The bird who kicked the wasp's nest: Red-throated Caracara predation, nesting and territorial behaviour

by

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Ethics Statement

Abstract

Red-throated Caracaras are enigmatic but seldom studied raptors of tropical American forests. They are known to prey on social wasps and exhibit cooperative breeding, but little quantitative data have been published. We investigated Red-throated Caracara nesting, predation and social behaviour in the field in French Guiana from 2008 to 2013. We closely studied two nests with automated camera systems and found a high level of cooperative behaviour among adults tending nests. Seven individuals were involved in bring prey to and guarding a nest in 2009. Our observations of caracaras nesting in bromeliads confirmed that the majority of their diet was comprised of the brood of social wasps, although they also brought millipedes and fruits to the nest.

The social behaviour of the caracaras included intense territorial behaviour, including specific vocalizations and displays in response to conspecifics or playback of caracara calls. Caracaras also attacked conspecific decoys, and we observed them attacking members of other groups on two occasions in 2011.

The caracaras provided their chicks with nests of a diverse assortment of wasp genera, including *Polybia*, *Pseudopolybia*, *Leipomeles*, *Apoica* and *Parachartergus*, and the proportional abundance of these taxa is not congruent with published studies on generic abundances. In addition, while army ants had previously been considered top predators of social wasps, we calculated that the caracaras, as specialist predators, could rival or exceed army ants as a mortality factor for social wasps.

It had been hypothesized that these caracaras rely on a powerful chemical repellent to protect themselves from the stings of their defensive prey, but we found no evidence of such a repellent. We used a video recording arena to observe caracara predation behaviour on nests of various species of *Polybia*. We observed that the caracaras are indeed stung by some species of wasps, but the caracaras mount high-speed aerial strikes against such nests, knocking them to the ground or striking them repeatedly until the adult wasps depart in an absconding swarm. The caracaras exploit this absconding response when attacking highly defensive wasp species in order to minimize stings while obtaining the wasp brood.

Dedication

This thesis is dedicated to Jean-Marc Thiollay, a pioneer in tropical raptor conservation and the first scientist to study the Red-throated Caracara in detail. Without his work, I would never have studied these amazing birds.

Acknowledgements

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James Carpenter of the American Museum of Natural History and Max Winston at the Field Museum of Natural History were instrumental in determining species ID's for wasps and army ants respectively. Your taxonomic expertise is much appreciated!

I would like to specially acknowledge the time, effort and sacrifices of my wonderful colleagues Onour Moeri and Tanya Jones who went with me to French Guiana: the stressful times and the spider bites you suffered were not in vain!

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Executive Summary

Red-throated Caracaras (*Ibycter americanus*) are highly unusual and enigmatic raptors of the American tropics. The work in this thesis comprises investigations into their life history and relationships with other species. In the first chapter, we consider vertebrates as predators of stinging social wasps and bees. There are very few animals that habitually seek out social wasps and bees as prey items, but the Red-throated Caracara is one such specialist predator. We review the adaptations these animals have to deal with their stinging prey, and the vertebrate-specific defenses of wasps and bees. In the second chapter, we describe for the first time the nesting behaviour of Red-throated Caracaras. We document the types of food brought to chicks, revealing that social wasps comprise 60-76% of their diet. We also describe well-developed cooperative breeding by groups of 5-7 caracaras. The third chapter examines the potential predatory impact these birds have on social wasps, which may rival that of another group of well-known wasp predators, the army ants. The fourth chapter deals

with social and territorial behaviours we recorded during our work. Red-throated Caracaras are highly vocal and territorial and do not tolerate other groups of Red-throated Caracaras in their territories. We analyze their vocalizations and describe territorial behaviours ranging from territorial calling and display to outright attack of intruders. In the final chapter, we examine the intriguing hypothesis that the caracaras are chemically defended against their stinging prey, and we provide evidence that this is not the case. Although there are some interesting chemicals to be found on Red-throated Caracaras, they do not protect the birds from counterattacks by wasps. Instead, the birds exploit the evacuation behaviour of their prey, damaging or disturbing the nests sufficiently so as to cause the wasps to abandon them and cease stinging. This allows the caracaras to take the brood of the wasps while minimizing their exposure to the stings of the adults. These chapters add to our knowledge of the Red-throated Caracara and their place in the ecosystems in which they live.

Chapter 1.

Vertebrate Predation on Stinging Social Wasps and Bees - Attack Strategies and Countermeasures

Sean McCann, Sean O'Donnell and Gerhard Gries

A modified version of this chapter will be submitted to *American Midland Naturalist*

1.1. Abstract

Social bees and wasps (Hymenoptera) are important pollinators, predators, and scavengers in many ecosystems. Yet, factors affecting the population densities of these insects are poorly understood. Predation is thought be an important mortality factor but has rarely been studied. Here we describe the current knowledge of vertebrate predation on social wasps, highlighting the attack strategies of vertebrate predators and the defense strategies of their social hymenopteran prey. Wasp colonies defending their nest against birds and mammals risk losing essential workers. Thus, nest defense is less likely in small-colony species and in large-colony species if a nest is in an incipient stage with limited brood and nest-building investment. Nest defense strategies can be active and passive. They are diverse and include nesting in cavities, on distal branches out of reach for heavier mammals, concealment of nests, fortification of nests with tough mud or woven-felt envelopes, Batesian mimicry of sound, stinging or venom spraying, nesting in association with protective ants, aggregated nesting for pooled anti-predator defense, and strategic retreat (absconding), a process during which the colony loses its offspring but retains its workers and queens. The adaptations and strategies of vertebrates to cope with the defenses of the insects are equally diverse. They include thick fur or feather "coats" as a form of protection from stings, innate or acquired immunity to insect venom, attack at night when insects are docile and will not fly, attack

of primarily small and less defended nests, killing workers in repeated bouts of attacks and thus depleting a nest’s defense line, mounting rapid and repeated fly-by attacks on nests and inflicting severe, absconding-inducing mechanical nest damage, and finally knocking nests to the ground where they are abandoned. That there are few specialist predators of social wasps and bees may reflect on the effective defenses offered by these insects. Alternatively, it may indicate that population densities of these insects are often low, or strongly fluctuate, and thus cannot support many specialist predators.

1.2. Introduction

> “Despite the ease with which the behavior is elicited, however, defensive
>
> behavior remains remarkably little-studied in the social wasps.” (Jeanne and Keeping, 1995).

Eusociality provides many benefits to a species, including greater net reproduction. Colonies of eusocial insects such as ants and termites typically have large numbers of developing offspring that depend on adults for food, cleaning and defense (Andersson, 1984). A colony of eusocial insects is a “factory inside a fortress” (Wilson and Hölldobler, 2005) where large aggregations of offspring represent a large collective investment on the part of the colony, and workers are responsible for both effective defense and efficient rearing of brood.

Although social bees and wasps are widespread and abundant in many ecosystems, detailed life history studies of species are rare. Predation, in particular, has seldom been studied, even though it is deemed to be a substantial mortality factor in the life history of many social wasps and bees (Jeanne, 1975).

The defensive responses of many stinging social wasps and bees are amazing to behold. Unlike ants and termites that are flightless and move relatively slowly across a surface, eusocial wasps and bees are very capable fliers and can swiftly attack potential nest predators by stinging, biting or venom-spraying (Hermann and Blum, 1981). Millions of years of evolution have yielded defense strategies of social insects that combine speed, efficiency and biochemical weaponry capable of discouraging vertebrate predators from attacking. Nonetheless, many vertebrates occasionally or habitually seek nests of social wasps and bees, and feed on their brood. In this literature review, we will summarize current knowledge of vertebrate predation on stinging social wasps and bees, highlighting attack and defense strategies.

1.2.1. Vertebrate predators of stinging social wasps and bees

There are many anecdotal reports in the popular literature on mammals and birds that occasionally or habitually prey on nests of social wasps and bees. Table 1 summarizes these records, describing the insect genera that are preyed upon, and classifying the respective vertebrate as an occasional, habitual, or specialist brood predator of social wasps and bees. For the purposes of this analysis, we considered specialists to be those species for which ≥ 30% of the diet is bee or wasp brood. Among mammals, representatives of the bear and weasel families prey particularly often on the brood of wasps and bees but true “specialists” who depend on this diet are rare. Even specialists do not prey exclusively on wasp and bee brood. Not listed in Table 1 are the wax-eating Honeyguides that are considered scavengers and the Bee-eaters (Meropidae) that consume adult bees or wasps rather than their brood (Kastberger and Sharma, 2000).

1.2.2. Does vertebrate predation substantially impact populations of stinging bees and wasps?

The population effects of predation on the demography of any animal species is difficult to quantify. The cryptic nesting habits of social wasps and bees (e.g., *Leipomeles,* Fig. 1.1) (Williams, 1925), or their nesting high in trees (Richards, 1978), make it difficult to survey sources of nest mortality. Nonetheless, nest predation can be an important mortality factor for certain species of stinging wasps and bees. Ant predation is assumed to be the principal cause of wasp nest mortality in the tropics (Jeanne, 1975; Kukuk *et al.*, 1989), but demographic studies supporting this assumption are remarkably rare. One such study documents substantial wasp colony mortality caused by various scouting and recruiting ants, but mortality estimates may have been biased because nests were surveyed only in lower strata of the forest (Bouwma *et al.*, 2007). Reportedly high predation rates on social wasps by vertebrate predators, particularly specialist predators, might exert substantial pressure on wasp populations (Huang *et al.,* 2004, McCann *et al.,* 2010, Windsor, 1976, Strassmann, 1981, Strassmann *et al.*, 1988, Gibo and Metcalf, 1978). However, the paucity of longitudinal demographic studies on most tropical social wasps and bees does not justify generalizations about the impact of predation on wasp populations.

1.3. Factors that determine defensive effort

Despite the significant investment that a colony has made in brood and nest building, defending a nest against vertebrate predators entails significant risk to worker wasps, largely due to the size differential between the wasps and the attacking vertebrate. Whether a wasp or bee colony will mount a defense may depend on many factors including colony size. Small-colony species, or incipient colonies of large-colony species with limited brood and nest-building investment, may abandon rather than defend the nest against vertebrate predators, thus reducing the risk of losing essential workers

The stage of the colony cycle also affects the propensity to defend. The number of offspring in the nest and their stage of development are often good predictors for the likelihood of defense, with a greater investment being correlated with a greater propensity to defend (West-Eberhard, 1982). Because colony size and number of offspring are correlated, the contributing effect of each factor is difficult to determine but there is clearly a relationship between reproductive investment and strength of defense (London and Jeanne 2003). This also applies to birds, where the overall brood investment often determines the strength of the defense against nest predators (Gottfried, 1979; Andersson *et al.*, 1980); but see Knight and Temple, 1986. In social insects, the underlying mechanisms resulting in increasingly stronger defense with increasingly greater reproductive investment are unclear, but may involve sensing the number of nest mates and offspring in the nest. Part of the mechanisms may be a brood pheromone but this has yet to be studied in detail (Conte *et al.*, 1990; London and Jeanne, 2003).

1.4. Stinging, venom and venom spraying

The stinger and venom apparatus of social wasps and bees is homologous to that of their solitary counterparts (Piek, 1986), however the social species use their stingers primarily in colony defense and intra-colonial combat, rather than in foraging (but see Olson, 2000). Solitary bees and wasps gain some anti-predator protection from their stinging defense, but social wasps and bees engage in coordinated defensive stinging as a strategy to deter potential nest predators (Seeley *et al.*, 1982; Dani *et al.*, 2000; Reed and Landolt, 2000).

The venoms of social wasps and bees contain many chemicals such as histamine, serotonin and dopamine that cause immediate pain and subsequent inflammation (Banks and Shipolini, 1986; Nakajima, 1986). Stinging efforts of workers in a social wasp colony are often coordinated and directed for maximum effect via chemical signals (Heath and Landolt, 1988; Sledge *et al.,* 1999; Dani *et al.*, 2000), auditory or vibratory signals (Nascimento *et al.*, 2005), or visual signals (O'Donnell *et al.*, 1997).

Alarm pheromones improve the effectiveness of a colony's defense against vertebrates and help protect the nest's integrity. With often only a small point of attachment to substrate, the nest integrity of many social wasps is vulnerable to large animals (Jeanne, 1975), and timely, pheromone-mediated mobilization of defensive workers is crucial to preventing catastrophic nest damage. Alarm pheromones communicate danger and compel action in workers who otherwise may not notice the predator. Furthermore, if pheromones also "mark" the predator, defending workers have a common target for their attack (Bruschini *et al.*, 2010). In many species, the stinger of workers is proportional to their body size, and is shorter and/or more barbed than that of queens (Piek, 1986). Highly barbed stingers are more likely to remain in the skin of vertebrate predators and to deliver more venom as the stinger and associated glands are torn from the abdomen. This phenomenon is known as sting autotomy, and occurs in several lineages of aculeate Hymenoptera, including ants, honeybees, bumblebees and several wasps (Mulfinger *et al.*, 1992, Hermann, 1971). Sting autotomy may inflict significant pain and impairment on predators or intruders, help mark intruders with pheromone as shown in honeybees (Wager and Breed, 2000), and facilitate a highly coordinated attack. Sting autotomy results in the death of workers and is expected to have evolved primarily in large-colony-size species that can sustain the “self-sacrifice” of workers, however this has seldom been investigated and the overall pattern is unclear (Macalintal and Starr, 1996). In contests between large hymenopteran nests and mammalian or avian raiders, sting autotomy could provide a useful advantage. Pheromone-marked intruders could become subject to concerted attacks and could be pursued well beyond the vicinity of the nest, thus lowering the probability of repeated attacks by the same intruder. Even without sting autotomy, many wasp species have pheromones in venom and head glands that alert the colony or mark intruders (Post *et al.*, 1984; Veith *et al.*, 1984; Heath and Landolt, 1988; Jeanne, 1991; Kojima, 1994; Landolt *et al.*, 1995; Sledge *et al.*, 1999; Dani *et al.*, 2000; Bruschini *et al.*, 2006). If alarm or marker pheromones are present in the venom, a worker wasp may deposit a small amount on the skin, feather or fur surface of predators during an attempted sting, an action that might suffice to mark predators for a coordinated attack by the entire colony.

Venom spraying by worker wasps, unlike attempting to sting, is probably a safer strategy to inflict pain and damage on vertebrate intruders. In this mode of defense, venom is sprayed from the stinger towards the predator’s face or eyes causing pain and blindness (Jeanne and Keeping, 1995).

1.5. When predators get stung

Venoms of social Hymenoptera cause immediate pain when injected into the skin of vertebrates during a stinging event. The pain-causing amine and kinin chemicals also induce an accelerated rate of red blood cell destruction (hemolysis) (Nakajima, 1986). Wasp or bee stings can certainly cause a prospective predator to flee, especially if pursued by a buzzing swarm of defending insects. If these insects can shift the predator’s behavior from foraging to escaping, they may prevent it from relocating and preying on the nest.

Bee and wasp venoms not only cause pain for an attacked intruder, they can also be lethal (Schmidt *et al.*, 1986; Schmidt, 1990). Human fatalities associated with venom pathology from social wasp and bee stings are documented in numerous reports

(Vetter *et al.*, 1999). Venom pathology causes fatalities also among smaller vertebrates (Thapa and Wongsiri, 2003). Interestingly, social Hymenoptera have venom much more toxic to vertebrates than venom of solitary species (Schmidt, 1990), presumably because they use the sting for nest defense against vertebrates rather than foraging for invertebrates. This might indicate that the direct killing or incapacitation power of these venoms is important to the defense of nests, beyond simply causing pain and evasive flight. Indeed, some bee and wasp venoms (Schmidt *et al.*, 1986) can have fatal consequences to vertebrates, and potentially these species may simply kill any vertebrate that attempts to attack their nests. Nonetheless, even the most toxic venoms do not seem to deter all predators, because taxa as formidable as *Vespa* (Lee, 2011) and *Apis dorsata* (Thapa and Wongsiri, 2003) are preyed upon by vertebrates.

1.6. Are stings effective deterrents to vertebrates?

The defensive capabilities of some wasp colonies deter vertebrate predators. According to classic ethological research, a predator avoids individual stinging insects when it has learned to associate their aposematic coloration with a negative stimulus (Brower and Brower, 1962). This avoidance behavior suggests that stinging can be an effective deterrent to predation on individual adult wasps. In this aversive conditioning, the predator learns to associate foraging on wasps with the pain of getting stung. The aposematic coloration of social wasps and bees, their warning sounds (Overal, 1981; Seeley *et al.*, 1982; Nascimento *et al.*, 2005) and visual displays (O'Donnell *et al.*,1997) can all serve as conditioning stimuli.

Nesting associations among birds and wasps in the tropics suggest that the presence of a formidable wasp nest protects associates from vertebrate predators (Robinson, 1985; Joyce, 1990; Joyce *et al.*, 1993; Haemig, 2001; Beier *et al.*, 2006). Some of these studies give firsthand accounts of bird nest predators being deterred by social wasps. Similarly, less defensive wasp species gain protection by nesting in association with larger, more formidable wasp species (Windsor, 1972; Starr, 1988). If formidable social wasps can serve as an effective deterrent to vertebrate predators of bird nests, the wasps must also be capable of defending themselves. Because the trait of stinging cannot be removed from these insects, a controlled study on its effectiveness is not possible, but the maintenance of various morphological and behavioral adaptations attests to the continued effectiveness of stinging.

1.7. Defensive strategies of stinging social wasps and bees

1.7.1. Concealment of nests

Many stinging bees and wasps select nest sites, or substrates for nest placement, that offer some protection from ants (Dejean *et al.*, 1998; Corbara *et al.*, 2009). Although less studied, it is likely that stinging bees and wasps may also select sites which reduce the risk of predation by vertebrates. Visual camouflage of nests is common across many taxa of wasps and bees (Richards, 1978; Seeley *et al.*, 1982). Placement of aerial nests beneath overhangs and leaves conceals nests from above while shading them and making them less conspicuous. Such nest placement also provides protection from inclement conditions such as excessive rain, and is common in many eusocial vespids. Nests may also be built adhering to tree trunks, with bark elements added as camouflage to the envelope, as seen in certain species of *Parachartergus* (Strassmann *et al.*, 1990; Jeanne and Keeping, 1995).

Habitual placement of nests close to the forest floor and beneath leaves by many species is likely an adaptation against avian predators that would have to fly in a very narrow cone of space to detect such nests. As the forest floor is cooler than higher strata of the forest, “floor-level” nests likely experience a tradeoff between reduced predation risk, and thermal disadvantage (Fetcher *et al.*, 1985) with slower brood development and longer colony cycles.

Leipomeles wasps have taken nest concealment to extremes. They build their nests beneath leaves and cover combs with an envelope resembling leaf venation (Fig. 1.1), so that predators searching from below cannot easily detect a nest (Williams, 1925). *Parachartergus* species conceal their nest by attaching it to a solid substrate and by decorating the envelope to resemble that substrate (Strassmann *et al.*, 1990). This tactic can be quite effective at masking the appearance of a nest.

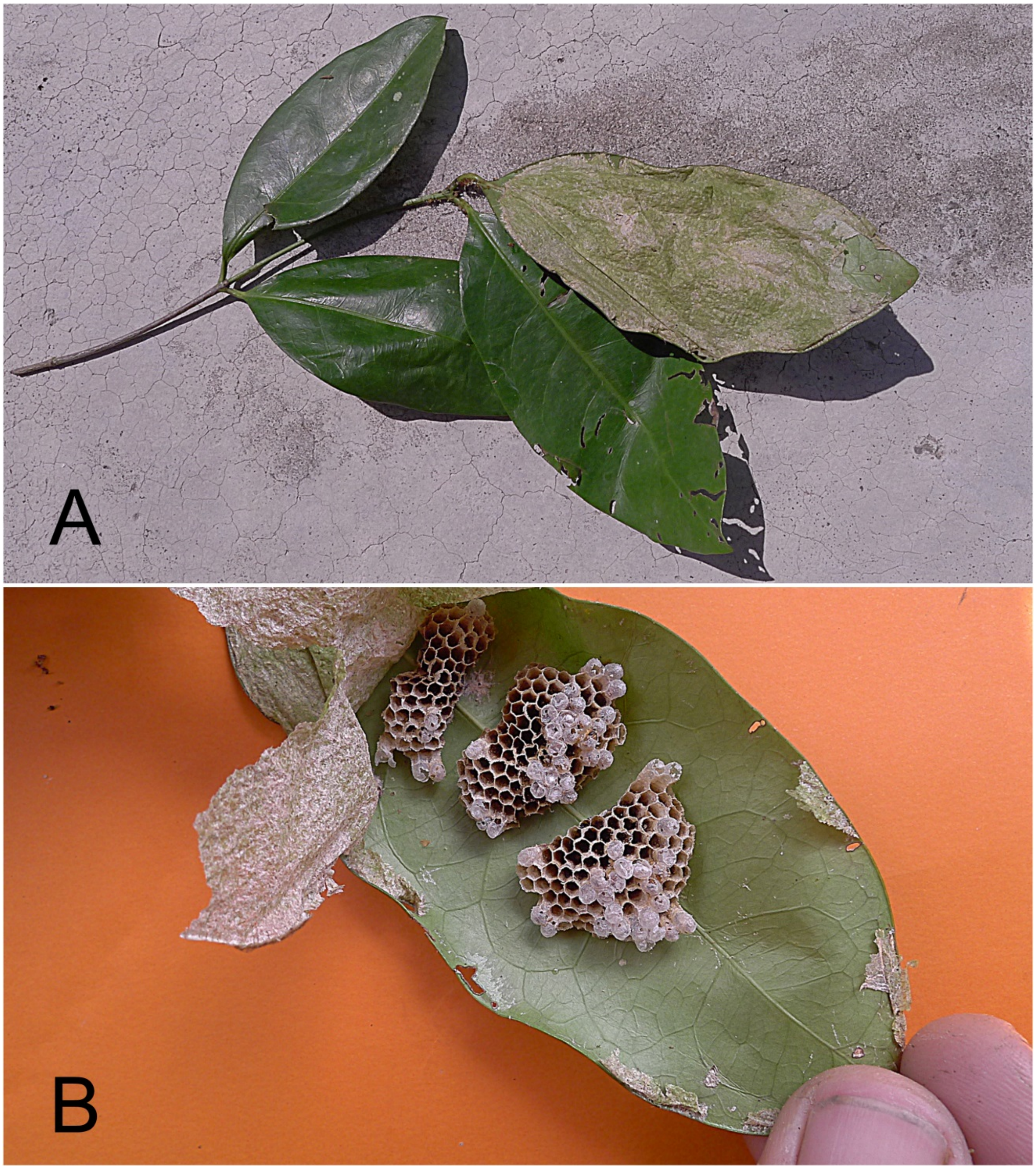

Figure 1.1. Nest of *Leipomeles dorsata* with an envelope (A) that resembles the underside of a leaf. Such nest camouflage may prevent vertebrate predators from locating the nest and preying on the brood comb (B). Photos by Alex Popovkin, Bahia Brazil, taken in January 2013, used under the terms of a Creative Commons 2.0 License.

1.7.2. Physical fortification of nests

Physical fortification of bee or wasp nests represents an effective defense irrespective of whether or not a colony can mount a potent stinging defense. Physical fortification of nests may involve their placement in rock or wood cavities, or in stony underground terrain. This tactic is found in various taxa of bees and wasps. In combination with stinging, it is probably very effective against many vertebrate predators except for bears (Ursidae) that are strong diggers and some mustelids such as ratels (*Mellivora capensis*). Physical nest fortification, however, has limited utility against ants that can raid into any cavity that may house wasps or bees (Seeley *et al.*, 1982; O'Donnell and Jeanne, 1990).

A notable exception to this may be seen in *Agelaia myrmecophila* and *A. hamiltoni*, two species of wasp that nests in holes excavated in the massive carton nests of ants of the genus *Azteca.* These wasps would be largely inaccessible to both army ants and most vertebrate predators (Richards, 1978, London and Jeanne, 2000).

Unlike cavity-nesting wasps, wasps that build aerial nests often fortify them by incorporating material into the nest envelope that renders it almost impenetrable (Fig. 1.2). The fortress-like nest of *Polybia emaciata* offers an effective physical defense against mammalian predators, but seems less effective against some birds (Skutch, 1959; Windsor, 1976). Some species in the *Polybia* subgenus *Pedotheca*, such as *Polybia singularis* and *P. spinifex,* build mud nest envelopes (Hozumi and Inagaki, 2010) that weigh up to 5 kg (Richards, 1978). Such massive nests, with envelopes encircling supporting branches, are difficult for many (avian) predators to open or break off. Moreover, the narrow nest entrances appear defensible against ants. Similar nest fortifications are achieved by other Epiponini such as *Chartergus* and *Epipona* (Fig. 1.3) that build nests out of tough, felt-like materials (Richards, 1978) Interestingly, these nests are commonly found high up in trees, beyond the reach of most army ants.

Figure 1.2. Nest of *Polybia singularis* with a thick envelope of mud, and a robust attachment to the tree limb. Such a nest may weigh as much as 5 kg (Richards, 1978) and may provide effective deterrent to vertebrate predators.

Figure 1.3. Nest of *Epipona* spp. with a tough, felt-like envelope that is broadly and securely attached to large branches. These nest features may protect against vertebrate predators. Photo by Robert Jeanne, used with permission.

1.7.3. Pooled defense

The phenomenon of multiple colonies of formidable insects nesting in close proximity to one another may be a result of selection for improved defense through pooling of resources (Kastberger and Sharma, 2000). Colony aggregations have been observed (Fig. 1.4) in *Polybia rejecta*, a large wasp with sting autotomy, alarm pheromones and a pugnacious temper (Jeanne, 1978). Conclusive data are lacking on the relative rates of predation on gregarious *versus* solitary nesters, but there is evidence that nest defense against vertebrate predators is shared between aggregated colonies of the giant honey bee *Apis dorsata* (Kastberger and Sharma, 2000). Large numbers of *A. dorsata* nesting gregariously killed a Crested Honey Buzzard (*Pernis ptilorhynchus*) which is a specialist bee and wasp predator (Thapa and Wongsiri, 2003).

Figure 1.4. Nesting aggregation of *Polybia rejecta*. These colonies may pool defense in order to drive off vertebrate predators. Photo by Robert Jeanne, used with permission.

1.7.4. Mimicry

The emission of coordinated, snake-like hissing sounds in response to colony disturbance represents an interesting defensive tactic in some bees (*Apis*) (Koeniger *et al.*, 2010) and bumble bees (*Bombus*) (Kirchner and Röschard, 1999). As experimentally demonstrated, this type of sound deters would-be predators such as mice (Kirchner and Röschard, 1999) and may be an example of auditory Müllerian mimicry. Other types of auditory signals may supplement visual displays and stinging to drive predators away from a defending nest (Overal, 1981; Nascimento *et al.*, 2005).

1.7.5. Nesting in association with other Hymenoptera

Several Neotropical social wasps build nests in close association with certain species of ants, actively maintaining nest sites free of the resident ants (Herre *et al.*, 1986; Joyce, 1990; Servigne, 2003). These ants densely occupy trees and defend them vigorously against all invertebrate intruders including army ants (Chadab, 1979a). Trees with resident ants may also deter vertebrate predators, especially those which cannot fly (Haemig, 2001). Studying, for example, the facultative nesting associations of *Polybia rejecta* with *Azteca* ants (Richards, 1978) would reveal whether and to what extend these associations help alleviate vertebrate predation. Similarly, wasps nesting in association with a formidable species presumably gain protection from vertebrate predators. For example, *Mischocyttarus immarginatus* does nest in association with the larger and more defensive *Polybia occidentalis*, being almost an obligate associate (Starr, 1988; London and Jeanne, 1997).

1.7.6. Absconding - a strategic retreat

Hymenoptera that found their nests as swarms of reproductive females and workers are termed swarm-founders and have evolved in the taxa *Provespa*, *Vespa*, Epiponini, Ropalidiini, Apini and Meliponini (Matsuura and Yamane, 1984; Cronin *et al.*, 2013). Swarm-founders leave their nest *en masse* when conditions for nesting become impossible, for example after catastrophic nest damage (West-Eberhard, 1982). If a nest is destroyed by weather or is threatened by an enemy that cannot be defeated, swarm-founders will cut their losses, depart, and re-found a nest in another location. This type of nest abandonment is termed absconding and seems unique to swarm-founders. An absconding colony loses its offspring but retains its reproductive females and the work force. In some genera, workers of the absconding swarm return to the old nest site and scavenge nest materials and/or protein (Seeley *et al.*, 1982; Sarmiento-M., 1999). In contrast, independent colony founders wherein single inseminated females initiate new colonies alone fight off predators as long as they are able, and attempt to re-found in the same location (Strassmann, 1981).

Several wasp species abscond in response to *Eciton* army ants (Chadab, 1979a; O'Donnell and Jeanne, 1990), a predator too formidable to meet with defense.

Absconding in response to the chemically-coordinated army ant raids with tens (or hundreds) of thousands of workers is almost a foregone conclusion, but the wasps' response to a vertebrate predator is less certain. The circumstances under which a swarm-founding colony will abscond or attempt to fight off the predator are not well understood. Conceivably, a threshold of disturbance needs to be crossed before swarm-founders abscond. If a nest is dislodged and has dropped to the ground and sustained damage, the colony will typically abandon the nest because it is now subject to surface predators such as ants (Chadab, 1979b). Vertebrate predators, especially birds, appear to take advantage of the wasps' absconding behavior in response to severe nest damage or dislodgment. In rapid and repeated fly-by attacks, Red-throated Caracaras (*Ibycter americanus*) inflict heavy nest damage, await the absconding response from a safe distance, and then return to feed on the brood in the abandoned nest (Fig. 1.5) (McCann *et al.*, 2013).

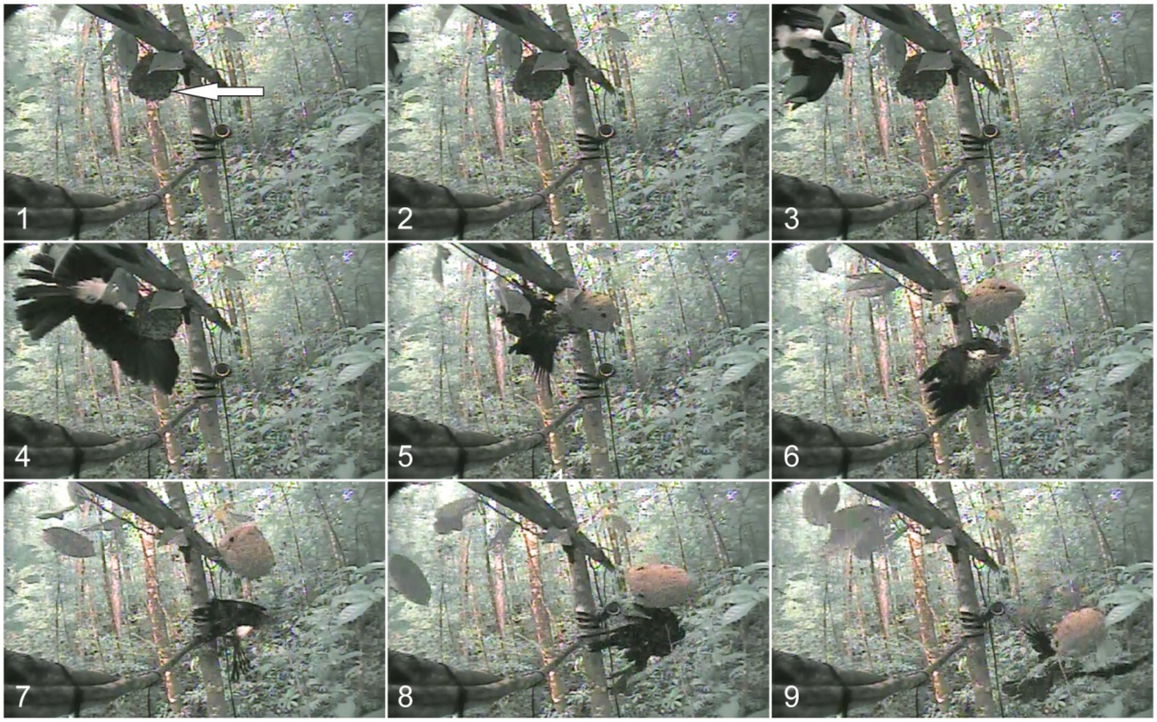

Figure 1.5. Fly-by attack of Red-throated Caracara on nest of *Polybia jurinei*. Single-frame images of a video recording revealing the fly-by attack of a Red-throated Caracara (ventral view) on a large nest of *Polybia jurinei* (arrow in panel 1).

1.8. Attack strategies of vertebrates

1.8.1. Attacking only small nests

Small colonies of *Polistes*, *Mischocyttarus*, *Apis cerana* (Seeley *et al.*, 1982), and of small Epiponini species do not vigorously defend against nest attackers. Instead, they appear to rely on nest crypsis for protection against large predators, to readily abscond and to re-found in the same site (McCann *et al.*, 2013). This type of “defense” probably allows a great many species of vertebrates to prey with impunity or little danger on these types of nests, provided they can find them. Drawing on our own records (McCann *et al.*, 2010), Red-throated Caracaras provision their chicks with many such small nests, or they feed on them *in situ* with no defense offered by the wasps. Testing nest defense by the small-bodied *Polybia bistriata*, we noticed that a determined attack by a human does not elicit stinging behavior, whereas casual movement in front of the nest sometimes does. In no instance did these wasps counterattack Caracaras during predation events (McCann *et al.*, 2013).

1.8.2. Morphological defenses

Morphological adaptations such as thick plumage, thin nares (nostrils) and tight, scale-shaped face feathers physically protect *Pernis* Honey-buzzards from wasp stings (Sievwright and Higuchi, 2011). This physical defense, however, may not be absolute because nest defending social insects can still drive off attacking buzzards (Cobb, 1979) or even kill them (Thapa and Wongsiri, 2003). Similarly, thick fur and recessed small eyes enable bears to withstand stinging attacks of bees and wasps, and to prey on these social insects worldwide (Bigelow 1922; Joshi *et al.*, 1997; Mattson, 2002).

1.8.3. Chemical defenses

Many mustelids prey on wasps habitually (Quick, 1951; Simmons, 1973; Kingdon, 1977; Strassmann, 1981; Hirakawa and Sayama, 2005), but they are not considered true specialist predators. Their predatory habits are difficult to observe, as they forage at night when social insects are reluctant to fly and sting, and are less able to mount a coordinated nest defense. Earlier reports of honey badgers (*Mellivora* *capensis*) secreting musk gland chemicals that narcotize or disable honeybees (Kingdon, 1977) could not be confirmed in more recent studies (Begg, 2002; Begg *et al.*, 2003). Similarly, the hypothesis that Red-throated Caracaras employ wasp repellents (Thiollay, 1991) has not been supported by chemical analyses of feathers and behavioral studies of their predation tactics (McCann *et al.*, 2013).

1.8.4. Innate and acquired immunity to venoms

Some specialist and routine predators of venomous snakes have innate immunity to many of the toxins their prey deliver in their bite (Jansa and Voss, 2011, Voss and Jansa, 2012), illustrating one means by which these specialist predators deal with well-defended prey. Similar immunity mechanisms may exist in specialist predators of wasps and bees, but these mechanisms have yet to be studied. Some predators such as honey badgers with innate immunity to snake venom are also habitual predators of honeybees (Begg, 2002), and may have some immunity to honeybee venom.

Immunity to bee and wasp venoms has likely a strong phylogenetic component, suggesting that the evolution of predatory interactions among didelphid marsupials and venomous snakes commenced in a common ancestor of many of the extant species. Strong predator-prey interactions may also have provided section pressure for the acquisition of defensive biochemistry by specialist avian predators of social bees and wasps, including the Bee Eaters (Meropidae), Honey Guides (Indicatoridae), and kites of the subfamily Perninae Within the Perninae, many species are reportedly bee and wasp predators, including species in the genera *Pernis* (Harrison 1931; Hagen and Bakke 1958; Itamies and Mikkola 1972; Huang *et al.*, 2004), *Henicopernis* (Gilliard, 1967), *Lophoictinia* (Hobson, 2006) and *Leptodon* (Windsor, 1976). Because all these genera belong to a monophyletic group (Lerner and Mindell, 2005), they likely share a common ancestor that preyed on stinging social insects. Whether and to what degree any of these birds have immunity to bee and wasp venoms is yet to be studied.

1.8.5. Attrition or slaughter

When vertebrates continually harass a nest of social wasps or bees, and kill workers in the process, they deplete a nest’s defense line until no defenders are left to put up a fight. The Summer Tanager (*Piranga rubra*) apparently employs this strategy of attrition when it attacks nests of large wasps (Alvarez del Toro, 1950). Ratels employ a similar strategy when they dig out honeybee nests (Begg, personal communication), repeatedly attacking the same nest over several days, with each attack meeting weaker resistance by the bees. This strategy resembles the “slaughter” phase of hornet attacks on nests of social bees and wasps, where the initial attack stage is a massacre of defending worker bees or wasps (Burgett and Akratanakul, 1982).

1.8.6. High-speed strikes on nests

Aerial nests of swarm-founders are subject to attacks by predatory birds. Birds strike these nests and inflict mechanical damage, knock entire nests or portions thereof to the ground (Koeniger *et al.*, 2010), or in mid-flight pluck nests from their substrate (Thiollay, 1991). In Red-throated Caracara predation events on wasp nests that we video recorded, the birds repeatedly struck large nests and thus induced absconding (McCann *et al,.* 2013), after which they consumed the defenseless wasp larvae and pupae (Fig. 1.5). Interestingly, high-speed strikes by Honey Buzzards on nests of Giant Honeybees induce an intriguing defense response. The bees conceal the hanging nest comb with a curtain of workers (Fuchs and Tautz, 2011), thus making it difficult for the attacking birds to judge the position of the comb and to strike it.

White Faced Capuchin monkeys (*Cebus capucinus*) employ a similar though likely less successful version of these aerial attacks (Fragaszy *et al.*, 2004) when they detach wasp nests from substrate and then race away with them through the forest canopy in the attempt to escape the defending wasps. Common squirrel monkeys (*Saimiri sciureus*), in contrast, knock wasp nests to the ground (Boinski and Timm, 1985) before they feed on the wasp larvae.

Birds also engage in high-speed attack tactics when they dislodge or pluck off nests of independent-founders (Alvarez del Toro, 1950; Strassmann, 1981). These tactics apparently reduce the risk of getting stung while securing the brood for consumption in a safe location.

1.9. Conclusion

Long-term studies are sorely needed to understand the impact of predation on the demographics of flying social Hymenoptera. Tropical species in particular suffer from a lack of studies and an abundance of supposition. Species in tropical rainforests are the least studied of all, lacking even basic information about colony abundance. Conclusions about the type of predation regimes endured by social wasps and bees in tropical rainforests are thus premature. Vertebrate predation may contribute significantly to colony mortality, especially when avian predators such as Red-throated Caracaras and Honey Buzzards are members of the tropical forest community.

Given that strategies exist to cope with the defenses of social wasps, one wonders why there are not more vertebrate predators including birds, mammals and perhaps even reptiles, that habitually or occasionally prey on social wasps and bees. A simple explanation might be that predation is a difficult phenomenon to witness and that it requires extensive resources to study.

That there are only few specialist predatory birds of social bees and wasps may reflect the potent defenses offered by these fast-flying, fast-stinging, and large-colony-size insects. Alternatively, it may indicate that population densities of social bees and wasps are often low, or strongly fluctuate, and thus cannot support specialist predators. In any case, the specialist and habitual predators of social insects offer the valuable lesson that no insect species is immune from predation.

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Tables and Figures

Table 1.1. Vertebrate predators of stinging social wasps and bees. "Class" denotes whether an animal is an occasional (O), habitual (H), or specialist predator (S). Habitual predators had numerous reports of predation on social wasps and bees. Specialist predators derive ≥30% of their diet from the brood of social wasps and bees, at least in some seasons.

Vertebrate species	Family	Class	Wasp or bee species	References cited
Gray-headed Kite, *Leptodon cayanensis*	Accipitridae	H	*Polybia occidentalis*	(Windsor, 1976; Ferrari, 1990)
Oriental Honey-buzzard, *Pernis ptilorhynchus*	Accipitridae	S	*Polistes* spp. *Parapolybia* spp.	(Huang *et al.*, 2004)
European Honey Buzzard, *Pernis apivorus*	Accipitridae	S	*Vespula vulgaris*, *Vespula* sp. , *Bombus* sp.	(Harrison, 1931; Hagen and Bakke, 1958)
American Kestrel, *Falco sparverius*	Falconidae	O	*Polybia occidentalis*	(Raw, 1997)
Red-throated Caracara, *Ibycter americanus*	Falconidae	S	*Synoeca septentrionalis*, *S. surinama, Polybia emaciata, P, bistriata, P. jurinei, P. scrobalis, P. belemensis, P. affinis*	(Skutch, 1959; Voous, 1969; McCann *et al.*, 2013)
Blue Crowned Motmot, *Momotus momota*	Momotidae	O	Unidentified Vespidae	(Sandoval *et al.*, 2008)
White woodpecker, *Leuconerpes candidus*	Picidae	O	*Polybia scutellaris*	(Bertoni, 1912)
Lineated Woodpecker, *Dryocopus lineatus*	Picidae	O	*Metapolybia cingulata*	(Raw, 1997)
Blue Jay, *Cyanocitta cristata*	Corvidae	O	*Polistes exclamans*	(Pulich, 1969)
Summer Tanager, *Piranga rubra*	Thraupidae	H	*Polistes*, *Polybia, Metapolybia*	(Hamaher, 1936; Alvarez del Toro, 1950; Windsor, 1976)
Common treeshrew, *Tupaia glis*	Tupaiidae	O	*Apis* spp.	(Seeley *et al.*, 1982)

Vertebrate species	Family	Class	Wasp or bee species	References cited
Yellow-throated Marten, *Martes flavigula*	Mustelidae	O	*Apis* spp.	(Wegner, 1949)
Japanese Marten, *Martes melampus*	Mustelidae	O	*Vespula* spp.	(Hirakawa and Sayama, 2005)
Long-tailed weasel, *Mustela frenata*	Mustelidae	O	*Dolichovespula maculata*	(Quick, 1951)
European badger, *Meles meles*	Mustelidae	O	*Vespula* spp.	(Simmons, 1973)
Honey badger, *Mellivora capensis*	Mustelidae	H	*Apis mellifera*	(Kingdon, 1977; Begg, 2002; Begg *et al.*, 2003)
Striped Skunk, *Mephitis mephitis*	Mephitidae	H	*Polistes exclamans, Bombus fervidus, Apis mellifera*	(Plath, 1923; Strassmann, 1981)
Raccoon, *Procyon lotor*	Procyonidae	O	*Vespula maculifrons*	(MacDonald and Matthews, 1981)
Black bear, *Ursus americanus*	Ursidae	H	*Dolichovespula arenaria*, *Vespula maculifrons*	(Bigelow, 1922; MacDonald and Matthews, 1981; Reed and Akre, 1983)
Sun bear, *Ursus malayanus*	Ursidae	H	*Apis* spp.	(Seeley *et al.*, 1982; Koeniger *et al.*, 2010)
Sloth bear, *Ursus ursinus*	Ursidae	H	*Apis* spp.	(Joshi *et al.*, 1997)
Brown bear, *Ursus arctos*	Ursidae	O	*Vespula* spp., *Bombus* spp.	(Mattson, 2002)
White-faced Capuchin, *Cebus capucinus*	Cebidae	O	*Polybia* spp.	(Joyce, 1990; Fragaszy *et al.*, 2004)
Central American Squirrel Monkey, *Saimiri oerstadi*	Cebidae	O	*Polybia* spp.	(Boinski and Timm, 1985)
Rhesus macaque, *Macaca mulata*	Cercopithecidae	O	*Apis* spp.	(Seeley *et al.*, 1982)

Chapter 2.

Nesting and Nest-Provisioning of the Red-throated Caracara (*Ibycter americanus*) in Central French Guiana

Sean McCann, Onour Moeri, Tanya Jones, Sean O'Donnell and Gerhard Gries

KEY WORDS: *Red-throated Caracara; Ibycter americanus; nesting; nest provisioning; diet; cooperative breeding*; *French Guiana*

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2.1. Introduction

The Red-throated Caracara (*Ibycter americanus*) is found in lowland tropical rainforests from Central America to southern Brazil. Recent morphologic and molecular analyses placed it in its own monotypic genus, a sister group to the genus Caracara (Griffiths 1999). Although *I. americanus* is reported to be a specialist predator of paper wasp colonies, it also consumes bees, termites, fruits, millipedes, other arthropods (Skutch 1959, Thiollay 1991), lizards (Lowery and Dalquest 1951), and items such as ants stored in the nest of wasps (Voous 1969).The breeding biology of *I. americanus* is not well known. Some form of cooperative brood care with more than two birds engaging in nest-guarding and provisioning has been reported (Thiollay 1991, Whittaker 1996), but neither the nest itself nor the young have been described. Here, we present data obtained from video recordings at two nest sites in Central French Guiana that provide the first glimpse of nesting and provisioning behavior of *I. americanus*.

2.2. Methods

From 25 January to 16 March 2008 and 27 January to 19 April 2009 we observed *I. americanus* at the Nouragues research station in French Guiana (4°05' N - 52°41'W) where Thiollay (1991) also conducted his studies. The topography around the research station is dominated by a 400-m granitic inselberg, the top of which is bare rock, grading into rock savannah, low forest, and dense tropical lowland rainforest. *Ibycter americanus* forages primarily in the lowland forests (Thiollay 1991).

We located one nest in each of 2008 and 2009 by following *I. americanus* in daylight and by observing and listening for caracara vocalizations. At dawn, members of the group called loudly and flew together from their night roosts to the nest tree. There, they called again several times before departing. During this ‘‘morning chorus,’’ the brooding bird was replaced by another group member.

The 2008 nest was in a large *Aechmea* bromeliad on a branch of a mature *Chrysophyllum lucentifolium* (Sapotaceae) tree 45 m aboveground (Fig. 2.1), as determined by a laser rangefinder/inclinometer (LaserAce 300H, Measurement Devices, Aberdeen, Scotland). The 2009 nest was in another large *Aechmea* bromeliad 40 m above ground in a tall tree (Fig. 2.1) of unknown taxonomic identity (due to its lack of flowers or fruit during the observation period). This site was 300 m to the southeast of the 2008 nest site, and was likely used by the same group of birds.

Figure 2.1. Trees in the Nouragues Reserve (French Guiana) bearing a large *Aechmea* bromeliad 40–45 m aboveground (indicated by arrow) that served as a nesting platform for a group of Red-throated Caracaras (*Ibycter americanus*) in 2008 and 2009.

To record the behavior of *I. americanus* at these nests, we installed video recording equipment. In 2008, we fitted the nest with a video camera attached to a digital video recorder (Honeywell Systems HDR4X4, Honeywell Security, Louisville, Kentucky, U.S.A.). We installed the camera on a branch ca. 1.2 m above the nest, pointing down; camera installation including climbing up and down the tree took 2 hr. We recorded a total of 99.9 hr of behavior during the daylight hours (06:00–18:30 H) of 6–16 March, with 2 d of down time due to technical difficulties. The video recorder was set to record, with motion activation, 10 frames per second at a 640 X 480 resolution with no audio input. A mostly-feathered nestling was present during camera installation in 2008.

In 2009, we fitted the nest with two video cameras and a Swann DVR41150H digital video recorder (Swann Communications, Santa Fe Springs, California, U.S.A.). We installed one camera on a branch 70 cm above the floor of the nest pointing down, and the other on a branch lateral to, and 1 m away from, the nest. Camera installations took a total of 7 hr, which we limited to 2 hr/d to minimize disturbance to the birds. We recorded 448 hr of behavior during the daylight hours (06:00–18:30 H) of 5 March to18 April, with 5 d of down time. A single egg was present during camera installations in 2009.

To retrieve the DVR and to change batteries, we visited both the 2008 and 2009 nest before dawn and after sunset, thus minimizing disturbance to the birds. When we had remained at the nest site until after dawn, we egressed as quietly as possible. We terminated video recordings in both years when field assistants had reached their maximum allowed stay of 3 mos.

To facilitate recognition of individual birds and to study their behavior and role as group members, we captured some birds in 2009 and affixed a colored Darvic band (Avinet Inc., Dryden, New York, U.S.A.) to one tarsus. Birds were lured by a hand-crafted and -painted conspecific decoy made of closed-cell polystyrene foam and placed next to the net, and by playback of recorded calls emitted from a Roland Microcube portable guitar amplifier (Roland Corporation, Los Angeles, California, U.S.A.). We captured one bird twice in 2008 and four different birds in 2009; we weighed three of the birds captured in 2009 (females: 600 g and 678 g, respectively; male: 550 g), and took blood samples from all birds captured in 2009 as well as feather samples from the 2009 nestling, for PCR-based sex identification (Griffiths et al. 1998).

Four birds had colored bands on their tarsi, allowing us to compare their behavior and that of at least two unmarked birds. Viewing our 2008 and 2009 video data using the video editing software VirtualDub (Lee 2007), we were able to determine when the single egg hatched in 2009. We also attempted to identify all food items brought to the nest and classified them into prey types for analyses of the nestling’s diet. For each of 2008 and 2009, we determined the proportion of each food type in the diet, calculated provisioning and visitation rates, and compared these rates between the two years. For statistical analyses of these data we employed a Wilcoxon rank-sum test using normal approximation and the software program S-Plus 8© (Insightful Corporation).

2.3. Results

Based on our observations from the ground and during camera installations in nest trees, we concluded that there was no nest structure and no nesting material other than bromeliad leaves that adult birds shred lengthwise. This shredding behavior apparently clears an area in the center of the bromeliad in which the egg or nestling resides. The bromeliad serves as a shelter for a single egg and nestling.

The egg, observed in 2009, was ovoid, circa 6 cm in length, and light tan speckled with purple-brown. It hatched on 28 March, as determined from video recordings.

We noted that early in development, the young nestling in 2009 was covered dorsally in fuzzy gray down (Fig. 2.2), with white down on thighs and the cloacal area, similar to the pattern on adults. Down beneath the mandible was patchy and white. The face and throat were bare, as in adults. The eyes were chestnut brown in color and the skin of the face and throat was yellow, as were the cere and the legs. In 2009, when the nestling was about 22 d old, the skin of the face and throat was becoming gray. The bill was black in contrast to the yellow bill of adult birds. On 1 April 2009, five days post-hatching, the nestling had a large parasitic fly larva inside the right orbit, with the spiracular plate slightly protruding through the lower eyelid (Fig. 2.2 A). Neither this maggot nor evidence of it was found on 18 April, although there was another protruding just behind the head. Feathers of the 22-d-old nestling included primaries, secondaries, primary coverts, greater coverts, and alula in the pin stage, with some barbs breaking free (Fig. 2.2B).

Figure 2.2. Nestling Red-throated Caracaras (*Ibycter americanus*) residing in *Aechmea* bromeliads. (A) Nestling 5 d post-hatching on 1 April 2009; (B) The same nestling as in A on 18 April 2009; (C) Unknown-age nestling on 21 February 2008 provisioned with a large millipede and remains of a wasp nest; (D) The same nestling as in C on 5 March 2008.

For the 2008 nestling on 21 February (Fig. 2.2 C), contour feathers such as the scapulars were well-developed. On 5 March 2008, nearly all juvenal feathers were developed (Fig. 2.2 D). From our video recordings and photographs, it was difficult to precisely deduce the length of the nestling period. The 18 April 2009 nestling in Fig. 2.2 B was 22 d old and less developed than the 2008 nestling (shown on21 February, Fig. 2C), which fledged 35 d later as determined by P. Chatelet (CNRS Guyane). Thus, it may take at least 57 (22 + 35) d from hatching to fledging. The 2009 chick fledged at an undetermined date. We observed and recognized it in 2010 based on the color band on its tarsus.

During the egg phase, adult birds made 0.56 (±0.18 SD) visits/hr to the nest (n = 22 d), during daytime hours in 2009. Daytime incubation bouts lasted on average 1.46 (±1.20 SD) hr.

During the nestling phase, adult birds visited the nest 2.20 (±0.45 SD) times/hr (n = 10 d) in 2008 and 1.76 (±0.52 SD) times/hr (n = 18 d) in 2009. Visitation rates were significantly greater in 2008 than in 2009 (rank-sum normal statistic: 2.78, $P < 0.05$).

Adult birds brought food to the nest on average 1.77 (±0.37 SD) times/hr in 2008, and 0.91 (±0.30 SD) times/hr in 2009. Food provisioning was significantly more frequent in 2008 than in 2009 (rank-sum statistic: 4.08, $P < 0.05$). Based on colored leg bands and sex-determination tests, at least six adult-plumage birds (two confirmed females, two males, two unknown sex) attended and provisioned the nestling in 2009. One adult female performed all of the overnight egg incubation and overnight brooding of the female nestling. As recorded on videos in 2008 and 2009, adult birds brought 186 and 192 items, respectively, to the nestling. Most of them (58.6% in 2008; 78.6% in 2009) were wasp nests or fragments thereof (Fig. 2.3). They were delivered to the nest significantly more often than all other food types combined in both 2008 (rank-sum statistic: 2.34, $P < 0.05$) and 2009 (rank-sum statistic: 4.30, $P < 0.05$). Wasp nests often were brought attached to substrate such as leaves or twigs. Large spirostreptid millipedes (Fig. 2.2 C) were the second most commonly delivered food item, accounting for 21% of food items in 2008 and 12.5% in 2009. Of millipede carcasses, only the anterior segments 1–4 were fed to the nestling. Small fruits from several plant species were also brought to the nest but these could not be conclusively identified from the video footage. The remaining 8.6% of food brought to the nests in 2008 and 5.7% in 2009 could not be identified but all were smaller than the other items.

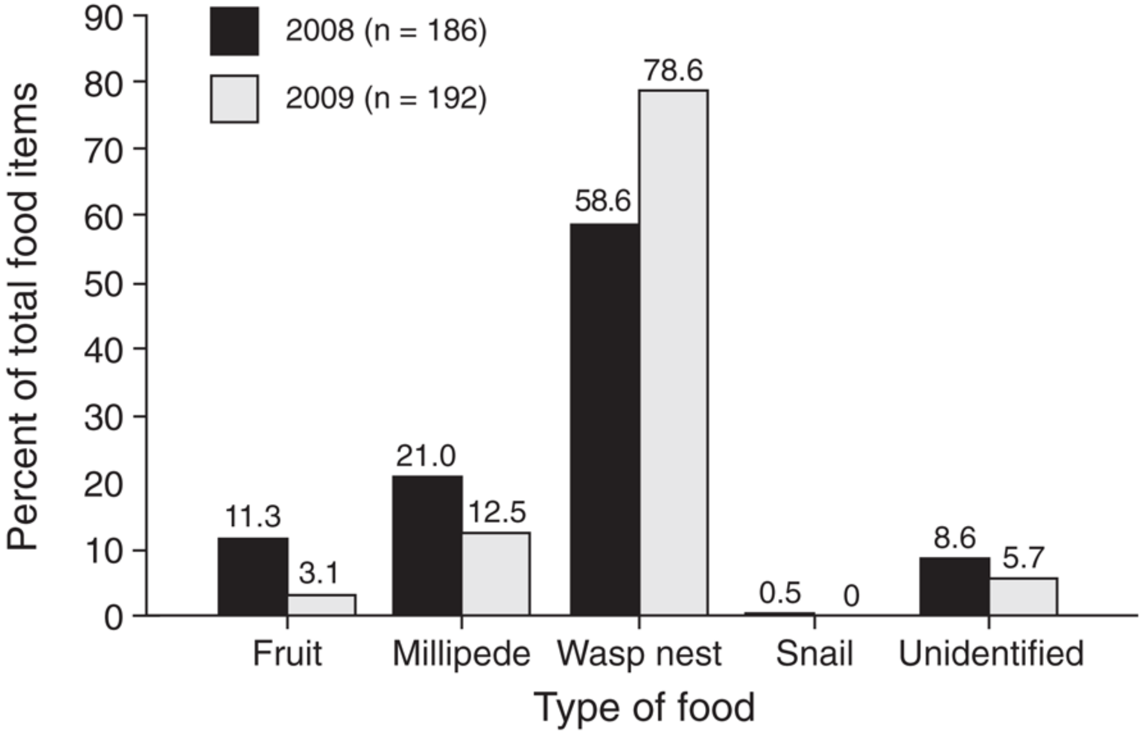

Figure 2.3. Food items provided to a single nestling of *I.americanus* in each of two years. Data were compiled based on 112.4 hr and 448 hr of video recordings of provisioning behavior during the daylight hours (06:00–18:30 H) of 6–16 March 2008 and 5 March to 18 April 2009, respectively. Numbers above bars indicate the percent of a respective food type.

2.4. Discussion

We provide the first detailed observations of the nest of I. americanus. Both Thiollay (1991) and Whittaker (1996) report nest trees as large trees with many epiphytes but do not report details of the nest structure or nesting behavior. Our data indicate that I. americanus may not construct a nest but instead utilize natural platforms such as bromeliads as nesting sites. Our video recordings and observational data substantiate earlier reports that I. americanus may be a cooperative breeder. Using video recordings of nestling provisioning, we found that food items brought to the nestling included wasp nests, fruits, and millipedes, as previously reported by Thiollay (1991) but did not include positively identified bees, termites, ants (Skutch 1959, Thiollay 1991) or vertebrates (Lowery and Dalquest 1951) as dietary constituents. Broodcontaining wasp nests were the most prevalent of all food items that were provided to the nestling. On each day, many wasp nests were brought to the nest, implicating wasp larvae as an important dietary component for the nestling's development. The ecological niche of *I. americanus* as a regular predator of wasp nests seems unique in the American tropics. Wasp nests with mature brood as a ready source of concentrated protein are usually well defended by adult wasps (Smith et al. 2001), suggesting that I. americanus can overcome the wasps' defense while preying on their nests. Although we present new information on the nesting and nest-provisioning biology of this intriguing raptor species, many aspects are yet to be studied. These include, but are not limited to, (1) the relatedness and role of group members in the group studied here and those in neighboring groups; (2) comparison of the social structure of I. americanus with that of other cooperative-breeding raptors; and (3) the strategy that enables I. americanus to prey on well-defended nests of social wasps.

ANIDACIÓN Y APROVISIONAMIENTO DE NIDOS DE *IBYCTER AMERICANUS* ENGUYANA FRANCESA CENTRAL

RESUMEN.—Utilizamos cámaras de video para estudiar un nido en cada una de dos estaciones reproductivas de un grupo de *Ibycter americanus* en Guyana Francesa. Encontramos que *I. americanus* no construyó un nido, sino que utilizó plataformas naturales, como bromelias, para anidar. Las aves adultas trajeron alimento al nido en promedio1.77 (±0.37 DE) veces/hr en 2008 y 0.91 (±0.30 DE) en 2009. La mayoría de los ítems alimenticios (58.6% en 2008; 78.6% en 2009) fueron nidos de avispas o fragmentos de éstos. Con base en anillas coloridas y determinación del sexo, por lo menos seis individuos con plumaje de adulto (dos hembras, dos machos, dos de sexo desconocido) atendieron y aprovisionaron a los polluelos en 2009. [Traducción del equipo editorial]

2.5. Acknowlegements

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Chapter 3.

Falconid raptor rivals predatory impact of army ants on social wasps

Sean McCann, Tanya Jones, Onour Moeri, Catherine Scott, Sean O'Donnell, and Gerhard Gries

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3.1. Abstract

Paper wasps are diverse in Neotropical rainforests but the factors that affect their abundance are poorly understood. Army ants (Ecitoninae) are generally thought to have the greatest predatory impact on populations of social wasps, but there is emerging evidence that predatory birds could also be a significant mortality factor. Our objectives were to (1) identify the genera of wasps preyed upon by *Ibycter americanus,* a specialist falconid predator of Neotropical social wasps, (2) quantify wasp nest predation by *I. americanus*, and (3) compare wasp nest predation rates by *I. americanus* with calculated rates of wasp nest predation by army ants. In 2008 and 2009, we video recorded chick provisioning at *I. americanus* nests in French Guiana and found that adult birds brought nests of 10 genera of mainly swarm founder wasps. In 2012, we noted that three of four sympatric *Eciton* species raided into trees and thus potentially preyed upon the brood of paper wasps at the same site. We quantified the population density of one *Eciton* species, calculated its rate of wasp nest predation, and compared this predation rate to that of *I. americanus.* We conclude that *I. americanus* rivals the predatory impact of army ants on some populations of Neotropical social wasps. *Ibycter americanus* and other diurnal vertebrate predators may exert strong selection on wasp defensive behavior, resulting in defensive adaptations that include selection of specific nest sites as well as physical fortification and visual crypsis of nests.

Keywords Red-throated Caracara · *Ibycter americanus* · prey spectrum · army ant · *Eciton* · French Guiana

3.2. Introduction

Social paper wasps (Hymenoptera: Vespidae: Polistinae) are conspicuous members of Neotropical insect communities (Jeanne, 1991). Their nests can contain large amounts of brood and thus are subject to considerable predation pressure (London and Jeanne, 2003). Paper wasps mount stinging and venom-spraying defenses against vertebrate predators when their nests are threatened (Jeanne and Keeping, 1995; Jeanne, 1996; Jeanne, 1981; Judd, 1998; Nascimento et al., 2005; O'Donnell et al., 1997).

The ecological impact of vertebrate and invertebrate predators on wasp abundance can be inferred from estimates of their predation rates. Ants are ubiquitous in tropical habitats (Jeanne, 1979), and have been implicated as primary predators of social wasps in rainforests (Jeanne, 1975). Surface-raiding species of *Eciton* army ants are well documented as predators of Neotropical social wasps (Bouwma et al., 2003; Jeanne, 1975; O'Donnell and Jeanne, 1990) and likely have induced the evolution of specific adaptations in wasps, such as nest evacuation (Chadab, 1979a, b), recruitment-trail diversion (West-Eberhard, 1989), and the deposition of ant-repellent substances to nest petioles (Jeanne, 1996). Vertebrate predators, in turn, are likely to have induced the evolution of other anti-predator adaptations that are characteristic of many social wasps including massed stinging attacks (London and Jeanne, 2003), cavity nesting (Jeanne, 1991), physical fortification (Hozumi and Inagaki, 2010) and visual crypsis of nests (Richards, 1978; Williams, 1925).

Vertebrates as predators of social wasp nests have received little attention. Nest attacks by the Gray-headed Kite, *Leptodon cayanensis*, a generalist raptor (Ferrari, 1990), frequently induce nest abandonment by the wasp *Polybia occidentalis* in Costa Rican tropical dry forest (Windsor, 1976). The Summer Tanager, *Piranga rubra* (Alvarez del Toro, 1950; Hamaher, 1936), and the White-faced Capuchin monkey, *Cebus capucinus,* are also opportunistic predators of wasps (Fragaszy et al., 2004). In contrast to these occasional predators, the Red-throated Caracara, *Ibycter americanus* (Boddaert), is a specialist predator of paper wasps (McCann et al., 2010). It can drive wasp species as formidable as *Synoeca septentrionalis* (Skutch, 1959; Voous, 1969), or *Polybia jurinei* (McCann et al., 2013), off their nests before raiding them. These observations suggest that the brood of paper wasp colonies is an important dietary constituent of *I. americanus*, and that the birds may exert substantial predation pressure on sympatric paper wasps.

Our objectives were to (1) describe the genera of wasps preyed upon by *I. americanus* in a Neotropical rainforest, (2) estimate predation rates on social wasps, and (3) compare these predation rates with estimates of predation rates by army ants.

3.3. Materials and methods

3.3.1. Video recordings of food items brought to *I. americanus* chicks

In 2008 and 2009, we fitted single *I. americanus* nests near the Nouragues research station in French Guiana (4°05' N - 52°41'W) with video recording equipment. Each nest contained a single chick. The 2008-chick had already hatched by the time we commenced filming for 12 consecutive days. We filmed the 2009-chick from hatching until it was 22 days old (McCann et al., 2010).

In 2008, the video equipment consisted of a Honeywell HRD4X4 digital video recorder (Honeywell Security, Louisville, Kentucky, U.S.A), recording video at 10 frames per second and a resolution of 640 × 480 pixels. Video input was from a waterproof color video camera. In 2009, we fitted the nest with a Swann DVR4-1150 4 Channel DVR (Santa Fe Springs, California, U.S.A.), recording video from two Lorex SG6183W cameras (Baltimore, Maryland, U.S.A.) at 15 frames per second and a resolution of 640 × 520 pixels. In both years, we programmed the DVRs to record when triggered by motion detection during daylight hours. We powered the DVRs by a rotating set of two 74 Ah deep-cycle automotive batteries that we installed daily before dawn and removed after dusk for re-charging. The video systems recorded chick provisioning for 112 h in 2008 (from 5-16 March) and for 211 h in 2009 (28 March to 18 April).

3.3.2. Identification and counting of wasp nests

We viewed the video recordings at reduced speeds, ranging from 0.5× speed to frame-by-frame analysis using VirtualDub software (www.virtualdub.org). We identified nests of wasps, or fragments thereof, to genus using an illustrated key to paper wasp nest architecture (Wenzel, 1998) as a guideline, and drawing on extensive field experience with Neotropical paper wasps (S. O'D.). Neotropical paper wasps build distinctive nests that can often be readily ascribed to genus based on combinations of comb structure and arrangement, envelope paper color and texture, and nesting substrate (Fig. 3.1). We pooled all other items brought to the chick, such as millipedes and fruits (McCann et al., 2010), in a non-wasp category, which we do not consider further here. If we could not identify nests to the genus level, we recorded whether they belonged to the group of swarm-founding or independent-founding species by noting the color of the pupal cell caps. We assigned brood combs with bright white pupal caps to the group of swarm-founders (wherein reproductive females and workers found new colonies), and those with darker pupal caps to the group of independent-founders (wherein single inseminated females initiate new colonies). If an assignment was not possible, we recorded the nest as "undetermined".

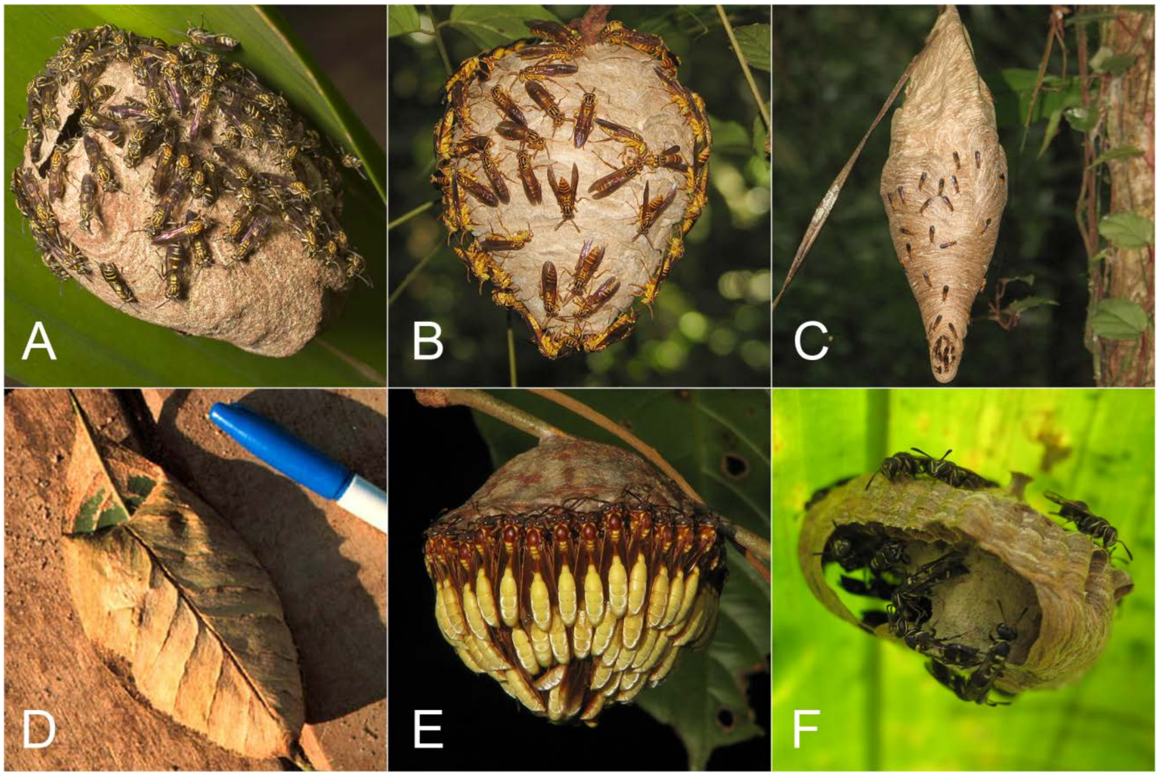

Figure 3.1. Photographs of nest types preyed upon by *Ibycter americanus* representing the following wasp genera: (A) *Polybia*, (B) *Pseudopolybia*, (C) *Angiopolybia*, (D) *Leipomeles*, (E) *Apoica,* and (F) *Protopolybia.*

We estimated the number of discrete nests preyed upon by *I. americanus*. Taking into account that adult birds sometimes cooperatively dismantle and transport multiple fragments of a wasp nest, we counted as one wasp nest those pieces of wasp nest that were of the same genus, had similar characteristics (e.g., paper color or brood cell size), and were brought to the nest within 30 min of each other (henceforth termed “unique nest delivery”). We assumed that similar nest fragments brought on different days, or separated in time by > 30 min, originated from different wasp colonies. We compared proportions of genera of wasps brought to *I. americanus* chicks with the proportional generic abundance in sampling surveys from across tropical America (Jeanne, 1991) using the latter as a hypothetical distribution for a G-test for goodness of fit (Zar, 1996). For this analysis, we excluded cavity-nesting genera, and pooled the two stelocyttarous (with layers of comb connected by narrow central pedicels) nest-building genera *Angiopolybia* and *Pseudopolybia* to match our dataset.

3.3.3. Estimates of predation rates

To estimate the predation rate of *I. americanus* on social wasps, we multiplied two population density estimates of *I. americanus* [0.015 individuals/ha (Thiollay, 1989), 0.004 individuals/ha (Haugaasen and Peres, 2008)] by the mean number of unique nest deliveries brought to the 2008- and 2009-chicks to infer a minimum and maximum daily per-hectare predation rate on social wasps. The estimates conservatively assume that adult birds consume brood from at least as many wasp nests as do chicks and that unique nest deliveries represent whole nests destroyed. We then multiplied the per-hectare predation rate by 400 to estimate the daily number of nests destroyed in a 400-ha *I. americanus* territory (Thiollay, 1991).

The army ants *Eciton burchellii* and *E. hamatum* are known to raid above ground level into vegetation, and hence to prey on paper wasp nests (Chadab, 1979b; O'Donnell and Jeanne, 1990). We found both species at the Nouragues station in November and December of 2012. To estimate army ant densities, we followed recent recommendations and modifications (Vidal-Riggs and Chaves-Campos, 2008) to the trail walk method (Franks, 1982). We carried out a total of 15 walks along three trails that were respectively 3.5, 4.0 and 6.7 km long. We began our walks in the afternoon such that the time at the midpoint of walks was 1500. The total distance we walked was 72 km. We took specimens of workers for species identification from each *Eciton* raid we encountered and noted the position and time on a handheld GPS unit. We also spent 5 minutes examining each raid noting whether or not the ants were raiding up trees.

We calculated population densities of *E. burchellii* using Franks' (1982) method. This method uses repeated trail walks (censuses), counting intersections with *Eciton* raids, and then calculates a density based on the number of encounters according to the following equation:

$$S = \frac{\pi N A}{2L}$$

where S is the total length of raids in the area (A) under investigation, and L is the length of each census path. The total length is thus computed, and the number of colonies is estimated by dividing the total length of raids by the average raid length at the midpoint of the census, and adjusted to account for the proportion of colonies in the area not engaged in raids (i.e., we divide by 0.757, to account for colonies in the statuary phase which are not raiding). We used 77 m as the mean raid length for the calculation as the time at midpoint of walks was 1500 (raids lengthen at 14 m/h, maximal raid length = 105 m at 1700). Because the trail walking method has not been evaluated for species other than *E. burchellii,* we restricted our calculations to *E. burchellii.* We do, however, present encounter rates for three other species of *Eciton*. We calculated weighted mean encounter rates for each species with 95% confidence intervals computed using the percentile method from 10000 bootstrap replications in R (Canty and Ripley, 2014; Davison and Hinkley, 1997).

To estimate rates of wasp nest predation, we obtained the typical minimum (1) and maximum (3) number of wasp nests taken per day by *E. hamatum* raids from data reported by Chadab (1979a). As no data are available on wasp nest predation by *E. burchellii*, we assumed that *E. hamatum* and *E. burchellii* take wasp nests at an equal rate. We justify this assumption considering that *E. burchellii* has larger colonies, but unlike *E. hamatum,* is not a specialist predator of social ants, bees or wasps (Kaspari et al., 2011). We multiplied this rate by our estimated population density of *E. burchellii* to obtain a minimum estimate of *E. burchellii* predation rates on wasp nests in a 400-ha *I. americanus* territory. To obtain a maximum estimate of *E. burchellii* predation rates, we calculated rates using the maximum population density reported for *E. burchellii* (Swartz, 1997).

3.4. Results

3.4.1. Video recordings of food items brought to the chick

In 2008, *I. americanus* adults brought 185 recognizable food items to their chick, 111 (60%) of which were wasp nests or nest fragments with 103 of these representing unique nest deliveries. In 2009, 146 (76%) of 191 food items were wasp nests or fragments, with 135 of these being unique nest deliveries. In 2008 and 2009, the chick received on average 12.4 and 7.8 unique nest deliveries per day, respectively (Table 3.1).

Table 3.1. Genera of paper wasp nests brought to a single chick by a group of adult Red-throated Caracaras, *Ibycter americanus,* in each of two observation periods (5 March to16 March 2008; 28 March to 18 April 2009) at the Nouragues Research Station in Central French Guiana. All are swarm founders except *Polistes* and *Mischocyttarus*.

Wasp genus	2008	2009	Both years	% of total
Polybia	46	35	81	34.0
Pseudopolybia	9	21	30	12.6
Angiopolybia	2	12	14	5.9
Leipomeles	11	2	13	5.5
Apoica	3	3	6	2.5
Protopolybia	4	1	5	2.1
Angopolybia or *Pseudopolybia*[a]	0	3	3	1.3
Mischocyttarus[b]	2	1	3	1.3
Polistes[b]	2	1	3	1.3
Parachartergus	1	1	2	1.3
Brachygastra	0	1	1	0.8
Unknown swarm founder	17	34	51	32.4
Unknown independent founder	2	1	3	1.3
Undetermined	4	19	23	9.6
All genera	103	135	238	100
Total swarm founders	93	114	207	87
Total independent founders	6	3	9	3.8
Mean (SD) per day[c]	12.39 (2.68)	7.8 (2.30)	9. 28 (3.12)	
Mean (SD) per hour	1.03 (0.22)	0.65 (0.19)	0.77 (0.26)	

[a] Nests were stripped of their envelope and by visual examination could thus not be assigned to one of two possible genera.

[b] Independent-founding genera

[c] Determined from the mean hourly rate calculated by day and multiplied for 12 foraging hours per day.

3.4.2. Identity and processing of wasp nests

In 2008 and 2009, most wasp nests brought to the chick belonged to swarm-founding genera (Table 3.1). In 2009, more nests than in 2008 could not be assigned as either swarm- or independent-founding genera due lower video quality.

Nests of 10 genera of wasps, including *Polybia, Pseudopolybia, Angiopolybia, Leipomeles, Apoica, Protopolybia, Mischocyttarus, Polistes, Brachygastra* and *Parachartergus* were preyed upon by *I. americanus* (Table 3.1). Nests of most wasp genera were brought whole and still attached to substrate. Exceptions were stelocyttarus-type nests such as those of *Angiopolybia* spp. and *Pseudopolybia* spp., which were most often stripped of their envelope. Larger *Polybia* spp. nests were frequently brought as individual combs.

In 2008 and 2009, 90% and 83%, respectively, of nests delivered to the chick could be assigned to genus. The genera of wasps brought to the chicks did not reflect the proportional abundances in sampling surveys (Jeanne, 1991) (G = 331.4, df = 18, $p < 0.001$, Fig. 3.2). *Ibycter americanus* provisioned with proportionally fewer nests of *Mischocyttarus* and *Polistes,* and far more nests of *Angiopolybia*/*Pseudopoplybia*, *Leipomeles* and *Apoica* than expected based on surveys and collections by human observers.

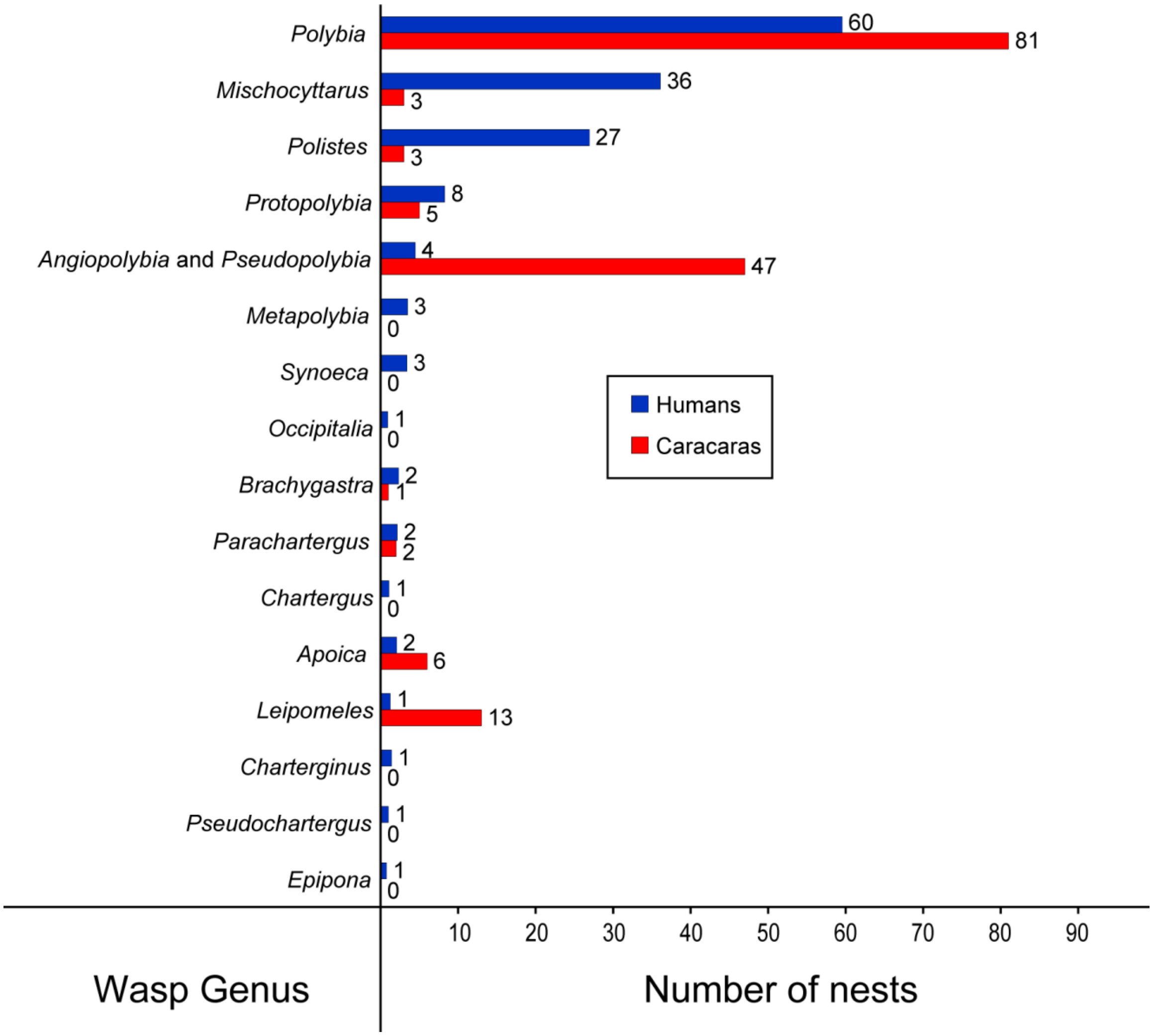

Figure 3.2. Total numbers of wasp nests of various genera taken by caracaras in 2008 and 2009 (red bars) and expected from human surveys (blue bars) Expected values were calculated from summaries in Jeanne (1991), excluding genera absent in French Guiana, and cavity-nesting genera. Numbers of *Angiopolybia* and *Pseudopolybia* are combined to match the *I. americanus* data set.

Among the identifiable nests, those of *Polybia, Pseudopolybia,* and *Leipomeles* were most frequently brought to the chick (Table 3.1, Fig. 3.1). Adult wasps were never evident on nest fragments brought to the chick, although stingless bees (Apidae: Meliponinae) and scavenging wasps, most likely *Ageleia* and *Angiopolybia* (O'Donnell, 1995), were often visible flying near the chick in the *I. americanus* nests.

3.4.3. Army ants found at the Nouragues Station

We encountered four species of *Eciton* army ants in our trail walks, most commonly *E. burchellii* and *E. hamatum* (five encounters each), and nearly as often *E. drepanophorum* (Smith, 1858) (four encounters). We also found three colonies of *E. vagans*. We regularly observed *E. burchellii, E. hamatum* and *E. drepanophorum,* but not *E. vagans,* raiding up trees, up to heights of greater than 5 m (Table 3.2).

Table 3.2. Encounters of four species of *Eciton* army ants during 15 trail walks, totaling 72 trail kilometers, at the Nouragues Research Station in Central French Guiana between November and December 2012. Means are weighted with weights corresponding to the length of the trail walk; 95% confidence intervals were constructed using 1000 bootstrap replicates of original sampling data using the percentile method (Canty and Ripley, 2014). Also indicated are the number of instances where we observed each species raiding 5 m or higher into trees.

Eciton species	Weighted mean (95% CI) encounters per km	Total encounters	Observations of raids up trees
E. burchellii	0.070 (0.0365, 0.1163)	5	3
E. hamatum	0.070 (0.0450, 0.1168)	5	1
E. drepanophorum	0.056 (0.0268, 0.0785)	4	2
E. vagans	0.028 (0.0080, 0.0523)	2	0

3.4.4. Estimates of wasp nest predation rates by *I. americanus* and *E. burchellii*

Estimates of wasp nest predation rates by *I. americanus* ranged between 0.117 to 0.186 wasp nests per hectare per day, or 46.7 to 73.4 nests per day in a 400-ha territory of *I. americanus* (Table 3.1). Based on our own data (Table 3.3) and data reported in the literature, estimates of maximum wasp nest predation rates by *E. burchellii* ranged between 24.8 to 132 nests per day in a 400-ha territory depending on the ant density we used for estimation (Table 3.3).

Table 3.3. Calculation of wasp nest predation rates by the army ant *Eciton burchellii* and by the falconid predator *Ibycter americanus* based on population densities reported in this study or the literature. We included our estimate for *E. burchellii*, as well as the highest estimate reported for an Amazonian forest population.

Predator	Swarms/ha or birds/ha (SE)	Estimated number of nests/ha/day[d] (SE)	Estimated number of nests/ day in 400-ha territory (SE)
E. burchellii	0.021[a] (0.01)	0.06 (0.031)	24.8 (12.4)
E. burchellii	0.110[b]	0.33	132
I. americanus	0.015[c]	0.117–0.186[e]	46.7–74.4

[a] This study, [b] Swartz 1997, [c] Thiollay 1989 (6 birds/400 ha)
[d] Assuming each swarm of *E. burchellii* raids at most 3 nests per day, as reported for *E. hamatum* (Chadab, 1979b; Teles Da Silva, 1982)
[e] Based on calculations that a single *I. americanus* preys on 8-12 wasp nests per day (see Table 3.1).

3.5. Discussion

3.5.1. Evidence for selective predation by *I. americanus*

Video recordings of *I. americanus* chick provisioning behavior allow us to draw two main conclusions. First, *I. americanus* does not often prey on wasp genera such as *Agelaia* that build nests in tree cavities or other physically well-protected locations. Secondly, in comparison with exhaustive Neotropical wasp nest surveys (Jeanne 1991), *I. americanus* was better able to find or subdue nests of *Angiopolybia*/*Pseudopolybia*, *Leipomeles* and *Apoica*. Notably, *I. americanus* brought 13 *Leipomeles* nests to its chicks over 32 days of nest camera recordings, whereas biologists collected *Leipomeles* only once during a 2-month study in Guyana (Richards and Richards, 1951). This discrepancy may be due to differences in the distribution of *Leipomeles* in Guyana and Central French Guiana, or because the birds are simply better at finding the cryptic *Leipomeles* nests (Williams, 1925) than are human observers. Furthermore, *Pseudopolybia* was not noted in Guyana by Richards and Richards (1951), being even less abundant than *Leipomeles* (Jeanne, 1991), yet it accounted for 12.5 percent of the total wasp nests provided to the chicks in our study. This too may be due to the birds' superior ability to find *Pseudopolybia* nests that often contain surrounding foliage in their envelope, making them difficult to detect (Richards, 1978). We ourselves found only one

Pseudopolybia nest during our stay in each of 2008 and 2012, and none in 2009, 2010 and 2011. Caracaras may be better at finding wasp nests than human observers, or the birds may forage in higher above-ground strata than scientists can typically investigate. This search restriction should be taken into account when designing quantitative sampling protocols for tropical social wasps.

Most wasp nests that caracaras delivered to chicks were from swarm founders. Swarm founder nests may be more abundant or larger, and thus more profitable to prey on, than nests of independent-founders. Many swarm-founders also leave their nest *en masse* when threatened by an enemy that cannot be defended, a behaviour that caracaras appear to exploit (McCann et al., 2013). Other species of large wasps including *Synoeca* spp. (Skutch, 1959; Voous, 1969) and *Polybia dimidiata* (McCann et al., 2013) appear equally unable to defend their brood against *I. americanus*. Our recordings of chick provisioning with nests of large and aggressive *Polybia* spp. and *Pseudopolybia* spp. imply that none of these wasps which make an aerial nest with a paper envelope is able to mount an effective defense against *I. americanus*.

3.5.2. Comparison of wasp nest predation by *I. americanus* and army ants

Bouwma *et al.* (2007) compared potential predatory impact of army ants (e.g., *E. hamatum*) with that of scouting and recruiting ants (e.g., *Camponotus* and *Crematogaster* spp.) on populations of social wasps in Neotropical forests. For *E. hamatum*, wasp nest predation rates range between 1-3 nests per swarm per day (Chadab 1979b). The ubiquitous scouting and recruiting ants, in contrast, encounter social wasps more frequently, although these ants may not be as successful as raiders.

Our estimated wasp nest predation rate of *I. americanus* ranged between 0.117 to 0.185 nests per hectare per day, or 47 to 74 nests per day in a 400-ha territory (Table 3.3). Our estimated wasp nest predation rate of *Eciton* spp. was highly variable, ranging from 0.06 to 0.33 nests/ha/day. These rates translate to *E. burchellii* raids harvesting 43 to 132 wasp nests per day in a 400-ha *I. americanus* territory. During the statary phase, which comprises about 60% of the colony cycle, *Eciton* spp. appear to reduce raiding, and hence their intake of wasp nests (Chadab, 1979b; Franks, 1982; Rettenmeyer, 1963), suggesting that the lower value of our bracketed estimates (43 nests per day per 400 ha) is the more realistic. If so, the predatory impacts of *I. americanus* and *E. burchellii* on social wasp populations are comparable.

Several authors have estimated *E. burchellii* raid densities (Franks, 1982; Swartz, 1997; Vidal-Riggs and Chaves-Campos, 2008; Willson, 2004) but densities of column-raiding species such as *E. hamatum* have not been included in these estimates. Nonetheless, similar trail-walk encounter rates of *E. hamatum* and *E. burchellii* suggest that these species often occur at similar densities when they overlap in range (O'Donnel et al., 2007; Powell, 2011). Likewise, there are no published accounts of *I. americanus* population densities. In French Guiana, the territory size of *I. americanus* is estimated to be 400 ha (Thiollay, 1991).

3.5.3. Final remarks

Neither *I. americanus* nor army ants completely eradicate the social wasp colonies they attack. Most adult wasps escape to found a new nest following a predatory attack (Chadab, 1979a,b; O'Donnell and Jeanne, 1990). Both bird and ant predators, however, typically cause total destruction of the wasp brood. As the wasps need several weeks to build a nest and rear brood (London and Jeanne, 2003), they lose considerable investment during a predation event. Thus, attacks by both *Eciton* and *Ibycter* decrease wasp colony fitness and select for anti-predation behavior in wasps.

As an effective diurnal predator of social wasps, *I. americanus* has likely induced specific adaptive defenses in wasps such as fortification and visual crypsis of nests. Adults of *I. americanus* did not provision the chick with nests of *Chartergus* or *Epipona* species which construct visually conspicuous nests of tough felt-like paper and attach them broadly to large distal branches high in tree canopies (Richards, 1978, S'O'D. pers. obs.). As a result of this physical fortification, nests of *Chartergus* or *Epipona* may be inaccessible to *I. americanus*, as might be nests of *Polybia singularis* and *P. spinifex* which have massive hardened mud envelopes (Hozumi and Inagaki, 2010; O'Donnell and Jeanne, 2002; Richards, 1978). Moreover, *Epipona* spp. appear not to abscond in response to mechanical nest disturbance (S. O'D., pers. obs.) and to keep up a vigorous stinging defense which may make it difficult for caracaras to prey on such nests.

Ant predation likely induced other adaptations of wasps including nest site selection on plants devoid of predatory ants (Corbara et al., 2009), nesting associations with *Azteca* ants which confer protection against army ants (Herre et al., 1986), and deposition of ant-repellent substances on nest petioles (Jeanne, 1996).

There are possible tradeoffs in nest site selection by Neotropical paper wasps sympatric with *I. americanus*. Nests on high distal branches may experience a lower likelihood of ant predation (Corbara et al., 2009) but may also become visually more apparent and thus prone to bird attacks. Conversely, nests in cavities may be well protected from bird attacks but are more likely to be raided by ants (O'Donnell and Jeanne, 1990). Long-term demographic studies of wasp nests could provide insight into these tradeoffs.

In conclusion, *I. americanus* preys upon diverse genera of social wasps, some of which are large, aggressive and able to mount a formidable stinging defense. As a specialist predator, *I. americanus* causes significant brood loss in swarm-founding wasp species and may affect their abundance and nest site selection to a degree comparable to that of army ants.

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Chapter 4.

Territorial displays, vocalizations and inter-group interactions of the Red-throated Caracara, *Ibycter americanus*

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4.1. Abstract

We studied territorial behavior and vocalizations of the Red-throated Caracara, *Ibycter americanus* (Boddaert), at the Nouragues Reserve in French Guiana during the rainy seasons of 2008 to 2011. We recognized and characterized distinct contact, alarm, territorial and solicitation calls. In response to playback of territorial calls and presentation of a caracara decoy, groups of *I. americanus* engaged in territorial displays, consisting of group calling and exaggerated body movements, followed by physical attacks on the decoy. During territorial conflicts in 2011, we observed competing rallying between groups as well as physical attacks by members of one group upon the other. This intensive territorial conflict may have disrupted a nesting attempt by a three-member group in 2011. Our results show that *I. americanus* groups do not tolerate foreign group members in their territories, and that they use territorial displays and aggression to drive intruders away.

KEY WORDS: Red-throated Caracara; *Ibycter americanus*; territoriality; vocal behavior; aggression; French Guiana

4.2. Introduction

The Red-throated Caracara (*Ibycter americanus*) is an unusual member of the Falconidae. As a specialist predator of social wasps, it seeks wasp nests and feeds on the brood of social wasps as a staple dietary component (Thiollay 1991, McCann et al. 2010). *Ibycter americanus* engages in cooperative breeding, with up to six adult birds provisioning a single offspring (Thiollay 1991, McCann et al. 2010, 2013). The birds often travel in groups (Huber 1932; Schulenberg et al. 2007) and are noted for their extremely loud and raucous vocalizations (Schomburgk 1845, Sclater 1858, Huber 1932, Skutch 1959, Thiollay 1991). These vocalizations, however, have not yet been well characterized, and their significance is not clear. It has been suggested that the birds defend year-round territories against conspecifics using vocalization and display (Thiollay 1991).

Our objectives were to (1) record and describe vocalizations of *I. americanus* and note the specific context in which they occur; (2) observe the behavior of *I. americanus* when exposed to playback of calls in the presence or absence of a conspecific decoy; (3) describe visual displays and note the specific context in which they occur; and (4) document instances of group interactions and describe associated behaviors.

4.3. Methods

4.3.1. Study Area

We studied three groups of *I. americanus* at and around the Inselberg Camp within the Nouragues Reserve in French Guiana (4°05' N - 52°41'W), during January to April (the rainy season), 2008-2011 and in addition two other groups further away within the reserve. The reserve is a large, relatively undisturbed lowland rainforest habitat situated in the Montagnes de Balanfois region, about 100 km SSW of Cayenne. The landscape surrounding the camp is dominated by the Inselberg des Nouragues, a large, 411-m high granitic mountain. The dense, low-altitude (50-250 m above sea level) primary forest transitions up the Inselberg to low-forest, tropical scrub, and finally rock savannah (Charles-Dominique 2001). Our research area included lower-altitude mature forest surrounding the Inselberg Camp where Thiollay (1991) found *I. americanus* most frequently. The canopy height across this area ranges from 25-45 m, with some emergent trees such as the 2008-nest tree *Chrysophyllum lucentifolium* (Sapotaceae) being > 50 m tall. We also made observations at the Saut Pararé camp, which is 5.7 km from the Inselberg Camp on the Arataye River, and at a point midway between the two camps. Several creeks traverse this landscape, the major waterway being Crique Nouragues. Extensive trail systems cover two large plateaus rising from the banks of the creek. The Inselberg camp afforded a good overview of part of the Crique Nouragues valley and the larger of the two plateaus.

In 2008 and 2009, there was one active *I. americanus* nest within 600 m of the Inselberg camp on the larger plateau, although the nests were at different sites each year (located 150 m apart). The nesting group at this site in 2009 included two males and two females and the chick that were individually color-banded (McCann et al. 2010), as well as 2-3 unmarked birds of unknown sex. In 2010, no nesting occurred near this site during our field season, although we saw three of the five marked birds and the 2009-chick during video recordings (McCann et al. 2013). In 2011, the same nest site that had been used in 2009 was being prepared for occupation by a group of three birds that did not contain any marked individuals.

4.3.2. Recording of Vocalizations and Behavioral Observations

We heard and recorded vocalizations of *I. americanus* during the field seasons in 2008-2011. We recognized four types of distinct-sounding calls and noted the behavioral context in which they occurred. In 2009, we completed 55 daily observation and audio recording sessions at the active *I. americanus* nest, noting weather conditions and the time of the first calls. To ensure that we recorded the first calls of the day, we arrived at the nest site well before dawn.

In all four field seasons, we opportunistically observed *I. americanus* during walks within the trail system, and from the vantage of the camp. We made notes on calls and observed behaviors paying particular attention to interactions between groups. We video recorded territorial interactions wherever possible, documenting some of them by means of a nest camera placed in the bromeliad that was being prepared by the birds as a nesting platform in 2011.

4.3.3. Analysis of Published Calls

To determine whether our qualitative call categories were representative of *I. americanus* throughout its range, we downloaded the entire suite of recorded *I. americanus* calls from both the Macaulay Library and Xeno-Canto, and converted the MP3 files into WAV files using Oxelon Media Converter.

We selected recordings for analysis that (based on spectrograms) had good audio quality, low levels of competing sounds, and appeared to be vocalizations of single rather than multiple birds (although this was not possible for chorusing calls). We excluded multiple recordings made by the same recordist within the same year at the same location. For each selected recording, we chose a single exemplar of one call type and measured the following parameters: duration and fundamental frequency of first syllable, and duration and peak frequency of the entire call series (repeatedly uttered syllables).

We assigned calls to one of four call types according to our *a priori* category of call type which was based on qualitative sound characteristics of each call type. Among all sound files we analyzed, we assigned 49 calls as alarm calls, 17 as contact calls, and 13 each as begging or territorial calls. To obtain an equal sample size for each call type, we randomly selected 13 alarm calls and 13 contact calls to be included in statistical analyses. We applied Box-Cox transformations to all data prior to analyses to achieve multivariate normality (Sakia 1992, Venables and Ripley 2002). We ran a quadratic discriminant analysis (Venables and Ripley 2002) with cross-validation to determine whether calls were correctly assigned to *a priori* categories based on backward elimination of the parameters we measured (the final model included fundamental frequency of first syllable, duration of first syllable, and duration of entire call series). We then ran univariate ANOVAs on assigned call type predicting each response variable, followed by Tukey’s HSD post-hoc tests. We used R 2.15.2 for all statistical analyses.

4.3.4. Call Playback

Using a portable speaker, we played back recorded calls to determine whether different types of calls elicit distinctive behavioral responses from *I. americanus*. We used playbacks at five sites in the forest surrounding the Inselberg camp, three sites near Saut Pararé camp, and at one site midway between the two camps. We began broadcasting calls from a playback site when we heard caracaras, and initiated playbacks every 3-4 minutes thereafter. During call playbacks, we observed behaviors of caracaras either from a blind with the audio equipment 5-10 m away from it, or - predicting a different type of behavioral response - in the open with the sound speaker hand-held by one of two observers.

4.3.5. Decoy Presentation

We exposed *I. americanus* to decoys that we had carved from closed-cell polystyrene insulation foam and painted with water-based acrylic paints to resemble a caracara. Between 800 h and 1600 h, we presented the decoy in each of three settings: (1) on the forest floor with no obstructing undergrowth (n=26 presentations), (2) on the forest floor with an overhanging *Astrocaryum* palm frond partially concealing the decoy (n=1), and (3) in the forest clearing of the camp (n= 5). For each presentation, observers resided in a blind and attracted birds to the location using playback of four types of calls. We noted or video-recorded all behaviors exhibited by the birds near the decoy.

4.4. Results

Note: Each of the following behaviors and vocalizations has exemplars uploaded to a dataset on figshare.com. Details are found in Appendix B.

4.4.1. Call Types

We distinguished four audibly distinct types of calls. The contact call (Fig. 4.1, A, B, C, Table 3), a monosyllabic “kyeeer” (Schulenberg et al. 2007), is a single, high-pitched scream that decreases slightly in pitch across the call. The solicitation call (Fig. 4.1 D) is soft and plaintive, and may be best described as an elongate high pitched “keeeeeeeeuhhhh”. Its spectrogram resembles the contact call in that it decreases in pitch across the call, but it is significantly longer (Fig. 4.1, Table 4.1). In two recorded repetitive solicitation calls, there were on average 0.5 calls per second, and these calls were often repeated by a single bird. The territorial call (Fig. 4.1 E), a guttural “Caw-uh, Caw-uh, Caw-uh” with each uttered syllable echoed by group members, is generally lower-pitched than the other call types. The alarm call (Fig. 4.1 F) is a staccato “CacacaCaaw”. In some cases, the final syllable of the alarm call resembles the contact call when viewed as a spectrogram (Detail in Fig. 4.1. F).

Contact calls were most often made by a flying bird and soon after echoed by other caracaras accompanying it. Birds arriving at the nest at dawn first produced contact calls (Fig. 4.1 B) and then territorial calls (Fig. 4.1 C, D), a sequence that we defined as “dawn chorus”. Solicitation calls were made by flying birds together with contact calls, and by birds trailing behind a group of foragers. Solicitation and contact calls were also made by birds when they were in the nest in 2008 and 2009. Unlike Thiollay (1991), we did not witness allofeeding in response to solicitation calls, possibly because we did not often directly observe birds making solicitation calls, and we did not have audio for our nest camera study (McCann et al. 2010). Solicitation calls were often repeated by a single bird.

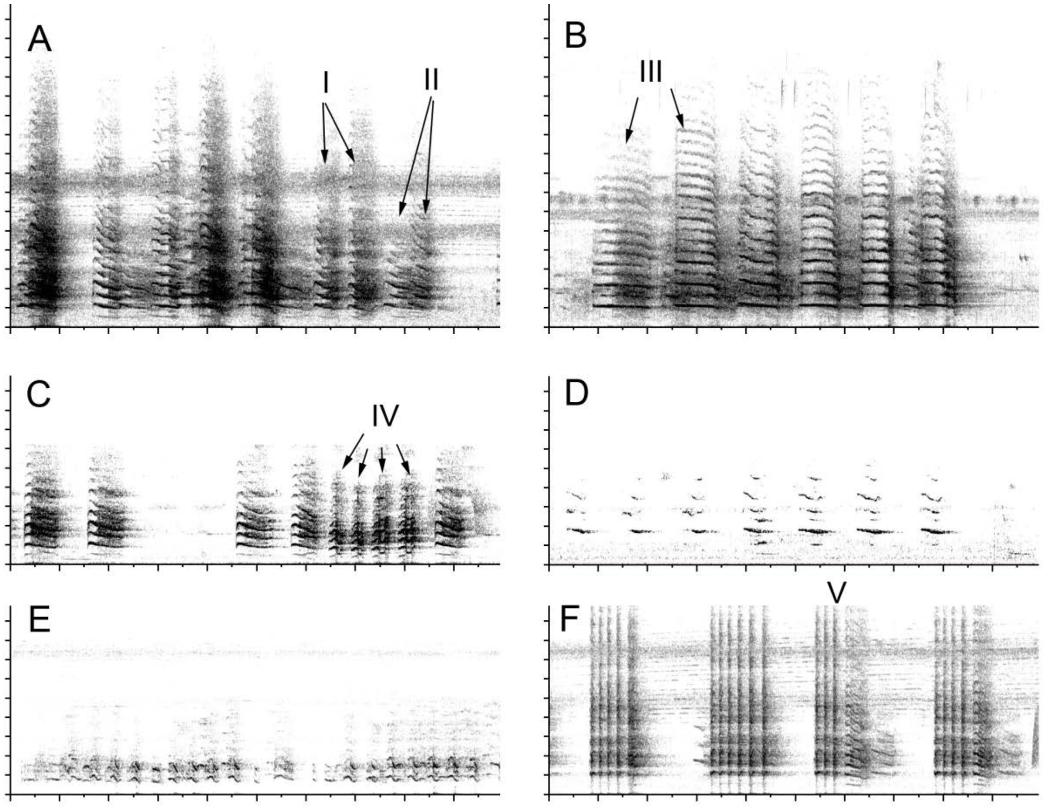

Figure 4.1. Spectrograms of five representative calls or call series of *Ibycter americanus* recorded at the Nouragues Reserve in French Guiana. (A) Contact calls of group members during flight: I indicates single calls uttered by one bird, II overlap in calls from one bird echoing another. (B) Contact calls during arrival at the nest tree at dawn: III indicates elongate syllables characteristic of these contact calls. (C) Beginning of dawn chorus - repeated contact calls followed by four notes of a territorial call (IV). (D) Solicitation call produced by a single bird. Note similarity to the contact calls. (E) Territorial call: produced by several birds, many syllables are chorused by others in the group. (F) Alarm calls: V indicates a characteristic alarm call sequence. The last syllable of this phrase resembles the contact call.

When we climbed the nest tree to install or repair nest cameras on four occasions in 2008 and on five occasions in 2009, several birds in attendance produced alarm calls continuously, from one to three hours each time depending on the length of the disturbance. Territorial calls were typically accompanied by visual territorial displays (see below) and expressed in the presence of other groups of caracaras, when exposed to playback of recorded calls, or spontaneously when group members gathered at the nest tree at dawn.

4.4.2. Analyses of Published Call Types

The quadratic discriminant function analysis indicated that calls can be correctly assigned to a predetermined call-type category by a combination of duration and fundamental frequency of the first syllable, and the duration of the entire call sequence (Wilks' lambda = 0.009, $F_{9,112} = 73.2$, $p < 0.0001$). The model assigned 48 of 52 calls (92.3%) correctly to one of four call-type categories (Table 4.1). ANOVAs indicated that there were significant differences among call types based on dominant frequency of the first syllable ($F_{3,48} = 22.2$, $p < 0.0001$), length of the first syllable ($F_{3,48} = 66.9$, $p < 0.0001$), and length of the entire call ($F_{3,48} = 72.2$, $p < 0.0001$). Post hoc analyses revealed that contact calls did not differ from alarm calls or territorial calls in terms of dominant frequency of the first syllable, contact calls and begging calls did not differ in terms of duration of the first syllable or duration of the entire call sequence, and begging calls did not differ from alarm or contact calls in terms of duration of the entire call sequence. All other comparisons yielded statistically significant differences (Table 4.1).

Table 4.1. Quadratic discriminant function analysis of published *I. americanus* calls, showing details of fundamental frequency as well as duration of first syllable and entire call sequence. Within each of columns 3-5, data with different lowercase letters are significantly different (Univariate ANOVA followed by Tukey's HSD post-hoc tests; differences are significant with an experiment-wise α of 0.05. Statistical tests were performed on Box-Cox transformed data; actual values shown).

Call type	n	Fundamental frequency (Hz) of 1st syllable mean (± SD)	Duration (s) of 1st syllable mean (± SD)	Duration (s) of call sequence* mean (± SD)	Proportion correctly assigned
Alarm	13	1249 (442) b	0.19 (0.03) a	1.62 (0.59) a	1.00
Begging	13	2194 (735) a	1.10 (0.27) b	1.09 (0.22) b	0.92
Contact	13	1138 (289) bc	0.84 (0.20) b	0.87 (0.20) b	0.85
Territorial	13	952 (152) c	0.55 (0.33) c	23.54 (16.27) c	0.92

*Entire call sequence defined as the series of continuously vocalized syllables separated by no more than 0.3 s of silence.

4.4.3. Response to Playback.

In response to playback of all four types of calls, groups of *I. americanus* immediately approached the speakers and initiated a territorial display from a nearby perch (Table 4.2), provided that human observers were concealed in blinds. This territorial display consisted of a gathering of up to seven birds followed by the chorusing territorial call (Fig. 4.1, C, E). The bird that initiated the territorial calling was immediately surrounded by nearby group members, one or more of which answered each syllable of the territorial call. The territorial call was accompanied by a visual display in which a calling bird inclined its head and turned it from side to side, with the bill pointing up and the throat expanded (Fig. 4.2, Appendix B). While calling, caracaras raised their wings, either together over the head, or alternately behind the back, thus exposing their white flanks or belly, which rendered the white parts visible from all directions (Fig. 4.2).

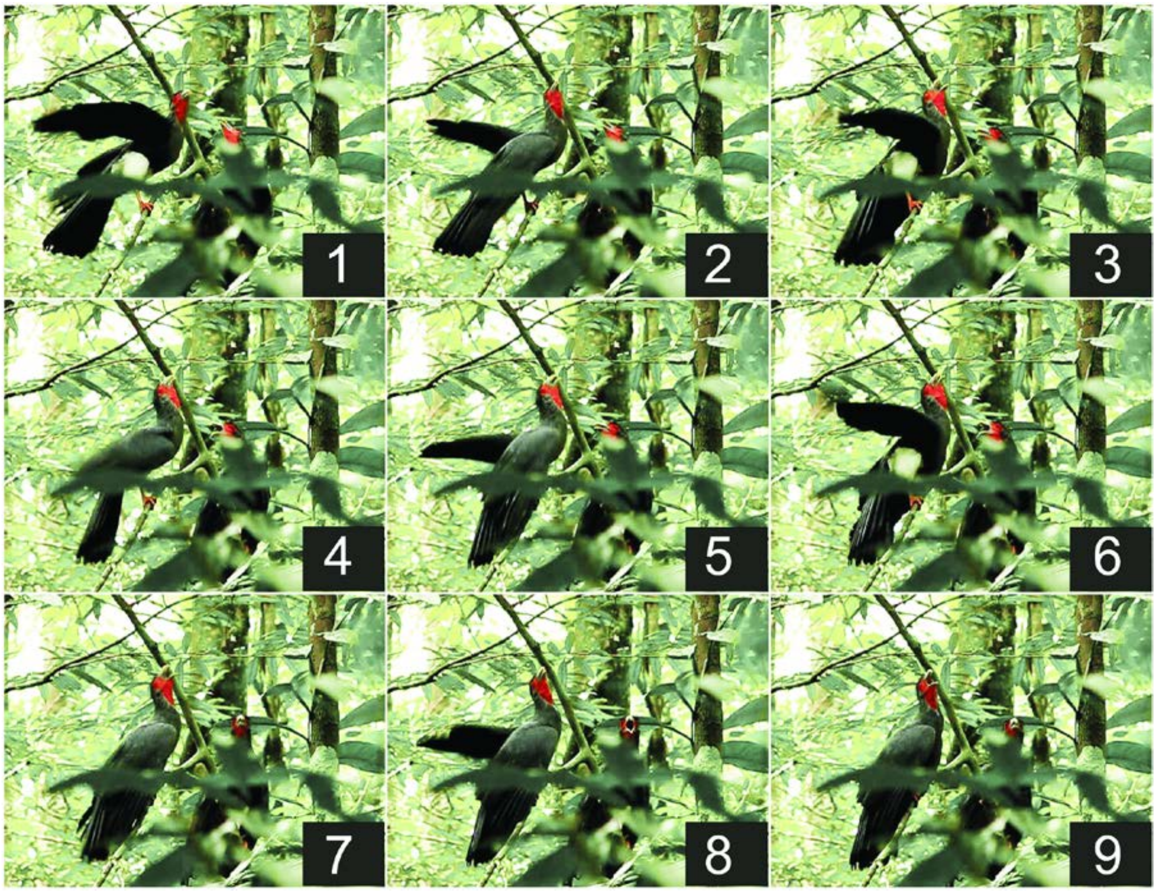

Figure 4.2. Territorial display of two *Ibycter americanus* adapted from a video recording. While calling, the birds raise their wings alternately above the back, thus exposing their white flanks (right wing in frames 1, 3, and 6; left wing in frames 2, 5, and 8), concurrently elevating their beak and turning their head from side to side. Calling birds perch close together and echo each other's syllables. This series of frames has been desaturated slightly to emphasize the birds against the background. The original video can be viewed unaltered on the SFU Library website (Appendix A).

Table 4.2. Summary of behaviors exhibited by *I. americanus* in response to the presentation of both a decoy (see Figure 3) and concurrent playback of various call types or in response to just playback of calls.

Stimulus presented	Location	n (number of instances)	Type of response by birds
Decoy & territorial call	Clearing in camp	5	Territorial call & visual display, stooping attacks, strikes to head of decoy
Decoy & territorial call	Forest, open understory	26	Territorial call & visual display, stooping attacks, strikes to head of decoy
Decoy & territorial call	Forest, decoy concealed from above	1	Territorial call & visual display, investigation flights, approach on foot, striking/grasping head of decoy (3 times)
Alarm call	Forest, various locations	6	Territorial call & visual display
Territorial call	Forest, various locations	>50	Territorial call & visual display
Contact call	Forest, various locations	18	Territorial call & visual display
Begging call	Forest, various locations	3	Territorial call & visual display
Various calls, observers outside blind	Forest, various locations; clearing in camp	20	Alarm & territorial call at a distance

4.4.4. Response to the Presentation of Decoys

Presentation of a decoy coupled with playback of territorial calls induced the same territorial display described above (Table 4.2). In addition, several of the birds approached in flight to within several meters of the decoy or perched within 5 m of it in the understory. Repeating the playback of calls every two minutes prompted individual birds to attack the decoy, usually within 15 minutes of their arrival. In general, the birds stooped at the decoy from a height, striking its head with their talons (Fig. 4.3). On three occasions, a single female caracara (individually identifiable, later marked, sexed and released) approached the decoy on foot and struck at the head with her talons (Appendix A).

Figure 4.3. Stooping attack of *Ibycter americanus* on a conspecific decoy, adapted from a video recording. Note that the head is targeted. Time (s) elapsed is shown in black numerals. This video can be viewed at the SFU Library website (Appendix A).

4.4.5. Territorial Behaviors

During the 2008- and 2009-nesting seasons, individual caracaras, presumably from the resident group, arrived simultaneously at the nest tree at dawn. Likely, all caracaras of the resident group arrived but they were difficult to count in the darkness of the dawn. Upon arrival, the birds first produced an extended series of contact calls (Fig. 4.1 C), then territorial calls and displays, and contact calls again before they left. This sequence, henceforth referred to as a "dawn chorus," usually lasted 2-5 min. During a dawn chorus, the brooding/incubating adult left the nest and another bird replaced it. In 2009, the group engaged in a dawn chorus on 34 of 35 days on which we made video/audio recordings, prior to egg hatching. The group remained silent only on one unusually rainy morning. After the egg hatched, we recorded a dawn chorus at the nest on all 20 mornings during which we made observations at the nest. When caracaras arrived as a group at the nest tree later in the day, they also chorused but we do not know whether they always did.

In 2011, a group of three birds commenced nest preparation behavior at a large epiphytic bromeliad in an emergent tree 600 m from the camp, the same bromeliad that a group of birds had used as a nest site in 2009 (McCann et al. 2010). These birds were able to engage in nest preparation and territorial display unopposed for at least three days after which time their territorial calls attracted neighboring groups. When one group arrived within sight of the nesting group, the arriving group commenced territorial displays and territorial calling in emergent trees 300-500 m from the nest tree. High in these trees within sight of one another, the two groups - apparently observing each other - engaged in alternate bouts of territorial calling. While one group remained silent the other was calling. Between these bouts of calling, one or both groups often flew to another emergent tree that was closer to, or farther from, the other group. Both groups were usually separated by 100-300 m. Bouts of calling between groups continued until the nesting group retreated far (≥ 1 km) out of sight to the northwest. On 15 of the 19 days when territorial confrontations occurred, they ended within 1-2.5 h with the nesting group retreating from the nest tree. On three occasions, calling bouts between the nesting group and another group ended at dusk, with both groups remaining near each other and calling bouts resuming the next morning.

The 3-bird nesting group was physically attacked by members of one or more groups on several occasions. On 3 April 2011, we filmed (from camp) a bird from the southeast group flying at, and attempting to strike, a bird on the nest. This event was simultaneously filmed by the automated nest camera. On this occasion, the attacking bird was apparently warded off with a counterattack by another member of the nesting group. About 20 min later, another bird from a second group made stooping attacks on birds of the nesting group that were calling in the nest tree.

On 9 April 2011, we observed three more physical attacks between members of two different groups in the forest 200 m to the northeast of the nest tree. We had followed the nesting group from the Inselberg camp to this location where they encountered the other group. When we arrived, the two groups were already engaged in territorial calling and displays. After bouts of territorial calling, several birds from one group began to chase birds from the other group. During these attacks an aggressor extended its talons, but in all instances we observed that the attacked birds avoided physical contact by taking evasive action.

In total, the 3-bird group attempting to use the nest tree near the Inselberg camp in 2011 was confronted with territorial displays or physical attacks by one or more other groups on at least 19 of the 26 days that the 3-bird group perched in and called from the nest tree. On 15 of these 19 days, members of the 3-bird group were eventually driven away from the nest tree. Between 9 April and 25 April 2011 (the day we left the field site) the group never returned to the nest tree.

4.5. Discussion

Results of our study support the conclusion that territoriality is a prominent life history trait of *I. americanus.* Gathering of birds in response to playback of four types of calls followed by territorial calls and visual displays, physical attacks on decoys, territorial rallying at the nest site, and territorial rallying with physical attacks between competing groups, all suggest that establishing and defending a territory is critically important for the survival of a group and its reproductive success.

Group territoriality in *I. americanus* at our study site may be linked to the their highly specific diet. With larvae and pupae of social wasps being the primary food source (McCann et al. 2010) that is supplemented by fruits, termites, and possibly lizards (Lowery and Dalquest 1951, Skutch 1959, Voous 1969, Thiollay 1991, McCann et al. 2010, 2013), the birds are challenged to locate many often small and cryptic wasp nests in a highly complex forest environment. Intraspecific competition for hunting territory may thus be high. Moreover, wasp nests are also preyed upon by other vertebrates (Windsor 1976, Raw 1997, Fragaszy et al. 2004), and by army ants, which are considered to be one of the major predators of social wasps in tropical rain forests (Jeanne, 1991). This competition may put significant strain on the prey base of *I. americanus.* Scarceness of, or competition over, prey may then have contributed to the evolution of cooperative breeding by *I. americanus,* a strategy which has been documented in several studies (Thiollay 1991, Whittaker 1996, McCann et al. 2010). The low reproductive output of *I.*

americanus, such as raising a single chick by a group of up to six birds (McCann et al. 2010), indicates a strongly k-selected life history. Low mortality, limited dispersal, as well as narrow diet breadth and high levels of territorial behavior are usually linked in cooperatively-breeding birds (Bennett and Owens 2002). While mortality and dispersal abilily of *I. americanus* are still unknown, cooperative breeding and narrow diet breadth have been well documented (McCann et al. 2010, 2013). It is not surprising then that groups of *I. americanus* exhibit pronounced territorial behavior and conflicts. Another cooperatively breeding raptor, the Harris' Hawk (*Parabuteo unicinctus*), also engages in aggressive behavior at territorial boundaries and around nest sites both within and outside the breeding season (Dawson and Mannan 1991).

The intensive conflict we observed around the nesting site warrants further examination. Based on our observations, the territorial calls of the nesting group drew the attention of neighboring groups which then contested the territory. Their continued vocal opposition and physical attacks drove the nesting group away on most days, and eventually prompted it not to return to the nest site. One might wonder then why the nesting group advertised its presence and why it persisted in attempting to defend the nesting site. Short supply of good nesting sites is a very plausible explanation. Both of the nest trees we observed were somewhat unusual, being large emergent trees with large bromeliads and limited connectivity to the canopy, presumably favoured as a means to limit access by predators such as monkeys (McCann et al. 2010). If Red-throated Caracaras do not build their own nests but instead seek bromeliads in tall trees as a nest platform (McCann et al. 2010), then the availability of nesting sites could indeed be a limiting factor. Intraspecific competition for nest sites is well documented in species with specific nest-site requirements such as cavity nesters (Newton 1994).

Territoriality in *I. americanus* is expressed in a number of vocal and visual territorial displays, including aggressive and potentially damage-inflicting behavior. The vocal repertoire included not only territorial calls but also alarm, contact and solicitation calls. Solicitation calls did not appear to be consistently linked to any particular behavior such as solicitation or allofeeding between foraging birds as described by Thiollay (1991), but they may still function in these contexts. The dawn chorus with contact and territorial calls, as part of this repertoire, occurred regularly during the breeding season. This type of morning calling has also been described for other Neotropical falcons, such as *Micrastur* (Thorstrom et al. 2000a, 2000b) and *Herpetotheres* (Miller et al. 2010), and may contribute to territorial advertisement. In response to playback of four types of calls, groups of *I. americanus* investigated immediately and initiated territorial displays which included chorusing territorial calls accompanied by visual displays. In response to decoys, *I. americanus* launched physical attacks with open talons directed at the decoy's head. Such attacks directed at a real intruder could injure one or both birds.

Our observations of physical confrontation between rallying groups and attacks on decoys indicate that territorial display followed by aggression could represent a continuum of escalating territorial conflict. Conceivably, a sequence of events during territorial disputes unfolds as follows: (1) one group calls at a territorial boundary and attracts a neighboring group; (2) both groups engage in competing territorial displays, possibly escalating into physical attack; and (3) one group retreats.

The various calls of these caracaras are audibly distinct and seem to be tied to specific social circumstances. Alarm calling is frequent in the presence of humans and other predators, and in the context of the nest site seems to function to mobilize group members for defense. Territorial calling appears to function in defense of territory against conspecifics and in gathering the group together at nest sites. These call types should be noted by observers of *I. americanus* in the field.

The social and vocal behaviors of *I. americanus* make it especially vulnerable to human-mediated population decline. By travelling and perching in groups and conspicuously alarm calling, they are prime shooting targets, as has been noted (Sclater 1858, Taylor 1860, Huber 1932). As one of the most conspicuous raptors in French Guiana (Thiollay 1989), *I. americanus* is reported to be persecuted frequently by hunters because its alarm-calling may disturb game animals (Thiollay 2007).

While we have obtained detailed information about territorial behavior and vocalizations of groups of *I. americanus* in our study area, this raptor remains poorly studied and further research on almost every aspect of its life history is warranted. Bionomic parameters such as mean size of social groups, kinship among group members, individual philopatry, courtship and mating behavior are all unknown. Even home range size has been estimated only once in one region (Thiollay 1991). In other regions where populations of *I. americanus* are low or declining, such as Costa Rica (AOCR (Comité Científico de la Asociación Ornitológico de Costa Rica) 2005), studies on home range size requirements and dispersal will be vital to devising appropriate conservation strategies.

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Chapter 5.

Strike Fast, Strike Hard: the Red-throated Caracara Exploits Absconding Behavior of Social Wasps during Nest Predation

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5.1. Abstract

Red-throated Caracaras *Ibycter americanus* (Falconidae) are specialist predators of social wasps in the Neotropics. It had been proposed that these caracaras possess chemical repellents that allow them to take the brood of wasp nests without being attacked by worker wasps. To determine how caracaras exploit nests of social wasps and whether chemical repellents facilitate predation, we: (1) video recorded the birds attacking wasp nests; (2) analyzed surface extracts of the birds' faces, feet, and feathers for potential chemical repellents; and (3) inflicted mechanical damage on wasp nests to determine the defensive behavior of wasps in response to varying levels of disturbance. During caracara predation events, two species of large-bodied wasps mounted stinging attacks on caracaras, whereas three smaller-bodied wasp species did not. The "hit-and-run" predation tactic of caracaras when they attacked nests of large and aggressive wasps reduced the risk of getting stung. Our data reveal that the predation strategy of caracaras is based on mechanical disturbance of, and damage to, target wasp nests. Caracara attacks and severe experimental disturbance of nests invariably caused wasps to abscond (abandon their nests). Two compounds in caracara foot extracts (sulcatone and iridodial) elicited electrophysiological responses from wasp antennae, and were also present in defensive secretions of sympatric arboreal-nesting *Azteca* ants. These compounds appear not to be wasp repellents but to be acquired coincidentally by caracaras when they perch on trees inhabited with *Azteca* ants. We conclude that caracara predation success does not depend on wasp repellents but relies on the absconding response that is typical of swarm-founding polistine wasps. Our study highlights the potential importance of vertebrate predators in the ecology and evolution of social wasps.

5.2. Introduction

It is well recognized that ants are important predators of social wasps, and that wasps exhibit ant-specific defensive adaptations [1–3], but until recently little attention has been paid to the role of vertebrate predators in social wasp evolution. Few vertebrate predators are known to specialize on the brood (larvae and pupae) of social wasps as their primary food source, but behaviors such as stinging, venom spraying [4], biting [5,6], and physical fortification or camouflage of wasp nests [7–9] suggest selection for specific anti-vertebrate defensive tactics. Among vertebrate predators are birds such as the Honey Buzzards of the Old World [10–12] and the Red-throated Caracara, *Ibycter americanus*, of the New World [13–15]. The Red-throated Caracara (henceforth “caracara”) is unusual among the Falconidae in that it has well-developed cooperative breeding, with up to six adult individuals participating in brood care [13]. Caracaras are also known to forage in groups and to share large wasp nests [15]. In a previous study [13] we showed that wasp nests account for 59-77% of food items brought to caracara chicks, implying that caracara adults routinely engage in wasp nest predation.

While Honey Buzzards have dense facial plumage and long narrow nares (nostrils) that presumably shield them from stinging wasps [16], these types of physical protections are not evident in caracaras, which lack plumage on the face and throat (Fig. 5.1 A, B). Instead, chemical rather than physical defenses have been posited to protect caracaras from attacking wasps. Thiollay [15], studying caracaras in French Guiana, observes: “The most striking adaptation of the Red-throated Caracaras was their ability to repel totally even the strongest and most aggressive wasps. As soon as one bird reached a nest, all the insects abandoned it and never attacked the raider, nor followed it when it carried the nest away. The wasps flew at a distance around the bird, rarely coming nearer than 1 m as long as it was on the nest." Thiollay concludes: "The fact that wasps never attacked, nor even closely approached the caracaras raiding their nests suggests the involvement of some powerful chemical repellent. This repelling power is known to the local Indians and hunters, who readily eat raptors but who do not consume the caracaras because of their reportedly strong smell and taste.". Thiollay's intriguing hypothesis has some antecedents. During a collection trip to Mexico, Lowery and Dalquest [17] relate that caracaras were considered by the local indigenous people to have a toxic substance on their feathers, and Weldon and Rappole [18] report malodorous qualities of caracaras.

Figure 5.1. Photographs of Red-throated Caracaras. A. Red-throated Caracara perched on a branch near the Pararé Camp of the Nouragues Reserve in Central French Guiana, April 2011; note the bird's bare face and throat. B. Procedure of swabbing the skin of the bird's face with hexane-soaked cotton to remove skin surface chemicals. Feet and feathers were sampled in a similar fashion.

Chemical defenses in birds have rarely been documented. The Pitohui (*Pitohui dichrous*) is known as toxic to indigenous people of New Guinea [19] and possesses homobatrachotoxin as a potent anti-predator poison. The Green Woodhoopoe (*Phoeniculus purpureus*) is said to have a foul-smelling secretion that deters predators [20]. Uropygial gland secretions of the Crested Auklet (*Aethia cristata*) are implicated as chemical protectants against ectoparasites [21,22], whereas some shearwaters (Procellariidae) eject stomach oils that they use to repel or even kill avian attackers [23].

Most species of social wasps preyed upon by caracaras are swarm-founding members of the tribe Epiponini that abandon their nests in response to strong physical disturbance [24]. Triggering this absconding response of swarm-founding wasps may allow caracaras to prey on wasp nests without being severely stung. It is also possible that caracaras are immune to the venom of their prey, and simply withstand the stinging defense.

Here we tested the hypothesis that caracaras possess a chemical repellent that protects them from wasp attacks, and the alternate hypothesis that caracaras inflict severe mechanical damage on wasp nests and then rely on the absconding response of wasps. To test these hypotheses and to gather data on how caracaras attack nests of social wasps, we took three approaches: (1) we built a recording arena with four video cameras, supplied the arena with active wasp nests, lured in caracaras by playback of their territorial calls, and video recorded caracaras attacking the nests (2) we captured caracaras, took solvent-soaked cotton swabs of their faces, feet and feathers, and analyzed swab extracts for potential defensive or repellent chemicals; and (3) we inflicted mechanical damage on wasp nests to determine whether it causes wasps to abscond without stinging.

5.3. Methods

5.3.1. Study site

We conducted our fieldwork at the Inselberg and Pararé camps of the Nouragues Reserve in Central French Guiana (100 km SSW of Cayenne, 4°05' N - 52°41'W), an undisturbed lowland rainforest (55-410 m ASL) closed to most human activity for approximately 40 years [25]. This area has year-round populations of caracaras and a trail network to facilitate access to the forest [15].

5.3.2. Observations of wasp nest predation by caracaras

In each of four field seasons (2008-2011) totaling 11 months, we observed caracara predation on wasp nests while we were on regular walks through the forest.

During observations of wasp nest predation we attempted to identify adult wasps by visual inspection or by collection of brood or callow workers from nests.

5.3.3. Controlled recordings of wasp nest predation by caracaras

In 2010 and 2011, we recorded caracara predation on wasp nests in a recording arena (Fig. 5.2) constructed about 100 m northeast of the Inselberg Camp. We fitted the arena with four 540 TV line resolution security video cameras (Aartech Canada, Oshawa ON, Canada) and fed video signals to a 4-channel security digital video recorder (Channel Vision DVR 4C, Channel Vision Technology Costa Mesa, CA, USA) housed in a shelter within the camp. At night, when the otherwise aggressive wasps are docile and remain on their nests, we transferred active wasp nests from the surrounding forest to the arena. We used a ladder to access the arena and attached the nests with spring clips to crosspieces 7 m above ground (Fig. 5.2).

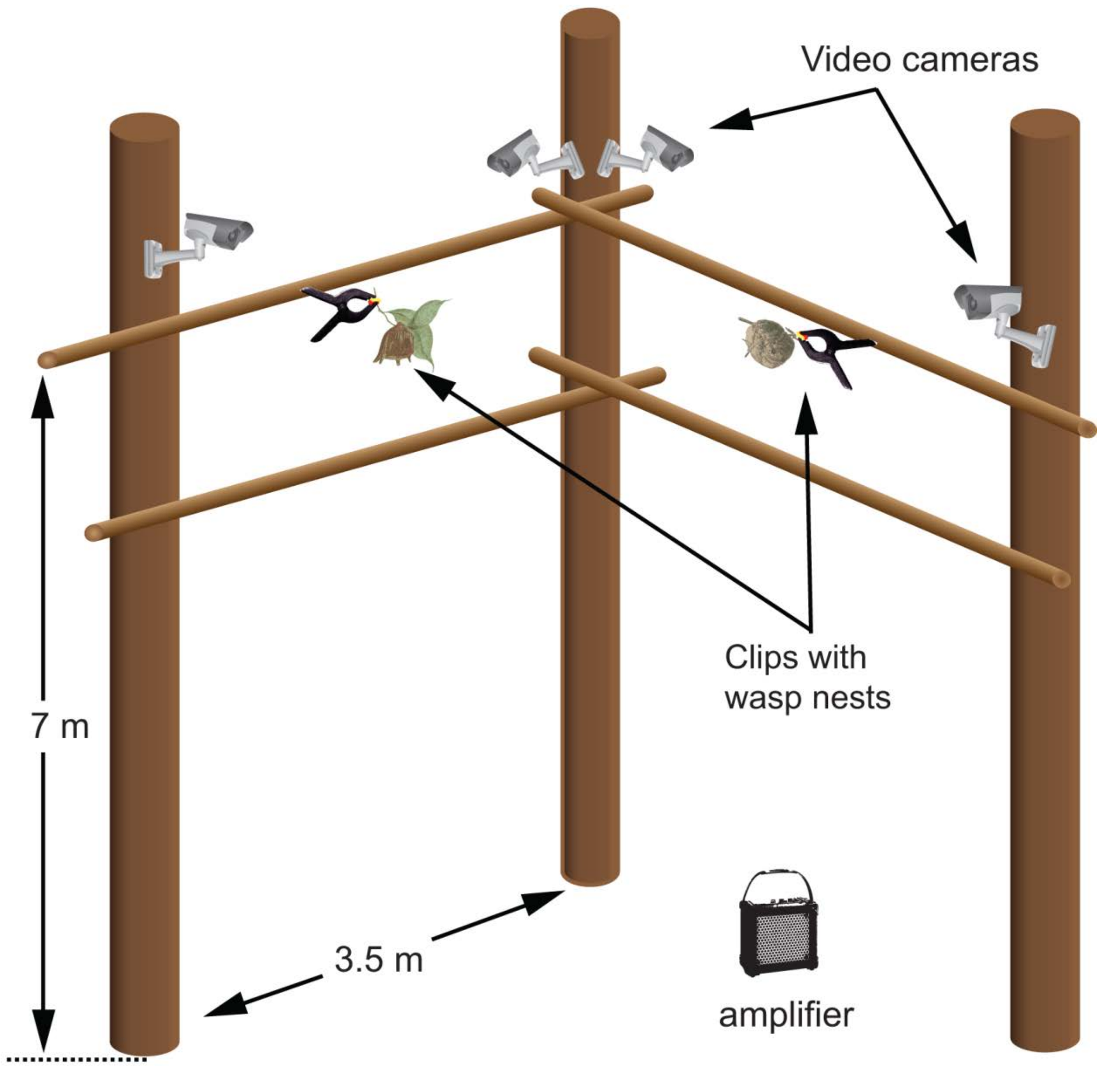


Figure 5.2. Drawing of the recording arena. We designed and constructed this arena to video record attacks of Red-throated Caracaras on active wasp nests which we transferred at night (when aggressive wasps are docile) to the arena from surrounding forest.

The arena was designed to record two nests concurrently. Upon motion detection, the DVR was set to record video at either 640 × 288 pixel resolution at 24 frames per second (FPS), or at 640 × 480 resolution at 15 FPS, depending on the number of cameras employed. A 5-s pre-recording buffer ensured that the entire sequence of events prior to motion detection was recorded. This pre-recording buffer transfers the footage 5 s prior to motion detection to the hard drive, a technology commonly found on security DVRs.

We played back caracara calls using a Roland Edirol R-09 portable field recorder and a Roland Microcube amplifier (Roland Corporation, Los Angeles, CA, USA) to attract birds to the camp, and then switched the playback device to a second amplifier located immediately below the arena.

We recorded 11 attacks by caracaras on nests of five wasp species (four nests each of *Polybia bistriata* and *P. jurinei,* and one nest each of *P. scrobalis*, *P. belemensis* and *P. affinis*). These nests were attacked within 2-27 days after transplantation. We selected *Polybia* nests for recordings because they were most frequently brought as prey to a caracara nestling in two seasons of provisioning observations [13]. Also, *Polybia* wasp species represent a wide range of body size and aggressiveness, and are diverse and widespread across the geographic distribution of caracaras.

For each attack, we viewed the video to determine whether caracaras were attacked and possibly stung by wasps, as evidenced by wasps flying towards a caracara to intercept the bird, or by caracaras scratching or plucking wasps off their faces and feathers. We also calculated the time it took caracaras to complete the attack, defined as the period within which a caracara first appeared perched in the field of view of one of the cameras until it tore into the wasp nest with its beak, or knocked the nest off the plant substrate. If caracaras were apparently driven from the nest area by the wasps, we recorded the time elapsed until the birds returned. We recorded an “absconding response of wasps” when all wasps departed from the nest envelope.

We calculated the Spearman’s Rank Correlation Coefficient as a measure of correlation between the size of wasp nests and the time caracaras required to complete nest attacks [26]. We used a Wilcoxon Rank-Sum test to compare the time for completion of attacks between nests that were defended and those that were not. We performed all tests in R 2.15.2.

5.3.4. Acquisition of potential repellents from the faces, feathers or feet of caracaras

We captured five caracaras in the forest surrounding the Inselberg camp by luring them into a mist net with a hand-carved conspecific decoy and playback of territorial calls [13]. The permits for the attraction and capture procedure were approved by the Animal Care and Use Committee of Simon Fraser University (Protocol number 849B-07) as well as the Direction Régionale de l'Environnement de Guyane (DIREN), and all permits complied with all relevant regulations. We took great care to avoid injury to birds, hooded them to minimize stress, marked them with colored Darvic plastic bands, and released them unharmed. We smelled each bird and noted any unusual or unpleasant odors. Following standard procedures [27], we surface-extracted the bare skin of each bird's face and neck, the scaly skin of its feet and tarsi, and its contour feathers on the back and breast, using in sequence cotton swabs soaked in distilled hexane or methanol to extract chemicals of potentially different polarity. Swabs of the face and throat typically left a yellowish stain on the cotton (Fig. 5.1 B). We then placed the cotton swabs in glass vials, added 200 µl of solvent, and kept samples at -4 ºC until they could be analyzed in the laboratory.

5.3.5. Gas chromatographic-electroantennographic detection analysis of cotton swab extracts of the caracaras' faces, feathers or feet

We anticipated that any defense chemicals of caracaras repellent to sympatric prey wasps would need to be perceptible to wasps and thus would elicit antennal responses which then could help determine the key components for chemical identification. Therefore, we collected adult wasps from two *P. occidentalis* nests (4°52'44"N, 52°20'06"W) and used their antennae in gas chromatographic-electroantennographic detection (GC-EAD) analysis [28,29] of combined cotton swab extracts from the caracaras' faces, feathers and feet. *Polybia occidentalis* is a representative prey species with broad Neotropical distribution and a high degree of sympatry with caracaras. For GC-EAD analyses, we used a Hewlett-Packard (HP) 5890 gas chromatograph fitted with a GC column (30 m × 0.25 mm ID) coated with DB-5MS (J&W Scientific, Folsom, California, USA). For each recording (n = 15), we removed an antenna from a wasp's head, and suspended it between two glass capillary electrodes (each 1.0 × 0.58 × 100 mm; OD × ID × length; A-M Systems, Inc., Carlsborg, Washington, USA) filled with saline solution [30]. We further analyzed compounds that elicited consistent antennal responses by GC-mass spectrometry (MS) on a Varian Saturn 2000 Ion Trap GC-MS fitted with the DB-5MS column, using separate hexane extracts of the caracaras' face, feathers and feet. The temperature program for GC-EAD and GC-MS analyses was 50˚ C (for 3 min), 20˚ C per min to 280˚C (held for 5 min).

5.3.6. Collection and analyses of defensive secretions from *Azteca* ants

Three compounds in caracara foot extracts [2-heptanone, sulcatone, an iridodial isomer] (see Results) are also known to occur in defensive secretions of dolichoderine ants, including *Tapinoma* spp. [31] and *Azteca* spp. [32]. *Azteca chartifex* is abundant at our study site, which led us to predict that caracaras coincidentally acquire chemicals from *A. chartifex* or other dolichoderine ants when they alight on ant-inhabited trees. To compare chemicals present in *Azteca* ants with those present on caracaras, we located (near the Pararé Camp) the large carton nests of *Azteca* nr. *chartifex* (more specific taxonomic determination was not possible based on our collections of worker ants), placed glass capillary tubes (1.5 × 100 mm) into the terminal end of these nests, extracted defensive secretions from the tubes with hexane, and stored these extracts at -4º C prior to GC-MS analysis as described above.

5.3.7. Physical disturbance of wasp nests

To determine whether physical damage, as might be inflicted by caracaras, would trigger a stinging defense or an absconding response of wasps, we conducted the following four manipulations, in sequence, on ten nests of *P. bistriata.* We (1) tapped the nest substrate three times while grasping the nest base with a gloved hand; (2) stroked the nest three times with a gloved hand while grasping the nest substrate; (3) tore the nest envelope with a sharp object while grasping the nest base with a gloved hand; and (4) tore the nest from the plant substrate, placed it on the ground, and tapped it with a finger. We waited two days between applications of each of the four treatments to an individual nest. In each replicate of each treatment, we counted the number of wasps attempting to sting. The final disturbance was replicated only 9 times, as the tenth nest had been raided by ants in the interim. The average nest size was 5.9 ± 1.3 cm (mean ± SD) at its widest point, and each nest contained capped brood (as determined after nest destruction).

5.4. Results

5.4.1. Field observations of wasp-nest predation by caracaras

During 11 months of field work, we witnessed attacks by caracaras on two wasp nests. In most instances when we approached, the birds ceased foraging, alarm-called, and flew off. However, on 28 January 2008, we observed a group of five caracaras feeding on the brood of a large *Polybia dimidiata* nest (~50 cm diameter) located 20 m above ground. The nest had large holes in the upper and lower envelope. As many as three birds were perched on the nest at a time. While we observed the event for 36 min, and filmed it for 20 min, a large number of wasps flew around the birds at a distance of several meters, but no wasps approached the birds (Appendix A, Video S1). We made a second observation of a single caracara feeding on a small (10 cm diam.) *Polybia* nest, but we did not witness the commencement of this attack, nor were we able to collect workers for identification.

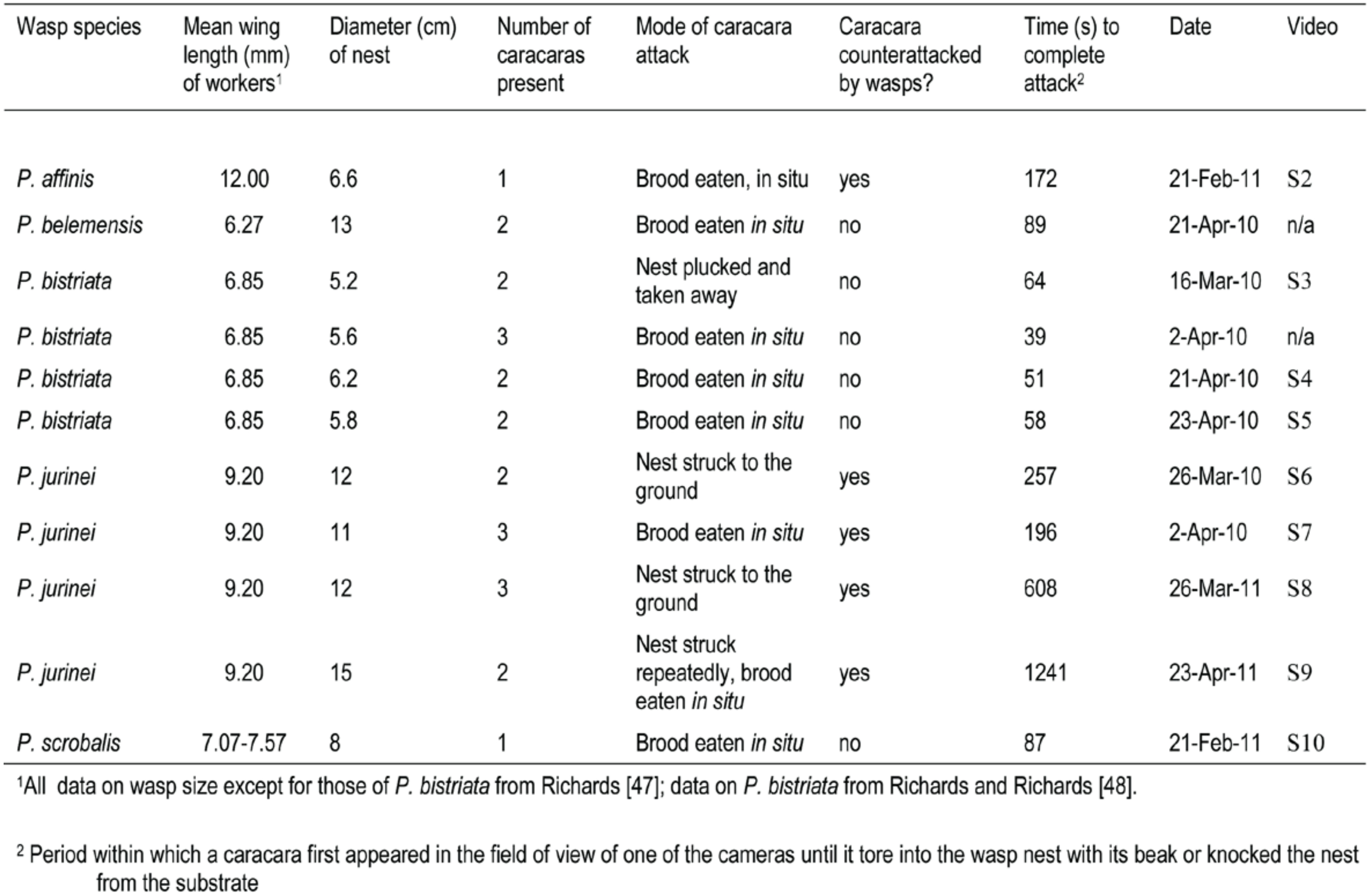
5.4.2. Controlled recordings of wasp nest predation by caracaras

Caracaras successfully attacked all nests of *P. bistriata, P. belemensis* and *P. scrobalis* (Table 5.1). In no instance did the wasps mount a detectable defense, but instead flew away upon nest disturbance. Caracaras ate the brood of all small nests but one *in situ*. In the exceptional event, a color-banded female attacked a *P. bistriata* nest, plucked it with her beak from the branch, and flew off with it.

In two of the attacks on *P. bistriata* nests, the caracaras repeatedly pulled on the nest substrate, dislodging or driving most of the wasps off in the process. As soon as the caracaras disturbed the nest or tore into the envelope, the remaining wasps departed (Appendix A, Video S3, S4).

During the attack on the *P. affinis* nest, the caracara first landed beside the nest, coming under attack by wasps flying off the envelope. The bird departed, then returned and approached on the upper crosspiece and had a wasp attack its face on the left side. The bird scratched off the wasp with its left foot, and henceforth experienced no further counterattacks, not even when it was tearing into the nest and consuming the brood (Appendix A, Video S2).

Table 5.1. Summary of video-recorded observations of caracara attacks on nests of various species of *Polybia* wasps.



Wasp species	Mean wing length (mm) of workers[1]	Diameter (cm) of nest	Number of caracaras present	Mode of caracara attack	Caracara counterattacked by wasps?	Time (s) to complete attack[2]	Date	Video
P. affinis	12.00	6.6	1	Brood eaten, in situ	yes	172	21-Feb-11	S2
P. belemensis	6.27	13	2	Brood eaten *in situ*	no	89	21-Apr-10	n/a
P. bistriata	6.85	5.2	2	Nest plucked and taken away	no	64	16-Mar-10	S3
P. bistriata	6.85	5.6	3	Brood eaten *in situ*	no	39	2-Apr-10	n/a
P. bistriata	6.85	6.2	2	Brood eaten *in situ*	no	51	21-Apr-10	S4
P. bistriata	6.85	5.8	2	Brood eaten *in situ*	no	58	23-Apr-10	S5
P. jurinei	9.20	12	2	Nest struck to the ground	yes	257	26-Mar-10	S6
P. jurinei	9.20	11	3	Brood eaten *in situ*	yes	196	2-Apr-10	S7
P. jurinei	9.20	12	3	Nest struck to the ground	yes	608	26-Mar-11	S8
P. jurinei	9.20	15	2	Nest struck repeatedly, brood eaten *in situ*	yes	1241	23-Apr-11	S9
P. scrobalis	7.07-7.57	8	1	Brood eaten *in situ*	no	87	21-Feb-11	S10

[1] All data on wasp size except for those of *P. bistriata* from Richards [47]; data on *P. bistriata* from Richards and Richards [48].

[2] Period within which a caracara first appeared in the field of view of one of the cameras until it tore into the wasp nest with its beak or knocked the nest from the substrate

In contrast to *P. bistriata*, caracaras suffered counterattacks from defending wasps during all attacks on *P. jurinei* nests. These included four instances of wasps flying from their nest to intercept a caracara approaching in flight (e.g. Appendix A, Video S7). During one of the caracara attacks, the wasps' counterattack was so fierce that it prompted the birds to temporarily retreat four times (Appendix A, Video S6), although the birds usually returned within 10-90 seconds (Table 5.2). During two predation events, caracaras mounted rapid fly-by attacks on the nest, striking it with their talons and eventually causing the nest to fall to the ground (Appendix A, Videos S6, S8, and Fig. 5.3) where the birds consumed the brood. In the attack on the smallest *P. jurinei* nest (Appendix A, Video S7), a caracara was counterattacked both in flight and after alighting near the nest, prompting the bird to scratch and pluck wasps from its plumage. However, when two caracaras began tearing into the nest envelope, the wasps absconded.

Table 5.2. Number of instances where caracaras were driven away by attacking *Polybia* workers.

Wasp species	Number of times caracara(s) were driven away	Time (s) to return of caracara(s)	Date	Video
P. scrobalis	1	46	21-Feb-11	S10
P. jurinei	3	40, 20, 98	26-Mar-10	S6
P. jurinei	1	10	2-Apr-10	n/a
P. jurinei	2	51, 11	26-Feb-11	S7
P. jurinei	1	960	23-Apr-11	S9

Figure 5.3. Fly-by attack of Red-throated Caracara on nest of *Polybia jurinei*. Single-frame images of a video recording revealing the fly-by attack of a Red-throated Caracara (ventral view) on a large nest of *Polybia jurinei* (arrow in panel 1) that we had transferred to the recording arena (see Figure 2). In the corresponding video S6, it is apparent that the wasps take off from the nest envelope to intercept the bird approaching from the left side (panels 1-3). Note that the nest is dislodged by the bird's talons (panel 4).

In the attack on the largest *P. jurinei* nest, a single caracara flew low over the nest, and while passing was attacked by several wasps. After this, the caracara struck the crosspiece holding the nest four times and the nest directly a single time, before a caracara perched next to the nest and began tearing into it with its beak. At this point, the remaining wasps absconded, leaving the caracara to eat the brood *in situ* (Appendix A, Video S9).

The two species of wasps (*P. jurinei*, *P. affinis*) that defended their nests against caracara attacks have workers that on average are larger than the workers of those species (*P. belemensis*, *P. bistriata, P. scrobalis*) that offered no defense (Table 5.1, Appendix A, Fig. S1). Furthermore, caracaras took longer to complete attacks on species that did defend their nest (median 257 s, range 172-1240 s) than on those that did not (median 61 s, range 39-89 s; Wilcoxon Rank-Sum Statistic: 30, n = 5, m = 6, $p <$

0.01 (Table 5.1). There was also a strong positive correlation between the time taken to complete attacks and the diameter of nests (Spearman's $\rho = 0.82$, $p < 0.01$, Table 1, Appendix A, Figure S1).

5.4.3. Gas chromatographic-electroantennographic detection (GC-EAD) analysis of cotton swab extracts of the caracaras' faces, feathers and feet

We captured caracaras 16 times in the course of our fieldwork, and none of the birds we captured had unpleasant odors during handling. Because chemical constituents in hexane and methanol extracts were similar, we present analytical results pertaining to only the hexane extract. GC-EAD and GC-MS analyses of combined cotton swab extracts of the birds' faces, feathers or feet revealed three compounds that consistently elicited antennal responses from wasps: 6-methyl-5-hepten-2-one (sulcatone), an epimer of *cis, trans*-iridodial, and myristic acid (Fig. 5.4, see Document S12 {Appendix A} for detailed analytical and synthetic descriptions). Although present in cotton swab extracts, other iridodial isomers did not elicit antennal responses. GC-MS analyses of separate face, feather, and feet extracts revealed that sulcatone, 2-heptanone and iridodial were present in foot extracts but not face or feather extracts.

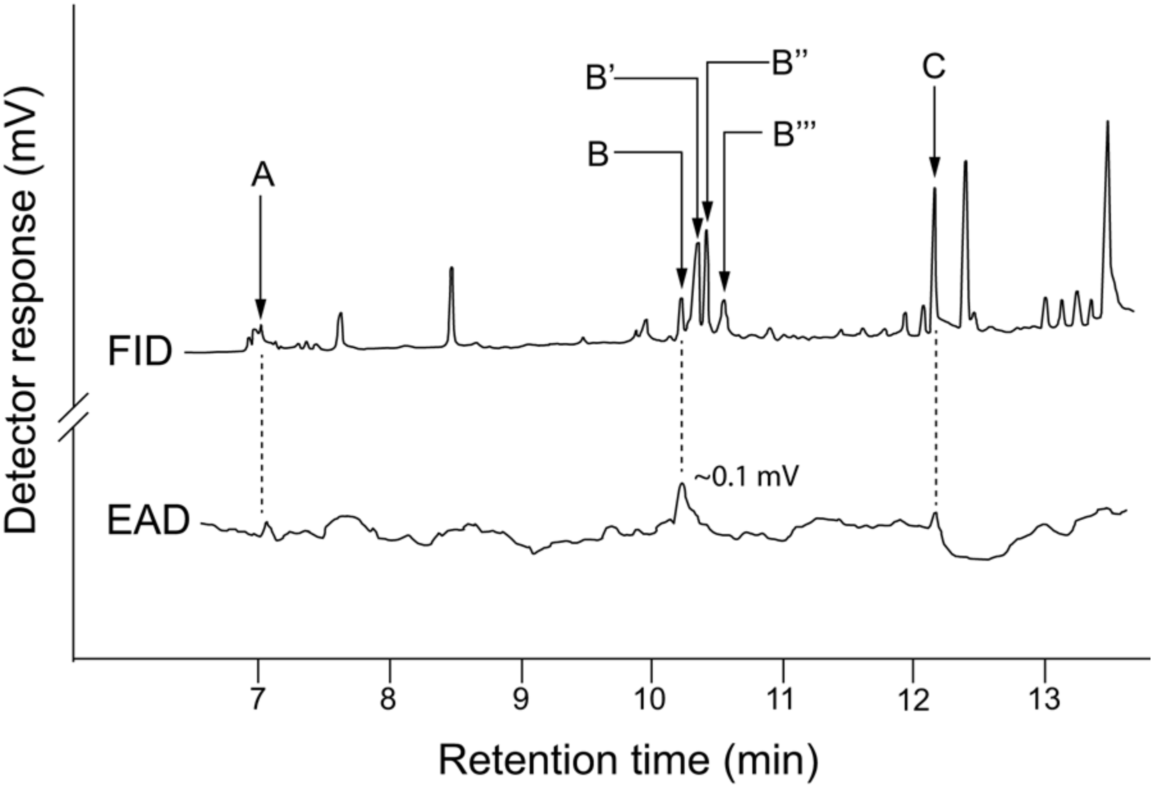


Figure 5.4. Gas chromatographic-electroantennographic detection analysis of combined cotton swab extracts of a caracara's face, feathers and feet. Representative recording (n = 15) of flame ionization detector (FID) and electroantennographic detector [EAD: antenna of a female wasp of *Polybia occidentalis*] responses to aliquots of combined cotton swab extracts of a Red-throated Caracara's face, feathers and feet. 6-Methyl-5-hepten-2-one (A), an epimer of *cis, trans*-iridodial (B), and tetradecanoic acid (C) elicited consistent antennal responses. B', B'' and B''' refer to other iridodial isomers. Chromatography: splitless injection, injector and detector temperature: 240 °C; DB5-MS column; temperature program: 50 °C (3 min), 20 °C per min to 320 °C; see methods for details.

5.4.4. Collection and analyses of defensive secretions from *Azteca* ants

When we disturbed *Azteca* nests by inserting a glass capillary tube in the nest carton, many ants emerged and attacked the capillary tube by biting and secreting pygidial gland content. This defensive secretion appeared as a white, sticky fluid (Appendix A, Video S11). GC-MS analyses of these gland secretions revealed 2-heptanone, sulcatone and several isomers of iridodial. The two ketones and the same isomers of iridodial were also present in caracara foot extracts (Fig. 5.5), but not in the face or feather extracts.

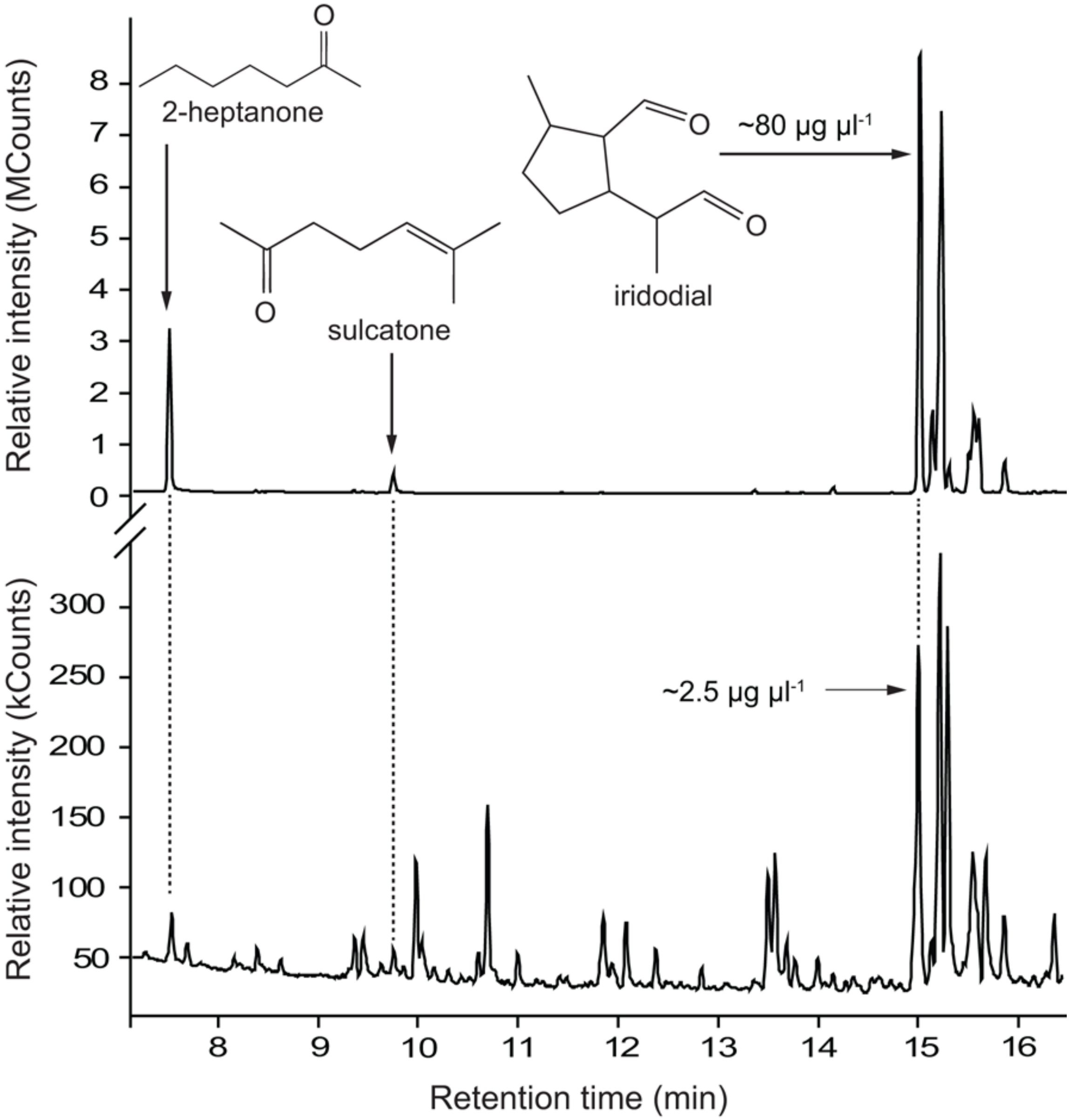


Figure 5.5. Comparison of chemicals from the Red-throated Caracara and *Azteca* nr. c*hartifex* ants. Total ion chromatograms of aliquots of a defensive secretion extract of *Azteca* nr. *chartifex* ants (top) and a cotton swab foot extract of Red-throated Caracaras (bottom). Dashed lines refer to compounds present in both samples. Note the occurrence of 2-heptanone, sulcatone and an epimer of *cis, trans*-iridodial in both extracts. Chromatography: Varian 3800/Saturn 2000 Ion Trap GC-MS; splitless injection; injector temperature 240 °C; DB5-MS column; temperature program: 50 °C (3 min.) 20°C per min. to 280°C; see methods for details.

5.4.5. Physical disturbance of *P. bistriata* nests

No physical mode of nest disturbance [tapping (1), stroking (2), envelope tearing (3), and placement on the ground (4)] elicited stinging responses from wasps. During modes 1-3, the wasps flew about and settled on nearby vegetation but did not attempt to sting. Subsequent to disturbance modes 1-3, the workers returned to their nests after several minutes. In contrast, each nest we detached from the substrate and placed on the ground was abandoned within seconds (Table 5.3), and the workers did not return.

Table 5.3. Stinging and evacuation behavior by worker wasps of *Polybia bistriata* in response to various types of disturbance of their nest. Absconding is defined as all wasps leaving the nest and not returning.

Type of disturbance	n	Wasps attempting to sting	Evacuation
Tapping	10	0	Partial
Stroking	10	0	Partial
Tearing	10	0	Partial
Knocking down nest	9	0	Absconding

5.5. Discussion

Our data support the following conclusions: (1) caracaras engage in a “hit-and-run” predation tactic when they attack nests of highly aggressive and defensive wasps; (2) the resulting nest damage prompts wasps to abscond; (3) the caracaras’ tactic of forcible physical attack and flight reduces the risk of getting stung; (4) there are no detectable repellent chemicals on faces and feathers of caracaras; and (5) the chemicals on the caracaras’ feet likely originate from *Azteca* ants, but do not seem to fend off attacking wasps.

Our video recordings of wasp nest predation by caracaras did not support the hypothesis of a chemical defense that protects caracaras from counterattacking social wasps. On the contrary, caracaras were vigorously attacked (even in flight) and likely stung by two of the wasp species we studied. The caracaras avoid excessive wasp attacks by inducing absconding of the colony before they feed on the brood or carry the nest away.

When a caracara attacked, small-bodied workers of *P. bistriata* nests did not attempt to sting the bird, as they did not attempt to sting us when we experimentally disturbed their nests. Facing a determined and persistent attacker, *P. bistriata* does not attempt to defend. However, large wasp species, such as *P. jurinei*, do attempt to sting the attacking bird for some time, but given sufficient disturbance of the nest they will also abscond. The specific defense behavior exhibited by each wasp species likely reflects their ability, or inability, to repel large avian predators, and may be related to relative sting potency and worker numbers. Previous research has shown that small-bodied wasp species are generally less likely to defend than large-bodied species, and nests with a large brood are more predisposed to defend than nests with little brood [33]. Unsurprisingly, it took caracaras longer to complete an attack when the wasp nest was defended, although ultimately they destroyed all the nests.

The lack of stinging attacks by *P. bistriata* during experimental physical disturbance surprised us, because during unrelated activities this species did sting us several times when we accidentally brushed against a nest. The wasps' stinging defense in response to a slight nest disturbance may warn intruders to stay away from the nest, whereas intense disturbance may signal that attack by a determined predator is well under way and that defense is futile. In any case, *P. bistriata* workers responded similarly to disturbance by caracaras and humans.

In birds, the decision of parents to defend brood depends on their investment in the brood and their ability to drive a predator away [34]. Similarly, wasps may adjust defensive tactics depending on the predator they face. By abandoning a nest in response to the determined attack of a caracara, reproductive female and worker wasps preserve their potential to reproduce in the future, while sacrificing their current investment in eggs, brood, and nest materials. Other severe nest disturbances such as those caused by tree falls and army ant attacks also induce absconding in swarm-founding polistines [24,35,36], suggesting that coordinated abandonment of nests is a tactic that may minimize losses of worker wasps when a nest is faced with annihilation.

Larger wasp species, such as *P. jurinei*, seem to be capable of temporarily driving the caracaras away. Although the caracaras' fly-by attacks may reduce the probability of getting stung, it is conceivable that caracaras are stung repeatedly by counterattacking wasps. Excessive wasp or bee stings can be dangerous to many animals [37], and may have killed a Crested Honey Buzzard *(Pernis ptilorhynchus*) when it was counterattacked by honeybees [38]. Wasp venom resistance analogous to the snake-venom resistance of didelphid marsupials [39] could offer an alternative means of protection to caracaras, but this is yet to be studied.

The hit-and-run predation tactic of caracaras when they attack large wasp nests resembles the recently-documented behavior of Oriental Honey Buzzards attacking hornet nests [40]. The Honey Buzzards work in groups and apparently take turns in striking a hornet nest with their bodies and feet during fly-by attacks. Caracaras also cooperate during foraging [15]. In two of our videos documenting attacks on *P. jurinei* nests, two birds participated (Table 5.2). In one case, two birds tore into the envelope, in the other each of two birds struck the nest with their talons. We also documented several birds tearing into and sharing the brood of a large *P. dimidiata* nest. Group-living and cooperative foraging may be strategies that help caracaras share the risks and rewards of attacking formidable prey, such as *Synoeca* spp. [14,41] and *P. dimidiata* [this study]. The advantages of group foraging in other species include minimizing the variation in daily success among cooperating individuals [42], which is important if prey is patchily-distributed and difficult to find.

The vulnerability of wasp nests to caracara attacks sheds light on other defensive adaptations of social wasps against vertebrate predators. Many social wasps in the Neotropics have visually cryptic nests, which likely reduce the rate of detection by diurnal vertebrate predators such as caracaras [9,43]. Furthermore, many nests are located in dense tangles of branches and vines which may not only reduce detection by avian predators but also render rapid fly-by attacks difficult or impossible. Aggregated nesting, as the aggressive *P. rejecta* does in some locations [44], may allow several colonies to pool defenses against caracara predation. Such a tactic has been reported for some Asian honeybees defending against Bee-eaters (Meropidae) [45]. Finally, the massive mud nest envelopes of *Polybia* subgenus *Pedotheca* wasps (e.g. *P. singularis*) [7,8], and the tough felt-like nests of *Chartergus* and *Epipona* wasps [46–48], may make it difficult for avian predators to inflict critical nest damage or to dislodge nests from branches. Such nests may render the caracaras' hit-and-run tactic impossible, although further studies would be needed to support this hypothesis.

The predation behavior of caracaras causes disturbance and damage to targeted wasp nests and induces absconding of worker wasps. This type of tactic does not necessarily require a strong chemical repellent to protect the birds from wasps [15], as absconding wasp colonies cease defensive stinging. The hypothesis of a chemical repellant was likely formulated [15] because the initial stage of the caracara attack and the absconding response of the wasps were not witnessed closely.

The types of compounds [iridodial, sulcatone, 2-heptanone, myristic acid] we found in foot samples of caracaras are not likely to fend off rapidly-flying wasps, and in fact some species of wasp build their nests in close association with ants that secrete iridodial, sulcatone and 2-heptanone for defense [32,49]. The co-occurrence of these compounds on the feet of caracaras and in defensive secretions of *Azteca* ants implies that these compounds are ant-derived. Caracaras may acquire these compounds coincidentally while perching on trees inhabited with *Azteca* ants that vigorously attack animals on their trees, and/or while preying on *P. rejecta,* which is commonly commensal with *Azteca* ants [44].

Alternatively, caracaras may intentionally seek *Azteca* ants to anoint their feathers with ant secretions for protection from ectoparasites. This “anting” behavior has been reported in one other Neotropical falconid [50], but in that case the ant was an ecitonine, not a dolichoderine. Other anting birds, though, have been reported to seek iridodial-secreting ants [51]. However, because none of these ant-derived compounds was present in the feather samples of caracaras, intentional anting by caracaras probably cannot account for their presence. Nonetheless, the presence of these compounds on caracaras highlights a surprising connection between seemingly unrelated members of a tropical forest community, mediated by commensalism between ants and wasps, and predation by birds on wasps.

In summary, the predation tactic of caracaras is based on severe disturbance and damage to target wasp nests and ultimately relies on the absconding response of swarm-founding wasps. The hit-and-run predation tactic of caracaras when they attack the large nests of highly aggressive wasps reduces the risk of getting stung by counterattacking wasps. Further studies should investigate whether caracaras have immune adaptations to cope with wasp venom as the birds seem to suffer some stings during attacks on large wasp nests. In turn, the effect of defensive adaptations of social wasps, such as aggregate nesting of *P. rejecta* [40], and physical nest fortification by *P. singularis*, *Epipona* spp., and *Chartergus* spp., on the predation success of vertebrate predators merits further investigation.

5.6. Acknowledgements

We thank P. Gaucher and P. Chatelet for technical assistance in the rainforest, J. Carpenter of AMNH for identification of wasp specimens, and J. Morrison and two anonymous reviewers for constructive comments and meticulous reviews. Helpful commentary on ants was provided by J. Orivel of UMR-EcoFoG, Kourou, French Guiana, and by J. Longino of Evergreen State University. We thank JM Thiollay for having inspired this study.

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Appendix A Supplementary Material

Chapter 4

Table I. List of video, photographic and audio data documenting various types of behaviours of *Ibycter americanus* from Chapter 4. All files can be accessed as a collection and downloaded from the SFU Library website.

File name	Medium	Description of file content
Contact calls	Audio	Contact calls by several birds
Solicitation calls 1 & 2	Audio	Repeated solicitation calls
Alarm calls	Audio	Alarm calling in response to human
Alarm calling 1	Video	Single bird alarm calling in response to human
Alarm calling 2	Video	Alarm calling in response to human climber
Territorial calls 1 & 2	Audio	Territorial calls in response to playbacks
Territorial displays 1 & 2	Video	Territorial display in response to call playback
Territorial displays 3 & 4	Video	Territorial display in response to a competing display by another group
Decoy attack 1	Video	Physical attacks on decoys: female caracara approaches a decoy on foot and seizes the head
Decoy attacks 2 & 3	Video	Caracara of unknown sex stoops down and strikes a decoy in a clearing of the Inselberg Camp
Dawn chorus	Audio	Recording of dawn chorus at active nest tree
Intraspecific aggression	Video	Two video recordings of aggressive interactions between the Southwest group and a 3-bird group attempting to use the 2009 nest site

Chapter 5

Table II. List of supplemental data from Chapter 5. All media files can be accessed and downloaded from the SFU Library website, or accessed on the PLOS ONE website. Document S12 and Figure S13 below.

Item	Description
Video S1	Red-throated caracaras consuming brood from a nest of *Polybia dimidiata*, 28 Jan. 2008.
Video S2	Red-throated Caracara attacking nest of *Polybia affinis*, 21 Feb. 2011.
Video S3	Red-throated Caracara attacking nest of *Polybia bistriata*, 16 March 2010.
Video S4	Red-throated Caracara attacking nest of *Polybia bistriata*, 21 April 2010.
Video S5	Red-throated Caracara attacking nest of *Polybia bistriata*, 23 April 2010.
Video S6	Red-throated Caracara attacking nest of *Polybia jurinei*, 26 March 2010.
Video S7	Red-throated Caracaras attacking nest of *Polybia jurinei*, 2 April 2010.
Video S8	Red-throated Caracaras attacking nest of *Polybia jurinei*, 26 March 2011.
Video S9	Red-throated Caracara attacking nest of *Polybia jurinei*, 23 April 2011.
Video S10	Red-throated Caracara attacking nest of *Polybia scrobalis*, 21 February 2011.
Video S11	Collection of defensive secretion from *Azteca* NR *chartifex* workers, 18 November 2012.
Document S12	Detailed analytical and synthetic procedures used in determination of iridodial and other chemicals recovered from caracara foot-swab extracts.
Figure S13	Time taken for caracaras to complete attacks on wasp nests depends on nest size and wasp defensive behavior.

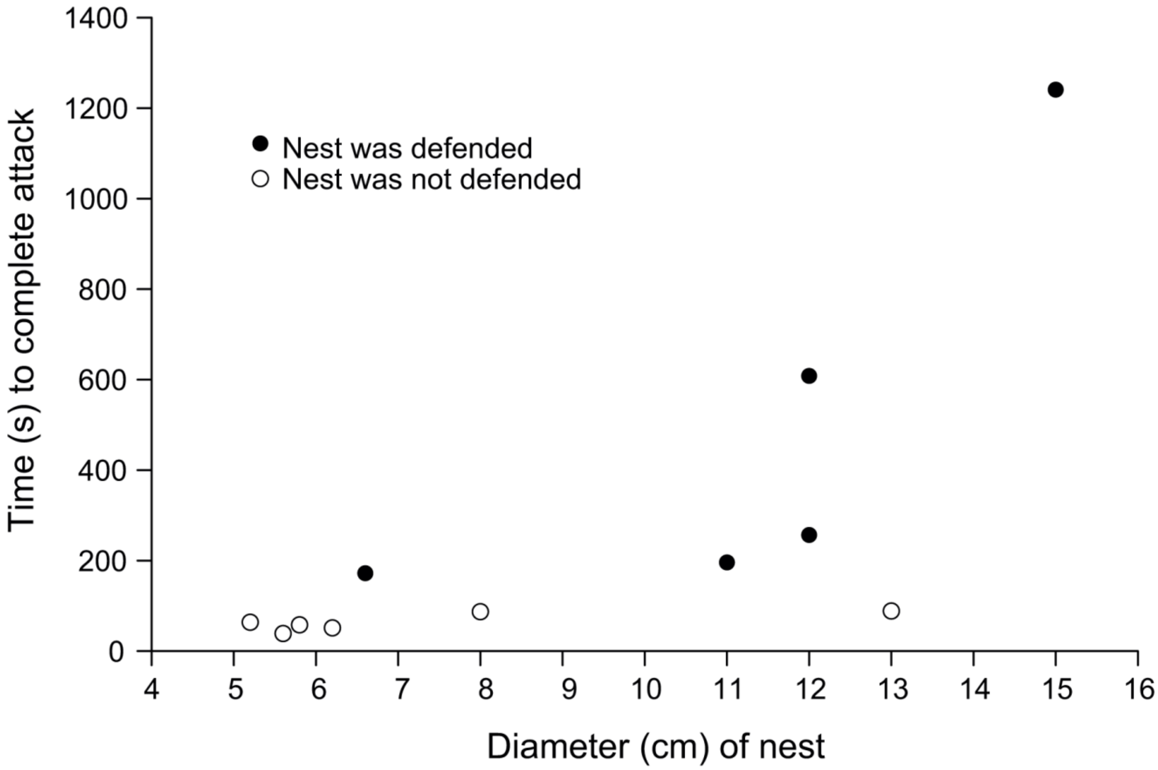

Figure S13. Time taken for caracaras to complete attacks on wasp nests depends on nest size and wasp defensive behavior.

Document S12. Chemical analyses

Identification of compounds in cotton swab extracts of caracara feet that elicited responses from wasp antennae

We identified the three compounds that elicited responses from wasp antennae in cotton swab extracts of caracara feet (A, B, and C in Fig. 5.4) as 6-methyl-5-hepten-2-one (sulcatone) (A), one or two epimers of cis, trans-iridodial (B), and tetradecanoic acid (C). Compound A had identical GC retention and mass spectrometric characteristics as an authentic standard (sulcatone) purchased from Sigma-Aldrich. Compound C had identical retention and mass spectrometric characteristics as synthetic tetradecanoic acid we prepared by oxidation of tetradecanol. The mass spectrum of compound B resembled that of nepetalactol or an iridodial (the corresponding di-aldehyde) [29]. The three compounds eluting immediately after compound B (B', B" and B"' in Figure 5.4) had a similar mass spectrum to B, suggesting that they are isomers of B.

Isomers of iridodial are abundant constituents in secretions of the ant Tapinoma nigerrimum [29], and on a BPX5 column (equivalent to a DB-5 column) elute in the following order: cis, trans, trans, trans (2 epimers), and trans, cis (2 epimers) [1,2]. As the cis, trans-iridodial eluted first, and the EAD-active compound B in (Fig. 4) was the first eluting isomer, we hypothesized that B is one or both epimers of cis, trans-iridodial.

To confirm this structural assignment, we initiated synthesis taking into account that cis, trans-nepetalactol and corresponding iridodials can be obtained from nepetalactone [2,3][51,52]. We purchased the essential oil of *Nepeta cataria* (Liberty Natural products Inc., Portland, Oregon, USA) which contains cis, trans- and trans, cis-nepetalactones in a 2.25:1 ratio by GCMS, similar to other reports of similar material [4]. We purified the nepetalactones in the essential oil by flash chromatography [pentane (95) : ether (5)] and treated them with 1,8-diaza-bicyclo(5.4.0)undec-7-ene in xylene, yielding the cis, trans-neptalactone as a single isomer. We then reduced this isomer with diisobutylaluminium hydride to afford cis, trans-nepetalactol as the major product. The reaction mixture also contained two minor products (~5%) which we assigned to be the corresponding iridodials of cis, trans-nepetalactol based on their mass spectra and a previous study [3] reporting that cis, trans-nepetalactol contained 5-8% of the corresponding iridodials (1R,2S,5R,8R-iridodial and 1R,2S,5R,8S-iridodial), which form as part of a chemical equilibrium. The first of two iridodials coeluted with B and had an identical mass spectrum. Based on these analyses, we conclude that EAD-active B in Figure 5.4 is a one or both epimers of cis, trans-iridodial.

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Appendix B.

Black-throated Antshrike preys on nests of social paper wasps in central French Guiana

Sean McCann, Onour Moeri, Tanya Jones and Gerhard Gries

This appendix has been accepted for publication in the journal *Revista Brasileira de Ornithologia*, pending revisions

Abstract

We studied predation by birds on nests of neotropical social paper wasps at the Inselberg camp of the Nouragues Reserve in Central French Guiana, a minimally-disturbed lowland rainforest habitat. Seven meters above ground, we built recording arenas and fitted them with motion-detecting video cameras. We transferred active wasp nests from surrounding forest to the arenas to film bird predators of wasps. In a video recording taken on 13 April 2010, we documented predation by a male Black-throated Antshrike, *Frederickena viridis,* on nests of *Polybia scrobalis* and *P. bistriata*. In rapid fly-bys, the antshrike repeatedly struck the wasp nests with his beak and in the process knocked parts of the nest to the ground. After the wasps absconded, he perched next to the nest of *P. bistriata* and fed on the wasp larvae and pupae. This predation tactic and type of prey was previously not known for *F. viridis.* Also, *F. viridis* apparently forages in higher strata of the forest than previously recorded.

KEY WORDS: Black-throated Antshrike, predation, social wasps, *Polybia*, *Frederickena viridis*

We studied predation by birds on nests of neotropical social paper wasps around the Inselberg Camp within the Nouragues Reserve in French Guiana (4°05' N - 52°41'W) (McCann *et al.* 2013), a low-altitude rainforest habitat far from human settlement (Charles-Dominique 2001). In the rainy season (January-April) of 2010, we recorded bird predation on wasp nests in recording arenas (McCann *et al.* 2013) that we had constructed about 7 m above ground in three trees 100 m northeast of the camp. Each arena consisted of four crosspieces, the two upper ones of which each bearing a spring clip for the attachment of a transplanted wasp nest. We transplanted nests from surrounding forest at night to avoid losing worker wasps from the nests. We equipped the arena with four 540 TV line resolution security video cameras (Aartech Canada, Oshawa ON, Canada) and recorded video with a 4-channel security digital video recorder (ChannelVision DVR 4C, ChannelVision Technology Costa Mesa, CA, USA) housed in a shelter within the camp. The DVR recorded video at 15 frames per second at 640 × 480 pixel resolution, with a 5 s recording buffer to record events prior to motion detection.

For recording sessions in April 2010, we mounted a nest of *Polybia scrobalis* and *P. bistriata* (Figure 1) in the arena. The *P. scrobalis* nest (8 cm in diameter, 5 cm high) was still attached to a large *Philodendron* leaf, and the *P. bistriata* nest (8 cm in diameter, 7 cm high) was attached to an *Astrocaryum* palm leaf.

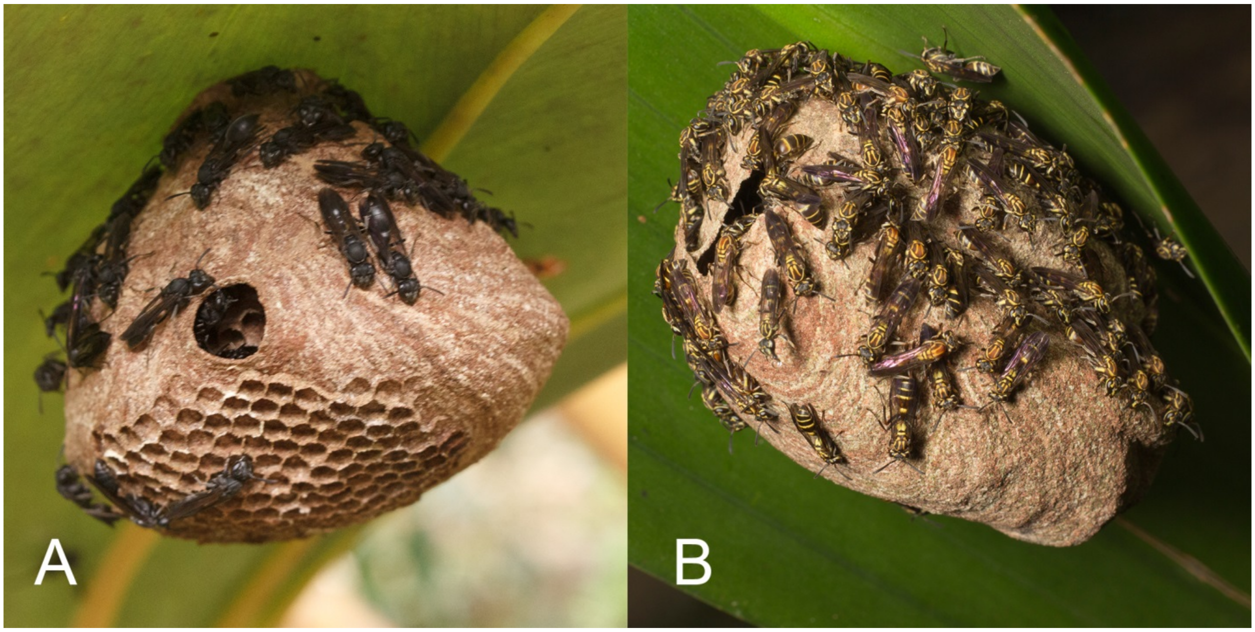

Figure 1. Representative photographs of nests of *Polybia scrobalis* (A) and *Polybia bistriata* (B) that were preyed upon by a male Black-chinned Antshrike*.*

On the morning of 13 April 2010, a male Black-throated Antshrike, *Frederickena viridis,* attacked both wasp nests in rapid fly-by strikes (See Video A1, Appendix A), hitting the nests with his beak. In the attack on the *P. scrobalis* nest which commenced at 06:38, the antshrike struck the nest from below and repeated the same type of attack 24 s later. In total, he struck the nest 5 times in this manner. Several times between strikes, he perched nearby looking at the nest. He also killed and dropped two adult wasps which appeared to be attacking him. During the last strike on the *P. scrobalis* nest at 6:40:24, a large portion of the nest fell to the ground.

At 6:49:04, the antshrike struck the *P. bistriata* nest with his beak from below, and repeated the same type of attack six times between 6:49:40 and 7:19. At 7:19:14, he perched immediately adjacent to the nest, and at 7:19:25 he began to eat larvae and pupae from the remains of the nest. No adult wasps molested the antshrike at this time. The bird fed for 76 s and departed at 7:21:03. It is noteworthy that this Black-chinned Antshrike foraged in a 7-m above-ground stratum which is higher than typically reported for this species (Zimmer & Isler 2003).

One hour following the antshrike's attacks, we examined the fragments of both nests that were still attached to substrate and found no remaining brood. Similarly, nest fragments on the forest floor that the antshrike had dislodged were void of brood, likely because the antshrike had eaten the brood after knocking these nest fragments to the ground. Swarms of adult wasps from both nests clustered on leaves near their former nest site. These swarms of reproductive females and workers will disperse, seek new nest sites, and found new colonies, a phenomenon known as absconding (Jeanne 1991, West-Eberhard 1982). The antshrike appeared to exploit the absconding response of these swarm-founding polistine wasps when it knocked their nests to the ground, affording him undefended brood. Absconding behaviour of swarm-founding polistine wasps was also evident during attacks on *Polybia* nests by the Red-throated Caracara, *Ibycter americanus,* a specialist falconid predator of social wasps (McCann *et al.* 2010, 2013). Unlike the antshrike, caracaras were not attacked by *P. scrobalis,* possibly because they are much larger and are seen as an enemy that cannot be defeated.

In conclusion, we present the first record of a Black-throated Antshrike attacking nests, and eating the brood of social wasps. Whether wasp larvae and pupae constitute regular or occasional prey items for the Black-throated Antshrike is yet to be investigated, as is the question whether other ant birds also prey on wasp nests.

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Associated Video

Video A1 shows a Black-chinned Antshrike preying on two *Polybia* nests. It can be accessed and downloaded from the SFU Library website.