Fighting behavior and prior residency advantage in the territorial dragonfly, *Perithemis tenera*

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Many factors, including residency status, body size, age, and energetic reserves, have been implicated as possibly determining the winner in animal contests. In this study I investigated which of these factors were correlated with the outcomes of naturally-occurring territorial contests between male ambohelwing dragonflies (*Perithemis tenera*). Ambushing contests consist of non-contact interactions and are characterized by a series of distinct stages that represent different levels of escalation. Prior residents did tend to win, but surprisingly this residency advantage only occurred in interactions that were not escalated. For both non-escalated and escalated interactions, body size (wing length) did not influence the outcome. Age was correlated with outcome for escalated interactions, with the younger of the pair tending to win. Winning males had also spent less time in male-male interactions both the day of the interaction and during their entire life, suggesting that energy reserves may also affect the outcome of contests. In contrast to escalated interactions, age and time spent in male-male interactions was not related to the outcome of non-escalated interactions. The difference between the two opponents' sizes, ages, and time spent in positions male-male interactions did not correlate with duration or escalation level of contest. These results suggest that non-escalated interactions may occur when intruders are simply assessing the quality of the site. Contests that do not escalate, and thus the prior residency advantage, are probably a result of the intruder not challenging for ownership because the value of the territory is too low.

KEY WORDS: territoriality, fighting, prior residency advantage, age, dragonfly, *Perithemis tenera*.

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INTRODUCTION

Biologists have paid considerable attention to contest behavior over the past few decades. This body of literature has indicated that asymmetries in the physical characteristics of an individual, for example its body size, age, or energy level, are related to its resource holding potential ("RHP"; PARKER 1974) and hence frequently affect who wins the contest (e.g. THORNHILL & ALCOCK 1983, ARCESE & SMITH 1985, LIEMAR et al. 1991, HUGHES 1996, PLANTOW & SVERINSSON 1996, MAIN et al. 2001). Resource value asymmetries may also influence contest outcome, especially when taken in relation to differences in RHP (e.g. PARKER & RUBENSTEIN 1981, SVERINSSON-SENN & PARKER 1981, AUSTRE 1983, DICK & ELMQUIST 1990, TORRISI 1997). In addition, a less intuitive relationship frequently has been found between an individual's residence status and its probability of winning a contest, such that prior residents usually win the majority of fights (e.g. DAVIES 1978, HAYT & SALMON 1978, JACOBS & DILL 1980, THORNHILL & ALCOCK 1983, GRIEBEL & THOMPSON 1991, ROSENBERG & ENQUIST 1991, MERON et al. 1992, TORRISI 1997, FAME & MESSING 1998, CHELLAPPA et al. 1999, TAKAHASHI et al. 2001). Proposed explanations for this prior residency advantage have included the possible higher RHP or resource value for residents as compared to intruders, as well as the possible use of arbitrary decision rules such as "residents always win" (MANNABA SMITH & PARKER 1976, DAVIES 1978, PARKER & RUBENSTEIN 1981, KLEIB 1982).

Some of the most intriguing systems in which to study fighting behavior are those species in which the contests do not involve contact between the participants (e.g. many flying insects; BAKER 1972, VAN BEEKER 1986, ALCOCK 1993, SWITZER & SCHULZ 2000). In such taxa, seemingly intuitive relationships that hold in many other systems (e.g. between body size and outcome) may not apply (ALCOCK 1993). Some species with such non-contact, flying contests can be found in the insect order Odonata, the dragonflies and damselflies (CORBET 1999). Odonates are often excellent subjects for studying contest behavior; they are generally easy to observe and may have frequent contests over resources and/or females (reviewed in FITZPATRICK & WELLINGTON 1983, THORNHILL & ALCOCK 1983, CORBET 1999). Thus, it is not surprising that numerous researchers have investigated contest behavior in odonates. Interestingly, though, some discrepancy exists among odonate species as to what characteristics lead to an adult male winning a territory contest (Table 1; see also CORBET 1999). The one factor that seems to have a consistent effect on outcome is residency, but often these studies did not attempt to determine the underlying cause of the observed residency advantage.

In this study, I test possible causes for residency advantage and contest outcome in a territorial dragonfly, the Eastern amberwing (Perithemis tenera). Male anberrwings defend territories around oviposition sites on still or slow moving bodies of water (JACOBS 1955; SWITZER 1997a, 1997b). Non-territorial males rarely obtain any matings with females (unpublished data) and territory residents often spend many hours within a day on the same territory and frequently return to the
<table>
<thead>
<tr>
<th>Suborder</th>
<th>Species</th>
<th>Size</th>
<th>Age</th>
<th>Energy</th>
<th>Previous experiences</th>
<th>Omnivory</th>
<th>Residency</th>
<th>References</th>
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<tr>
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<td>Wroe &amp; Wroe 1984, Wroe 1988</td>
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</table>

"+" means that the factor was tested and was correlated with contest outcome, "-" means the factor was tested and was not correlated with contest outcome, and "-" means the factor was not tested or mentioned. The symbols are given if studies conflict in their results. The evidence for the result could have been direct or indirect. Direct evidence includes studies that looked for correlations between winners and losers of particular contests. Indirect evidence (+) includes studies that found patterns (e.g., might be related to contest outcome, such as correlations between territorial status (e.g., resident or floaters) and body size.)
same territory the next day (Switzer 1997a, 1997b; unpublished data). Residents approach intruding males and these pursuits occasionally lead to physical interactions between the males (Jacobs 1955, Switzer & Eason 2000). Interactions between residents and intruders rarely include physical contact (Jacobs 1955, Switzer & Schultz 2000). In fact, contact only occurs either when one of the males has landed somewhere in the territory and the other male is "bouncing" on the first male's back seemingly trying to get the perching male to resume flying, or when a resident male is guarding an ovipositing female and grabs and flies with an intruding male (Switzer & Schultz 2000); both of these situations are relatively rare (Switzer & Schultz 2000; pers. observ.). In this paper, I first show that interactions between male amoeboforms consist of a relatively orderly progression through a series of distinct behaviors, which are interpreted as different levels of escalation. I then investigate what factors affect the outcome of these interactions and what characteristics may explain whether contests become escalated.

METHODS

This study was conducted on a small farm pond in east-central Kansas, USA (see Switzer 1995 for a description of the study site). I captured males throughout the summer and gave them an alphanumeric code on their right forewing with a permanent marker. Males marked in this manner could be identified without recapture by using binoculars. The length of the right forewing was also measured for many males. Males did not hold territories on other ponds after being territorial at this study pond (Switzer 1995).

Jacobs (1955) described three categories of interactions between territorial males and intruders: (i) "roundabout flights", where the resident flies around the intruder while the intruder is examining the resident's oviposition site; (ii) "hovering", where the resident and intruder remain relatively stationary in the air near the oviposition site; and (iii) "pursuit flight", where one male chases another at high speed out over the water. The categories I used to describe male-male interactions were similar to those of Jacobs (1955), with two clearly distinct additions. First, I added the category of "bouncing" (figure 8c), in which one or both males either bounce or swing in small circles about each other near the oviposition sites. Second, "circle chases", in which one male periodically circled over the oviposition site, was then chased by the other male out over the water away from the site, after which the first male circled over the site again. This sequence of behaviors resulted in a circling of the two males over the site and over the water. Thus, I recorded 6 distinct categories of interactions: (1) roundabout flight; (2) hover; (3) pursuit flight; (4) bounce (figure 8c); (5) circle chase; and (6) end of flight (i.e., one male remaining in the area from the two that were interacting). I did not record brief chases (i.e. lasting only a few seconds) by the resident, including those directed toward passing males, intruding neighbors, or heterospecific insects (Switzer & Eason 2000, Schultz & Switzer 2001). Thus, I distinguished between these chases and interactions in which the intruder remained within the territory (e.g. examining oviposition sites; Jacobs 1955; Switzer 1997b).

During scan observations of the pond, I noted the location and category of each male interaction. Any change in the category of the interaction was noted from that time, including the end of the interaction. In order to utilize data from unmarked males, I needed to operationally define the end of the interaction. Because a male leaving the area for a few minutes generally (in 64/72 interactions involving two marked males) means an ended end of the interaction between those males (i.e. they did not resume that day), I treated any interactions between unmarked males that were separated by 5 min or more as different interactions. The winner was defined as the individual remaining in the area at the end of the interaction; data were not included in the analyses if both males remained in the area at the end of the interaction (e.g. as occurred between neighbors).
My analyses of outcome are conducted pairwise within the individual resident/stranger pair (dyad). Because my unit of analysis was the dyad, I used only one interaction per dyad (cf. Doughty & Bedroom 1991, Stamps & K刪除ecky 1994, K株va et al. 1997), choosing the first interaction for those dyads that had more than one interaction. Except for my descriptive analysis of transitions between interaction categories, all analyses used dyads that contained either at least one marked male or had both sexes marked (these two possibilities are treated separately in the results). Even for these analyses allowing a simple unmarked male, pseudoreplication was unlikely because for a given marked male I only included one interaction with any unmarked male. However, I recognize that using unique dyads as a measure of analysis, while appropriate for contest, does leave the potential for pseudoreplication. Therefore, I repeated my analyses of the determinants of outcome and escalation using only one observation per male. In almost all cases, the trends were of the same direction and magnitude, although in some cases the results changed from statistically significant to not significant because of the smaller sample size. Accordingly, I report the results of both unique dyad and unique individual analyses when analyzing the factors that may affect outcome of contests and when the results differ between the two levels of analysis; otherwise, I report only the values from unique dyads.

Testing for the effects of body size, age, and energy reserves required operational measures of these three characteristics. First, my measure of body size was the length of the male's right forewing (cf. Pickre 1984, Thornehill 1984, Thornehill & Oso 1987). Right forewing length is correlated with other measures of body size for male ambearings (i.e., right forewing length, right hindwing length and width, thorax length, thorax width, face width, abdomen length, and dry mass; all Kendall's $\tau > 0.34$, all $P < 0.001$, unpublished data), and thus was a reasonable measure of overall body size. Second, because males were captured throughout the summer, I was able to use the number of days since they were marked as a measure of relative age (Switzer 1997a, 1997b). Third, like many anisopteran dragonflies (pers. obs.), male ambearings lost a contest usually left the area quickly after a contest, making it possible to immediately capture opponents for fat extraction (unlike, e.g., Calopteryx damselflies; Maküss & Wagger 1990, Macker & Rollins 1994, Pickett & Street 1996). Therefore, to estimate energy reserves, I assumed that interactions were energetically costly (e.g. May 1984, Pickre 1984, Street 1996) and that more time spent interacting meant more energy spent (Pickett & Street 1996, Deeman 1998). Like many other odonates, ambearings rarely fed while defending a territory (Jacobs 1955, Padis 1983, Switzer 1995, Baisd & May 1997), so males would be unable to restore fat reserves while on a territory. Thus, males that had interacted more would have decreased their energy reserves relatively more. For each dyad, my two measures of remaining energy reserves were the number of minutes each had spent in male-male interactions prior to that interaction either just within that day or total (i.e., including his previous visits to the pond). This reasoning obviously assumes that males start out with approximately the same energy reserves, either at the beginning of a day or at the start of their reproductive life; therefore, conservative conclusions will focus simply on the effect of the amount of time in male-male interaction rather than the interactioned relationship with energy.

Some analyses needed estimates of territory quality and competition for territories. To estimate territory quality, I ranked arbitrary 3 m sections of shore according to their mating rate (i.e. number of matings that occurred per minute they were occupied by a male) (Switzer 1997a, 2002a, 2002b). 3 m corresponds roughly to the minimum average territory size for a male (Jacobs 1955, Switzer 1992a, Switzer & Evans 2000). Many other aspects of male ambearing behavior (e.g. order of site occupation, frequency of site occupation, total amount of contests per section, site fidelity, etc.) correlate with this ranking as would be expected if mating rate were correlated with territory quality (Switzer 1997a, 2002a). To estimate competition, I assumed that competition was positively correlated with the number of males on the pond (Switzer 1992a), in support of this assumption, as the number of males on the pond increases, the total duration of male-male interactions on the pond and the proportion of time spent in male-male interactions on any given section increases (Switzer 2002a). I censused the pond every hour, counting the total number of males, and used the census that was closest in time to the particular contest when assigning a density to that contest.
Means are reported as ± SE. Non-parametric statistics are used for many analyses as the data did not meet the assumptions of parametric statistics; these non-parametric statistics take tied values into account when appropriate. Sample sizes differ among tests because not all information was available for some males.

RESULTS

Interaction sequence

All categories could lead to the end of an interaction; in fact, the “end” was the most frequent next interaction category for all categories except hover. Pursuit flights tended to occur late, if at all, in an interaction. To examine the general category sequence of interactions more closely, I calculated the transitions between categories for the set of interactions that included a pursuit flight (Fig. 1). Bounce/figure 8s and roundabouts tended to occur early in interactions, hovers tended to occur in the middle, and circle chases and pursuit flights tended to occur toward the end of an interaction.

![Diagram showing transitions between interaction categories](image)

Fig. 1. — Transitions between the six categories of male interactions in umbreling dragonflies for contexts that included a pursuit flight. Width of the arrow indicates the size of the transition percentage between those two categories. Numbers on arrowheads refer to the actual numbers of transitions. The general category sequence can be determined by following the most likely transitions (the biggest arrows) from a given category. For clarity, transition percentages of less than 5% are not shown (n = 91 contexts with 258 total transitions).
Based on this typical sequence of categories, I ranked the interaction categories in the following categorical order: bounce/figure 8 < roundabout flight < hover < circle chase < pursuit flight. Because both bounce/figure 8s and roundabouts occurred at the beginning of interactions, but rarely led to one another (Fig. 1), and because these two categories very rarely occur as the only 2 categories in a given interaction (and never in those data), I arbitrarily ranked roundabouts higher than bounce/figure 8s. As will become apparent below, this decision did not affect the results. Using one interaction per dyad, I recorded the highest ranking category observed in the interaction as a whole. Interactions escalating only to bounce or roundabouts were significantly shorter in duration than the other interactions (Fig. 2). Therefore, the transitions between categories, the interaction duration, and the characteristics of the behaviors themselves (see Methods) all support the idea that a general sequence of behaviors exists in amherwing interactions and that the different behaviors represent different levels of escalation.

Fig. 2. — Durations of contests in amherwing dragonflies, including the stated level as the highest level of escalation; data include dyads with at least one male marked. The overall effect of category on duration was significant (ANOVA using log-transformed durations; F(5,29) = 31.2, P < 0.0001). The numbers above the SE bars are the sample size. The horizontal bars connect categories that were not significantly different (P > 0.05) using Bonferroni pairwise comparisons.
Factors affecting outcome

Interestingly, none of the contests, regardless of level of escalation, were between a resident and one of his neighbors. Instead, the interactions that occurred between a resident and his neighbor were generally brief chases. This suggests that resident male ambushes were not at risk of losing their territory to a neighbor; rather, territory contests occurred between the resident and males currently without a territory. One possible factor affecting the outcome of such contests is residency. Considering all categories of interactions together, residents were not more likely to win a contest than intruders (at least one marked male: 42/85 fights won by resident, Binomial test $P > 0.50$; both males marked: 23/45 fights won by resident, Binomial test $P > 0.50$). However, if these interactions are separated by their level of escalation (as above), two interesting patterns emerge (Fig. 3). First, residents did not usually give up without escalating. In only 6/85 contests did the resident leave the territory without escalating to at least a hover; in contrast, 18/85 intruders did so (Fisher’s Exact Test; $P = 0.009$). Second, residents did win the majority of contests with roundabouts or bounces (figure 8s as the highest ranking category). However, when chases, circle chases, or pursuits were the highest category, residents and intruders were more equally likely to win, with intruders actually having a slight edge (Fig. 3). The difference in residency advantage (i.e., proportion of interactions won by the resident) across levels of escalation is statistically significant ($\chi^2 = 13.7, df = 4, P < 0.009$). When data were limited to interactions with both

Fig. 3. — Percentage of contests won by resident ambushing dragonflies for different levels of escalation. Numbers above bars are sample size; data include contests for when at least one male was marked in the dyad.
males marked, the percentages were virtually identical to those in Fig. 3, but the trend was not significant due to the lower sample size ($\chi^2 = 7.55, df = 4, P = 0.15$).

Thus, interaction levels differed in duration and the importance of residency. I took this into account in the rest of the analyses by lumping bouts/figure 8 and roundabout interactions into a "non-escalated interaction" group, lumping the remaining interactions into an "escalated interaction" group.

I compared the wing length, age (as measured by date since marking), and the amount of previous time spent in male-male interactions between the winner and loser of individual contests (Table 2). No significant trend existed between any character and the outcome of non-escalated contests. In escalated contests, however, a clear pattern existed for age; losers of escalated contests were significantly older than winners (Table 2). Trends also existed for wing length and the amount of time spent fighting. However, the significance of these trends depended on whether individuals or dyads were used as the unit of analysis. With the exception of wing length, the magnitude of the difference was similar for individuals and dyads, suggesting that the difference in significance level is due to lower statistical power for individual analyses.

The age effect appeared to be a major factor overriding the residency advantage described above; residents lost when they were older than the intruder, but if

<table>
<thead>
<tr>
<th>Contest type</th>
<th>Characteristic</th>
<th>Mean difference (winner-loser)</th>
<th>n* 1</th>
<th>Wilcoxon T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-escalated</td>
<td>Wing length</td>
<td>−0.068 ± 0.24 mm (0.21 ± 0.21 mm)</td>
<td>5</td>
<td>7</td>
<td>&gt; 0.70</td>
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<td></td>
<td>Age</td>
<td>5.8 ± 3.2 days (2.0 ± 1.66 days)</td>
<td>6</td>
<td>4.5</td>
<td>&gt; 0.50</td>
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<td>Previous time interacting (that day)</td>
<td>−7.7 ± 6.7 min (&lt; 0.05 ± 1.5 min)</td>
<td>6</td>
<td>6</td>
<td>&gt; 0.70</td>
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<tr>
<td></td>
<td>Previous time interacting (total)</td>
<td>554 ± 87 min (95.1 ± 51.8 min)</td>
<td>8</td>
<td>2</td>
<td>0.10</td>
</tr>
<tr>
<td>Escalated</td>
<td>Wing length</td>
<td>−0.45 ± 0.19 mm (&lt; 0.038 ± 0.17 mm)</td>
<td>12</td>
<td>14</td>
<td>0.063</td>
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<tr>
<td></td>
<td>Age</td>
<td>−2.9 ± 0.83 days (&lt; 2.2 ± 0.06 days)</td>
<td>17</td>
<td>1.5</td>
<td>0.0015</td>
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<td></td>
<td>Previous time interacting (that day)</td>
<td>8.4 ± 6.39 min (&lt; 12.7 ± 5.9 min)</td>
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<td>9</td>
<td>0.35</td>
</tr>
<tr>
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<td>Previous time interacting (total)</td>
<td>59.7 ± 31.7 min (&lt; 56.9 ± 31.9 min)</td>
<td>17</td>
<td>40</td>
<td>0.09</td>
</tr>
</tbody>
</table>

* n = the total number of pairs in the analysis. The sample size for calculating T was smaller in some tests due to differences between some opponents being zero (Zwi 1999).
they were either the same age or younger, they won roughly 50% of the contests (Fig. 4; \( \chi^2 = 8.47, df = 2, \text{P} = 0.01 \)). To examine whether smaller differences in age between the opponents was responsible for the outcomes that ran counter to the pattern in Fig. 4 (i.e., residents lost when younger), I compared the absolute difference in ages for the contests that fit the pattern (i.e., residents won when younger) to those that did not (i.e., residents lost when younger). The magnitude of the age difference did not affect outcome \( \text{(dyads; residents won when younger: 5.14 ± 1.1 day difference, } n = 7; \text{residents lost when younger: 4.33 ± 2.0 days, } n = 6; \text{Mann-Whitney, } U = 12, z = 1.30, \text{P} = 0.19 \). Therefore, the losing, younger residents were not losing because they were close to the same age as the intruders. In contrast to escalated interactions, for non-escalated interactions, no significant pattern existed between the relative age of the resident and the likelihood of winning and the trend was in the opposite direction from that of escalated interactions \( \text{(dyads: 6/7 residents lost when younger, 1/3 lost when older; Fisher's exact test; } P = 0.18 \). In summary, one can reliably pick the winner of a non-escalated contest by choosing the resident, and the winner of an escalated contest by choosing the younger male.

I correlated age with the amount of time a male spent in male-male interactions to assess the degree to which these two factors may have independent effects.

Fig. 4.—Probability of a territorial resident amending winning an escalated contest in relation to his age relative to the intruder. Numbers above the bars are the sample sizes. Figure is for unique dyads; pattern is the same using individuals as unit of analysis (6/8 residents won when same age as intruder, 5/8 residents won when younger than intruder, 0/6 residents won when older than intruder; \( \chi^2 = 20.4, df = 2, \text{P} = 0.005 \).}
on the outcome of escalated contests. As expected, the maximum recorded age for a male and the cumulative amount of time he spent in male-male interactions during his life were strongly correlated (Kendall's rank correlation, \( t = 0.57, z = 6.38, P < 0.0001 \)). However, the correlation between daily interaction time and age was only weakly correlated and of borderline significance when all males and ages were pooled (\( t = 0.053, n = 296, z = 1.91, P = 0.056 \)). When analyzed individually, only 25/42 males had positive correlations between their age and their daily interaction time at that age (Binomial test: \( 6.5 > z > 0.2 \)). The lack of a correlation between age and daily interaction time suggests that the effects of these two variables on outcome may be independent.

**Escalated versus non-escalated contests**

Differences in territory quality, availability of territories, or RHP may have been responsible for whether particular contests escalate. For example, individuals may have been more likely to escalate if the territory was of relatively high quality. However, territory quality, as measured by rank of the section of the pond margin on which the resident's outposition site was located, did not significantly differ between escalated and non-escalated contests (escalated: \( 26.8 \pm 1.0, n = 64 \); non-escalated: \( 24.9 \pm 1.6, n = 25 \); \( U = 662.5, P = 0.21 \)). In addition, the rank of sites for evictions was not consistently different than the rank of sites on which the resident won (escalated contests: eviction rank: \( 27.1 \pm 1.3, n = 37 \); non-escalation rank: \( 26.6 \pm 1.9, n = 25 \); Mann-Whitney: \( U = 456.5, z = 0.086, P = 0.93 \); non-escalated contests: eviction rank: \( 22.8 \pm 2.8, n = 6 \); non-eviction rank: \( 25.3 \pm 2.0, n = 18 \); Mann-Whitney: \( U = 45.5, z = 0.57, P = 0.57 \)). The proportion of fights that resulted in an eviction was slightly higher on sites with quality above the average site rank compared with those below the average rank, but the difference was not significant for escalated or non-escalated contests (escalated: 8/16 evictions on low-ranking sites versus 29/46 on high-ranking sites; Fisher's exact test, \( P = 0.39 \); non-escalated: 2/8 evictions on low-ranking sites versus 4/16 on high-ranking sites; Fisher's exact test, \( P = 0.99 \)). Finally, for escalated contests, the duration of fights that resulted in an eviction was not significantly different than those in which the resident won (evictions: \( 25.03 \pm 3.0 \text{ min}, n = 37 \); non-evictions: \( 32.6 \pm 4.8 \text{ min}, n = 25 \); \( U = 368.5, P = 0.18 \)).

Contests may have been more likely to escalate if territories were relatively scarce, increasing the value of each particular site. To test for competition effects, I compared the number of males on the pond between escalated and non-escalated contests; no significant pattern was detected (escalated: 16.0 ± 0.92 males, \( n = 51 \); non-escalated: 15.2 ± 1.4 males, \( n = 22 \); \( U = 492.5, P = 0.84 \)). Thus, density of males did not seem to affect the escalation of contests.

If males were assessing RHP during contests, the degree of escalation and/or the duration of the contest would be predicted to correlate with the absolute magnitude of the RHP difference between the two males (Parker 1974, Endest & Lemaire 1983). The participants in non-escalated contests did not have a larger absolute difference compared to those in escalated contests for any of the possible RHP characteristics (wing length: non-escalated: \( 0.54 \pm 0.13 \text{ mm}, n = 10 \); escalated: \( 0.57 \pm 0.08 \text{ mm}, n = 24 \); Mann-Whitney: \( U = 102, z = 0.68, P = 0.50 \); age: non-escalated: \( 5.7 \pm 1.6 \text{ days}, n = 15 \); escalated: \( 4.6 \pm 0.76 \text{ days}, n = 38 \); Mann-Whitney: \( U = 229, z = 1.11, P = 0.27 \); previous interaction time that day: non-escalated: \( 2.9 \pm 1.3 \).
Prior residency advantage

For numerous animals, including many insects, territory residents win the majority of fights (e.g., ROSEBERRY 1982, TINOSAKI & ALCOCK 1983, LEHMAR & ENQUIST 1984; Table 1). The most common explanations invoked for this pattern are that either individuals are following an arbitrary convention such as "residents always win" or that asymmetries exist in either RHP or resource value that favor the resident. For example, DAVIES (1978) suggested that intruders of speckled wood butterflies (Pararge aegeria) simply defer to residents once roles are established (but see STUTT & WELLNER 1998). ROSENBERG & ENQUIST (1991) found that resident Wedemeyer’s admiral butterflies (Limenitis wedeneyeri) were larger than the intruders, and suggested that size was correlated with RHP in this species (ROSENBERG & ENQUIST 1991). WAGER (1988) found that escalated fights were most common in black-winged damselflies (Calopteryx maculata) when both opponents had residency at the same territory, which led to the perceived resource value being high for both participants (see also DAVIES 1978, KEEFS 1982, GRIBBIN & THOMPSON 1991). However, pursuing passer-bys or intruder occupancy probes (GRAFEN 1987) may also lead to observations of residents typically "winning", when no true contest had occurred. Below I first discuss whether occupancy probes or passer-bys fit the observed patterns in amberwing contests, and then discuss which of the more traditional explanations for prior residency advantage may apply.

In the current study, a prior residency advantage only existed in non-escalated contests, and for these contests, none of the measured, potential correlates with RHP were significantly associated with winning. One possible explanation for this pattern of residency advantage is that these non-escalated contests were simply reactions by the resident to males passing by his territory. Resident male amberwings do experience quick intrusions from males passing linearly across their territories, and these passes often elicit a pursuit from a resident male (SWITZER & EASON 2000, SCHULTZ & SWITZER 2001). Such brief intrusions, however, were not included in the data analyzed in this study. Rather, the non-escalated contests considered here could last for several minutes and these non-escalated interactions fre
quently progressed to more escalated stages. Thus, although ambergings do react to passage; these reactions do not explain the prior residency advantage described here. Nor do the results fit the pattern of occupancy probes. If intruders were probing territories for resident occupancy (GRAFIN 1987), the probe would be expected to only last as long as it took to determine that a resident was there, at which time the intruder would leave. However, in contrast to those conditions, the non-escalated interactions described in this paper could last minutes and did not terminate when the resident responded. Therefore, occupancy checks also do not appear to explain the prior residency advantage in ambergings.

Of the more traditional explanations for a residency advantage, neither an arbitrary convention or a RHP asymmetry appear consistent with the data. Residents did not win all contests; instead, the advantage was only apparent in contests that did not escalate. Thus, they do not appear to be following a resident always wins' convention. Furthermore, contrary to what would be predicted by the effect of an RHP asymmetry, residents and intruders did not differ in my measures of RHP in the non-escalated contests, nor did these contests have a large difference in RHP than the escalated contests.

However, resource value asymmetries, perhaps as a result of a resident's experience on the territory (KREBS 1982), may have lead to the residency advantage. Residents may value a particular territory more because they have already paid the "start-up costs" in terms of predation risk, energy and time associated with settlemen (JACOBS 1955, unpublished data); therefore, if a resident settled on a new territory, he would have to pay these costs again, while the intruding male has to pay these costs for any territory (see also TOBAS 1997). In addition, if previous matings occurred at the site, a fact which would be known by a resident but not by naive intruders, the resident may increase his assessed value of territory quality (SWITZER 1997a, 1997b). Alternatively, intrinsic, individual differences may exist in the assessment of site value (see also below) for residents and those intruders that do not escalate. In other words, these intruders "losing" non-escalated interactions may have left the site even if the site were not already occupied. Furthermore, non-escalated interactions in ambergings occurred when the intruder was examining ownership-free (i.e., assessing resources) within the resident's territory. Therefore, intruders seemed to contest for territory ownership only under particular circumstances, and these circumstances seem more likely to be related to resource value than relative RHP.

However, non-escalated contests did not consistently occur on lower quality sites than those for escalated contests, as would be expected if site quality affected the decision to escalate (e.g., RZECZKO 1979, LEMAR & ENQUIR 1984). But the same section, and even the same resident, may experience both escalated and non-escalated contests within a site (SWITZER 2002a), which suggests that males may vary in their evaluation of site quality. Such individual differences in other criteria or assessments would not be surprising for this species; ambergings may differ in their preference for particular oviposition substrates (JACOBS 1955, SWITZER 1995) and an individual's experience at a site affects his site selection (SWITZER 1997a, 1997b). In any case, while it seems relatively clear that arbitrary convention or RHP cannot explain the residency advantage in this species, further studies will be necessary to determine the role of resource value asymmetries.

Interestingly, the prior residency advantage in ambergings, while perhaps related to resource value, may not be the result of a true contest (in the sense that both participants were attempting to obtain ownership of the resource;
WILMAN & WILKUND 1983, GRAFFEN 1987). Instead, I propose that the resident wins because the intruder determines (after assessing possible oviposition sites) that the territory is too worth fighting for and does not contest for ownership (cf. LINDBRO 1992). True contests occur in situations in which the intruder assesses the territory to be of sufficient value for settlement, relative to his expected net benefit from contesting to search. This proposal is consistent with observations of intruder behavior in ambervings: during the non-escalated interactions, the intruder's behavior is more directed toward oviposition sites than to the resident, while the opposite is generally true for escalated interactions. However, because intruders are examining resources prior to leaving, the situation in ambervings may differ from systems in which an "information asymmetry" exists favoring the resident. In those systems, residents base their contest behavior on the actual value of the site, while intruders base their behavior on the average resource value in the area (SIGURDSDOTTIR & PARKER 1981, AUGUST 1983, RIECHERT 1984, HACK et al. 1997). The pattern of intruders leaving immediately after assessment, as seen in ambervings, is more commonly associated with contests decided by RHP (and therefore assessment of RHP) than resource value (e.g., MARYNARD SMITH & PRICE 1973, RIECHERT 1978, TURNER 1994). This suggestion — that intruder assessment of the resource is leading both to the decision to escalate and to the lack of a prior residency advantage in escalated contests — is also consistent with theoretical studies conducted by LEIDMAR & EQUEST (1984) and EQUEST & LEIDMAR (1987). They found that in an owner-intruder game with an uncorrelated role asymmetry (e.g., not related to RHP) and no information asymmetry on resource value, the probability of residents winning fights decreased with increasing resource value. Therefore, if the contested territory was judged by both the resident and intruder to be of sufficiently high value, escalated contests would occur and no residency advantage would be observed.

Non-escalated contests in which residents win also occur in other species of odonates, but the proposed explanations for these contests differ. For example, WAGG (1988) and MARDEN & WAGG (1990) suggested that brief (less than 15 sec) interactions in C. macroptera were cases where intruders were respecting the intruder-resident asymmetry: residents vary in energetic reserves and only intruders with high energetic reserves persist in contests. PANKRIN & Sivas-Jerret (1996) proposed that non-escalated interactions in the damselfly Calopteryx splendens occur when the intruder is an old and weak male, for whom the chance of finding a vacant territory is greater than the chance of winning the fight. In ambervings, residents briefly chase passing males quite frequently (see above) but I do not know whether these intruders are passing, non-competitive males. However, as stated earlier I did not include such brief pursuits in this current analysis. More importantly, the RHP difference between residents and intruders did not significantly differ between non-escalated and escalated interactions for any of the measured characteristics. This lack of a difference would not be expected if an intruder was assessing his RHP relative to the resident and escalating if he were of comparable or higher RHP (PARKER 1974, MARYNARD SMITH & PARKER 1976, EQUEST & LEIDMAR 1983).

Effects of RHP

In contrast to non-escalated contests, some of my measures of RHP did correlate with the outcome of escalated contests, as GRAFFEN (1987) proposed would be the case for true contests for a resource. Interestingly, however, size did not corre-
In support of Alcock's hypothesis, the non-contact escalated contests in amberswings were won by those males who were younger and who had fought relatively less prior to the given contest, not those who were of larger size. Both of these characteristics are consistent with the idea of condition-dependent outcome, especially if time spent in interactions is correlated with energy reserves. Age is frequently associated with competence ability in odonates (e.g. Forsyth & Montgomery 1987, Tsuchi & Ono 1987). The importance of energy reserves has been demonstrated in experimental studies of Calopteryx damalis (Marden & Wäge 1990, Marrey & Rollins 1994, Plastow & Siva-Jothy 1996), whose contests are also predominantly non-contact in nature. Whether age and energy reserves have independent effects on outcome in amberswings is still unclear. The relationship between age and time spent interacting within a day was quite weak, which suggests that they may have independent effects, but this evidence is suggestive at best. Age and energy reserves are often correlated in odonates (Marden & Wäge 1990, Marrey & Rollins 1994, Plastow & Siva-Jothy 1996), which makes it difficult to tease the effects of these two factors apart. However, it is feasible that other factors besides energy, such as the condition of the wings, are also correlated with age (e.g. Koenig & Alman 1985) and may likewise influence outcome.

In conclusion, the patterns apparent in amberswing contest behavior indicate that prior residency advantage differed depending on the level of escalation and suggest that RHP and resource value may serve different roles depending on the level of escalation. Of course, some combination of RHP and resource value (e.g. Alcock 1983) may be important for the outcome of amberswing contests; I was unable to investigate such combinations with these data. However, overall the results provide some important considerations for all studies investigating contest behavior in general and possible residency advantage in particular. Field studies of prior residency advantage often do not distinguish between levels of escalation, and may even include cases where passing males were approached by the resident or other cases of brief intrusions (e.g. Olsson & Siva 2000). Researchers should be careful when interpreting these reactions to brief intrusions as "contests"; the intruding male may not be assessing the resource or resident, in alone challenging for possession (see also Wicksman & Wiklund 1983). Second, even within relatively extended contests, it may be useful to explore differences among escalation levels between residents and intruders. Future studies of prior residency advantage may be able to distinguish whether RHP or resource value primarily explains residency advantage by carefully recording assessment behavior and escalation levels and analyzing these data appropriately.
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REFERENCES


Fighting behaviour in ambushing dragonflies


