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BODY SIZE RELATIONSHIP BETWEEN *SPHECIUS SPECIOSUS* (HYMENOPTERA: CRABRONIDAE) AND THEIR PREY: PREY SIZE DETERMINES WASP SIZE

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ABSTRACT

Eastern cicada killers, *Sphecius speciosus* Drury, are large, ground-nesting, mass-provisioning wasps that use cicadas to feed their offspring. Previous studies have reported that female *S. speciosus* provide each male offspring with 1 or rarely 2 cicadas, and each female offspring with 2 or rarely 3 cicadas, regardless of cicada size. We collected samples of male and female cicada killers and samples of their cicada prey from 12 locations in 10 different states of the USA. We measured right forewing length of the wasps and dry body mass of the cicadas as indicators of size; ANOVA revealed significant differences in mean masses among local populations of cicadas. We predicted that wasp size would also vary among locations, and would be positively correlated with mean size of local cicada prey. ANOVA did reveal significant differences in mean wing length in both male and female wasps among study sites. Regression analysis, with local mean cicada mass as the independent variable and local mean wasp wing length as the dependent variable, suggests that the size of available cicada prey is a good predictor of size for both male and female *S. speciosus*.

Key Words: cicada killer, cicada, body size variation, mass-provisioning

RESUMEN

Asesinas de cicádidos, *Sphecius speciosus* Drury, son avispas grandes que anidan en la tierra, aprovisionan en masa, y usan cicádidos por alimentar sus hijos. Investigaciones previos han reportado que la hembra *S. speciosus* da a cada hijo 1 o raramente 2 cicádidos y cada hija 2 o raramente 3 cicádidos no obstante a tamaño. Coleccionamos machos y hembras de matadores de cicádidos y sus presas de 12 lugares en 10 estados diferentes de los EE.UU. Medimos la longitud de la aleta delantera derecha y la masa del cuerpo seco de las avispas; ANOVA muestre diferencias significas en masas promedias entre poblaciones locales de cicádidos. Predecimos que el tamaño de avispas varie tambien entre lugares, y corelaciona positivamente con el tamaño promedio de presa local. ANOVA monstró diferencias significativas en la longitud promedio de la aleta delantera en ambos machos y hembras entre lugares que estudiamos. Análisis de regresión, usando masa promedia de cicado local como la variable independente y la longitud de la aleta delantera de la avispa local como la variable dependente, sugere que el tamaño de los cicádidos que son presas es un buen predictor del tamaño para ambos machos y hembras de *S. speciosus*.

Translation provided by the authors.

Solitary nest-provisioning Hymenoptera may be subdivided into 2 broad categories based on the relative timing of provisioning and offspring developmental events: progressive provisioners, those in which the female provisioning period overlaps with the larval development period, and mass provisioners, in which females complete provisioning and seal off each nest cell before the egg hatches (Evans & O'Neill 2007). In provisioning Hymenoptera generally, the body size of offspring is often subject to wide variations within a given population; numerous studies have documented that a primary determinant of this variation is the amount of the provision provided. This positive relationship between provision mass and offspring size has been reported for a wide range of mass provisioners, for example, the spider wasp, *Pepsis thisbe* Lucas (Punzo 1994), the red mason bee, *Osmia rufa* L. (Seidelmann 2006), and the European beewolf, *Philanthus triangulum* Fabricius (Strohm 2000).

Eastern cicada killers, *Sphecius speciosus* Drury, are large, colonial, mass-provisioning wasps. Females dig nest burrows in sandy soil and provision individual nest cells with cicadas they capture and paralyze in nearby trees. Several published studies, including Dow (1942a, 1942b), Lin (1979), and our own unpublished observations, indicate that the number of cicadas provided to each offspring is fairly consistent; male offspring are given 1, rarely 2, cicadas, whereas female offspring are given 2, rarely 3, cicadas regardless of cicada size. If, as in many other provisioning wasps, the size of individual offspring in cicada killers is determined largely by provision mass, then females should, on average, be much larger than males. This pattern of sexual dimorphism has been described in all published reports of relative male and female size in this species (Evans & O'Neill 2007) and it is a pattern that we have observed in all populations that we have previously studied. In fact, Coelho (1997) found that mean female mass was nearly 2.5 times that of mean male mass.

Sphecius speciosus is found in nearly all states of the USA east of the continental divide (Holliday & Coelho 2006). Over this range they hunt a wide variety of cicada species, which vary considerably in size. Lin (1979) noted that *S. speciosus* he captured in Louisiana were heavier than those captured by Dow (1942b) in New York; he concluded that this size difference might be a consequence of the difference in size of their respective cicada prey. However, to our knowledge, no previous study of cicada killers, or of any other provisioning wasp, has focused on regional variation in body size of the wasps or on how such variation might be related to variation in size of their prey. The idea for this study arose from comparisons we made between samples of the wasps from Big Bend National Park, TX and from Hasty, CO, and samples of their respective prey. In the former location, only relatively small cicadas are available as prey, and in the latter, only large cicadas are active where and when the wasps were found. The conspicuous difference in size of the wasps from these 2 locations prompted us to collect cicadas and wasps from a wide range of geographic locations and to determine if a direct relationship exists between the size of wasps and the size of available cicada prey among these locations. If, indeed, female *S. speciosus* from all locations provision nest cells with a consistent number of prey, and if offspring size is largely determined by provision mass, then we should be able to predict local mean wasp size from the mean size of available cicada prey.

MATERIALS AND METHODS

Cicadas were collected at the 12 locations shown in Table 1 with 3 different methods. At locations where we found large nesting aggregations of wasps, we collected cicadas brought to the nest area by provisioning females. We either captured female wasps and their prey together, or we retrieved cicadas that females abandoned at the openings of their nest burrows. We were able to induce abandonment by plugging nest openings with dowels after we saw females leave their nests. When females would return to the plugged burrows with provisions, they would abandon the cicadas at the plug, and we would later collect the cicadas. At locations where we did not find large nesting aggregations of wasps (Big Bend National Park, TX and Hasty, CO), we captured cicadas in trees or shrubs at the same sites where we collected wasps. At these 2 locations, we only collected cicadas of species known to be used there as provisions by female wasps. At Big Bend National Park, *Diceroprocta cinctifera* Uhler was the only species we saw taken by female wasps, and it was the only cicada found in abundance at the sites where and when we collected wasps. At Hasty, CO, 2 species of cicadas of similar size, *Tibicen dealbata* Davis and *Tibicen dorsata* Say, were the only cicadas found in abundance, and we did observe female wasps provisioning with both species. We field-collected cicadas of these 2 species as we encountered them during efforts to collect *S. speciosus*. Coelho (1997) and Grant (2006) found that cicadas captured by female *S. speciosus* were not significantly different in size or sex than those captured haphazardly by the researcher. Consequently, we are confident that cicadas we collected at the Hasty, CO and Big Bend, TX sites are representative of cicadas that *S. speciosus* use as prey.

All cicadas were killed with ethyl acetate. In the lab we dried them in an oven at 60°C to constant mass and then weighed them to the nearest mg with an Ohaus Adventurer Pro AV53 balance (Ohaus Corp., Pine Brook, NJ). We used dry mass as a measure of body size for cicadas, as we considered it to be a reasonable indicator of the possible energy content available to larval wasps.

We collected male and female *S. speciosus* at each location. Some of these specimens were preserved in 95% ethanol for subsequent DNA analysis. Others were individually marked and released. As many wasps in our samples were not available for measurement of dry mass, we used right forewing length as a measure of body size. Wing length was measured to the nearest 0.05 mm with calipers as the distance from the end of the right wing to the distal tip of the tegula. We did oven-dry 204 females and 335 males from 9 different locations at 60°C to constant mass and found that forewing length is highly correlated with dry mass (R^2 for females = 0.734, R^2 for males = 0.640). Consequently, we are confident that wing length is a good indicator of cicada killer size. In fact, Ohl and Thiele (2007) presented evidence that wing length is a good variable to use as an indicator of body size in apoid wasps in general.

TABLE 1. LOCATIONS OF COLLECTION SITES, INCLUDING SPECIES OF CICADAS COLLECTED AND DESCRIPTIVE STATISTICS OF THE CICADA SAMPLE DRY MASSES (G) AT EACH LOCATION, LISTED IN INCREASING ORDER OF SAMPLE MEAN SIZE.

Location (lat., long.)	Cicada Species	*n*	Mass (mean ± SD)
Newberry, FL (29.65251, -82.48536)	*Neocicada heiroglyphica* Say *Diceroprocta olympusia* Walker *Tibicen resonans* Walker *Tibicen similaris* Smith and Grossbeck	24	0.169 ± 0.176
Big Bend NP, TX (29.18176, -102.96310,)	D*iceroprocta. cinctifera* Uhler	50	0.248 ± 0.042
Montague, MA (42.57079, -72.51535)	*Tibicen canicularis* Harris	5	0.347 ± 0.067
Westford, MA (42.580309, -71.471410)	*Tibicen lyricen* DeGeer	35	0.383 ± 0.077
Easton, PA (40.69785, -75.20733)	*Tibicen chloromera* Walker *Tibicen linnei* Smith and Grossbeck	157	0.436 ± 0.100
Channahon, IL (41.444226, -88.172465)	*T. chloromera* *T. lyricen*	113	0.497 ± 0.074
Blacksburg, VA (37.22679, -80.42671)	*T. chloromera* *T. linnei,* *Tibicen pruinosa* Say	20	0.510 ± 0.107
Raleigh, NC (35.76862 -78.67775)	*T. chloromera,* *T. pruinosa* *Tibicen davisi* Smith and Grossbeck	14	0.512 ± 0.176
Highland Heights, KY (39.03209, -84.46302)	*T. chloromera* *T. pruinosa*	26	0.520 ± 0.066
Branson, MO (36.64549, -93.26323)	*T. chlolomera* *T. pruinosa*	16	0.552 ± 0.064
Hasty, CO (38.05198, -102.96346)	*Tibicen dealbata* Davis *Tibicen dorsata* Say	37	0.716 ± 0.022
St. Johns, FL (30.02820, -81.60472)	*T. chloromera* *T. resonans* *T. similaris* *Tibicen figurata* Walker	32	0.716 ± 0.335

We used two-way ANOVA (SPSS) to compare mean wing lengths of wasps between sexes and among geographic locations. We used one-way ANOVA to compare mean dry masses of cicadas among locations. Reduced major axis (RMA) and ordinary least squares (OLS) regressions, with cicada mass as the independent variable, were both used to determine if relationships exist between the mean dry mass of cicadas and the mean wing length of male and of female *S. speciosus* among locations. OLS regression assumes that the X values have no error (Warton, et al. 2006), but the X values in these analyses do have error, as they are means of local cicada sample dry masses. Consequently, RMA analysis was performed with PAST 1.81 (Hammer, et al. 2006). However, Warton, et al. (2006) state that if the goal of a line-fitting procedure is to predict Y from X, then OLS could be suitable, especially if the correlation coefficient, *r*, is high. As one of our goals was to determine if Y (local wasp size) can be predicted from X (local cicada size), we performed both OLS and RMA analyses.

RESULTS

Descriptive statistics of the body mass samples of cicadas are listed in Table 1, along with the species of cicadas used for provisions by female *S. speciosus* at the different locations. Females provisioned nests primarily, but not exclusively, with species of *Tibicen,* results consistent with those reported by Evans and O'Neill (2007). ANOVA revealed a significant difference among sample mean cicada dry masses from these locations (F = 48, $P < 0.001$, $df = 11$).

ANOVA also revealed a significant difference in mean wing length between sexes of wasps (F = 735, $P < 0.001$, df = 1) and among wasps sampled from different locations (F = 25, $P < 0.001$, df = 11). Overall mean female wing length (27.65 ± 2.33 mm, n = 401) was much greater than that of males (22.27 ± 1.76, n = 628). Due to the sexual size dimorphism, subsequent analyses were done separately for the sexes. As we only collected 3 females at the Hasty, CO site, they were excluded from subsequent analyses.

OLS regression analysis with cicada dry mass as the independent variable revealed that a significant positive relationship does exist between mean cicada dry mass and mean female *S. speciosus* wing length ($P < 0.001$, $R^2 = 0.824$); the relationship approaches significance for males (P = 0.055, $R^2 = 0.322$) (Fig. 1). In the regression analyses, one data point, the mean cicada dry mass and the mean wing length of males from Newberry, FL, is an outlier (maximum Cook's distance = 2.387). In fact, if that point is removed from the male analysis, the relationship becomes highly significant ($P < 0.001$, $R^2 = 0.834$, maximum Cook's distance = 0.852). We believe that this is a biologically unique data point for reasons discussed below. MRA regression analyses led to the same conclusions as those based on OLS regression analyses; for females the regression equation was $y = 8.62x + 23.84$ ($P < 0.001$, $R^2 = 0.847$), for males (excluding the outlier sample) the equation was $y = 6.88x + 18.95$ ($P < 0.001$, $R^2 = 0.832$).

DISCUSSION

In provisioning wasps, offspring size is largely determined by the mass of the provision they receive. In progressive provisioners, e.g., most species of *Bembix*, because providers directly feed larvae, the development of each offspring can be monitored, and the total provision mass given to them can be adjusted accordingly (Evans & O'Neill 2007). In mass-provisioning wasps, however, providers have no direct contact with larvae, because provisioning of each nest cell is completed before the egg laid in a cell hatches. Despite this lack of interaction between provider and offspring, in many mass provisioners the number of prey given to each offspring varies. For example, *Sceliphron laetum* F. Smith mass-provisions each nest cell with spiders of variable size; the number of prey given to each offspring is adjusted according to the size of the prey so that all nest cells receive a fairly constant spider mass (Elgar & Jebb 2004). The European beewolf mass-provisions its nest cells with honeybees, which are of fairly uniform size, but the number of honeybees given to each offspring can vary with changes in environmental factors such as prey availability (Strohm & Linsenmair 1997).

Though the relationship between provision mass and offspring size has not been directly studied in cicada killers, reported patterns of provisioning and sexual size dimorphism suggest that this general relationship applies to them as

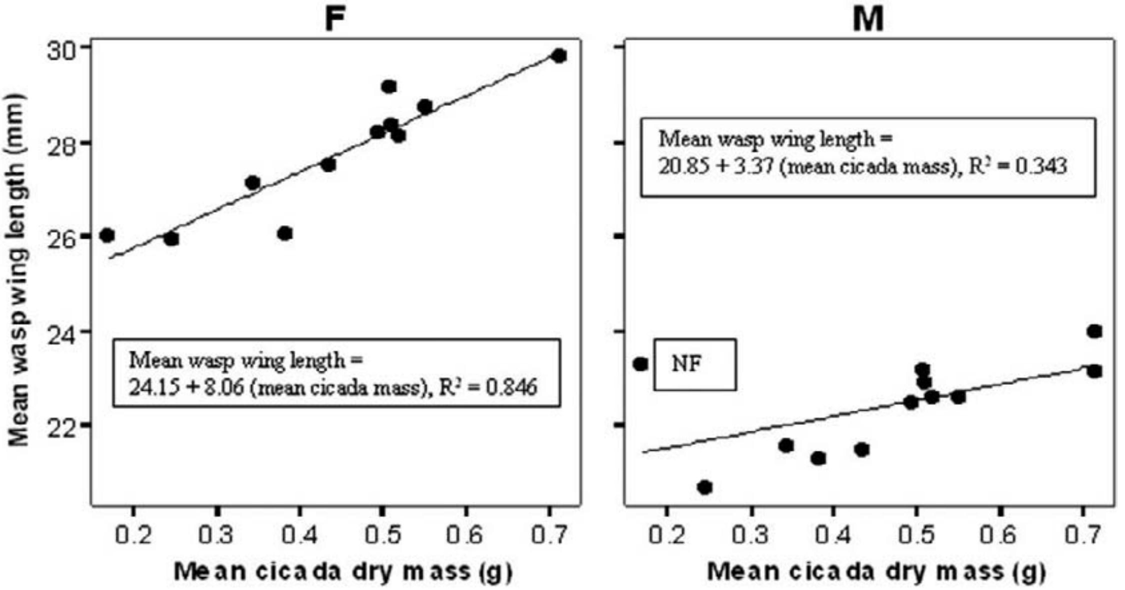

Fig. 1. Scatterplots, including OLS regression lines and equations describing the lines, showing the relationship between sample mean cicada dry mass and sample mean *S. speciosus* forewing length among different study locations. Separate graphs are shown for females (left) and for males (right). The data point for males from Newberry, FL is indicated by "NF".

well. However, unlike many other mass provisioners, cicada killers appear to provide each nest cell with a nearly constant prey number rather than with a relatively constant prey mass. At the population level, the consequence of this behavior is that the mean size of the wasps should track the mean size of the cicadas available in the local environment, unless female wasps hunt selectively by prey species, sex, or size. However, *Sphecius* females appear to be opportunistic, rather than selective, hunters (Grant 2006). The result of this opportunism is the central finding of this study: mean size of male and female *S. speciosus* varies among geographic locations, and is directly dependent on the size of cicada prey available in the local environment.

Selection Pressures Influencing Provisioning Behavior

Why have cicada killers apparently evolved to provision nest cells with fairly consistent number of prey? As mass provisioners, cicada killers have evolved to exploit a very specialized food resource: relatively large annual cicadas, mainly of the genus *Tibicen*. At most locations we have studied, female *Sphecius* hunt primarily either 1 prey species or they hunt multiple species that are of similar size, because that is generally what is available to them. Examples of the latter hunting pattern are the *S. speciosus* in Hasty, CO that hunt *T. dorsata* and *T. dealbatus*, both very large cicadas, and *Sphecius grandis* Say in the Chiricahua Mountains of Arizona, which hunt *T. duryi* and *T. parallela* (Hastings 1986), which are also very similar in size. As a consequence of this common pattern of prey availability, at most locations *Sphecius* females provision their nests with prey that are relatively uniform in size.

Each provisioning event by a female *S. speciosus* is apparently quite costly. For example, Coelho (1997) presented evidence of the physical and physiological difficulty of prey carriage, Grant (2006) estimated that provisioning events take at least 1.5 h, and Coelho and Holliday (2008) found that it takes a female 99 min to complete a male nest cell; 157 min are required for a female nest cell. Given that only a certain number of provisionings can be made during a female's lifetime, the more cicadas supplied to each offspring, the fewer offspring can be produced. In addition to the substantial energy and time costs of provisioning are potential costs incurred by the risk of nest parasitism. In *S. speciosus*, nest cells remain open as they are being filled with provisions. Therefore, the risk of parasitism of a given nest cell is likely to increase directly with the number of prey placed in the cell (Seidelmann 2006). At many of the locations visited in this study we observed miltogrammine flies, known to be parasites of cicada killer nests, near openings of *S. speciosus* nest burrows. In fact, at the Channahon, IL location, we observed miltogrammine flies deposit larvae on cicadas as they were being carried into nest burrows by female wasps. Given all of the above costs of provisioning, there must be strong selection pressure on females to minimize the number of cicadas provided to each offspring.

Large-male mating advantage has been reported in *S. grandis* (Hastings 1989) as well as in *S. speciosus* (Coelho & Holliday 2000). Large males obtain a disproportionate number of matings, presumably because they are better able to defend territories within areas of emergence of virgin, receptive females. Consequently, female wasps could possibly increase the success of individual sons by stocking nest cells with 2 or more cicadas. However, small males can and do obtain copulations by employing alternative mating tactics (Hastings 1989; Coelho & Holliday 2000). Additionally, Coelho (1997) discussed how the law of diminishing returns applies to the flight performance of insects; parental investment in larger offspring yields a decreasing return in flight performance. Consequently, a female investment strategy of producing a few, large male offspring, as opposed to producing more, but smaller males might not be favored by selection. The observed provisioning pattern in *S. speciosus* of most male offspring being given 1, or rarely 2, cicadas appears to be an adaptive compromise that may have evolved in response to these conflicting selection pressures.

A similar argument can be applied to the provisioning of nest cells that will yield female offspring. Apparently, due to the difficulty of prey carriage (Coelho 1997), small female *S. speciosus* have relatively low provisioning success (Hastings 1986; Pfennig & Reeve 1989; Grant 2006) and, presumably, low reproductive success. Could not provisioning females, therefore, increase the reproductive success of their daughters by providing each with 3 or more, rather than just 2, cicadas? As with production of sons, the production of daughters involves allocation of a limited maximum total number of cicadas that may be caught in a female's lifetime among the offspring, in addition to the increased risk of nest cell parasitism likely associated with increased number of cicadas supplied per cell. Though the smallest females do appear to have reduced hunting success or, at least appear to be constrained to hunting only the smallest available prey (Grant 2006), all but the smallest females from most study sites appear to be capable of carrying all sizes of cicadas available in their habitat; a notable exception is discussed below. Consequently, on average, the common provisioning pattern of allocating 2 cicadas per daughter will usually produce daughters large enough to be successful providers, and allocation of more than 2 cicadas to any daughter would be wasted parental effort, resulting in production of fewer offspring.

Cicadas and Cicada Killers in Newberry, Florida

Though cicada prey are fairly uniform in size at most locations of this study, in Newberry, FL cicadas with a dry mass range between 0.096 g (*Neocicada hieroglyphica*) and 0.860 g (*Tibicen resonans*) were collected from provisioning female wasps. If, as we contend, the size of cicada prey determines the size of cicada killers, then the size range of the wasps should parallel the large range that exists in the prey. This was the case, at least in females, which had a wing length range between 22.3 and 33.0 mm, the largest range among all sites sampled. Additionally, the coefficient of variation in wing length for the sample of females from Newberry was 10.1%, which was the highest among all sites; the next highest being 8.2% for the sample of females from Easton, PA. Most Newberry females had wing lengths of 26.0 mm or less, which, based on our calculated relationship between wing length and dry mass ($y = 32.836x - 600.99$) would correspond to dry masses of 0.253 g or less. Based on the prey carriage limit of 2.5X the female body mass proposed by Coelho (1997) and Grant (2006), we would expect these relatively small females to be limited to carrying prey with a dry mass of 0.633 g or less. The relatively large *Tibicen* present in this local environment are significantly heavier than this theoretical limit, and, therefore, are too large for most females in this sample to carry in flight. In fact, 22 of the 24 cicadas brought to nests by Newberry females were the relatively small *Neocicada hieroglyphica* and *Diceroprocta olympusia*. While we did observe large females provisioning with small cicadas, we saw no female with a wing length shorter than 26.0 mm provision with one of the 2 relatively large *Tibicen* species. Apparently, most females at this site are constrained to hunting only the small cicadas. As prey capture occurs in canopies of tall trees, we were unable to determine whether or not small females capture and paralyze large cicadas but fail to return with them to their nests. Certainly large females at this location are at an advantage, because a wider size range of prey is available to them. So why are most females small? Inflexibility of provisioning behavior coupled with the predominance of small cicadas in the environment could account for this.

As we only collected 9 male *S. speciosus* at Newberry, we remain cautious about drawing inferences from this sample. However, the mean wing length of these males was 23.3 mm, higher than that of all male samples except for that of the St. Johns, FL sample, which was 24.0 mm. This contrasts sharply with what was observed for females from this location. In fact, there appears to be relatively little sexual size dimorphism within this local wasp population (Table 2). Is it possible that female wasps of this population provide their male and female offspring with equal numbers of prey? Alternatively, perhaps females only oviposited unfertilized (and, therefore, male) eggs on relatively large prey.

The size of wasps from the Newberry site raises another question relevant to the basic thesis of this paper: Why are the females at this location so small when the females from St. Johns, FL, a location only about 100 km to the east, are so large (Table 2)? The striking disparity in female wasp size between these locations exists in spite of the fact that females from both locations hunt at least 2 of the same species of cicadas (Table 1). The answer could simply be that at the former site small prey species (*D. olympusia* and *N. hieroglyphica*) are much more abundant than they are at the latter site. If this is the case, then these data provide more support for our central hypothesis that provisioning females stock nest cells with a fairly constant number of prey, rather than with a constant cicada mass.

TABLE 2. DESCRIPTIVE STATISTICS (*N*, MEAN ± SD) OF RIGHT FOREWING LENGTH (MM) OF MALE AND FEMALE *S. SPECIOSUS* SAMPLES FROM ALL STUDY LOCATIONS, LISTED IN SAME SEQUENCE AS IN TABLE 1.

	Males		Females	
Location	*n*	mean	*n*	mean
Newberry, FL	9	23.3 ± 1.86	43	26.0 ± 2.62
Big Bend NP, TX	63	20.7 ± 1.90	24	25.9 ± 1.76
Montague, MA	8	21.6 ± 1.22	15	27.1 ± 2.17
Westford, MA	48	21.3 ± 1.25	38	26.0 ± 1.79
Easton, PA	85	21.5 ± 1.48	75	27.5 ± 2.25
Channahon, IL	113	22.5 + 1.70	75	28.2 + 2.17
Blacksburg, VA	51	23.2 ± 1.50	21	29.2 ± 1.56
Raleigh, NC	70	22.9 ± 1.51	25	28.3 ± 1.70
Highland Heights, KY	50	22.6 ± 1.48	29	28.1 ± 2.15
Branson, MO	84	22.57 ± 1.33	30	28.73 ± 1.60
Hasty, CO	21	23.1 ± 1.92	3	not in analysis
St. Johns, FL	26	24.0 ± 1.53	25	29.8 ±1.70

This study has determined that variation in body size exists among regional populations of cicada killers, and that wasp size can be predicted from the size of available prey. Though the explanation for this relationship remains unclear, the variation in wasp size could be entirely due to variation in provision mass given to offspring by females adapted to provide offspring with a relatively consistent number of prey. Alternatively, regional variation in wasp size might have evolved by selection. We view this study as a starting point for a more thorough investigation of regional variation in body size within all North American species of *Sphecius* and the causes that underlie the variation. Additional research of the populations of *S. speciosus* in northern Florida, and the wide diversity of prey that they utilize, should provide us with an improved understanding of this issue. Consequently, we will focus most of our research efforts there over the next few summers.

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