The Behavioral Significance of Male Body Size in the Tarantula Hawk Wasp *Hemipepsis ustulata* (Hymenoptera: Pompilidae)

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Abstract

Large males of the tarantula hawk wasp *Hemipepsis ustulata* appear to have an advantage in the competition for mates. Large males are more likely to acquire perch territories used to scan for incoming receptive females and territorial males appear more likely to mate than non-territorial males. In addition, among the males that do secure a mate, those that intercept a female on a territory are larger than those that do so elsewhere. Despite the mating advantages apparently enjoyed by larger males of this species, average male size has remained essentially constant over the last 25 yr. Moreover, larger males are not seen to employ certain competitive tactics that might otherwise enhance their reproductive success. Thus, larger males did not preferentially visit the most popular landmark territory compared to a site that attracted fewer visitors overall. Nor were larger males more likely to return to potential territories after marking, capture, and release, either immediately or on a subsequent day. Finally, although large males made up a significantly greater proportion of the males captured at two territories as the 2005 flight season progressed, over all the years of the study, receptive females have not been concentrated in the latter part of the flight seasons.

Introduction

Males often vary considerably in body size within a species and, when this is true, larger males typically enjoy a competitive advantage in both vertebrates (Andersson 1994) and invertebrates (Thornhill & Alcock 1983; Blanckenhorn 2000; Strohm & Lechner 2000). Although there are exceptions (e.g. Hernandez & Benson 1998; Lefevre & Muehter 2004), the standard pattern of a large male advantage raises the question, what maintains small males in these species?

The tarantula hawk wasp *Hemipepsis ustulata* is a highly size variable species of wasp in which male body weight can range from 6 to 56 mg (Alcock & Bailey 1997). During the spring mating season, males of this species perch in and defend shrubs and small trees (especially the foothills palo verde) on hilltops and ridgelines. Territorial residents defend their sites for several hours each morning. These males leave their perches to fly after male visitors, chasing them away quickly or (much less commonly) engaging them in elaborate upward spiraling flights until the intruder retreats (or a takeover occurs). In keeping with the typical pattern, the larger individuals appear to be competitively advantaged in these contests. For example, territorial residents are larger than 'replacement' males that claim a site soon after the original male's experimental removal (Alcock 1979; Alcock & Carey 1988; Kemp & Alcock 2003). Territorial males appear to increase their chances of mating because, as is characteristic of territorial hilltopping insects (Shields 1967; Alcock 1987), receptive females fly to perch sites held by territorial males (Alcock 1981).

Assuming that territory holders of *H. ustulata* do have a mating advantage, we can use this wasp species as a model to answer a number of questions about the evolution of body size in a species in which large males are more successful at defending landmark mating locations. In this paper we focus on five questions:

First, do large males really enjoy a mating advantage over their smaller rivals? Large males do have an advantage in competition for territories, but it is not known whether this translates into a fitness advantage. We examine this possibility by summarizing the data on the size of mating males collected between 1980 and 2005.

Second, does the mean size of males vary over time? We would expect to see a trend toward larger male body mass, if large males do indeed tend to mate more often than small males, and if body size is heritable. We check this possibility by comparing the mean head-width (a close proxy for body weight, r = 0.97; Alcock & Bailey 1997) in male populations sampled between 1980 and 2005.

Third, does size affect when during the 2–3 mo long flight season males appear on the hilltops to compete for mating territories? Given that large males appear to have a territorial advantage, one prediction is that larger males should time their flight activity for that period when receptive females are most available. We will test this prediction by assessing whether larger males are more likely to be present in that part of the flight season when most matings occur.

Fourth, do relatively large males target the more popular sites, namely those that are occupied more consistently than others over the lengthy flight season (Alcock 1981)? The rank order of sites remains much the same from year to year (Alcock 1983, 2000), suggesting that males of *H. ustulata* evaluate territory quality similarly. We therefore predict that large males, given their competitive advantage, should preferentially inspect the more highly sought-after locations. We test this prediction by examining the size distribution of males captured over the 2005 flight season at two territories of different attractiveness to male tarantula hawks.

Last, are larger males more motivated to acquire a territory? Given that several mate-locating tactics apparently exist in this species, with some males flying long routes that take them to many landmarks while others perch in and defend certain plants (Alcock 1981), one possibility is that small males are less inclined to practice the territorial tactic as opposed to the patrolling option. The accumulation of larger males as territorial residents would then be a direct consequence of a motivational difference rather than a difference in the competitive abilities of large vs. small males (although differences in competitive ability may have led to the evolution of size-dependent motivational strategies). We predict that if small males are less motivated to acquire territories then they will be less willing to return to a vacant site once captured at that site and subsequently released. We test this prediction by examining the relationship between male body size and the readiness of visitor males to return to a vacant territory where they were captured soon after arriving.

Methods

The Study Site

We conducted this study along ridges in the Usery Mountains, a collection of hills ranging up to about 900 m north of Mesa, AZ in Maricopa County. The habitat is typical of the upland Sonoran Desert with scattered shrubs, cacti and small trees, notably creosote bush (*Larrea divaricata*), saguaro cactus (*Carnegia gigantea*), and foothills palo verde (*Parkinsonia microphyllum*). Further description of the area can be found in (Alcock 1979; Alcock & Schaefer 1983). Conspicuous shrubs, cacti, and palo verdes growing along the ridge attract territorial males of *H. ustulata*, which perch on these favored shrubs and trees, one male per plant, from which they launch flights to chase away intruders and to capture and mate with incoming receptive females. Non-territorial males appear to be patrollers that visit territories, but, as noted, they are almost always quick to depart when challenged by a territorial male as they approach the defended site (Alcock & Bailey 1997).

The Sample of Mating Males

At least one mating was observed in each of the 10 yr between 1980 and 2005 when observers were present at the study site(s) during the spring flight season. When a mating was seen, the location of the pairing was recorded and every effort was made to identify the male. Unmarked males were captured, if possible, in order to measure their head-widths and to supply them with identifying marks (see below).

The Mean Head-Width of Populations across Years

In the spring of 1980, 1981, 1987, 1988, 2001, 2004, and 2005 between 119 and 424 males were captured at one of two ridge transects several hundred meters

in length, one at the highest part of the Usery Mountains while the other was about a kilometer distant lower on the slope. The head-width of each captured male was measured with a pair of dial calipers accurate to 0.05 mm. Each male was given a distinctive color-coded mark using Liquid Paper Typewriter Correction Fluid or Liquitex Acrylic Paints or Deco Color Opaque Paint Markers, and then was released. The data on male sizes were collected over many days beginning as early as the second week of March and continuing to mid-June. at the latest, although the flight season sometimes did not begin until early April and sometimes ended in late May. In all years except 2005, the samples were gathered as an observer walked a transect checking a number of territories while attempting to capture, measure and mark all unmarked males seen perched on the plants in question.

In 2005, a different protocol was used in which an observer captured every male that appeared in palo verde#1 and palo verde#2 over a 2 h period in the morning on 25 d beginning April 8 and ending June 15 (with intervals of two or three days between samples as a rule). The 2 h period began about 0800 Mountain Standard Time (M.S.T.) early in the season and shifted toward 0600 M.S.T. as the weeks passed and temperatures rose. The two palo verdes were chosen for the purpose of collecting residents and visitors because these trees have for many years been regularly occupied by territorial males during the flight season, with palo verde#2 the single most consistently claimed site on the upper part of Usery Peak (Alcock 2000).

If a male marked on a given day returned to either of the two palo verdes during that 2 h period, the male was captured, placed in a small plastic vial, and held in a cooler until the end of the sampling interval so as not to have to recapture the same male repeatedly. At the end of the sample period, all captive wasps were warmed in the sun and released from their vials. During each period, a record was made of the location, identity, time of capture, head-width, and wing-wear of every captured individual. Wing-wear (a correlate of age) was scored on a 4-point scale from 1 (no wear), to 2 (a nick or two), to 3 (evenly tattered outer edges of the forewings), to 4 (severe and irregular tattering of the outer parts of the forewings).

Statistical Analyses

The head-widths of male *H. ustulata* are normally distributed (Fig. 1; see also Kemp & Alcock 2003);
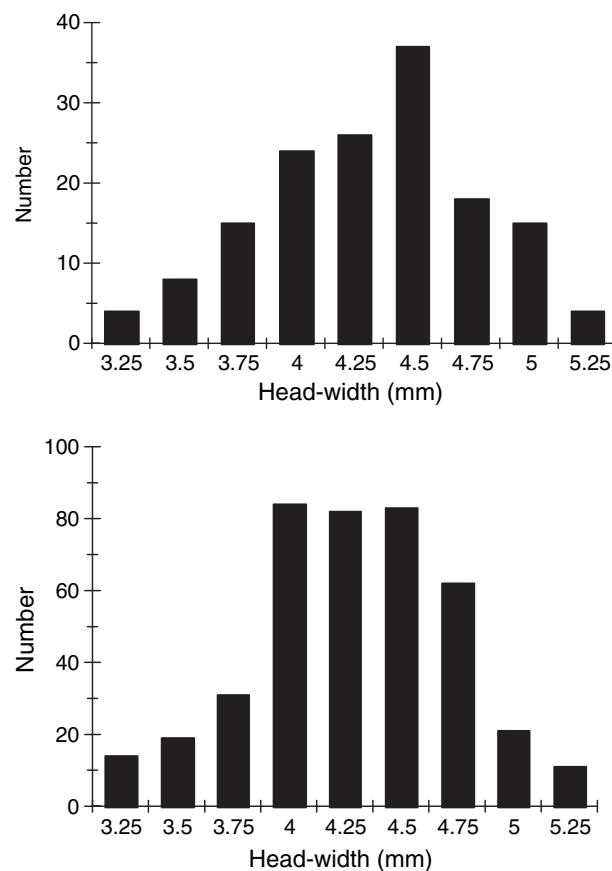
Fig. 1: Stability in the size distribution of male tarantula hawks, *Hemipepsis ustulata*, captured in the Usery Mountains in 2004 (top) and 2005 (bottom). To convert head-width to body mass, the following equation applies: fresh body mass (mg) $= 0.754 *$ head-width$^{3.87}$ ($n = 69$; from Kemp & Alcock 2003)

hence, we use t-tests and Pearson's correlation coefficient to evaluate group differences and bivariate relationships. In the case of the 2 h samples conducted in 2005, we constructed most parsimonious linear/non-linear models of (1) whether, and (2) when, males returned to the site in 1 h following their capture and release. Only males caught and released in the first hour were used in these analyses, excluding individuals that were strongly suspected to be residents because of their early appearance at a site over 2 or more days (these males have a history of attachment to their territory). To avoid pseudoreplication we only used the first record of males that were captured on more than one day. We included site (palo verde#1 or palo verde#2), date, time of release, and head-width, as well as the interactions of all variables with site. Wing-wear was not included in these models because it was redundant in the presence of the variable date (owing to a

very strong relationship between these variables; see results). Model fit was evaluated using Akaike's information criterion (AIC), which is better suited to the analysis of observational data, and provides for more robust solutions in the presence of unbalanced random variables. Further, in keeping with the principles of information theoretic analysis (Burnham & Anderson 2002), here we report and interpret results from the top three best-fitting models. Analyses were conducted using STATISTICA v7.0.

Means are presented ±1SD.

Results

The Effect of Body Size on Male Mating Success

Matings were seen during 10 field seasons between 1980 and 2005, but the total recorded was only 33 despite repeated visits to the study site by one or more observers who spent 2–4 h in the area during the morning activity period of the wasp. The observed copulations occurred between 27 March and 22 May. The precise dates of some older records (n = 8) have unfortunately been lost; of the remaining cases, four were recorded in March, 15 in April and six in May. The time of observed matings ranged from 0657 to 1125 M.S.T. Although 10 and 9 matings, respectively, were recorded at the two sites most popular with territorial males (palo verde# 2 at the peak itself and palo verde# 17 lower in the mountains), at least one copulation was seen at six other locations.

The mean head-width of the 13 known territorial males was 4.58 ± 0.32 vs. 4.26 ± 0.36 mm for the eight non-resident mating males (t = 2.13, df = 19, p < 0.05).

In addition, seven other males mated after they had replaced a territorial resident that had been temporarily removed from his site during various experiments. The residents, which were held in a cooler prior to release, had significantly larger head-widths (4.74 ± 0.26 mm) than their temporary replacements (4.24 ± 0.33 mm; paired t-test; t = 2.98, df = 12, p < 0.03).

If we pool all mating males, resident and non-resident, and then add the residents that had been captured shortly before a mating occurred on their territory (on the assumption that they would have mated had they not been removed), the mean head-width of this sample (n = 28) is 4.53 ± 0.36 mm, which is significantly larger than the mean head-width for the entire 2005 sample of 4.38 ± 0.45 mm (t = 1.77, df = 450, p = 0.04, one-tailed test).

Table 1: Mean ($\pm$ 1 SD) head-widths of male *Hemipepsis ustulata* at the Usery Mountains, AZ sampled between 1980 and 2005
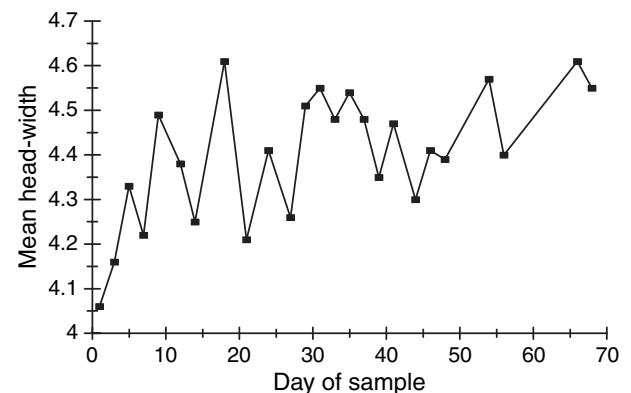
Year	n	Head-width
1980	210	4.41 ± 0.51
1981	125	4.40 ± 0.42
1987	142	4.32 ± 0.42
1998	272	4.37 ± 0.45
2001	119	4.30 ± 0.41
2004	151	4.41 ± 0.46
2005	424	4.38 ± 0.45

Stability in Male Body Size

Although size variation among males of *H. ustulata* is pronounced and highly persistent from year to year (Fig. 1), the mean male head-widths of the populations sampled over 25 yr have remained essentially constant (Table 1), despite the apparent large male mating advantage.

Body Size and the Timing of Male

The mean head-width of samples of unmarked males taken at two territories gradually increased over the 2005 flight season (Fig. 2), leading to a positive correlation between the mean head-width of the sampled males and the date of the collection (r = 0.59, n = 25, p < 0.005). But over all 10 yr of the study, matings were not concentrated in the latter part of the season, May and June (n = 6 copulations observed), compared to March and April (n = 14 matings observed; chi-square goodness of fit to randomly expected frequencies; $\chi_1^2 = 1.96$, p > 0.05). This result does not support the prediction that

Fig. 2: The mean head-widths of samples of unmarked males captured at two palo verdes used by territorial *Hemipepsis ustulata* on 25 d during the 2005 flight season. Mean daily sample size = 16.2 ± 7.4; range = 5–35; day 0 = Apr. 11

larger males time their emergence to coincide with the period when more matings occur.

Body Size and the Probability of Visiting Territories of Different Quality

As noted, male tarantula hawks have, over the years, been more attracted to palo verde#2 than palo verde#1 (Alcock & Carey 1988; Alcock 2000). So, for example, a male was present in palo verde#2 on 95 censuses in 2001 whereas palo verde#1 had a defender in place on only 68 censuses (Alcock, unpublished data). In 2005, an average of 18.7 males were captured at palo verde#2 during the 2 h sample periods, whereas palo verde#1 attracted only 7.1 males on average. The maximum number of visitors during any one sample was 35 for palo verde#2 compared to 14 for palo verde#1.

There was no difference, however, in the mean head-widths of the two populations of males: unmarked individuals taken at at palo verde#2 (n = 228) had a mean head-width of 4.43 ± 0.47 vs. 4.31 ± 0.40 mm for males (n = 102) captured at palo verde#1 (t = 0.08, p > 0.5). This result, admittedly involving only a single paired comparison, does not support our prediction that larger males should favor the more popular perching site.

Body Size and the Probability of Returning after Capture and Release

During the 2005 study, some male wasps did return to the two palo verdes after having been captured and released at these sites. For the 105 males that returned on the day of capture itself, the mean time to return was 33.6 ± 24.2 min. In addition, a group of 124 marked males returned to the study on days subsequent to the day of capture. For these males, the interval between first and last sighting was 9.6 ± 7.8 d (n = 124) with a maximum of 38 d, figures similar to those recorded in other years (Alcock 2000).

The proportion of males in the daily samples that had been captured and marked on previous days declined over the flight season (Fig. 3), but not because the pool of recently marked males was also declining. (The correlation between the number of males marked in the previous 8 d and the number of marked males captured during the 2 h sample on the ninth day was just 0.23; n = 24; p = 0.27). Instead, the steady decrease over the season in the number of marked males coming to palo verde# 1 and palo verde#2 on more than one day probably occurred because of increased mortality arising from an ageing male population, given the strong correlation between mean wing wear score and date (r = 0.87, n = 24, p < 0.001; Fig. 4).

In any event, if large males are more likely to acquire territories, especially those of high quality, then we would expect that returning males should be larger-than-average individuals. However, males returning to either palo verde#1 or#2 on the day of their capture in 2005 had a mean head-width of 4.39 ± 0.46 mm (n = 114), a figure nearly identical to the overall mean head-width of 4.38 ± 0.45 mm (n = 424). Nor were males that returned on subsequent days after their initial capture especially large; this group had a mean head-width of 4.40 ± 0.47 mm (n = 124).

We constructed multivariate models of the probability of males returning in the hour following their
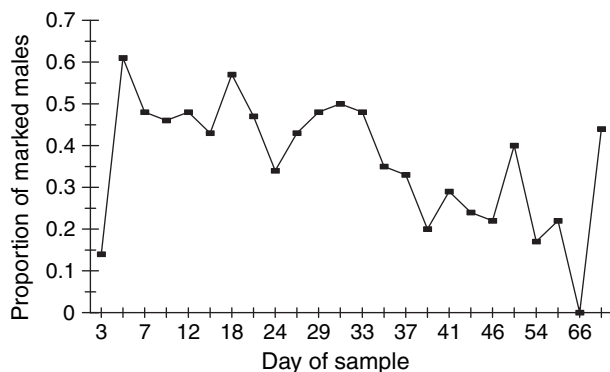
Fig. 3: The proportion of all males captured at two palo verdes on 25 d during the 2005 flight season that had been marked on any previous day. Mean daily sample size = 25.7 ± 9.4; range = 8–46; day 0 = Apr. 11
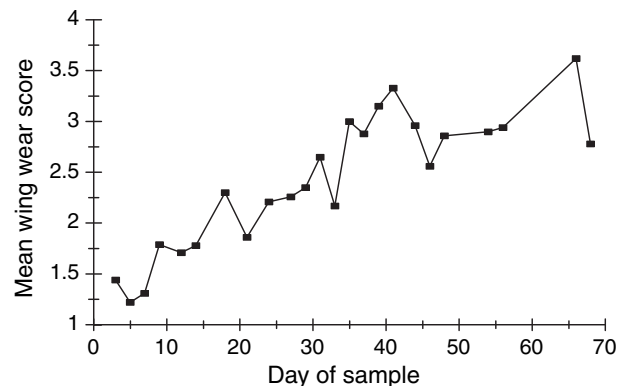
Fig. 4: The mean wing-wear score of samples of males captured at two palo verdes used by territorial *Hemipepsis ustulata* on 25 d during the 2005 flight season. Mean daily sample size = 25.7 ± 9.4; range = 8–46; day 0 = Apr. 11

Table 2: Results of the modeling of (a) whether or not males returned to their site of initial capture in the next hour, and (b) among those males that did return, how quickly they returned. The three best-fitting models for each case are presented (lower AIC values indicate better fit). The parameters included in each model are listed along with an estimate of their significance (adjudged using the Wald statistic), and their unique covariance with the dependent variable (semi-partial correlation). Significant model terms are in bold.

Question	Model	Model fit (AIC)	Model significance	Parameters included	Significance	Effect size (semi-partial r)
(a) Male return?	1	175.44	$G_2 = 8.15$, p < 0.05	1. **Site**	Wald = 5.14, p < 0.05	0.116
0 = 'no'				2. Time of day	Wald = 2.66, p = 0.10	−0.161
1 = 'yes'	2	175.60	$G_3 = 9.98$, p < 0.05	1. Site	Wald = 3.62, p = 0.06	0.157
				2. Time of day	Wald = 0.83, p = 0.36	−0.088
				3. Site × Time of day	Wald = 1.87, p = 0.17	−0.112
	3	175.94	$G_3 = 9.64$, p < 0.05	1. **Time of day**	Wald = 5.52, p < 0.05	−0.167
				2. Site	Wald = 2.99, p = 0.08	0.123
				3. Date	Wald = 1.48, p = 0.22	−0.084
(b) How quickly?	1	273.09	$G_1 = 5.42$, p < 0.05	1. **Time of day**	Wald = 6.31, p < 0.05	0.390
	2	273.15	$G_2 = 7.37$, p < 0.05	1. **Time of day**	Wald = 5.32, p < 0.05	0.343
				2. Site	Wald = 2.33, p = 0.13	−0.229
	3	273.51	$G_2 = 7.01$, p < 0.05	1. **Time of day**	Wald = 5.15, p < 0.05	0.349
				2. Date	Wald = 1.83, p = 0.18	−0.190

capture. The three most parsimonious models were statistically significant and implicated site and time of day as relevant predictors (Table 2a). Site was coded 1 = palo verde#1 and 2 = palo verde#2; hence, the positive semi-partial correlations for this variable suggest that the males captured from palo verde#2 were more likely to be seen again within an hour. To a lesser extent, males that were captured earlier in the first hour were also more likely to be recaptured within an hour. In addition, the best fitting models of when (in the hour following their capture) males returned to the site included time of day as the major predictor (Table 2b). Here, the positive semi-partial correlations also suggest that males were more likely to return quickly when caught earlier in the day. Note, however, that head-width did not feature in any of the most parsimonious models. The lack of an effect because of head-width in these analyses does not support the hypothesis that differently sized males possess different motivational strategies with respect to site residency.

Discussion

Male Size and Mating Success

Although non-territorial males of *H. ustulata* are clearly capable of capturing receptive females that will mate with them, some females in search of a mate do reach the hilltop territories and mate with males defending these sites. Given that the single territorial residents at palo verdes#1 and #2 faced from 6 to 18 non-territorial visitors on average in a

2 h period, the fact that we saw 20 matings by known territory holders (permanent and replacement residents) compared to just eight by non-territorial males suggests that territorial males have a mating advantage. Given that territorial males have consistently been found to be larger on average than non-territorial males, as shown in the current study as well as in Alcock (1979) and Alcock & Bailey (1997), we tentatively conclude that large males have a mating advantage in this species. Note, however, that we never attempted to systematically measure the mating success of territorial vs. non-territorial males because the probability of seeing even one mating on any given day was so low.

If we accept that large males of *H. ustulata* are more likely to mate, then we can ask whether there has been an evolutionary shift toward larger body size over time. A shift of this sort could occur either from an increase in the frequency of alleles that contribute to the development of larger body size in males or to an increase in the frequency of other alleles that lead adult females to lay haploid (male) eggs on larger spider prey. The data, however, show no hint of an increase in mean male head-width over 25 yr. In fact, despite different sample sizes and even different sampling methods, the mean male head-width (and the variance in male sizes) has remained remarkably constant during this time.

This result is suggestive of stabilizing selection either on male body size per se or, more probably, on female provisioning patterns. The wasps appear to be laying haploid (male) eggs on the same distribution of prey sizes from year to year, despite

fluctuations in rainfall that almost certainly affect the numbers and sizes of spider prey present in different years. Despite likely variation in the resource base available to nesting females, the size distribution of their sons has remained much the same in all 10 sample yr.

Stability in the mean body size of males could arise from reduced returns to females that produce extra-large sons as opposed to large daughters, as has been documented for the wasp *Philanthus triangulum* (Strohm & Linsenmair 2000). In the case of tarantula hawk wasps, the allocation of a large spider prey to a son may yield less fitness than if the prey were donated to a daughter, giving her higher fecundity and greater capacity to deal with large spiders herself when an adult. Similar decisions about the allocation of provisions may also contribute to stability in mean male head-widths recorded in the anthophorine bees *Centris pallida* and *Amegilla dawsoni*, whose females distribute different amounts of pollen and nectar to their sons and daughters (Alcock 1984, 1995, 1996).

In addition to the costs to mothers of producing especially large sons, there may be other tradeoffs that affect the fitness of larger-than-average males, such as decreased longevity, increased risk of predation, added time to development and reduced aerial maneuverability (e.g. Peckarsky et al. 2002; Stoks 2000; Thompson & Fincke 2002).

Behavioral Decisions by Large Males

The year 2005 was the first in which we detected a statistically significant tendency for larger males to appear later in the season than smaller ones. However, in 1986 males collected in the second half of the flight season were also somewhat larger than those taken and measured earlier (Alcock 1987). In addition, turnovers in ownership at consistently occupied territories have resulted in gradual increases in the size of territorial defenders there over some flight seasons (Alcock 1981, 1987).

Several proximate explanations exist for this pattern, including developmental constraints that slow the emergence of large males as well as greater mortality or dispersal of smaller males. But whatever the underlying proximate causes, the fact that smaller males appear to precede larger ones into the mate-locating habitat has ultimate consequences as well. In some insects, the small males that emerge sooner than larger ones avoid direct competition for mates with their more powerful rivals for a portion of the flight season (e.g. Alcock 1997; Jann et al. 2000). In

these species, small males are, however, generally active when relatively few females are available. In *H. ustulata*, however, smaller males are common during the period when receptive females are fairly abundant, given that more matings occurred in the first half of the flight season (March and April) than in the latter part (May and June). Why large males should tend to wait to be territorial in the second half of the flight season is therefore something of a mystery.

Although body size may affect male emergence decisions, size did not influence other potentially strategic aspects of male behavior. Thus, larger males did not visit the more popular palo verde#2 in preference to the less attractive territorial site, palo verde#1, even though palo verde#2 has consistently been the focus of intense competition among male tarantula hawks (Alcock 2000). Likewise, a male's size had no affect on the likelihood that he would return to the territorial sites examined in 2005, either on the day of capture or on subsequent days. In other words, although male body size apparently influences the probability that a male will become territorial at top-ranked sites, nevertheless the effect of body size is small or nil with respect to guiding patrolling males toward potential territorial sites of different quality or in motivating them to return a given location after an initial visit. Perhaps the effects of body size on male behavioral tactics are modest in this species because of the absence of direct physical combat in *H. ustulata* (Kemp & Alcock 2003). In any event, body size must not be the only attribute that affects male success in the competition for mates in this tarantula hawk wasp.

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