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Original Article

Mechanisms of reduced interspecific interference between territorial species

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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.

Key words: **agonistic character displacement, habitat partitioning, habitat preference, microhabitat, interference competition, interspecific territoriality, Odonata**

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

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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 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 and 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 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 (Supplementary Table S1).

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 (Supplementary Figure S1), and released where they were captured. Each day, two to five 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 7483 males and made 34,614 observations. A male was considered a territory holder if he was observed in the same location (± 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 ≤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 ≥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 $2d_id_i$ where d_i and d_i 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 the following: 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 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; Supplementary Table S2).

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 (Supplementary Table S3).

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); LDA was implemented with the LDA default in R package MASS 7.3–53.1 (Venables and Ripley 2002).

Table 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

RESULTS

Species differences in microhabitat use

The first three principal components (PCs) accounted for 83.4% of the variance in microhabitat use (Table 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; Supplementary Figure S2). 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

Table 2

Results of LDA and multivariate regression analyses (MVA) of species differences in microhabitat use

		LDA species classif.			LDA coefficients (standardized)				MVA
Pop. pair	Spp. code	# correct	# wrong	% correct	Perch height	Stream width	Current speed	Canopy cover	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 Supplementary Table S1 for site info and species names.
$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Table 3

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

		Observed freq.		Expected freq.		
Pop. pair	Spp.	Intrasp. fights	Intersp. fights	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 for site info.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$ after sequential Bonferroni correction.

Table 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 $R^2 = 0.54$, $F(3, 21) = 10.4$, $P < 0.001$.

positive loading for stream width and a negative loading for current speed (Table 1; Supplementary Figure S2). 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 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 2). As shown by the species means and LDA coefficients, all four microhabitat variables proved useful for differentiating between sympatric species (Tables 2; Supplementary Table S3).

Interspecific fighting

Across the 25 pairs of sympatric populations, we collected data on 1974 territory holders and 1793 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 3). There was considerable variation in this relationship across species, as reflected by the wide range of chi-square values (Table 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 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 1a), while in others the reduction was explained by species discrimination (Figure 1b) or both spatial segregation and species discrimination (Figure 1c). Yet there were some sympatric populations for which these factors could not fully explain the reduction in observed interspecific fights (Figure 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 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 three-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

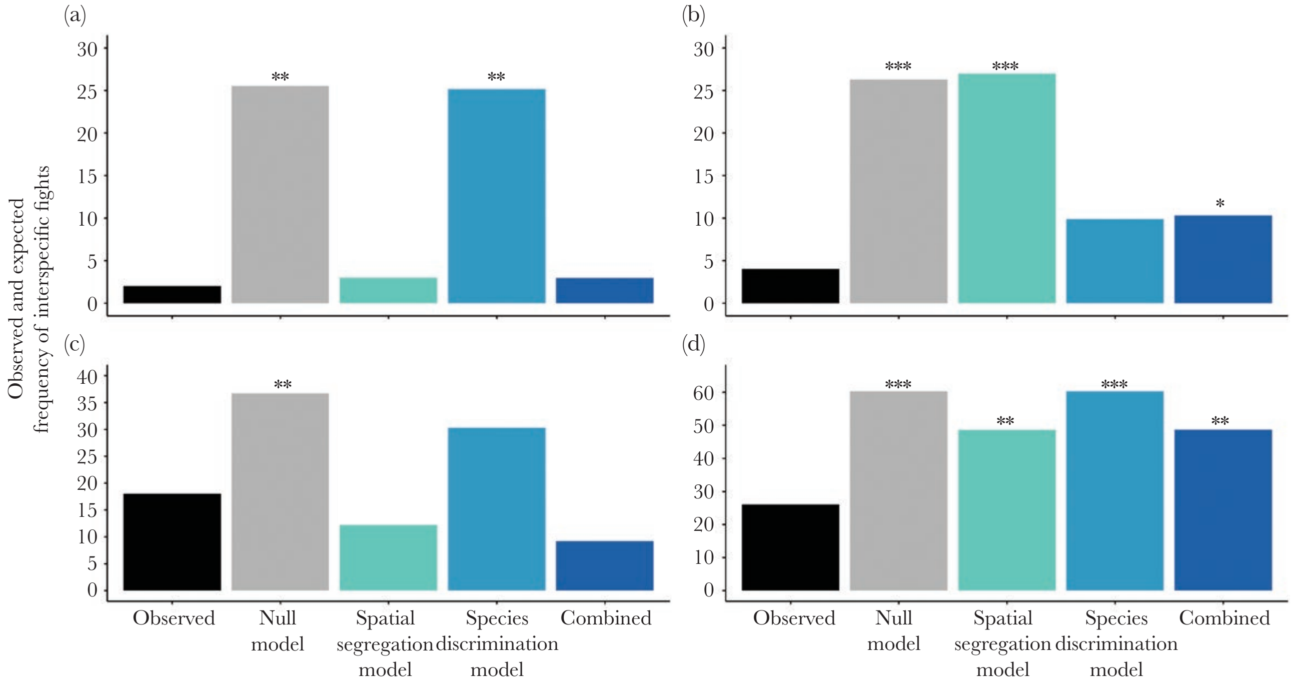

Figure 1

Observed and expected numbers of interspecific fights, based on different methods of calculating the expectation, for selected sympatric population pairs (see Supplementary Figure 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 LS 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 GO 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 SL 2016). Combined refers to the model that calculates expected fighting rates based on both spatial segregation and competitor recognition. See Table 3 for statistical results comparing all 25 sympatric population pairs.

Table 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. Mean	SE	V	P
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

was greater between sympatric populations with low and high HA compared to those with intermediate HA (Figure 2; speciesXHA: −0.68 ± 0.14, $z = -4.91$, $P < 0.0001$; speciesXHA^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 2; stream width, speciesXHA: −4.64 ± 1.88, $z = -2.47$, $P = 0.013$; speciesXHA^2: 5.95 ± 1.45, $z = 4.11$, $P < 0.0001$; current speed, speciesXHA: 0.16 ± 0.074, $z = 2.20$, $P = 0.028$; canopy cover, speciesXHA: 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 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 ± 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 (Supplementary Table S4).

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 2) and are more spatially segregated (Figure 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 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

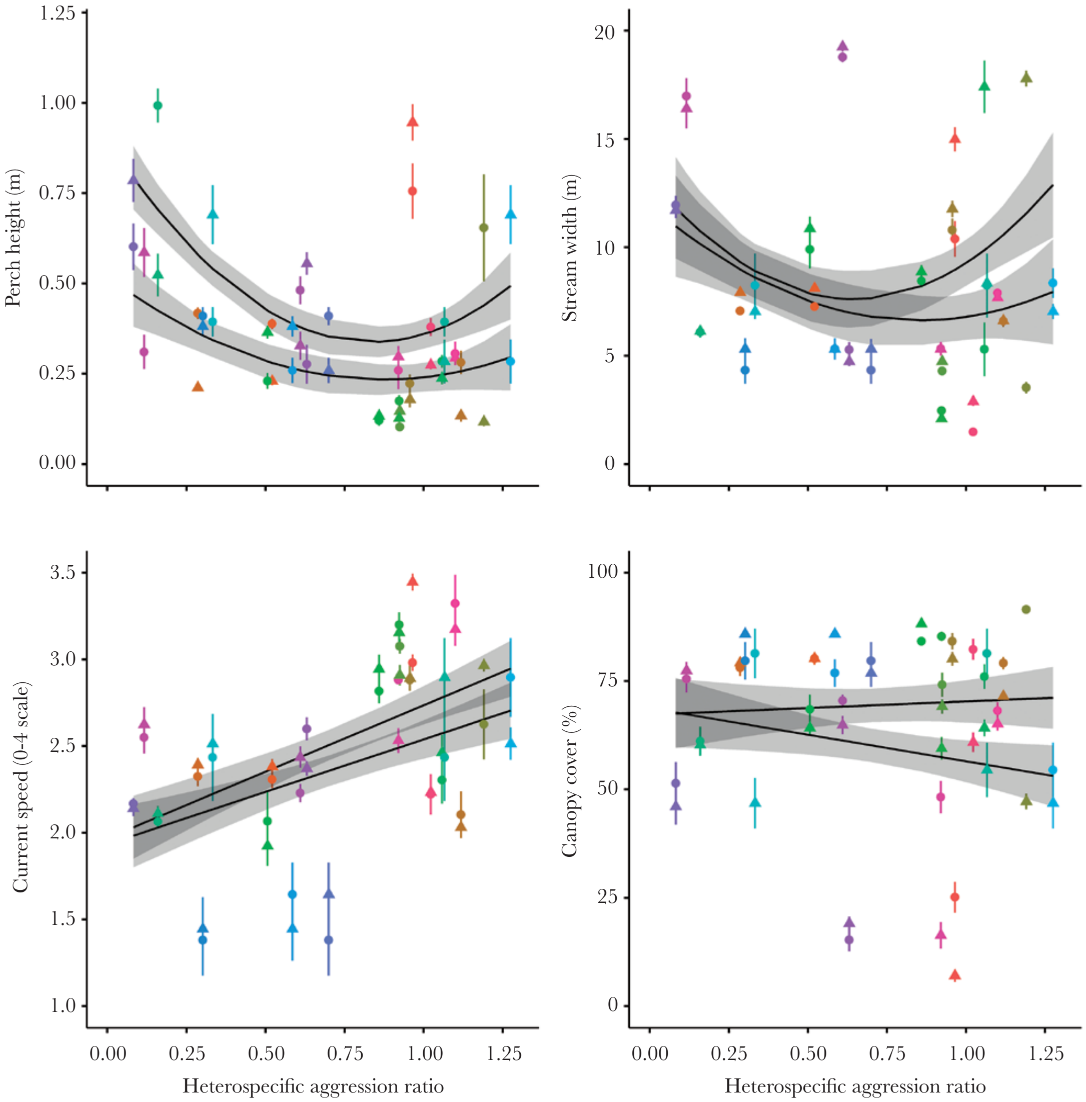

Figure 2

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**.

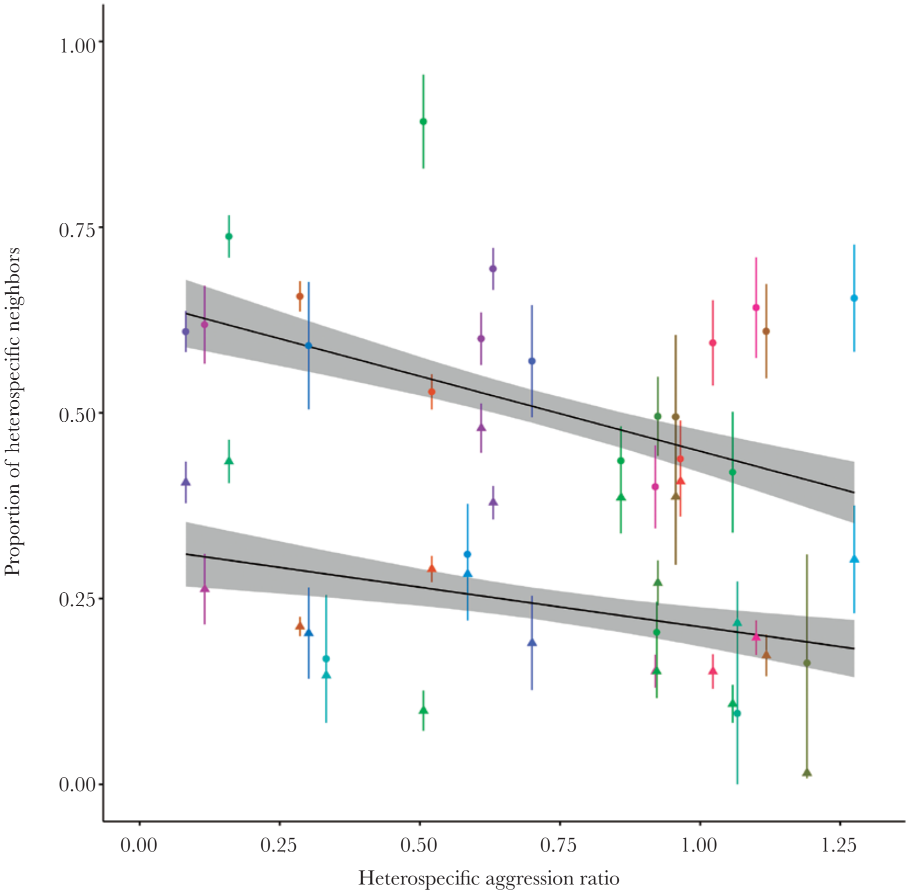

Figure 3

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 2.

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, b; 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 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 2). Considering that species with low levels of heterospecific aggression have overlapping territories (Anderson and 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 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 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 5). However, the observed number of interspecific fights was still significantly below the expected number in many populations (Figure 1, Supplementary Figure S3). Species differences in microhabitat use, which were found in all but two sympatric population pairs (Table 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, personal observation), 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.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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