Dancers and Followers in a honeybee colony differently prioritize individual and colony nutritional needs

Keziah Katz and Dhruba Naug

Department of Biology, Colorado State University

Corresponding author: Keziah Katz

Department of Biology

1878 Campus Delivery, Fort Collins, CO 80523, U.S.A.

Telephone: (570) 872 - 4159

Email: Keziah.Katz@colostate.edu

1 The evolution of sociality is often accompanied by nutritional conflicts and the evolution
2 of mechanisms to resolve them. The foraging behaviour of eusocial animals such as the
3 honeybee, *Apis mellifera*, is generally considered to be largely regulated by the colony
4 nutritional state, with a subset of individuals foraging for the entire group. Previous work based
5 on the information primacy hypothesis has however found that satiated honeybee foragers
6 explore (sample resources) more and exploit (consume resources) less in response to their
7 individual nutritional state. We therefore hypothesized that individual and colony nutritional
8 states differ in their influence on individuals of different behavioural phenotypes such as Dancers
9 and Followers, who are akin to producers and scroungers, respectively. This leads to the
10 prediction that these two behavioural groups will differ with respect to their exploration-
11 exploitation trade-off and in terms of how they prioritize individual and colony nutritional states.
12 We tested our predictions by creating a mismatch between individual and colony nutritional
13 states. Our results show that Dancers and Followers do not differ in their levels of exploration
14 and exploitation, but Dancers are more responsive to colony nutritional state than Followers with
15 regard to managing their exploration-exploitation trade-off. We discuss these results in the
16 context of how these two behavioural phenotypes may differ in their sensitivity to the different
17 nutritional pathways regulating worker behaviour in a eusocial colony and the evolution of
18 sociality in general.

20 **Keywords**

21 Exploration, exploitation, producer, scrounger, behavioural phenotype, eusociality,
22 intragroup conflict, nutrition, foraging, honeybees

24 Social groups are typically characterized by not only cooperation, but also conflict among
25 group members. While such within-group conflict has been mostly studied in the context of
26 reproductive allocation (Keller & Reeve, 1994; Ratnieks et al., 2006), the basic principle behind
27 such conflicts also applies in the context of altruistic foraging. Members of a group may differ in
28 terms of their nutritional requirements and an individual's own requirements might not
29 necessarily match those of the group as a whole. Integration of nutritional needs and metabolic
30 complementation have been considered key prerequisites to the evolution of group living, and
31 are regarded as critical drivers in the evolution of eukaryotes through endosymbiosis and the
32 evolution of multicellularity (Blackstone, 2013). Mechanisms that mediate any nutritional
33 conflicts among the lower-level components are therefore critical in order for higher-level units
34 to evolve through cooperation.

36 Nutritional conflicts are likely to be especially strong when a subset of group members
37 must obtain nutrition for the entire group. This is most obvious in the case of eusocial insects,
38 where a subset of individuals – the foragers – meet the nutritional demands of the entire colony.
39 It has been well established that the foraging behaviour of honeybee workers is regulated to a
40 large part by the nutritional state of the colony (Seeley, 1995), but recent work suggests that the
41 nutritional state of an individual also plays a strong regulatory role in determining the foraging
42 behaviour of individual bees (Toth et al., 2005). While colony and individual nutritional states
43 are normally tied to each other, uncoupling the two shows that fed bees in starved colonies
44 behaved more similarly to bees in fed colonies than bees in starved colonies (Schulz et al., 1998),
45 and that honeybee foragers at a higher nutritional state forage less often than bees at a lower
46 nutritional state in a shared colony environment (Mayack & Naug, 2013). These studies suggest

that honeybee foragers use information about both individual and colony nutritional states to make their foraging decisions.

The nutritional state of an animal has been predicted to be the primary driver of a key foraging decision – whether to explore or exploit. Foragers must divide their time between gathering information about available resources (exploration) and applying that information to utilize the best available resource (exploitation; Hill et al., 2015); these activities cannot be performed simultaneously and must trade-off with one another. The information primacy hypothesis predicts that animals will give precedence to information gathering (exploration) when they have a nutritional surplus and will prioritize food gathering (exploitation) when they are at a nutritional deficit (Inglis et al., 2001), thus allowing them to adaptively manage their own nutritional budget over time. A manipulation of the individual nutritional state in honeybees showed that those at a higher nutritional state explored more and exploited less compared to bees at a lower nutritional state, in support of this hypothesis (Katz & Naug, 2015). However, since the foraging decisions of honeybees are known to be subject to the nutritional state of the colony, it is important to evaluate if colony nutrition has a similar influence on the exploration-exploitation trade-off.

Within a colony, some bees use the waggle dance to transmit foraging information to other bees which follow the dance. This allows us to divide the foragers into two behavioural phenotypes, information gatherers (the Dancers) and information consumers (the Followers) – colony-level units of exploration and exploitation. This Dancer-Follower framework thus allows an evaluation of the exploration-exploitation trade-off at the group level and helps us to

determine if the colony nutritional state drives an adaptive allocation of individuals into these two behavioural phenotypes. The behaviour of Dancers and Followers can also be interpreted in light of the producer-scrouter framework, according to which foraging groups consist of producers, which locate new food patches, and scroungers, which take advantage of the producer's find and feed at the same patch (Barnard & Sibly, 1981). As Followers forage at patches originally located by Dancers, it can be argued that these Followers are similar to scroungers while Dancers are similar to producers.

In this study, we manipulated colony nutritional state to study how it dictates the colony level distribution of behavioural phenotypes and their behaviour, as per the information primacy hypothesis. Our 1st prediction is that colonies at a higher nutritional state will have a higher proportion of Dancers than colonies at a lower nutritional state and that Dancers will show an overall higher level of exploratory behaviour. By creating either a match or a mismatch between individual and colony nutritional states, we also examined how Dancers and Followers prioritize individual and colony needs with respect to their exploration and exploitation behaviour. Our 2nd prediction is that when colony and individual nutritional states are similar and therefore “matched,” all bees will respond to an overall high nutritional state by exploring more and respond to an overall low nutritional state by exploiting more. However, when the two states are “mismatched” and the individual state differs from that of the colony, it presents a nutritional conflict to the bees. Our 3rd prediction is that under such a mismatch, Dancers would be more sensitive to colony nutritional state, as per the producer-scrouter framework. The test of these three predictions addresses if the two behavioural phenotypes, Dancers and Followers, differ in

their predispositions to show exploration and exploitation behaviours, differ in their response to nutritional conflict, and if the information primacy hypothesis scales to the colony level.

METHODS

Observation of In-Hive Behaviour

We set up two observation hives, each with one brood frame and about 3,000 bees, and created two nutritional treatments at the colony level. A colony with higher nutrition (“Full colony”) was created by providing it with a frame that had at least 75% honey and a colony with lower nutrition (“Empty colony”) was created by providing it with a frame that contained no more than 10% honey. These two nutritional treatments were rotated between the two colonies on a weekly basis to control for any confounding effects of colony identity for a total of 9 weeks of data collection. About 500 individually tagged newly emerged bees were added to each colony after the nutritional rotation each week. Allowing 2.5 days for the nutritional treatment to have an effect, we then observed the dance floor of each colony for 2 hours each week, using scan sampling to identify the bees performing a waggle dance or following a waggle dance. The scan sampling consisted of dividing the dance floor into squares that were 1/6th of the entire frame in size, sampling these squares sequentially for a duration of 1 minute each and recording the identities of all tagged bees found performing a waggle dance or following a waggle dance within the square during this period. Based on which of these two activities a bee was observed to perform during this entire observation period, we categorized each bee as either a “Dancer” or a “Follower,” ignoring bees observed both dancing and following (3.5% of observed bees).

Two-Alternative Proboscis Extension Response Assay

We captured a subset of these Dancers and Followers and harnessed them in plastic straws. The bees were starved for 3 hours inside a dark incubator maintained at 25°C and 60% relative humidity to increase their motivation for learning an appetitive stimulus. We trained these bees to associate an odour with a sucrose reward using an appetitive conditioning procedure involving the Proboscis Extension Response (PER) assay (Bitterman et al., 1983). Sucrose placed on the antenna (the unconditioned stimulus, US) was paired with an odour (eugenol or 1-octanol; the conditioned stimulus, CS) to elicit a proboscis extension (a conditioned response, CR) in 6 conditioning trials. Each trial consisted of presenting the odour for 6 seconds with the final 2 seconds of the odour pulse coinciding with the presentation of the sucrose reward, with an 11 minute inter trial interval (ITI).

Subsequent to the conditioning procedure, we created a high and a low nutritional treatment at the individual level, by feeding half the bees with 30 µl of 30% sucrose solution (“Fed bees”) and not feeding the other half (“Starved bees”), thus giving us a 2 x 2 nutritional treatment consisting of Fed and Starved bees from Full and Empty colonies. We kept these bees in an incubator, under the same conditions as described above, for 3 hours to allow the individual nutritional treatment to have an effect before subjecting them to a two-alternative assay (Shafir et al., 1999) designed to test for exploration and exploitation behaviour (Katz & Naug, 2015). The assay consisted of presenting each bee with the odour they were previously conditioned to and a novel odour on opposite sides of her head. Each odour was presented twice for 0.8 seconds with 0.2 seconds of odourless air in between successive odour pulses in the pattern ABAB. The number of head turns made by a bee as she sampled the two odours was interpreted as a measure

of exploration and the duration of its proboscis extension was interpreted as a measure of exploitation (Katz & Naug, 2015).

Statistical Analysis

All data were analysed using ANOVAs chosen through step-wise AIC model selection. AIC selection for predicting colony proportion of Dancers started from a model including a three-way interaction between colony nutrition, day, and colony identity. AIC selection for predicting individual behaviour started from a model including the three-way interactions between the two nutritional states and behavioural phenotype, and the main effects of colony identity and conditioning odour. Head turning (count data) was square root transformed to allow for parametric analysis. In order to control for any differences among individuals in overall activity level, a measure of relative exploration was calculated by converting head turns to a duration and calculating the proportion of time that each bee spent head turning out of total time spent active (head turning or extending her proboscis). Bees that did not extend their proboscis at least once during the conditioning procedure, or failed to perform either of the measured behaviours during the two-alternative assay were excluded from all analyses, resulting in a final sample size of 178 bees. The effects of colony and conditioning odour were dropped from all ANOVAs due to minimal contribution to explanatory power during model selection. A single combined plot for each behavioural response variable is presented to emphasize the similarity of trends found among them. The parameter eta squared (η^2) is presented as a measure of effect size; 0.01 is considered a small effect size, 0.06 is considered a moderate effect size, and 0.14 is considered a large effect size (Maher et al., 2013).

Ethical Note

Large outdoor naturally foraging colonies of honeybees were maintained by the authors, with most colonies consisting of two deep boxes with 9 frames each. Bees were euthanized following the two-alternative assay by freezing. No licences or permits were required for this research.

RESULTS

In-Hive Behaviour

The proportion of Dancers within a colony (Number of Dancers / Number of Dancers + Followers) was not influenced by colony nutritional state (ANOVA: $F_{1,19} = 2.03$, $p = 0.16$, $\eta^2 = 0.07$). This does not support our 1st prediction that the proportion of Dancers within a colony would be higher in colonies at a higher nutritional state. The proportion of Dancers was, however, affected by the day in the season a colony was observed with the proportion increasing as the summer progressed over the nine weeks of observation ($F_{1,19} = 8.67$, $p = 0.008$, $\eta^2 = 0.30$). The interaction between day and colony nutritional state was not included in the AIC selected model.

Proboscis extension duration

The duration for which a bee extended her proboscis (exploitation) was significantly influenced by a three-way interaction between her individual nutritional state, colony nutritional state, and behavioural phenotype (Fig. 1A, Table 1), as well as by each of these factors alone. This indicates that Dancers and Followers did not respond identically to colony and individual nutrition. Under mismatched nutrition, Fed Followers extended their proboscis very briefly, as

would be predicted for a bee prioritizing individual nutrition, while Fed Dancers extended their proboscis for an intermediate duration, as would be predicted for a bee responding to both individual and colony nutrition. This supports our 3rd prediction that Followers would be less sensitive to the colony nutritional state than Dancers. This prediction is also supported by the significant two-way interactions between behavioural phenotype and colony nutritional state (Fig 1B), which indicates that Dancers and Followers respond differently to the effects of colony nutritional state. The significant interaction between behavioural phenotype and individual nutritional state (Fig 1C) indicates that Dancers and Followers also respond differently to the effects of individual nutrition, Dancers being slightly less sensitive to individual nutrition than Followers. The non-significant two-way interaction between individual and colony nutritional states (Fig 1D) indicates that the effect of individual nutrition on exploitation is similar in Full and Empty colonies. In general, a Follower extended her proboscis for a significantly shorter duration than a Dancer, which is contrary to our 1st prediction that Followers would be less exploitative than Dancers. However, a Fed bee extended her proboscis for a significantly shorter duration than a Starved bee and a bee from a Full colony extended her proboscis for a significantly shorter duration than a bee from an Empty colony, supporting our 2nd prediction that bees would increase their exploitation behaviour when both colony and individual nutritional states are low.

Table 1

Predictor	F	P	η^2
Individual	9.4	0.002	0.030
Colony	5.17	0.02	0.016
Phenotype	10.1	0.001	0.032
Individual * Colony	1.0	0.30	0.003
Individual * Phenotype	6.3	0.01	0.020
Colony * Phenotype	5.5	0.01	0.017
Individual * Colony * Phenotype	5.9	0.01	0.018

Table 1: ANOVA of proboscis extension duration. Predictors are individual nutritional state, colony nutritional state, and behavioural phenotype (N = 178; all predictor df = 1). η^2 presented as a measure of effect size.

Figure 1: Exploitation (A - D), exploration (E - H), and relative exploration (I - L) of bees categorized as Dancers (triangles) or Followers (circles), or both pooled together (squares). Bees were manipulated to be Fed (filled shapes) or Starved (open shapes), or both pooled together (crossed shapes). Matched nutrition indicates similar colony and individual nutritional states (e.g. a Fed bee in a Full colony), while mismatched nutritional states indicate dissimilar colony and individual nutritional states (e.g. a Fed bee in an Empty colony). Legends describe the subplots (N = 178) below them. Data consist of means with standard error bars. Means within each subplot that share the same letter are not statistically different at $\alpha = 0.05$ (Tukey post-hoc).

Head turning

The number of head turns made by a bee (exploration) was not significantly influenced by a three-way interaction between her individual nutritional state, colony nutritional state, and behavioural phenotype (Fig 1E, Table 2). There was a significant two-way interaction between behavioural phenotype and colony nutritional state (Fig 1F), which indicates that a Dancer and a Follower responded differently to colony nutritional state. A Dancer turned her head more when she was from a Full colony than when she was from an Empty colony, but a Follower turned her head similarly, irrespective of colony nutrition, supporting our 3rd prediction that Followers would be less sensitive to colony nutritional state than Dancers. There was no significant interaction between behavioural phenotype and individual nutritional state (Fig 1G), indicating that Dancers and Followers were similarly influenced by individual nutrition. There was a significant two-way interaction between individual and colony nutritional states (Fig 1H), indicating that bees responded differently to the combined effects of individual and colony nutritional states. Fed bees turned their heads more than Starved bees in Empty colonies, but not in Full colonies, which partially supports our 2nd prediction that bees would increase their exploration in response to a higher level of nutrition at the individual and the colony level. The lack of a significant main effect of behavioural phenotype on head turning behaviour is contrary to our 1st prediction that Dancers would be more exploratory than Followers. However, individual nutritional state had a significant main effect on head turning, and a Fed bee performed significantly more head turns than a Starved bee, supporting our 2nd prediction that bees would increase their exploration behaviour when their individual nutritional state is high.

Table 2

Predictor	F	P	η^2
Individual	32.8	< 0.001	0.145
Colony	2.7	0.09	0.012
Phenotype	1.9	0.16	0.008
Individual * Colony	6.1	0.01	0.027
Colony * Phenotype	8.7	0.003	0.038

Table 2: ANOVA of number of head turns. Predictors are individual nutritional state, colony nutritional state, and behavioural phenotype (N = 178; all predictor df=1). η^2 presented as a measure of effect size.

Relative exploration

The number of head turns (exploration) and the duration of proboscis extension (exploitation) were negatively correlated (Pearson's correlation: $n = 178$, $r = -0.60$, $p < 0.001$), indicating that these behaviours trade-off with one another. However, since a Dancer both extended her proboscis for a longer duration and turned her head more frequently than a Follower, this higher overall activity level of Dancers hinders a direct comparison between the two behavioural phenotypes in terms of their exploration and exploitation. We therefore converted the head turning data from count to duration (based on the duration of a single head turn, measured as 0.58 ± 0.16 seconds from a subset of randomly selected trials) and calculated a measure of relative exploration – the proportion of time spent by a bee turning her head out of the total time spent active in head turning and proboscis extension. Dancers were indeed significantly more active overall than Followers (ANOVA: $F_{1, 174} = 9.3$, $p = 0.002$, $\eta^2 = 0.032$). In addition, Starved bees were significantly more active overall than Fed bees ($F_{1, 174} = 74.8$, $p < 0.0001$, $\eta^2 = 0.281$), and bees from Empty colonies were significantly more active overall than

bees from Full colonies ($F_{1, 174} = 4.2$, $p = 0.04$, $\eta^2 = 0.016$). No interactions were included in the AIC selected model.

The relative exploration of a bee was found to be significantly influenced by the three-way interaction between her individual nutritional state, colony nutritional state, and behavioural phenotype (Fig. 1I, Table 3). This indicates that Dancers and Followers did not respond identically to the effects of colony and individual nutrition. Under mismatched nutrition, Fed Followers showed low relative exploration, as would be predicted for a bee prioritizing individual nutrition, and Dancers showed intermediate relative exploration, as would be predicted for a bee responding to both individual and colony nutrition. This supports our 3rd prediction that Followers would be less sensitive to colony nutrition than Dancers. The two-way interactions between behavioural phenotype and colony nutritional state (Fig 1J) and between behavioural phenotype and individual nutritional state (Fig 1K) were significant, suggesting that Dancers and Followers respond differently to the effects of colony and individual nutritional states. The two-way interaction between individual and colony nutrition was not significant (Fig 1L), indicating that the effect of individual nutrition on relative exploration is similar in Full and Empty colonies. Relative exploration was also significantly affected by each of these factors alone. The relative exploration of a Fed bee was significantly higher than a Starved bee, and the relative exploration of a bee from a Full colony was significantly higher than a bee from an Empty colony. These findings support our 2nd prediction that bees would increase their exploration behaviour when colony and individual nutritional states are high, and increase their exploitation behaviour when colony and individual nutritional states are low. However, the finding that the relative exploration of a Follower was significantly higher than a Dancer is once

again contrary to our 1st prediction that Dancers would be more exploratory and be less exploitative than Followers.

Table 3

Predictor	F	P	η^2
Individual	11.0	0.001	0.034
Colony	6.8	0.009	0.021
Phenotype	13.6	< 0.001	0.042
Individual * Colony	0.4	0.49	0.001
Individual * Phenotype	6.6	0.01	0.024
Colony * Phenotype	9.8	0.002	0.030
Individual * Colony * Phenotype	5.4	0.02	0.016

Table 3: ANOVA of relative exploration. Predictors are individual nutritional state, colony nutritional state, and behavioural phenotype (N = 178; all predictor df =1). η^2 presented as a measure of effect size.

DISCUSSION

Bees consistently explored more and exploited less when their individual nutritional states were high. Colony nutritional state had a similar effect, such that bees from Full colonies explored more and exploited less than bees from Empty colonies. Both these results are consistent with our prediction and the previous findings regarding the effect of individual nutritional state on the exploration-exploitation trade-off (Katz & Naug, 2015) according to the information primacy hypothesis (Inglis et al., 2001). It initially appears that colony nutritional state has a much smaller effect on exploration than individual nutritional state (as measured by the η^2 of the respective main effects; Table 2). However, further analysis reveals that individual

and colony nutrition both have comparable influences on how bees divide their time between exploration and exploitation, as defined by relative exploration (Table 3). The apparent larger effect of individual nutritional state can instead be attributed to the higher overall activity level of Starved bees. This corroborates previous findings that changes in overall activity level is a key behavioural mechanism by which individuals deal with changes in their own nutritional state when confronted with conflicting signals about the nutritional state of the colony (Mayack & Naug, 2013), adding to the growing evidence of individual nutritional state playing a vital role in the regulation of worker behaviour in eusocial colonies.

The higher overall activity level of a Dancer led to both more head turns and a longer duration of proboscis extension compared to a Follower (Fig 1A, 1E). However, once this difference in overall activity level was accounted for, there was little difference between Dancers and Followers under identical colony and individual nutritional states (Fig 1I). Neither was more exploratory than the other, which is contrary to our prediction that Dancers would be more exploratory. The sole exception to the similar behaviours of Dancers and Followers is in the comparison of Fed Dancers and Fed Followers under mismatched nutrition. Fed Followers from an Empty colony exploit much less than Fed Dancers from an Empty colony (Fig 1A) and Fed Followers from an Empty colony have a much higher relative exploration than Fed Dancers from an Empty colony (Fig 1I). A related trend can be seen in our initial measure of exploration, Dancers explore more in Full colonies than they do in Empty colonies, but Followers explore equally regardless of colony nutritional state (Fig 1F). Dancers therefore altered their behaviour in accordance with the colony state to a greater extent than did Followers, and did so in a manner that is consistent with the information primacy hypothesis. This suggests that Followers are more

inclined to disregard the colony nutritional state and instead act primarily in accordance with their individual nutritional state, which can be construed as acting in a more “selfish” manner than Dancers. This is consistent with our prediction that Followers, as a scrounger-type phenotype, would prioritize individual nutrition more than Dancers.

If the allocation of Dancers and Followers within a colony responds to the colony nutritional state as individual bees respond to individual nutritional state (Katz & Naug, 2015), the information primacy hypothesis predicts that colonies with high food stores will have more Dancers and fewer Followers than colonies with little food stores and *vice versa*. However in contrast to our prediction, colony nutrition had no effect on the proportion of Dancers in a colony and Dancers were not more exploratory than Followers in the individual behavioural assay. This suggests that either 1) the information primacy hypothesis does not scale to the group level or, 2) Dancers and Followers are equally exploratory, or both. One cannot also completely rule out that our study maybe lacked sufficient power to detect the effect of the treatments on the proportion of Dancers in the colonies, or that our experimental manipulation cannot completely disentangle the effects of individual and colony nutritional state, or that the head turning behaviour is influenced by factors besides exploratory tendency. The proportion of Dancers within a colony however increased over the season, which indicates that there are possibly additional mechanisms in the colony that regulate how a colony allocates its efforts into Dancers and Followers, and exploration and exploitation.

Considering the extent to which an individual’s behavioural decisions are the product of their own interests and are influenced by the interests of others have widespread application for

understanding animal behaviour. Several studies have investigated a parallel between the producer-scrouter and the explore-exploit framework (Koops & Giraldeau, 1996; David et al., 2011; Kurvers et al., 2012; Mehlhorn et al., 2015). In the context of social foraging, which provides individuals with the opportunity to either produce (or discover) resources or to scrounge upon the ones produced by others, the payoff to each of these two strategies is defined by a negative frequency dependent relationship. Increased relatedness between such foragers can lead to higher levels of scrounging when producers are kin-selected to be more tolerant of scroungers (Mathot & Giraldeau, 2010). Eusocial insects such as honeybees present extreme examples of such kin groups and one can speculate that higher order sociality and altruistic foraging in these groups might have evolved out of such producer-scrouter systems – with producers becoming increasingly tolerant of scrounging kin to the eventual extreme of promoting and guiding scrounging kin to finding a resource for group-level benefits. The evolution of primate food sharing is sometimes similarly attributed to tolerated theft of food from a producer, especially when a resource patch is too ephemeral or large to exploit by oneself (Bliege Bird & Bird 1997; Blurton Jones, 1984, 1987; Stevens & Cushman, 2004; but see Gurven, 2004).

It has been suggested that there are two different nutritional pathways which regulate foraging behaviour in bees (Toth et al., 2005; Toth & Robinson, 2007; Ament et al., 2010). The pathway related to the individual nutritional state is similar to that of solitary animals while the one related to the colony nutritional state is likely a more recent adaptation to group living and may be mediated through social interactions. Our demonstration that the behavioural changes triggered by manipulation of the two nutritional states differ among Dancers and Followers suggests that the Followers may be less sensitive to the pathway related to colony nutritional

state than Dancers. This may be adaptive at the colony level as individuals of different sensitivities allow a finer tuning in terms of the exploration-exploitation trade-off rather than when the behaviour of all individuals are similarly constrained by a single nutritional state. The difference in the sensitivity of Dancers and Followers to these nutritional pathways may explain the role of Dancers as altruistic producers and Followers as scroungers of information from Dancers. The results from this study show that both individual and colony nutritional states are accounted for in the foraging decisions made by a honeybee forager and that individuals of different behavioural phenotypes vary in the degree to which these two states influence these decisions.

REFERENCES

- Ament, S. A., Wang, Y., & Robinson, G. E. (2010). Nutritional regulation of division of labor in honey bees: toward a systems biology perspective. *Wiley Interdisciplinary Reviews- Systems Biology and Medicine*, 2(5), 566-576.
- Barnard, C. J., & Sibly, R. M. (1981). Producers and scroungers: A general model and its application to captive flocks of house sparrows. *Animal Behaviour*, 29(2), 543-550.
- Bitterman, M. E., Menzel, R., Fietz, A., & Schäfer, S. (1983). Classical conditioning of proboscis extension in honeybees (*Apis mellifera*). *Journal of Comparative Psychology*, 97, 107-119.
- Blackstone, N. W. (2013). Why did eukaryotes evolve only once? Genetic and energetic aspects of conflict and conflict mediation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1622), 20120266. doi: 10.1098/rstb.2012.0266

395 Bliege Bird, R. L., & Bird, D. W. (1997). Delayed reciprocity and tolerated theft: The behavioral
 396 ecology of food-sharing strategies. *Current Anthropology*, 38(1), 49-78.

397 Blurton Jones, N. G. (1984). A selfish origin for human food sharing: tolerated theft. *Ethology*
 398 and *Sociobiology*, 5(1), 1-3.

399 Blurton Jones, N. G. (1987). Tolerated theft, suggestions about the ecology and evolution of
 400 sharing, hoarding and scrounging. *Social Science Information*, 26(1), 31-54. doi:
 401 10.1177/053901887026001002

402 David, M., Cézilly, F., & Giraldeau, L.-A. (2011). Personality affects zebra finch feeding success
 403 in a producer–scrounger game. *Animal Behaviour*, 82(1), 61-67. doi:
 404 <http://dx.doi.org/10.1016/j.anbehav.2011.03.025>

405 Gurven, M. (2004). To give and to give not: The behavioral ecology of human food transfers.
 406 *Behavioral and Brain Sciences*, 27, 543-583.

407 Hills, T. T., Todd, P. M., Lazer, D., Redish, A. D., & Couzin, I. D. (2015). Exploration versus
 408 exploitation in space, mind, and society. *Trends in Cognitive Sciences*, 19(1), 46-54. doi:
 409 <http://dx.doi.org/10.1016/j.tics.2014.10.004>

410 Inglis, I. R., Langton, S., Forkman, B., & Lazarus, J. (2001). An information primacy model of
 411 exploratory and foraging behaviour. *Animal Behaviour*, 62, 543-557.

412 Katz, K., & Naug, D. (2015). Energetic state regulates the exploration–exploitation trade-off in
 413 honeybees. *Behavioral Ecology*, 26(4), 1045-1050. doi: 10.1093/beheco/arv045

414 Keller, L., & Reeve, H. K. (1994). Partitioning of reproduction in animal societies. *Trends in*
 415 *Ecology and Evolution*, 9, 98-102.

416 Koops, M. A., & Giraldeau, L.-A. (1996). Producer–scrounger foraging games in starlings: a test
 417 of rate-maximizing and risk-sensitive models. *Animal Behaviour*, 51(4), 773-783. doi:
 418 <http://dx.doi.org/10.1006/anbe.1996.0082>
 419 Kurvers, R., Hamblin, S., & Giraldeau, L. A. (2012). The effect of exploration on the use of
 420 producer-scrounger tactics. *PLoS ONE*, 7(11). doi: 10.1371/journal.pone.0049400
 421 Maher, J. M., Markey, J. C., & Ebert-May, D. (2013). The other half of the story: effect size
 422 analysis in quantitative research. *CBE-Life Sciences Education*, 12(3), 345-351.
 423 Mathot, K. J., & Giraldeau, L.-A. (2010). Within-group relatedness can lead to higher levels of
 424 exploitation: a model and empirical test. *Behavioral Ecology*, 21(4), 843-850. doi:
 425 10.1093/beheco/arq069
 426 Mayack, C., & Naug, D. (2013). Individual energetic state can prevail over social regulation of
 427 foraging in honeybees. *Behavioral Ecology and Sociobiology*, 67(6), 929-936. doi:
 428 10.1007/s00265-013-1517-6
 429 Mehlhorn, K., Newell, B. R., Todd, P. M., Lee, M. D., Morgan, K., Braithwaite, V. A., . . .
 430 Gonzalez, C. (2015). Unpacking the exploration–exploitation tradeoff: A synthesis of
 431 human and animal literatures. *Decision*, 2(3), 191-215. doi: 10.1037/dec0000033
 432 Ratnieks, F. L. W., Foster, K. R., & Wenseleers, T. (2006). Conflict resolution in insect societies.
 433 *Annual Review of Entomology*, 51, 581-608.
 434 Schulz, D. J., Huang, Z. Y., & Robinson, G. E. (1998). Effects of colony food shortage on
 435 behavioral development in honey bees. *Behavioral Ecology and Sociobiology*, 42(5), 295-
 436 303.
 437 Seeley, T. D. (1995). *The wisdom of the hive: the social physiology of honey bee colonies*
 438 Cambridge: Harvard University Press.

- 439 Shafir, S., Wiegmann, D. D., Smith, B. H., & Real, L. A. (1999). Risk-sensitive foraging: choice
440 behaviours of honeybees in response to variability in volume of reward. *Animal*
441 *Behaviour*, 57, 1055-1061.
- 442 Stevens, J. R., & Cushman, F. A. (2004). Cognitive constraints on reciprocity and tolerated
443 scrounging. *Behavioral and Brain Sciences*, 27(04), 569-570.
- 444 Toth, A. L., Kantarovich, S., Meisel, A. F., & Robinson, G. E. (2005). Nutritional status
445 influences socially regulated foraging ontogeny in honey bees. *Journal of Experimental*
446 *Biology*, 208, 4641-4649.
- 447 Toth, A. L., & Robinson, G. E. (2007). Evo-devo and the evolution of social behavior. *Trends in*
448 *Genetics*, 23(7), 334-341.

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