Title: Eavesdropping selects for conspicuous signals

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Animal communication signals generally evolve to become increasingly conspicuous for intended receivers [1]. However, such conspicuous signals are also more susceptible to eavesdropping: exploitation by unintended receivers [2]. It is typically thought that eavesdroppers harm signalers and select against conspicuous signals [3]. But, if signal conspicuousness deters eavesdroppers by indicating a cost, all receivers benefit. This may occur when eavesdroppers exploit food recruitment signals but need to fight for food access [4]. Using eusocial insects, stingless bees, we show that conspicuous signals can indicate competitive costs and enable signalers to escape eavesdropper-imposed costs. The dominant eavesdropper, *Trigona hyalinata,* avoided higher levels of *T. spinipes* pheromone that indicate a food source difficult to win, and showed attraction to lower pheromone levels that indicate a relatively undefended resource. Our decision analysis model reveals that eavesdropping individuals who assess takeover costs can benefit their colony by recruiting to weakly defended resources and avoiding costly takeover attempts.

Stingless bees are important tropical pollinators that live in diverse communities with high competition for floral resources. Many deposit species-specific pheromones around rich, persistent resources to recruit nestmates [5]. Foragers odor mark (deposit pheromone droplets) with approximately equal intensity at all food sources deemed worth recruiting to [6]. Many marking species intensely defend resources [7]. Thus eavesdroppers may have to fight for the advertised resource, recruiting nestmates and increasing the colony's energetic expenditure. Our focal species produce chemically distinct recruitment pheromones in labial glands (LG), and differentiate conspecific from heterospecific pheromones [4, 8]. *Trigona hyalinata* displaces *T. spinipes* from desirable food [7], but must recruit more nestmates to do so when the contested resource is heavily occupied.

To test if more odor marks indicate a more visited and therefore better guarded food source, we measured *T. spinipes* pheromone deposition and recruit arrival. We trained individual foragers to visit a rich sucrose feeder 100 m from their nest and then permitted them to freely recruit nestmates (see Supplemental Experimental Procedures). The number of foragers increased with the number of recent odor marks, and continued to rise once pheromone intensity plateaued (Fig. 1A). Forager abundance significantly correlated with the cumulative number of odor marks in the current (r=0.94) and preceding (r=0.75) 5-min periods (Fig. S1A). Thus, the species-specific chemical composition [4, 5, 8] and the number of odor marks provide the information eavesdroppers need to infer costs of accessing an advertised resource.

Next, we determined if *T. hyalinata* matches its eavesdropping responses to these inferred costs. Individual *T. hyalinata* foragers were given a choice of two feeders, one with no pheromone and one with a specific number of *T. spinipes* odor marks (see Supplemental Experimental Procedures). We presented pheromone from two sources: labial glands dissected from *T. spinipes* foragers' heads, and fresh odor marks deposited on filter paper strips by nearby *T. spinipes* colonies. *Trigona hyalinata* foragers exhibited a similar non-linear eavesdropping response to LG extract and to fresh odor marks (Fig. 1B,C). The bees were highly attracted to a low number of marks (0.075 bee equivalents, 4 marks), indicating they recognize competitors' pheromones as signals of high-quality food sources. Attraction to few odor marks persisted for the full 15 min of a trial despite pheromone volatilization (Fig. S1B). However, the bees strongly avoided a larger number of odor marks that correspond to significant fight effort (0.1 and 0.2 bee equivalents, ≥ 9 marks). Bees may not detect very small numbers of marks (0.05 bee equivalents, 2 marks). This strategy of determining resource access costs by eavesdropping on foraging information may be common. Diverse social insects show behavior consistent with assessing

food accessibility via the resident's size, group size, familiarity or aggression (Table S1).

To examine this more general case, we developed a decision analysis model (see Supplemental Experimental Procedures, Fig. S2A,B) that tests if more conspicuous signals (increased recruitment pheromone deposition) lead to higher takeover costs for eavesdroppers. This model determines the fight duration at which individual eavesdroppers should switch from approaching to avoiding non-nestmate odor marks to maximize the colony's energetic yield (Fig. 1D). It also calculates the relative cost of making sub-optimal eavesdropping decisions (Fig. 1E).

We used our model to predict eavesdropping behavior for three stingless bee species (*T. hyalinata*, *T. spinipes* [4], *Melipona rufiventris* [8]; see Supplemental Experimental Procedures), and compared predicted with measured patterns. When parameterized for experimental conditions, our model predicts well. Decisions that maximize colony fitness (daily energetic gain) agree with empirical eavesdropping data (Fig. 1D,E). Our model predicts that *T. hyalinata* and *M. rufiventris*, but not *T. spinipes*, colonies benefit when individual eavesdroppers match responses to perceived access costs (Fig. S2C-E). Live *T. hyalinata* and *M. rufiventris* foragers show clear preferences for or against odor-marked feeders, but *T. spinipes* foragers do not (Fig. 1B,C). Attraction to heterospecific odor marks is beneficial when takeover occurs within ~1 h of resource detection by a *T. hyalinata* eavesdropper, and is never good for a *M. rufiventris* eavesdropper. Model results further showed that *T. spinipes* colony fitness is the same for all eavesdropping decisions (Fig. S2E). However, *T. hyalinata* and *M. rufiventris* incur significant costs from sub-optimal decisions (Fig. 1E). Thus, strong energetic constraints can select for eavesdroppers that assess the accessibility of advertised resource, but not all species are subject to these constraints.

The current paradigm suggests that signalers should use less conspicuous communication

to avoid eavesdropping [2, 3]. However, we show that there is not always a conflict between optimizing a signal to escape from eavesdropping and to benefit the intended receiver. Further, we demonstrate an additional situation when individuals should not copy others [9]: when copying is costly. Conspicuous signals can provide valuable information about a resource's accessibility, enabling eavesdroppers to avoid costly competitive interactions. Thus, competing eavesdroppers may be a selective force for keeping signals conspicuous. Most eavesdropping studies focus on detecting predators, prey or mates [2]. Eavesdropping within a trophic level deserves more attention because such eavesdropping can influence signal evolution and has high potential to influence the structure of ecological communities [10].
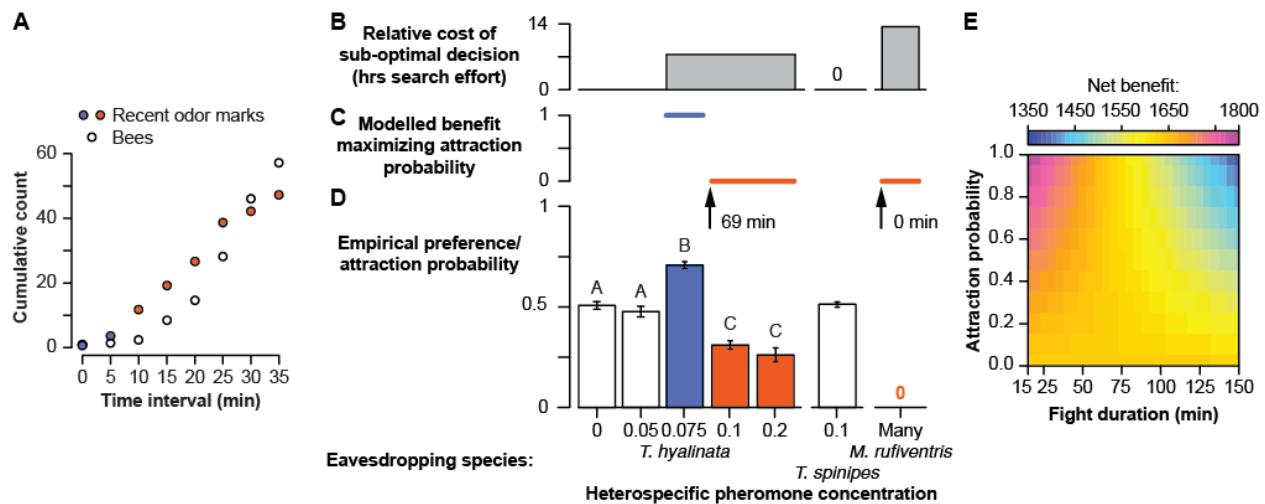
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Figure Legend

Figure 1. **Empirical and modeled stingless bee recruitment (A) and eavesdropping (B-E) behavior.** Empirical data show attraction (light gray dots, bars and lines) or avoidance (black), and the corresponding number of marks eliciting each response. A) Average buildup of *T. spinipes* odor marks and recruits over time. B & C) *Trigona hyalinata* eavesdropping responses depend on the quantity of *T. spinipes* pheromone encountered (B: LG extract, C: fresh odor marks; ANOVA including both pheromone sources: $F_{7,80}$=40.89, p<0.0001). A bee equivalent is the total contents of labial glands from one bee. Bars show mean ± SEM proportion of bees in a trial that preferred the pheromone. Letters indicate statistically different groups. The box encloses data collected in this study. D) Calculated fight efforts (times) at which the model predicts eavesdroppers will switch from attraction to avoidance. These values cannot be computed when the eavesdropper does not detect the recruitment pheromone (0, 0.05 bee equivalents), or when the relative cost of sub-optimal decisions is zero. E) Modeled energetic benefit to the colony when the eavesdropper makes a fitness-maximizing decision relative to sub-optimal decisions, standardized to hours of search effort.
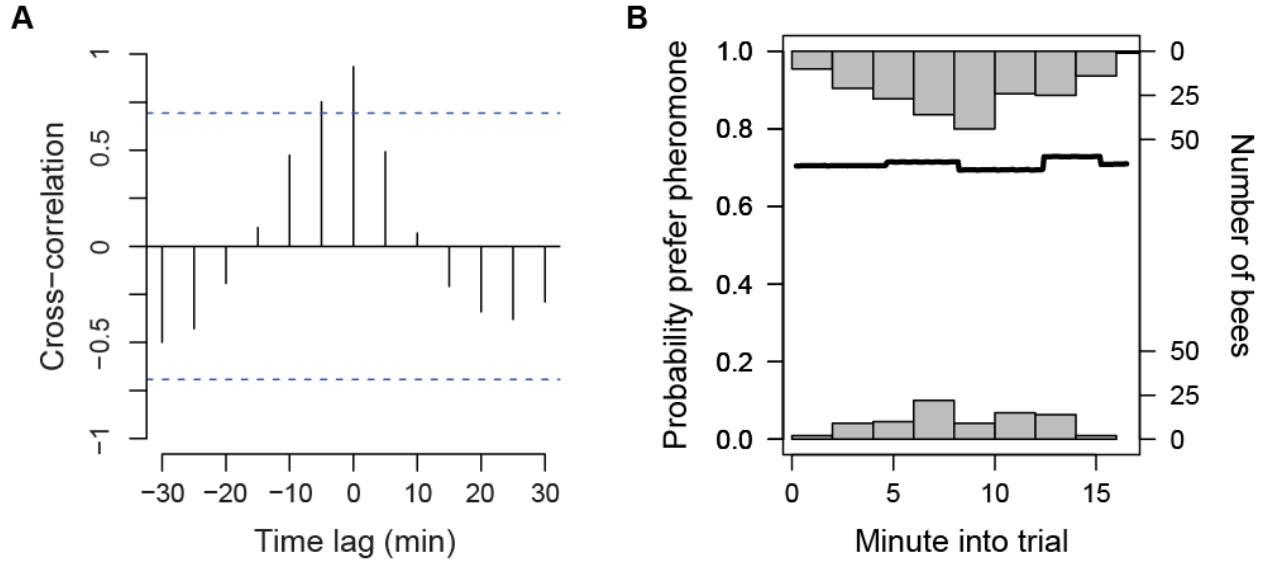
Supplemental Data

A

B

Figure S1. Detailed data from empirical recruitment and eavesdropping experiments. A) Temporal cross-correlation between *T. spinipes* odor mark and recruit numbers. Dashed lines show 95% confidence limits. Data are from five trials (each at a unique location) conducted with two colonies. **B)** Choices of individual *T. hyalinata* foragers in trials with weak *T. spinipes* recruitment pheromone (0.075 bee equivalents, 4 marks) do not change over time (GLMM: n=20 trials, time coefficient=0.0005±0.04, z=0.01, p=0.99). The thick black line shows fitted values from the GLMM (logit link), which included colony and odor source type as fixed effects and trial as a random effect. Histograms show the number of bees selecting the odorless (bottom) or pheromone-bearing (top) feeder in each 2 min time block. Model visualization follows recent recommendations [S1, S2].
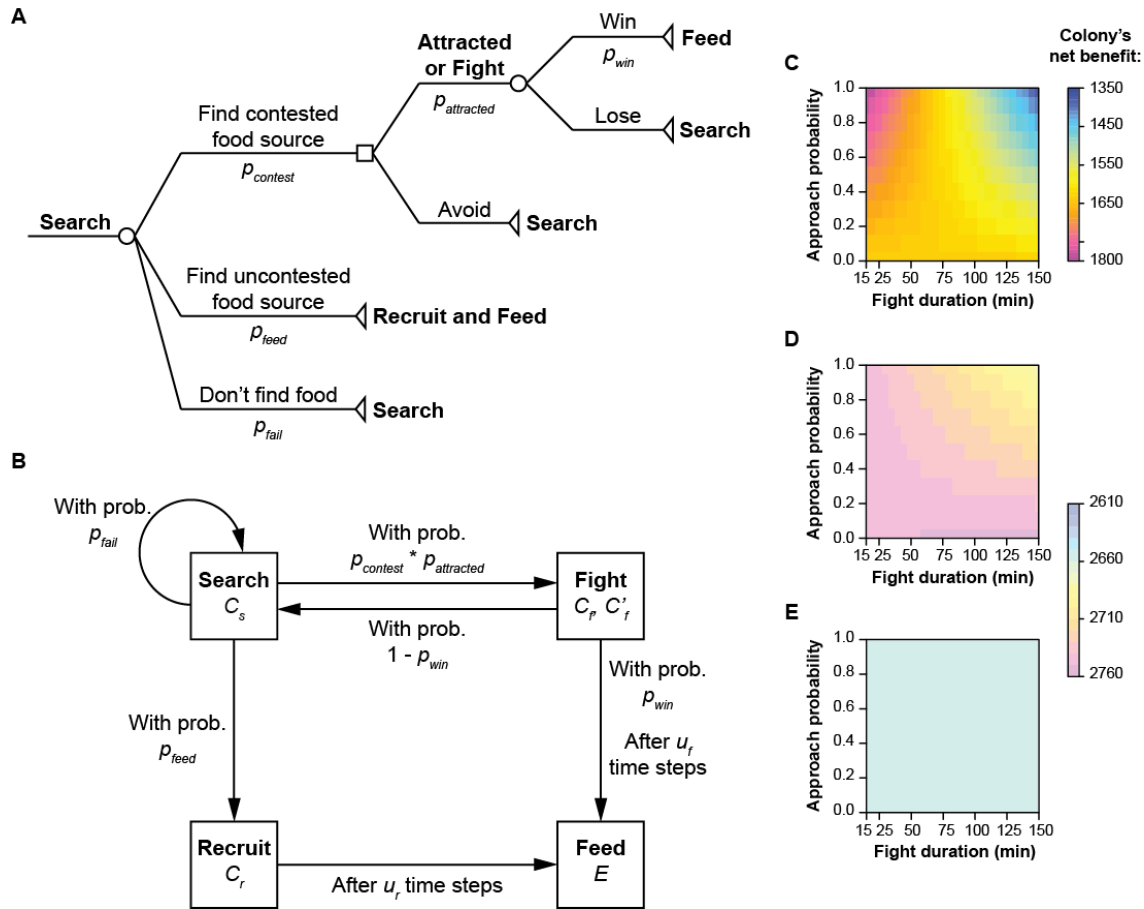
Figure S2. Eavesdropping model schematics (A, B) and outputs for three stingless bee species (C-E). A) Decision tree and **B)** flow diagram for the decision analysis model of stingless bee eavesdropping. In the decision tree, circles indicate chance nodes, squares decision nodes, and triangles end nodes. Behavioral states are shown in boxes in the flow diagram and are in bold type on the decision tree. The flow diagram shows each state and the rules governing transitions between states. Symbols under behavior states are the costs and benefits associated with each state. Subscripted ps are probabilities associated with each node. Supplemental Experimental Procedures describe each parameter and show values used when we parameterized the model for three stingless bee species. Heat diagrams (right column) show model behavior when parameterized for **C)** *T. hyalinata* eavesdropping on *T. spinipes* [this study], **D)** *M. rufiventris* eavesdropping on *T. spinipes* [S3] and **E)** *T. spinipes* eavesdropping on *T. hyalinata* odor marks [S4]. Colors indicate predicted net benefits across a range of eavesdropping decisions (y-axis) at each fight duration simulated (x-axis). Quantile regression coefficients (± SEM) and p-values for the attraction probability-fight duration interaction term are: *T. hyalinata* -15.46 ±0.58, *p* <0.0001; *M. rufiventris* -2.82 ±0.52, *p* <0.0001; *T. spinipes* 0 ± 0.40, *p* = 1.00. Other regression terms for the *T. hyalinata* model are: intercept 1632.61 ± 5.97, *p* < 0.0001; fight duration -0.10 ± 0.33, *p* = 0.77; attraction probability 213.18 ± 9.63, *p* < 0.0001. Other regression terms for the *M. rufiventris* model are: intercept 2746.73 ± 5.12, *p* < 0.0001; fight duration 0.28 ± 0.30, *p* = 0.35; attraction probability 8.46 ± 8.80, *p* = 0.34. Other regression terms for the *T. spinipes* model are: intercept 2656 ± 4.40, *p* < 0.0001; fight duration 0.00 ± 0.23, *p* = 1.00; attraction probability 0.00 ± 7.42, *p* = 1.00.

Table S1. Social insect studies that show patterns consistent with inferring resource access costs via eavesdropping on signals or "spying" [S5] on unintentional cues

Decision-making taxon	Information source	Information modality	Exploited information	Pattern
Termites				
Cryptotermes secundus drywood termite	*Coptotermes acinaciformis* drywood termite	Substrate-borne vibration	Vibrations indicate edible food; dominant species' vibrations indicate food is inaccessible	Incoming subordinate avoids dominant's vibrations [S6]
Wasps				
Vespula maculifrons yellowjacket	*Vespula germanica, Vespula vidua* yellowjackets	Visual	Presence of other wasps indicates a food source; wasps larger than the incoming one may exclude or eat it [S7]	Smaller wasps avoid occupied feeders when live near larger species [S8, S9], but are attracted to them at sites where larger species are rare or absent [S10]
Vespula consobrina yellowjacket	*V. maculifrons, V. vidua* yellowjackets	Visual		Wasps are only attracted to feeders occupied by a smaller species [S9]
Polistes fuscatus paper wasp	*V. maculifrons, V. vidua* yellowjackets	Visual	Presence of other wasp indicates a food source; incoming wasp's large size increases probability of rapid takeover	Larger wasps are attracted to occupied feeders [S8, S9, S11]
V. germanica yellowjacket	*V. maculifrons* yellowjacket			
Polybia occidentalis paper wasp	*Polybia diguetana* paper wasp			

Ants				
Formica pratensis formicine ant	*Formica cunicularia, Formica exsecta* formicine ants	Visual	Presence of other ant indicates movement towards food; food can be taken from subordinate species	Show attraction to known subordinate species but avoid unfamiliar species of unknown relative dominance [S12]
Dolichoderus debilis [S13] (published as *Monacis debilis*) dolichoderine ant	*C. carinata* [S13] (published as *Crematogaster limata parabiotica*) myrmicine ant	Visual or chemical	Co-nesting subordinate species' recruitment indicates a food source; dominant species must recruit conspecifics to take over the source	Dominant species recruits only recruits when few subordinates are on the food source [S14]
Camponotus femoratus camponotine ant, *Polyrhachis rufipes* formicine ant	*Crematogaster levior* crematogastrine ant, *Gnamptogenys menadensis* ectatommine ant	Chemical	Pheromone trail indicates a food source; incoming ant's dominant status increases probability of rapid takeover	Dominant species are attracted to subordinate species' pheromone trails [S15, S16]
Acromyrmex octospinosus, Atta cephalotes attine (leaf-cutting) ants	*A. octospinosus, A. cephalotes* attine ants	Chemical	Pheromone trail indicates a food source; high activity on the trail indicates the food source is heavily exploited	Follow heterospecific trails when they are empty, but not when they contain large numbers of heterospecific ants [S17]
To be included in this table, animals had to respond to food location information provided by competitors. We do not include research on bees' use of chemical "footprint" cues because the information they provide is highly context dependent [S18]. We also exclude studies of ant trail sharing that do not test trail following behavior.				

Supplemental Experimental Procedures

Study site and species

We conducted empirical work at the Universidade de São Paulo, Ribeirão Preto in southeastern Brazil. Multiple wild colonies of *T. hyalinata* and *T. spinipes*, plus 17 other species [S19], inhabit the campus and have been observed contesting natural food sources. Our focal species lay odor trails to recruit nestmates to rich resources [S20–S22], overlap in distribution [S23], exhibit similar floral utilization and have a clear dominance relationship [S24].

Recruitment experiment

We quantified the information pheromone concentration provides by measuring the relationship between concentration and forager abundance at a food source. We trained one *T. spinipes* forager 100 m from the nest with a dilute sucrose solution that did not elicit recruitment (0.375 M). At 100 m we switched to a higher concentration (0.99 M), and permitted the trained bee to freely odor mark and recruit nestmates. Bees odor mark by rubbing their mandibles against the edge of a leaf or other similar substrate [S25]. A single rubbing event is considered one odor mark [S20]. During the following 40 min, we counted the numbers of (1) odor marks placed on the feeder and (2) new recruits (each marked with non-toxic paint). For each trial (*n*=5, at unique locations, with two *T. spinipes* colonies), we calculated the (1) cumulative number of bees and (2) total number of recent odor marks (within the past 20 min, matching *T. spinipes* recruitment pheromone's retention time [S21]) in each 5-min time interval. We analyzed data in R [S26], with α=0.05.

Eavesdropping experiment

We tested responses of foragers from three *T. hyalinata* colonies to pheromones from two to three *T. spinipes* colonies, following published methods [S4]. The table below shows sample sizes. Trail-making stingless bees tend to odor mark visually conspicuous objects [S21, S27]. In the fresh odor mark trials, we therefore collected specific numbers of fresh odor marks on clean vertical strips of filter paper placed around a feeder to which *T. spinipes* foragers were recruiting. We replaced strips if we did not collect the correct number of marks within 5 min, to avoid significance decreases in odor mark potency from volatization. For each trial (individual choices from at least 10 bees over 15 min), we determined the proportion of bees landing on the feeder with pheromone, hexane or (in blank control trials) an arbitrarily selected feeder. After applying an arcsine square root transformation and ensuring our data met parametric assumptions, we tested the effect of pheromone concentration on eavesdropping behavior with a three-way ANOVA that included colony identity and odor source (labial gland extract — LG — or fresh marks), and a post-hoc Tukey's HSD test. Post-hoc testing also permitted calibration of LG concentration to fresh odor marks. Neither colony nor odor source affected eavesdropping behavior (colony: $F_{2,80}$=0.94, p=0.40; source: $F_{1,80}$=2.42, p=0.12). To determine if weak odor marks (0.075 BE, 4 marks) significantly volatilized during trials (15 min), we ran a generalized linear mixed model (logit link) with feeder choice as the response variable, time into the trial, colony and pheromone source as fixed effects, and trial as a random effect. We visualized results using the popbio package [S2].

	Treatment								
Sample sizes and bee participation in the *T. hyalinata* eavesdropping experiment	**Labial gland extract (bee equivalents)**					**Fresh odor marks (# marks)**			
	0	**0.05**	**0.075**	**0.01**	**0.02**	**0**	**2**	**4**	**≥ 9**
Trials conducted	16	10	14	19	10	6	6	6	4
Colonies tested	3	2	3	3	2	2	2	2	2
Mean number of choices per trial	19.00	13.60	14.21	16.53	13.20	17.83	14.50	17.67	14.75

One bee equivalent (BE) is the total labial gland contents from one bee. Data for 0 BE, 0.1 BE, and many marks include our published results [S4] as well as data from an additional *T. hyalinata* colony.

Eavesdropping model

We developed a decision analysis model of intra-guild eavesdropping to test the role of takeover costs in eavesdropping decision making. Decision analysis models integrate uncertainties, cost and benefit values, and preferences to formally address the factors affecting a decision [S28] and compare the relative value of each decision [S29]. They have provided valuable insights in fields such as medicine [S30], management [S31], conservation [S32] and homeland security [S33]. The facility with which such models handle multi-input decisions and uncertainty about exact parameter values [S29] make them useful for analysis of animal decision-making under natural conditions.

Key model assumptions

Assumption	Justification	Implementation
1) Stingless bee eavesdropping decisions maximize colony energetic net gain.	For eusocial organisms like stingless bees, the colony is the unit of reproduction and the target of natural selection. Thus, although eavesdropping decisions are made by individual bees, the responses have evolved to maximize colony fitness [S34].	Our model tracks energetics of the whole colony.
2) Takeover of food sources with more competitors requires greater effort by eavesdroppers.	See [S35, S36]	We explicitly model recruitment effort as a function of fight duration, but do not include competitor densities in the model.
3) Fight costs reflect metabolism and not physical harm.	Interspecific stingless bee fights typically yield low mortality [0 to several dead bees per fight, S37].	The major cost of taking over a food source in our model is the energy expended in recruiting enough nestmates for successful takeover.
4) A marked resource does not significantly deplete during the modeled day	Mass-flowering (big bang) trees and shrubs that maintain large numbers of flowers over several days [S38] elicit nestmate recruitment [S39–S42]. Further, personal observation suggests that bees cease marking food sources within a day or two of discovery, since the colony sends sufficient foragers to the food source in the morning. Thus marked food sources are still flowering.	Eavesdroppers that successfully gain access to an occupied or unoccupied resource feed at the same level for the entire simulated day.

Our model steps through one day (8 h) in 5-min intervals, and outputs the colony's net

energetic gain or loss at the end of the day. The colony is the unit of reproduction for social insects. Thus the colony, rather than individual fitness, is typically thought to drive evolution of individual behaviors [S34]. Fig. S3 shows the successive choices a forager makes. Probability of attraction to a heterospecific-occupied food source corresponds to empirically-measured eavesdropping responses. Fights last a specified duration, and represent all assessment, recruitment of nestmates and interaction with the resident bees involved in a potential takeover event. Search, fight and recruitment costs come from metabolic expenditure by active and inactive bees. Collecting nectar yields an energetic benefit, which enables the colony to sustain current activity, increase its honey stores and produce more brood [S43]. Detailed parameter derivations and estimations, including additional data collected and biologically-realistic parameter value sources, are listed below. The model was implemented in Python [S44]. We ran the model across a fully-factorial set of fight duration and attraction probability combinations (see table below), with 1000 repetitions of each combination.

To describe the joint effects of fight duration and attraction probability on net benefit, we implemented quantile regression with the R package quantreg [S45], and visualized regression results via the lattice package [S46]. Like traditional least-squares regression, quantile regression estimates response variable values conditional on one or more predictor variables. We chose quantile regression because medians minimize the influence of extreme values, and this technique does not require certain parametric assumptions [S47, S48] that our simulated data failed to meet. Because of our large sample sizes, we used the Frisch-Newton interior point method for model fitting and the Huber sandwich method for inference statistics [S45].

From the fitted regression, we calculated two descriptors of eavesdropping behavior and its consequences: the attraction-avoidance threshold and efficiency gain. The former is the fight

effort at which the model predicts eavesdroppers switch from attraction to avoidance. Efficiency gain indicates the relative energetic benefit of making a fitness-maximizing decision compared to sub-optimal alternatives. Efficiency gain increases as the net benefit from making a fitness-maximizing decision increases relative to sub-optimal alternatives such as attempting to take over a food source that is too heavily defended. High efficiency gain implies significant costs resulting from sub-optimal decisions. We calculated the attraction-avoidance threshold by setting the partial derivative of the fitted linear model (Eq. 1) with respect to attraction probability equal to zero and solving for fight duration (Eq. 2). Efficiency gain quantifies the impact of showing attraction above the threshold. We defined attraction as showing an attraction probability of at least 0.65, based on stingless bee odor preference experiments [e.g. S49, S50]. We then compared the net benefit of runs above and below the attraction-avoidance threshold, calculating average net benefit of each portion of the parameter space by integrating the regression equation. To compare model results when different parameter values were used, we standardized efficiency gain to the unit hours of search effort (based on each simulated eavesdropper's search cost parameter value). The table below shows parameter values used to model eavesdropping behavior of the three species for which we have empirical data.

(Eq. 1) $\hat{E} = b_0 + b_{uf} + b_{pattracted} * p_{attracted} + b_{uf*pattracted} * u_f * p_{attracted}$

(Eq. 2) $threshold = \dfrac{-b_{pattracted}}{b_{uf*pattracted}}$

We derived model parameters (see table below) from bee traits and habitat variables, from our own and published experiments. Values not known for stingless bees are based upon literature values reported for honey bees. Here we define each such value and describe how we calculated it. We also detail data collected to parameterize the model.

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Decision analysis parameter descriptions and parameter values used

Parameter	Definition	*T. hyalinata* eavesdropping on *T. spinipes*	*Melipona* eavesdropping on *T. spinipes*	*T. spinipes* eavesdropping on *T. hyalinata*
			Simulated species pair	
Energetic parameters				
C_s	Search cost	-6.06 kJ	-0.98 kJ	-1.78 kJ
C_r	Recruitment cost	-6.06 kJ	-0.98 kJ	-1.78 kJ
C_f	Fight cost (per step)	-6.06 kJ	-0.98 kJ	-1.78 kJ
C'_f	Fight cost, last fight step	-6.50 kJ	-1.26 kJ	-2.21 kJ
E	Net energy gain while feeding	23.79 kJ	34.54 kJ	32.29 kJ
State durations				
u_r	Recruitment duration		2 steps (10 min)	
u_f	Fight duration (from food discovery through attempted takeover)		3 – 30 steps (15 – 150 min)	
Probabilities				
$p_{contest}$	Probability of finding an occupied/contested resource	0.02	0.01	0.01
p_{feed}	Probability of finding an unoccupied resource	0.04	0.05	0.07
p_{fail}	Probability of finding no food	0.94	0.94	0.92
$p_{attracted}$	Attraction probability – probability of showing attraction to the occupied resource and recruiting nestmates to attempt takeover		0, 0.1, 0.2, … , 0.9, 1	
p_{win}	Probability of winning a fight	0.5	0.1	0.25

All parameter values reflect five minutes of activity.

Constants

The constant **α** is the honey bee mass-specific resting metabolic rate, 5.38E-5 J/s/mg

[S51]. Multiplying α by a stingless bee species' average fresh weight (*w*, mg) yields the resting

metabolic rate for that species. Fresh weight is often considered an inferior measure of body size

[S52], but in stingless bees it strongly correlates with measures of sclerotized body parts, such as

head width (Spearman's rank correlation: r_S=0.87, *n*=16 species, *p*<0.0001). Fresh weights and

head widths come from the literature [S53–S59] and our own measurements of head widths

[S24] and weights (*Frieseomelitta varia* 11±0.3 mg, *M. quadrifasciata* 69±1.2 mg, *Nannotrigona*

testaceicornis 6±0.2 mg, *Scaptotrigona* aff. *depilis* 16±0.2 mg, *T. hyalinata* 25±0.6 mg, *T.*

spinipes 20±0.3 mg) of foragers not carrying nectar or pollen.

The constant **β** is the honey bee mass-specific active metabolic rate, 4.23E-4 J/s/mg

[S51].

The constant **γ** is the energetic value of 30% weight/weight (0.99 M) sucrose solution,

5.68 J/µL [S60, S61]. Bees were trained to this sucrose concentration for our eavesdropping

experiments, and 0.99 M is therefore the food quality that they expected to find at our test

feeders. Our *M. rufiventris* simulation used γ=13.08 J/µL to reflect the 60% weight/weight

sucrose solution used by Nieh et al. [S3]

The constant **δ** is the density of a 30% weight/weight sucrose solution at 20º C, 1.13 J/µL

[S62]. We use it to determine how much extra weight a bee carries on her return trip to the nest,

with a full crop.

The constant **ζ** is the proportion of workers in a colony that search for food: 0.025 [S63].

We use it to calculate the probability a food source is already occupied by the signaling species.

The constants **η** and **θ** are the intercept and slope of the line predicting crop load from

body size. We determined this relationship to reduce the number of bee traits required to

calculate net energy gain (*E*). Using published data [S54, S64–S67] and crop loads of 100 sated

T. hyalinata foragers measured with 20 μL micropipettes (Hirschmann® Laborgeräte ringcaps®; 10.6±0.22 μL), we found that crop load is a linear function of body size (linear regression: $F_{1,5}=29.41$, $p=0.0002$, $r^2=0.95$; crop load=0.91+0.36*fresh weight).

Bee traits

The variable w is the fresh weight of a bee with an empty crop and no corbicular pollen. We measured fresh weights of *T. hyalinata* and *T. spinipes* as described above. To parameterize the model for *Melipona* eavesdropping, we averaged fresh weights from two species similar in size to *M. rufiventris*: *M. quadrifasciata* (see above) and *M. panamica* [67 mg, S54].

The variables c and c_2 are the average sizes of the eavesdropping and signaling colonies, respectively. Lichtenberg et al. [S24] describe our method for screening published colony sizes and list sources for *T. hyalinata* (15,000 workers) and *T. spinipes* (5,500 workers). *Melipona rufiventris* colony sizes are unknown, so we averaged all published *Melipona* colony sizes [S27, S54, S68–S77] plus four *M. panamica* colonies measured by Meg Eckles (542, 346, 678, 498 workers) to yield a mean colony size of 900 workers (19 species, range 50-3000).

The variable R measures recruitment intensity as the number of nestmates feeding at the same resource, averaged across the entire recruitment process and subsequent feeding. We measured *T. hyalinata* recruitment intensity in a manner similar to that described for *T. spinipes* in the main text, but with each trial (6 total, 2 colonies) lasting for 3 h. Because the feeding state includes the build-up of bees after the initial group of recruits arrives and the asymptotic number of foragers after recruitment, we calculated R in the following manner. First, for each trial we calculated the average number of recruits for time durations starting from the fourth model step (the earliest bees could feed) through the final step, successively adding one step. Based upon

our observations, we hold forager numbers steady after 3 h. We averaged these duration-specific recruit counts across trials, then across durations to obtain a final estimate of the number of bees feeding during any one 5-min interval (160.70 for *T. hyalinata*). Repeating this procedure with our *T. spinipes* recruitment data and published *Melipona* recruitment curves [S3, S74, S78], we estimated R values of 194.38 for *T. spinipes* and 38.75 for *M. rufiventris*. This process assumes the resource does not deplete over the course of the day (see assumptions table).

The variables t_v, t_e and t_n are the times bees spend doing each of three activities while collecting food: flying between nest and food source, ingesting nectar at the food source and unloading nectar in the nest. We measured feeding time and time away from the feeder for 59 bees during the *T. hyalinata* recruitment experiment described above. We then estimated the flight distance between feeder and nest as the hypotenuse of a right triangle with base 25 m (the distance between nest and feeder) and height 4 m (the approximate vertical distance between nest and feeder). Combining this distance (27.16 m) with stingless bee flight speed [4.25 m/s, S79], we separated the time away from the nest into in-flight and in-nest components. This yielded *T. hyalinata* times of 23.39±0.57 s, 73.58±1.94 s and 12.78 s, respectively. We used these same values for *T. spinipes*, but for the larger *M. rufiventris* relied on data collected by MH for *Melipona seminigra* foraging on 50% weight/weight (1.80 M) sucrose solution 50 m from the nest (25.93 s in flight, 15.80 s in the nest).

The variables n_1 and n_2 are the nest densities of the eavesdropping and signaling species, respectively. For *T. hyalinata* and *T. spinipes*, we estimated nest densities from nest counts on the Universidade de São Paulo, Ribeirão Preto campus and the campus' area, excluding the lake and buildings [574.61 ha, S19]. *Melipona* estimates come from a Brazilian cerrado plot [S80].

Habitat variables

The variable d is the density of flowering plants in the simulated habitat. We used bimonthly counts of the number of flowering individuals of 26 tree species in a 1 ha cerrado plot [S81] and the 224 woody plant species observed in this plot [S82] to estimate the density of flowering plants present at any given time. Flowering plant density averaged 0.16 plants/m^2, ranging from 0.007 to 0.70 plants/m^2 across the year.

The variable A is the area covered in 5 min by a bee searching for food. We estimated this area by simulating bee flight using R software [S26]. Searching bumble [S83] and honey [S84] bee flight patterns can be described by Lévy flight (with μ=2), a type of random walk where step lengths follow a probability distribution with a power-law tail. We simulated Lévy flight of bees flying for 5 min at searching flight speed (2.13 m/s), which is approximately half the speed of foragers for honey bees [S84]. To determine the area covered by the simulated flight, we calculated the square root of the product of the two eigenvalues of the flight's radius of gyration tensor. This value is a good estimator of the arithmetic mean of a random walk [S85]. The tensor's eigenvalues and associated eigenvectors quantify the widest and narrowest dimensions of the flight [S86]. We simulated 100,000 flights and determined the median flight area. Using the median allowed us to minimize the influence of flights with steps larger than is biologically realistic (0.3% of the simulated flights).

Parameter derivations

Energetic parameters depend on metabolism of active (flying or recruiting) and inactive (inside the nest or ingesting food) bees, and on the energetic value of ingested nectar. In the Search state (C_s), the colony has one active bee (who is searching for food) while the rest of the

colony remains inactive (Eq. 3).

(Eq. 3) $\qquad C_s = C_r = C_f = -0.3w\left[\alpha(c-1)+\beta\right]$

       Recruitment covers the time from food discovery until the recruited nestmates first feed. It involves a greater variety of behaviors than searching, but is not yet described in sufficient detail for parameterization from first principles. We thus assume that, on average, recruitment cost (C_r) equals search cost. For much of the recruitment process the original searching bee is flying and creating an odor trail (pers. obs.), exhibiting excitatory runs inside the nest [S49] or inactive. Only during the last minute or two of recruitment are a large number of bees showing high activity.

       Our model divides fighting into two stages: recruitment of sufficient nestmates to take over the discovered resource (Assumption 3), and flight to and in the vicinity of the food source while the resident species is displaced [S4]. Thus the majority of time in the Fight state is spent recruiting and incurs a cost (C_f) equal to the recruitment cost. We elevate costs slightly during the last time step in the Fight state (C'_f) to reflect increased activity of recruited nestmates (Eq. 4).

(Eq. 4) $\qquad C'_f = -0.3w\left[\alpha c + R(\beta - \alpha)\right]$

       Net energy gain while feeding (E) incorporates gross energy collected as nectar (or sucrose solution in experiments), metabolic costs of inactive bees in the nest and metabolic costs of foragers (Eq. 5). We model foragers as having an active metabolic rate while flying between nest and food source, and inactive while standing on the food source imbibing nectar or inside the nest unloading nectar.

(Eq. 5) $\qquad E = 0.3\left[\dfrac{R}{t_v+t_e+t_n}\left[w\left(\gamma\theta - \beta t_v\left(1+\dfrac{\delta\theta}{2}\right)-\alpha(t_e+t_n)\right)+\gamma\eta - \dfrac{\beta\delta\eta t_v}{2}\right]-\alpha w(c-R)\right]$

Bees remain in the Fight and Recruit states for fixed numbers of time steps. We set recruitment duration (u_r) to 2 steps, representing bees highly motivate to feed. In all recruitment trials described above, recruits began to feed during the second 5-min time interval. Since fights involve recruitment and takeover, we model fights as requiring at least one time step more than recruitment. We systematically varied fight duration (u_f) across an empirically supported range, using only integer values to keep model implementation reasonable. The longest published takeover, between *Trigona corvina* and *T. silvestriana*, was 2.5 h [S87]. We thus set the maximum fight duration as 30 steps.

We calculated search-related probabilities from bee nesting traits, floral availability and search behavior. These probabilities depended on two other probabilities: encountering food ($1 - p_{fail}$) and a food source being occupied before discovery (Eq. 6). Contested food sources were thus discovered and occupied (Eq. 7), while uncontested food sources were discovered and unoccupied (Eq. 8). We estimated the baseline p_{fail} value by dividing the average number of *T. hyalinata* and *T. spinipes* foragers landing in any 5 min of an eavesdropping trial (6.27 and 6.05, respectively) by the average 100 bees at the training feeder at the start of a trial [S4]. Similar data are lacking for *Melipona* spp., so we applied this value to the *Melipona* simulation. *Trigona spinipes* appear to have a broader foraging niche than most Neotropical stingless bee species [S4, S88]. To account for this, we slightly increased their probability of finding food.

(Eq. 6) $$p_{occupied} = \frac{(1 - p_{fail})\zeta c_2 n_2}{dAn_1}$$

(Eq. 7) $$p_{contest} = \frac{(1 - p_{fail})^2 \zeta c_2 n_2}{dAn_1}$$

(Eq. 8) $$p_{feed} = \varepsilon - \frac{\varepsilon \zeta c_2 n_2}{dAn_1}$$

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Author Contributions

EML designed and performed experiments, designed and implemented the model, analyzed data and prepared the manuscript; JGZ designed the model and edited the manuscript; MH designed and performed experiments, and edited the manuscript; JCN designed experiments, analyzed data and prepared the manuscript.