0.39 (2)
18	n	0.23 (2)	9.90 (2)	2.07 (1)	68.44 (1)	0.89 (1)
18	t	0.36 (1)	10.87 (1)	1.92 (2)	64.19 (2)	0.10 (2)

19	n	0.28 (1)	5.30 (2)	2.30 (2)	76.00 (1)	0.42 (1)
19	o	0.24 (2)	17.4 (1)	2.46 (1)	64.21 (2)	0.11 (2)
20	f	0.39 (1)	8.24 (2)	2.43 (2)	81.36 (1)	0.10 (1)
20	o	0.28 (2)	8.35 (1)	2.90 (1)	54.49 (2)	0.22 (2)
21	f	0.39 (2)	8.24 (1)	2.43 (2)	81.36 (1)	0.17 (1)
21	t	0.69 (1)	7.03 (2)	2.51 (1)	46.83 (2)	0.15 (2)
22	o	0.28 (2)	8.35 (1)	2.90 (1)	54.49 (1)	0.65 (1)
22	t	0.69 (1)	7.03 (2)	2.51 (2)	46.83 (2)	0.30 (2)
23	f	0.38 (1)	5.31 (2)	1.44 (2)	85.84 (1)	0.28 (2)
23	o	0.26 (2)	5.31 (1)	1.64 (1)	76.84 (2)	0.31 (1)
24	f	0.38 (2)	5.31 (1)	1.44 (1)	85.84 (1)	0.20 (2)
24	t	0.41 (1)	4.33 (2)	1.38 (2)	79.66 (2)	0.59 (1)
25	o	0.26 (2)	5.31 (1)	1.64 (1)	76.84 (2)	0.19 (2)
25	t	0.41 (1)	4.33 (2)	1.38 (2)	79.66 (1)	0.57 (1)

The species index (in parentheses) corresponds to the species index used in mixed-effects

regression models (see main text). Spatial segregation refers to the proportion of heterospecifics

in territory holders' neighborhoods. See Table S1.1 for population pair and species codes.

Table S1.4. Results of the mixed-effects regression models for all possible subsets of the data excluding two species pairs at site GO01.

GO01 species pair included	Model	Estimate	SE	95% CI	ΔAIC
o-f (1,889)	all four microhabitat variables	4.62	0.84	(2.97, 6.27)	
	perch height	0.29	0.12	(0.06, 0.52)	3.58
	stream width	8.32	1.61	(5.15, 11.48)	23.79
	current speed	0.15	0.08	(-0.003, 0.29)	
	canopy cover	17.73	2.34	(13.14, 22.32)	
f-t (1,892)	all four microhabitat variables	3.93	0.84	(2.29, 5.58)	
	perch height	0.29	0.12	(0.05, 0.53)	2.42
	stream width	8.52	1.64	(5.30, 11.74)	23.84
	current speed	0.14	0.07	(-0.01, 0.28)	
	canopy cover	15.87	2.35	(11.26, 20.49)	
o-t (1,894)	all four microhabitat variables	4.26	0.83	(2.64, 5.88)	
	perch height	0.43	0.11	(0.21, 0.64)	14.37
	stream width	6.09	1.49	(3.18, 9.01)	13.85
	current speed	0.15	0.07	(0.01, 0.30)	
	canopy cover	16.31	2.33	(11.75, 20.87)	

Results from postestimation test of contrasts of the hierarchical linear mixed models (see main text) comparing microhabitat use to the interaction between species category and heterospecific aggression (HA) ratio. We only report ΔAIC when the quadratic HA ratio is a better fit than the linear HA ratio. See Table S1.1 for species codes; sample size for the models when a given species pair is included is in parentheses.

Figure S1.1. Photos of the species included in this study (males on the left, females on the right). Two photos of *H. titia* are shown to represent the variation in wing coloration of this species. Pictures were taken with a Canon EOS digital camera with a Canon 100mm macro and MT-24EX macro flash. The scale bar is a millimeter scale.

H. cruentata	
H. occisa	
H. miniata	
H. americana	
H. vulnerata	
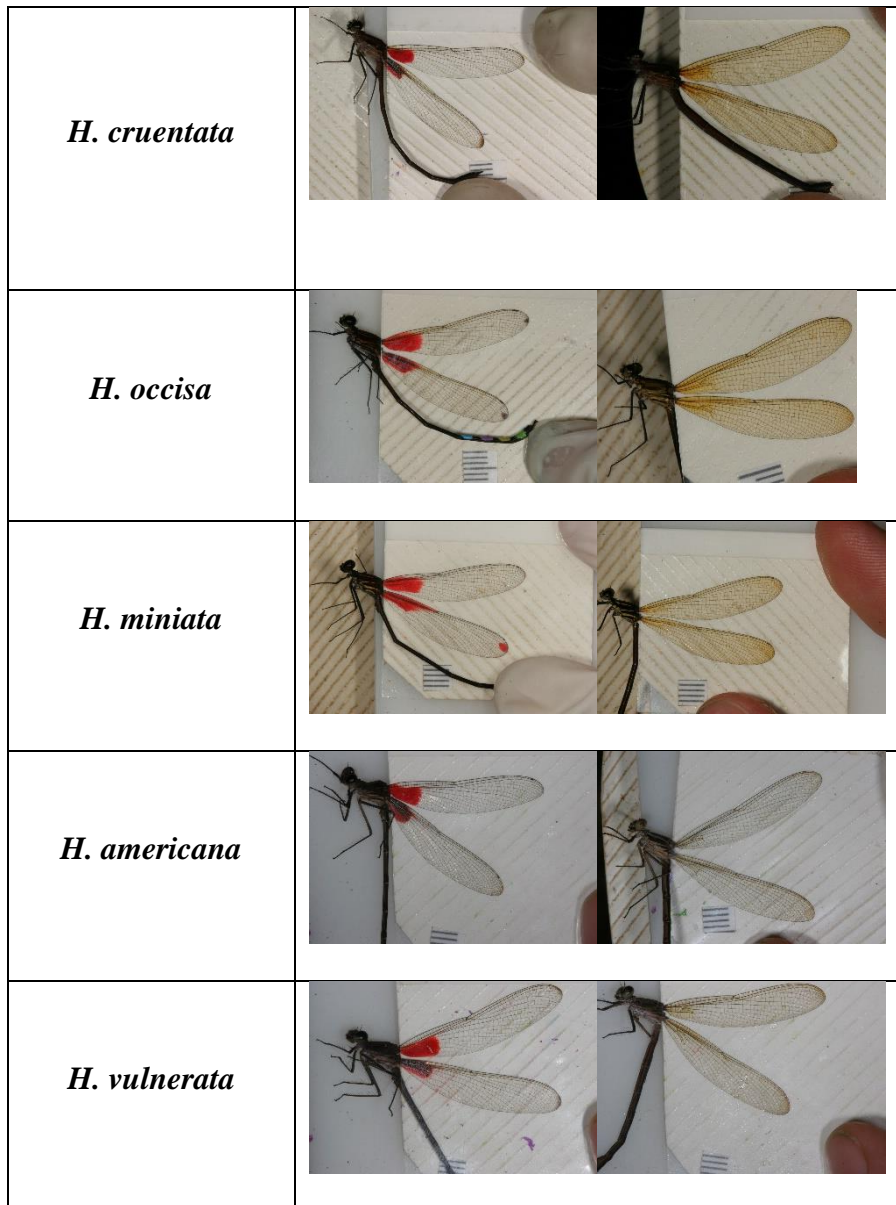
H. sempronia	
H. capitalis	
H. majuscula	
H. fuscoguttata	
H. titia	

Figure S1.2. Principal component analysis on the four microhabitat features across all populations in our study. Each point represents the average microhabitat values at each male's territory (n = 1,974). (a) PC1 vs PC2; (b) PC1 vs PC3. Microhabitat variables: canopy = canopy cover, current = current speed, width = stream width, height = perch height. Arrow lengths indicate the magnitude of the loadings (see Table 1.1).
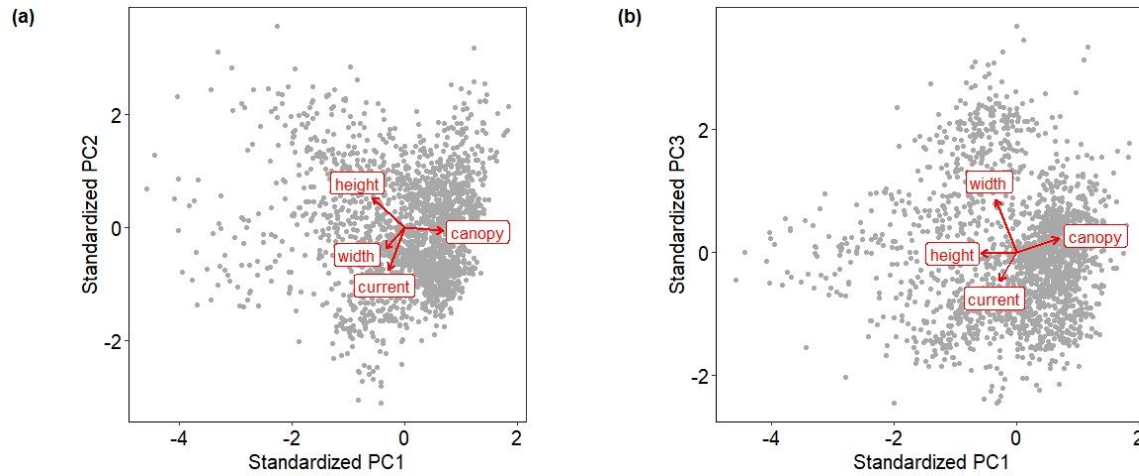
Figure S1.3. The number of observed and expected interspecific fights. From left-to-right, the groups are: the total number of observed interspecific fights, and the number of expected interspecific fights according to: the null model, the spatial segregation model based on the proportion of heterospecific males in territory holders' neighborhoods, the competitor recognition model based on the aggressive response of territory holders to heterospecific intruders relative to conspecific intruders, and the combination of both the spatial segregation and competitor recognition models. Sites are indicated below the x-axis; refer to Table S1.1 for which species are present at each site. We compared the observed to expected frequency of interspecific fights using a Wilcoxon test and indicate significant differences with: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ after sequential Bonferroni correction.
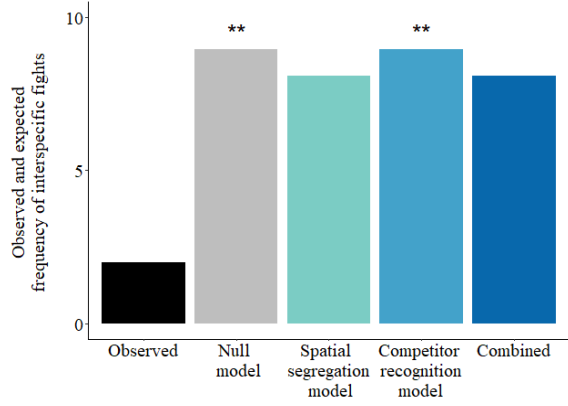
H. occisa - H. cruentata at CT 2006
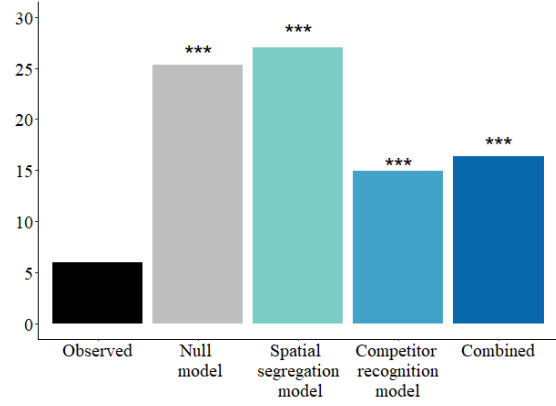
H. occisa - H. titia at PA 2007
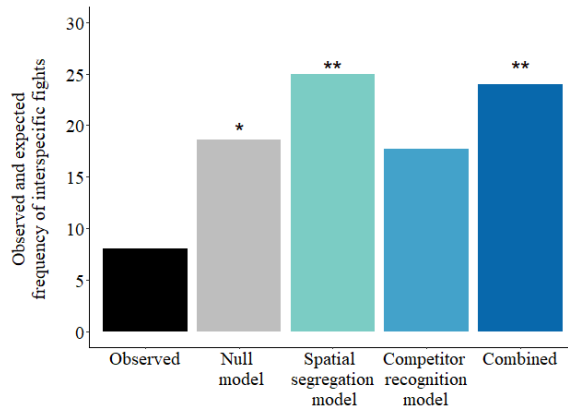
H. americana - H. titia at AR 2008
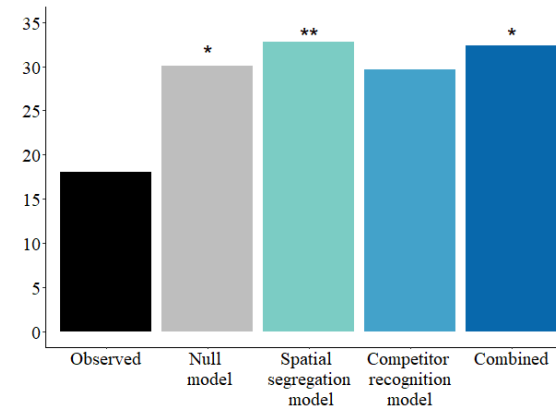
H. americana - H. titia at CV 2008
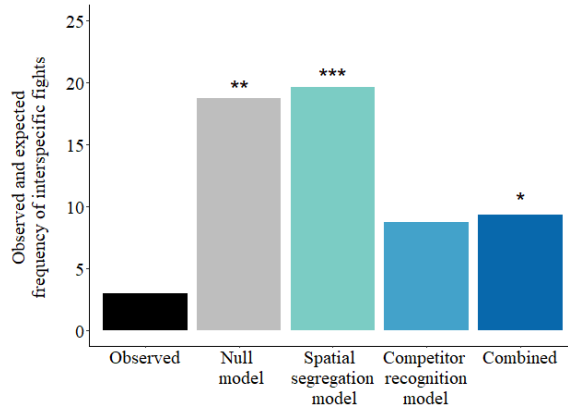
H. americana - H. titia at CV-L 2008
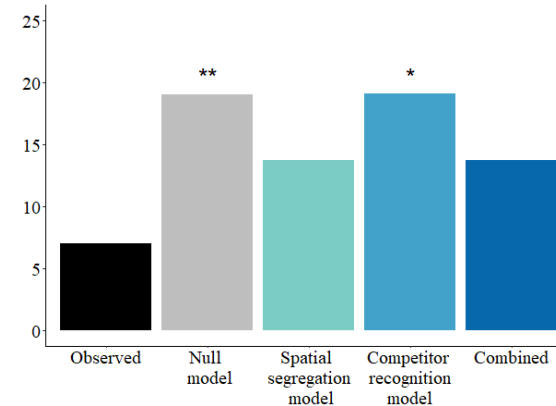
H. americana - H. cruentata at EL 2008
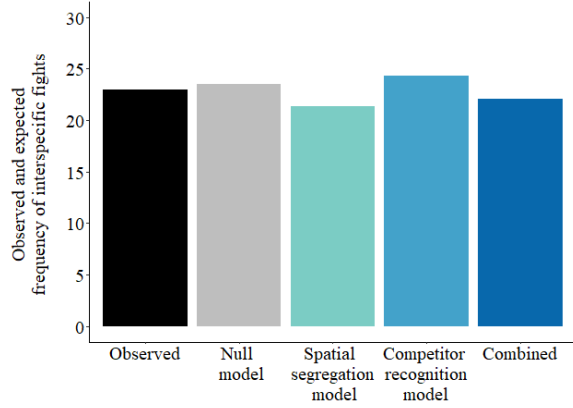
H. cruentata - H. vulnerata at PX 2010
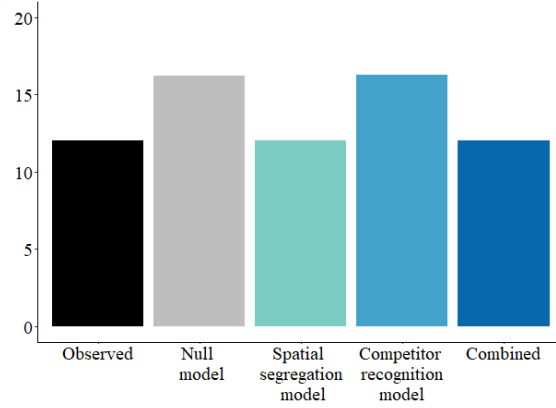
H. americana - H. vulnerata at BC 2012
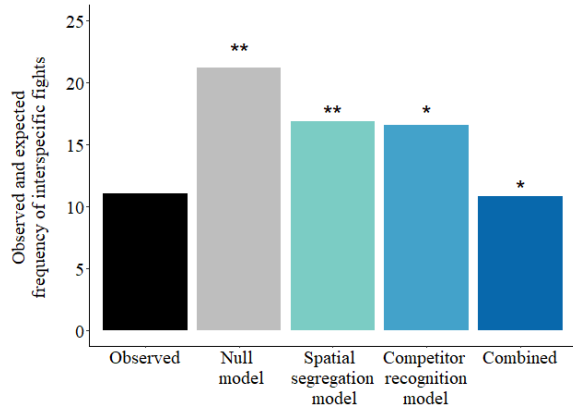
H. occisa - H. titia at PA1 2012
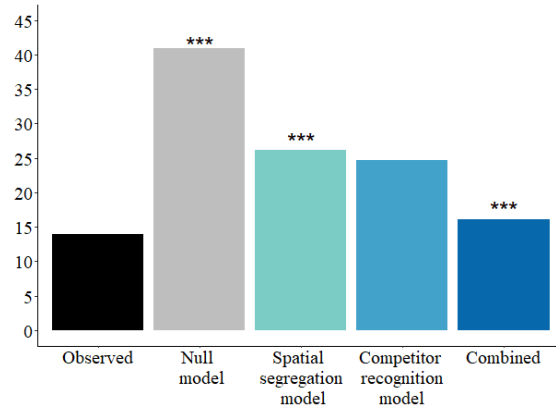
H. occisa - H. titia at PA2 2012
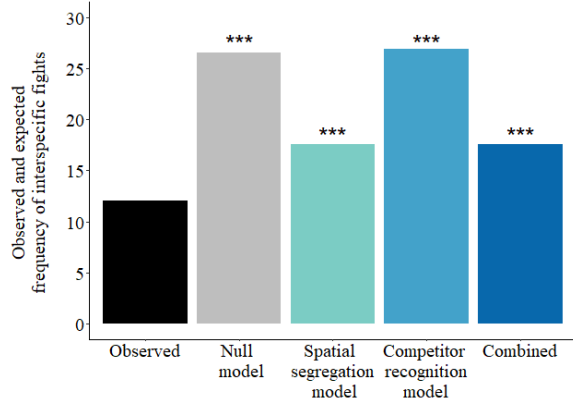
H. occisa - H. sempronia at ES 2013
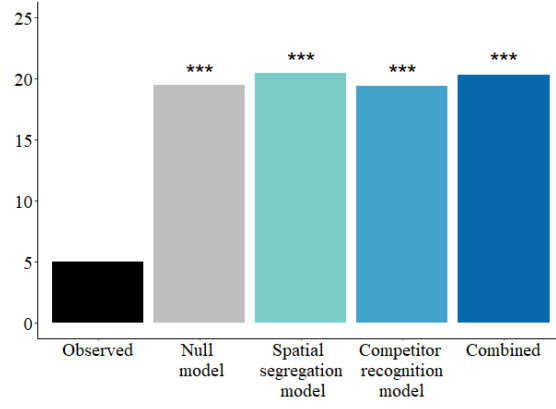
H. occisa - H. capitalis at RT02 2015
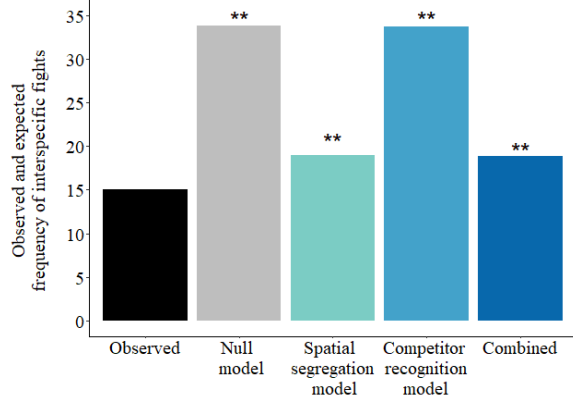
H. cruentata - H. capitalis at MV05 2016
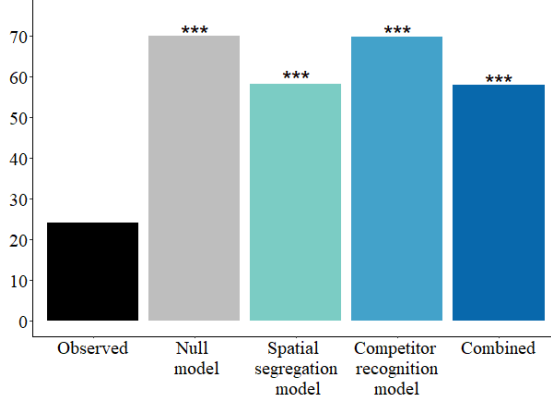
H. occisa - H. capitalis at RT02 2016
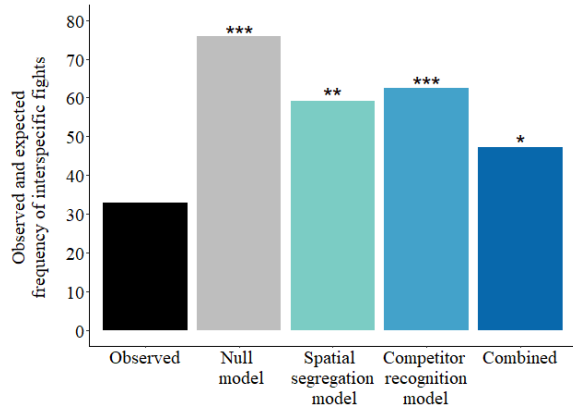
H. titia - H. miniata at ESRB 2017
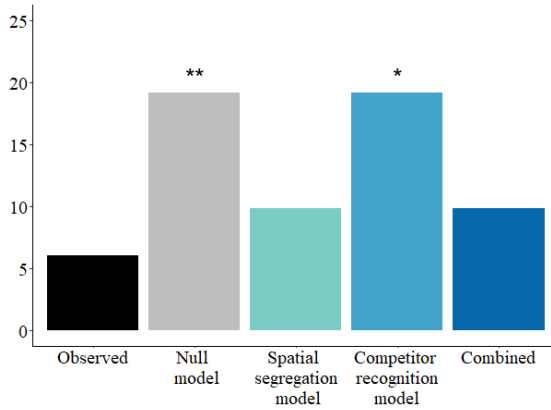
H. occisa - H. miniata at LH03 2017
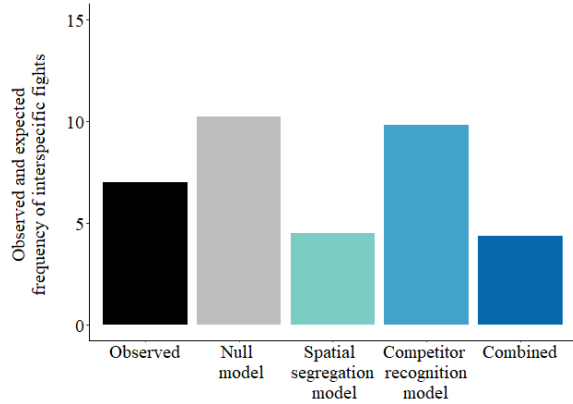
H. occisa - H. fuscoguttata at GO01 2016
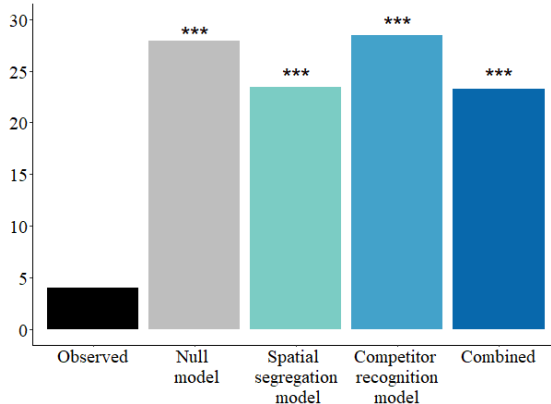
H. occisa - H. titia at GO01 2016
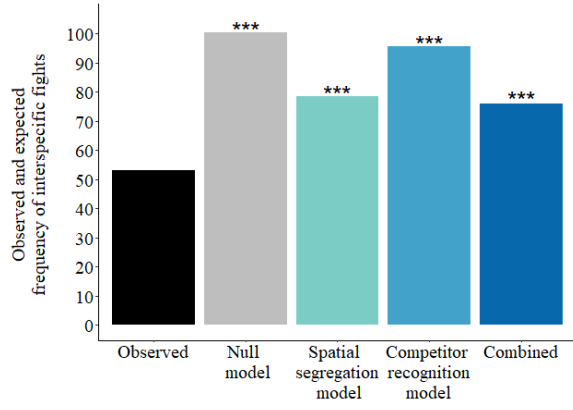
H. occisa - H. fuscoguttata at GO01 2017
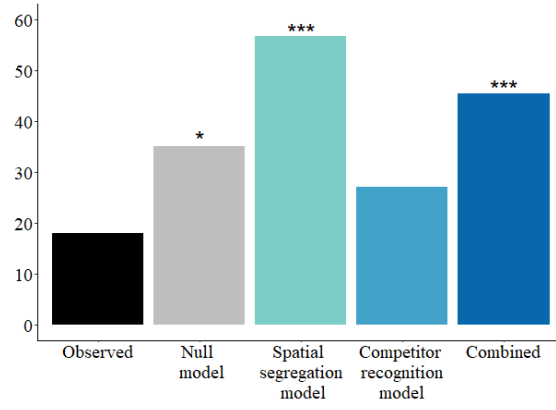
H. fuscoguttata - H. titia at GO01 2017
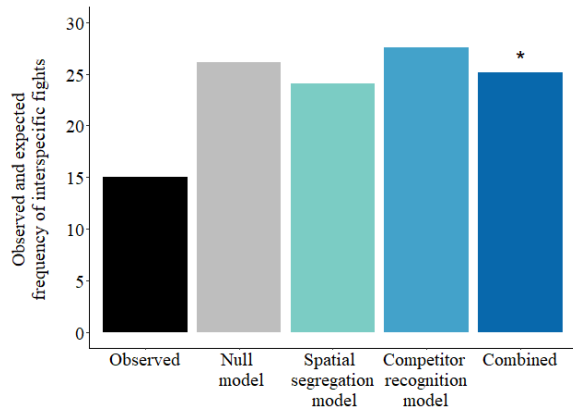
H. occisa - H. titia at GO01 2017

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Chapter 2: Agonistic character displacement, not ongoing competitive displacement, drives microhabitat divergence between sympatric rubyspot damselflies (*Hetaerina* spp.)

ABSTRACT

Aggressive interference can drive sympatric species apart in habitat use in two distinct ways. First, competitive displacement occurs when a dominant species forces a subordinate species into suboptimal habitat. Second, agonistic character displacement (ACD) in habitat preference can reduce the frequency of agonistic encounters over evolutionary time. Few, if any, cases of ACD in habitat divergence have been documented, but a recent study found that species differences in microhabitat use are strongly correlated with heterospecific aggression in rubyspot damselflies (*Hetaerina*), which could be due to competitive displacement, ACD, or some combination of these processes. We carried out removal experiments to test for competitive displacement in four *Hetaerina* species pairs by testing two key predictions: in the absence of the dominant species, the subordinate species will (I) move into areas it was excluded from and (II) shift its microhabitat use toward that of the dominant species. We found no support for either prediction and, therefore, reject the competitive displacement hypothesis. By process of elimination, we infer that the species probably diverged in microhabitat preferences through ACD.

INTRODUCTION

Niche partitioning between ecologically similar species tends to facilitate coexistence (Schoener 1974, Chesson 2000). Niche partitioning can arise from interactions between species over both ecological and evolutionary time. When the presence of one species narrows the realized niche of another species in ecological time, this is referred to as competitive displacement (Reitz and

Trumble 2002). Competitive displacement can arise from indirect (exploitative) or direct (interference) competition between species, and result in sympatric species occupying different parts of a habitat mosaic or environmental gradient (DeBach 1966, Reitz and Trumble 2002). Interspecific competition can also cause species' ecological niches and habitat preferences to diverge over evolutionary time (i.e., character displacement; Pfennig and Pfennig 2009, Price and Kirkpatrick 2009).

Competitive displacement caused by interference competition, usually in the form of interspecific territorial aggression, is well documented, and has often been inferred to be the cause of species replacements along elevational and habitat gradients (Cody and Walter 1976, Connell 1983, Robinson and Terborgh 1995, Robertson 1996, Price and Kirkpatrick 2009, Jankowski et al. 2010, Pasch et al. 2013, Eurich et al. 2018, Freeman et al. 2019). Ecological character displacement (ECD) is also well documented and widely regarded to be a major driver of niche differentiation between species that compete indirectly for resources (Pfennig and Pfennig 2009). In theory, agonistic character displacement (ACD) could be an important cause of niche differentiation between species that compete directly for resources or mates (Grether et al. 2009, 2017). To the best of our knowledge, there are no well-documented empirical examples, but ACD is relatively new and untested in this context. Some putative cases of competitive displacement or ECD might actually be cases of ACD instead.

Aggression between closely related species can be an adaptive response to exploitative competition for mates or resources, or a maladaptive byproduct of intraspecific aggression (reviewed in Grether et al. 2009, Peiman and Robinson 2010, Drury et al. 2015). In either situation, aggressive interactions are costly, and shifts in habitat use that reduce the frequency of aggressive interspecific encounters are likely to be favored by selection. Empirically, shifts in

habitat use caused by interspecific aggression (i.e., ACD) can be difficult to distinguish from those caused by exploitative competition (i.e., ECD), but theoretically, these are distinct evolutionary processes (Grether et al. 2013).

In this paper, we provide evidence that ACD has driven sympatric species of rubyspot damselflies (*Hetaerina* spp.) apart in habitat use. Interspecific aggression in this genus appears to be maintained by mate competition arising from reproductive interference (Drury et al. 2015, 2019, Grether et al. 2020). Mature males defend mating territories along streams and rivers and attempt to mate with females that inadvertently fly through territories while searching for oviposition sites (Johnson 1963, Córdoba-Aguilar et al. 2009, Guillermo-Ferreira and Del-Claro 2011). Males recognize females using visual cues and the females of most sympatric species are very similar phenotypically (Drury et al. 2015, 2019, Grether et al. 2015). Consequently, males often attempt to mate with heterospecific females, which results in reproductive interference and local mate competition between species (Drury et al. 2015, Grether et al. 2020). Across species pairs, heterospecific aggression can largely be predicted from the level of reproductive interference (Grether et al. 2020). Heterospecific aggression, in turn, is predictive of species differences in microhabitat (McEachin et al. 2021).

Nearly all sympatric species of *Hetaerina* differ, on average, in the microhabitat characteristics of male territories, but as would be expected under both the competitive displacement and ACD hypotheses, sympatric species that respond more aggressively to each other in simulated intruder tests differ more in territory microhabitat (McEachin et al. 2021). This pattern cannot be accounted for by ECD because *Hetaerina* territories are only used for mating (Weichsel 1987, Grether 1996, Córdoba-Aguilar et al. 2009). The competitive displacement and ACD hypotheses are not mutually exclusive – both could have contributed to

the pattern – but if one of these two alternative hypotheses could be rejected, the other would be strengthened by process of elimination (Platt 1964).

We carried out removal experiments to test the competitive displacement hypothesis on four of the 14 sympatric *Hetaerina* species pairs studied by McEachin et al. (2021). Territory holders of at least one of the two species in each pair are highly aggressive to heterospecific male intruders (Grether et al. 2020), and the species differ significantly in territory microhabitat (McEachin et al. 2021). If the species differences in microhabitat were due to competitive displacement, removal of the dominant species should have resulted in the subordinate species (I) moving into areas from which it was previously excluded and (II) shifting in microhabitat use toward that of the dominant species. Neither of these predictions were met. Having rejected the competitive displacement hypothesis, we infer that the correlation between microhabitat differences and heterospecific aggression documented by McEachin et al. (2021) must be a product of interspecific aggression in the evolutionary past (i.e., ACD). This may be the strongest evidence to date that interspecific aggression causes species to diverge in habitat preferences and thereby increases niche differentiation.

METHODS

Study sites and behavioral observations

We studied four different species pairs of *Hetaerina* damselflies at four sites in Costa Rica from March to July in 2016 and 2017 (Table S2.1). At each site, we established a 200-300m transect where we fastened a cord along the bank of the stream with numbered flags in 1 m increments. Within the transect, we captured the males, marked their abdomens with unique color combinations using paint pens, photographed, and released them where they were captured

(Anderson et al. 2011). Each day, 2-4 observers continuously walked along the transect and recorded the locations of males to the nearest 0.1 m on hand-held computers. A male was considered a territory holder if he was observed in the same location ($\pm$ 2 m) close to the surface of the water for at least two consecutive days (Anderson and Grether 2010).

Microhabitat Sampling

We measured the same microhabitat variables as McEachin et al. (2021): perch height, stream width, current speed, and canopy cover. Perch height was estimated to the nearest 0.1 m each time an observer recorded a male's location. Every 2 m along the transect, we measured the width of the stream to 0.1 m and recorded current speed near both banks and in the middle of the stream on an ordered categorical scale from 0-4, with 0 for still water and 4 for fast-moving, turbulent water. A concave spherical densiometer (Forestry Suppliers, Inc.) was used to measure canopy cover every 5 m along the transect. Where the stream width was < 3 m, canopy cover was measured in the middle of the stream. Where stream width was $\geq$ 3 m and < 10 m, canopy cover was measured on both banks; and where stream width was $\geq$ 10 m, canopy cover was measured in the middle and near both banks. Canopy cover ranges from 0 to 100 percent, where higher values indicate shadier habitat. To characterize each territory holder's microhabitat use, we calculated the average observed perch height and interpolated between the two closest stream width, current speed, and canopy cover measurements. For the purpose of calculating Euclidean distances between individual territory holders in microhabitat use, we used principal components analysis (PCA) to convert the four microhabitat variables to four orthogonal axes (Table S2.2). We used the mean values of the microhabitat variables of all territory holders present in the study transects prior to the experimental removals as the input for the PCA. The PC loadings were then

used to calculate PC scores for the new territory holders that settled in the removal sections after removal.

Removal experiments

To test for competitive displacement, we removed territory holders from alternating sections along the study transects and monitored resettlement for 1 week, which is an appropriate temporal scale for these animals. At each site, we designated 4-6 removal sections ranging from 10-30 m in length (Figure S2.1). We caught all territory holders in each removal section and released them on the same stream >100 m above or below the transect, which was sufficient to keep them from returning during the experiment. Removals were done on a single day at each site, except at site RS, where removals were done on two consecutive days in sections 1-3 and 4-6, due to logistical constraints (Figure S2.1). During the resettlement period, we continued to mark any unmarked males found in the transect, but we released them immediately (without taking photographs) to minimize handling effects on settlement behavior. Due to heavy rain and flooding, we could only monitor territory settlement for 2 days post-removal at site RB.

To test prediction I, that in the absence of the dominant species, the subordinate species will move into the removal sections from which it had been displaced, we compared the relative density of territory holders in the removal sections before and after removal. We calculated relative density from the perspective of the species that was overrepresented in each removal section as a standardized way to compare changes in relative density across all sites and removal sections. A species was considered overrepresented if the relative density of territories in the removal section was greater than the relative density of territories over the length of the transect. The competitive displacement hypothesis predicts that the relative density of the overrepresented

62

species should decrease in the early post-removal settlement period, compared to the pre-removal period, and then gradually increase again as the absolute density increases and males of the subordinate species are pushed out of the mutually preferred microhabitats and into less preferred microhabitats. We compared the mean relative density of the overrepresented species in each removal section over the 7 days before removal to the mean relative density over the first 2 days as well as the first 7 days after removal, using Wilcoxon matched pairs signed ranks tests.

To determine whether sympatric species used different microhabitats before the experimental manipulation, we compared:

$d(Species\ 1_B, Species\ 1_B)$ to $d(Species\ 1_B, Species\ 2_B)$, and

$d(Species\ 2_B, Species\ 2_B)$ to $d(Species\ 2_B, Species\ 1_B)$,

where d stands for Euclidean distance and the B subscripts stand for "before" removal.

To test prediction II, that the microhabitat use of one species shifted toward that of the other species during the post-removal resettlement period, we compared:

$d(Species\ 1_A, Species\ 2_B)$ to $d(Species\ 1_B, Species\ 2_B)$, and

$d(Species\ 2_A, Species\ 1_B)$ to $d(Species\ 2_B, Species\ 1_B)$,

where the A subscripts stand for "after" removal. To determine whether either species shifted in microhabitat use (at all) between the pre-removal and post-removal settlement periods, we compared:

$d(Species\ 1_A, Species\ 1_B)$ to $d(Species\ 1_B, Species\ 1_B)$, and

$d(Species\ 2_A, Species\ 2_B)$ to $d(Species\ 2_B, Species\ 2_B)$.

Each of the above tests were carried out on all four species pairs using paired t-tests or Wilcoxon matched pairs signed ranks tests, depending on whether the data were normally distributed (Table S2.3).

RESULTS

At all four sites, the first three principal components accounted for $\geq 80\%$ of the variance in microhabitat use (Table S2.2). At sites GO and RB, PC1 had a large positive loading for stream width and a large negative loading for current speed, while at sites RS and RT, PC1 had a large positive loading for both stream width and canopy cover (Table S2.2). Before the experimental removal, the Euclidean distance in multivariate PC space was significantly smaller between conspecifics than heterospecifics in all cases except *H. occisa* at RT (Table 2.1; Figure 2.2). Thus, these species pairs differ in microhabitat use and could have undergone competitive displacement or ACD.

Contradicting competitive displacement prediction I, the mean relative density of the overrepresented species did not change significantly between the pre-removal period (0.75 ± 0.05 territory holders per square meter) and the first 2 days (0.68 ± 0.07) or 7 days (0.71 ± 0.07) post removal (Table 2.2). Contradicting competitive displacement prediction II, the experimental removal had no significant effect on the mean Euclidean distance between species, from either species' perspective, in any of the four species pairs (Figure 2.1). At site GO, the mean Euclidian distance between *H. occisa* territory holders decreased between the pre- and post-removal periods, but there was no significant change in microhabitat use in either species at the other three sites (Table S2.4b; Figure 2.2).

DISCUSSION

McEachin et al.'s (2021) 13-year study of 14 sympatric species pairs of rubyspot damselflies provided an unprecedented level of support for the general hypothesis that interspecific

aggression increases spatial habitat partitioning. They were not, however, able to determine whether interspecific aggression drives species apart in habitat use through agonistic character displacement (ACD) in microhabitat preferences, competitive displacement, or some combination of these two mechanisms. We carried out a removal experiment to test for competitive displacement in a subset of the species pairs, all of which are interspecifically territorial (Grether et al. 2020) and differ in microhabitat use (this paper; see also McEachin et al. 2021). If the species differences in microhabitat were caused by competitive displacement, removing all territory holders from experimental sections should have resulted in specific changes in species composition and microhabitat use during the resettlement period. None of the predicted changes occurred. Thus, we infer that competitive displacement cannot account for the observed species differences in microhabitat use.

Ruling out competitive displacement greatly strengthens the hypothesis that these species diverged in microhabitat preferences because of selection against interspecific fighting in the past (i.e., ACD). Other results of the removal experiment also suggest that the species differ in microhabitat preferences. In the post-removal period at site GO, the microhabitat use of the new *H. occisa* territory holders contracted toward the species' centroid (Figure 2.2), as would be expected if males settled in the preferred areas first, according to their species-specific microhabitat preferences. In general, males that established new territories in the removal sections tended to perch where conspecific territory holders had previously perched (S.M. pers. obs.), which also points to species-specific microhabitat preferences.

Interspecific aggression is very common in some taxonomic groups, including insects, fishes, reptiles, amphibians, birds and mammals (Robinson and Terborgh 1995, Palomares and Caro 1999, Linnell and Strand 2000, Grether et al. 2009, Peiman and Robinson 2010, Martin et

al. 2017, Moran and Fuller 2018, Drury et al. 2020), and could be a major driver of divergence in habitat preferences, but as yet there are few well-documented examples. *Ficedula* flycatchers present a potential case for the combination of competitive displacement and ACD in breeding habitat. In allopatry, pied flycatchers (*F. hypoleuca*) preferentially defend breeding territories within deciduous forests (Lundberg and Alatalo 1992), but on the Swedish island of Öland, pied flycatchers are being pushed out to coniferous forests by recent colonization of aggressively dominant collared flycatchers (*F. albicollis*) (Qvarnström et al. 2009). An older hybrid zone in central Europe shows similar habitat segregation (Saetre et al. 1999), where aviary experiments demonstrated that pied flycatchers that occur within the hybrid zone actually preferred coniferous vegetation (Adamík and Bureš 2007), which suggests that pied flycatcher populations on Öland may evolve to prefer the poorer habitat type (Rybinski et al. 2016). However, the mechanism driving habitat segregation between these flycatcher species remains unclear. As collared flycatchers colonized Öland just 50 years ago (Qvarnström et al. 2009), pied flycatchers may be exhibiting a plastic response in habitat use (Rybinski et al. 2016). Additionally, as these species overlap extensively in diet (Veen et al. 2009) and hybridize (Saetre et al. 1999), habitat segregation may be driven by ECD or RCD (Vallin et al. 2012). Offspring may also imprint on their natal habitat and learn to prefer the habitat of their parents (Rybinski et al. 2016).

In another possible example, red-legged (*Rissa brevirostris*) and black-legged (*R. tridactyla*) kittiwakes exhibit interspecific aggression (Kenyon and Phillips 1965, Byrd and Williams 1993) and differences in nest site preference (Kildaw 1999). A resource-addition experiment showed that competitive displacement is not occurring, but habitat divergence resulting from aggressive interference in the past (i.e., ACD) cannot be ruled out (Kildaw 1999). However, with data from only two populations at one site, it cannot be determined whether ACD

has driven the observed differences in nest site preference. In addition, the matching of morphology and life history of *R. brevirostris* to the features of preferred nest sites is indicative of allopatric adaptation to environmental conditions independent of interspecific competition (Kildaw 1999).

There are many examples of interspecific interference competition affecting habitat use, but most can comfortably be classified as competitive displacement. For example, asymmetric aggression or dominance hierarchies have been found to maintain species distributions and nonoverlapping territories (Edgehouse et al. 2014, Klatt et al. 2015, Kajtoch et al. 2015, Martin and Bonier 2018, Culbertson and Herrmann 2019). However, there are other intriguing examples in reef fish (Bay et al. 2001, Canterle et al. 2020), land snails (Kimura and Chiba 2010), and lizards (Stuart et al. 2014), where habitat partitioning may not be due to just current agonistic interactions like competitive displacement.

One of the criteria in demonstrating ACD is showing that the displaced character is not a pleiotropic effect of another evolutionary process (Grether et al. 2009). This raises a challenge because niche differentiation is also a predicted outcome of reproductive character displacement (RCD), sometimes referred to as reinforcement (Gröning and Hochkirch 2008, Grether et al. 2009, Pfennig and Pfennig 2012). Furthermore, RCD takes precedent over ACD when a displaced character reduces both interspecific aggression and reproductive interference (Okamoto and Grether 2013). There are many cases of species pairs that are both interspecifically aggressive and exhibit reproductive interference (Drury et al. 2015), and in order to conclude that habitat differentiation in these species is the result of ACD, one must show that species differences in habitat use reduces aggressive interference and not reproductive interference. For example, *Mnais costalis* and *M. pruinosa* exhibit both aggressive and

reproductive interference (Nomakuchi and Higashi 1996), including hybridization (Hayashi et al. 2005), and utilize different microhabitats in sympatry (Okuyama et al. 2013), but because females oviposit within the male's territory, RCD is a more likely candidate for evolutionary divergence in habitat preference over ACD.

It is unlikely that RCD can explain the relationship between heterospecific aggression and species differences in microhabitat preference in *Hetaerina*. Unlike *Mnais* and *Ficedula* mating systems, *Hetaerina* males do not display courtship rituals to attract females (Weichsel 1987, Dale and Slagsvold 1996, Tsubaki et al. 2010). Rather, males attempt to clasp females that happen to fly through their territory in search of oviposition sites. While males initially clasp females in or near their territory, pairs rarely copulate and oviposit within the male's territory. As such, the only opportunity for female choice to drive microhabitat preference is in selection for oviposition sites. However, preferred oviposition sites are likely determined by environmental conditions and physiological demands on ova and larvae development as opposed to avoiding reproductive interference. Nevertheless, we cannot entirely rule out the possibility that male microhabitat preference tracks female microhabitat preference that evolves through RCD. Testing whether female microhabitat preferences are mediated by reproductive interference would require data on female oviposition sites and rates of reproductive interference as a function of microhabitat availability, which is an area of ongoing research.

CONCLUSIONS

Species distributions between ecologically similar species are invariably affected by interspecific interactions. Here, we tested whether species differences in microhabitat use have occurred as a result of competitive displacement. Territory holders appear to settle in areas consistent with

species-specific microhabitat preferences and are not influenced by current aggressive interactions with heterospecifics. As we are able to rule out competitive displacement, our results, together with the findings from McEachin et al. (2021), are among the first to empirically demonstrate that agonistic character displacement drives species differences in microhabitat preference between interspecifically territorial species. However, theory suggests that this phenomenon should be more common than there is current evidence for. Future studies should examine divergence in habitat preference as a mechanism that reduces agonistic encounters between interspecifically aggressive species.

Table 2.1 Mean (± SE) Euclidean distances between conspecific and heterospecific territory holders in microhabitat PC space before removal. Test statistics are from paired t-tests or Wilcoxon matched pairs signed ranks tests (bold). See Table S2.1 for species codes.

Site	Sp	n	Conspecific Mean ± se	Heterospecific Mean ± se	Test statistic	p
GO	1	30	2.63 ± 0.06	2.86 ± 0.09	-2.22	0.034
	2	30	2.34 ± 0.07	2.86 ± 0.07	**21.00**	< 0.001
RB	1	98	2.58 ± 0.04	2.77 ± 0.05	**1357.00**	< 0.001
	2	26	2.57 ± 0.07	2.77 ± 0.08	-3.17	0.004
RS	1	40	2.37 ± 0.06	2.86 ± 0.1	**93.00**	< 0.001
	2	41	2.46 ± 0.08	2.86 ± 0.1	**2.00**	< 0.001
RT	1	78	2.61 ± 0.08	2.61 ± 0.09	**1551.00**	0.96
	2	89	2.41 ± 0.07	2.61 ± 0.06	**563.00**	< 0.001

Table 2.2 Mean relative density of the overrepresented species in removal sections for 7 days before removal, the first 2 days after removal, and the first 7 days after removal. NA indicates that no territory holders of either species were present. Wilcoxon matched pairs signed ranks test (V) compared the mean relative densities before and after removal. See Table S2.1 for species codes.

Site	Rem. section	Overrep. species	7 days Before	2 days after	V(p)	7 days after	V(p)
RT	1	2	0.82	0.77	63.00(0.82)	0.80	56.00(0.48)
	2	1	0.50	0.45		0.49	
	3	2	0.82	0.75		0.69	
	4	2	0.82	0.50		0.44	
	5	1	0.51	0.53		0.60	
RS	1	2	1.00	NA		1.00	
	2	2	1.00	1.00		1.00	
	3	1	0.75	0.50		0.43	
	4	1	0.69	1.00		1.00	
	5	1	0.63	1.00		1.00	
	6	2	1.00	0.75		0.80	
GO	1	2	0.71	0.33		0.37	
	2	1	0.55	0.67		0.28	
	3	2	0.54	NA		1.00	
	4	1	0.95	1.00		0.78	
RB	1	2	0.50	0.83		-	
	2	2	0.23	0.17		-	
	3	2	0.23	0.39		-	
	4	2	0.56	1.00		-	

Figure 2.1 Mean (± se) Euclidean distance in microhabitat PC space to heterospecific territory holders, calculated from the perspective of species 1 (red) and species 2 (blue) before (circle) and after (cross) removal. Data are presented in Table S2.4a.
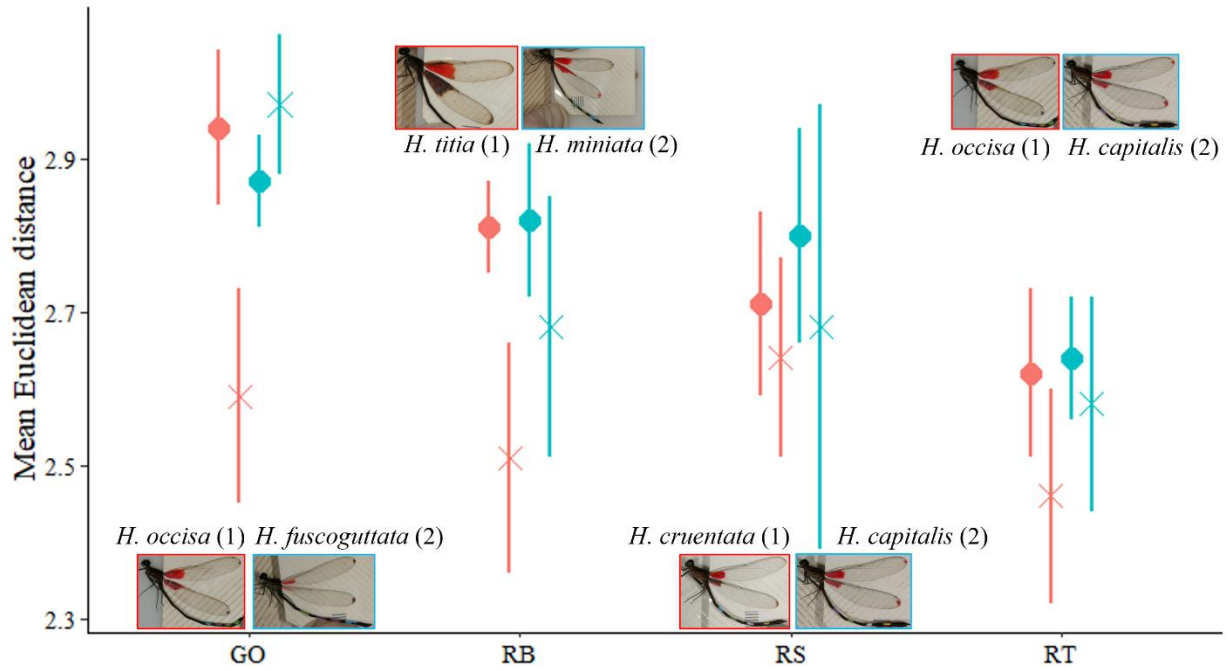
Figure 2.2 Principal component analysis on the four microhabitat features of territories inside removal sections at sites (a) GO, (b) RB, (c) RS, and (d) RT. Each point represents the average microhabitat values at each territory of species 1 (red) and species 2 (blue) before removal (circle) and after removal (cross).
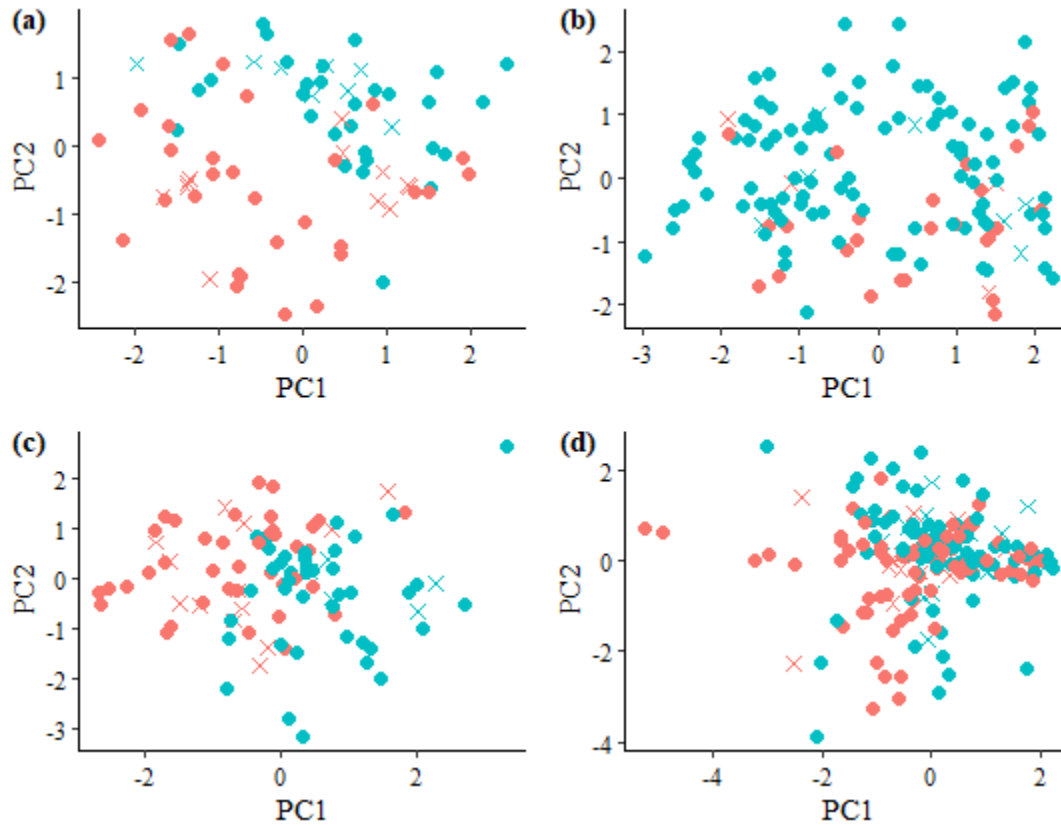
Chapter 2 Supplementary Materials

Table S2.1 A list of study sites. Species codes are in parentheses.

Site	Year	Species	No. territory holders	No. removal sections	Latitude	Longitude
RT	2016	*H. occisa* (1)	106	5	10.949	-85.5116
		H. capitalis (2)	117			
RS	2016	*H. cruentata* (1)	61	6	10.2783	-84.8189
		H. capitalis (2)	51			
GO	2017	*H. occisa* (1)	43	4	8.643	-83.1953
		H. fuscoguttata (2)	41			
RB	2017	*H. titia* (1)	110	4	9.71961	-82.9657
		H. miniata (2)	31			

Table S2.2 Microhabitat principal component loadings.

Site	Microhabitat variable	PC1	PC2	PC3	PC4
GO	Perch height	0.241	0.663	0.570	-0.421
	Stream width	0.648	-0.117	-0.531	-0.533
	Current speed	-0.722	0.136	-0.302	-0.608
	Canopy cover	0.020	0.727	-0.549	0.412
	Proportion of variance	0.354	0.303	0.241	0.103
RB	Perch height	-0.121	0.911	-0.361	-0.160
	Stream width	-0.643	0.072	0.060	0.760
	Current speed	0.580	-0.067	-0.603	0.544
	Canopy cover	-0.486	-0.401	-0.709	-0.317
	Proportion of variance	0.479	0.264	0.171	0.086
RS	Perch height	0.391	-0.710	0.016	0.586
	Stream width	0.539	0.182	-0.814	-0.117
	Current speed	-0.405	-0.665	-0.342	-0.526
	Canopy cover	0.626	-0.144	0.469	-0.606
	Proportion of variance	0.335	0.272	0.213	0.180
RT	Perch height	-0.438	0.231	-0.842	-0.215
	Stream width	0.592	-0.238	-0.519	0.569
	Current speed	0.098	0.916	0.104	0.376
	Canopy cover	0.669	0.227	-0.107	-0.699
	Proportion of variance	0.378	0.269	0.222	0.132

Table S2.3 Normality tests on the Euclidean distances using the Shapiro-Wilk test. See Table

S2.1 for species codes; A and B subscripts stand for "after" and "before" removal.

Site	Distance	n	W	p
GO	$Sp1_B$ to $Sp1_B$	18	0.96	0.56
	$Sp1_B$ to $Sp2_B$	18	0.96	0.66
	$Sp1_A$ to $Sp1_B$	12	0.93	0.36
	$Sp1_A$ to $Sp2_B$	12	0.92	0.25
	$Sp2_B$ to $Sp2_B$	22	0.92	0.08
	$Sp2_B$ to $Sp1_B$	22	0.98	0.91
	$Sp2_A$ to $Sp2_B$	8	0.86	0.13
	$Sp2_A$ to $Sp1_B$	8	0.91	0.37
RB	$Sp1_B$ to $Sp1_B$	51	0.96	0.12
	$Sp1_B$ to $Sp2_B$	51	0.97	0.14
	$Sp1_A$ to $Sp1_B$	7	0.94	0.65
	$Sp1_A$ to $Sp2_B$	7	0.92	0.45
	$Sp2_B$ to $Sp2_B$	19	0.94	0.23
	$Sp2_B$ to $Sp1_B$	19	0.95	0.39
	$Sp2_A$ to $Sp2_B$	4	0.90	0.41
	$Sp2_A$ to $Sp1_B$	4	0.95	0.72
RS	$Sp1_B$ to $Sp1_B$	20	0.93	0.13
	$Sp1_B$ to $Sp2_B$	20	0.91	0.08
	$Sp1_A$ to $Sp1_B$	13	0.96	0.80
	$Sp1_A$ to $Sp2_B$	13	0.95	0.56
	$Sp2_B$ to $Sp2_B$	21	0.77	< 0.001
	$Sp2_B$ to $Sp1_B$	21	0.84	0.00
	$Sp2_A$ to $Sp2_B$	5	0.85	0.19
	$Sp2_A$ to $Sp1_B$	5	0.87	0.29
RT	$Sp1_B$ to $Sp1_B$	45	0.72	< 0.001
	$Sp1_B$ to $Sp2_B$	45	0.71	< 0.001
	$Sp1_A$ to $Sp1_B$	18	0.85	0.01
	$Sp1_A$ to $Sp2_B$	18	0.75	< 0.001
	$Sp2_B$ to $Sp2_B$	65	0.78	< 0.001
	$Sp2_B$ to $Sp1_B$	65	0.81	< 0.001
	$Sp2_A$ to $Sp2_B$	20	0.77	< 0.001
	$Sp2_A$ to $Sp1_B$	20	0.78	< 0.001

Table S2.4 The mean Euclidean distance in microhabitat PC space from territory holders before removal to (A) heterospecifics before removal (Before-Before) and after removal (Before-After), and (B) conspecifics before removal (Before-Before) and after removal (Before-After). Test statistics are from paired t-tests when values followed the normal distribution and Wilcoxon matched pairs signed ranks tests (in bold) otherwise. See Table S2.1 for species codes.

A			Before-Before		After-Before			
Site	Sp	n	Mean ± se	n	Mean ± se	Test statistic	p
GO01	1	18	2.94 + 0.1	12	2.59 + 0.14	-2.05	0.053
	2	22	2.87 + 0.06	8	2.97 + 0.09	0.96	0.35
ESRB	1	51	2.81 + 0.06	7	2.51 + 0.15	-1.90	0.09
	2	19	2.82 + 0.1	4	2.68 + 0.17	-0.50	0.64
MV05	1	20	2.71 + 0.12	13	2.64 + 0.13	-0.43	0.67
	2	21	2.8 + 0.14	5	2.68 + 0.29	**45.00**	0.66
RT02	1	45	2.62 + 0.11	18	2.46 + 0.14	**324.00**	0.22
	2	65	2.64 + 0.08	20	2.58 + 0.14	**613.00**	0.71
B							
GO01	1	18	2.67 + 0.09	12	2.41 + 0.09	-2.07	0.049
	2	22	2.28 + 0.06	8	2.14 + 0.12	**-1.04**	0.32
ESRB	1	51	2.64 + 0.09	7	2.49 + 0.09	-1.37	0.20
	2	19	2.57 + 0.07	4	2.65 + 0.29	0.25	0.82
MV05	1	20	2.26 + 0.07	13	2.29 + 0.09	**0.24**	0.81
	2	21	2.39 + 0.13	5	2.05 + 0.21	**36.00**	0.31
RT02	1	45	2.63 + 0.1	18	2.51 + 0.13	**342.00**	0.34
	2	65	2.48 + 0.09	20	2.41 + 0.13	**663.00**	0.90

Figure S2.1 The timeline of removal experiments at the four different sites. See Table S2.1 for the species present at each site. Removal sections are in parentheses when territory holders were removed on different days at a site.
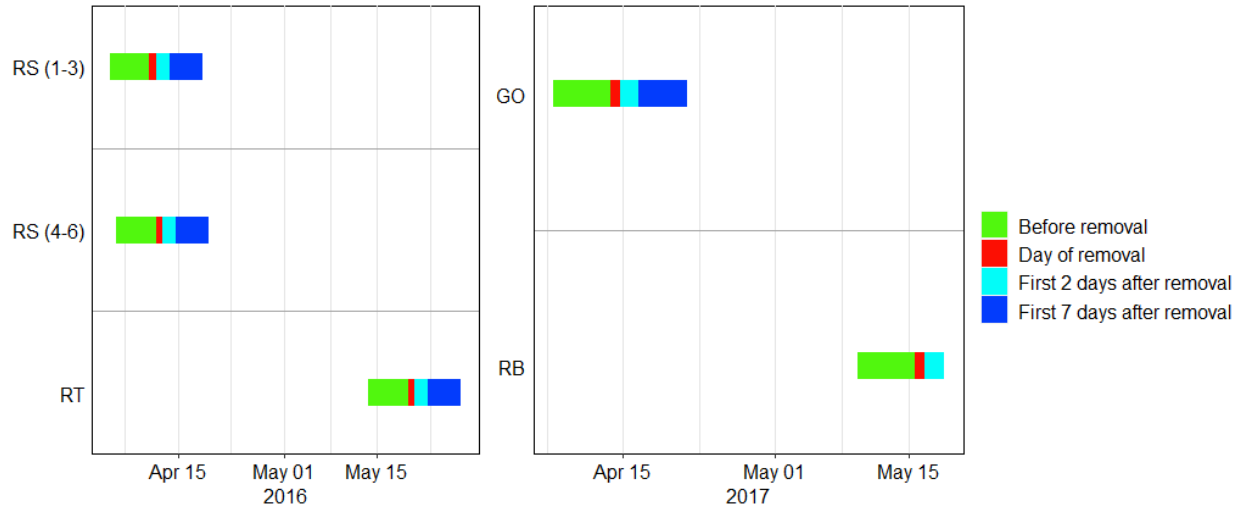
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Chapter 3: Conspecific attraction and microhabitat preferences drive spatial partitioning between interspecifically aggressive rubyspot damselflies (*Hetaerina*)

ABSTRACT

Territory holders use various forms of information during habitat selection. Individuals acquire private information about the physical environment, while the presence of conspecifics, a kind of public information, can promote the differential settlement of individuals near conspecifics. Habitat partitioning and conspecific attraction both have the potential to drive spatial segregation between interspecifically aggressive species. We examined the mechanisms of spatial segregation in 42 populations, including 9 different species, of interspecifically territorial *Hetaerina* damselflies. Most of the populations exhibited territory clustering, which can be explained by heterospecific repulsion, conspecific attraction, or microhabitat preferences. A previous study found no evidence of competitive displacement and therefore rules out heterospecific repulsion. By comparing the observed level of territory clustering to null distributions, calculated from population-specific environmental niche models, we could differentiate between the effects of conspecific attraction and microhabitat preferences on microhabitat selection. The null distributions predicted the distribution of territories based on microhabitat availability alone. Conspecific attraction occurred when observed clustering exceeded that of the null distributions, whereas microhabitat selection based on microhabitat preferences occurred when observed clustering followed the null distributions. Most populations showed a combination of territory clustering that both exceeded and followed the clustering of the null distributions. Thus, we present evidence that both conspecific attraction and microhabitat

preferences serve as mechanisms of microhabitat selection that promote spatial partitioning between interspecifically aggressive species.

INTRODUCTION

Habitat selection is an important process for animals that affects survival and reproduction (Morris 1992, 2003, Hall et al. 1997, Kirkton and Schultz 2001). Many factors determine how an individual selects a given habitat, such as innate preferences (Johnson 1980, Brown et al. 1994, Martin 1998), thermal or physiological tolerance (Martin and Martin 2001, Wiens 2011, Pasch et al. 2013), natal imprinting (Davis and Stamps 2004, Berner and Thibert-Plante 2015), and the presence of conspecifics (Courchamp et al. 1999, Stamps 2001, Morris 2002, Doligez et al. 2003, Jeanson and Deneubourg 2007). If environmental conditions are stable over time, species can evolve innate habitat preferences (Rausher and Englander 1985, Danchin et al. 2004, Berner and Thibert-Plante 2015). Otherwise, animals must be able to acquire information during their lifetime (Buckley 1997, Seppanen et al. 2007). In some cases, animals acquire personal information about the physical habitat by interacting with the environment through trial and error (van Bergen et al. 2004, Danchin et al. 2004). In other cases, animals acquire public information by observing how others interact with the environment (Valone 1989, 2007, Doligez et al. 2003, Danchin et al. 2004, Campobello and Sealy 2011, Szymkowiak et al. 2017).

The use of public information is considered to be a widespread phenomenon (Danchin et al. 2004). Individuals may acquire information from both heterospecifics and conspecifics. For example, individuals may avoid interspecific competition by settling in areas without heterospecifics (i.e., heterospecific repulsion or avoidance; Byers 1993, Fletcher 2007, 2008, Erfanifard and Khosravi 2019). Conversely, individuals may be more likely to select patches

with conspecifics than patches without conspecifics (i.e., conspecific attraction; reviewed in Buxton et al. 2020). For example, many species of territorial songbirds are more likely to settle in patches with conspecifics present than empty patches (Ward and Schlossberg 2004, Farrell et al. 2012). Similarly, female *Nephila clavipes* spiders follow conspecific chemical cues and form aggregations independently of prey density (Fitzgerald and Ives 2017).

Conspecific attraction can improve fitness when animals cannot use non-social cues to assess habitat quality (Stamps 2001, Fletcher Jr. 2006). Several ultimate explanations have been proposed to explain the evolution of conspecific attraction, such as the reduction in costs related to searching for and settling in suitable habitat and Allee effects (reviewed in Stamps 2001). Stodola and Ward (2017) developed an individual-based model that suggests conspecific attraction can be adaptive when environmental conditions are stable, but detrimental when conditions change rapidly. Conspecific cueing, a specific case of conspecific attraction where conspecifics act as accurate indicators of habitat quality, has long been cited as a fitness benefit of conspecific attraction (e.g., Muller 1998, Shima and Osenberg 2003, Johnson et al. 2006, Farrell et al. 2012, Mariette and Griffith 2012). In fact, most studies in a recent review by Buxton et al. (2020) proposed habitat quality as the adaptive benefit for conspecific attraction. There may also be multiple ultimate explanations for conspecific attraction in a given system. For example, Donahue (2006) developed an empirically-based fitness model based on settlement of the porcelain crab (*Petrolisthes cinctipes*) and found that positive density dependence and indicators of quality habitat together (i.e., both Allee effects and conspecific cueing) explain conspecific attraction.

Conspecific attraction causes spatial clustering (Perry and Andersen 2003, Schlossberg and Ward 2004, Mills et al. 2006) and may therefore drive spatial segregation between sympatric

88

species. Spatial partitioning is common among interspecifically aggressive species (Gotelli 2000, Jankowski et al. 2010, Pigot and Tobias 2013, Ulrich et al. 2017). For example, damselfish communities along coral reefs maintain fine-scale, nonoverlapping territories through aggressive interactions (Eurich et al. 2018). *Ficedula* flycatchers are interspecifically aggressive and use conspecific cues for nest-site settlement (Qvarnström et al. 2009, Vallin et al. 2012, Kivela et al. 2014, Rybinski et al. 2016). However, we found just one study (Gotelli et al. 2010) that demonstrated conspecific attraction as a mechanism that promotes spatial segregation between interspecifically aggressive species. As such, the role of conspecific attraction in spatial partitioning between interspecifically aggressive species remains understudied.

Here, we examine the effects of conspecific attraction on spatial partitioning between several species of interspecifically territorial rubyspot damselflies (*Hetaerina* spp.). Mature males in this genus defend mating-based territories along streams and rivers (Johnson 1963, Córdoba-Aguilar et al. 2009, Anderson and Grether 2011). Territory holders perch close to the surface of the water and attempt to clasp females as they fly by searching for oviposition sites (Weichsel 1987). Where sympatric heterospecific females have similar wing coloration, males attempt to mate with heterospecific females at similar rates to conspecific females (Drury et al. 2015, 2019, Grether et al. 2020). A strong positive correlation between heterospecific aggression and heterospecific clasping rates suggests heterospecific aggression is an adaptive response to reproductive interference in this system (Drury et al. 2015, Grether et al. 2020).

Several features of the habitat have been shown to be important for microhabitat selection in *Hetaerina* territory holders, including canopy cover, current speed, and stream width (Johnson 1966, 1973, Anderson and Grether 2011, McEachin et al. 2021). While stream width is not necessarily an aspect of the microhabitat *per se*, it reflects an axis upon which territory holders

can spatially separate. Submerged vegetation has also been found to be associated with territories, however, adult damselflies are apparently unable to detect submerged vegetation from above the water's surface (Weichsel 1987). Females, who oviposit in submerged vegetation, tend to find oviposition sites by trial and error, while males, who do not submerge, are unlikely to be able to see submerged vegetation from above the surface (Weichsel 1987). As such, males may acquire public information and be more likely to defend a site where females spend more time submerged at oviposition sites. Similarly, male eastern amberwing dragonflies (*Perithemis tenera*) are more likely to return to territories where they have higher reproductive success (Switzer 1997). Conspecific attraction may be adaptive if established territory holders are accurate indicators of sites where encounters with females are more likely.

Conspecific attraction and microhabitat partitioning have the potential to facilitate spatial partitioning between interspecifically aggressive species of *Hetaerina*. A long term study by McEachin et al. (2021) found a strong positive correlation between heterospecific aggression and species differences in microhabitat use (see also Anderson and Grether 2011). The two most likely hypotheses to explain this correlation are competitive displacement and agonistic character displacement, however, the results of a removal experiment show that competitive displacement does not occur in this system (McEachin and Grether 2021). Therefore, evidence suggests species may have evolved divergent microhabitat preferences over time as a response to past interspecific aggression (McEachin and Grether 2021, McEachin et al. 2021). There was also a negative correlation between heterospecific aggression and the proportion of heterospecific neighbors (McEachin et al. 2021), suggesting interspecifically aggressive sympatric species are spatially segregated. The absence of competitive displacement (McEachin and Grether 2021) indicates that heterospecific repulsion or avoidance does not drive spatial segregation. Thus, in

addition to microhabitat partitioning, conspecific attraction may contribute to the spatial segregation between interspecifically aggressive *Hetaerina* territory holders.

We examined the effects of conspecific attraction and microhabitat preferences on spatial segregation in 42 populations across 9 different species of *Hetaerina* territory holders. Because species that exhibit conspecific attraction form clusters of individuals (Perry and Andersen 2003, Schlossberg and Ward 2004, Mills et al. 2006), we measured the degree to which conspecific territories were clustered throughout each study site. We considered instances where populations were more clustered than expected based on microhabitat availability to be evidence for conspecific attraction. Instances where populations were as clustered as expected based on microhabitat availability were considered evidence that territory settlement was based on microhabitat preference. Differentiating between conspecific attraction and microhabitat preference improves our knowledge of the mechanisms responsible for spatial partitioning between interspecifically aggressive species.

METHODS

Study sites and territory clustering

We studied 42 populations representing 9 different species of *Hetaerina* damselflies in the United States, Mexico, and Costa Rica between 2005-2017 (Table S3.1). The study period at each site was approximately 1-3 weeks long (see Table S3.1). In order to examine the spatial distribution of territory holders, we mapped the locations of territories at each site. We established a 200-300 m transect and fastened a cord along the bank of the stream with numbered flags in 1 m increments. Within the transect, we captured males, marked their abdomens with unique color combinations using paint pens, and released them where they were captured

(Anderson et al. 2011). Each day, 2-4 observers continuously surveyed the transect and recorded the locations of males to the nearest 0.1 m on hand-held computers. We considered a male to be a territory holder if he was observed in the same location ($\pm$ 2 m) close to the surface of the water for at least two consecutive days (Anderson and Grether 2010).

Conspecific attraction is expected to result in clustering of territory holders within the available habitat. To examine spatial distribution of territory holders, we determined the extent to which the locations of territories were clustered, randomly spaced, or uniformly spaced using a linearized version of Ripley's (1977) K function called the L function (Besag 1977). Ripley's K compares the observed spatial clustering to that expected under a Poisson distribution at various spatial scales by drawing circles of increasing radius (r) around each point and counting the number of other points within that circle, scaled by the intensity (for equations and detailed explanations of these statistical methods see Loosmore and Ford 2006, Baddeley et al. 2014, Diggle 2014). In our application, the points were the territory midpoints of individual males.

The L statistic, $\sqrt{\frac{K(r)}{\pi}}$, is a linearized, variance-stabilizing transformation of K that is more intuitive and interpretable than raw K values. We calculated L using radii (r) between 0.5 and 20 m in 0.5 m increments and generated a 95% simulation envelope using n = 99 Monte Carlo simulations. To simplify the visualization of the degree of clustering, we calculated the proportional deviation from the simulation envelope by taking the difference between L and the upper end of the simulation envelope and dividing by the upper end of the simulation envelope at each radius. If the proportional deviation is greater than 0, the territories are considered to be clustered, relative to complete spatial randomness (Baddeley et al. 2015). Analysis on clustering was carried out using the spatstat package in R (Baddeley et al. 2015).

Microhabitat availability and environmental niche models

It has previously been shown that sympatric *Hetaerina* species are separated along several different axes of microhabitat variables, including canopy cover, stream width, and current speed (Anderson and Grether 2011, McEachin et al. 2021). Therefore, it is possible that microhabitat partitioning can account for the spatial clustering of conspecific territory holders. To determine whether microhabitat availability explained the clustering of territories, we built population-specific environmental niche models (ENMs) to simulate territory settlement based on microhabitat availability. The expected spatial distributions from the ENMs provide a null distribution against which to compare observed distributions of territories to disentangle the effects of microhabitat preferences and conspecific attraction on territory clustering.

To build the ENMs, we measured the availability of stream width, current speed, and canopy cover and assigned values of each microhabitat variable to each male's territory. Every 2 m along the transect, we measured the width of the stream to 0.1 m and recorded current speed near both banks and in the middle of the stream on an ordered categorical scale from 0-4, with 0 for still water and 4 for fast-moving, turbulent water. A concave spherical densiometer (Forestry Suppliers, Inc.) was used to measure canopy cover every 5 m along the transect. Where the stream width was < 3 m, canopy cover was measured in the middle of the stream. Where stream width was ≥ 3 m and < 10 m, canopy cover was measured near both banks; and where stream width was ≥ 10 m, canopy cover was measured in the middle and near both banks. Canopy cover ranges from 0 to 100 percent, where higher values indicate shadier habitat. To calculate the value of the microhabitat features at each territory, we interpolated between the two closest stream width, current speed, and canopy cover measurements. At some sites, there were two or more

channels where the river forked, and the channels often differed in microhabitat. We therefore analyzed channels separately.

We similarly assigned values of each microhabitat variable to background points within the study transect. For each channel, we generated a list of all possible locations within the study transect at a 0.1 m resolution (i.e., a grid of locations with 0.1 m x 0.1 m cells). To obtain values of microhabitat variables at each cell in the grid, we interpolated between the two closest stream width, current speed, and canopy cover measurements in the same way that we calculated microhabitat values at territories. We then rasterized each microhabitat vector to use as input for the ENMs. Each microhabitat variable had a resolution of 0.1 m, and the extent was set by the boundaries of the transect. We used Maxent to obtain the probability of occurrence at each cell based on the available microhabitat and the microhabitat use of territory holders. Maxent, or maximum entropy modeling, is a machine learning algorithm for modeling species distributions and environmental niches (Phillips et al. 2006). By using environmental measurements and presence data as inputs, Maxent produces a probability distribution that predicts the probability of occurrence at each point in a given landscape (Phillips et al. 2006, Elith et al. 2011, Merow et al. 2013). It has become widely used across ecological studies for a variety of purposes, including the mapping of species distributions onto environmental covariates (Wollan et al. 2008, Monterroso et al. 2009, Elith et al. 2011). Many studies use Maxent to predict species distributions on large geographic scales, but it appears to perform better at smaller scales (Suárez-Seoane et al. 2014, Manzoor et al. 2018). One limitation many studies face is that environmental data often does not exist at fine scales (i.e., microhabitat), but we were able to measure microhabitat data on a very fine scale.

94

We used the MIAMaxent package in R to carryout Maxent modeling on each population (Vollering et al. 2019). Maxent output includes relative probabilities of occurrence at each cell in the grid in the form of probability ratio output (PRO). A PRO of 1 indicates average probability of occurrence at a given location, and higher PRO values indicate a higher likelihood of occurrence. In theory, there is no maximum PRO value. However, to simulate populations based on microhabitat availability and the probability of occurrence, it was necessary to use probabilities between 0 and 1 (see below). Therefore, we normalized the PRO values by subtracting them from the minimum PRO and dividing the difference by the maximum PRO. We used the area under the curve (AUC) of the receiver operating characteristic (ROC) to evaluate model performance. Models with AUC > 0.7 are considered to have good model performance (Swets 1988).

We then drew random samples, with replacement, from the list of all possible locations within the transect. For each random location, we used the rbinom function in R (R Core Team 2021) to calculate a Bernoulli variable (0 = absence, 1 = occurrence) using the normalized probability of occurrence from the Maxent model. To simulate a population, we continued the process until the number of occurrences matched the number of observed territories. We simulated 1,000 populations, referred to as the null distribution, for each observed population in each channel of each site. To determine the degree to which null distributions showed clustering at different spatial scales, we calculated L using radii between 0.5 and 20 m in 0.5 m increments along with the 95% simulation envelope.

The observed degree of clustering was compared to the null distributions to differentiate between the extent to which conspecific attraction and microhabitat preferences drive microhabitat selection. We considered there to be evidence of conspecific attraction if the

observed degree of clustering exceeded the degree of clustering in the null distributions.

However, if the observed degree of clustering was not different from the degree of clustering in

the null distributions, we considered this as evidence of microhabitat selection based on

microhabitat preferences. Thus, to determine whether the observed degree of clustering differed

from what would be expected if males settled according to microhabitat availability alone, we

compared the clustering of territories in observed populations to the null distributions from the

ENMs. First, we calculated the proportional deviation of L from the upper end of the simulation

envelope across all radii for the null distributions and calculated the bootstrapped 95%

confidence intervals (CI) of the proportional deviations. We then compared the observed

deviations to the bootstrapped 95% CI to differentiate between the effects of conspecific

attraction and microhabitat preferences. We assigned the categories "none," "low," "moderate,"

and "high" according to the classification scheme in Table 3.1 to describe the degree to which

populations were clustered (Table 3.1). If the observed deviations are positive and above the

95% CI, then territories are more clustered than expected based on microhabitat availability,

suggesting conspecific attraction drives territory distributions. However, if observed deviations

fall within the 95% CI, then territories are as clustered as expected based on microhabitat

availability, suggesting males settle based on microhabitat preferences.

RESULTS

Of the 42 total populations, 81% (n = 34) exhibited at least a low degree of territory clustering

(Table S3.2). Of the 8 populations with no territory clustering, the corresponding null

distributions of 7 of these populations also did not show clustering. The mean AUC score from

the Maxent models was 0.74 ± 0.01, suggesting the Maxent models performed reasonably well

for a majority of the populations; AUC > 0.7 is generally considered to represent acceptable performance (Swets 1988, Lüdemann et al. 2006, el Khouli et al. 2009, Safari et al. 2016). Only 1 population had an AUC score < 0.6. The Maxent models for 30 populations had AUC scores > 0.7 (Table S3.2); we only included these 30 populations for further analysis. Of these 30 populations, 83% (n = 25) had territories with some clustering, a majority of which showed a moderate (n = 10) or high (n = 10) degree of clustering (Table 3.2).

Null distributions were considered to show clustering if the entire 95% CI was > 0 at a given radius (i.e., the lower end of the 95% CI > 0). Most null distributions showed no clustering at any scale. In fact, just 23% (n = 7) of the null distributions showed some degree of clustering based on microhabitat availability (Table 3.2). Each of these 7 null distributions showed either a moderate or high degree of clustering.

Each of the 25 populations with observed territory clustering showed evidence of conspecific attraction because they exhibited more clustering than expected based on the null distributions (Table 3.2). A majority of these populations exceeded the clustering of null distributions across a large or moderate range of radii (Table 3.2). Just 5 populations showed no evidence of clustering, and the respective null distributions also did not show any clustering (Table S3.2). At least one population of every species showed more clustering than expected compared to the null distributions (Table S3.2).

There were no populations where the observed degree of clustering was the same or less than the null distributions across all radii (Table S3.2). However, there was still evidence that microhabitat preferences partially drove microhabitat selection because the populations that showed a low degree, and many that showed a moderate degree, of clustering beyond that of the null distributions tended to also fall within the 95% CI across some radii (Figures 1c-f; S2-S3).

97

Thus, most populations showed clustering that could be explained by some combination of microhabitat preferences and conspecific attraction.

DISCUSSION

In this study, we present evidence of widespread conspecific attraction across many populations of interspecifically aggressive *Hetaerina* species. Not only did a large majority of the populations in our study have spatially clustered territories, but much of the clustering was beyond that predicted by microhabitat availability. We also presented a novel way to account for microhabitat availability by generating null distributions using environmental niche models (ENMs) to simulate territory settlement. The null distributions represent the expected distribution of territory holders if they settled according to microhabitat availability alone. Thus, we can differentiate between conspecific attraction, where observed clustering exceeds the clustering of null distributions based on ENMs, and microhabitat preference, where patterns of observed clustering follow null distributions.

While conspecific attraction explains much of the spatial clustering of territories, microhabitat preference still plays a large role in territory settlement in *Hetaerina*. The clustering of territories in many populations closely followed the null distribution across various spatial scales. For example, the clustering of territories in population 9 closely followed the null distribution across a majority of radii (Figure 3.1f). Many of the populations in our study follow a similar pattern; only 5 populations were more clustered than the null distributions across all radii (Figure 3.1a; Figure S3.4). Therefore, because the clustering of territories both exceeds and follows the clustering of the null distributions, our findings suggest *Hetaerina* territory holders

respond to both the physical microhabitat as well as the presence of conspecifics, where territories are clustered within a species' preferred microhabitat.

Our findings demonstrate that conspecific attraction and microhabitat preferences can promote spatial partitioning between interspecifically aggressive species. A previous study found that the higher the levels of heterospecific aggression in *Hetaerina* species, the greater the spatial segregation and species differences in microhabitat use (McEachin et al. 2021). Spatial segregation is a common outcome among interspecifically aggressive species (Robinson and Terborgh 1995, Grether et al. 2009, Jankowski et al. 2010, Eurich et al. 2018) and many studies have found that aggression itself can be the cause of spatial partitioning, for example, through competitive displacement (Reitz and Trumble 2002, Pasch et al. 2013, Edgehouse et al. 2014, Kajtoch et al. 2015, Martin and Bonier 2018). However, McEachin and Grether (2021) showed that competitive displacement does not occur in *Hetaerina* and, as a result, suggested microhabitat preferences diverged over time through agonistic character displacement. While species have diverged in microhabitat preferences, there is still some overlap between sympatric species (McEachin et al. 2021). As territory holders respond to species-specific microhabitat preferences, they become nonrandomly distributed across the stream, but not necessarily clustered. Conspecific attraction can act to cluster males within species-specific microhabitat and reduce the probabilities of encountering heterospecifics within areas of microhabitat overlap by responding to the presence of conspecifics and not just microhabitat features. Therefore, conspecific attraction and microhabitat preferences both contribute to the spatial partitioning between interspecifically aggressive species.

The acquiring of information from interactions with the physical environment is considered private or personal information, whereas public information is acquired by observing

other individuals (Valone 1989, Danchin et al. 2004). As *Hetaerina* territory holders exhibit both microhabitat preferences and conspecific attraction, it is likely they acquire both personal and public information before settling. For example, canopy cover has been shown to be a particularly important axis of microhabitat for *Hetaerina* territory holders (Anderson and Grether 2011, McEachin et al. 2021) and ectotherms generally (Shelly 1982, Huey 1991, Tsubaki et al. 2010, Okuyama et al. 2013). Males may be able to detect areas with suitable canopy cover due to the effects on thermoregulation. Stream current speed has also been found to be an important microhabitat feature for territory settlement (Anderson and Grether 2011, McEachin et al. 2021), and because males perch close to the surface of the water, they may be able to detect appropriate current speeds. However, Weichsel (1987) found that male *H. americana* are apparently unable to detect submerged vegetation, the substrate in which females oviposit, even though reproductive success is higher among territory holders with submerged vegetation nearby. This apparent contradiction can be better understood in the context of acquiring public information. Territory holders tend to be more perch attached (i.e., site faithful) if they are reproductively successful (Weichsel 1987). If males are more likely to observe territory holders with longer tenures, this may be a proximate explanation for conspecific attraction and the association between territories and microhabitat features such as submerged vegetation.

It is somewhat counterintuitive that territorial animals are more likely to settle in an area with conspecifics than without conspecifics because *Hetaerina* territory holders readily attack conspecific intruders. Consequently, conspecific attraction increases the probability of encountering a competitor and, thus, the frequency of intraspecific fights. However, there is likely some advantage to perching near a reproductively successful male. While this increases competition for mates, it may also increase the likelihood of encountering a female. Many

ultimate explanations have been proposed to explain the evolution of conspecific attraction in territory holders, such as reducing costs associated with search time (Stamps 2001). Search costs are varied, but include increased risk of mortality due to predation and expenditure of extra time and energy which takes away from opportunities to mate or defend a site (Lima and Dill 1990, Danielson 1992, Morris 1992, Lubin et al. 1993). For example, green and golden bell frogs reduce search time by selecting habitat based on the presence of conspecifics (Pizzatto et al. 2016), and Farrell et al. (2012) suggest conspecific cueing in wood warblers may be especially beneficial during the pre-settlement phase when environmental conditions are not consistent from one year to the next. Conspecific cueing occurs when conspecifics act as accurate signals of habitat quality (Stamps 2001, Donahue 2006). For example, a territorial species of grasshopper, *Ligurotettix coquilletti*, is more likely to settle on a bush with other males present than an empty bush, and conspecifics may act as indirect cues of habitat quality (Muller 1998). While habitat quality may refer to the quality of the bush itself, females are also attracted to bushes with several males, so the quality of the habitat may refer to factors related to reproductive success rather than some physical aspect of the environment. Similarly with *Hetaerina* damselflies, conspecific territory holders may indicate quality microhabitat in that they are near submerged vegetation (Weichsel 1987) and thus may be in locations likely to encounter females. According to the interception hypothesis (Bick and Bick 1965), males intercept females who are searching for oviposition sites (Weichsel 1987). Although tandem pairs rarely oviposit within the male's territory, settling near potential oviposition sites may increase encounter rates with females and decrease the distance flown to an oviposition site, and therefore increase a male's reproductive success. Conspecific cueing may increase a male's chance of settling in such sites.

Conspecific attraction may also increase the likelihood that, in the event of territory turnover, males will settle in the same part of a territory that was occupied by the previous territory holder. In fact, in many instances, we observed mature males perching in the exact location that a previous territory holder had perched (S.M. pers. obs. unpublished data). Most territories are approximately 2-4 m^2 and include many different available perches, so there is no reason to expect *a priori* that new territory holders utilize the exact same perch as previous territory holders. However, immature males may be able to acquire public or private information before actively defending a territory. Male *Hetaerina* reach reproductive maturity 6-14 days after emerging (Grether 1996a), during which time males have the opportunity to observe conspecifics. The red patch on male wings is a secondary sexual character that acts as a proximate signal of reproductive maturity (Grether 1996b), and immature males have small patches that are much lighter in color, eliciting little-to-no aggressive response from territory holders. Before attempting to settle in a new territory or takeover a preexisting territory, immature males may have the opportunity to "try out" various territories and perches (i.e., acquiring private information *sensu* Valone 1989, Danchin et al. 2004), thus gaining experience and information from the environment. This information may then be used to occupy a territory immediately after the eviction or death of the previous resident.

CONCLUSIONS

Microhabitat selection in *Hetaerina* territory holders appears to be driven by a combination of conspecific attraction and microhabitat preference. In almost all populations examined in our study, the clustering of territory holders exceeded (conspecific attraction) or matched (microhabitat preferences) that predicted by microhabitat heterogeneity. We developed a novel

method of testing for conspecific attraction, while controlling for microhabitat availability, by comparing observed populations to populations that were simulated using ENMs. Our findings improve our understanding of the mechanisms driving habitat selection by demonstrating conspecific attraction and microhabitat preferences both contribute to the spatial partitioning between interspecifically aggressive species.

Table 3.1 Categories of the degree of clustering of territories.

Category	Description and radii covered	Examples
None	No clustering observed.	Figure 3.1g-h; Figure S3.1
Low	Clustering observed over < 2 m of a range of radii.	Figure 3.1e-f; Figure S3.2
Moderate	Clustering observed between 2-10 m over a range of radii.	Figure 3.1c-d; Figure S3.3
High	Clustering observed over > 10 m over a range of radii.	Figure 3.1a-b; Figure S3.4

Table 3.2 The degree to which territories in observed populations and null distributions exhibit clustering. See Figure 3.1 and Figures S3.1 – S3.4 for visualizations of the degree of clustering.

	Number of populations
Total with AUC > 0.7	30
Observed populations with territory clustering	25
Low degree of clustering	5
Moderate degree of clustering	10
High degree of clustering	10
Null distributions with territory clustering	7
Low degree of clustering	0
Moderate degree of clustering	3
High degree of clustering	4
Observed populations with territories more clustered than null distributions	25
Low degree of clustering	10
Moderate degree of clustering	7
High degree of clustering	8

Figure 3.1 The spatial clustering of territories, as measured by the deviation of the observed L-statistic from the upper end of the confidence envelope (solid black line) and the 95% CI from null distributions (gray). We show representative examples of populations with (a-b) high, (c-d) medium, (e-f) low, and (g-h) no degree of clustering that exceeded that of the respective null distributions. From a – h, population numbers are: 3, 26, 12, 15, 1, 9, 40, and 27. See Table S3.1 for population numbers and Figures S3.1 – S3.4 for the remaining populations.
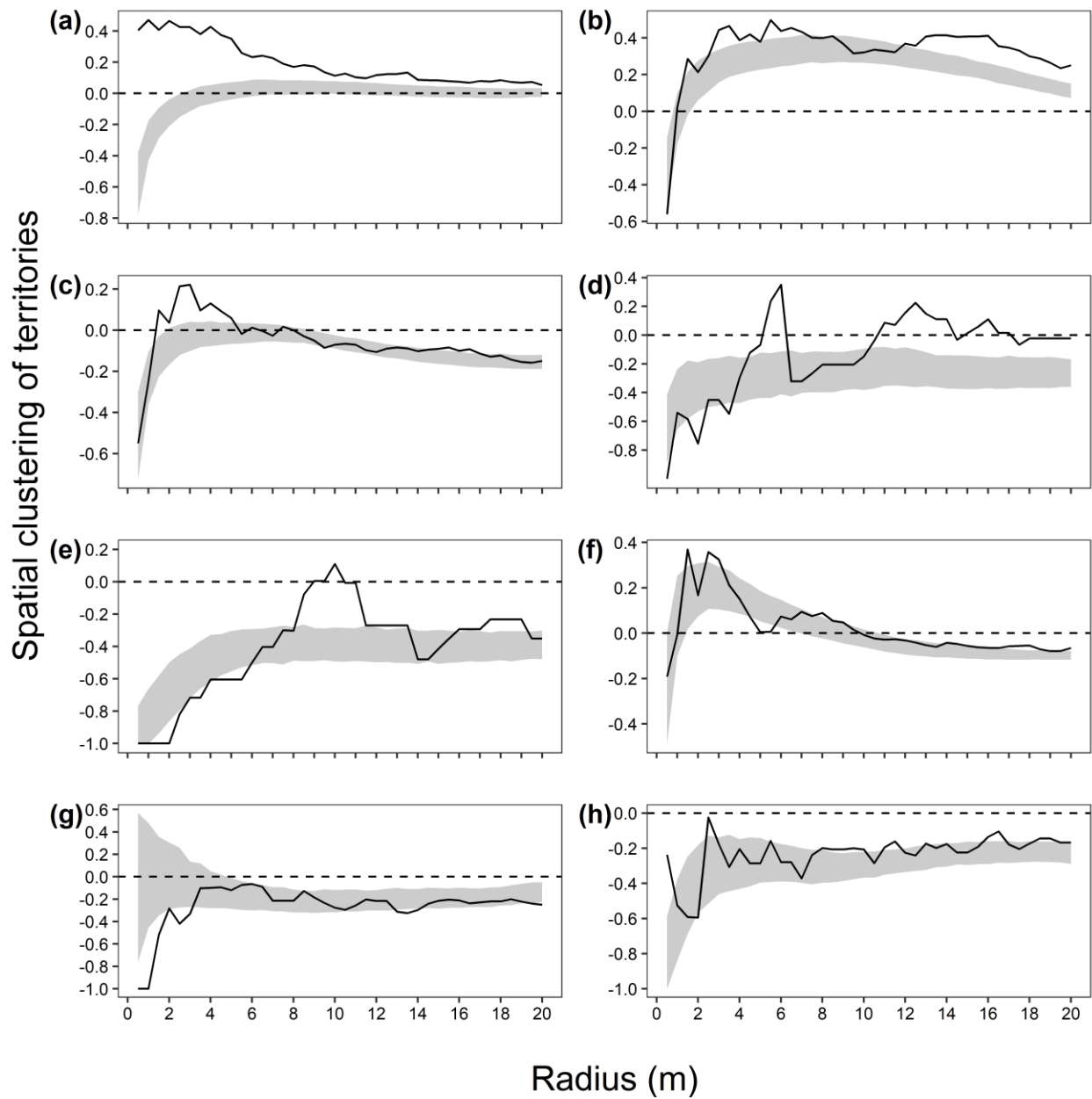
Chapter 3 Supplementary Materials

Table S3.1 A list of populations (n = 42) in this study.

Pop. no.	Study period	Site	Channel	Species
1	Jul-06	CT	s	*H. occisa*
2	Jul-06	CT	x	*H. occisa*
3	Jun-07	OT	2	*H. titia*
4	Jun-07	OT	2	*H. occisa*
5	Jul-07	PA	x	*H. occisa*
6	Apr – May 2008	AR	x	*H. titia*
7	Apr – May 2008	AR	x	*H. americana*
8	Apr-08	CV	x	*H. titia*
9	Apr-08	CV	x	*H. americana*
10	Aug-08	CV-L	x	*H. americana*
11	Aug-08	CV-L	x	*H. titia*
12	Aug-10	PX	x	*H. cruentata*
13	Aug-10	PX	x	*H. vulnerata*
14	Jul-12	BC	1	*H. americana*
15	Jul-12	BC	2	*H. vulnerata*
16	Jul-12	BC	2	*H. americana*
17	Jul-12	BC	3	*H. americana*
18	Jul-12	BC	3	*H. vulnerata*
19	Apr-12	PA1	n	*H. titia*
20	Apr-12	PA1	n	*H. occisa*
21	Apr-12	PA1	s	*H. occisa*
22	Apr-12	PA1	s	*H. titia*
23	Apr-12	PA1	u	*H. titia*
24	Apr-12	PA1	u	*H. occisa*
25	Apr-13	ES	x	*H. sempronia*
26	Apr-13	ES	x	*H. occisa*
27	Aug-15	RT	u	*H. occisa*
28	Aug-15	RT	x	*H. occisa*
29	Aug-15	RT	x	*H. capitalis*
30	Jul-16	GO	x	*H. occisa*
31	Jul-16	GO	x	*H. fuscoguttata*
32	Jun-16	LH	x	*H. occisa*
33	Mar – Apr 2016	RS	x	*H. cruentata*

34	Mar – Apr 2016	RS	x	*H. capitalis*
35	Aug-15	RT	x	*H. occisa*
36	Aug-15	RT	x	*H. capitalis*
37	Jul-16	GO	x	*H. fuscoguttata*
38	Jul-16	GO	x	*H. occisa*
39	Jun-16	LH	n	*H. occisa*
40	Jun-16	LH	u	*H. miniata*
41	Apr - May 2017	RB	x	*H. titia*
42	Apr - May 2017	RB	x	*H. miniata*

Table S3.2 The degree of territory clustering in observed populations and null distributions.

AUC is the area under the curve of the receiver operating characteristic from Maxent models.

We only included populations with AUC > 0.7 when comparing observed populations to null

distributions. See Table S3.1 for population numbers.

	Degree of clustering			
Pop. no.	Null distributions	Observed populations	Observed > null	AUC
1	None	Low	Low	0.99998
2	None	None	None	0.72629
3	None	High	High	0.77915
4	None	High	None	0.64269
5	High	Moderate	None	0.58931
6	High	High	None	0.73111
7	None	None	None	0.67226
8	None	Low	Low	0.73696
9	Moderate	Moderate	Low	0.75806
10	None	Moderate	Low	0.75338
11	None	Moderate	None	0.87231
12	None	Moderate	Moderate	0.75295
13	None	None	None	0.67286
14	High	None	None	0.67593
15	None	Moderate	Moderate	0.85658
16	None	Moderate	None	0.68594
17	None	High	Moderate	0.75458
18	None	None	None	0.75792
19	None	Low	None	0.66973
20	High	Moderate	None	0.71579
21	None	Moderate	Moderate	0.71421
22	None	Moderate	None	0.61924
23	None	Moderate	Moderate	0.73478
24	None	Moderate	None	0.62002
25	None	Low	Low	0.8309
26	High	High	High	0.70998
27	None	None	None	0.8128
28	None	Low	Low	0.82377
29	High	Low	None	0.60836
30	None	Moderate	Moderate	0.8467

31	None	None	None	0.82219
32	None	High	None	0.64305
33	High	High	High	0.85513
34	None	Moderate	Moderate	0.76043
35	Moderate	High	High	0.74504
36	None	Moderate	None	0.6141
37	None	High	High	0.70914
38	None	High	High	0.83028
39	None	Low	Low	0.70603
40	None	None	None	0.82515
41	Moderate	High	High	0.7027
42	None	High	High	0.71841

Figure S3.1 The deviation of the observed L-statistic from the upper end of the simulation envelope (solid black line) and the 95% CI of the null distribution (gray). Populations (a) 2, (b) 18, and (c) 31 showed no degree of clustering that exceeded that of the null distribution. See Table S3.1 for population numbers.
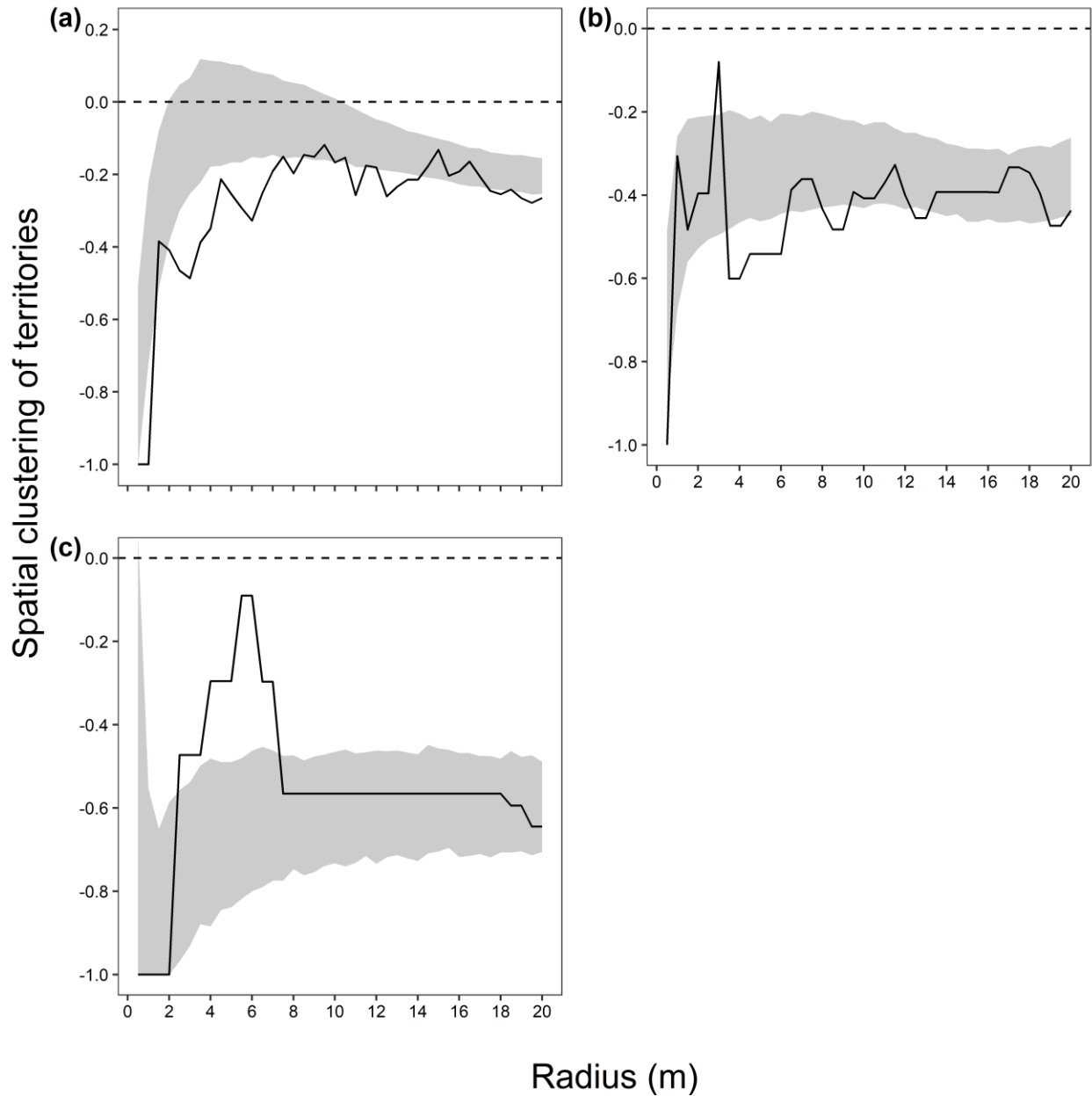
Figure S3.2 The deviation of the observed L-statistic from the upper end of the simulation envelope (solid black line) and the 95% CI of the null distribution (gray). Populations (a) 6, (b) 8, (c) 10, (d) 11, (e) 20, (f) 25, (g) 28, and (h) 39 showed a low degree of clustering that exceeded that of the null distribution. See Table S3.1 for population numbers.
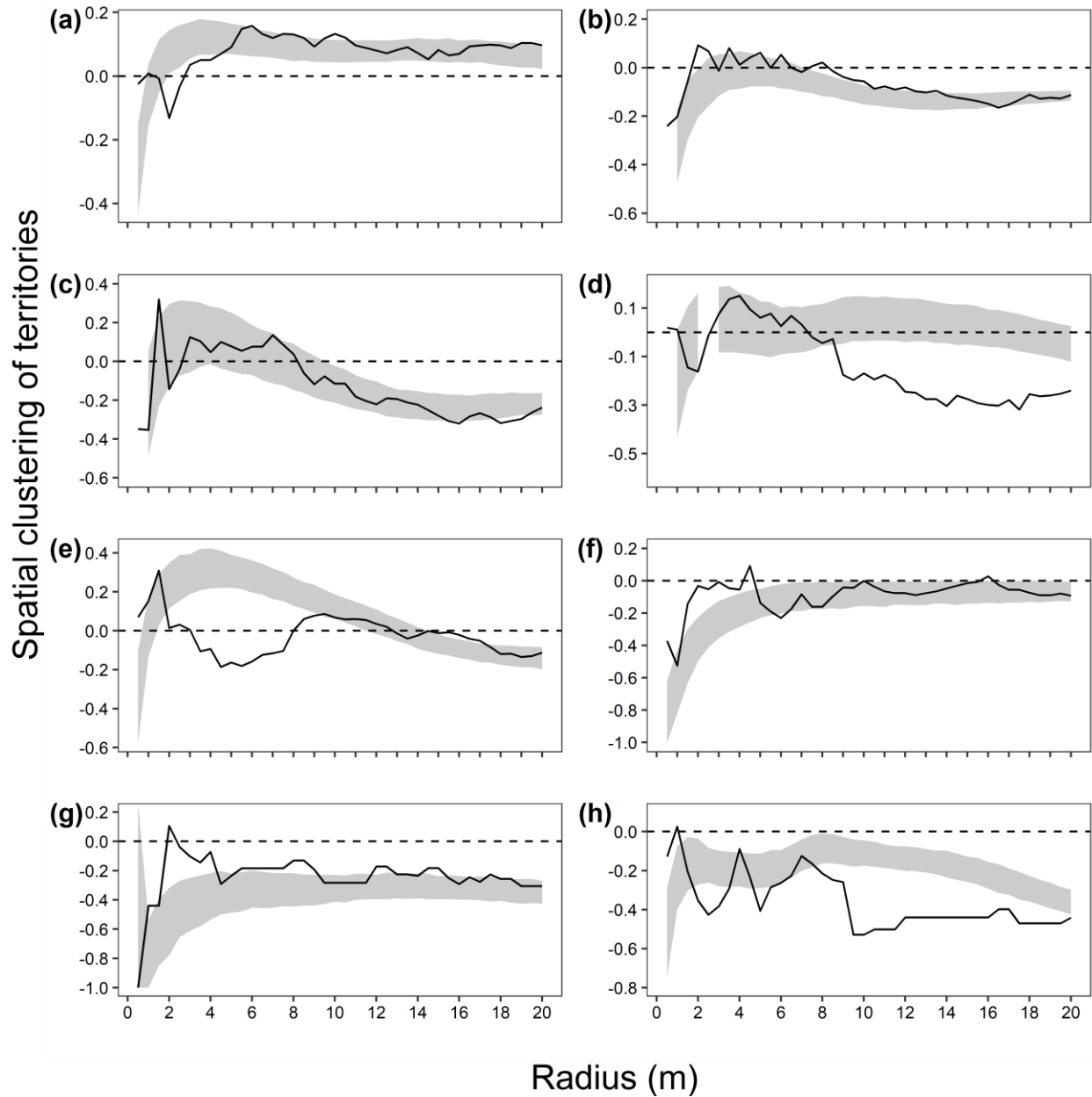
Figure S3.3 The deviation of the observed L-statistic from the upper end of the simulation envelope (solid black line) and the 95% CI of the null distribution (gray). Populations (a) 17, (b) 21, (c) 23, (d) 30, and (e) 34 showed a moderate degree of clustering that exceeded that of the null distribution. See Table S3.1 for population numbers.
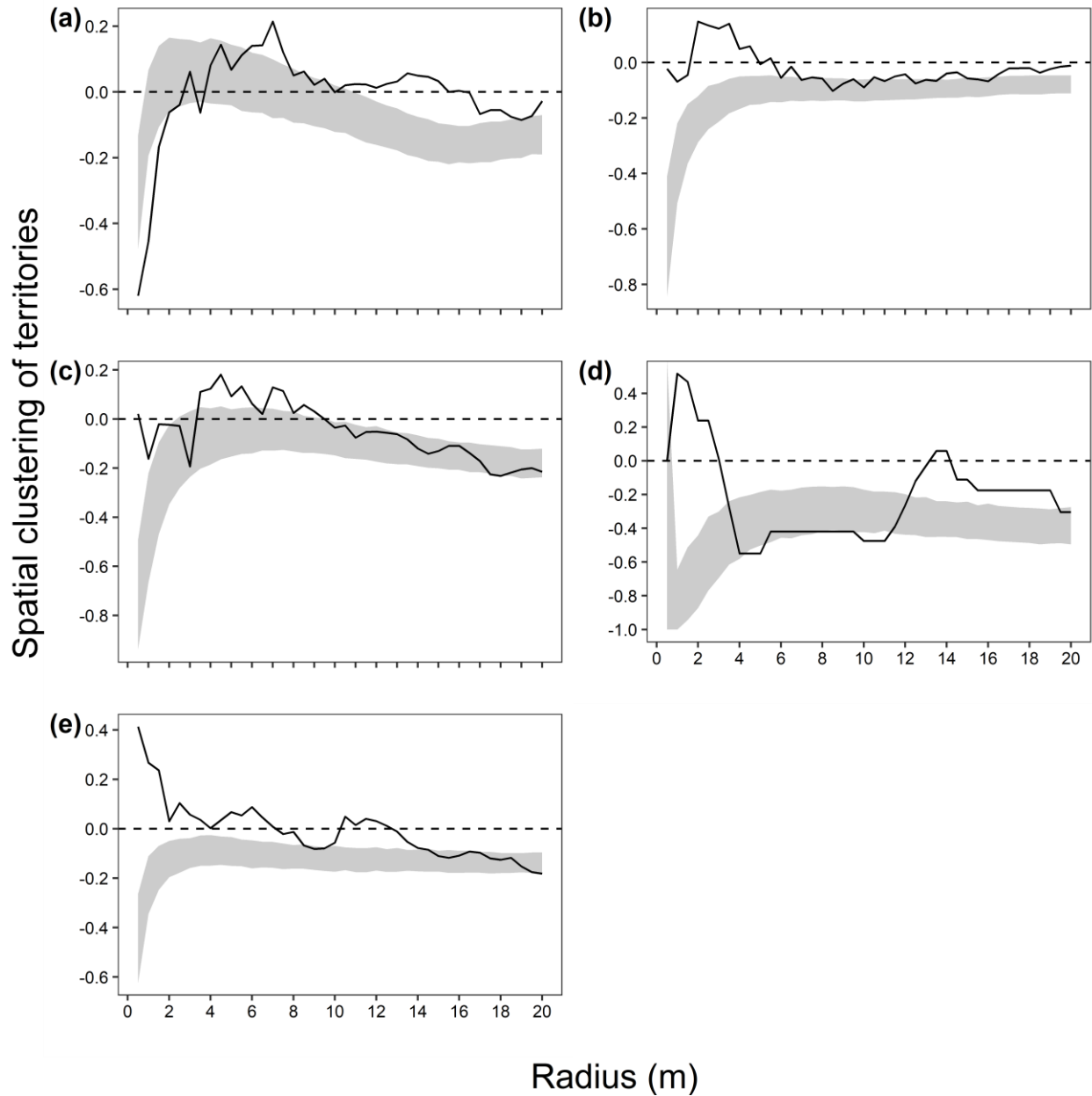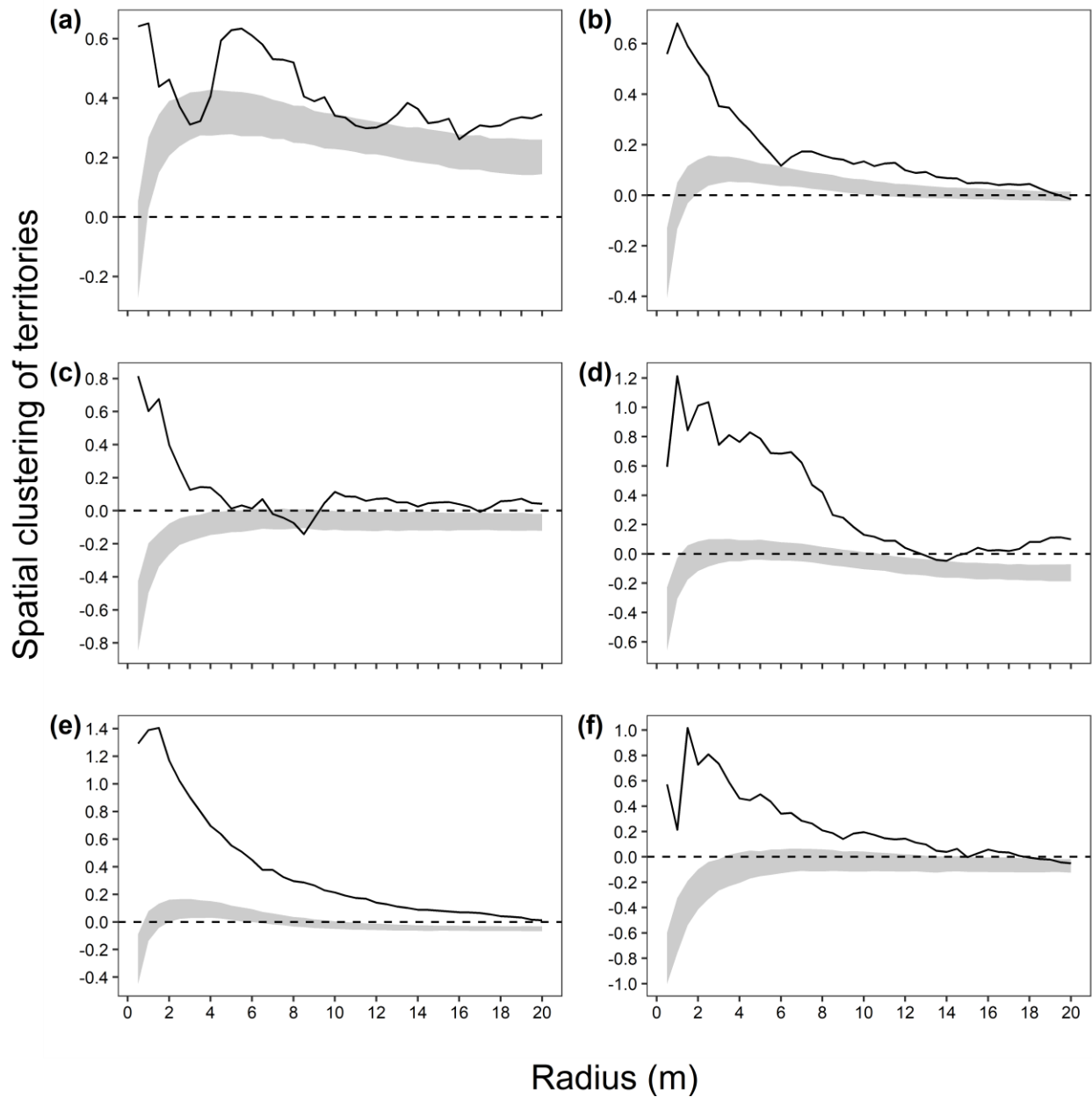
Figure S3.4 The deviation of the observed L-statistic from the upper end of the simulation envelope (solid black line) and the 95% CI of the null distribution (gray). Populations (a) 33, (b) 35, (c) 37, (d) 38, (e) 41, and (f) 42 showed a high degree of clustering that exceeded that of the null distribution. See Table S3.1 for population numbers.

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