Title

The ecology and behavior of the sand wasp Steniolia nigripes (Hymenoptera: Crabronidae): natural history, resource utilization, and reproductive tactics

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The Ecology and Behavior of the Sand Wasp *Steniolia nigripes* (Hymenoptera: Crabronidae): Natural History, Resource Utilization, and Reproductive Tactics

A dissertation submitted in partial satisfaction of the requirements
for the degree Doctor of Philosophy in Biology

by

Gilene Mikali Young

2014

ABSTRACT OF THE DISSERTATION

The Ecology and Behavior of the Sand Wasp *Steniolia nigripes* (Hymenoptera: Crabronidae): Natural History, Resource Utilization, and Reproductive Tactics

by

Gilene Mikali Young

Doctor of Philosophy in Biology

University of California, Los Angeles, 2014

Professor Peter Nonacs, Chair

Differences in reproductive strategies are often hypothesized as the adaptive result of frequency-dependent and condition-dependent selection. However, conventional explanations of mating systems based on ecology do not include the fitness effects of interactions between the sexes. Ecological factors, phenotypic variation, and intersexual interactions must all be examined in order to understand the evolution of reproductive behavior. I investigated the natural history, ecology, and behavior of the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae), using both field observations and controlled behavioral trials. The sand wasps (Bembicinae) are a large, highly diverse group of wasps with extensive variation in male and female reproductive behavior across species. *Steniolia nigripes* shows reversed sexual size dimorphism and a previously undescribed resource-based territorial strategy in males. The results of this research indicate that the distribution of *S. nigripes* is determined primarily by the availability of prey used to provision offspring. Seasonal changes and social environment also affect the distribution and behavior of both male and female wasps. A small minority of male wasps hold territories consisting of plants that females visit for prey and nectar. These territorial males are significantly larger and more aggressive than other males, indicating that body size may be important to male competitive success. However, there is no clear evidence of female mating preferences based on either the size or the behavior of males, despite the frequent harassment of females by territorial males in the field. This species thus demonstrates unusual and highly variable morphological and behavioral phenotypes. Studying unique species such as *Steniolia nigripes* provides a rich opportunity for a comparative understanding of the evolution of body size and reproductive tactics.

The dissertation of Gilene Mikali Young is approved.

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2014

This dissertation is dedicated to my father, Dr. Stephen K. Young, and my sister,
Dr. Chantal D. Young, who have never doubted me for a second.

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Introduction

Background

Understanding behavioral and morphological variation within species is a continuing challenge in evolutionary biology. Differences in reproductive strategies are most often explained in the adaptive context of frequency-dependent and condition-dependent selection (Gross 1996; Alonzo and Warner 2000). Ecological factors can significantly influence the time and investment individuals dedicate to mating, as well as the costs and benefits involved in mating (Rowe et al. 1994; Watson, Stallmann, and Arnqvist 1998). However, traditional theories relating ecology and mating systems (Emlen and Oring 1977) do not account for the effects that the behavior of one sex can have on the fitness of the other (Alonzo 2007). While sexual reproduction has often been viewed as a cooperative endeavor involving both sexes, a conceptual shift is occurring that favors a more antagonistic coevolution in which male and female interests are opposed (Tregenza, Wedell, and Chapman 2006).Sexual conflict can have important consequences for both male and female fitness (Chapman et al. 2003; Arnqvist and Rowe 2005; Tregenza, Wedell, and Chapman 2006). Thus, understanding the evolution of reproductive strategies requires examining intersexual interactions in addition to ecological and individual effects on fitness.

Body size has the potential to affect intrasexual competition in males and females, mate choice, and conflict between male and female reproductive behaviors in multiple ways (Bonduriansky 2009). Sexual size dimorphism can determine the balance of power between two conflicting individuals, thereby influencing whether males or females have control over mating

(Ding and Blanckenhorn 2002). Large male size may improve a male’s chances of either defeating rival males or inducing a female to mate. Large female size can have critical effects on parental provisioning and fecundity (Bosch and Vicens 2006), as well as a female’s ability to deter unwanted mating attempts. Female resistance may select for increased male body size or strength (Jormalainen 1998; Arnqvist and Rowe 2002), which could impact selective pressures acting on both males and females. Furthermore, variation in resource availability can affect body size differently in males and females, so ecological conditions may modify the degree of sexual size dimorphism within species (Teder and Tammaru 2005).

Sand wasps (Crabronidae: Bembicinae) present a unique opportunity to study the importance of phenotypic variation in sexual interactions, because there is variability in sexual dimorphism and mating behavior across species. Sand wasp males can be highly aggressive, but are usually smaller than females (O’Neill 1985), so it is unlikely they are able to actually coerce females. Rather, their aggression may be an attempt to irritate females to the point that they mate out of convenience (Thornhill and Alcock 1983), or a means to prove their quality as mates. However, larger males can attain greater mating success (O’Neill and Evans 1983; O’Neill, Evans, and O’Neill 1989) in bembicine species in which males must hold onto females during flight in order to mate (Thomas and Nonacs 2002). Male-biased sexual dimorphism has also been shown to improve a male’s success in achieving copulation with reluctant females in other wasps (Teder 2005). In the bembicine wasp *Steniolia nigripes*, males are larger than females (Thomas and Nonacs 2002) and very aggressive, which is consistent with conflict over mating opportunities. Given this variability in sexual dimorphism and male aggressive behavior, the importance of sexual conflict may vary across species in this single tribe of wasps, but many species have not been studied (Evans 2002).

Outline of the Thesis

This thesis has two primary objectives. First, to describe the natural history, ecology, and behavior of *S. nigripes*, a species that is both unique and previously unstudied. Second, to investigate the mating system and reproductive behavior of *S. nigripes* in greater depth. Here I provide a brief summary of the structure of the thesis and of the major results reported.

In the first chapter, I discuss the natural history of *S. nigripes*, focusing on behavioral descriptions. There is little information available in the scientific literature about *S. nigripes*, so this chapter is designed as an introduction to the species and a resource for future researchers. I report my observations and knowledge largely without quantitative data.

The second chapter examines the ecology and habitat use of *S. nigripes*. In particular, I use statistical modeling to determine what factors predict the distribution of male and female wasps within their habitat. The models include sex, plant species, plant quality, habitat type, date, the presence of wasps of the opposite sex, and the presence of prey species as potential factors. The presence of other wasps and the abundance of prey are the strongest predictors of wasp presence, although plant species, habitat type, and date all have significant effects.

Thirdly, I describe the behavioral ecology of *S. nigripes* by investigating the relationship between the above-mentioned factors and the *type* of behavior performed, rather than merely presence/absence of wasps. The temporal progression of the season is the best predictor of both male and female behaviors. The behavior of wasps also differs based on the plant species they are visiting, and males and females respond differently to different plant species. In general, females spend more time foraging than males, and show less variation in their behavior.

In the fourth chapter, I focus on male aggressive behaviors, particularly territoriality. Although other species of sand wasps may defend female nesting or emergence sites, *S. nigripes* represents the only known case of resource-based territoriality. Territorial males are larger than non-territorial males. Furthermore, larger males are more aggressive, hold the most highly contested territories, and hold territories for longer. The success of large males in territory holding could clarify why *S. nigripes* shows reversed sexual size dimorphism, with males that are significantly larger than females.

Finally, I examine mating preferences in *S. nigripes* using arena trials. Unexpectedly, there is no evidence of an effect of male size and/or aggression levels on female mate preferences. Females do not consistently prefer any of the measured male traits. However, females do not entirely avoid males either, indicating a lack of strong aversion to possible mating attempts. This study suggests that females evaluate territory quality and may mate according to the resources controlled by a male, rather than directly evaluating male characteristics.

Body size is likely to affect the outcome of sexual selection in *S. nigripes* in multiple ways. Studying these questions will provide information on the fundamental processes of evolutionary biology underlying reproductive behavior, reproductive success in males and females, and the maintenance of phenotypic variation in populations.

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Chapter 1:

The natural history and behavior of the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae)

Abstract

Sand wasps (Crabronidae: Bembicinae) demonstrate an array of interesting behavioral and morphological traits (Evans 1966; O'Neill 2001; Evans and O'Neill 2007), but many of the approximately 1,700 species have not been investigated in depth. I studied a population of *Steniolia nigripes* located at the Granite Mountains in the Mojave Desert, California, from 2008 to 2013. This species has been studied very little and is almost nonexistent in the scientific literature. I present information on the distribution and habitat of these wasps, as well as seasonal patterns in population size and location. I also discuss the response of *Steniolia nigripes* to environmental variation. In addition, I describe the behavior of wasps of both sexes, including foraging, prey selection, aggression, and space use. This paper represents the first truly comprehensive description of *S. nigripes* natural history and behavior.

Introduction

Solitary wasps have long been of special interest to behavioral biologists, including the foundational ethologist Niko Tinbergen. Many solitary wasps are large, brightly colored, and fascinating to observe. Although they do not cooperate in nest-building as social species do, solitary wasps often aggregate in large numbers. These features have attracted naturalists to the study of solitary wasps for well over a century (O'Neill 2001; Pulawski 2014).The sand wasps

(Crabronidae: Bembicinae) are an appealing group of wasps with great variation in their behavior and extensive species diversity (Bohart and Menke 1976). Indeed, the Bembicinae are the second largest subfamily of the sphecid wasps, containing over 80 genera and more than 1,700 species (O'Neill 2001; Pulawski 2014). This diversity of species and the corresponding diversity of behavior present in the Bembicinae offer unique opportunities for comparative study.

Sand wasp females dig nests in the ground, both in isolation and in subsocial aggregations. In many species, males gather near females in mass swarms termed "sun dances"(Rau and Rau 1918). Males often form highly mobile, aggressive groups (Thomas and Nonacs 2002; Evans and O'Neill 2007), and competition among males can be dangerous to females in these aggregations (O'Neill and Evans 1983; Thomas and Nonacs 2002). In most bembicine species, females are larger (by up to 2.5 times) than males (O'Neill 2001; Evans and O'Neill 2007), but there are a few exceptions in which sexual size dimorphism is either absent or reversed (Evans and O'Neill 2007). *Steniolia nigripes* is one of the very few species of sand wasps with fully reversed sexual size dimorphism, such that males are substantially larger than females (Thomas and Nonacs 2002; Evans and O'Neill 2007). This species occurs in the Eastern Mojave Desert in California, as well as the Owens Valley and the Sonoran Desert zones of Southern California (Bohart and Gillaspy 1985). Despite its unique patterns of size dimorphism, *S. nigripes* has been studied very little and is almost nonexistent in the scientific literature. Here, I describe my general findings and observations about an eastern Mojave Desert population in order to expand our understanding of sand wasp natural history. Investigating unusual species such as *S. nigripes* provides context for future studies, and an important contrast for comparative research.

Location, Habitat, and Seasonality

I examined the sand wasp *Steniolia nigripes* at the Granite Mountain Desert Research Center (GMDRC) from 2008 to 2013. The GMDRC is a University of California reserve located within the Mojave National Preserve, 128 km east of Barstow, CA (34° 48’ 20” N, 115° 39’ 50” W). The Granite Mountains range from 1,128 – 2,071 m above sea level and include a variety of habitats characteristic of the Sonoran, Great Basin, and Mojave Desert ecosystems. The average precipitation is only 23 cm per year, with high interannual variability. The slopes of the Granite Mountains consist primarily of fractured granitic boulders, which produce a highly complex habitat structure. Compared to the surrounding areas, this type of rock retains more snowmelt and rain runoff (Sweeney Granite Mountains Desert Research Center 2014). Due to their unique transitional location, wide elevation range, and precipitation retention, the Granite Mountains are impressively diverse in both flora and fauna (Sweeney Granite Mountains Desert Research Center 2014).

Steniolia nigripes is found primarily on the southeastern side of the Granite Mountains, where average annual precipitation is estimated to be 2-4 cm greater than in other parts of the range. In 2008-2010 I extensively surveyed the Granite Mountains and other nearby ranges in order to determine the distribution of *S. nigripes*. The population at the Granite Mountains appears to be quite isolated, as I did not find *S. nigripes* more than approximately 5 km from the GMDRC.I searched in possible habitats within 25 km of the Granite Mountains, including the Providence Mountains and the Kelso Dunes, as well as on other aspects of the Granites. *Steniolia nigripes* was not detected in these surrounding regions, although they do live near multiple springs within the Granite Mountains. The vast majority of the population is located in the areas of Granite Cove and nearby White Fang (**Figure 1.1**), both of which contain several large washes fed by the Cove Spring. Smaller numbers of wasps may be found along Kelbaker Road within 2 km of the GMDRC entrance. I located *S. nigripes* mainly in washes and near roads, where more water is available and plants flower more often.

Although many species of sand wasps form large, easily found aggregations, *S. nigripes* is most readily found in the field by observing flowering plants. *Steniolia nigripes* visits a number of plant species for nectar feeding and hunting (see Chapters 2-3), and is abundant enough in washes to be present on most flowering plants. The only widespread wash plant that is not used by *S. nigripes* is creosote bush (*Larrea tridentata*); other characteristic wash plants,

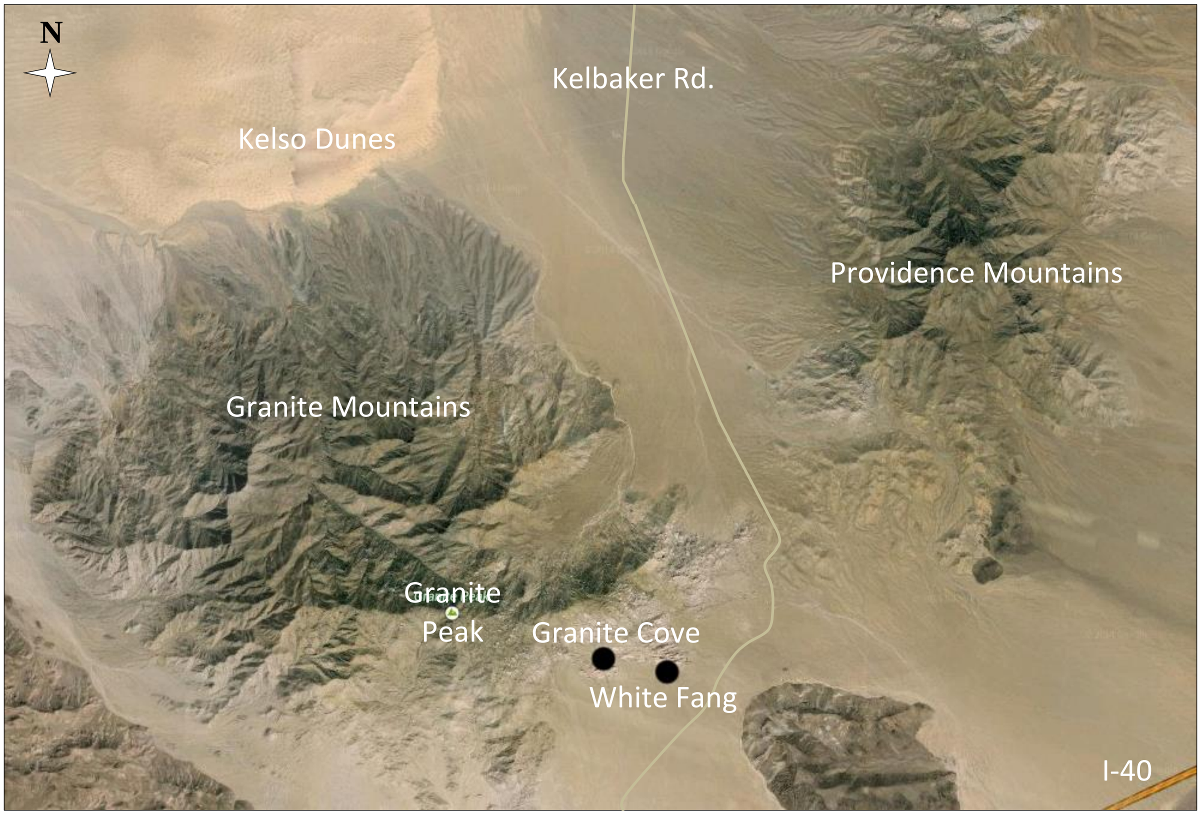

Figure 1.1. Map of the Granite Mountains and surrounding areas. Black dots represent the major locations of *S. nigripes*. Image © Google 2014.

such as catclaw acacia (*Acacia greggii*) and sandpaper plant (*Petalonyx thurberi*), are frequented. There is no apparent explanation for why *S. nigripes* avoids creosote bush. Wasps are most commonly seen flying or foraging in washes, often following boundaries such as wash banks or a road edge. They also use mixed creosote shrub and woody succulent habitat near washes for foraging and nesting. Nesting seems to occur mainly on wash banks, but I rarely found nest holes despite extensive searching. It thus seems likely that nest holes are closed when the wasp is away. Specific plant selection and species use are explored further in Chapters 2 and 3.

In 2009 only, I found another subpopulation of wasps along the trail leading up from Granite Cove to Granite Peak, where the trail intersected with a shady part of the spring bed containing standing water. This area was highly populated by many different species of insects, since water is a scarce resource. *Steniolia nigripes* females were clearly hunting insects that had come to collect water. Males flew over the water in groups of 3-5, chasing each other and females, but I was unable to discern any territoriality (i.e., behaviors that males used to aggressively exclude others from specific locations). Due to the difficult terrain, it was not obvious where the wasps were feeding and nesting, but I found no evidence that wasps individually marked in this location mixed with those at lower elevations. Interestingly, the wasps at the spring were significantly larger than those in Granite Cove and White Fang (**Table 1.1, Figure 1.2**). In particular, females at higher elevations closer to the spring were approximately 30% larger than females in low washes. Furthermore, females at the spring chased larger potential prey items (such as robber flies, Asilidae) than those in other locations. Thus, it is possible that large size in this population may be an adaptation to the size of available prey items. However, in 2010, *S. nigripes* was not present at the spring, though another sand wasp species (likely *Stictiella* sp.) occupied the same area. This second species does not emerge every year in the Granite Mountains, and I did not observe them in 2008 or 2009. From 2011 to 2013, the area did not have any standing water, perhaps explaining why no wasps were present. The possible relationship between *S. nigripes* body size and proximity to water sources in wet years requires further investigation, since it may have important consequences for male and female behavioral tactics.

Location Code	**Location Description**	**Females**		**Males**	
		Average Body Length (mm)	N	Average Body Length (mm)	N
1	Low elevation sandy wash	13.254 ± 1.213	23	18.456 ± 1.290	22
2	Mid elevation sandy wash	15.263 ± 1.215	25	18.077 ± 1.290	15
3	Higher elevation wash with standing water	17.591 ± 1.217	37	19.942 ± 1.290	9

Table 1.1: Mean (± SD**) body size of females and males at each location.**

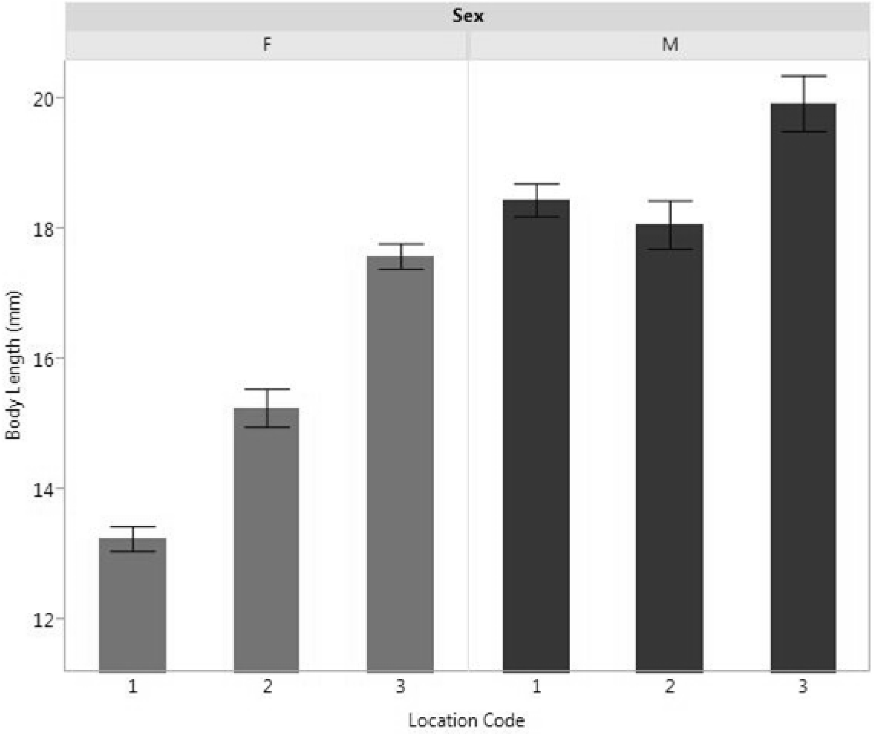

Figure 1.2. **Body size vs. elevation.** Body size of both male and female *S. nigripes* increases at higher elevations closer to a water source. Location 1: low elevation sandy wash; Location 2: mid elevation sandy wash; Location 3: higher elevation wash with standing water. Data are from 2009 only.

Steniolia nigripes appears to be a bivoltine species in the Granite Mountains, with two non-overlapping reproductive periods every year. There are two peaks in *S. nigripes* populations per year, the first occurring in June and the second in September, following the monsoonal rains which make up a substantial proportion of yearly precipitation. Based on tracking of marked individuals, individual wasps live for up to 2-3 weeks. The two population peaks represent separate generations. In the spring of 2013, I observed a strongly female-biased sex ratio in the population, perhaps as a result of extreme drought conditions – female wasps are smaller than males, and thus require less food during development. Without very many males present, female wasps are forced to create sons rather than daughters, since they cannot acquire sperm with which to fertilize their eggs. In the fall of 2013, the population was strongly male-biased, suggesting that these individuals were the offspring produced by the many unmated females in the spring. These males were also slightly smaller than males of previous years (see **Table 4.2**), further implying an effect of resource limitation in 2013. Thus, spring populations yield offspring in the fall, and vice versa, rather than in two separate yearly cycles.

Steniolia nigripes are highly sensitive to shifts in weather, on all temporal scales. Population emergence depends on warming spring temperatures. In 2012, when the spring was colder and windier than usual, wasps emerged several weeks late. Most striking, however, is their strong response to daily and hourly weather changes. Typically, wasps do not appear unless the temperature reaches at least 28°C, and they are most active when temperatures are around 32°C. If the weather is particularly cloudy or windy, wasps will not be active, regardless of temperature. In fact, even momentary shading caused by a cloud passing in front of the sun will result in the sudden disappearance of wasps. Once direct sunlight returns, wasps will immediately reappear. It is not entirely clear where they go in these short cloudy intervals, but they are likely resting on the ground under or near plants. Similarly, high winds (common in the Mojave) will cause wasps to retreat due to the difficulty of controlled flight in windy conditions. Given the highly variable climate of the Mojave, the flexibility of *S. nigripes* in response to shifting conditions may be an important adaptation.

Male Behavior

Aside from mating, the daily behavior of male *S. nigripes* may be classified into two broad categories: foraging and aggression. All males forage, but there is significant variation in the amount and type of aggressive behavior. The diet of adult males appears to consist entirely of nectar collected from flowering bushes. When foraging, a male lands on a flower and visibly extend his labium (lower lip or tongue), which is exceptionally long in all *Steniolia*. The wasp will quickly insert and remove his labium from each flower in a small area of 3 centimeters at most, with no clear pattern. He usually does not try every flower. When finished with one area, he flies in a short hopping motion to another area, and repeats the feeding movements. However, males often alternate between foraging and other behaviors. This is especially true of highly aggressive males, which need to forage, but rarely spend more than a few seconds at a time foraging. Rather, highly aggressive males only feed when no potential competitors (or mates) are nearby. Males will forage at a variety of plant species, and transition from species to species as they bloom.

Male aggressive behavior takes several forms. The most commonly observed aggressive behavior is patrolling flowers. A patrolling male will circle over the top of a plant, usually around 10 cm above the plant. Patrolling males fly in a stereotyped, repeated path from plant to plant, although they may stop to forage, change direction, or interact with other insects along the path. A small number of males patrol the same plants consistently, and prevent other males from patrolling there via aggressive interactions. These males patrol and defend certain areas for days at a time (see Chapter 4). When a male encounters another insect while patrolling, several outcomes can result. Some males chase any insect they see, whether it is another male, a female, or an entirely different insect species. Alternatively, some males patrol and chase, but do not actively pursue other individuals as often. When two or more males meet, they chase and circle each other in flight for up to 10 seconds. Chases usually take males away from the plant territory, and end when one male flies away and the other (victorious) male returns to the plant. Aggressive interactions may involve multiple individuals, with 5 or more males chasing each other or a female and covering large areas. If no especially aggressive males are present, several wasps may investigate and forage on a single plant, but patrolling males typically prevent other males from nearing the plant they are defending.

When a patrolling male detects a female, he will attempt to interact with her immediately. More aggressive males will dive rapidly onto a female, grab her, and attempt to mate with repeated stabbing motions of the abdomen. However, females typically resist these attempts, and will often escape from the male’s hold. Once a female is out from underneath the male, she may fly away entirely, or the male may continue to chase her up into the air. Due to the swift, elevated nature of these interactions, it is nearly impossible to observe mating taking place in the field. Most commonly, a male will be observed pursuing a female, but not actually contacting her. In some cases, this may be a combination of territorial behavior and mating behavior.

Male *S. nigripes* exhibit variation in abdominal color that appears related to body size. In general, male wasps have bright yellow and black patterning. However, in larger males the yellow is tinted green or blue, and especially large males may appear more blue than yellow (**Figure 1.3**). Females do not show any blue coloration, regardless of body size. In other species of solitary wasps, color variation can have a strong effect on thermoregulation because darker colors absorb more solar radiation than light colors (Willmer and Unwin 1981; Willmer 1983; O'Neill 2001). Large body size also affects thermoregulation, as larger wasps warm more quickly and maintain higher body temperatures while active (Willmer and Unwin 1981; Willmer 1985a; Willmer 1985b), in addition to experiencing larger energetic costs during flight (Larsson 1990). Thus, large dark insects may be more active at cooler temperatures, while small bright insects may be more active at higher temperatures (Willmer 1983). The size-linked color variation in male *S. nigripes* is potentially an adaptation for the differing physiological requirements of aggressive behavior and foraging. Due to the high energetic demands of flight, large aggressive males may be subject to higher heat stress. For example, in the sand wasp *Bembecinus quinquespinosus*, larger males engage in more intensive scramble competition,

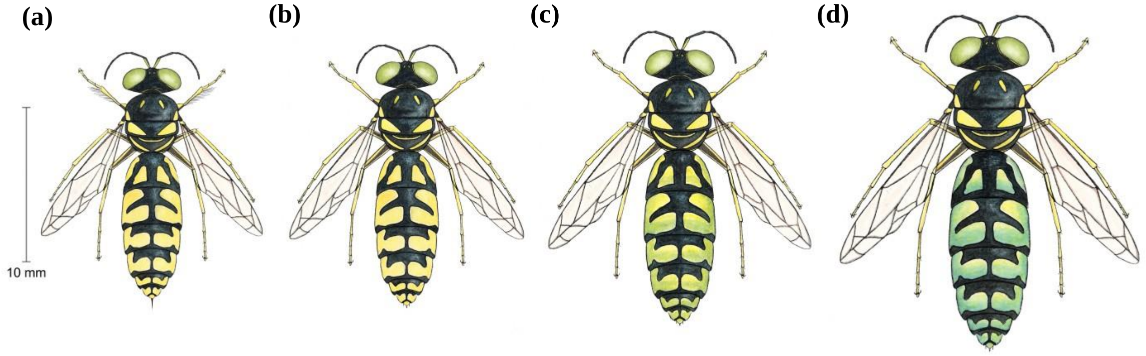

Figure 1.3. Size and color variation in *S. nigripes*. a. female, **b-d.** male. Illustration by Julie Himes.

experience hotter microenvironments, and show higher proportions of yellow instead of black coloration (O’Neill and Evans 1983; O’Neill et al. 1989). However, *S. nigripes* males differ in color tint, rather than proportion of light to dark colors, so it is not entirely clear what drives the size-linked color variation in this species.

Female Behavior

Female *S. nigripes* spend the majority of their time on food acquisition, either for themselves or for their offspring. However, females are also highly vigilant, and responsive to the presence or movement of any other insects. The foraging of adult females appears very similar to that of males – they take nectar from flowers using their long tongues and move frequently between flower clusters. Before foraging on flowers, a female will almost always observe the plant from a short distance, either in flight or resting on the ground. Females often circle plants or clusters of plants, flying very near the ground and landing occasionally. These behaviors were termed active vigilance and resting vigilance due to the female’s high awareness of and responsiveness to any nearby insects. A female typically avoids proximity to other insects, unless she is hunting. If she does not encounter other insects during this time, she will proceed to the flowers to forage. Unlike males, who remain near the tops of plants, female wasps often forage on low flowers.

Female wasps of different body sizes demonstrate variable space use on plants. I observed females in the field and recorded their body size and relative location on the plant (bottom third, middle third, or top third). Body size was either directly measured from captured females, or visually estimated as small (11-12 mm), medium (13-14 mm), or large (15 mm or more). The accuracy of these estimates was frequently checked by subsequently catching the female and measuring the precise body length. Female body size was strongly related to the relative height of the female on the plant, for both measurement techniques (**Figures 1.4-1.5**). Typically, the higher portions of the plant are where most of the flowers are located, and hence where most insects may be found. Smaller females may be attempting to avoid interactions with other insects by remaining low on plants. Larger females go farther up on plants, where they are

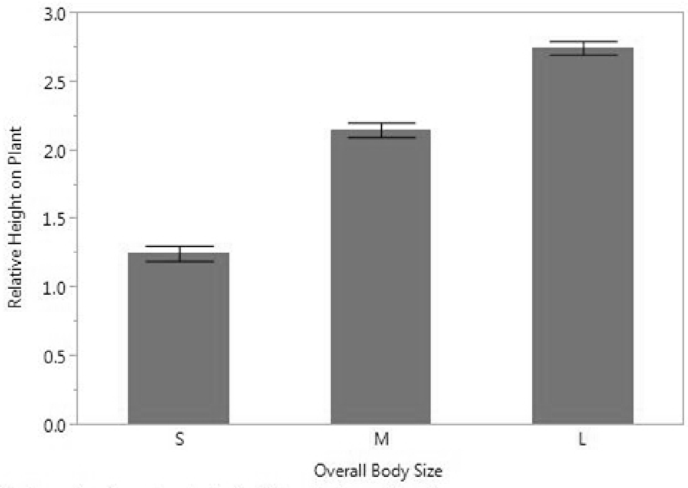

Figure 1.4. Relative female body size and space usage on plants. Small females remain at low heights, while larger females will fly to higher parts of the plant (N = 240, $\chi^2 = 142.5$, *df* = 2, p < 0.0001).

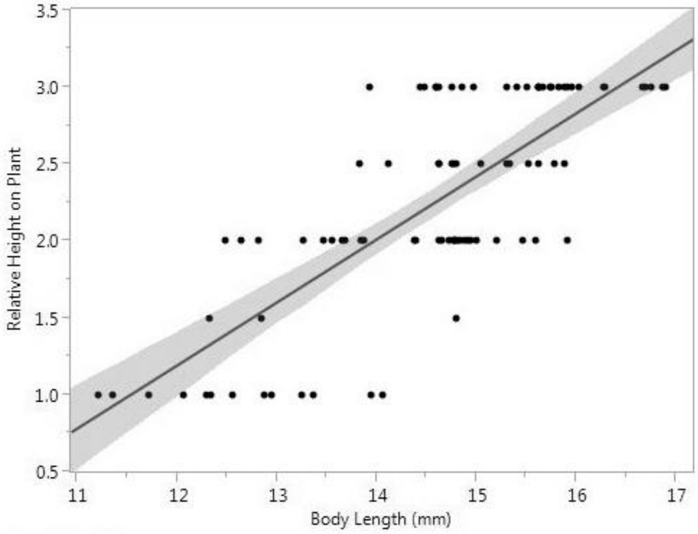

Figure 1.5. Female body size vs. height on plants. Female body size is strongly correlated with how high they will travel on plants (N = 87, Spearman's ρ = 0.714, p < 0.0001).

more likely to encounter harassment from males or other insects. Higher areas also likely have lower ambient temperatures, which may be an advantage to wasps of larger body size (Willmer 1985b; Larsson 1990). Females do not appear to defend portions of plants in any way.

Female hunting behavior is quite distinct from nectar foraging. When hunting, females will often hover nearly motionless, observing potential prey from a short distance. This hunting vigilance is accompanied by a high-pitched noise produced by the rapid, contained wing movement necessary for hovering. A hunting female may slowly move within the inner branches of a plant, while continuing to hover. This behavior is easily differentiated from nectar feeding because the female rarely lands. When tracking a potential prey, a female will begin hovering in a single spot, increase her wing speed (as evidenced by increased volume and pitch of wing noise), and then quickly dive towards the prey. She grabs the prey insect with her legs and mandibles, and immediately attempts to sting it. It is not uncommon for a hunting dive to fail. Insects may fly away before the female can catch them, struggle to such an extent that she loses her grip, or escape before she is able to sting sufficiently. In some cases the female may sting the insect once to slow it down, land while still holding on to it, and sting a second time. Once a female has successfully immobilized the prey, she will carry it in flight to a nest hole using her legs.

Although females may occasionally pursue honey bees or robber flies, *S. nigripes* have never been observed successfully capturing anything other than Diptera, and the most common prey choice is small Diptera. These dipterans may belong to any of a number of apparently widespread species, but are usually Bombyliidae approximately 3-8 mm in length. This is consistent with observations of other *Steniolia* species (Evans and O'Neill 2007). Most

Bembicini are progressive provisioners (Evans and O'Neill 2007), meaning that females provide hatched larvae with a continuous supply of new prey items. This is assumed to be the case in *S. nigripes*, but as the nests were difficult to find, it was not possible to directly examine nest contents. Given the extensive sexual size dimorphism in *S. nigripes*, offspring provisioning must be sex-biased so that daughters receive substantially fewer or smaller prey items than sons.

Female *S. nigripes* have an extensive fringe of setae, called rake spines, on the front legs, which are used for nest digging (Bohart and Gillaspy 1985; O'Neill 2001). Like other sand wasps, they usually dig in variably sandy substrate, either along the banks of washes or in open areas such as parking lots or clearings (Evans 1966; Evans and O'Neill 2007). The nests may be either clumped or solitary, as is more common in the Granite Mountains. When clumped, nest aggregations are small, ranging up to approximately 10 nest holes which may be as close as several centimeters to each other. Nests are difficult to find, and it is more common to find either a single individual nest or trial holes only. Many sand wasps create huge, obvious aggregations of hundreds or even thousands of nests (Evans 1966; Evans and O'Neill 2007), so the nests of *S. nigripes* are less well suited to study than those of other species. Marking of individual females indicates that females dig more than one nest, often right next to each other. It is not clear whether these holes represent false nests or in fact contain multiple larvae, and both strategies have been found in other species of sand wasps (Evans 1966; O'Neill 2001; Evans and O'Neill 2007).

Future Directions

These observations, and the research reported in the following chapters, represent the first comprehensive study of *Steniolia nigripes*. This species is a fairly derived sand wasp (Bohart and Gillaspy 1985) with a number of intriguing characteristics, including male territoriality, color variation, reversed sexual size dimorphism, intersexual aggression, and variable use of resources. However, there is still much that is unknown about this species. For example, sand wasps either sleep in shallow burrows or in clusters on branches (Evans 1966; Evans and O'Neill 2007), but it is not clear where *S. nigripes* spends the night. Further study is needed on many aspects of their life history, especially the timing of reproduction and dispersal. In addition, future research should investigate the fecundity of wasps of various sizes, and the extent to which size is heritable. This species potentially presents a rich study system applicable to a variety of research questions.

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Chapter 2:

Habitat use, population abundance, and spatial variation in the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae)

Abstract

This study examines habitat use by the sand wasp *Steniolia nigripes* in the Granite Mountains, located within the Mojave National Preserve, California. I surveyed plants of six different species from May to October of 2010, measuring wasp presence by sex, plant quality, abundance of dipteran prey, and landscape features in order to determine if ecological factors predict the distribution of *S. nigripes*. Statistical analysis using generalized linear mixed models indicated that male and female wasps used the same plants, and that plant choice was driven more by opportunities to catch prey for nest provisioning than opportunities to forage on nectar. Arroyos sustained larger wasp populations than any other type of habitat. Although male and female presence were positively correlated, wasp use of a minority of sites and plant species occasionally differed between the sexes, suggesting additional ecological effects not yet measured.

Introduction

Sand wasps (Crabronidae: Bembicinae) are a widely distributed, charismatic group, well known to casual entomologists for their bright colors, large size, and observable nesting behaviors. However, little has been reported on bembicine wasps in the scientific literature. Most commonly reported are the nesting behavior and prey use of a few better-studied species, mainly in such genera as *Sphecius*, *Bembix*, *Microbembix* and *Bembecinus* spp. (Evans 1966; O'Neill, Evans, and O'Neill 1989; Evans 2002; Evans and O'Neill 2007). Although many bembicine wasps may appear superficially similar, there is variation in habitat use, behavior, and sexual size dimorphism across even closely related species (Toft 1987; Evans and O'Neill 2007). Accounts of a wide variety of ecological, behavioral, and morphological traits in sand wasps suggest a potentially rich area for study (Evans and O'Neill 2007).

This study investigates the microhabitat use, population abundance, and spatial variation in the species *Steniolia nigripes*. This species occurs in the Eastern Mojave Desert in California, as well as the Owens Valley and the Sonoran Desert zones of Southern California. *Steniolia nigripes* is one of the very few species of sand wasps with fully reversed sexual size dimorphism, such that males are substantially larger than females (Thomas and Nonacs 2002; Evans and O'Neill 2007). This species also demonstrates a unique resource-based territorial strategy (see Chapter 4), which has not been described in any other bembicine wasp. Plants serve two purposes; first, as nectar sources for foraging adult wasps, and second, as sites where females find prey with which to provision their offspring. Males compete for and defend plant resources that females visit, and size is a key component of male territorial success (Ch. 4). Ecology can have profound implications for mate searching strategies such as territoriality (Alcock 1979; Thornhill and Alcock 1983; Kemp and Alcock 2003; Peixoto et al. 2012; Oliveira et al. 2013), so considering the ecological context of this novel behavior is critical. In this paper, I will examine a number of ecological factors, including landscape features, intraspecific abundance, and the presence of prey species, in order to determine what affects the distribution of male and female *S. nigripes* within their habitat.

Methods

Study site

Research was conducted from May 25 through October 1 of 2010 at the Granite Mountains Desert Research Center (GMDRC). The GMDRC is a University of California reserve located within the Mojave National Preserve, 128 km east of Barstow, CA (34° 48' 20"N, 115° 39' 50" W). The Granite Mountains range in elevation from 1,128 – 2,071 m asl and include a variety of habitats characteristic of the Sonoran, Great Basin, and Eastern Mojave Desert ecosystems. Sand wasps such as *Steniolia nigripes* primarily live in lower-elevation sandy washes at this location, and are more prevalent at the foot of the Granite Mountains than in surrounding areas. Six sites were chosen for study, all within 3 km of the GMDRC (**Figure 2.1**).

Observations of marked individuals indicated that each site represented a separate population of wasps, as individual wasps were never seen outside of a single area. There were no obvious barriers to dispersal among sites, except for the scattered distribution of wash plants. All sites included either a wash or a road, where more water is available due to runoff from seasonal rains. Each site was classified into one or more location types: mixed (woody and creosote scrub vegetation); wash (broad sandy arroyo, typically with steep banks); dirt road (surrounded by mixed vegetation); or paved road (with sand or gravel substrate on either side). When a site included more than one location type, plants were individually assigned a location type based on their precise location. Two of these sites were outside the boundaries of the GMDRC along Kelbaker Road, which is the primary thoroughfare through the Mojave National Preserve but usually receives low levels of traffic. The remaining sites were within the GMDRC and thus experience very little disturbance. Two sites included multiple subpopulations of wasps which were within 50 m of each other but did not appear to mix, based on repeated observations of marked individuals.

Sampling Design

Across the 6 sites, a total of 240 individual plants were labeled and examined over the course of the season. Plants were chosen randomly at each site, and included 6 species that *S. nigripes* commonly visits: catclaw acacia (*Acacia greggii*); California buckwheat (*Eriogonum fasciculatum*); flat-top buckwheat (*Eriogonum plumatella*); threadleaf snakeweed (*Gutierrezia*

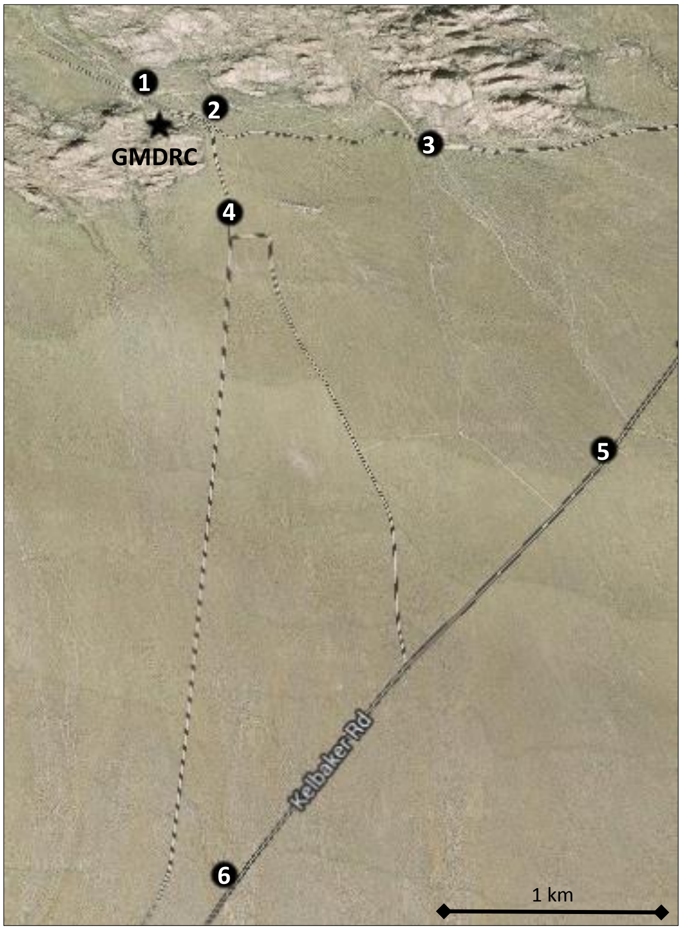

Figure 2.1. Map of study sites relative to the GMDRC. Location types were as follows: Site 1, mixed and wash; Site 2, mixed; Site 3, wash; Site 4, dirt road; Site 5, mixed and paved road; Site 6, paved road. Image © Google 2014.

microcephala); sandpaper plant (*Petalonyx thurberi*); and threadleaf ragwort (*Senecio flaccidus*). Each of these species reaches peak flowering at different points in the progression of the season. Plants were only included in observations when they had green stems, since wasps do not visit dry plants. Green plants were observed every 1-2 weeks, for a total of up to 8 observations over the course of the season.

For each plant, the height, area, and number of flowers blooming was measured. Area was estimated as an ellipse using the formula $A = 0.25\pi d_1 d_2$, where d_1 and d_2 are the two longest perpendicular axes crossing the center of the plant (as in Arango et al. 2000). Plant size was then calculated as the volume of an elliptical cylinder. When it was unfeasible to count each flower individually, number of flowers was extrapolated from a 15cm x 15cm quadrat. In addition, the insects present at each plant were counted for 1 minute. Most plants are less than 1m tall, allowing observers to see the entire plant at once. When plants were taller, observers walked around the plant to see all sides. During each minute, observers recorded the number, behavior, and sex of all *S. nigripes*, and the number of small to medium sized Diptera (representing the available prey for *S. nigripes*, and thus not including large dipterans such as robber flies and flower flies) visiting the plant.

Statistical Analyses

A generalized linear mixed effect model was constructed to predict the distribution of *S. nigripes* on plants. Fixed effects included the presence of *S. nigripes* of the opposite sex, quantity of Diptera, plant volume, flower quantity, and location type (see above). Fixed effects were tested for collinearity with Pearson's correlations. Plant species and plant ID were included as nested random effects to account for multiple measurements across species and individual plant, and to compare ecological factors not related to plant type (Bolker et al. 2008). Four separate models were tested (presence/absence and number of wasps for each sex) to evaluate whether wasp presence correlated to plant characteristics, presence of prey, presence of other wasps, or landscape effects. In order to test for interactions between plant community variation and location type, an additional two models (presence/absence of each sex) were tested with only plant species and location type as fixed effects, and plant ID as a random effect. The relative explanatory power of each variable was assessed by comparing models with the Akaike Information Criterion corrected for small sample size (AICc), using the lme4 package in R 3.0.2 (R Core Team 2013; Bates et al. 2014).

Results

For all models, the presence of the opposite sex was an important component predicting the distribution of wasps. Female presence was the strongest predictor of male presence (β = 0.17, ΔAICc = 51.24, $w_i < 0.001$) and of the number of males on a plant simultaneously (β = 0.32, ΔAICc = 57.05, $w_i < 0.001$). Similarly, male presence was the strongest predictor of female presence (β = 0.19, ΔAICc = 49.05, $w_i < 0.001$) and of number of females (β = 0.302, ΔAICc = 48.13, $w_i < 0.001$). Removing the effect of the opposite sex always resulted in the model with the highest AICc (**Tables 2.1-2.4**).

Table 2.1. Summary of models explaining the presence or absence of male wasps on plants.

Model	AICc	ΔAICc	*K*	w_i
Full model – volume	898.93	0	7	0.513
Full model – flowers	899.04	0.11	7	0.486
Female + flies + flowers + volume + location type (full model)	913.91	15.08	8	<0.001
Full model – location type	918.76	19.83	5	<0.001
Full model – flies	925.67	26.74	7	<0.001
Full model – female	950.17	51.24	7	<0.001

"Female" represents the presence or absence of female wasps. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=1383.

Table 2.2. Summary of models explaining the number of male wasps on a plant simultaneously.

Model	AICc	ΔAICc	*K*	w_i
Full model – flowers	2532.75	0	7	0.936
Full model – volume	2539.54	6.79	7	0.032
Female + flies + flowers + volume + location type (full model)	2545.76	13.11	8	0.001
Full model – flies	2552.55	19.80	7	<0.001
Full model – location type	2558.45	25.70	5	<0.001
Full model – female	2589.80	57.05	7	<0.001

"Female" represents the presence or absence of female wasps. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=1383.

Table 2.3. Summary of models explaining the presence or absence of female wasps on plants.

Model	AICc	ΔAICc	*K*	w_i
Full model – flowers	1080.49	0	7	0.974
Full model – volume	1087.81	7.32	7	0.025
Male + flies + flowers + volume + location type (full model)	1095.02	14.64	8	<0.001
Full model – flies	1103.56	23.07	7	<0.001
Full model – location type	1128.45	47.96	5	<0.001
Full model – male	1129.54	49.05	7	<0.001

"Male" represents the presence or absence of female wasps. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=1383.

Table 2.4. Summary of models explaining the number of female wasps on a plant simultaneously.

Model	AICc	ΔAICc	K	w_i
Full model – flowers	2463.11	0	7	0.981
Full model – volume	2471.14	8.03	7	0.018
Male + flies + flowers + volume + location type (full model)	2476.49	13.49	8	0.001
Full model – location type	2499.91	36.80	5	<0.001
Full model – flies	2500.85	37.74	7	<0.001
Full model – male	2511.24	48.13	7	<0.001

"Male" represents the presence or absence of female wasps. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (K), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=1383.

Including fly presence improved the model for both sexes. Increasing fly populations were related positively to male presence ($\beta = 0.03$, ΔAICc = 26.74, $w_i < 0.001$), number of males ($\beta = 0.04$, ΔAICc = 19.80, $w_i <0.001$), female presence ($\beta = 0.03$, ΔAICc = 23.07, $w_i < 0.001$), and number of females ($\beta = 0.06$, ΔAICc = 37.74, $w_i < 0.001$). Models with lower AICc scores always included the effect of flies (**Tables 2.1-2.4**). However, the effect of flies was substantially less than that of the opposite sex.

The number of flowers on a plant and the volume of a plant were both much weaker predictors of wasp presence, and produced similar effects in the models (**Tables 2.1-2.4**). The inclusion of either flowers or volume was important for all models, but including both never improved the model. For 3 of 4 response variables, volume produced a lower AICc than flowers, but the difference was usually small.

Location type was also a component of the best models for all four response variables, with washes being the preferred location for both sexes (**Figure 2.2**). Areas with mixed vegetation were the second most visited by both sexes. Although males visited both dirt and paved road sites equally, females were almost never found along a paved road. The composition of the plant community varied in the different habitat types (**Figure 2.3**), with both dirt and paved road sites containing fewer species than washes or mixed habitats. Males and females generally used the same species of plants, but not always (**Figure 2.4**). Male wasps were much more likely to be found on *Acacia greggii* than females, while females preferred both species of *Eriogonum*. Males and females both used *Petalonyx thurberi* extensively.

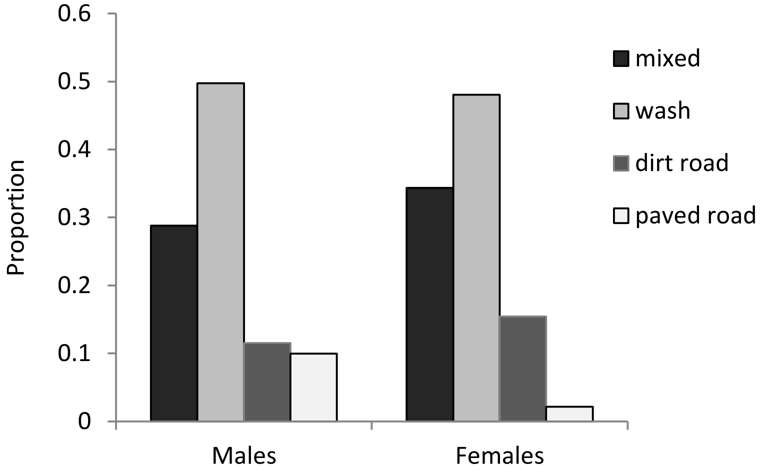

Figure 2.2. Proportion of observations including *S. nigripes* at locations of each type. Location type had a significant effect on the presence of males ($\chi^2 = 79.1$, *df* = 3, $p < 0.001$) and on the presence of females ($\chi^2 = 114.9$, *df* = 3, $p < 0.001$).

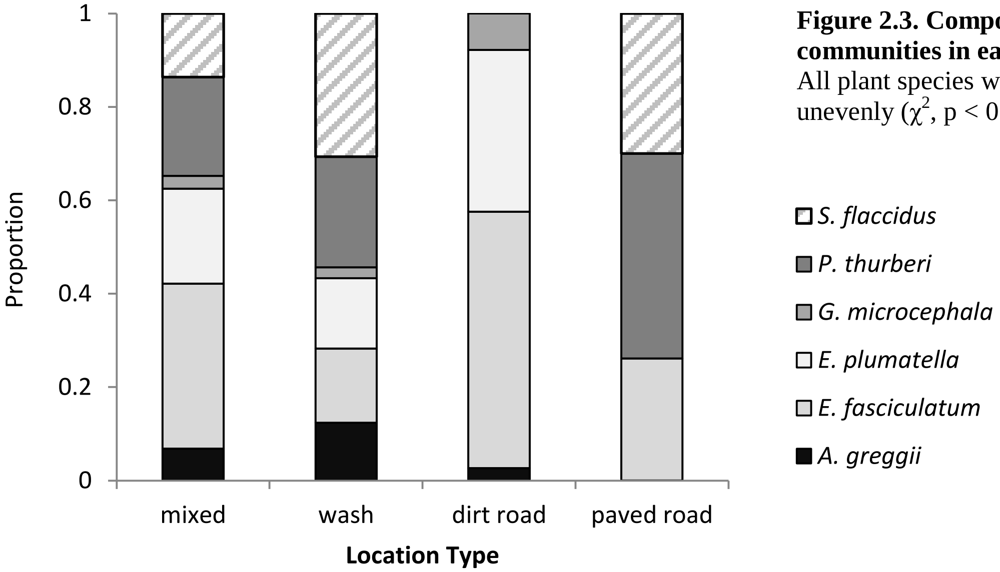

Figure 2.3. Composition of plant communities in each location type. All plant species were distributed unevenly (χ^2, $p < 0.001$ for all).

In order to separate the effect of plant species (**Fig. 2.4**) from the variation in plant communities by location type (**Fig. 2.3**), two additional models were tested to determine if plant species and location type interacted. The best model for each sex included both species and location type separately, and did not include an interaction effect (**Tables 2.5-2.6**).

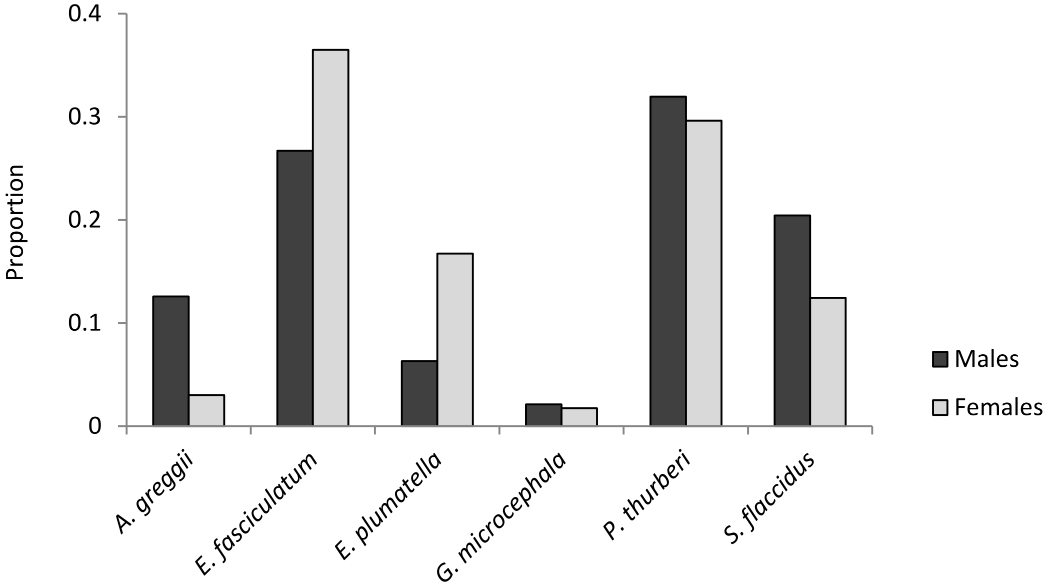

Figure 2.4. Proportion of observations including *S. nigripes* on each species of plant. Plant species has a significant effect on the presence of males (χ^2=78.5, *df*=5, p<0.001) and of females (χ^2=138.2, *df*=5, p<0.001).

Model coefficients (**Table 2.7**) indicated that the best plant predictor of male presence was *A. greggii*, followed closely by *P. thurberi*. Females were most often found on *P. thurberi* and the two species of *Eriogonum*. Both males and females were more likely to be found in washes than anywhere else.

Not all plant species flowered for the entire study period. Rather, each species had a distinct peak in flowering at different times (**Figure 2.5**).

Table 2.5. Summary of models testing the interaction between plant communities and locations in predicting the presence of male wasps.

Model	AICc	ΔAICc	*K*	w_i
Species + location type	1043.10	0	9	0.761
Species * location type	1045.42	2.32	19	0.239
Location type	1070.58	27.48	4	<0.001
Species	1085.16	42.06	6	<0.001

The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=1388.

Table 2.6. Summary of models testing the interaction between plant communities and locations in predicting the presence of female wasps.

Model	AICc	ΔAICc	*K*	w_i
Species + location type	1140.71	0	9	0.953
Species * location type	1144.06	3.96	19	0.047
Location type	1180.06	39.35	4	<0.001
Species	1242.50	101.79	6	<0.001

The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=1388.

Table 2.7. Model coefficients for the effect of each species of plant and type of location on male and female *S. nigripes*. Predictors are arranged in order of decreasing *β*.

Males	Plant Species	*β*
	A. greggii	0
	P. thurberi	-0.021
	S. flaccidus	-0.582
	E. fasciculatum	-0.629
	G. microcephala	-1.016
	E. plumatella	-1.767
	Location Type	*β*
	Wash	0.183
	Dirt road	0
	Paved road	-0.972
	Mixed	-0.987

Females	Plant Species	*β*
	P. thurberi	1.873
	E. fasciculatum	1.669
	E. plumatella	1.133
	S. flaccidus	0.655
	G. microcephala	0.569
	A. greggii	0
	Location Type	*β*
	Wash	0.459
	Dirt road	0
	Mixed	-0.827
	Paved road	-2.578

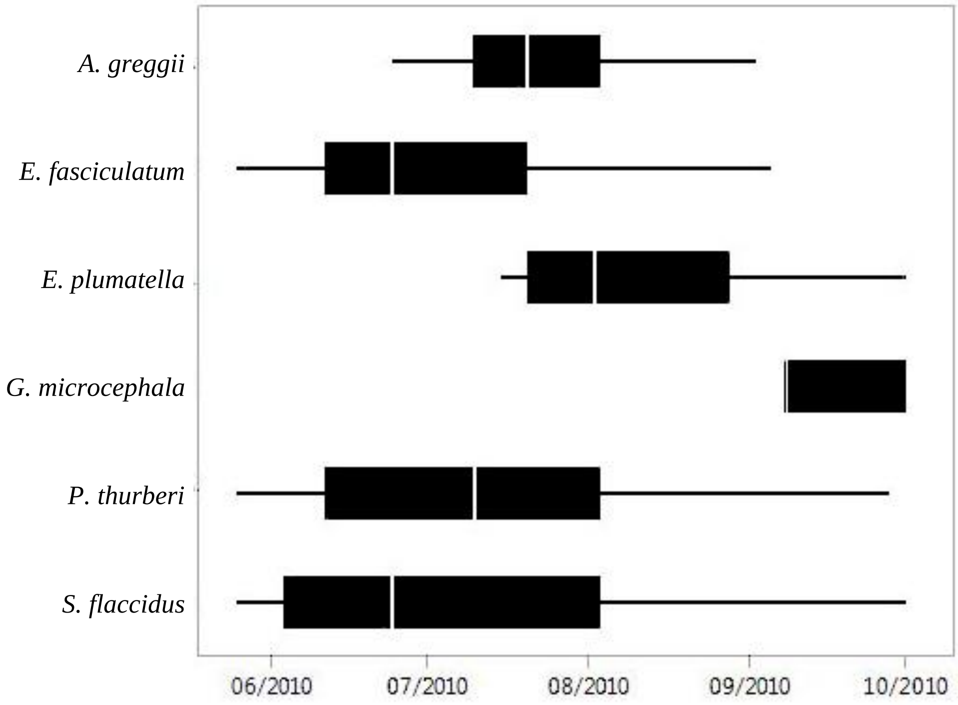

Figure 2.5. Flowering periods of each plant species. Boxes are defined by median and quartiles. Whiskers represent the total measurement period for each species.

Discussion

The models tested in this study indicate that the most important factor predicting wasp presence was the presence of wasps of the opposite sex. Therefore, male and female wasps typically visit the same individual plants, across multiple plant species and locations. Given that the effect of fly abundance was more important in the models than either measure of plant quality (flowers and volume), plant preferences are likely driven by females, who hunt primarily flies (Evans 2002; Evans and O’Neill 2007). If adult foraging opportunities (i.e., nectar) are crucial to *S. nigripes*, we would expect to see a strong effect of plant quality. Rather, the ability of females to find and catch prey items for offspring provisioning appears to matter more than the food resources available for adult consumption. Therefore, it is likely that males choose plants based more on the presence of females than on the quality of the plant, which leads to a correlation of male and female wasp presence.

However, the presence of males cannot always be explained by the presence of females. For example, during the two weeks in July in which *A. greggii* flowers, males can be found almost exclusively on large *A. greggii* trees, even though females continue to visit other plant species. These plant preferences generally parallel the distribution of wasps across location types, since locations differ in plant community composition. In particular, higher female use of *Eriogonum* could explain the patterns of female distribution along dirt and paved roads (see **Fig. 2.2**), since dirt roads are dominated by *Eriogonum* while paved road sites contain the smallest proportion of *Eriogonum* (**Fig. 2.3**). Alternatively, the substrate surrounding paved roads may be less suitable for nesting, making them unappealing to females. Males visit and defend plants alongside paved roads, which females avoid. It is not clear if this mismatch between males and females is due to females avoiding anthropogenic disturbance, site assessment error by males, or if it is an adaptive behavior. Males may be visiting certain plant species for sex-specific benefits, such as a required nutrient intake balance for pheromone production (Kaspi et al. 2000) or concentrated nectar output to fuel territorial behavior (Toft 1984).

Both male and female wasps use a variety of different plant species over the course of the season. Each species has a flowering duration that is much shorter than the length of the wasp season. In this area, *S. flaccidus* typically blooms first in late May, followed by *E. fasiculatum* in June, *P. thurberi* and *A. greggii* in July, *E. plumatella* in August, and *G. microcephala* and a second flowering of *S. flaccidus* in September (**Fig. 2.5**). Although the exact dates may vary from year to year, the flowering order remains consistent every season. Wasp populations track these blooming periods, so that wasps are always found near whichever plants are blooming within the habitat. This ability to use many plant species is likely adaptive for *S. nigripes*, since it allows wasp populations to flourish for nearly half of each year. However, because plant blooms in the desert are strongly influenced by seasonal rains, the abundance of *S. nigripes* is also dependent on weather and climate patterns (see Chapter 1).

In other species of sand wasps, males often gather in areas of high female presence (Evans and O'Neill 2007). However, males typically aggregate in nesting or emergence areas. In contrast, *S. nigripes* males aggregate around plants that females are visiting. Quality of offspring provisioning resources, rather than nectar for adult consumption, explains which plants females visit. Thus, offspring provisioning appears to be a key factor predicting the distribution and habitat use of this species. Offspring provisioning determines adult body size in the Hymenoptera, and larger body size can provide advantages to both males (Alcock 1979; O'Neill et al. 1989; Barthell and Daly 1995; Teder 2005; Reece et al. 2007) and females (O'Neill 1985; Kim 1997; Bosch and Vicens 2006; Shreeves and Field 2007; Coelho et al. 2008). In particular, male body size in *S. nigripes* is strongly related to success in territory holding (see Chapter 4). Hence, the unique mating system of *S. nigripes* may underlie the importance of provisioning resources for this species.

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Chapter 3:

Ecological factors predicting behavioral variation in the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae)

Abstract

This study investigated the relationship between ecology and behavioral variation in the sand wasp *Steniolia nigripes* in the Granite Mountains, located within the Mojave National Preserve, California. I surveyed plants of six different species from May to October of 2010, measuring wasp behavior by sex, plant quality, abundance of dipteran prey used for nest provisioning, and landscape features in order to determine if ecological factors predict behavioral variation in *S. nigripes*. In particular, I examined the proportion and frequency of foraging, vigilance, and aggressive behaviors. Statistical analysis using generalized linear mixed models indicated that the behavior of male and female wasps varied primarily based on the progression of the season. The behavior of both sexes also varied across plant species, but plant quality did not have a strong effect. The presence of prey and the presence of male wasps both influenced female behavior, but male behavior was not related to either prey or female presence. Overall, females spent more of their time foraging than males, and their behavioral budgets were less affected by ecological factors.

Introduction

In desert ecosystems, extreme fluctuations and heterogeneity in environmental conditions are common. Desert organisms thus face a wide range of variation in their surroundings, including factors such as precipitation, soil moisture content, temperature, nitrogen fixation, and soil particle size (Schlesinger et al. 1990; Schowalter et al. 1999; Titus et al. 2002). When water and nutrients are limited, species must evolve to take advantage of resources when they are available, so seasonal changes may lead to corresponding variation in animal behavior. The ecological context of any behavior may be different nearly every time it occurs, based on the surrounding organisms, daily or seasonal conditions, or the characteristics of the individual performing the behavior. Thus, individuals may benefit by altering what behaviors they prioritize in different environments. Plasticity in behavior allows animals to adjust to better match their environment at any given moment (Aluja and Birke 1993; Charmantier et al. 2008), while limited plasticity may result in non-optimal behavior (Sih et al. 2004).

Most organisms experience different needs at different points in their life history. As a result, we can expect to find seasonal differences in behaviors such as foraging, aggression, and nesting (e.g., Blanckenhorn and Perner 1996). Individuals must face changes both in their own physical capabilities and requirements, and in the resources available to them. For example, the foraging strategy of a particular species can vary over time in response to shifts in nutritional needs (Kaspi et al. 2000), behavioral priorities such as acquiring mates (Blanckenhorn et al. 1995), the presence of predators (Anholt and Werner 1995), or plant community composition (Hobbs 1985; Stamp and Bowers 1990). Males and females may use resources in different ways (Aluja and Birke 1993), and distinct selective environments can produce variable behavioral syndromes over entire populations (Dingemanse et al. 2007). It is therefore impossible to fully understand the behavioral repertoire of any animal without understanding how ecological and environmental factors may alter an individual’s behavior.

This study investigates behavioral variation over time and space in the sand wasp species *Steniolia nigripes* (Crabronidae: Bembicinae). This species occurs in the Eastern Mojave Desert in California, as well as the Owens Valley and the Sonoran Desert zones of Southern California. *Steniolia nigripes* is one of the very few species of sand wasps with fully reversed sexual size dimorphism, such that males are substantially larger than females (O'Neill 2001; Thomas and Nonacs 2002; Evans and O'Neill 2007). This species also demonstrates a unique resource-based territorial strategy (see Chapter 4), which has not been described in any other bembicine wasp. Males compete for and defend plant resources that females visit, and size is a key component of male territorial success (Chapter 4). Ecology can have profound implications for mate searching strategies such as territoriality (Alcock 1979; Thornhill and Alcock 1983; Kemp and Alcock 2003; Peixoto et al. 2012; Oliveira et al. 2013), so considering the ecological context of this novel behavior is critical. In this paper, I will examine a number of ecological factors, including landscape features, intraspecific abundance, and the presence of prey species, in order to determine what affects the behavior of male and female *S. nigripes*. Given the variability of desert environments, I expect to see strong seasonal patterns in *S. nigripes* behavior. In particular, the late summer monsoonal rains should lead to increased foraging, since many desert plants bloom only in response to rain.

Methods

Research was conducted from May to October 2010 by systematic observation of 240 plants of 6 species, across 6 sites at or near the Granite Mountains Desert Research Center. Measurements included plant species, location type (wash, road, or mixed scrub), number of flowers on the plant, plant size, number of dipteran prey at the plant, and the number, behavior, and sex of all *S. nigripes*. See Chapter 2 for a detailed description of the study site and sampling design.

Behavioral Measurements

Separate ethograms for male and female *S. nigripes* were created based on previous personal observations. Observed behaviors were classified into groups for analysis. Behavioral categories for male wasps included foraging (feeding on nectar), aggression (patrolling plants and chasing other insects), and other (traveling, resting, etc.). For females, the behavioral categories were foraging (feeding on nectar), hunting (predatory hovering or attempts on Diptera), nesting (digging in the substrate), vigilance (hovering or resting next to a plant, usually followed by foraging), and other. Male behaviors were labeled aggressive because male wasps actively pursued and engaged with other insects. Aggressive interactions usually led to short aerial conflicts. Female behaviors were labeled vigilant because females were highly reactive, immediately turning towards, observing, and flying away from other insects, including male conspecifics. Females never instigated aerial conflicts, and generally avoided interaction with other wasps.

Statistical Analyses

Logistic regression models were constructed to predict the behavior of *S. nigripes* based on the presence of *S. nigripes* of the opposite sex, date, quantity of Diptera, plant species, plant volume, flower quantity, and location type. Fixed effects were tested for collinearity with Pearson’s correlations. Separate models were tested for each sex to evaluate whether wasp behavior correlated to plant characteristics, presence of prey, presence of other wasps, or landscape effects. The relative explanatory power of each variable was assessed by comparing models with the Akaike Information Criterion corrected for small sample size (AICc), using the lme4 package in R 3.0.2 (R Core Team 2013; Bates et al. 2014). Further statistical tests were used to examine the effect of each variable individually, as needed.

Results

For both male and female wasps, date was by far the most important variable predicting behavior (male ΔAICc = 54.28, $w_i < 0.001$; female ΔAICc = 53.04, $w_i < 0.001$). Removing the effect of date always resulted in the model with the highest AICc, as compared to the removal of other variables (**Tables 3.1-3.2**).

Table 3.1. Summary of models explaining the behavior of male wasps on plants. The best possible model included only date, species, and flowers.

Model	AICc	ΔAICc	*K*	w_i
Full model – location type	438.92	0	11	0.841
Full model – flies	444.02	5.10	14	0.066
Full model – volume	444.58	5.66	14	0.050
Full model – female	445.20	6.28	14	0.036
Female + date + flies + species + flowers + volume + location type (full model)	448.49	9.58	15	<0.001
Full model – flowers	456.51	17.59	14	<0.001
Full model – species	461.48	22.56	9	<0.001
Full model – date	493.20	54.28	14	<0.001

"Female" represents the presence or absence of female wasps. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=286.

Table 3.2. Summary of models explaining the behavior of female wasps on plants. The best possible model included only date, species, flies, and male.

Model	AICc	ΔAICc	*K*	w_i
Full model – location type	736.12	0	11	0.977
Full model –species	743.82	7.69	9	0.021
Full model – flowers	748.57	12.44	14	0.002
Full model – volume	751.60	15.48	14	<0.001
Full model – male	754.11	17.99	14	<0.001
Full model – flies	755.96	19.83	14	<0.001
Male + date + flies + species + flowers + volume + location type (full model)	756.12	19.99	15	<0.001
Full model – date	789.16	53.04	14	<0.001

"Male" represents the presence or absence of male wasps. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (*K*), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=317.

In May, when males emerge before females, males split their time evenly between aggression and foraging (**Figure 3.1**). In June and July, males primarily behaved aggressively, while foraging was predominant in August and September (**Figure 3.1**). The proportion of foraging and aggressive behaviors in males varied significantly over time (N = 286, logistic regression, $p < 0.001$).

Females were observed starting slightly later in the year than males. In June, females spent the majority of their time on vigilance behaviors (**Figure 3.2**). In July and August, foraging and hunting behaviors increased, and foraging was the predominant behavior in September (**Figure 3.2**). Females were only rarely observed nesting. The proportion of foraging and vigilance behaviors varied significantly over time (N = 318, logistic regression, $p < 0.001$).

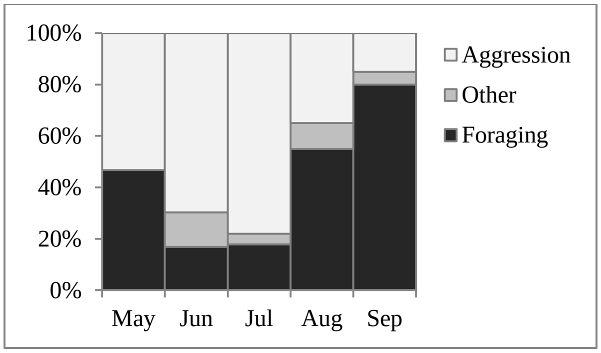

Figure 3.1. Proportion of male *S. nigipes* behaviors over time. Male aggression was highest in June and July, while foraging was dominant in August and September.

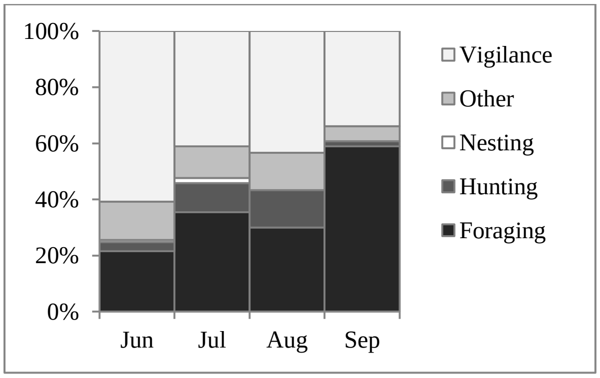

Figure 3.2. Proportion of female *S. nigipes* behaviors over time. Female vigilance was highest in June. Hunting increased in July and August, and foraging was dominant in September.

Males and females behaved differently while visiting different species of plants (**Figure 3.3-3.4**). Plant species was a better predictor of male behavior than of female behavior (male ΔAICc = 22.56, $w_i < 0.001$; female ΔAICc = 7.69, $w_i = 0.021$). Plant species alone had a significant effect on male behavior type (N = 286, $\chi^2_{10} = 43.9$, $p < 0.0001$) and on female behavior type (N = 318, $\chi^2_{20} = 38.4$, $p = 0.008$). Males performed the most aggressive behavior on *A. greggii*, which is used by males much more often than females (see Chapter 2). The only species where foraging was more common than aggression in males was *S. flaccidus*. For all other plant species, aggression was the most frequently observed male behavior. Overall, females spent a higher proportion of their time foraging than males. Vigilant behavior was most common on *E. fasciulatum* and *P. thurberi*, which bloom in June and July respectively. Hunting occurred mostly on *P. thurberi* and *S. flaccidus*.

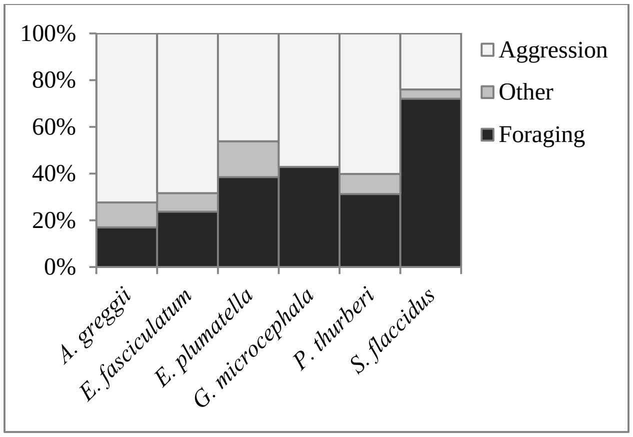

Figure 3.3. Proportion of male *S. nigipes* behaviors by plant species. Male aggression was highest on *A. greggii*, and the dominant behavior on all species except *S. flaccidus*.

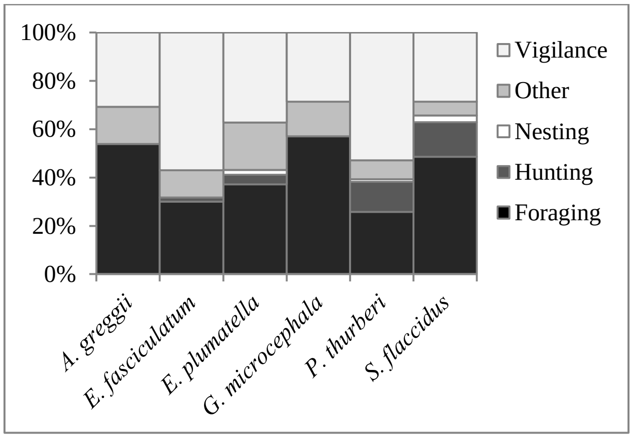

Figure 3.4. Proportion of female *S. nigipes* behaviors by plant species. Females spent more time foraging than males, and divided their time less consistently across species.

Location type did not predict the behavior of either sex, and removing location type always improved the model (**Table 3.1-3.2**). Location type alone had no significant effect on either male (N = 286, $\chi^2_6 = 6.2$, p = 0.41) or female (N = 318, $\chi^2_{12} = 13.3$, p = 0.35) behaviors. Plant quality measurements were not important to female behavior (**Table 3.2**), but number of flowers did predict male behavior (ΔAICc = 17.59, $w_i < 0.001$). In contrast, the number of Diptera had little effect on male behavior (ΔAICc = 5.10, $w_i = 0.066$), but did predict female behavior (ΔAICc = 19.83, $w_i < 0.001$). In particular, females were observed hunting more often at plants with larger numbers of Diptera.

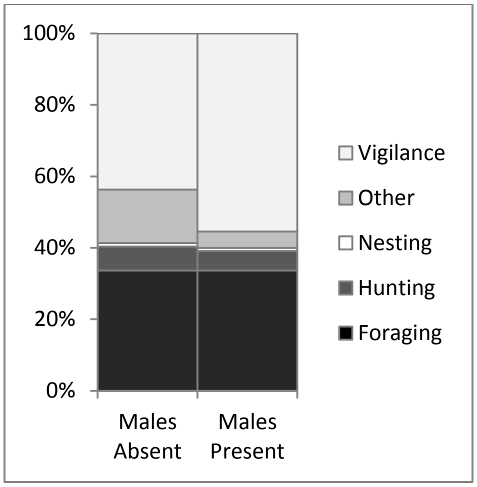

Figure 3.5. Proportion of female *S. nigipes* behaviors with and without males present. Female vigilance increased when males were present.

Finally, the presence of males had some effect on female behavior (ΔAICc = 17.99, $w_i < 0.001$), but the reverse was not true (ΔAICc = 6.28, $w_i = 0.036$). In the presence of males, female vigilance increased significantly (N = 318, $\chi^2{}_1 = 5.92$, p = 0.02), but foraging and hunting remained consistent (**Figure 3.5**).

Discussion

This research indicates that the behavior of male and female *S. nigripes* fluctuates substantially over the course of a season. For both sexes, date had a stronger effect on behavior than any other factor. Individual wasps do not live for the entire duration of the season, so these behavioral shifts occur at the scale of the population. Male and female wasps show similar patterns in behavior, and foraging increases in both sexes later in the year. Aggression in males and vigilance in females decrease at the same time, though whether the two are directly related is unclear. Male presence does relate to increased vigilance in females independently of date.

The influential effect of date may be due to the importance of thermoregulation in insects, as they are highly susceptible to fluctuations in temperature (see Chapter 1). Temperature can impact behavioral efficiency, sustainable activity levels, physiological processes, and the pace of development in insects (Stamp and Bowers 1990; Amor et al. 2011). Both daily and seasonal temperatures play a large role in insect activity patterns (Hobbs 1985; Larsson 1990; Albrecht and Gotelli 2001; Kurczewski 2008). Flight is an energetically costly behavior and generates a significant amount of body heat, which can lead to overheating and exhaustion in insects that fly constantly (Vande Velde and Van Dyck 2013). Although this study did not directly investigate the costs and benefits of different temperatures, substantial behavioral variation over the season indicates that temperature is most likely an important environmental factor for *S. nigripes*. At non-optimal temperatures, wasp flight may be slower or less agile, which could have profound consequences for behaviors such as hunting and agonism.

Because each of the plant species observed blooms at slightly different times (see Chapter 2), it is difficult to disentangle the effect of plant species from that of date. For example, male aggression is highest in July, and on *A. greggii*, which flowers in July. Similarly, male foraging is highest in May and September, which are the two flowering periods of their preferred foraging plant, *S. flaccidus*. For females, vigilance was highest in June, and on *E. fasciculatum*, which flowers in June. However, date was a better predictor of both male and female behavior than plant species, suggesting that the behaviors of *S. nigripes* relate more to seasonal changes.

Plant quality had no effect on females, but did predict male behavior. However, this effect was most likely due to the strong effect of plant species on male behavior. The species associated with the greatest change in male behavior, *S. flaccidus*, has many fewer flowers than the other species, often by several orders of magnitude. It is therefore difficult to directly compare plant quality between *S. flaccidus* and the other five plant species. Although wasps spend a lot of time foraging, plant quality does not affect female behavior and is not a strong predictor of the presence of either males or females (see Chapter 2), suggesting that nectar acquisition is likely not a primary objective for adult *S. nigripes*. Instead, females seem to prioritize offspring provisioning, and forage as necessary in order to achieve hunting success.

Although female presence is highly related to male presence, the proximity of females does not affect the type of behavior that male wasps perform. This may be because males are often occupied with obtaining and defending territories (see Chapter 4), and rely on territory ownership as a means of encountering females. Thus, though female presence may drive male presence, males do not immediately change their behavior when females are nearby. Alternatively, the relevant shifts in male behavior may not have been measured by this study. When females are present, males might be expected to direct their aggressive dives and chase flights towards females rather than other males. Here, no distinction was made based on the intended recipient of male behaviors. It is likely that males did indeed pay attention to females, but simply did not alter their overall level of aggression.

The effects of these ecological factors on the behaviors of *S. nigripes* are similar but not identical to their effects on the abundance and distribution of *S. nigripes*, as reported in Chapter 2. Both behavior and abundance vary on different plant species, but are not strongly related to the characteristics of individual plants. The abundance of dipteran prey used to provision offspring is more important for female presence and behavior than any plant characteristics, and male presence appears to be driven primarily by female presence. The only factor that clearly affects abundance and behavior differently is location type, which does predict the presence of both male and female wasps, but not their behavior. The lack of a relationship between location type and behavior indicates that wasp behavior does not vary between populations, even though populations are distributed unevenly throughout the habitat.

In summary, behavioral variation in *S. nigripes* appears to correspond to seasonal changes, rather than differences in microhabitat. Insects commonly alter their foraging behavior according to seasonal differences (e.g., Lynch et al. 1980; Whitford et al. 1981; Albrecht and Gotelli 001; Irwin and Maloof 2002). In parasitoid wasps, seasonal life history and habitat changes can impact host search time and selection (Roitberg et al. 1992), which can have further implications for adult body size (Sequeira and MacKauer 1993). Interestingly, adult *S. nigripes* females appear to trade off hunting for host prey and foraging for themselves (see Figure 3.2). The number and size of provisions provided to the offspring determines offspring size and subsequent adult sexual size dimorphism (O’Neill 1985; Rosenheim et al. 1996; O’Neill and O’Neill 2003; Shreeves and Field 2007; Radmacher and Strohm 2010). Thus, seasonal fluctuations in female activity budgets may lead to fluctuations in size variation in the following generation. Female parental investment, and therefore offspring size and sex ratio, are likely to vary with seasonal resource availability (Torchio and Tepedino 1980; Frohlich and Tepedino 1986; Strohm and Linsenmair 1997; Alcock et al. 2005).

Seasonal variation in abiotic conditions can also have profound impacts on the costs and benefits of male aggressive behavior. For example, territorial ownership may be more important when certain microenvironments are especially valuable, such as when ambient temperatures are not ideal (Wickman and Wiklund 1983). Competitive ability is also likely to vary seasonally, due to the effects of shifting nutritional availability and ontogeny (Kemp et al. 2006). When resources are ample, males can spend less time foraging and more time competing with other males (Kolluru and Grether 2004). Thus, seasonal variation in male aggression in *S. nigripes* may correspond to the availability of their preferred forage plants. Indeed, the highest levels of male aggression occur on those plant species that are most attractive to males (see Figure 3.3 and Chapter 2). Male aggression is highest during the flowering times of their preferred plants (see Figures 2.5 and 3.1).

The highly variable environmental conditions characteristic of a desert ecosystem may therefore have a substantial effect on *S. nigripes*. In this species, shifts in behavior correspond to population turnover (see Chapter 1), so plasticity during an individual's lifetime may not be necessary. Instead, population level changes may produce seasonal behavioral polyphenism (Brakefield and Reitsma 1991). Arthropod species do not always respond identically to environmental fluctuations, and their differential responses can have broad consequences for plant-insect dynamics and thus the larger ecological functioning of an ecosystem (Schowalter et al. 1999). Further study into the specific conditions related to behavioral variation in *S. nigripes* may elucidate how this species will respond to future environmental change, and what effects that could have on the ecosystem.

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Chapter 4:

Size variation and a novel territorial strategy in the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae)

Abstract

Males of the solitary Hymenoptera often engage in either scramble competition or female defense polygyny in order to obtain mating opportunities. In the sand wasps (Crabronidae: Bembicinae), males may defend female nesting or emergence sites. I found a unique resource-based territorial strategy in the sand wasp *Steniolia nigripes*, a species with reversed sexual size dimorphism. Males defend plants that females visit for prey items and nectar, and aggressively exclude other males. Wasps were individually marked and their behavior was observed in the field. Approximately 10% of male *S. nigripes* exhibited territorial behavior. These males were significantly larger and more aggressive than others, monopolized the most contested plants, and remained on plants for longer periods of time. *Steniolia nigripes* shows unusual patterns in both male reproductive behaviors and sexual size dimorphism. Large body size thus appears to be a critical determinant of success in male-male competition in this species.

Introduction

Territorial defense is a commonly used strategy in a wide variety of animal species, especially in males as a path to increased reproductive success (Andersson 1994). The ability to hold a territory can provide an individual with increased access to resources, higher frequency of mating opportunities, and a means of demonstrating their attractiveness to potential mates.

Although territoriality takes a number of different forms, the reproductive strategies used by territorial males can be placed into three general categories (Davies 1991; Peixoto et al. 2012). First, in female defense polygyny, males may directly monopolize access to females, either as a harem or through scramble competition. Second, in resource defense polygyny, males defend some environmental resource that females need, such as food or nesting sites. Third, in lekking species, males hold territories in areas with a high female encounter rate but no particular inherent value otherwise. Which of these mate searching strategies is used by males can have profound impacts on the overall mating system of a species.

The type of male territoriality in a given species is strongly influenced by the distribution of resources (including females) in the environment (Thornhill and Alcock 1983; Peixoto et al. 2012). The distribution of receptive females is a particularly key distinction between female defense and resource defense. In order for female defense to occur, females must be concentrated in space and time. In the Hymenoptera, female nesting or emergence sites are often aggregated, providing the opportunity for female defense polygyny and scramble competition (Alcock et al. 1977; O’Neill 1983). Nesting areas are one of the primary locations for male-female interaction in many wasp species (Alcock et al.1977). Furthermore, the control of clumped emergence sites is especially critical when female mating rate is low and females are most receptive to mating when they are virgins. However, when females are less highly concentrated, resource defense may be more advantageous. Female Hymenoptera must spend large portions of their adult lives provisioning their offspring, and thus experience high energetic demands (Honek 1993; Kim 1997; Blanckenhorn 2000; Shreeves and Field 2007). Therefore, males may search for females at foraging sites where females are either foraging themselves or hunting prey for their offspring.

Males of species with more widely distributed females and higher energetic demands on the females are thus expected to adopt resource defense territoriality.

In the sand wasps (Crabronidae: Bembicinae), females dig nests in the ground, both in isolation and in subsocial aggregations. In many species, males gather near females in a highly mobile, aggressive group (Thomas and Nonacs 2002; Evans and O'Neill 2007). Scramble competition among males can be dangerous to females in these aggregations (O'Neill and Evans 1983; Thomas and Nonacs 2002). Approximately 10 species of sand wasps show male territoriality centered on either nesting or emergence sites (Evans and O'Neill 2007). Typically, males will hover a few centimeters above the ground and wait for females to exit their nests. Males may compete for these spots, but it is common to see a single male at a nest entrance as well. However, there is no known example of a bembicine wasp defending resources other than nests (Evans and O'Neill 2007).

One of the most common traits associated with territoriality is male size. When females are larger than males, mating success is often driven by female choice and male scramble competition (Ding and Blanckenhorn 2002). When males are larger, the mating system is more likely to include resource defense by males, polygyny, and forced copulation (e.g., Heske and Ostfeld 1990; Andersen 1997; Jormalainen 1998; Teder 2005). Male insects are usually smaller than females, and female-biased sexual size dimorphism is common due to the energetic demands of producing eggs and provisioning offspring (Rosenheim et al. 1996; Teder 2005; Bosch and Vicens 2006; Shreeves and Field 2007). Although smaller males are the norm, large male body size correlates with territory holding ability in a number of species of Hymenoptera (Alcock 1996; Alcock 1997; Oliveira and Schlindwein 2010; Oliveira, Carvalho, and

Schlindwein 2012). There is considerable variation in the direction and degree of sexual size dimorphism across even closely related species (Andersson 1994), often associated with variation in male mating tactics (Brockmann 2008; Oliveira et al. 2012).

In most bembicine species, females are larger (by up to 2.5 times) than males (O'Neill 2001; Evans and O'Neill 2007), but there are a few exceptions in which sexual size dimorphism is either absent or reversed (Evans and O'Neill 2007). Field studies suggest that larger males are more likely to be found in species where males must carry females in flight in order to mate (e.g., *Bembecinus quinquespinosus*, Evans and O'Neill 2007). One of the most notable cases of reversed sexual size dimorphism is the sand wasp *Steniolia nigripes*, in which males are substantially larger than females (Thomas and Nonacs 2002, **Figure 4.1**).

In *S. nigripes*, males do attend nesting sites, but they also aggregate and chase each other in groups in a pseudo-lekking behavior (Thomas and Nonacs 2002). These male groupings often travel near flowering plants, and wasps are found more easily in the field by focusing on flowering plants, rather than searching for nesting sites (see Chapter 1). Here I present evidence

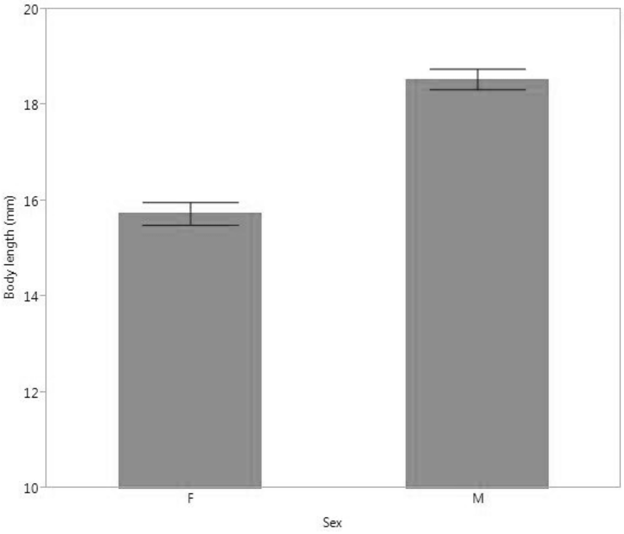

Figure 4.1: Reversed sexual size dimorphism in *S. nigripes*. Males are approximately 20% larger than females. Data are from 2009.

for a novel territorial strategy in *S. nigripes* based on resource defense, a behavior previously undescribed in the Bembicinae. I propose that the success of this novel behavior is linked to the unique body size patterns in *S. nigripes*. If male body size is sexually selected, then size should affect the ability of male wasps to attain and hold quality territories, and contest success in direct male-male interactions. Furthermore, I hypothesize that males of different sizes should employ alternative behavioral strategies, resulting in variation in plant resource utilization. These predictions were evaluated using behavioral observations of individually marked male wasps in the field.

Methods

This study was conducted during the summers of 2009 through 2013 at the Granite Mountains Desert Research Center, a University of California reserve located within the Mojave National Preserve, 128 km east of Barstow, CA (34° 48’ 20” N, 115° 39’ 50” W). The Granite Mountains are a high-elevation (1,128 – 2,071 m above sea level) range located in the east Mojave Desert, in the transition zone between Sonoran, Great Basin, and Mojave Desert ecosystems. Sand wasps such as *Steniolia nigripes* live primarily in lower-elevation sandy washes. These areas generally consist of a broad, open stream bed with soft substrate, bordered by steep banks leading to mixed woody and creosote scrub vegetation. Wasps frequent a number of characteristic wash plants, including catclaw acacia (*Acacia greggii*), sandpaper plant (*Petalonyx thurberi*), and threadleaf ragwort (*Senecio flaccidus*).

Wash vegetation is distributed in nearly-straight lines along washes, creating natural transects. The first transect was approximately 200 m in length and included 30 *P. thurberi* bushes, plus 4 large *A. greggii* trees. These plants were clumped into 3 patches separated by about 40 m of empty sand. The second transect was between 60 and 100 m in length, depending on the year, and included 30 to 35 *S. flaccidus* plants. While the *S. flaccidus* plants were also somewhat clumped, the grouping was much less distinct than that of *P. thurberi*. I observed Transect 1 in June and July, when *P. thurberi* and *A. greggii* are flowering, and Transect 2 in September, when *S. flaccidus* flowers following the monsoonal rains.

Prior to observation, wasps were captured on or near plants along the transect using an insect net. The body length (anterior boundary of the eyes to the tip of the abdomen) and head width (maximum lateral distance between outer boundaries of the eyes) of each wasp were measured with a digital caliper while they were immobilized within the net. I then gave each male wasp a unique combination of thorax markings with extra-fine tipped DecoColor paint markers. Female wasps were all labeled with a single color to enable easy distinction from males. The behavior, sex, location, size, and markings of the wasp were recorded after every capture, and the wasps were released back to their original plant. For statistical analysis, male size was scaled from 0 to 1 across all seasons, in order to avoid the effects of year-to-year variation in wasp size.

Observers walked along a transect in both directions, for a total of 2 to 4 observations of each plant per day. Observers remained at each plant for 60 s and recorded the sex, behavior, and identity of every wasp that visited the plant during that time period. Plants were characterized as “popular” if multiple wasps were present on the plant simultaneously. Wasps were considered territorial if they were observed performing aggressive and/or patrolling behaviors on the same plant for more than one day in a row. A total of 126 males were marked and observed over four seasons. Each time a marked male was observed, its behavior and corresponding aggression score (**Table 4.1**) were recorded. All aggression scores for a single individual were then averaged for data analysis.

Aggression Score	Behavior
1	Foraging
2	Foraging and patrolling
3	Patrolling
4	Chasing (or patrolling and chasing)

Table 4.1. Scoring of aggressive male behaviors. See Chapter 1 for detailed descriptions of each behavior.

Results

Male wasps ranged from 14.04 mm to 21.53 in body length (mean ± SD: 17.221 ± 1.187 mm). Male head width varied from 3.60 mm to 6.65 mm (mean ± SD: 4.834 ± 0.637 mm). Body length and head width were highly correlated; henceforth only body length will be used to represent size, because body length was easier to measure and thus more likely to be accurate. Across all subpopulations, male body size was strongly related to male aggression (Spearman's $\rho = 0.5658$, $p<0.0001$, **Figure 4.2**). Larger males were responsible for most of the aggressive behavior, including chasing and patrolling. Smaller males were mainly observed foraging.

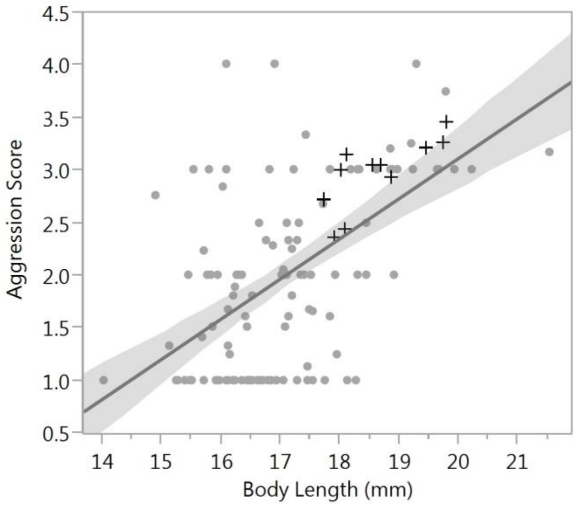

Figure 4.2: Body length vs. aggression. Larger males were more aggressive (Spearman's $\rho = 0.5658$, $p < 0.0001$). Circles represent non-territorial males, and crosses represent territorial males.

Of 126 males, 11 were identified as the primary territory holders. Territorial males were significantly larger than non-territorial males (Wilcoxon rank-sum test, $W = 1073.5$, $p = 0.0001$, **Figure 4.3a**). Non-territorial males overlapped in size with females, while territorial males were always larger than females (**Figure 4.4**). Male size varied from season to season (**Table 4.2**), but in all cases territorial males were significantly larger (**Figure 4.5**).

Season	All Males		Non-territorial Males		Territorial Males		
	Average Body Length (mm)	**N**	**Average Body Length (mm)**	**N**	**Average Body Length (mm)**	**N**	**% Size Difference**
06/2011	18.985 ± 1.187	22	18.877 ± 1.245	19	19.663 ± 0.187	3	4.2
09/2011	17.743 ± 0.861	24	17.582 ± 0.848	20	18.545 ± 0.316	4	5.5
09/2012	16.909 ± 1.094	14	16.750 ± 1.103	12	17.865 ± 0.205	2	12.4
09/2013	16.510 ± 0.863	66	16.464 ± 0.834	64	17.995 ± 0.134	2	9.3
Combined	17.221 ± 1.327	126	17.087 ± 1.294	115	18.626 ± 0.751	11	9.0

Table 4.2: Average body sizes of non-territorial and territorial males across seasons. All values are mean ± SD.

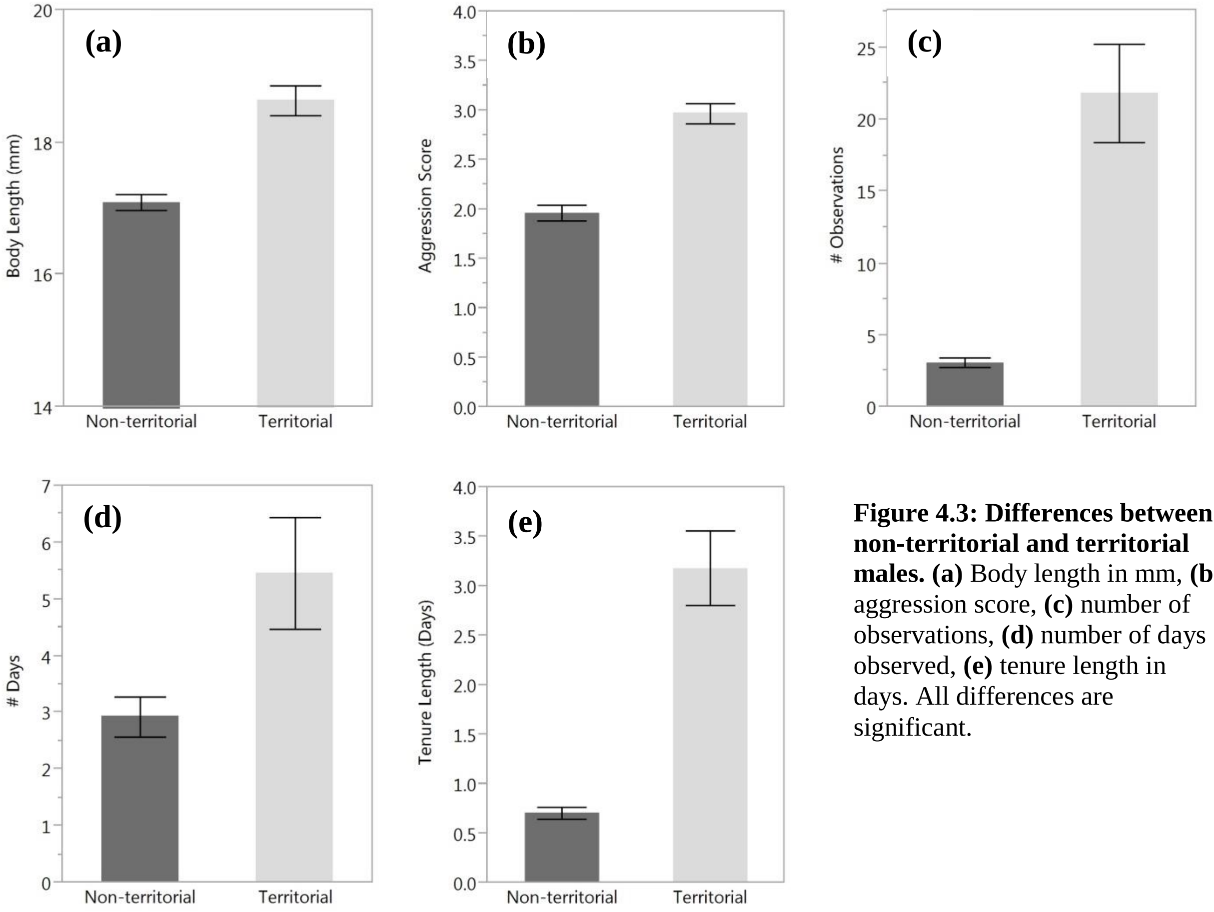

Figure 4.3: Differences between non-territorial and territorial males. **(a)** Body length in mm, **(b)** aggression score, **(c)** number of observations, **(d)** number of days observed, **(e)** tenure length in days. All differences are significant.

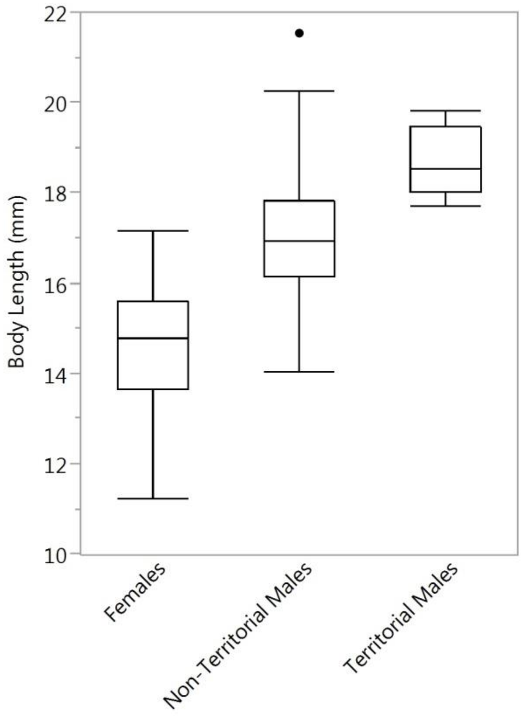

Figure 4.4: Size comparison of females, non-territorial males, and territorial males. Non-territorial males may encounter females that are larger than they are, whereas all territorial males are larger than any females.

Table 4.3. Summary of models explaining aggression levels in male wasps.

Model	AICc	ΔAICc	K	w_i
Territorial + body length	273.08	0	2	0.721
Body length	274.97	1.90	1	0.279
Territorial	313.10	40.02	1	<0.001

"Territorial" represents whether males were territorial or non-territorial. The table shows the Akaike Information Criterion, the difference in AIC from the best model, the number of parameters (K), and the Akaike weight of each model (w_i). Models are arranged in order of increasing AICc. N=126.

In addition to being larger, territorial males were more aggressive than non-territorial males (Wilcoxon rank-sum test, W = 1080, p < 0.0001, **Figure 4.3b**). However, comparison of multivariate models (**Table 4.3**) indicated that increased aggression in territorial males was a result of large body size, not territoriality per se. No other variables (number of observations, number of days, or tenure length) independently correlated to body length.

Territorial males were observed significantly more often (Wilcoxon rank-sum test, W = 1258.5, p < 0.0001, **Figure 4.3c**), over significantly more days (Wilcoxon rank-sum test, W = 1062, p = 0.0006, **Figure 4.3d**). Number of observations varied from season to season (**Figure 4.6**) due to field work scheduling, so the number of observations was scaled from 0 to 1 as with body length. In non-territorial males, there was no relationship between overall aggression and the number of times a wasp was observed (N = 115, Spearman's ρ = 0.160, p = 0.088), nor the number of days (N = 115, Spearman's ρ = 0.042, p = 0.658), indicating that increased observation was indeed linked to territoriality and not merely general activity.

Finally, territorial males were observed on the same plants (i.e., their tenure as territory owner) for a longer period of time (Wilcoxon rank-sum test, W = 1209.5, p < 0.0001, **Figure**

4.3e). Non-territorial males often visited the same plants for multiple days in a row, and thus had a tenure length, but did not consistently perform aggressive behaviors while there.

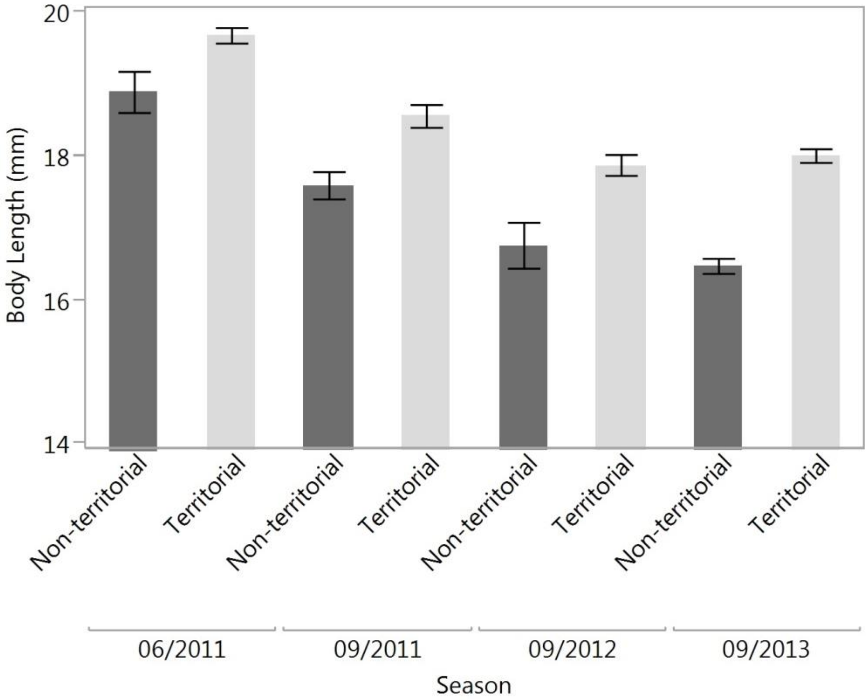

Figure 4.5: Variation in body length from season to season. In all cases, territorial males were significantly larger than non-territorial males.

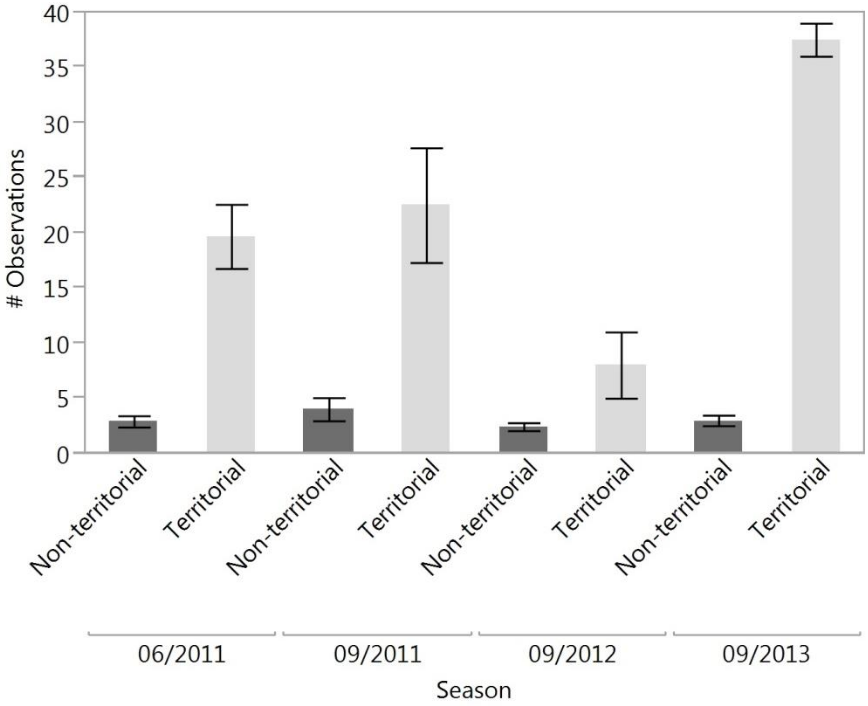

Figure 4.6: Variation in number of observations of each male from season to season. In all cases, territorial males were observed significantly more often than non-territorial males.

A minority of the plants (12-40%, depending on the season) were found to be popular, meaning that multiple wasps were seen at the plant at one time. At these popular plants, aggressive chases were more likely to occur, and occurred more often. The most popular plants were highly contested and a chase could be observed as often as twice a minute. Larger males engaged in more chasing behavior overall, and were more likely to hold highly-contested territories. In those cases where both participants in a chase could be identified, the larger male was the instigator 80% of the time and the victor (defined as the wasp that returned to the plant territory after a chase) 80% of the time.

Discussion

The results of this study indicate that approximately 12% of male *S. nigripes* consistently hold territories based on plant resources. Territorial males were observed much more frequently than non-territorial males, indicating higher local site fidelity. Furthermore, territorial males were larger than non-territorial males, suggesting that body size is a critical trait in male *S. nigripes*. Larger males were more aggressive, held territories more often, and held more popular territories. Larger males were more likely both to start and to win direct physical conflicts with other males. Large body size thus appears to strongly affect male success in territory holding in this species. Although male size, number, and distribution varied from year to year, the same patterns of territoriality held across generations and locations.

This type of territorial strategy, in which males defend environmental resources rather than females themselves, has not previously been described in any species of sand wasp (Evans and O’Neill 2007). The males of most described crabronid wasps engage in some combination of scramble competition and female defense polygyny (O’Neill 2001; Alcock 2007), particularly when virgin females emerge more or less simultaneously within a limited area. Some crabronids and a number of other solitary wasps, notably tarantula hawks (Pompilidae: *Hemipepsis ustulata*), defend landmark territories that allow for higher encounter rates with females (Alcock 1979; Alcock and Carey 1988; Elliott and Elliott 1992; Alcock 2007). For example, many species employ hilltopping, where males compete for highly visible areas on exposed ridges. This mating system is a form of lek polygyny, since territories contain no particular resources and serve primarily as landscape features (Alcock 1979; Alcock 2007), and may be especially useful when females are widely dispersed (O’Neill 1983). The use of wash plants as territories in *S. nigripes* may thus represent both hot spot lekking and resource defense polygyny. Indeed, Thomas and Nonacs (2002) observed *S. nigripes* lekking in large numbers near female nesting sites, rather than plant resources as I found. The male reproductive behavior of this species is most likely highly variable, and may be dependent on population size and resource availability year to year.

It is important to note that success in male-male competition is not necessarily indicative of actual reproductive success. In order to assess the relative advantages provided by territorial and non-territorial behavior, paternity across generations must be examined. If the territorial strategy is indeed more advantageous, territorial males should obtain greater genetic representation in the next generation. Since *S. nigripes* populations can be found in the same locations from year to year, and territorial wasps show high site fidelity, multi-generation studies are feasible in this system.

Given that territoriality in *S. nigripes* is strongly related to body size, the selection pressures produced by male-male competition may have driven the evolution of reversed sexual size dimorphism in this species. Furthermore, the resource-based strategy used by *S. nigripes* indicates that male-biased sexual dimorphism may be associated with this form of territoriality, rather than female-based or lekking territoriality. Body size can affect an individual's success in intrasexual competition in males and females, mate choice, and conflict between male and female reproductive behaviors (Bonduriansky 2009). Reversed sexual size dimorphism, once evolved, could subsequently shift the patterns of sexual selection acting on a species (Ding and Blanckenhorn 2002).

In this species, large male body size appears to be an adaptation for male-male competition. However, large size could provide fitness benefits in other ways, such as thermoregulation (Willmer and Unwin 1981), desiccation prevention (Schilman et al. 2007), or antipredator defense (O'Neill 1983). Large male size is also favored in harassment scenarios, where males must physically overcome females in order to mate (Arnqvist and Rowe 2002; Ding and Blanckenhorn 2002; Teder 2005). *S. nigripes* males are highly aggressive towards females as well as other males, and females typically avoid contact with males. In the field, mating attempts occur when a male wasp dives onto a female, and often lead to an airborne struggle. Further study could elucidate if large male size may be an adaptation for coercive mating in this species. Even if large male size is not used for coercive mating, the harassment performed by territorial males could still lead to sexual conflict (Arnqvist and Nilsson 2000; Teder 2005; Córdoba-Aguilar 2009). If females suffer substantial costs from male harassment, they should prefer to interact with smaller males, even though larger males are more successful in intrasexual competition. Males investigate every passing insect, so they are unlikely to leave females alone even after mating. Sexual conflict has the potential to create sustained polymorphism in mating tactics (Alonzo 2007), since males using strategies that enhance their mating success may not be the males that most benefit females (Warner et al. 1995). Thus, conflict between female preference and male-male competition could explain the maintenance of extensive variation in body size in *S. nigripes*.

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Chapter 5:

Female mate preferences in the sand wasp *Steniolia nigripes* (Hymenoptera: Crabronidae)

Abstract

Mating preferences can be a key source of selective pressures, since their expression leads directly to differential reproductive success. In particular, female preferences for alternative male reproductive tactics could have considerable effects on the relative success of each tactic. In cases where males aggressively compete for control of territories, females may prefer the males with the best territories. Alternatively, females may prefer to interact with males who do not harass them. I tested for female mate preferences in the sand wasp *Steniolia nigripes* (Crabronidae: Bembicinae), a species in which male size correlates with aggression and success in territory holding. Contrary to predictions, females did not express preferences for males of particular sizes, aggression levels, or activity levels. These results suggest that female *S. nigripes* directly evaluate territory quality, rather than the characteristics of their potential male partners. Access to resources may therefore be more important than mate quality in this species.

Introduction

The selection of a reproductive partner is one of the most important decisions of any sexual animal's lifetime. For every mating attempt, organisms must invest time and energy in producing gametes and finding, attracting, and copulating with their partners (Watson et al. 1998; Gowaty and Hubbell 2009). Further investment is often necessary to rear viable offspring.

Variation in ecological factors such as food supply, sex ratio, nest site availability, and density can thus have a strong effect on the costs and benefits involved in reproduction, and therefore the dynamics of sexual selection (Rowe et al. 1994; Fricke et al. 2009). In addition, mating with nonpreferred partners can have negative consequences for the fitness of both the reproducing individual and their offspring (Drickamer et al. 2000; Drickamer et al. 2003; Gowaty et al. 2003; Anderson et al. 2007; Gowaty et al. 2007). Thus, it is in generally in every individual's best interest to maximize their ability to choose a mate. When males and females do not agree in their preferences, sexual conflict arises.

Mate choice based on preferences for certain characters is a critical driving force for evolutionary change (Andersson 1994; Hoekstra et al. 2001). In particular, female choice can have profound consequences on the relative fitness of alternative reproductive behaviors in males (Alonzo and Warner 2000). Certain male tactics may induce higher mating costs in females, via aggressive mate harassment (Watson et al. 1998; den Hollander and Gwynne 2009), forced copulation (Arnqvist and Nilsson 2000), external or internal injury (Blanckenhorn et al. 2002; Hotzy and Arnqvist 2009; Johns et al. 2009), lowered survival or fecundity (Crudgington and Siva-Jothy 2000; Rice 2000; Meader and Gilburn 2008), or toxic accessory substances in the ejaculate (Chapman et al. 1995; Eberhard and Cordero 1996; Arnqvist and Nilsson 2000). If females may suffer higher costs when mating with certain males, then the response of females to males of various sizes and aggression levels is expected to vary. Universal female avoidance of males would suggest that each mating, regardless of the mate, carries a direct cost to females that causes them to avoid mating completely(Gavrilets et al. 2001), thus providing evidence for sexual conflict (Mühlhäuser and Blanckenhorn 2002; Chapman et al. 2003).

This study investigates the mating preferences of female *Steniolia nigripes* (Crabronidae: Bembicinae), a desert sand wasp species with high levels of male aggression (Thomas and Nonacs 2002, Chapters 1 and 4). Females are often avoidant of males in the field (see Chapter 1), and will generally fly away immediately if a male approaches them. Large aggressive males will attempt to chase and catch females. If male harassment has negative fitness consequences for females, then females should either avoid all males, or particularly avoid the most aggressive males. Furthermore, large females that are better able to withstand male harassment should show weaker preferences. In contrast, if females prefer certain males based on their territory holding ability, females should interact more with large aggressive males. Female choice, whether evidenced by avoidance or preference, is expected to relate to either the size of the chooser or the size of the potential mate.

Methods

Mate preference trials were conducted indoors to reduce interference from environmental cues. The mate preference arena was circular and divided into thirds (**Figure 5.1**). Each third included a small paper container ("choice") on the outside of the circle, separated from the interior by a mesh screen. The floor of the arena contained a thin layer of gravel to provide a more natural surface and a grip for wasps that flipped onto their dorsal side. The entire arena was covered with a clear polycarbonate sheet 1 cm above the bottom surface, to prevent the wasps from flying. Video was recorded through the polycarbonate sheet from directly above the arena. The arena was rotated periodically to account for any female bias to one side.

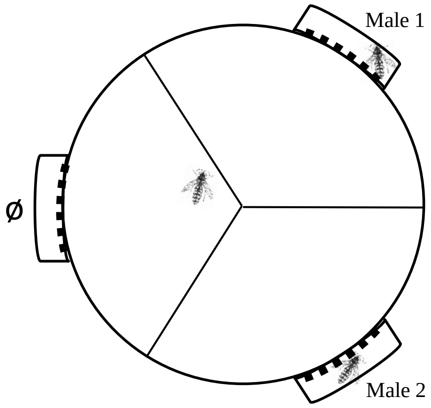

Figure 5.1. **Diagram of the arena used for preference trials.** Areas labeled "Male 1" and "Male 2" contained a male wasp, while "ø" was empty. The female was free to move anywhere in the circle.

Three wasps were used for each mate preference trial (two males and one female). Wasps were captured while visiting plants. We recorded their behavior before capture, and measured body length and head width. Each of the two males was placed in one of the choice containers, with the third choice left empty. Once the males were in place, the female was added from the empty side of the arena, and video recording began immediately. Each trial lasted for 20 minutes. At the end of the 20 minutes, wasps were either collected into 100% glycerol for dissection, or

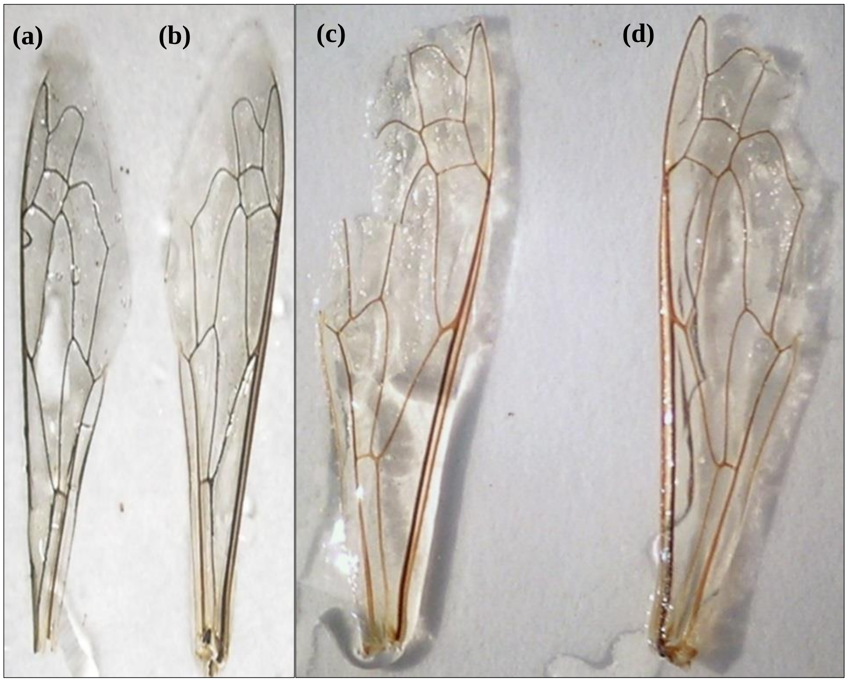

Figure 5.2. **Examples of wing wear scoring. a.** 0, **b.** 1, **c.** 5, **d.** 4.

marked with Decocolor paint markers and released in their original location. We later scored the wing condition of collected wasps (as in Alcock 2000) according to the following scale (**Figure 5.2**): 0, wing margins intact (no damage); 1, very slight damage (such as a small tear); 2, one small nick in wing edge; 3, two to four nicks; 4, more than four nicks, producing a frayed wing edge; 5, large pieces of wing missing (wing venation incomplete). An overall wing wear score was calculated for each individual by averaging the scores of all 4 wings.

We used JWatcher Version 1.0 for video scoring and analysis. Females were scored for the time spent in each area of the arena, the time spent on the screen of each "choice", and the time spent directly interacting with each male. For analysis, we chose screen time as the most relevant measure of preference, for two reasons. First, females spent a large amount of time exploring the arena, making area time an overly general measure. Second, interaction time was dependent on the male also being present on the screen, since males and females could only directly interact through the screen. If a male was elsewhere in the choice container, females could not physically interact with them. Subsequently, only results for screen time will be reported.

Results

Body length and head width were highly correlated for both males ($N = 58$, Spearman's $\rho = 0.857$, $p < 0.0001$) and females ($N = 29$, Spearman's $\rho = 0.752$, $p < 0.0001$). Henceforth, I will report results using only body length, as it is easier to measure and thus may be less susceptible to error. Activity level, calculated as the proportion of a trial in which an individual was moving, did not correlate to body size in either males (Spearman's ρ = 0.062, p = 0.751) or females (Spearman's ρ = 0.254, p = 0.184).

Females did not move evenly around the arena ($\chi^2 = 6.690$, *df* = 2, p = 0.035). Out of 29 trials, the female spent the most time on the empty screen only 5 times, compared to 24 trials where she spent more time with one male or the other. However, there was no clear pattern in which male she preferred. Male body length did not affect how much time females spent on each screen (Spearman's ρ = 0.138, p = 0.476). The size asymmetry between the two males also did not affect her screen time (Spearman's ρ = -0.104, p = 0.592). Furthermore, the female's body size did not affect the size of the preferred male (Spearman's ρ = -0.091, p = 0.640), nor whether she preferred larger or smaller males (Spearman's ρ = -0.077, p = 0.692). When only the trials in which there was a large difference in screen time were included, male body size was still not significant (N = 16, $\chi^2 = 2.250$, *df* = 1, p = 0.134). However, there was a nonsignificant trend for females to spend more time with the smaller male (11 cases out of 16, **Figure 5.3**).

Female wing wear did not predict the relative size of her preferred male (N=16, Spearman's ρ = 0.1422, p = 0.384). However, male wing wear correlated positively with the amount of time females spent on that male's screen (N = 31, Spearman's ρ = 0.475, p = 0.007, **Figure 5.4**).

Male activity levels had no effect on the female's screen time with each male (Spearman's ρ = 0.294, p = 0.122), and neither did relative male activity levels (Spearman's ρ = 0.092, p = 0.635). Similarly, female size did not correlate to the activity level of her preferred male (Spearman's ρ = -0.026, p = 0.894). There was also no difference in female screen time based on male aggression prior to capture (*F* = 0.064, *df* = 3, p = 0.978), nor based on their

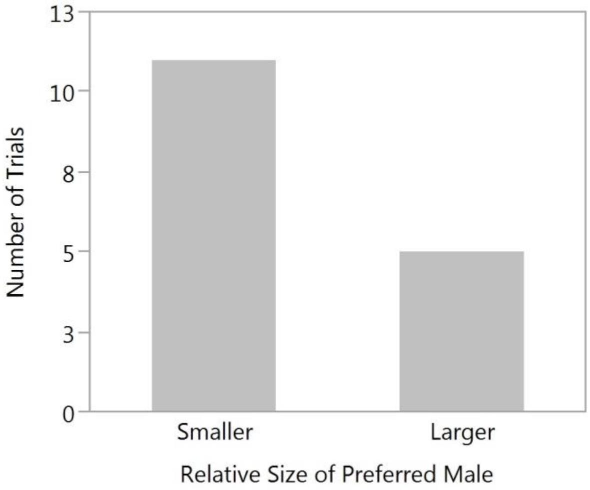

Figure 5.3. **Nonsignificant female preferences for males based on size.** In cases where the female spent much more time with one male than the other, she tended to prefer the smaller male (N = 16, χ^2 = 2.250, *df* = 1, p = 0.134).

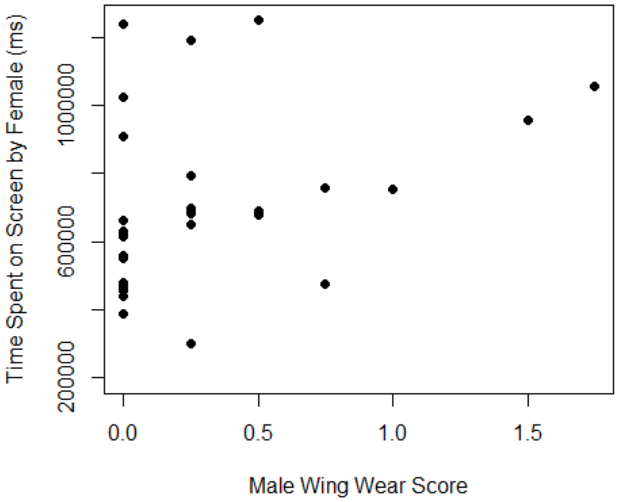

Figure 5.4. **Female preferences for males based on wing wear.** Females spent more time interacting with males with greater amounts of wing wear (N = 31, Spearman's ρ = 0.475, p = 0.007).

relative aggression (*F* = 0.488, *df* = 5, p = 0.782). Female body length did not relate to the aggression score of her preferred male (χ^2 = 2.718, *df* = 3, p = 0.602).

Since the arena was periodically rotated, the side each male was on was also analyzed. Male activity level differed significantly depending on which side of the arena they were on (*F* = 6.647, *df* = 1, p = 0.016, **Figure 5.5**). The side of the arena preferred by females also related to which way the arena was facing, although this effect was not significant (χ^2 = 2.718, p = 0.099).

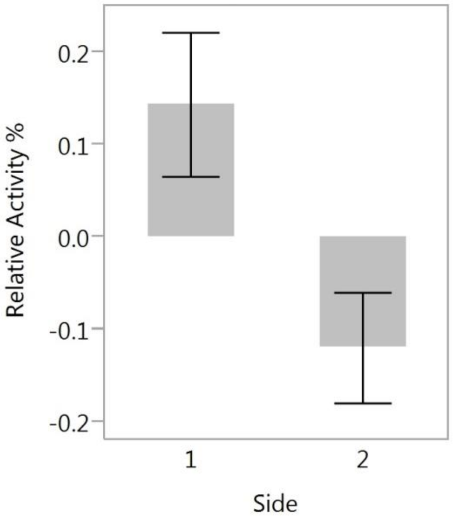

Figure 5.5. **Activity levels on each side of the arena.** Males were more active on one side of the arena than on the other (*F* = 6.647, *df* = 1, p = 0.016).

Discussion

Contrary to predictions, there does not appear to be any clear relationship between body size and mating preferences in *S. nigripes*. Although females often preferred one option in the arena, there was no clear pattern as to which option. Females spent time equally with larger and smaller males, and with more aggressive and less aggressive males. Male activity levels also did not appear to affect the females' preferences. Furthermore, the size of the female did not relate consistently to her preference. The only male characteristic that related to female attention was wing wear. Females spent more time with males that had wings in poorer condition. A preference for males with more worn wings could be a form of mate choice based on good genes, since wing wear indicates age and older males have been able to survive longer. However, variation in wing wear was low, and the majority of males had very little or no wing damage. The correlation between female preference and male wing wear was thus driven by only a few data points. Only three males showed wing wear greater than or equal to 1, and when those three males were removed, there was no effect of wing wear.

There are two primary potential explanations for the results of this study. First, females do not prefer some males more than others based on the male’s size, aggression, or activity, or based on the female’s size. This suggests that females do not have strong mating preferences, or at least do not associate with certain males in order to express mate choice. Rather, females respond fairly equally to all males. Alternatively, this study was simply unable to capture the variables affecting female mating preferences. It is possible that females base their attraction to certain males on factors other than those measured here. For this to be the case, the traits that females prefer must be entirely unrelated to size, aggression, or activity levels. More likely, females were not expressing mate preferences through their movement in the arena.

Wasps of both sexes are highly attuned to environmental factors, such as sunlight, air movement, and temperature (see Chapter 1). The arena trials were performed indoors for this reason. Although attempts were made to control for these variables, females may still have acted according to environmental factors. The arena was blocked off from the nearest windows by a piece of poster board, but it was impossible to control light from the skylights and doors elsewhere in the room. Male activity levels were relatively higher on the side of the arena nearest to the windows (**Figure 5.6**). It is therefore possible that females were more attentive to relative amounts of light than to any characteristics of the males in the arena.

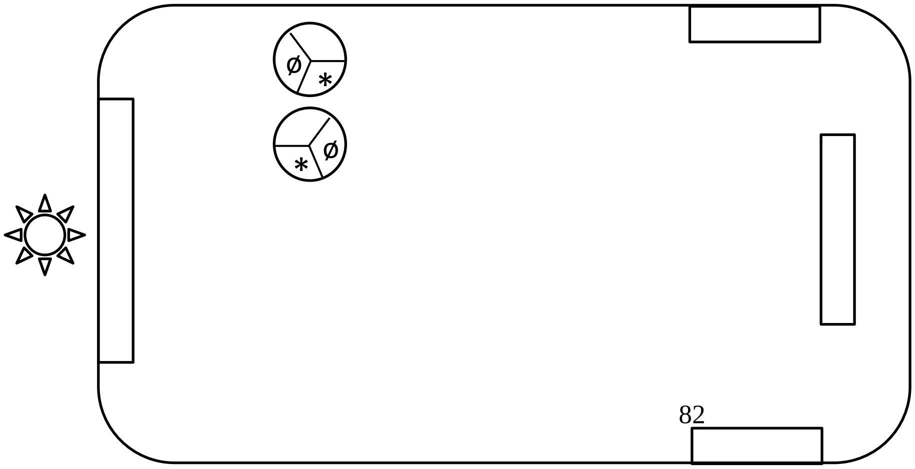

Figure 5.6. **Diagram of the room in which arena trials took place.** Each orientation of the arena is shown, with “ø” denoting the empty third, and an asterisk denoting the side where males were more active.

It is important to note that females did not necessarily avoid interacting with males. In most cases, females did not choose to remain in the empty portion of the arena. This lack of avoidance suggests that females are not especially averse to the presence of males, at least as long as the males are not actively harassing them. Female evasion of males in the field may be the result of a more general reluctance to engage with other insects, rather than a specifically male-directed behavior. Therefore, it is unlikely that variation in male size and behavior are an evolved response to female resistance.

Although the classic view of sex roles (Darwin 1871; Bateman 1948) emphasizes female choice, both sexes experience differing costs and benefits when mating with different partners (Watson et al. 1998; Rönn et al. 2008; Gowaty and Hubbell 2009), and both sexes should express mating preferences as a result (Gowaty et al. 2003; Clutton-Brock 2007). Mate choice by males appears to be widespread in insects (Bonduriansky 2001) and has been demonstrated in several wasp species, both solitary (Schoene and Tengo 1981; Alcock and Gwynne 1987) and social (Cappa et al. 2013). In some species, female mating success correlates with large body size (Alcock and Gwynne 1987; Kovacs et al. 2008). Males are expected to prefer large body size in females because it is often associated with higher fecundity (Bonduriansky 2001). Given the range of female body size variation in *S. nigripes* (see Chapter 1), it would be worthwhile to investigate the possibility of male mate choice in this species.

Although there may be additional variables that were not measured in this study, the results suggest that female mating preferences are not especially strong. Females are most likely not directly creating the selective pressure that has led to large male body size in this species. Females do not appear to use male body size to assess potential mates, despite the fact that large males are more successful in territory holding (see Chapter 4). Rather, females may evaluate territory quality over any inherent characteristic of the males holding those territories. The cues leading to female preference of some territories over others must be intrinsic to the territories, not the males. Females thus likely prioritize acquisition of the resources available on a territory over acquisition of a favorable mate. Indeed, the abundance of suitable prey items for provisioning offspring is the primary factor predicting the presence of female wasps (see Chapter 2). Given the intensity and duration of male territorial behavior, male-male competition for high quality territories may be a greater determinant of mating success than active female choice in *S. nigripes*.

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