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Nesting ecology of the Pacific cicada killer, *Sphecius convallis* Patton (Hymenoptera, Crabronidae), in the Sonoran Desert

Joseph R. Coelho[1], Jon M. Hastings[2], Charles W. Holliday[3]

1 *Biology Program, Quincy University, 1800 College Ave., Quincy, IL 62301, USA* **2** *Department of Biological Sciences, Northern Kentucky University, Highland Heights, KY 41099, USA* **3** *Department of Biology, Lafayette College, Easton, PA 18042, USA*

Corresponding author: Joseph R. Coelho (coelhjo@quincy.edu)

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Abstract

Factors affecting the ecology of a large population of Pacific cicada killers (*Sphecius convallis*) occupying a field of mine tailings in Ruby, AZ, were examined. Burrows were quite dense in certain areas around the periphery of the mine tailings, but were dispersed randomly within these areas. Approximately 1600 females (based on burrow counts) and 2500 males (based on mark-recapture) were recorded, yielding a total population estimate of 5000–6000 adults. Female wasps were able to dig much more rapidly in the mine tailings than their congeners *S. speciosus* in soils from PA, suggesting that the habitat suitability was a large factor in this robust population. Provisioning rate was comparatively slow, however, suggesting that cicada abundance in that year was not a contributor to the high population density. The presence of a sap-producing tree may have eased the energetic and thermoregulatory demands of the wasps. Although excavations revealed that the number of burrows and cells could easily maintain the population size, the lack of cicadas probably resulted instead in a population crash the following season.

Keywords

Wasp, soil, digging, dispersion, population, provisioning

Introduction

Four species of cicada killers (genus *Sphecius*) occur in North America (Coelho et al. 2011). The Eastern species (*S. speciosus* Drury) is best known, having received considerable attention from biologists as early as the late 19th century (Riley 1892). The other species, however, have been relatively neglected until recently. Pacific cicada killers (*Sphecius convallis* Patton, 1879; Hymenoptera: Crabronidae) have nested at Ruby, Arizona (Santa Cruz County) probably at least since 1940, and perhaps since the sandy galena ore mine tailings were deposited in the valley by the operations of the Montana and Ruby mines between the late 1800s and the 1930s (Ring et al. 2005). Their presence was recorded in a documentary film (BBC 1993), which prompted us to visit the site. In 2009, when we found a huge population. Prior to our work there were only treatments of the species' taxonomy (Krombein 1979; Bohart 2000; Holliday and Coelho 2006) and distribution (Coelho et al. 2011), but not its biology. We found that, like other cicada killers, *S. convallis* is endothermic, and regulates its body temperature (Coelho et al. 2016). The only prey species used by *S. convallis* at this site was *Hadoa parallela* (Davis, 1923)(Hemiptera: Cicadidae). The flight muscle ratio of *S. convallis* loaded with *H. parallela* is nearly optimal, contributing to a high foraging efficiency (Coelho et al. 2012). However, many prey cicadas are stolen by birds and conspecific females, which enter the burrows of others and lay eggs on their already-provisioned cicada (Coelho et al. 2019).

While these studies contributed greatly to our understanding of the biology of *S. convallis*, factors contributing to its large population size are not fully explained. Schmidt (2013) describes the general characteristics of the Ruby site, and the diversity of digger wasps and their parasites that thrive there. The goal of the present study is to examine some ecological factors potentially affecting the success of Pacific cicada killers in Ruby, Arizona.

Methods

Burrow density

We described the field site previously (Coelho et al. 2012), a pile of sand-like mine tailings centered on approximately 31°27'28"N, 111°14'00"W. We measured burrow density in three areas containing the highest density of cicada killer burrows, which we designate as Areas A, B and C (Fig. 1). The areas were measured using a series of rectangles with a large measuring tape. The number of burrows within each area was counted.

Burrow dispersion

Nest burrows were generally clustered around the periphery of the mine tailings; however, we wanted to determine the dispersion pattern of burrows within these aggregations. We

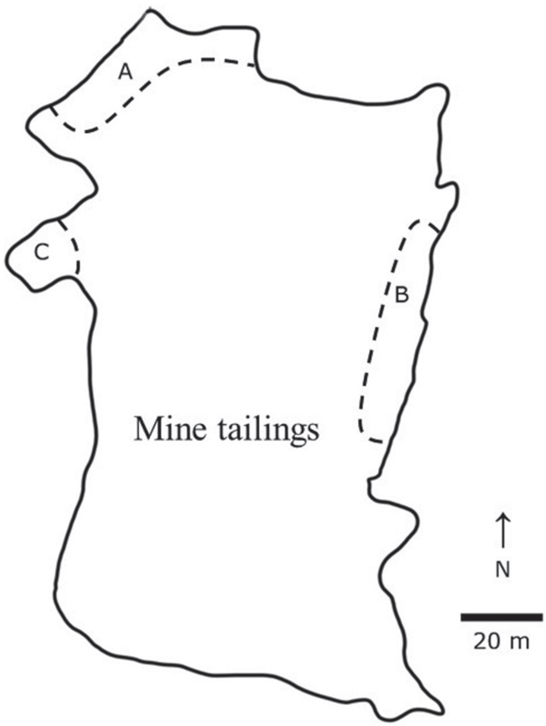

Figure 1. Map of burrow aggregation sites on the Ruby mine tailings.

had predicted that the burrows would be uniformly arranged in space, as that is the general impression they make to the eye, especially in high density areas. Known aggression between cicada killer females at high densities (Lin 1963; Hastings et al. 2008) should lead to the regular (uniform) dispersion pattern (Molles and Sher 2018). The nearest neighbor technique was performed (Clark and Evans 1954) using data from 09/08/2009, which was slightly past the peak of burrow density (see below). Two sites that appeared to be high (Willow and Hammock within Area A) and low (Areas B and C) density were examined.

Mark-recapture

We used a mark-recapture method to estimate the male population size of *S. convallis* in Area B, which had the highest apparent density of male wasps. We captured all of the male wasps that we could (195) on three successive days (7–9 August 2009), marked them on the scutum with an approximately 3-mm diameter dot of blue nail polish, confined them in a 2.43 × 2.43 m (8 × 8 feet) screen tent with a shaded roof for up to 4 hours during the capture period to prevent recaptures, and released them at the capture site (Fig. 2). On the morning of the fourth day (10 August) we captured all of the marked and unmarked male wasps that we could in Area B, confined them in the screen tent for up to 3 hours during the recapture period, and then counted them as

Figure 2. Screen tent used in estimating male cicada killer population size. Field of mine tailings in the background.

they were released. We used the Chapman (1951) estimator to calculate male population size. This method ignores the effect of any differential wasp mortality, which we expect to be minimal in the 3-d marking period.

Male population density (wasps/m^2) was calculated as the number of males estimated by the mark-recapture method divided by the area occupied by males in Area B. The total number of males in all three areas was crudely estimated by multiplying the density of males in Area B by the total number of square meters in all three areas.

Estimation of female population size and density

To estimate the sizes of the female *S. convallis* populations in the three areas, we counted the number of nest entrances in Areas A and B up to August 29 and in Area C up to August 31 as a proxy for female numbers. This method is a rough approximation and a minimum population estimate, as we observed many females moving from burrow to burrow and entering other females' burrows in apparent attempts at cleptoparasitism (see below). Female population density (wasps/m^2) was calculated as the number of burrows in each area divided by the area occupied by burrows in each area.

Phenology

We used our field notes and data sheets from our observations to track the abundance of males, females and burrows, as well as the frequency of matings through the season. For each data sheet, we recorded the number of males and females observed or used in experiments on that day. For mating observations, one may assume that one female and a variable number of males were in attendance.

Digging

We undertook measurements to determine whether the substrate was easier to dig in Ruby than in other locations. We located females that were in the act of digging or expanding their burrows. Digging behavior was essentially identical to that observed in *S. speciosus*, and digging rate was measured largely as described previously (Coelho and Holliday 2008). In brief, a pit was excavated in front of the burrow entrance and a small, plastic condiment cup was placed in front of it. Each load of soil was captured by the cup as the wasp backed out of the burrow and replaced with another cup while time was recorded for each event. Cups were individually marked and placed on the dashboard of an automobile placed facing the sun with one side window open and the other equipped with a solar-powered fan. In this way, the soil sample was dried to constant mass and weighed on an Ohaus Adventurer-Pro electronic balance to the nearest 0.001 g.

Sap tree census

Cicada killers frequently eat sap exuded from wounded trees, presumably as a source of carbohydrate fuel (CWH, personal observations). We examined the use of sap from a willow (*Salix* sp.), over the course of a day to determine how this type of foraging fit into the cicada killers' daily routine. On 11 August 2009, beginning at 05:30 h, we counted the number of cicada killers visiting the sap tree and measured the ambient temperature in the shade at the height of the sap-producing would every 15 min until 20:00 h.

Provisioning effort

Focal sites were chosen in which several burrows could be observed at once. We closely observed the provisioning activities of female *S. convallis* at two sites in Area A. Nesting females were marked, then observed so that provisioning behavior, and burrow entries and exits could be recorded along with the time they occurred.

Excavations

In order to estimate the total seasonal provisioning success of a subsample of nests, we dug up an area with 10–13 active burrows in Area A as the site of our studies of cicada provisioning success down to 0.7 m, below which the wasps did not dig because of a layer of gravel. To make sure that we found all nest cells, the area excavated included extended for an area of 1 m outside the area occupied by nest entrances.

Results

Burrow density

The nest aggregation areas had maximum densities of burrows as follows: Area A, 1213 burrows on 8/29 on 1505 m^2, or 0.81 burrows/m^2; Area B, 299 burrows on 8/29 on 3221 m^2, or 0.09 burrows/m^2; Area C, 76 burrows on 8/31 on 240 m^2, or 0.0.32 burrows/m^2. There were many other burrows spread out much more thinly on the central area of the sandy dune. Thus, a total of 1588 burrows were recorded for the high density sites alone on the dates we recorded them.

Burrow dispersion

All sites were relatively flat and unvegetated. Burrow density varied from just under 0.5 to 1.3 burrows/m^2. At all four sites, the ratio (R) of observed to expected distances was not significantly different from 1 (Table 1). Hence, all were consistent with a random arrangement of burrow entrances on the surface of the soil.

Mark-recapture

On August 10, the mark-recapture method indicated that there were 2556 male *S. convallis* in Area B (Table 2), yielding a population density of 0.79 wasps/m^2. Using this density and the total area of Areas A, B and C, this indicates that nearly 4000 males were present in the three areas. On August 29–31, burrow counting indicated a minimum total female population of nearly 1600 wasps in the three areas and an average density of 0.403 females/m^2. Near the end of the breeding season (September 17), the presence of fresh burrow excavation indicated that there were only 206 active burrows in Area A, 50 in Area B, and 36 in Area C, for a minimum total female population of 292 wasps (data not shown in Table 2).

Phenology

Males were first observed emerging at the site 7 August (Fig. 3). Females began to appear in small numbers and matings were observed. Male numbers began to fall around 10 August, and males became hard to find for the last set of experiments in which they were used on 3 September. We left the site on 17 September; while female foraging and burrow digging was still underway, no males had been seen for 14 days. Female density and activity seemed to be decreasing. Mating was observed as soon as females began

Table 1. Dispersion pattern of burrows in four nesting colonies of Pacific cicada killers.

Site name	Area C	Area B	Willow	Hammock
Number	114	171	118	87
Area (m^2)	240	200	88.6	66.1
Density (burrows/m^2)	0.475	0.855	1.33	1.31
R	1.04	0.973	0.94	0.957
K*	0.75	-0.667	-1.25	-0.772

*As the critical value of K is 1.96 at the 5% level, none of the values of R are significantly different from 1, which is consistent with random dispersion.

Table 2. Male and female population density estimates in three areas at Ruby, AZ.

Area	Male population	Male density (males/m^2)	Female population	Female density (females/m^2)
A	–	–	1213	0.806
B	2556	0.794	299	0.093
C	–	–	76	0.317
Total	3943*	0.794	1588	0.403

*estimated based on density of Area B and surface area of Areas A and C.

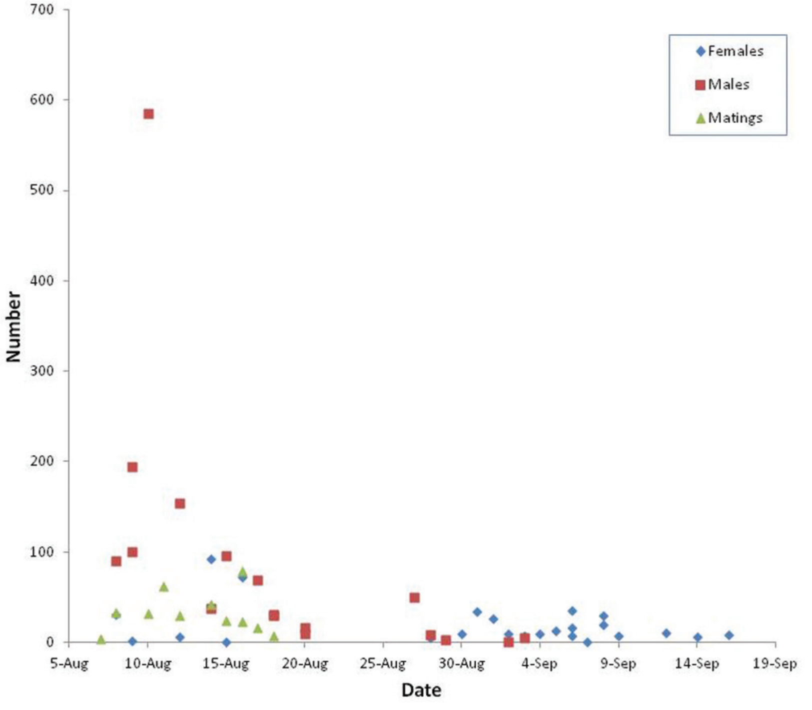

Figure 3. The timing of male emergence, female emergence and mating in *Sphecius convallis*.

to emerge on 7 August, peaked approximately on 13 August, then fell off quickly, no further matings being observed after 18 August.

The first burrow was observed on 14 August (Fig. 4). Their numbers increased rapidly to a peak of nearly 1600 by 30 August, but decreased steadily afterward.

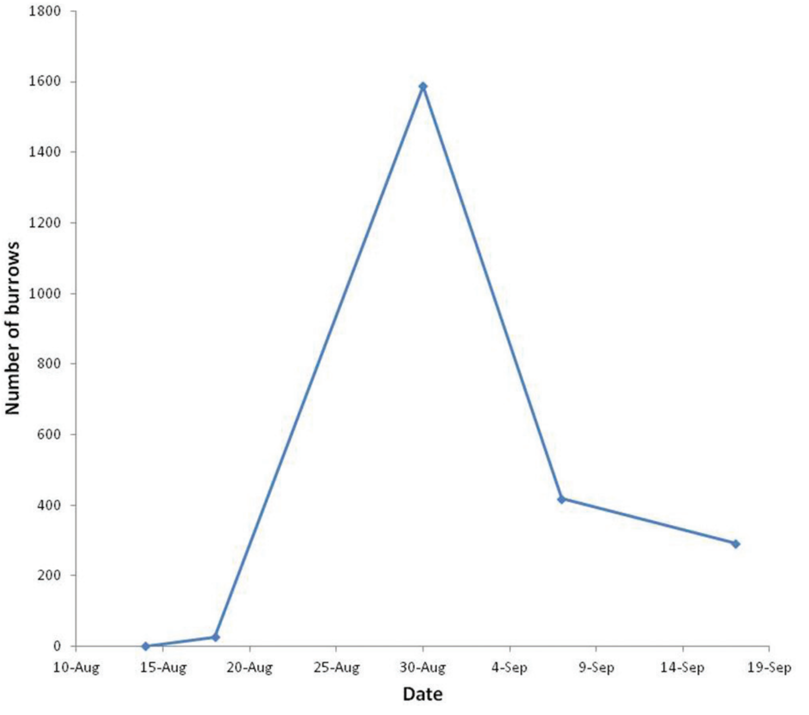

Figure 4. The timing of burrow construction in *Sphecius convallis*.

Digging

S. convallis at Ruby, AZ, removed soil at a rate of 1.46 g/min dry mass, while *S. speciosus* in Easton, PA, digs at a rate of 0.98 g/min (Coelho and Holliday 2008). These data exclude lapses when wasps were assumed to be loosening soil in the burrow. While the Ruby wasps took longer between digging bouts, their gross digging rate (1.33 g/min dry mass, which includes such intermissions) was still greater than even the net rate of Easton wasps with intermissions excluded. Hence, the rate of soil removal at Ruby is 48% higher than at Easton.

Sap tree census

There was considerable activity among cicada killers feeding at sap trees. A great deal of bumping and brief fighting between individuals, and, occasionally, other species, occurred as insects attempted to access the site of the sap flow (Fig. 5).

No cicada killers were observed at the sap tree until 0615 h, when 17 suddenly appeared. This event marked the early peak in wasp sap tree attendance, which plunged to 4 by 0715 h. The numbers climbed afterward to 22 at 1030 h. Thereafter, the number of cicada killers varied dramatically until late in the day, as attendance ranged as high as 26 at 1400 h, and plunged to zero between 1900 and 1945 h. As many wasps

Figure 5. *Sphecius convallis* feeding on sap at a willow tree, along with several flies. Note the foam in the wound in the tree's bark, probably made by yeast sugar fermentation.

were individually identifiable, having been marked in the course of other studies, we found that some wasps returned to the sap tree repeatedly during the day.

There was a weak but significant relationship between ambient temperature (°C) and sap tree attendance (number of wasps = 1.04(temperature) -16.1, $R^2 = 0.33$). Attendance increased linearly with temperature even though the data from the early peak ran counter to this trend.

Provisioning effort

During 348 hours spent observing an isolated group of 10–13 active burrows (the number of active burrows varied from day to day over the observation period) at one site in the picnic area, a total of 43 paralyzed cicadas were placed into the burrows by female *S. convallis*.

Excavations

Nest architecture was essentially the same as that observed in *S. speciosus*. We located a total of 104 nest cells, of which 14 were empty. Females use the soil from a new cell to backfill the previously completed cell (Dambach and Good 1943). Since the number of empty cells is approximately equal to the number of burrows, we can reasonably assume that all of the cells containing cicadas were completed. Of the remaining cells, 68 held one cicada, 20 had two cicadas and 2 had three cicadas. Of the 90 nest cells with fresh cicadas, 68 contained male eggs (male cicada killers are smaller than females because they get only one cicada on which to feed [Lin 1979]) and 22 had 2–3 cicadas and were females, yielding an apparent male:female ratio of 68:22 or 3:1.

In digging up the 10–13 burrows noted above, we also found nest cells from 2008 and perhaps earlier seasons (old nest cells): a total of 235 older nest cells with decayed, moldy and obviously old cicada and cicada killer cocoon remains in them were found.

Discussion

Density

Several estimates of population density of cicada killers can be extracted from the existing literature to compare to those here. The overall nest density in the largest colony of *S. speciosus* studied by Dambach and Good (1943) was ca. 0.1 nests/m^2; local areas of high density had ca. 0.75 nests/m^2. Eason et al. (1999) indicate a territorial male density of ca. 0.5 males/m^2. The density of nests in three aggregations in Easton, PA, ranged from 0.301–0.345 nests/m^2 (CWH, unpublished data). At a remarkably high population site in Channahon (Will Co.), IL, Hastings et al. (2008) estimated the density of nests at ~l.07/m^2 overall, and l.64/m^2 within a focal area. The density of males active within the focal berm was greater than 1.64/m^2. Burrow densities of our nesting aggregations of *S. convallis* exceed typical estimates and approach those of *S. speciosus* in Channahon. Hence, the data corroborate our observations that the Ruby site held a large population with high densities of burrows during the field season under study.

Several factors probably contribute to the abundance of cicada killers at the site. One is obviously the availability of cicadas, although long hunt times, low hunting success, and the low frequency of males singing (Coelho et al. 2019) suggest that the cicada population size was low during the year of this study. We can infer that the density of cicadas was much higher during the previous nesting season. Another factor appears to be the availability of nesting habitat. The mine tailings create sandy substrate that appears to be ideal for burrowing. Roots and rocks that could interfere with burrow construction are absent; whereas, the surrounding substrate is very rocky and unsuitable. The mine tailings have a large fraction of fine particles which hold water very well. As a result, just a few inches below the surface, the sand is moist and cohesive, so it does not have a tendency to collapse as would a coarser or drier sand. Also, an almost complete lack of vegetation resulted an open habitat, which cicada killers apparently prefer (Coelho et al. 2011), perhaps because it is easier to reach their nest entrances unhindered, especially while carrying a cicada.

Dispersion

Nesting aggregations were clumped within the field of mine tailings as a whole; however, within nesting aggregations, burrows were shown to have a random arrangement in space. A uniform pattern would have reflected territoriality and/or competition, which we did observe to some extent between females. Although one female was actually observed to steal a cicada from another, prey theft more often takes the form of a female sneaking into an unoccupied burrow and laying an egg on an already provisioned cicada while the burrow owner is away (Coelho et al. 2019). Hence, the direct agonistic encounters that might result in a uniform dispersion pattern are likely to be rare. In *S. speciosus*, nearby burrows tend to be owned by relatives (Pfennig and Reeve 1989), which may ease antagonism. A clumped arrangement might have reflected a preference for particular microhabitats, which appeared to be the case with higher densities around mesquite trees. The random dispersion pattern suggests that our perceptions were mistaken, and the wasps make no particular choice in where to dig their burrows.

Phenology

As has been observed in *S. speciosus* (Dambach and Good 1943) and *S. grandis* (Hastings 1989b), *S. convallis* is protandrous. Males emerge well before females and establish territories where virgin females are likely to emerge from their natal nests. The mating season occurs as females begin to emerge, but once all females have done so, opportunities for mating are rare (as females mate only once) and males begin to die off. Females continue provisioning through the end of summer, but begin to die off with the onset of cooler fall weather.

Role of soil type

Not only does the mine tailing field at Ruby provide a large area of suitable habitat relative to the surrounding rocky terrain, it appears to provide excellent conditions for digging. *S. convallis* at Ruby removed soil at a rate of ~1.5x that of *S. speciosus* in Easton, PA, (0.98 g/min, Coelho and Holliday 2008). The soft, easily dug, yet cohesive mine tailings appear to be ideal for cicada killer burrow construction. Soft soil can be dug much faster, while moisture retention maintains humidity in the nest cell. Hence, several hymenopterans have been shown to have nesting preferences for soil humidity and particle composition (see Potts and Willmer 1997). The slightly smaller great golden digger wasp (*Sphex ichneumoneus* (Linnaeus, 1758) also chooses flat, soft soil that is unlikely to collapse (Brockmann 1979). Less time spent digging translates into more time available for foraging. An analysis in our previous paper indicates that the fitness gains of such temporal advantages are large, in part because life span is relatively short (Coelho and Holliday 2008). This measure stands out strongly as a potential factor leading to the high density of *Sphecius convallis* at Ruby.

We expect that this population is isolated to a high degree from other Pacific cicada killer populations. The mine tailings provide an unnaturally favorable habitat. Although we searched the surrounding region (the southwest corner or "panhandle" of Santa Cruz County) extensively during this period, we never observed burrows or adult wasps in other places. It has long been our contention that cicada killers thrive on disturbance. In the eastern US, this means areas of open soil or very low vegetation, such as suburban lawns (Tashiro 1987) or sports fields (Lin 1967). Thus we suggest that cicada killers are a synanthropic species that do not require the presence of humans, but thrive where they occur.

Sap tree

The early peak in sap tree attendance is likely attributable to the wasps arising from nocturnal inactivity and requiring carbohydrate energy. The timing is strikingly similar to the early perching of males on basking trees (Coelho et al. 2016). The sap tree attendance drops quickly as the refueled wasps turn to the important activities of territory defense by males and nest construction and provisioning by females. As these activities use up energy and water, wasps return to the tree during the day. Fluctuations in attendance likely occur as individuals become unsynchronized. All abandon sap foraging as the sun sets, females returning to their burrows and males to night perches.

The direct relationship between sap tree attendance and ambient temperature is subject to a number of interpretations. It may be that, as activity increases with temperature, energy needs increase. However, as male territorial activity decreases during the afternoon (Coelho et al. 2016), this explanation fails. It is possible that increasing ambient temperature increases foraging on sap as the wasps require more water. Both males and females use evaporative cooling as part of their thermoregulatory strategy (Coelho et al. 2016). Although tree sap is fairly concentrated, it may provide a rare source of both fuel for activity and water for evaporative cooling. Preliminary measurements of crop fluid spontaneously released by Easton, PA, *Sphecius speciosus* under CO_2 anesthesia showed the presence of reducing sugars and yielded osmotic pressures of 1500–2000 mOsm/kg H_2O (CWH, unpublished data). Hence, the presence of the sap-producing tree may have eased both the energetic and thermoregulatory demands of the wasps, perhaps contributing to the size of the local population.

Provisioning success

The rate of provisioning, 8.1 h per cicada, is very low compared to that of *Sphecius speciosus* in Easton, PA, and is consistent with very low cicada availability in the local environment (we heard very few *H. parallela* males calling at Ruby). Hence, at least during our season of observation, it does not appear that high cicada density contributed to the high density of *Sphecius convallis*. It is likely, however, that cicada density was much higher during the prior nesting season, resulting in the high population observed in 2009. We suspect that *Sphecius convallis* and *H. parallela* are a case of predator and prey cycling out of phase in population size, but this possibility requires further investigation. There was, in fact, a much smaller cicada killer population the following year of approximately 150 individuals in the entire area (J.O. Schmidt, personal communication), as one might predict from such a model.

Sex ratios

The strongly male-biased offspring sex ratio may well have been caused by the low availability of cicadas, particularly when the high incidence of birds stealing the provisioners' cicadas and cleptoparasitism (Coelho et al. 2019) is taken into account. A cicada killer laying an egg on a "stolen" cicada must, of necessity, lay a male egg, as a female egg given a single cicada to eat would be too small to carry cicadas when she eclosed the next summer. Cells with two cicadas are unavailable to cleptoparasitic females, as they are immediately sealed with soil by the nest owner upon provisioning with the second cicada.

Estimates of total nest and cell numbers

The 104 nest cells in 13 burrows from 2009 average 8.0 cells per burrow, assuming the empty ones would have eventually received cicadas and eggs. Let us assume that another cell per burrow would have been added by the time all of the females were dead, making the average 9 nest cells per burrow. Using the highest values above for burrow densities in Area A (1213), Area B (299) and Area C (22), we have a total of 1534 known cicada killer burrows at Ruby, each with 9 nest cells, making an estimated 13,806 nest cells. Allowing for about 50% mortality (probably not a bad guess, given all of the parasitic velvet ants that were present and the high rate of dead/moldy grubs and cocoons we found in the nest cells we dug up), this gives us about 6900 wasps to appear the next summer at Ruby. The true number should be perhaps 25% higher, as we did not count all of the burrows present, but only those in the Areas A, B and C. Though these calculations suggest the potential to maintain the population at the same high level during the following year, it seems unlikely that the low cicada supply would support it. There was a much smaller cicada killer population the following year, as noted above. Hence, one should expect the cicada killer population to vary considerably from year to year, not to be as large as we encountered in 2009 every year.

Conclusion

In summary, it seems likely that the greatest factor drawing Pacific cicada killers to the Ruby site is the mine tailings themselves. The open habitat and the favorable soil make accessing nest entrances and digging substantially easier than in the surroundings. We took numerous hikes throughout the region during the period of the study, but we never saw any cicada killer burrows in other places; this absence was also reported to us by S. Hunter, the caretaker of the site for several years before our visit. In spite of substantial prey theft (Coelho et al. 2019), cicada killers were abundant there. Other factors contributing to the success of cicada killers might also be the presence of sap-exuding trees to provide them carbohydrate fuel and water. The abundance of cicadas in the trees surrounding the site, at least during previous years, likely also contribute to the high density of *Sphecius convallis* there. These factors, among others, combined to produce one of the largest populations of cicada killers ever described. It is not surprising that this is a human-altered site, as the high-density site in Channahon, IL, was for *Sphecius speciosus* (Hastings et al. 2008). Cicada killers thrive on disturbance, in part because it removes vegetation and changes soil structure, creating open areas for burrow digging and making burrow entrances more accessible to females returning with prey.

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