Intra- and Interspecific Prey Theft in Cicada Killers (Hymenoptera: Apoidea: Sphecius)

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Abstract

We studied prey theft in two cicada killer aggregations: Ruby, Arizona (Sphecius convallis Patton) and Easton, Pennsylvania (Sphecius speciosus Drury). Many prey (Tibicen parallelus Davis [Hemiptera: Cicadidae]) were stolen from S. convallis by kingbirds and Greater Roadrunners at Ruby. Seventy percent of kingbird attacks on provisioning wasps were successful. Using sand-filled trap nests baited with a cicada, we tested the hypothesis that conspecific females might kleptoparasitize by laying an egg on the cicada and closing the nest cell. At Ruby, 45% were so appropriated, and at Easton, 52%. Easton data showed that the longer a nest cell was left open, the higher the rate of kleptoparasitism. Hence, intraspecific kleptoparasitism likely occurs at high rates in both populations. Not needing to dig a burrow, or to hunt, capture, and carry a paralyzed cicada favors intraspecific kleptoparasitism in cicada killers. Low cicada availability and intense avian kleptoparasitism of cicada killers may intensify selection pressure for this behavior at the Arizona site. Pirating cicadas may be the only viable reproductive outlet for females that are small or in environments with few prey. We suggest that provisioned nest cell kleptoparasitism may have evolved in cicada killers as an alternative strategy to standard provisioning, given the dual uncertainties of adult body size and prey availability.

Key words: foraging, alternative strategy, kleptoparasitism, solitary wasp, ecological interactions

Solitary, predaceous wasps paralyze their prey, providing a ready opportunity for other organisms to steal this resource. Indeed, parasitization by satellite flies and mutillids are well documented (Dambach and Good 1943, Curran 1962, Lin 1963, Evans 1966, Schmidt 2013). However, prey theft from wasps by conspecifics and vertebrates has been described in only a few cases. Prey theft is likely to have effects on wasp population dynamics, reproductive strategies, and evolved behavior.

Members of the genus Sphex are known to have their large orthopteran prey stolen by House Sparrows and Grey Catbirds (Brockmann 1980, Benttinen and Preisser 2009, Lechner 2010). Acorn Woodpeckers and whiptail lizards (Cnemidophorus spp.)
have also been observed stealing cicadas from provisioning western cicada killers (Sphecius grandis Say; J. M. H., unpublished observations). The authors have observed various birds (including House Sparrow, J. R. C. and C. W. H.) attempting to steal cicadas from Sphecius speciosus (Drury 1773) in this way, but never in substantial numbers. Correspondents contributing to a cicada killer biogeography study (Coelho et al. 2011) noted House Sparrows, Brewer’s Blackbirds, Northern Cardinals, and American Crows taking prey cicadas (C. W. H., unpublished correspondence). Say’s Phoebe has also been observed stealing prey from cicada killers (BBC 1993).

Cicada killers are particularly likely to be targets of vertebrate prey theft, as North American cicadas are large prey items (0.15–3.50 g live mass) and generally contain no defensive chemicals.

In the course of investigations on the ecology of Pacific cicada killers (Sphecius convalis Patton 1879) in Ruby, Arizona, we observed various vertebrate predators systematically robbing cicada killers of their prey. One goal of this study was to quantify this activity and attempt to estimate its impact on the cicada killer population.

Cicada killers in the genus Sphecius (Dahlbom 1843) are large apoid wasps (Sann et al. 2018), which provision their young with one to as many as nine paralyzed ‘annual’ cicadas. Cicada killers have a typical, solitary wasp life cycle that has been described numerous times (e.g., Dambach and Good 1943). Females emerge in early summer, mate, dig a burrow, and begin provisioning nest cells. Females hunt cicadas in the neighboring trees and sting them, resulting in complete, irreversible paralysis. The cicada is flown back to the burrow, although overloaded wasps may be required to climb trees or other objects to gain altitude and resume flying. The cicada is sequestered in a cell in the burrow. The flight of the female wasp to the burrow while carrying a cicada provides the opportunity for prey theft by birds.

High-value prey also provide opportunities for theft by conspecifics. Evans (1957) reported prey-stealing in five species of Bembix. Villalobos and Shelly (1996) state that in the related wasp, Stictia heros (Fabr.), intraspecific prey theft is common. These observations suggest that prey theft might occur among cicada killers as well. In most of the United States, one or two cicadas in the genus Tibicen are used as nest cell provisions in nearly all Sphecius populations that have been investigated (Holliday et al. 2009, Hastings et al. 2010); Florida Sphecius spheniscus frequently use the tiny Neocicada hieroglyphica and compensate for the cicada’s small body mass by provisioning nest cells with up to nine cicadas. Male cicada killers are much smaller than females and male eggs are provisioned with one or more cicadas; female eggs are provisioned with two or more cicadas (Dow 1942). Female wasps know the sex of each egg before they lay it, as they dig larger underground nest cells for female eggs than for male eggs (Holliday, unpublished data from trap nest studies). They provision female eggs in the larger nest cells with more cicada prey than male eggs, usually one Tibicen for a male egg and two for a female (Holliday et al. 2009). When more than one cicada is to be placed in a nest cell, the female leaves the burrow open with the first cicada within while she is away hunting for additional cicadas. This behavior is in sharp contrast to that of the many progressively provisioning, solitary sand wasp species which close and even camouflage the burrow opening while they are away hunting for prey with which to feed their growing grubs (Evans and O’Neill 2007). Such burrow closure presumably protects the developing wasp grub and reduces prey theft by conspecifics and by other arthropods, as well as reducing kleptoparasitism by egg-laying mutillid wasps and by several families of flies.

At most cicada killer nesting aggregation sites, where nest density is relatively low, cicadas are occasionally dropped by the female in the course of trying to find or access her burrow. There they are left to rot, frequently consumed by ants or yellowjackets (Vespula spp.). (J. R. C., C. W. H., and J. M. H., unpublished observations). However, at sites with extremely high nest density (e.g., Will County, II; Hastings et al. 2008), females may pounce on others carrying cicadas, and dropped cicadas are immediately picked up by the provisioner or other female cicada killers (Lin 1963). These anecdotal observations suggested to us that, under the right conditions, competition for prey may become intense among cicada killers.

In the course of many summers of field research on Sphecius, we have often noticed female cicada killers entering the burrows of other females. Such ‘intruders’ spend from several seconds to an hour or more in the burrow they are visiting and are sometimes vigorously evicted by the ‘owner’ female inside the burrow or when she returns from foraging for food or cicada prey. Similar behavior is described by various other authors (Dambach and Good 1943, Lin 1963, Evans 1966, Lin and Michener 1972, Brockman and Dawkins 1979, Pfennig and Reeve 1989). We have often wondered whether or not such visits might result in the in situ piracy by an intruder of an open nest cell containing one or more paralyzed cicadas put in place by the burrow’s owner; demonstrating this behavior was one of the main purposes of our study. We designate this form of conspecific prey piracy ‘provisioned nest cell kleptoparasitism’ (PNCK) by cicada killer females. A second purpose of this study was to assess the presence and frequency of PNCK in two cicada killer populations in the United States: the Pacific cicada killer, Sphecius convalis population at Ruby, Arizona, and the Eastern cicada killer, Sphecius speciosus, population on the Lafayette College campus in Easton, Pennsylvania.

Materials and Methods

Field sites

Ruby, Arizona

The two cicada killer populations studied had a minimum of 50 or more nesting female wasps. A large population of Pacific cicada killers nesting on a 3.3-ha field of mine tailings in Ruby (Santa Cruz County), Arizona (31°27’33.18” N, 111°14’02.77” W, elevation 1268 m), hereafter referred to as Ruby, was the subject of a number of ecological studies in August to September 2009. Approximately 3.25 ha of fine, sandy tailings from an abandoned lead mine form a nearly level sand flat blocking two south-draining valleys, each of which has a small lake formed upstream of the tailings. These tailings are 2–5 m above the water levels of the lakes and provide a suitable site for the nest burrows of a breeding aggregation of several thousand Pacific cicada killers. In 2009, this aggregation provisioned its offspring exclusively with Tibicen parallela (Davis 1923 Hemiptera: Cicadidae) cicadas, which had an average body mass of 1.127 g; female S. convalis in this population had an average body mass of 0.991 g (Coelho et al. 2012). During the course of our 2-mo stay at Ruby, we made field notes of all cases of attacks on provisioning cicada killers. A focal area of the aggregation area was chosen to observe prey theft by kingbirds (Tyrannus spp.). This site had high burrow density (418 burrows along a 60-m transect) and was directly adjacent to vegetation that kingbirds used heavily as perch sites. Observations were carried out primarily in the morning hours when provisioning and prey theft were most frequent. Cases of kingbird attack on cicada killer/cicada pairs were recorded, as well as whether the attack was successful. If the attack was successful, the behavior of the bird while handling the cicada was recorded. Successful provisioning events by cicada killers were also recorded. Most kingbirds were photographed for confirmation of identity with a Canon EOS 40D digital SLR camera and Sigma 150–500 mm lens. Data are reported as mean ± SEM (N), unless otherwise indicated.
Sphecius speciosus was studied at Lafayette College, Easton, Northampton County, Pennsylvania (40°41′52″ N, 75°12′28″ W; elevation 103 m), hereafter referred to as Easton, in August 2008 and 2010. Data from 1989 to 1999 show that female wasps present at the southeast corner of Pardee Hall had a live body mass of 0.965 g ± 0.0103 (416); the corresponding numbers for males were 0.424 g ± 0.0048 (451). Females of this population dig nest burrows in architectural berms around and next to the south side of Pardee Hall. The clay soil in these berms is relatively fine but contains small stones which may cause cicada killers to abandon a partly finished burrow. This population provisions its offspring with two species of cicadas, *Tibicen lineatissima* (Smith and Grossbeck 1907), with an average body mass of 1.280 g, and *Tibicen tibicen* [Linne 1758; formerly *Tibicen chloromerus* (Walker 1830)], with an average body mass of 1.660 g (Holliday, unpublished data).

**Trap Nest Method**

To estimate the rate of conspecific PNCK by female cicada killers, we used sand-filled trap nests ‘baited’ with a freshly paralyzed cicada, taken from a cicada killer returning to provision a nest-cell, and placed in a simulated nest cell at the bottom of the trap nest. Trap nests were made using 75-cm length of 7.5 cm inside-diameter polyvinyl chloride water pipe (J.M. Eagle Corp.). The pipe was split along its length, reassembled with cellophane tape and filled with damp sand (‘Play Sand’, Home Depot Corp., 600 ml deionized water). A 7.5-cm-deep furrow leading away from the burrow opening that is characteristic of natural tumuli and through which the female wasp excavating a burrow pushes excavated soil to the edge of the tumulus (Fig. 3).

Natural cicada killer burrows have a tumulus of excavated soil at their mouths and we simulated this tumulus with an approximately 8-cm-high pile of damp sand at the mouth of the trap nest, complete with the 2-cm-deep furrow leading away from the burrow opening. To serve as a landmark for visiting cicada killers. In rainy weather, a styrofoam cover (the upper or lower half of a 24 x 24-cm clamshell takeout food package) was erected as a rain shield over the trap nest’s upper end using bamboo shish kebab skewers inserted through it at an angle into the ground and arranged so as to allow free access by wasps to the burrow. Trap nests were installed between 09:00 and 15:00 each day. Each trap nest at Easton was exposed to PNCK by the natural population of cicada killers in the area for 25 min, 45 min, or 24 h. The trap nests at Ruby were checked after 23–30 h of placing paralyzed cicadas in them.

To determine whether PNCK might be an alternative strategy for smaller females, we compared provisioning females (owners) to intruder females. We captured female wasps as they were provisioning nests, anesthetized them with CO₂, and weighed them to the nearest 0.001 g using an Ohaus Adventurer-Pro electronic balance. We also attached a unique number tag to the thorax of each wasp with cyanoacrylate glue before releasing it and used a matching numbered flag to mark its nest. We defined intruders as females that entered a nest marked with the number of another female. We observed intruding females enter marked nest burrows, waited for them to exit the burrows, then captured, anesthetized, and weighed them. Intruders were not marked; therefore, some could have been measured more than once. However, given the extremely large population size at Ruby, such repeated measures are likely to be few.

**Results**

**Bird Theft**

In total, 765 min (12.75 h) were spent making observations at the focal site for bird theft in Ruby over seven observation days from 3–15 September 2009. Cassin’s Kingbirds (*Tyrannus vociferans* [Passeriformes: Tyrannidae]) carried out the majority of attacks on provisioning cicada killers. Thick-billed Kingbirds (*Tyrannus crassirostris*) were less common in the area, carrying out only three successful and two unsuccessful attacks. Attacks by both species were very similar, except that Thick-billed Kingbirds were never observed to beat the cicada; hence, both species were lumped into the following analysis.

![Diagram of the trap nest. Dimensions provided in the text.](image-url)
We recorded 56 instances of kingbirds (both Cassin’s and Thick-billed) attacking provisioning female cicada killers. Of these, 39 (70%) were successful. Kingbirds carried out a successful theft for every 19.4 min of observation on average, and the number of successful attacks was equal to the number of successful provisionings (39) recorded during the same observation periods. The kingbirds usually perched on top of a mesquite bush (generally velvet mesquite, *Prosopis velutina*) or near the top of a dead agave (*Agave angustifolia*) inflorescence at the periphery of the sand dune, providing them with a good view of approaching provisioning cicada killers. At times, there were as many as five kingbirds thus perched. On a successful sally, a kingbird generally flew out, seized the cicada in its bill; the cicada killer surrendered its cicada at this point and the kingbird returned to a perch with it, landing on an agave mast or mesquite, though not always the same one from which the sally originated. The kingbird often subsequently beat the cicada against a branch (67% of cases, Fig. 4); sometimes a piece of the cicada fell off during this process. At times, the bird tossed the cicada in the air, presumably to reposition it for swallowing, which was always head first. We never observed kingbirds foraging on any other insects while at Ruby. On a few occasions, kingbirds were observed taking the wasp, but never during the focal observations.

We also documented nine cases of prey theft by Greater Roadrunners (*Geococcyx californianus* [Cuculiformes: Cuculidae]) during 32 d of working at Ruby. However, their method of attack differed greatly from that of kingbirds. Roadrunners walked the periphery of the mine tailings, where most of the burrows were located, generally staying in the shade of mesquites and other trees. When a provisioning wasp landed, the roadrunner ran to it, grasped the cicada in its bill before the wasp could enter a burrow, and ran back into the shade (Fig. 5) to eat it. The roadrunner sometimes tossed the cicada a few times before swallowing it. We also observed a single case of a woodpecker (most likely Ladder-backed Woodpecker) stealing a cicada.

Although few specimens were recovered during this particular study, all prey were presumed to be *Tibicen parallelus* Davis (Hemiptera: Cicadidae), as hundreds of specimens taken in the course of other studies (Coelho et al. 2012, 2016) at this time proved to be.

**PNCK**

All eggs found on paralyzed cicadas placed in trap nest cells were visually indistinguishable from those laid by female cicada killers in naturally provisioned trap nests used in other experiments in 2007–2011 (Fig. 6). Since other *Sphecius* species or other genera of large wasps which provision their nest cells with cicadas were never observed in either study area, we assume that all of the eggs we found on cicadas in our trap nests were laid by cicada killers of...
the appropriate species. PNCK rates were similar for *S. convallis* at Ruby and *S. speciosus* at Easton at ~50% (Table 1).

The longer a burrow holding a cicada was left unattended, the greater the odds that the cicada would be kleptoparasitized (Table 2). At Ruby, natural burrow owners were not significantly different in body size from intruders (Table 3, *t*-test, *P* = 0.67). We never recorded a numbered female (an owner) entering the nest of another.

**Discussion**

*Tibicen parallelus* is a large (1.1 g, Coelho et al. 2012), palatable insect, representing a fine prize for a bird. Loaded wasps are slow, loud, and the visual profile of the pair is much larger than either alone. Furthermore, the provisioning female is not very maneuverable. One simple measure of maneuverability is the ratio of flight muscle mass to body mass (flight muscle ratio [FMR]; Marden 1987). The mean FMR of unladen *S. convallis* females is 0.401, indicating a high degree of maneuverability (Coelho et al. 2012). However, once the wasp is carrying a cicada, the maneuverability is much lower as the FMR drops to a mean of 0.187, which is very near the marginal level for flight in Hymenoptera (0.18, Marden 1987). Flycatchers, having evolved as aerial predators, should find heavily loaded provisioning cicada killers easy to capture. Nesting in colonies makes cicada killers favorable targets, as a bird may easily intercept multiple wasps. It is not surprising that generalist predators such as kingbirds and roadrunners have learned to exploit such an abundant and conspicuous food item. A ladder-backed woodpecker was also observed attacking a provisioning wasp, and Say’s Phoebe is known to steal cicadas from *S. convallis* (BBC 1993); we did not observe this species attacking, though they were in the area. This bird species would otherwise be unlikely to capture many cicadas, as *T. parallelus* is cryptically colored, seldom flies, and remains largely inconspicuous in the environment (except for calling by the males). The FMR of *T. parallelus* is only 0.225 (Coelho et al. 2012), indicating that, in an aerial contest, the bird should have no difficulty capturing the cicada alone. Provisioning cicada killers eliminate crypsis and its attendant advantages to the cicada. The authors confirmed the palatability of *T. parallelus* by themselves consuming a number of freshly paralyzed specimens, roasted on a gas grill, without ill effect.

It is typical for kingbirds to engage in this style of foraging: sitting on a high perch and hawking insects (Palmer and Fowler 1975, Sibley 2000). The beating behavior is curious. Kingbirds are known to beat large insects, such as caterpillars, in order to discard the skin (Ball 1936). As the cicadas were completely paralyzed, it was needless to kill or incapacitate them. The kingbirds were perhaps carrying out innate behaviors that they use to immobilize large prey. Alternatively, the beating may make the cicadas easier to swallow and digest, as the head of *T. parallelus* is quite wide (10.7 ± 0.09 (32) mm, Coelho, unpublished data).

Kleptoparasitism of wasp prey by birds is sufficiently rare that Brockmann (1980), referring to *Sphex ichneumoneus*, claimed, ‘No other species of digger wasps are known to be harassed by birds in this way’. Avian kleptoparasitism was later documented on its congener *Sphex pensylvanicus* (Benttinen and Preisser 2009, Lechner 2010). In body mass, *Sx. ichneumoneus* averages 0.303 g, *Sx. pensylvanicus* 0.489 g, whereas their prey average 0.462 and 0.425 g, respectively (Coelho 2011). *Sphex* and *Spheciopterus* are large wasps with large prey, which presumably makes them worth the time and energy spent by birds to kleptoparasitize them. The weak stings of both genera probably do little to deter the birds’ thievery.

While House Sparrows attacking prey-loaded *Sx. ichneumoneus* most often approach them directly in flight, the prey are only stolen once the wasp has been driven down to or dropped it on the ground. House Sparrows, not surprisingly, lack the aerial ability of kingbirds...
Table 1. Apparent kleptoparasitism rates after 22–30 h in two species of *Sphecius*

| Species         | Location | No. kleptoparasitized | Total | Percent kleptoparasitized |
|-----------------|----------|-----------------------|-------|---------------------------|
| *Sphecius convallis* | Ruby, AZ | 13                    | 29    | 45                        |
| *Sphecius speciosus* | Easton, PA | 27                    | 52    | 52                        |

Table 2. The effect of trap nest exposure time on kleptoparasitism rate in *S. speciosus* at Easton, PA

| Time | No. kleptoparasitized | Total | Percent kleptoparasitized |
|------|-----------------------|-------|---------------------------|
| 25 min | 9                     | 49    | 18                        |
| 45 min | 10                    | 37    | 27                        |
| 24 h   | 27                    | 52    | 52                        |

Table 3. Body mass of owner and intruder female *S. convallis* at Ruby, AZ

| Role | Avg body mass (g) | SEM | N  |
|------|-------------------|-----|----|
| Intruder | 0.963            | 0.173 | 100 |
| Owner   | 0.981            | 0.127 | 162 |

Owners were not significantly different in size from intruders (*t*-test, *P* = 0.67).

*Sphecius convallis* appears to be better defended, yielding a value of 1. Finally, the foul odor produced by cicada killers on capture (J. R. C., C. W. H., and J. M. H., unpublished observations) appears to be stronger in *Sphecius convallis* than in the two other species. These three admittedly anecdotal observations could have evolved in response to predation and prey theft by birds.

Assuming that our trap nests are treated as genuine cicada killer nests by females, in Arizona and Pennsylvania *Sphecius* populations, about half of cicadas left in open nest cells in open burrows for 22–30 h are kleptoparasitized and used in situ as egg provisions by females other than the one that dug the nest cell. This trend probably accounts for the large number of intruder females we see.

Few females performing PNCK add a second cicada to the one they pirate, and the 7 of 46 pirating females that did so (15%) were only in Easton. This strategy is probably attributable to the real risk at Easton (24 min for an average successful hunt) that the original female will return with her second cicada, lay an egg, and close the nest cell while the ‘hopeful’ pirate is out hunting for a second cicada of her own. In normal nests, eggs laid on a single cicada are nearly always male (Dow 1942). Hence, one might predict that eggs laid during PNCK are predominantly male. Alternatively, half of the eggs laid on single cicadas could be female, leading to an ‘underclass’ of small females which may be forced to rely mostly on PNCK to reproduce. However, there was no size difference between PNCK females and nest owners, suggesting that the ‘single cicada produces a male’ rule applies to PNCK as well. When PNCK is frequent, it should lead to strongly male-biased sex ratio, as the fecundity of both owner and intruder will increase if they lay male eggs.

PNCK should be favored by natural selection, as it increases a female’s fecundity by increasing her potential number of offspring while simultaneously lowering the time/energy investment in the resulting offspring. Although females engaging in PNCK might sometimes encounter agonistic behavioral defense by the resident female from whom they are attempting to steal a provisioned nest cell (Lin 1963), we have never seen an interaction result in the death of one of the females. This effect should be greater at Ruby, with its 54.5 ± 9.9 (19) min successful hunt duration, versus 24 min at Easton (C. W. H., unpublished data), but that was not shown, as the rates of PNCK were about the same after 22–30 h at both sites.

Small females should have more difficulty capturing and returning with cicadas of a given size than large ones (Lin and Michener 1972, Coelho 1997, Coelho et al. 2012), so PNCK should be favored as possibly the only way that small females can reproduce in areas where only larger cicadas are available. However, this notion is not
supported by data from Ruby showing that owners and intruders are not significantly different in size. Perhaps, all females perform PNCK when they can, but it may be the only way that small ones can reproduce at all.

At high female population densities and/or in times of low prey availability (i.e., Ruby in 2009), PNCK should be far more advantageous than ‘honest’ provisioning of a wasp’s own nest cells and, thus, selected for. Cicada kleptoparasitism by birds at Ruby would make conspecific PNCK even more advantageous. However, we saw slightly greater rates of nest cell piracy at Easton in summer 2010 than at Ruby in 2009, so avian kleptoparasitism is not what was driving PNCK in Easton, as House Sparrow kleptoparasitism of cicadas carried by Cks has been seen only three times at Easton over about 20 yr of observations.

It appears that the large, paralyzed prey of cicada killers are attractive to a variety of thieves. Interspecific prey theft is common among birds (Brockmann and Barnard 1979), and it is not surprising that agile, generalist predators such as birds have discovered how to exploit the provisioning system of Sphecius. Intraspecific kleptoparasitism is, however, much more subtle. If we had not utilized trap nests, we would not have known that it was occurring at all. This cryptic alternative strategy provides a mechanism by which all females can potentially reproduce, despite large differences in their adult sizes and without regard to the size range of cicada prey available in their environment.

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