



Honey robbing: could human changes to the environment transform a rare foraging tactic into a maladaptive behavior?★

Clare C Rittschof¹ and James C Nieh²

Human environmental modifications have outpaced honey bees' ability to evolve adaptive regulation of foraging tactics, possibly including a tactic associated with extreme food shortage, honey robbing. Honey robbing is a high risk, high reward, and understudied honey bee tactic whereby workers attack and often kill neighboring colonies to steal honey. Humans have exacerbated the conditions that provoke such robbing and its consequences. We describe robbing as an individual-level and colony-level behavioral syndrome, implicating worker bees specialized for foraging, food processing, and defense. We discuss how colony signaling mechanisms could regulate this syndrome and then explore the ecological underpinnings of robbing—highlighting its unusual prevalence in the commonly managed *Apis mellifera* and outlining the conditions that provoke robbing. We advocate for studies that identify the cues that modulate this robbing syndrome. Additionally, studies that apply behavioral ecology modeling approaches to generate testable predictions about robbing could clarify basic bee biology and have practical implications for colony management.

Addresses

¹ University of Kentucky, Department of Entomology, S-225 Agriculture Science Center North Lexington, KY, 40546, United States

² University of California, San Diego, Division of Biological Sciences, 9500 Gilman Drive, MC 0116, La Jolla, CA 92093-0116, United States

Corresponding author: Rittschof, Clare C (clare.ritttschof@uky.edu)

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Human agricultural practices impact honey bee foraging tactics like robbing

Human agricultural practices have diverse and complex implications for honey bee behavior, health, and

beekeeping costs. Colony management, presently a requirement for successful pollination of many cash crops worldwide, is itself a source of honey bee stress. For example, during crop bloom in intensive agricultural landscapes, honey bees are densely packed into small areas, leading to nutritional stress from competition and lack of floral diversity [1]. The world-wide transport of *Apis mellifera* has introduced novel pathogens and invasive parasites, most notably the *Varroa* mite, which has decimated colony survivorship and productivity in most regions where it has taken hold. In addition to beekeeping practices, agricultural land use generally has large effects on bee nutrition. Crop bloom results in boom-and-bust periods of resource availability, and honey bee colony health strongly tracks these feast-famine cycles [2]. In the U.S.A., a general period of nectar dearth arises in the mid-late summer, in part from the loss of native flowering prairie lands that naturally bloom at this time [3]. The replacement of natural floral communities with crop and grazing lands can increase competition for food among bee species, or alternatively, decrease competition by eliminating natural refuges and wild bees altogether [4]. Changing climate and weather patterns may further limit nectar abundance [5], harming bee populations [6]. Honey bees, therefore, face diverse stressors in human agricultural environments, including the complex and significant effects of floral resource limitation.

Honey bees forage for kilometers across the landscape, and they have sophisticated adaptations that allow them to take advantage of sparse, ephemeral floral resources [7]. During extreme resource scarcity, they can deploy a comparably extreme foraging tactic known as honey robbing. Robbing colonies invade neighboring colonies and collect honey stores, sometimes numbering in the kilograms. Because honey is processed, concentrated nectar collected from millions of different flowers, bee colonies provide a large, diverse, and valuable food resource. However, robbing is relatively rare under natural conditions because it is a high-risk tactic, in which foragers attack, fight, and kill members of the 'victim' colony [8]. This places unique demands on the robbing colony, which must mount an offense, but also collect and store an unusually large quantity of food. Moreover, victim colonies can be infected with transmissible

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diseases and parasites, weakening them and reducing their defensive behavior, which simultaneously makes them more attractive and more costly robbing targets [9–11,12*,13]. Because robbing can result in widespread colony mortality, it is understudied, and it remains unclear whether or not colonies adaptively deploy this foraging tactic under the extreme conditions presented by agricultural practices. For example, foraging adaptations like nestmate recruitment using the waggle dance may actually work against colony productivity in extreme conditions of resource scarcity [14*]. Thus, there is evidence for maladaptive expression of colony level foraging tactics in highly modified environments. Honey robbing, which integrates nutritional stress with other disease and mortality costs, may be one such tactic.

Here, we provide an overview of robbing in honey bees, focusing on *A. mellifera*, the commonly managed western honey bee. We describe honey robbing as a complex behavioral syndrome at individual and colony levels, and we discuss how well-established honey bee communication mechanisms may operate in a robbing context. We explore the scope of this foraging tactic in other *Apis* species. Finally, we discuss the ecological contexts that promote robbing, and consider how humans have altered robbing risks and benefits. Robbing may be a sophisticated colony-level foraging tactic that becomes dysregulated under human-altered conditions. As a result, robbing may be triggered in maladaptive scenarios, ultimately increasing colony losses.

Honey robbing as a behavioral syndrome

In social insects, behavioral syndromes (suites of correlated behavioral traits), occur at both individual and colony levels. This behavioral organization is particularly complex in honey bees because of their large colony sizes (20 000–60 000 worker bees). Colony foraging regulation is sophisticated: tactics change in response to colony demography, size, and nutritional deficits [15,16], the quality, quantity, and proximity of available resources [17,18], and abiotic factors including temperature [19]. To adjust food collection, colonies can deploy different ratios of nectar and pollen foraging specialists [20], and individuals can adjust their foraging trip frequency, duration, and distance, as well as their use of social information about resource quality and location (the famous dance language [21], which is likely also involved in robbing).

At the individual level, little is known about traits that characterize robbing foragers. Foragers are divided into individuals that specialize on resin, nectar, pollen, or water collection. The latter three specializations are correlated with sensitivity to sugar concentration in a logical manner (nectar, pollen, and water foragers have respectively low, medium, and high sensitivities [22]). This logic implies that robbing bees could have unusually low sensitivity and thus high sugar response thresholds.

Robbers are unlikely to be a distinct foraging specialization given the seasonal and opportunistic nature of the tactic. However, there is some evidence that they may consistently possess other correlated traits. For example, even when kept safely in the lab, robbers have decreased longevity compared to non-robbing foragers, a pattern that lessens the potential costs to the riskier tactic [10]. There is also some evidence that robbing foragers, even without engaging in fights, are unusually aggressive [23*], a potentially adaptive trait since aggression may be required to overwhelm victim colony defenses.

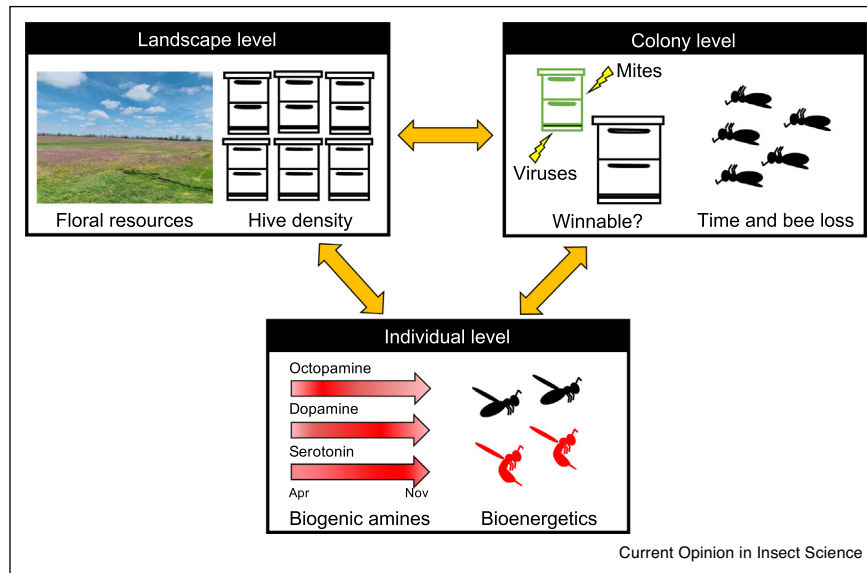
At the colony level, robbing is characterized by a conspicuous increase in foraging activity, requiring a concomitant increase in food storing abilities. Nectar foragers do not directly store their nectar load, but instead transfer it to receiver bees. The length of time a forager waits for a receiver affects the speed at which that forager leaves for another trip. During robbing, the rapid increase in foraging trip rate [23*] likely requires rapid, increased recruitment of receiver bees [24], and possibly a change in the feedback mechanism that regulates foraging activity (discussed below). The robbing colony's defensive specialists also have been implicated in the syndrome [23*]. Guard bees are specialists who defend against invading robber honey bees. Guards smell odors on incoming foragers and chase away non-nestmates [25]. Unsurprisingly, experiencing robber intrusion results in increased victim colony guard numbers and higher rates of non-nestmate rejection [26,27]. However, guards from robbing colonies that have not experienced such intrusions can also elevate their defensiveness, even towards their own foragers [23*]. The causes and consequences of this shift are largely unknown, although it suggests a correlation between robbing activity and invasion risk (Figure 1).

Colony signaling mechanisms and the regulation of robbing

Honey bees use social information and sophisticated communication mechanisms to modulate foraging behavior. Foragers perform waggle dances to signal the presence of good food resources [21], likely including a nest that can be robbed. In fact, the classic artificial sugar feeders used by researchers to decode the characteristics of the waggle dance more closely simulate a nest than a floral resource because flowers do not offer concentrated nectar *ad libitum*. Artificial feeders can provide very large quantities of high-concentration sugar solution that may simulate nest robbing [28*]. They also elicit guarding and patrolling (robbing behaviors), and attract hundreds of foragers to a single location [29]. Managed honey bee colonies are routinely fed during times of food dearth with artificial feeders containing sugar solutions, a human manipulation that may increase robbing, particularly given the lack of other food sources.

Using rich 'robbable' feeders placed outside the nest, researchers have identified two signals, tremble dancing

Figure 1



Mechanisms that co-regulate aggression and foraging in a robbing context. Robbing colonies display a behavioral syndrome characterized by simultaneous increases in foraging activity and aggression [23*,27,44*]. Because both foraging and aggression are high-energy behaviors [62,63], this co-regulation is surprising [64], and likely the result of interacting processes at the individual, colony, and landscape levels that are also under human influence. At the landscape level, floral resources alter competition among colonies [27,44*], while colony density can increase aggressive interactions due to processes like worker drift or increased availability of robbing targets. At the colony level, the decision to rob requires both increased aggression to fight bees from the victim colony and increased foraging activity to exploit the high-value food resource [23*]. Risks associated with robbing cause colonies to target 'winnable' small and often diseased colonies [10,12*,13]. The lost bees and time due to robbing pose additional costs that may modulate both foraging and aggression. Such costs may only appear over a long-term timeframe. At the individual level, studies document seasonal fluctuations in biogenic amines, including a peak in brain serotonin and dopamine levels during the robbing season [57]. These biogenic amines modulate honey bee aggression [55]. Seasonal shifts could reflect increased aggressive interactions with neighboring colonies, or a correlated response to floral resource scarcity that prepares colonies for defense. Bioenergetics are important for both foraging and aggression in honey bees, due in part to the high metabolic costs of flight [65]. However, brain metabolic dynamics, which are modulated by biogenic amines, distinguish foraging and aggressive specialists [59,66]. It is unclear how this neural mechanism is altered in the context of robbing.

and stop signaling, that regulate food collection and storage processes relevant to robbing. During a massive increase in nectar inflow (which could occur during robbing), there are insufficient receiver bees to collect food from incoming foragers. Forager wait time increases, and in response, they shift from waggle dancing to tremble dancing [30]. Tremble dancing may stimulate bees to engage in food receiving because the number of receivers increases after tremble dancing rises. This regulation is elegant since foragers cease recruiting new foragers to a food resource when the colony is unable to process it. New receiver recruitment can happen rapidly [31], but it is unknown whether this typical mechanism is sufficient to accommodate the influx of honey during robbing.

Robbing could trigger an additional signaling mechanism associated with resource competition. When foragers overwhelm an artificial feeder, they experience overcrowding [32] and fight with foragers from competing colonies [28*]. In this situation, foragers return to the nest and produce brief vibratory pulses called stop signals, directed at other waggle dancers recruiting for the same

overwhelmed resource. These signals cause foragers to stop dancing [28*]. Unlike the passive process by which tremble dancing supplants waggle dancing, the stop signal provides negative feedback to counter the positive recruitment effects of waggle dancing. The result is more rapidly reduced recruitment and a faster foraging behavioral shift at the colony level.

Different signals may allow colonies to weigh robbing risks and benefits during its incipient stages and abandon situations that are overly risky. For example, foragers that are not attacked at an overwhelmed feeder continue to waggle dance and recruit, while individuals who are attacked at a rich feeder (as could occur during the initial stages of robbing when a victim colony defends itself) produce stop signals and tremble dances [28*]. This case suggests a broader role for the tremble dance as a catalyst for reallocating colony labor [33]. Agent-based modeling of robbing suggests that stop signaling allows a colony to more efficiently stop robbing when the robbed colony can mount an effective defense [34]. Thus, stop signals can theoretically inform a conservative robbing decision-

making process. Such a process predicts that colonies preferentially attack weak colonies (which is supported by empirical evidence) and quickly call off attacks when strong colonies mount an effective defense [34], as supported by evidence of abandoned robbing attempts [8].

Robbing in different honey bee species

The existence of the defensive guard specialist whose effort is directly modulated by conspecific robber intrusion suggests that robbing occurs outside of the managed colony context (i.e., between non-managed *Apis mellifera* colonies). However, among the different *Apis* species, the most common observations of robbing come from apiaries, illustrating a potential impact of human manipulation. Colony management conditions may simultaneously increase passive worker drift and provoke non-nestmate aggression when resources become scarce, or when a robbing target presents itself. In *A. mellifera*, for example, managed colonies rob both within and among apiaries [12^{*}], and based on patterns of disease transmission, evidence of density-dependent robbing exists at the landscape, not just apiary, scale [35].

All *Apis* species create nests with highly concentrated resources that are attractive to interspecifics [36]. *Apis florea* [37], an open-nesting species, can rob *A. mellifera* colonies, and, surprisingly, given the generally smaller sizes of *A. florea* colonies and workers, can overcome *A. mellifera* [38]. *Apis cerana* (a cavity nesting species) is robbed by *A. mellifera* and *vice versa*, with *A. mellifera* possessing the competitive advantage [39]. Similarly, the open nesting *Apis dorsata* [37] can rob *A. cerana* [39], and *A. cerana* and *Apis koshevnikovi* (both cavity nesters) have been observed landing on *A. dorsata* nests to rob them [11].

Although robbing between species is broadly supported, it is less clear how common intraspecific robbing is for feral and wild honey bees. Compared to *A. mellifera*, there is little evidence of robbing, and surprisingly little intraspecific aggression in *A. florea*, *A. andreniformis* (an open nester), *A. dorsata*, and *A. cerana* [40]. However, *A. cerana* robbing and fighting were observed in managed colonies during honey harvesting [40], just as with *A. mellifera*. Robbing observations may be more frequent in apiaries because they are closely monitored, but the association with honey harvesting suggests that increased colony densities and honey availability due to management practices could increase robbing.

A. dorsata nest in clusters that could facilitate robbing. However, genetic analyses found only about 1.4% worker drift (defined as passive movement of workers to a non-natal colony) between colonies [41], suggesting adaptations to prevent drift, non-nestmate intrusion, or both. *A. dorsata* are relatively docile towards conspecifics, but they do become more defensive towards non-nestmates during the migratory season when a new nest has settled in their

vicinity. Actual robbing is still rarely observed [42]. Interestingly, managed *A. mellifera* colonies kept at a similar density show a drift rate that is 35-fold higher. *Apis mellifera* colonies naturally occur at much lower densities than the density of colonies found in most apiaries, which may have weakened natural selection against worker drift [43].

In addition to passive drift, robbing is a key mechanism for mite and virus transfer among colonies [12^{*}]. The prevalence of both stressors is correlated with landscape colony density, suggesting interactions among colonies from widely spaced apiaries. Forfert *et al.* [35] found a positive correlation between density and pathogen prevalence, comparing a minimum density of 0.32 colonies per km² to a maximum density of 1.4 colonies per km². Honey bee colonies are often managed at densities well above this maximum. In general, species variation in robbing could result from differences in the quantity of stored resources, nesting habits, dissimilarities in the risks and benefits of intraspecific aggression, management practices, or a combination of these factors.

Ecological conditions that provoke honey robbing

Floral resource limitation, specifically nectar scarcity, seems to be the main ecological condition that promotes robbing and can be exacerbated by a lack of natural floral resources in landscapes altered by humans. Nectar scarcity can be assessed by measuring visitation to sugar feeders placed in the vicinity of honey bee colonies. As floral resources dwindle, bees visit and collect food from feeders with progressively lower sugar concentrations [27,44^{*},45]. Although there is substantial landscape-level variation in floral resource abundance, in most moist temperate areas, nectar scarcity shows a predictable seasonal pattern that tracks robbing activity. Floral resources decline substantially in late summer [46]. Simultaneously, other factors compound the effects of food shortage, including increased competition from other bee species at their peak population abundance [47], heightened pressure to accumulate sufficient honey for the winter [48,49], and declining temperatures, which make nectar processing more energetically costly [50]. Further studies across a range of climate regions are needed to determine how robbing risk is predicted by any one of these seasonal changes. For example, in parts of Florida dominated by citrus, robbing risk increases after the end of the citrus bloom, even though this decline in floral resources occurs in early spring, removing the other seasonal pressures associated with the approach of winter [27].

Conclusions

Robbing is a sophisticated foraging tactic that carries great risks to honey bee colonies in human altered landscapes. Improved understanding of the mechanisms underlying

robbing is needed to understand its impacts and regulation. For example, the cues driving the simultaneous increase in foraging activity and aggression during robbing are unclear [23^{*}]. Guards could be confused by changes in nestmate odors that result from bees entering another nest. Guards may also respond to the heightened aggression displayed by robbing foragers, even though they are nestmates. Minor intrusion attempts by neighboring colonies could also cause these changes [26], and eventually escalate to robbing. If so, the use of migratory colonies for pollination could exacerbate robbing when colonies are set out closely spaced and bees begin to orient themselves in a new location. Other costs like pathogen and parasite transmission may be higher in high density conditions, and the impact of robbing in these contexts remains to be considered [51,52]. For beekeepers, the costs associated with robbing-related mortality and disease risk are compensated, to a degree, by the financial gains from pollination services. The state of this fragile balance could substantially impact the future of commercial beekeeping [53,54].

If colonies use floral resource abundance or other seasonal cues to anticipate robbing threats, they may proactively shift their defensiveness over the season. Food scarcity and defensive behaviors are correlated and peak in the fall when robbing is common, even without evidence of an acute robbing event [44^{*}]. Interestingly, brain titers of aggression-related biogenic amines, serotonin and dopamine [55,56], peak during August and September [57] when robbing peaks, but it is not known whether this variation arises from abiotic cues or robbing experience. Simultaneous expression of two high energy behaviors, aggression and foraging activity, is difficult to sustain, suggesting robbing has unknown colony level energetic consequences that may manifest over time. For individual robbers, it is unclear how foragers accommodate an increase in aggression, as these two phenotypes are typically mutually exclusive, including at the level of neural regulation [58,59]. Future work should address how the colony level features of the robbing syndrome are regulated by existing signals, and how robbing related behaviors are regulated at the individual level.

Determining the physiological and ecological mechanisms that modulate robbing (Figure 1) should improve our understanding of robbing and its consequences. For example, the cost of fighting over rich food sources is not necessarily, as might be expected, a mortality cost, but rather a cost of lost time. In the case of two stingless bee species, time spent fighting for an unwinnable resource takes away from time spent foraging for other resources, and thus mechanisms have evolved that allow species to avoid time-wasting combat [60]. A similar decision may be made by robbing honey bees. Is it better to rob or to forage for floral resources? It may also be illuminating to

integrate optimal foraging theory with game theory, an approach commonly used in studies of facultative kleptoparasitism (selective stealing of food resources [61^{*}]). Such modeling suggests that food stealing is affected by multiple factors, including fighting, but it is particularly influenced by population density (in our case, the number of colonies in each area, [35]), a factor that could be adjusted during agricultural pollination. In addition, decision analysis modeling could be used to better understand factors, such as the time costs and the probability of winning a rich resource, that a robbing or aggressive colony weighs [60]. In general, such modeling would be useful for understanding how collectives adapt to dynamic ecological conditions. Robbing, therefore, provides a case-study in the precariousness of social coordination in the face of accumulating stressors, particularly those exacerbated by human actions. In addition to its direct impacts on colony health, human intervention may result in maladaptive foraging tactics that lead to colony losses.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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