Avian kleptoparasitism of the digger wasp *Sphex pensylvanicus*

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Abstract—Kleptoparasitism (one organism stealing prey from another) is especially common in birds. Avian kleptoparasites should be especially likely to target insects such as digger wasps (Hymenoptera: Sphecidae) that occur in large aggregations and repeatedly deliver large prey to the same nesting site. We document kleptoparasitism of digger wasps (*Sphex pensylvanicus* L.) by sparrows (*Passer domesticus* (L.)) and catbirds (*Dumetella carolinensis* (L.)). During summer 2008, we observed 697 wasp provisioning attempts (return of a prey-laden wasp to a marked nesting site) in a mown field. One-third (244/697) of attempts were intercepted by birds, primarily sparrows, which increased their hourly total number and hourly number of successful attacks per capita. Wasps maintained a consistent rate of successful provisioning attempts but may not have been able to do so indefinitely. Energetic costs related to kleptoparasitism may exert strong selection pressures on affected digger wasps.

Résumé—Le cleptoparasitisme (dans lequel un organisme vole la proie d'un autre) est très répandu chez les oiseaux. Les oiseaux cleptoparasites sont particulièrement susceptibles de cibler les insectes tels que les guêpes fouisseuses (Hymenoptera: Sphecidae) qui forment d'importants rassemblements et livrent à répétition de grandes proies aux mêmes sites de nidification. Nous étudions le cleptoparasitisme des guêpes fouisseuses (*Sphex pensylvanicus* L.) par les moineaux domestiques (*Passer domesticus* (L.)) et les moqueurs chats (*Dumetella carolinensis* (L.)). Nous avons observé, durant l'été 2008, 697 tentatives d'approvisionnement (retour d'une guêpe porteuse de proies à un site de nidification marqué) dans un champ fauché. Un tiers (244/697) des tentatives ont été interceptées par les oiseaux, surtout par des moineaux, qui ont augmenté leur nombre total d'attaques par individu et d'attaques réussies par heure. Les guêpes ont maintenu un nombre constant de tentatives d'approvisionnement réussies, mais n'auraient peut-être pas pu conserver le rythme indéfiniment. Les coûts énergétiques reliés au cleptoparasitisme peuvent exercer de fortes pressions de sélection sur les guêpes fouisseuses.

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Kleptoparasitism, one organism stealing food from another, occurs in a range of taxa and ecosystems (Iyengar 2008) and is especially prevalent among birds, a taxon with both opportunistic and specialist kleptoparasites (Brockmann and Barnard 1979). Although birds primarily kleptoparasitize other birds, they also exploit various arthropods (*e.g.*, Curry 1986; reviewed in Brockmann and Barnard 1979). Specialists often steal less than 1% of host resources but opportunistic species can take up to one-third of a host's prey (reviewed in Iyengar 2008).

Ecological conditions that favour kleptoparasitism include a large concentration of hosts providing abundant predictable high-quality food (Brockmann and Barnard 1979). Concentrations of digger wasps (Hymenoptera: Sphecidae), solitary insects with females that often form dense nesting aggregations (Rosenheim 1990), provide such conditions. Adult females of the great black wasp, *Sphex pensylvanicus* L., a large (2.0–3.5 cm long) digger wasp, provision multiple-chambered underground nests with various Orthoptera (Frisch 1938), often spending many days to fully provision a nest

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(Brockmann 1985). Because the single larva in each chamber will consume two to six grasshoppers or katydids (Frisch 1938), an adult female returns to her nest repeatedly for several days or weeks. This behaviour may make *S. pensylvanicus* especially vulnerable to opportunistic kleptoparasites.

There have been only two reports of bird–wasp kleptoparasitism. Harassment by house sparrows (*Passer domesticus* (L.)) and American robins (*Turdus migratorius* L.) led to "near extermination" of an aggregation of great golden digger wasps, *Sphex ichneumoneus* (L.) (Ristich 1953). In a more detailed study, Brockmann (1980*a*) reported that although several bird species occasionally stole prey from *S. ichneumoneus*, persistent harassment by two to five house sparrows resulted in loss of 25% of the wasps' prey. However, such kleptoparasitism was only observed at a single wasp nesting site (Brockmann 1980*a*). Both reports suggest that only a small group of birds within a larger population adopt this behaviour.

Here we document avian kleptoparasitism of *S. pensylvanicus*, the first published account of this interaction affecting a digger wasp other than *S. ichneumoneus*. We provide a preliminary assessment of the impact on nest-provisioning rates and examine the potential costs of increases in bird density and aggression over the period of our observations.

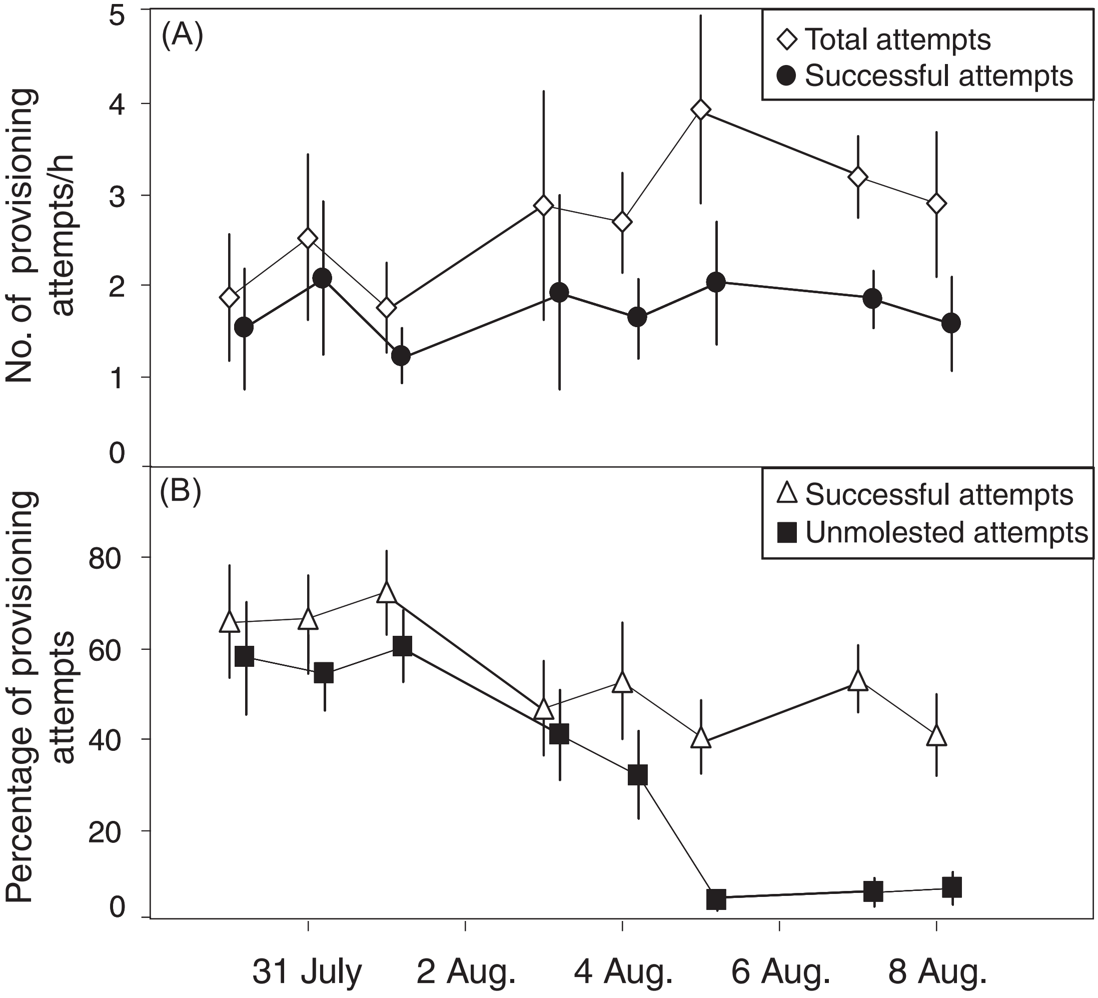
In 2008 we selected an aggregation of wasp nests in Foster, Rhode Island, United States of America (approximately 41°51′N, 71°45′W), based on personal observations of bird−wasp kleptoparasitism over the preceding two summers. Twelve active wasp nests were selected in late July; each was marked with a uniquely marked bamboo stake 10–15 cm long and observed for the duration of the study. We separately recorded harassment by wasps that we judged were probably (but not definitely) associated with any one of the 12 marked nests. Selected nests were clustered within in a "core" area of approximately 20 m^2 containing the majority of active nests; this allowed us to observe activity at all marked nests concurrently.

The study began approximately 1 week after nest provisioning began, when we first observed evidence of avian kleptoparasitism. From 30 July 2008 through 8 August 2008, a total of 27.6 h of observations were made between 10:00 and 15:00 on eight nonrainy days (wasps do not provision nests on rainy days). All observations were made 7–10 m from marked nests; neither birds nor wasps were disturbed by us at this distance (personal observation).

For each provisioning attempt by a wasp, defined as the return of a prey-laden wasp to a nest, we recorded the nest location and whether or not the provisioning attempt was interrupted by a bird. For each harassed provisioning attempt, we recorded the bird species (*P. domesticus* or gray catbird, *Dumetella carolinensis* (L.)) and whether provisioning was successful (the wasp entered the nest with a prey item) or unsuccessful (a bird stole the prey). We calculated the hourly rate of wasp provisioning attempts per nest on each of the eight observation days by dividing the total number of provisioning attempts per nest each day by the number of observer-hours. We also calculated the hourly rate and percentage of successful wasp provisioning attempts, as unharassed provisioning attempts plus harassed but successful provisioning attempts. The average hourly attack rate per bird and average percentage of successful attacks per bird were calculated by dividing the cumulative attack rate on a given day by the number of birds present on that day. We only counted birds as present if they were actively involved in kleptoparasitism or precursor activities (*e.g.*, perching on nearby vegetation and watching wasp movement in the core area).

We calculated a mean daily value (= replicate) of each metric for each of eight observation days (*n* = 8 replicates) by averaging the data from observed nests. Because we hypothesized that kleptoparasitic interactions would escalate over time, we analyzed the relationship between observation date and each metric using linear regression with date as the fixed factor. Differences between bird species were analyzed using one-way ANOVA (eight replicates per species). Data were checked for normality by visually inspecting the normal quantile plot and for homogeneity

Fig. 1. Daily data (mean ± SE) on nest provisioning by digger wasps (*Sphex pensylvanicus*) from 31 July 2008 to 8 August 2008 at Foster, Rhode Island, United States of America. (A) Numbers of total and successful provisioning attempts per hour. (B) Percentages of successful provisioning attempts and percentages of attempts during which the returning prey-laden wasp was not harassed by any birds. For visual clarity, solid symbols are slightly offset from open symbols.



of variance via the Brown−Forsythe test and Levene's test for unequal variance ($F_{1,13}$ = 1.29 and 1.82, respectively; both $P > 0.20$). All data analyses were performed in JMP 7.0.2 (SAS Institute Inc. 2007).

Of 697 observed provisioning attempts, approximately two-thirds (453) were successful. in the remaining 244 provisioning attempts, birds intercepted and stole the wasp's prey. Though the number of successful provisioning attempts per hour remained stable across the sampling period ($F_{1,6}$ = 0.13, $P > 0.5$), this consistency resulted from a marginally significant increase in the total number of provisioning attempts per hour ($F_{1,6}$ = 5.6, P = 0.056) (Fig. 1A). The percentage of unsuccessful attempts increased significantly, from 42% to 93% ($F_{1,6}$ = 40.3, $P < 0.001$), whereas the percentage of successful attempts decreased significantly, from 65% to 40% ($F_{1,6}$ = 10.7, P = 0.017) (Fig. 1B).

Between one and three catbirds and between three and five sparrows harassed returning wasps, with no difference in the overall success rates of the two species (catbirds and sparrows were successful in 70 ± 7.4% (mean ± SE) and 60 ± 6.9% of attacks per day, respectively; $F_{1,13} = 0.96$, $P = 0.34$). Catbirds harassed wasps intermittently but sparrows congregated at the nesting site and remained there throughout each observation period, so the total number and the number of successful attacks per hour by each bird were significantly higher for sparrows than for catbirds (total attacks: 0.39 ± 0.07 *versus* 0.15 ± 0.07 (mean ±SE); $F_{1,13} = 5.7$, $P = 0.032$; successful attacks: 0.21 ± 0.04 *versus* 0.09 ± 0.04; $F_{1,13} = 5.2$, $P = 0.039$).

The number of kleptoparasitizing sparrows increased significantly over the course of our observations ($F_{1,6} = 23.9$, $P = 0.003$), from three (30 July to 3 August) to four (4 August to 7 August) to five (8 August). This corresponded to increases in total number ($F_{1,6} = 15.4$, $P = 0.008$) and number of successful attacks per bird ($F_{1,6} = 9.3$, $P = 0.022$). The sparrows did not, however, become more efficient at obtaining prey; the percentage of successful attacks did not change over time ($F_{1,6} = 0.03$, $P = 0.86$).

Catbird behaviour changed little over time. There was no change in the per-capita hourly rate of total or successful attacks ($F_{1,6} = 0.71$ and 2.10, respectively; both $P > 0.15$), and the number of foraging catbirds fluctuated irregularly from one to three. Sparrows appeared to cause catbirds to abandon their pursuit of wasps, suggesting that interspecific avian competition can affect the efficacy of kleptoparasitism. Perhaps because of this, catbirds showed a nonsignificant decrease ($F_{1,6} = 4.47$, $P = 0.088$) in successful kleptoparasitism attempts.

Our research documents intense avian kleptoparasitism of the digger wasp *S. pensylvanicus* at one site. Our results differ from reports of avian kleptoparasitism of *S. ichneumoneus* (Ristich 1953; Brockmann 1980*a*) in that we document an increase in the frequency and impact of kleptoparasitism over time. The marginally significant increase in the total number of provisioning attempts, resulting in a constant rate of successful provisioning, may have been a response to kleptoparasitism. This has been demonstrated for at least one other solitary wasp: a species of *Ammophila* Kirby (Sphecidae) increases its rate of prey capture in response to experimental removal of prey (Field *et al.* 2007).

The increase in density of sparrows and their harassment of wasps demonstrate that this "opportunistic and adaptable" bird (Brockmann 1980*a*) increasingly exploited an opportunity to obtain food. We never observed birds attacking unladen wasps, which supports the hypothesis that such opportunistic kleptoparasitism may have arisen in response to birds' pursuit of large mobile insects, with the wasps serving as prey "vectors" rather than targets (Brockmann and Barnard 1979; Brockmann 1980*a*). However, increased interest in and harassment of prey-carrying wasps by sparrows were not correlated with increased success in obtaining food (*i.e.*, the percentage of successful sparrow attacks did not change over time). Ultimately, our study was too short to allow firm conclusions to be drawn about changes in the birds' foraging behaviour.

Despite a generally consistent rate of successful provisioning by wasps over the observation period, they may have been unable to maintain this pace indefinitely. Interference with nest provisioning, including removal of prey, can have an impact on wasp reproductive success (reviewed in Brockmann 1979; Field *et al.* 2007). Wasps incur considerable energetic costs during the capture and transport of prey items up to three times their body mass (Field *et al.* 2007), and kleptoparasitic fly maggots may consume their buried prey (Coelho and Ladage 1999). Although adult wasps have a life-span of approximately 6 weeks (Field 1989; review in Rosenheim 1990), prey abundance decreases in late August and September (Brockmann 1980*b*). The impact of kleptoparasitism may thus have increased in the weeks following our observations. Also, the increase in foraging rates necessary for wasps to compensate for bird harassment may affect the life-span of provisioning adults. The apparent rarity of bird−wasp kleptoparasitism and its restriction to specific locations suggest that such interactions may persist only for short periods of time. However, our research was motivated by our observation of bird–wasp kleptoparasitism at the same site during the preceding two summers. Cumulative avian kleptoparasitism (both within and across years) may exert strong pressures on wasp populations, perhaps even causing local extirpation (as suggested in Ristich 1953). It may also be that if wasp densities decrease to a level at which kleptoparasitism is energetically unprofitable, the birds leave, allowing remaining wasps to provision their nests without interference. How (and whether) *S. pensylvanicus* compensates for reductions in provisioning success driven by avian kleptoparasitism is an important area of future study.

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