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SIZE-SPECIFIC PROVISIONING BY CICADA KILLERS, *SPHECIUS SPECIOSUS,* (HYMENOPTERA: CRABRONIDAE) IN NORTH FLORIDA

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ABSTRACT

Eastern cicada killer wasps (*Sphecius speciosus* Drury) mass-provision underground nest burrows with cicadas they capture and paralyze in nearby trees. We studied provisioning by female cicada killers at 2 aggregations in north Florida where a variety of cicada species, with a large range in body size, are used as prey. We captured and measured samples of male and female wasps and we uniquely marked samples of females. We measured and identified paralyzed cicadas that we retrieved from females as they were provisioning their nests. We compared the body sizes of male and female wasps, and cicada prey, between locations. The mean body sizes of male wasps, female wasps, and cicadas from the St. Johns site were much larger than those from the Newberry site. We determined the relationship between the size of individual female wasps and the size of their prey at both locations. Previous studies had concluded that cicada killer hunting is opportunistic, with females provisioning their nests with cicadas of different sex, species, and size in proportion to their relative abundance in the environment. However, we found that individual female cicada killers at these locations exhibited prey specificity by size. Small wasps brought only small cicadas to their nests, as they are likely constrained from carrying large cicadas in flight. Large wasps, not similarly constrained, rarely provisioned with small cicadas. The wasps appear to selectively hunt the largest prey they can carry in flight. Evidence suggests that the cicadas retrieved from wasps at the Newberry site were smaller because small female wasps predominate there, and not because there is a difference in the body size distributions of the cicadas between the 2 local environments.

Key Words: mass-provisioning, size variation, prey size, selective hunting, solitary wasp

RESUMEN

La avispa asesina de cigarras del este (*Sphecius speciosus* Drury) recolectan provisiones masivas de cigarras que ellas capturan y paralizan en sus nidos subterraneos en árboles cercanos. Estudiamos como las hembras de la avispa asesina de cigarras aprovisionan sus nidos en 2 agrupaciones en el norte de la Florida donde una variedad de especies de cigarras, con una amplia gama de tamaños de cuerpo, son usadas como presas. Capturamos y medimos muestras de los machos y hembras de las avispas y marcamos unicamente las muestras de las hembras. Medimos y identificamos las cigarras paralizadas que fueron recuperadas de las hembras mientras que aprovisionaron sus nidos. Comparamos el tamaño del cuerpo de los machos y hembras de las avispas y de las presas cigarras en las dos localidades. Los promedios del tamaño de las avispas machos, avispas hembras y cigarras del sitio de St. John fueron mucho mas grandes que los del sitio de Newberry. Determinamos la relación entre el tamaño de los individuos de las hembras avispas y el tamaño de sus presas en ambas localidades. Estudios anteriores han concluido que la caseria por las avispas asesinas de cigarras es oportunistica, que las hembras aprovisionan sus nidos con cigarras de diferente sexos, especies y tamaños en proporción de su abundancia relativa en el ambiente. Sin embargo, encontramos que los individuos de las hembras de la avispa asesina de cigarras en estas localidades mostraron una preferencia por el tamaño de la presa. Avispas pequeñas llevaron solamente cigarras pequeñas a sus nidos, esto probablemente a que estan limitadas de llevar cigarras grandes mientras que vuelan. Avispas grandes, no estan limitadas y raramente aprovisionaron sus nidos con cigarras pequeñas. Parece que las avispas cazan selectivamente las presas más grandes que puede llevar cuando vuelan. La evidencia indica que las cigarras recuperadas de las avispas en el sitio de Newberry fueron mas pequeñas por que las avispas pequeñas hembras predominaron ahi, y no por que hay una diferencia en la distribución de tamaño del cuerpo de las cigarras entre los 2 ambientes locales.

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Eastern cicada killers, *Sphecius speciosus* Drury, are mass-provisioning wasps found in all but 2 states (Vermont and Maine) of the USA east of the continental divide (Holliday & Coelho 2006). Over this range they hunt cicadas of at least 30 species in 5 genera (Holliday et al. 2009); further, these prey cicadas vary considerably in size. Females dig nest burrows in well-drained soil, often forming large nesting aggregations, and provision nest cells with cicadas they capture and paralyze in nearby trees. Studies by Dow (1942a, 1942b), Lin (1979a), Coelho (1997), and Grant (2006) report that the number of cicadas provided to each offspring is fairly consistent, with sons given 1, sometimes 2, cicadas, whereas daughters are given 2, sometimes 3, cicadas regardless of cicada size. If, as in many other provisioning Hymenoptera, the size of individual offspring in cicada killers is determined largely by the mass of their provision (Punzo 1994; Strohm 2000; Seidelmann 2006), then female cicada killers should generally be much larger than males. This pattern of sexual size dimorphism has been described in all published reports of relative male and female size in this species (Evans & O'Neill 2007) and it is the pattern that we have observed in the many *Sphecius* populations that we have studied (Hastings et al. 2008).

Lin (1979b) presented evidence that female cicada killers hunt cicadas selectively by size, species, and sex. He concluded that females know the sex of the egg that they will lay in each nest cell in advance of their hunts. Presumably, when a female is hunting for a future daughter, she will not only dig a larger nest cell and provide it with 2 or 3 cicadas, but she will also hunt selectively for heavy prey individuals. As a result, daughters are provided with large provisions, enabling them to attain large body size. However, other studies of nest provisioning by female cicada killers have concluded that they are opportunistic, rather than selective, hunters (Coelho 1997; Grant 2006). Evidence presented in these more recent studies suggests that, at the population level, female cicada killers hunt largely at random with regard to the species, sex, and the size of cicada prey. Consequently, samples of cicadas taken from provisioning females were not very different from samples gathered from the environment.

Grant (2006) also investigated the possibility that, in the absence of overall size bias in provisions at the population level, individual wasps within the population might exhibit size-specific hunting, with large females hunting large prey and small females hunting small prey. However, he found there to be little evidence in support of individual size-selectivity other than that the smallest females were constrained from provisioning with the largest cicadas. This constraint was likely due to the inability of the small wasps to carry large prey in flight. Coelho (1997) came to similar conclusions.

In a previous study of cicada killers from 12 geographic locations, Hastings et al. (2008) found that the mean body size of male and female wasps and of their cicada prey varied among locations. They reported that a direct relationship existed between the mean size of cicada prey available in the local environment and the size of the wasps; in locations where cicadas were large, the male and female wasps were large; where prey were small, the wasps were small. This relationship between prey size and wasp size should exist if (1) female wasps are opportunistic hunters, (2) females provision their nest cells with a fairly consistent number of cicada prey, and (3) the size of wasps is largely determined by the mass of cicada prey provided to them by their mothers. At most locations of this study, wasps provisioned their nests primarily with 1 species of prey or with 2 species of similar size. However, at 2 locations in north Florida, Hastings et al. (2008) reported that several cicada species with a body mass range exceeding an order of magnitude were used as prey. They noted that the wasps from Newberry, FL were small and the wasps from St. Johns, FL were much larger, despite the fact that the locations were less than 100 km apart, and that at least 2 of the same species of cicadas were used as prey. They tentatively concluded that the size difference in wasps likely reflects differences in the relative abundance of prey of various sizes at the different locations; presumably small cicadas predominated in Newberry, large cicadas in St. Johns. They also concluded that further study of provisioning by cicada killers at these Florida locations was warranted and could provide improved understanding of hunting behavior in these wasps and of the causes of local variation in their body size. The present study is an expansion of this earlier work; our focus was on only these 2 locations in north Florida, and the application of additional sampling methods has provided us with a very different, and likely a clearer, understanding of cicada killer hunting and provisioning in environments with a broad diversity of potential cicada prey.

Materials and Methods

We conducted field research between 14 Jul and 5 Aug 2008 in 2 locations in north Florida. The study site in Newberry, FL (lat/long = 29.653005, -82.485275), a residential area, includes the front yards of 2 houses on the same block. The St. Johns County, FL site (30.028234, -81.604746) is within and around the stable and equipment shed of a small horse farm. We collected data on 16-19 Jul, 24-25 Jul, 31 Jul-3 Aug in Newberry, and on 14-15, 21-23, 28-30 Jul, and 4-5 Aug in St. Johns. Thirty wasps and 13 cicadas brought to nests by female wasps, collected 29 Jun-11 Jul at the Newberry site by a local resi-

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dent, who froze and dried them, are included in our analyses.

Male wasps were netted, killed with ethyl acetate, and weighed to the nearest mg (Adventurer Pro AV53 electronic scale, Ohaus Corp., Pine Brook, NJ). The right wing length (RWL) was measured to the nearest 0.01 mm with digital calipers (Cen Tech #47256, Harbor Freight, Camarillo, CA) as the distance from the distal end of the wing to the distal tip of the tegula. Female wasps were netted, anesthetized in 100% CO_2 (ISI Soda Siphon, iSi, GmbH, Vienna, Austria) for 30 s, weighed to the nearest mg, labeled with numbered paper tags affixed to the scutum with alpha-cyanoacrylate glue (Duro Quick Gel thick formulation, Henkel Corp., Avon, OH) and the RWL was measured as above. Recovery from anesthesia occurred in 90-120 s; the few wasps that did not recover promptly were killed with ethyl acetate and kept as voucher specimens. Of the 220 labeled females released in the 2 study areas, 124 (56.4%) were seen again after release, and many were seen regularly over the entire remaining period of the study.

Female cicada killers usually enter their burrows rapidly when returning with or without paralyzed cicadas and, therefore, we developed a method to detain them briefly to allow identification of wasp and prey. We detained female wasps and their prey together by plugging nest openings with dowels after we saw females leave their nests to hunt cicadas. When females returned to the plugged burrows with or without a paralyzed cicada, they would try to dig into the burrow along one side of the dowel; this allowed us time to identify the female by the numbered tag on her scutum and to identify the sex and, tentatively, the species, of her cicada. In some instances, after prey identification, the dowel was slowly removed from the burrow, allowing the wasp to enter with her prey and then replaced when she left the burrow to hunt again. However, in most instances we retrieved the cicada provisions from the female wasps; these cicadas were weighed and RWL was measured as noted above. Retrieved cicadas were killed in ethyl acetate and pinned for verification of our field identifications.

We noted that cicada prey, which were of several different species, were extremely variable in body size. 2 species, later determined to be *Neocicada hieroglyphica* Say, and *Diceroprocta olympusa* Walker, were much smaller than the others. We classified all individuals of these 2 species as small cicadas. Another species, later determined to be *Tibicen resonans* Walker, was significantly larger than all other species; we classified all *T. resonans* as large cicadas. We classified all other cicada species, which were of intermediate size, as medium cicadas.

We conducted focal studies of provisioning behavior by 59 labeled females in Newberry and 19 in St. Johns in order to determine how much time is required for females to find, capture, paralyze, and return with cicadas to their nest burrows. Clusters of several active burrows were continually observed by each researcher throughout the day. Whenever females would exit their burrows, we would block the openings and note the time of their exit. The time of the females' return with prey was noted, and the cicadas were identified. The plugs were then slowly removed without disturbing the wasps and they were allowed into their burrows with their prey cicadas. Hunt times were calculated as the time period between wasps' exit from the burrows and their return with cicadas. Occasionally females would return to their nests without prey; as we had no way of knowing whether such events were unsuccessful hunts or if the females were returning to their nests following bouts of feeding or other activity, we did not include these time periods in the hunt time calculations.

Direct sampling of the cicada communities at both locations was impractical for a variety of reasons, but primarily because the cicadas were active in the canopies of tall trees that were out of our reach and our view. We then attempted to use male cicada song counts as a crude method of determining the relative abundance of various cicada species. We learned to identify the songs of males of several local cicada species, including *Neocicada hieroglyphica*, *Diceroprocta olympusa*, *Tibicen tibicen australis* Davis, and *Tibicen resonans* by 2 methods, as follows: (1) we used a camcorder to record singing cicadas that we could identify; we then studied these recordings, and, (2) we studied recordings of songs of local cicada species that were available on an Internet site created by Walker & Moore (http://entomology.ifas.ufl.edu/walker/buzz/c700fl2.htm). Twice each morning and twice each afternoon, when the sun was not covered by clouds, we spent 10 min listening to cicada songs. Based on our perception of the relative number of males of each species that we heard singing, we made daily subjective rankings of the relative abundance of the various cicada species. We acknowledge the limitations of this crude census method. For example, it assumes equal proportions of males and females among the different species. It also assumes that there are no significant differences in how frequently and when, during the diurnal cycle, males of the different species sing. However, despite these shortcomings, we contend that the method provides useful information about the relative abundance of prey species in the local environments.

Data Analysis

We used independent-samples *t*-tests to compare the mean body sizes of cicadas retrieved

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from female wasps between locations, and to compare mean hunt times for small cicadas between locations. Lack of hunt time data for medium and large cicadas at the Newberry site precluded similar between-location comparisons for these prey size categories. Two-way ANOVA was used to compare mean wet body masses and RWL of wasps between sexes and between locations and one-way ANOVA was used to compare mean hunt times among different cicada prey size classes at the St. Johns location. For each of these statistical tests we used SPSS version 15.0.

The use of RWL, instead of wet mass, as a measure of body size in wasps and in cicadas increases our sample sizes for some analyses, and it is a measure of body size commonly used in wasp research (Ohl & Thiele 2007), including by Hastings et al. (2008), for populations of *S. speciosus* at the same locations as those of the present study. Consequently, some of our results make use of RWL as the measure of body size in the wasps and the prey. However, it is useful for us to be able to convert size measurements between RWL and wet mass. Therefore, we determined the relationship between these size variables in the wasps and in the cicadas using the statistics package R (R Development Core Team 2008). Coelho (1997) found no difference in the scaling of RWL and wet mass between male and female *S. speciosus*. Consequently, male and female wasp samples from both locations were combined for this analysis. R was used to determine the relationship between RWL and wet mass within samples of cicadas retrieved from female wasps.

We also used R to determine the relationship between the RWL of individual female wasps and the RWL of cicada prey they brought to their nests. For this analysis, we assumed that wasps of any given size provision their nests in an independent and identically distributed way. Therefore, we included each provisioning event by each female in the analysis, which included 96 provisioning events by 68 Newberry female wasps and 51 provisioning events by 28 female wasps from St. Johns. We combined data from the 2 locations for the analysis.

Results

Body size samples of male and female wasps from both locations are summarized in Table 1. ANOVA revealed significant differences in wet mass between the sexes ($F = 549_{405, 1}$, $P < 0.001$) and between locations ($F = 368_{405, 1}$, $P < 0.001$). At both locations females are much larger than males, and for both sexes, the wasps from St. Johns are much larger than those from Newberry. Similar results were obtained from comparison of RWL among the samples. These comparisons follow the same pattern reported by Hastings et al. (2008) for cicada killers sampled at these locations.

The species and descriptive statistics of the wet masses and RWL of cicadas retrieved from female wasps at the 2 locations are summarized in Table 2. Comparison of samples (independent-samples t-tests) of *N. hieroglyphica* and *D. olympusa,* and *T. t. australis* between locations revealed no significant difference in RWL, hence samples for each species from both locations were combined. No *T. resonans* were sampled from Newberry and no *T. similaris* or *T. pruinosus* were found at St. Johns. The cicadas fell into 3 size categories; we classify *N. hieroglyphica* and *D. olympusa* as small cicadas, *T. resonans* as large cicadas, and other *Tibicen* species as medium cicadas.

Table 3 summarizes the number of cicadas of the different size classes brought to nests by provisioning female wasps at each location. Also shown are the descriptive statistics of the body sizes of the cicadas that we retrieved from the wasps, all size classes combined, sampled from each location. At the Newberry site, females provisioned nearly exclusively with small cicadas, whereas the St. Johns females brought similar numbers of cicadas of the 3 size classes to their nests. The mean wet mass of the Newberry cicadas was much smaller than that of the St. Johns cicadas ($t = 12.4$, $df = 141$, $P < 0.001$); a similar result was found for the comparison of cicada mean RWL between locations ($t = 14.8$, $df = 156$, $P < 0.001$). As Hastings et al. (2008) previously found, the cicada provisions of the female wasps at the

Table 1. Descriptive statistics of body size measurements of male and female cicada killers from 2 locations in north Florida, USA. Shown are mean ± SEM for wet body mass in mg and for right wing length (RWL) in mm, and number of specimens, *n*.

	St. Johns	Newberry
Males		
wet mass (mg)	532.2 ± 11.1, $n = 110$	329.2 ± 9.0, $n = 73$
RWL (mm)	24.3 ± 0.2, $n = 110$	21.8 ± 0.1, $n = 90$
Females		
wet mass (mg)	1141.4 ± 33.4, $n = 90$	612.6 ± 12.6, $n = 129$
RWL (mm)	30.7 ± 0.3, $n = 93$	24.0 ± 0.2, $n = 142$

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TABLE 2. SIZE CATEGORIES OF DIFFERENT SPECIES OF CICADAS RETRIEVED FROM FEMALE CICADA KILLER WASPS AT NEWBERRY AND ST. JOHNS, FL. ALSO SHOWN ARE MEAN ± SEM WET MASS IN MG, MEAN RIGHT WING LENGTH (RWL) IN MM AND THE NUMBER OF SPECIMENS (*N*) FOR EACH SPECIES.

Cicada species	Size category	mg Wet mass (*n*)	mm RWL (*n*)
Neocicada heiroglyphica	small	339.5 ± 5.3 (87)	26.5 ± 0.1 (99)
Diceroprocta olympusa	small	419.4 ± 18.1 (14)	27.9 ± 0.3 (14)
Tibicen tibicen australis	medium	1897.2 ± 54.2 (24)	43.1 ± 0.3 (27)
Tibicen pruinosus	medium	1632.0 + 264.0 (3)	42.15 + 1.0 (3)
Tibicen similaris	medium		36. 97 (1)
Tibicen resonans	large	2723 ± 97.0 (18)	52.54 ± 0.5 (18)

TABLE 3. TOTAL NUMBER OF CICADAS OF EACH SIZE CATEGORY BROUGHT TO NESTS BY FEMALE *S. SPECIOSUS* AT EACH LOCATION. ALSO SHOWN ARE MEAN ± SEM, NUMBER (*N*) WET MASS AND RWL FOR SAMPLES OF CICADAS RETRIEVED FROM PROVISIONING FEMALES.

	Cicada size category			Mean Cicada Body Size	
Location	Small	Medium	Large	mg Wet mass (*n*)	mg RWL (*n*)
Newberry	294	7	0	389.96 ± 26.2 (90)	26.98 ± 0.3 (102)
St. Johns	61	68	43	998.31 ± 137.1 (53)	42.28 ± 0.3 (56)

Newberry location were generally much smaller than they were at the St. Johns site.

The relationship between RWL and wet body mass of wasps collected from both sites is shown in Fig. 1. The graph is a scatterplot of transformed data, obtained by taking the natural logarithm of both RWL and wet mass measurements for each wasp; linear regression was then performed on the transformed data. The high R^2 (0.94) indicates that RWL is an excellent predictor of wet body mass. Wet mass is an exponential, rather than a linear, function of RWL, which should be expected, as mass should increase as a cubic function of linear measurements such as wing length.

Fig. 2 displays the relationship between RWL and wet body mass, both variables log-transformed, for cicadas retrieved from female wasps, with all species from both locations combined. The relationship was the same for small and large cicadas; the best-fit line for medium cicadas followed a similar slope, but had a different Y-intercept, indicating that for any given RWL, the medium cicadas were slightly more massive than were cicadas of the other size categories. As with the wasps, wet mass is an exponential function of RWL, and the high R^2 (0.98), shows that RWL is an excellent predictor of wet mass in cicadas.

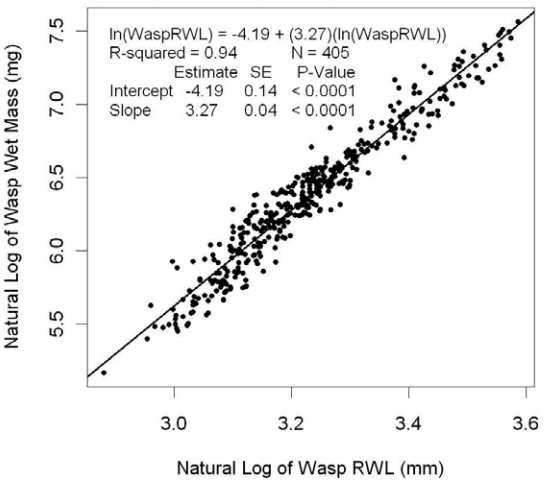


Fig. 1. The relationship between body wet mass in mg and right wing length (RWL) in mm in *S. speciosus*; samples of both sexes from both locations combined. In the scatter plot both variables have been log-normalized. The straight line of best fit and its equation are shown.

Prey Loads

Fig. 3 is based on a similar figure published by Grant (2006). In it we plot individual provisioning events by wet masses of the female wasp and her prey, as well as lines of various slopes passing through the origin; these lines represent possible relative prey and wasp masses and, for example, the line labeled "2" represents cicada masses twice that of their wasp captors. Newberry provisioning events are distinguished from those occurring at St. Johns. Relative prey loads varied greatly at both sites, with prey mass ranging from approx-

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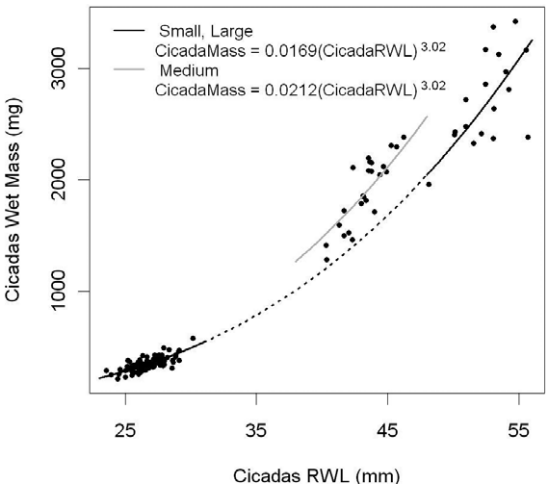


Fig. 2. The relationship between body wet mass in mg and right wing length (RWL) in mm in cicadas of all species retrieved from female *S. speciosus*, both locations combined. Also shown are the curves that best describe this relationship; the curve for medium wasps has a different Y-intercept than does the one for the small and large wasps.

imately 0.25 to 2.5 times the mass of the wasp. As in a New Jersey cicada killer population (Grant 2006), the upper limit for prey load appears to be 2.5, which is likely the physical limit of the wasps' ability to carry prey in flight (Coelho 1997). However, in contrast with Grant's findings, there is a much broader range of prey loads, with many wasps carrying cicadas significantly less than their own mass. In fact, many of the wasps had prey loads of less than 0.5. Most wasps from Newberry are small and therefore constrained from provisioning with medium and large cicadas, which are, on average more than 2.5 times their mass. They must, by necessity, provision with small cicadas, which generally weigh much less than they do. The few provisioning events in Newberry with medium cicadas involved the largest female wasps. The wasps in St. Johns, which are generally much larger, and are not similarly constrained, mainly provisioned with medium and large cicadas. As in Grant (2006), most provisioning events at St. Johns were clustered around the relative prey-load line with a slope of 2.0. Some St. Johns females provisioned with small cicadas; with only 2 exceptions, these were relatively small wasps. In other words, large wasps rarely provisioned with small cicadas.

The Relationship between RWL in Wasps and their Prey

In Fig. 4, individual provisioning events are plotted by the RWL of the provisioning female and the RWL of her prey. The data suggest a set of

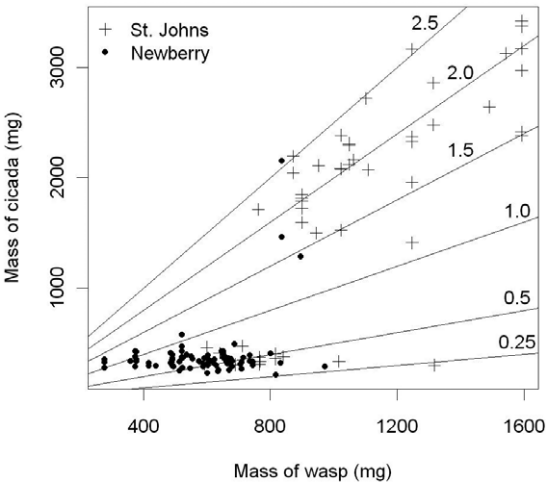


Fig. 3. Prey loads of individual female *S. speciosus* shown as body wet masses of the female wasp and her prey. Provisioning events occurring at Newberry are contrasted from those at St. Johns. Also shown are lines of various slopes passing through the origin; these lines represent possible relative prey and wasp masses, with the line labeled "2" indicating cicada masses twice those of their wasp captors. This figure is based on a similar one in Grant (2006).

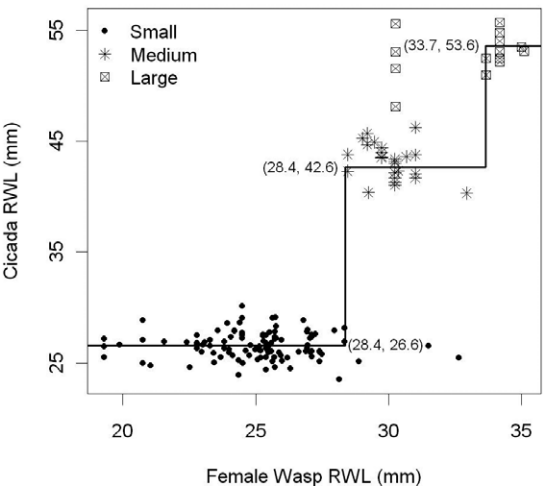


Fig. 4. Individual provisioning events are plotted by the right wing length (RWL) in mm of the provisioning female and the RWL of her prey. Provisioning events occurring at the 2 locations are combined. Also shown is the non-linear stair-step model that describes the relationship between wasp RWL and prey RWL. Symbols for provisioning events are distinguished by cicada size category. Coordinates of the switch-points of the stair-step model are shown in parentheses.

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stairs; small wasps provisioned with small cicadas, medium-sized wasps primarily with medium cicadas, and large wasps with large cicadas. We used a seven-parameter model of the following form to model the data:

$$\text{cicada RWL} = \alpha + \beta * S(\text{wasp RWL}; \mu_1, \sigma_1) + \gamma * S(\text{wasp RWL}; \mu 2, \sigma 2),$$

where S (x; μ, σ) is the normal cumulative distribution function centered at μ with standard deviation σ. This represents one choice out of many possible sigmoidal functions which we could have used to make the transition between 2 levels. We felt that such a model, made up of 3 distinct levels separated by smooth transitions, would capture the behavior of the predation as seen in the predation data. Upon using weighted non-linear regression to select the best parameters, we discovered that the result became effectively a step function, such that the values σ_1 and σ_2 were essentially zero (not significant at the $\alpha = 0.05$ level).

The best model we obtained is represented by the parameters presented in Table 4. We contend that predation is based on wasp size: there exist discrete switch-points in wasp RWL at which wasps suddenly switch to hunting larger prey. We suggest that this occurs at the RWLs at which the wasps are physically capable of carrying the larger cicadas. The case for the transitions occurring when the wasps become physically capable of carrying the larger cicadas is based in part on the mass ratio of the transition points in the stair-step model of RWL. The values of μ occur at points such that the wasp and cicada masses would be along the slope = 2.0 line of Fig. 3. That is, if we use the regression models described above to predict wasp and cicada masses corresponding to the points (28.372, 42.626) and (33.664, 53.586), we obtain masses of (856.9, 1793) and (1499, 2850), leading to mass ratios of 2.093 and 1.901, respectively.

Provisioning by Large Females in St. Johns, FL

With few exceptions, the Newberry wasps, as a consequence of their small size, are constrained to provision their nests with small cicadas. However, the St. Johns wasps are not similarly limited, and similar numbers of cicadas of the 3 size classes were brought to nests by the St. Johns females. Table 5 summarizes the number of cicadas of each size class brought to nests by female wasps at the St. Johns location. The wasps, like the cicadas, are divided into 3 size classes; the wasp size classes are defined by the stair-step model presented above. Small female wasps provisioned only with small cicadas, medium females primarily with medium cicadas, and large females almost exclusively with large cicadas. For the purpose of this analysis, if we assume that the overall provisioning result is an approximate census of the cicada prey in the local environment, then the relative frequencies of the small, medium, and large cicadas would be 0.35, 0.40, and 0.25, respectively. The large female wasps are presumably capable of carrying all available cicadas in flight to their nests. Consequently, if these large females had hunted opportunistically, the proportions of the size classes of their prey should be reflective of the relative frequencies of these cicada size classes. However, of the 30 cicadas brought to nests by large St. Johns females, none were small, only one was medium, and 29 were large. Assuming non-selective hunting, the probability of such an extreme hunting outcome is essentially zero ($\chi^2 = 82.2$, $df = 2$, $P < 0.001$).

Hunt Times

The mean ± SEM hunt time for small cicadas at the Newberry site was 23.5 ± 1.9 min ($n = 118$); it was not significantly different from the mean hunt time for small cicadas at the St. Johns site, which was 29.6 ± 7.0 ($n = 12$) (independent-samples $t = 0.94$, $df = 128$, $P = 0.349$). No hunt times were recorded for large cicadas at the Newberry site; only one was recorded for medium cicadas, and it was excluded from subsequent analysis. ANOVA revealed a significant difference in mean hunt times among cicada size categories at the St. Johns location ($F = 4.6_{30,2}$, $P = 0.019$, power = 0.731) with the mean hunt time for small cicadas

TABLE 4. PARAMETERS OF THE STAIR-STEP REGRESSION MODEL (SEE FIG. 4) OF THE RELATIONSHIP BETWEEN THE RWL OF *S. SPECIOSUS* FEMALES AND THE RWL OF THEIR CICADA PREY; DATA FROM BOTH LOCATIONS COMBINED. THE PARAMETERS DEFINE THE LOCATIONS AND SIZES (HEIGHTS) OF THE STEPS OF THE MODEL.

Feature of model	Parameter	Estimate	Standard error	*P*-value
Baseline height	α	26.588	0.342	<.0001
Size of first step	β	16.038	0.671	<.0001
Size of second step	γ	10.960	1.299	<.0001
Location of first step	μ_1	28.372	0.009	<.0001
Location of second step	μ_2	33.664	0.008	<.0001

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TABLE 5. THE NUMBER OF CICADAS OF EACH SIZE CLASS BROUGHT TO NESTS BY FEMALE *S. SPHECIUS* OF EACH SIZE CLASS AT THE ST. JOHNS LOCATION. WASP SIZE CLASSES ARE DEFINED BY THE STAIR-STEP MODEL PRESENTED ABOVE. SMALL WASPS HAVE RWL < 28.37 MM, MEDIUM WASPS HAVE RWL BETWEEN 28.37 - 33.66 MM, AND LARGE WASPS HAVE RWL > 33.66 MM.

	Cicada prey size class			
Wasp size class	Small	Medium	Large	Total
Small	47	0	0	47
Medium	14	67	14	95
Large	0	1	29	30
Total	61	68	43	172
Relative frequency	0.35	0.40	0.25	1.00

(29.6 ± 7.0 min, n = 12) being significantly shorter than the mean hunt time for medium cicadas (54.0 ± 5.8 min, n = 13) (Tukey post hoc multiple comparison, P = 0.021). No other significant differences in mean hunt times were found.

Cicada Communities

Our attempts to census the different prey species by song were met with several unanticipated challenges, including interruption of the attempts by changes in cloud cover; males generally did not sing unless direct sunlight was available. We had difficulty determining the exact number of individual males of each species singing at any given time. Consequently, our census data consisted only of subjective daily rank orders of abundance. For each day of study *N. hieroglyphica* were judged to be the most abundant followed by *D. olympusa*. *Tibicen resonans,* and *T. t. australis* were judged to be equally abundant and less common than the other 2 species. We concluded that at both locations, cicadas of each size class were active each day, and that small cicadas were more abundant than the medium and the large ones.

Our results suggest that female *S. speciosus* exhibit size-specific provisioning at these locations. Consequently, it is reasonable to expect the mean hunt time for each cicada size class to be inversely related to their abundance; it should take less time for a female wasp to find a cicada of appropriate size when those cicadas are more abundant. The fact that there was no significant difference in mean hunt times for small cicadas between locations is consistent with the conclusion that small cicadas were similarly abundant at the 2 study sites. Our finding that the mean hunt time for small cicadas was shorter than it was for medium cicadas at St. Johns is consistent with our judgment that small cicadas were more abundant than the medium ones there. We acknowledge that factors other than relative abundance of cicadas of the various size classes in the environment could affect mean hunt time. For example, cicada tree preference might be species-specific, and distances of trees of different species from the wasp aggregation could vary, thereby affecting travel time of provisioning wasps. Consequently, as with our estimates of relative abundance of different cicadas based on song frequency, we remain cautious in our assertions that the relative abundance of a cicada species can be inferred from mean hunt times.

Though none of the large *T. resonans* were brought to nests by female wasps in Newberry, we heard them singing each day that we were present in that location, and they are apparently common throughout the summer in that county (Walker & Moore 2009). Additionally, in our previous study at this location (Hastings et al. 2008) we did collect several of these large cicadas. Aside from the difference in the cicadas sampled by female wasps between locations, we found no evidence of any difference in the cicada communities between these study sites. As we now have evidence that female cicada killers, at least at these locations, do not capture the available prey cicadas randomly, we have no reason to assume that there is a significant difference in the composition of the cicada communities between Newberry and St. Johns; in fact, we suggest that they are quite similar.

DISCUSSION

Our findings that the sample mean body sizes of male wasps, female wasps, and cicada prey from St. Johns, FL are larger than those from Newberry, FL are consistent with the results reported by Hastings et al. (2008). However, these authors proposed that the size of the wasps is determined by the size of the prey available in the local environment. They stated that a possible explanation for the difference in size of the wasps between these locations was that the available cicada prey were, on average, smaller at the Newberry site than they were at St. Johns. Key assumptions of this explanation were that (1) female cicada killers hunt opportunistically (in other words, they sample the available cicadas at random), (2) females provision nest cells with a consistent number of cicadas, and (3) the size of offspring is directly related to provision mass. This first assumption is not supported by evidence presented here. In fact, we found that hunting by female *S. speciosus* is size-specific, and if hunting female *S. speciosus* in north Florida do not randomly sample cicadas from the available pool of potential prey, then the reasoning of this assumption lacks empirical support. Small wasps do not provision with large cicadas, probably due simply to mechanical constraints, and large

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wasps, though apparently not constrained, provision mainly with large cicadas. Though these results differ from those reported in other studies of *Sphecius*, size-specific provisioning has been observed in other mass-provisioning, Crabronid wasps such as the digger wasps *Cerceris arenaria* L. (Polidori et al. 2005) and *Palmodes laeviventris* Cresson (Gwynne & Dodson 1983).

We do not refute the findings of Coelho (1997), and Grant (2006), which concluded that female *S. speciosus*, at the locations of their respective studies, hunted opportunistically. However, at these locations, the available prey were relatively uniform in size. In contrast, in Newberry and St. Johns, Florida, we found that cicada killer wasps preyed on cicadas of distinct size classes, with a wet body mass range equal to or exceeding an order of magnitude (217-2150 mg in Newberry and 303-3421 mg in St. Johns). This diversity in prey size likely creates a very different set of selective influences on *S. speciosus* body size and provisioning behavior than is present at locations where prey cicadas are not so variable in size.

Hastings et al. (2008) further argued that their observed difference in the mean body size of cicadas retrieved from female *S. speciosus* between Newberry and St. Johns was likely due to a difference in the size distribution of available cicada prey in the respective local environments. However, we found no evidence that the relative species compositions and abundances of the cicada communities are different at these 2 locations. In fact, based on judgement of relative frequencies of songs of the various cicada species, and of hunt times required for wasp provisioning with them, we suspect that the cicada communities at the 2 locations are quite similar. Consequently, the difference in mean body size of cicadas we retrieved from wasps at the 2 locations might well be a result of the difference in size of the female wasps. The cicadas sampled by the wasps in Newberry were smaller because the wasps there were smaller, and not because small cicadas predominate there, and medium-sized and large ones predominate in St. Johns. As we did not directly sample the cicadas in the local environments, we state this conclusion with caution.

It is reasonable to assume that the size of individual adult *S. speciosus* is determined largely by the mass of the cicadas provided to them by their mothers, as is the case in some other Hymenoptera (Punzo 1994; Strohm 2000; Seidelmann 2006). Dow (1942b) presented evidence of this assumption, although the evidence was based on provision mass estimates, rather than on direct measurements of masses of cicadas provided to each offspring. Analysis of Dow's data reveals that, on average, conversion of provision mass to adult wasp mass is approximately 25% in *S. speciosus*, indicating that an adult wasp of 500 mg is likely to develop from a 2000 mg mass of cicada provisions. Preliminary data from the use of trap nests in an Easton, PA, cicada killer population in 2008 yield similar prey conversion efficiency for male offspring (24.6 ± 1.4%, n = 7; Holliday, unpublished data).

As Grant (2006) reported for New Jersey cicada killers, the prey loads we found for medium-sized and large female cicada killers in St. Johns were clustered around the relative prey-load line with a slope of 2.0 (Fig. 3); the prey were generally twice as massive as the provisioning female. Assuming a 25% conversion of provision mass to offspring mass, daughters given 2 such cicadas would achieve an adult size similar to that of their mother. The common provisioning pattern exhibited by *S. speciosus* whereby daughters are usually given 2 cicadas means that the size of daughters will tend to be similar to that of their mothers. Indeed, we hypothesize that the size of daughters in this species is probably directly related to the size of mothers. A testable prediction of this hypothesis is that in the St. Johns location, large females, which selectively hunt large cicadas, should produce larger offspring than those produced by medium-sized females, which more often bring medium cicadas to their nests. We hope to test this hypothesis in St. Johns in the near future by excavating nest cells and/or using trap nests.

We found that small female wasps at both locations provision only with small cicadas which, in nearly all cases, weighed less than their predator. Frequently, these prey had a wet mass less than one-half that of the female wasp. This result suggests that, unlike larger wasps, small female wasps must provide each daughter with many more than just 2 cicadas, assuming that daughters are similar in size to their mothers, and that about 25% of the provision mass is converted to adult wasp mass. Given these assumptions, a small female wasp hunting cicadas one-half her size must provide each daughter with 8 cicadas. In fact, this hypothesis is supported by preliminary evidence from our focal studies of provisioning females. We noted that females provisioning with small cicadas commonly exhibited bouts of continuous provisioning, with a final total of 7-9 cicadas, uninterrupted by digging activity. These bouts of uninterrupted hunting likely correspond to complete provisioning of nest cells for individual female offspring. Numerous uninterrupted provisioning bouts with 4 small cicadas also were observed, which we presumed to be completed nest cells for male offspring. We plan to test our interpretations of this provisioning activity when we return to these study sites in the near future, again by excavating nest cells and/or using trap nests. It is unlikely that the general pattern of provisioning previously described for this species (1, sometimes 2, cicadas for sons; 2, sometimes 3 cicadas for daughters), is exhibited by the small *S. speciosus* in north Florida. In this regard, these small wasps are probably

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similar to *Sphecius hogardii* Latreille in Cuba, which have been reported to provision nest cells with 4-6 cicadas, *Uhleroides walkerii* Guérin-Méneville (Genaro & de Varona 1998), which are slightly larger than the 2 species in the "small" size category in the present study.

This study has provided evidence of size-specific provisioning by female cicada killer wasps at 2 locations in north Florida; female wasps appear to provision nests with the largest available cicadas that they can carry in flight. At these locations, a much broader size range of potential prey is available than is apparently present where hunting by these wasps has been described as opportunistic. Perhaps selective provisioning by *S. speciosus* occurs at other locations where diverse sizes of cicada prey are found; this is a question we intend to investigate in the future.

This study also supports the finding of Hastings et al. (2008) that the wasps of both sexes and the cicadas brought to nests by female wasps are much larger in St. Johns than they are in Newberry, FL. However, in contrast with this previous study, we contend that the prey retrieved from female wasps at St. Johns are larger because the wasps hunting them there are larger, and not because there is a significant difference in the cicada communities between these locations. If, as we contend, the observed difference in size of cicada killers between Newberry and St. Johns cannot be attributed to a difference in size of available prey in the local environments, then what could account for the difference in the size of the wasps? At this point, any attempts at explanation would be speculative. However, we intend to investigate this issue over the next few years.

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