

Pursuit of Heterospecific Targets by Territorial Amberwing Dragonflies (*Perithemis tenera* Say): A Case of Mistaken Identity

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*Although they are defending mating territories, territory residents of a wide variety of insect species have been observed to pursue heterospecifics in addition to the conspecifics that intrude on their territories. One species that has such heterospecific pursuits is the Eastern amberwing dragonfly (*Perithemis tenera* Say) (Anisoptera: Libellulidae). In this study, we tested five alternative hypotheses for the function of heterospecific pursuits in amberwings: competition for resources, prevention of interference while mating, predator deterrence, foraging, and mistaken identity. Resident males pursued both male and female conspecifics, as well as a species of horse fly (*Tabanus* spp.) and butterfly (*Ancyloxypha numitor*). Other intruding odonates, including *Epitheca princeps*, *Erythemis simplicicollis*, *Libellula luctuosa*, *Pachydiplax longipennis*, and *Plathemis lydia*, were relatively ignored. Because the horse fly and butterfly were similar to amberwings in body size, color, and flight height, and because they are not predators or prey of amberwings, we concluded that the pursuit of these heterospecifics was due to mistaken identity. The characteristics of the horsefly and butterfly likely correspond to the cues that the male amberwings use to identify conspecifics, and the relative rarity of intrusions by these two species (as well as by female amberwings) probably made it more costly to discriminate and pursue only conspecifics than to make some mistaken pursuits.*

KEY WORDS: Odonata; dragonfly; territory defense; species recognition; mating behavior; vision.

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INTRODUCTION

Males of many species of insects defend territories associated with mating, and quite often, vision is used to detect both potential mates and intruding males (reviews by Wehner, 1981; Fitzpatrick and Wellington, 1983; Thornhill and Alcock, 1983; Land, 1997). During their tenure, resident males approach conspecific males and females that they detect. These approach flights have the function of defending the territory from competitors and obtaining matings and, thus, play a crucial role in an individual's reproductive success (Thornhill and Alcock, 1983; Fitzpatrick and Wellington, 1983).

However, even though males are defending mating territories, many territorial species have been observed to pursue "targets" other than conspecifics, including other insect species, noninsect animals, and even inanimate objects (reviewed by Fitzpatrick and Wellington, 1983). For example, males of *Asterocampa leilia*, a territorial butterfly, are known to chase not only heterospecific butterflies, but also bees, flies, wasps, and birds (Rutowski and Gilchrist, 1988). Likewise, male *Protoxaea gloriosa* (Hymenoptera) pursue larger butterflies and birds but ignore small bees and wasps (Hurd and Linsley, 1976). Heterospecific pursuits are sometimes very aggressive (Fitzpatrick and Wellington, 1983). For instance, Severinghaus *et al.* (1981) observed territorial male wool-carder bees (*Anthidium manicatum*) striking and biting intruding heterospecifics (e.g., other bee species), and these heterospecifics were commonly injured from the attacks. As with pursuits of conspecifics, these approaches toward heterospecifics may be costly for the territorial male in terms of energy, injury, and lost opportunities for mating or defense (Bitzer and Shaw, 1979; Singer, 1989; Brown and Alcock, 1990; Switzer and Eason, 2000), which adds to the mystery of why the pursuits occur.

Although observations of heterospecific pursuits are common, rarely have studies tested alternative hypotheses for their function. Instead, many studies either simply mention the pursuits anecdotally, treat them as mistakes, or assume that they serve a competitive function (e.g., Moore, 1964; Bitzer and Shaw, 1979, 1983; Maier and Waldbauer, 1979; Severinghaus *et al.*, 1981; Frantsevich and Mokrushov, 1984; Lin, 1961; Alcock and Alcock, 1983; Alcock, 1985; Alcock and Gwynne, 1988; Rutowski and Gilchrist, 1988; Pezalla, 1979; Pinheiro, 1990; Ravenscroft, 1994; Dreisig, 1995; Jones *et al.*, 1998; Wcislo, 1999). For instance, Pezalla (1979) concluded that *Libellula pulchella*, a territorial dragonfly, pursued heterospecifics because of competition for perches and space. This "competition hypothesis" is commonly invoked to explain heterospecific pursuits for noninsect taxa and for other types of territories (e.g., Gaudreault and Fitzgerald, 1985; Adams, 1994; Dearborn, 1998; Genner *et al.*, 1999). However, we have identified at least five functional

Table I. Summary of Alternative Hypotheses for Why Territorial Males May Pursue Heterospecific Targets and Their Predictions

Hypothesis	Function of pursuit	Predicted targets and observations
Competition	Attempting to exclude heterospecific competitors from territory	Species that share resources with the focal species; targets may or may not be contacted
Interference	Keeping heterospecifics from disturbing mating activities	Species that attempt to mate mistakenly with focal species' females (Singer, 1989); targets may or may not be contacted
Foraging	Attempting to catch prey	Species that are prey items; targets are occasionally contacted (and eaten) and the same pursuit behaviors are used as when foraging off territory
Mistaken identity	Attempting to mate with or defend territory from conspecifics	Target species similar in appearance to conspecifics (Corbet, 1999); targets are usually not contacted
Predator defense	Attempting to dissuade potential predators from remaining in area	Targets potential predators of adults, eggs, or young; targets may or may not be contacted (e.g., Curio, 1978)

hypotheses that exist for why residents of mating territories might pursue heterospecific targets: competition, mating interference, foraging, predator defense, and mistaken identity (Table I). An inspection of Table I reveals that, in general, these five hypotheses can be tested by identifying the type of targets that are pursued and nothing whether physical contact with the target occurs. In this study, we test these five hypotheses for the pursuit of heterospecific targets by the Eastern amberwing dragonfly (*Perithemis tenera*).

The amberwing dragonfly is a territorial species that defends small territories around oviposition sites on still or slow moving water (Jacobs, 1955; Switzer, 1997a,b). Territorial males perch within their territories and actively pursue male and female conspecifics that pass near their perch (Jacobs, 1955; Switzer and Walters, 1999; Switzer and Eason, 2000; Switzer and Schultz, 2000). Males remain reproductively active for approximately 1 week on average (Switzer, 1997a). Like many other odonates, territorial male amberwings also pursue heterospecifics occasionally (Moore, 1952, 1964; Pajunen, 1964; Nakamuta *et al.*, 1983; Miller and Miller, 1985; Moore, 1987; Singer, 1989; Gribbin and Thompson, 1991; Pezalla, 1979; Fraser and Herman, 1993; Switzer and Walters, 1999; for additional references see Corbet, 1999).

Previous studies on heterospecific pursuit in insects typically focused on species within closely related taxa. For instance, Singer (1989) investigated

aggression among three species of *Leucorrhinia* dragonflies, and Brown and Alcock (1990) and Jones *et al.* (1998) examined interspecific interactions between sympatric butterfly species of the genera *Vanessa* and *Pararge*, respectively. For our study, we were interested in a broader examination of all naturally occurring pursuits by territorial males. By taking this broad approach, we were able to test the above hypotheses and, at the same time, gain insight on the proximate mechanisms used for the detection of conspecifics by male amberwings.

METHODS

This study was carried out at a small pond (approximately 175 m in circumference) in Coles County, Illinois, during July and August 1999 [see Switzer and Eason (2000) for a description of the study site]. Dowel rods 5 mm in diameter were placed 0.75 m out from shore and 1 m apart for use as perches and to facilitate the measurement of distances. All male amberwings in this study used these dowels as perches from which they flew out after approaching insects. Male amberwings were captured and marked with an alphanumeric code on their right forewing; this procedure allowed them to be identified without recapture by using binoculars.

We conducted preliminary observations to narrow the list of relevant, potential target species (i.e., species resident males approached at least occasionally). Thus, commonly intruding insects that were not pursued (e.g., coenagrionid damselflies) were not included as possibilities, nor were species pursued commonly at ponds other than our study site [e.g., *Polistes* wasps (personal observations)]. As a result of these observations, we included the following six odonate species and two nonodonate species as potential targets. Potential odonate targets [common names follow Dunkle (1989)] included amberwings, widow (*Libellula luctuosa*), pondhawk (*Erythemis simplicicollis*), pirate (*Pachydiplax longipennis*), whitetail (*Plathemis lydia*), and the prince baskettail (*Epithea princeps*); nonodonate targets included a horse fly (*Tabanus* spp.) and a butterfly (*Ancyloxypha numitor*). Both sexes of amberwings were potential targets; however, only males of the other odonates were potential targets (females of these species were rare and did not elicit a response) and sex was not distinguished for the nonodonate species. Hereafter we refer to the butterfly and horse fly species as simply “butterfly” and “horse fly” to help distinguish them from the odonate species.

We conducted two types of focal observation studies to investigate heterospecific approaches; each focal on an individual lasted 10 min. For “intrusion focals,” we recorded all relevant flying insects that flew within a 2-m radius of where the focal male was perched. This radius corresponds roughly to their average detection distances at different angles of intruder approaches

and against different backgrounds (Switzer and Eason, 2000). This intrusion area included all of the area over the water and 0.25 m onto shore. When a potential target insect intruded, the identity of the target and the response of the male were recorded. The recorded response was binary: either the male flew toward the intruder or it did not.

“Approach focals” focused on the targets the male approached, regardless of how far the target was from the male (i.e., they could be beyond 2 m). For each target species the male pursued we recorded the identity of the target, the distance between the male and the target when the male began his approach (“starting distance”), and the closest distance between the male and the target during the approach (“approach distance”). Distances over 0.5 m were recorded to the nearest 0.5 m; distances less than 0.5 m were recorded to the nearest 0.25 m (i.e., 0 and 0.25 m).

We also determined the predominant flight height of each target species. To minimize pseudoreplication on the target species (which were not individually marked), we recorded flight heights every other day. At every other 10-m stretch of shoreline, we recorded the height above the water of the first individual of a particular target species that we observed.

We calculated the body size of the target species relative to male amberwings. For the odonates, we used the midpoint of the range of body length given by Needham and Westfall (1954). These values were found to be similar to the sizes of five individuals of each species that were captured locally. For the size of the horse fly and butterfly, we used the mean body length of five individuals captured at the study pond. Using wing length instead of body length yielded similar results.

All observations were taken between 1100 and 1730 h during times when males were present and active at the pond. Because amberwing behavior may be sensitive to weather conditions (Jacobs, 1955), we recorded ambient temperature and cloud cover hourly on days on which we were collecting behavioral data. We did not take data on cloudy days when the temperature was below 25°C to eliminate periods during which amberwing activity levels could have been reduced (Jacobs, 1955).

We present means \pm SE. Nonparametric statistics take ties into account when appropriate.

RESULTS

Intrusion Focals

The 50 focal males experienced a total of 4027 intrusions within 2 m of their perch by the relevant target species. Of these, most of the intrusions

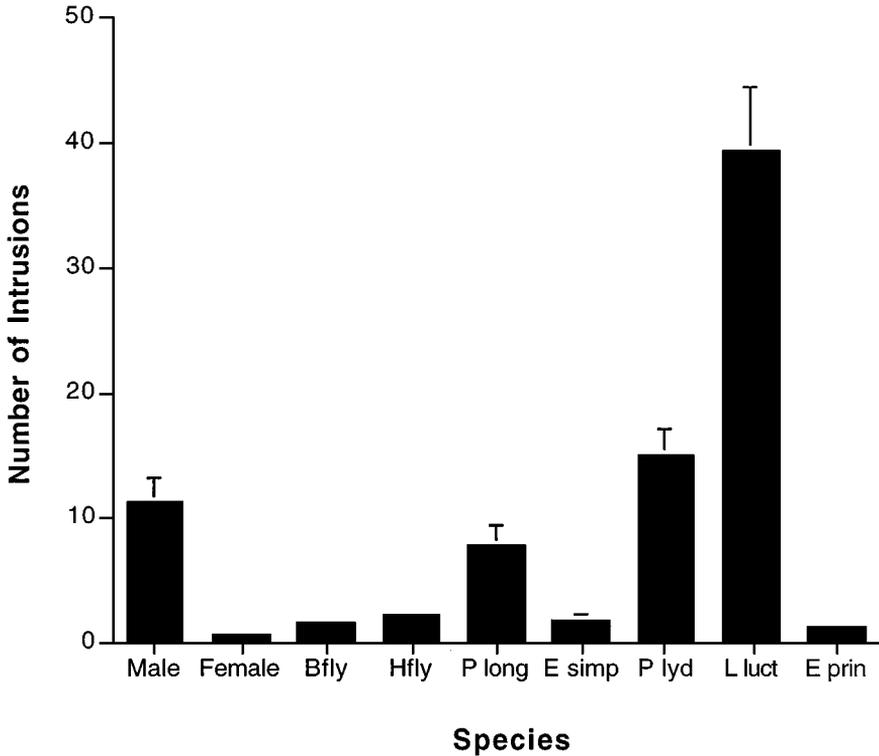


Fig. 1. Mean number of intrusions (\pm SE) per focal of target species; some SE are too small to be noticeable, given the scale of the figure. Male, male amberwing; female, female amberwing; Bfly, butterfly (*Ancyloxypha numitor*); Hfly, horse fly (*Tabanus* sp.); P long, *Pachydiplax longipennis*; E simp, *Erythemis simplicicollis*; P lyd, *Platthemis lydia*; L luct, *Libellula luctuosa*; E prin, *Epiheca princeps*. Sample size equals 50 focals for each target species except for horse flies ($N = 27$).

were by *L. luctuosa* and *P. lydia*, with fewer intrusions by others (Fig. 1). The proportion of intruding individuals that males responded to also significantly differed among species, with residents responding to conspecifics as well as to the horse fly and butterfly (Fig. 2) (Kruskal–Wallis, $H = 205.4$, $df = 8$, $P < 0.0001$). This difference among species remained when male and female amberwings were excluded from the analysis ($H = 49.4$, $df = 6$, $P < 0.0001$). To investigate whether the pattern in responses remained when examining the responses of individual males (and thus controlling for potential differences among males), we compared a male's response proportion to butterflies or horse flies to the maximum response that male had to any heterospecific odonate. A significant tendency existed for individual males to respond more to butterflies and horse flies than to the other heterospecific

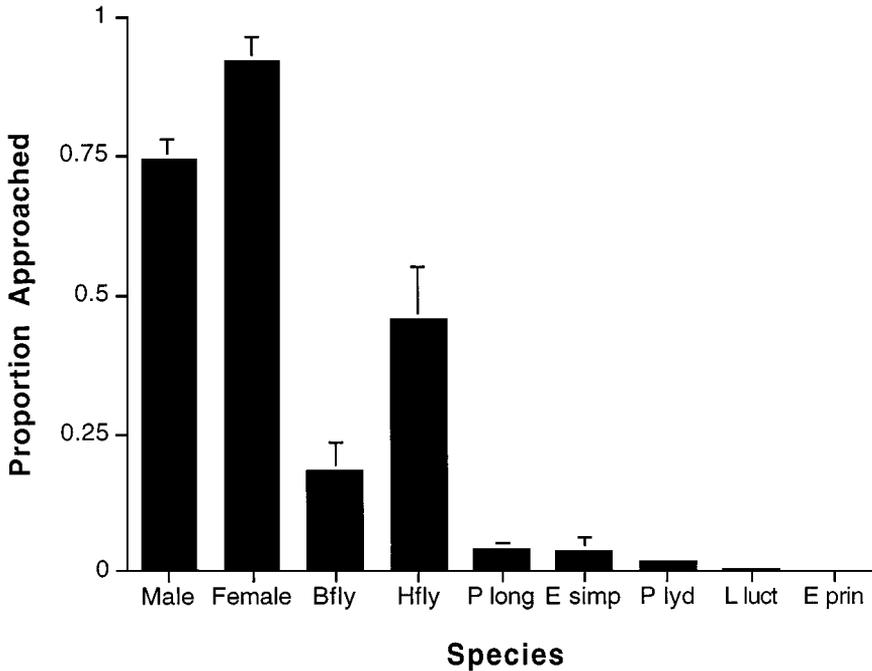


Fig. 2. Mean proportion (\pm SE) of intruding targets that were approached; some SE are too small to be noticeable, given the scale of the figure. Proportions of individual focals were averaged across males. Sample sizes (i.e., number of focal males): male (48), female (28), butterfly (31), horse fly (21), *Pachydiplax longipennis* (37), *Erythemis simplicicollis* (19), *Platthemis lydia* (44), *Libellula luctuosa* (49), and *Epiheca princeps* (22). Abbreviations are the same as for Fig. 1.

targets (Wilcoxon test: butterflies, $N = 18$, $T = 39$, $P = 0.043$; horse flies, $N = 18$, $T = 15$, $P = 0.002$).

We correlated the number of intrusions by a species to the proportion of these intrusions that elicited a response to examine whether those species with very high intrusion rates were responded to less frequently. A negative relationship between intrusion frequency and response did exist, but the correlation was not significant (Kendall's τ : with amberwings included in the analyses, $N = 9$, $\tau = -0.22$, $P = 0.40$; without amberwings, $N = 7$, $\tau = -0.14$, $P = 0.65$).

Approach Focals

The characteristics of how male amberwings responded varied among target species (Fig. 3). Not surprisingly, males responded when the target species was at a greater distance when the target was a conspecific (analysis

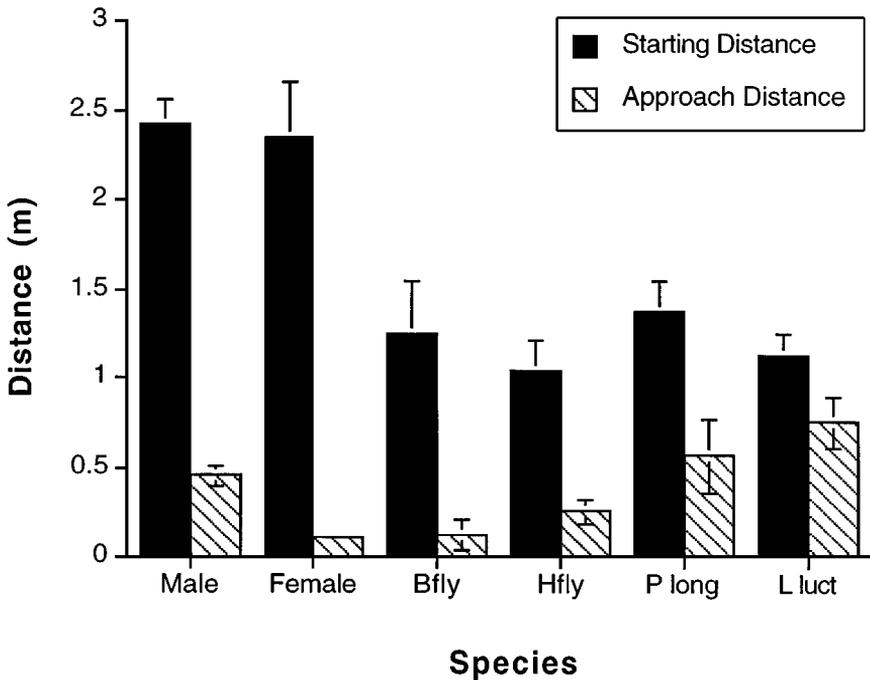


Fig. 3. Mean distances (\pm SE) at which the territorial male started to approach one of the target species and the distance of their closest approach; some SE are too small to be noticeable, given the scale of the figure. Multiple observations of the same target were averaged for each focal male. Sample sizes (i.e., number of focal males): males (47), females (26), butterflies (8), horse fly (9), *Pachydiplax longipennis* (8), and *Libellula luctuosa* (4). *Plathemis lydia*, *Erythemis simplicicollis*, and *Epitheca princeps* were not included because fewer than four focal males approached those species.

limited to those target species with at least four focal males responding; Kruskal–Wallis, $H = 27.4$, $df = 5$, $P < 0.0001$). In addition, they also varied in how closely they approached a target, with female amberwings, butterflies, and horse flies all being approached more closely on average than male amberwings (Fig. 3) ($H = 33.4$, $df = 5$, $P < 0.0001$). No target species besides female amberwings were ever contacted and no individuals of any target species were eaten.

Other Characteristics

Similarities between the physical and the behavioral characteristics of amberwings and those of the commonly pursued heterospecifics would

Table II. Summary of Characteristics of Conspecific and Heterospecific Targets Approached by Territorial Male Amberwings (Listed by Response Rank)^a

Species	Response rank	Intrusion rank	Color	Flight height	Relative size
Female amberwing	1	9	Brown	Same	1
Male amberwing	2	3	Orange/brown	Same	1
Horse fly	3	8	Brown	Same	0.96
Butterfly	4	6	Orange	Same	0.55
<i>Pachydiplax longipennis</i>	5	4	Blue	Higher	1.7
<i>Plathemis lydia</i>	6	2	White/black	Same	2.1
<i>Libellula luctuosa</i>	7	1	White/black/blue	Higher	2.1
<i>Erythemis simplicicollis</i>	8	5	Blue	Same	1.9
<i>Epithea princeps</i>	9	7	Brown	Higher	2.9

^aResponse rank and intrusion rank are based on pooled data from the territory intrusion focals; a ranking of 1 denotes the species that elicited the most responses or intruded the most frequently. Color includes the predominant color (of body and/or wings) as it appears to human observers. Flight height is relative to amberwing flight height, and size is body length relative to male and female amberwings. The horse fly was *Tabanus* sp. and the butterfly was *Ancyloxypha numitor*.

support the mistaken identity hypothesis. To compare characteristics among species, we examined the target species' flight height, size, and predominant color. Most target species flew close to the water surface. Those target species typically (i.e., with >50% of all individuals viewed during flight height scan samples) flying ≤ 0.25 m above the water included male amberwing (125 of 129 observations), female amberwing (5/5), *E. simplicicollis* (25/30), *P. lydia* (45/65), butterfly (28/28), and horse fly (2/3). Those target species typically flying higher included *P. longipennis* (0.25–0.5 m), *L. luctuosa* (0.5–0.75 m), and *E. princeps* (0.75 m). In general, the butterfly and horse fly species were the most similar to amberwings in size and overall color, with the butterfly being relatively orange like male amberwings and the horse fly being relatively brown like female amberwings and of a similar size (Table II).

DISCUSSION

Not surprisingly, territorial male amberwings pursued conspecific males and females; however, males also commonly pursued a species of butterfly and a species of horse fly that came close to their territories and they approached these two heterospecifics as closely as they did conspecifics. Other species, including other species of odonates, were infrequently pursued and when these species were pursued, they were not approached closely.

Our results are not consistent with four of the five hypotheses for heterospecific pursuit (Table I). First, our data do not support the competition

hypothesis. The butterfly does not share common resources (e.g., food, oviposition sites, or perches) with either larval or adult amberwings. The horse fly does not overlap in resource use with adult amberwings, but their larvae are reported to feed on aquatic insects (Lehmkuhl, 1979), so some overlap with larval amberwings may exist. However, the odonate species with whom amberwings had the most overlap in terms of larval and adult resources, such as *P. longipennis* and *P. lydia*, were infrequently pursued. Second, the interference hypothesis (Singer, 1989), which proposes that heterospecific targets are chased to keep them from disrupting mating behavior, can be rejected. Neither the butterfly nor the horse fly was ever observed to pursue amberwing females or disturb a mating pair; indeed, the horse flies never reacted in an observable manner to the pursuit by the male, and the butterflies reacted only rarely. Third, we can reject the foraging hypothesis. We never observed residents to eat the butterfly or horse fly species. In fact, the flight behavior of residents pursuing heterospecifics (i.e., a horizontal, rapid and unidirectional approach) resembled the pursuit of conspecifics, not the looping, more vertical flight behavior associated with feeding (personal observation). In addition, amberwings typically take prey that are much smaller than either the butterfly or the horse fly species (personal observation). Fourth, our results also are not consistent with the predator defense hypothesis. Neither the adult horse fly nor the adult butterfly is a known predator of the eggs, larvae, or adults of amberwings, although as stated earlier, it is possible that larval horse flies might eat aquatic insects such as amberwing larvae. Our observations suggest that the horse flies were always rapidly leaving the vicinity of the resident before the resident responded to them and that the horse flies did not alter their flight path as a result of the pursuit. Therefore, even if predator defense was occurring, it was unnecessary and ineffective. Furthermore, *E. simplicicollis*, which we have observed to capture and eat adult amberwings (unpublished data), and the other odonates, which have nymphs that certainly may eat amberwing nymphs, were rarely pursued.

Our results do, however, support the mistaken identity hypothesis. The butterfly and horse fly were most similar to amberwings in size, color, and flight height (Table II), with the butterfly and horse fly most closely resembling male and female conspecifics, respectively. Singer (1989) suggested that heterospecific pursuits may be the result of a perceptual constraint and individuals are responding to small, moving objects in the territory. Thus, because the butterfly species flew slowly around the perimeter of the pond, the argument could be made that, for the butterfly, males were simply reacting to prolonged movement within their territory. However, the territorial male amberwings are more specific than just responding to any small moving object.

For instance, many small insects (e.g., coenagrionid damselflies, dipterans other than horse flies) commonly intruded but were never approached, and a different butterfly species (*Everes comyntas*), of a similar size, shape, and behavior to, but a different color (i.e., blue/gray) than, the butterfly target in this study (*Ancyloxypha numitor*), occasionally intruded but was never pursued. Furthermore, in other areas, male amberwings have been observed to pursue *Polistes* wasps arriving at the pond to obtain water. These wasps resemble female amberwings in coloration and flight behavior and are only slightly larger (Dunkle, 1989; personal observation). Thus, the available evidence suggests that territorial male amberwings pursue heterospecifics because these heterospecifics resemble amberwings with respect to the proximate cues (e.g., color, flight height, flight style, size) used by males to identify conspecifics (Jacobs, 1955). Other odonates are rarely pursued because no odonates in our study area resemble amberwings; indeed, amberwings are relatively unique among dragonflies when size, color, and flight behavior are all considered (Needham and Westfall, 1954; Dunkle, 1989). Studies of other territorial species, including species of dragonflies, have also noted that the heterospecifics that are pursued tend to resemble conspecifics in appearance (e.g., Lin, 1961; Maier and Waldbauer, 1979; Dreisig, 1995; Corbet, 1999), suggesting that mistaken identity may be a cause of heterospecific pursuit in a variety of taxa.

The consequences of pursuing heterospecific targets, either to the resident male amberwing or to the target, are unclear. Singer (1989) hypothesized that the selectivity a male exhibits for discriminating between conspecific and heterospecific targets is a balance between the frequency of the heterospecific intruders and the cost of not responding to the intrusions; thus, one would expect to see discrimination if the target was common and/or if a delay in the response to a potential conspecific was costly. However, we found that the relationship between the intrusion frequency and the proportion of the intruders that elicited a response, while negative (and thus in the same direction as his hypothesis would predict), was neither strong nor significant. We did not attempt to quantify the costs of responding or not responding to intrusions. But because the frequencies of intrusion by the butterfly and horse fly were so low, it may be less costly for the resident male to expend the time and energy to approach these heterospecifics than not to approach them. For instance, female amberwings rarely intruded, so the risk of missing even one mating, combined with the relative rarity of the horse fly species, suggests that it may be less costly to approach the horse fly than to delay and/or identify them more critically. Additionally, not responding to a potential male may make it more costly to evict that male during a territory contest (Singer, 1989; Switzer and Eason, 2000), and again, the butterfly species intruded

much less frequently than conspecific males. Future studies could attempt to quantify these costs and/or compare the response frequency among locations that differ in how often the horse fly and butterfly species intrude.

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