

Foraging bumblebees do not rate social information above personal experience

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Abstract Foraging animals can acquire new information about food sources either individually or socially, but they can also opt to rely on information that they have already acquired, termed “personal information”. Although social information can provide an adaptive shortcut to new resources, recent theory predicts that investing too much time in acquiring new information can be detrimental. Here, we investigate whether foraging bumblebees (*Bombus terrestris*) strategically prioritize personal information unless there is evidence of environmental change. All bees in our study had personal information that one species of artificial flower was rewarding, and bees in the scent group then experienced social information about an alternative-scented species inside the nest, while a control group did not. On their next foraging bout, bees in both groups overwhelmingly used personal information when deciding where to forage. When bees subsequently learnt that the rewards offered by their preferred species had dwindled, bees that had social information were no quicker to abandon their personal information than control bees, but once they had sampled the alternative flowers, they showed greater commitment to that species than control bees. Thus, we found no evidence that social information is particularly important when personal information fails to produce

rewards (a “copy when established behaviour is unproductive” strategy). Instead, bees used social information specifically to complement personal information.

Keywords Social information use · Social learning strategies · Bumblebees

Introduction

Social animals are typically faced with three options when deciding where to forage. Individuals can acquire new information individually via exploration, acquire new information socially through the behaviour of other animals, or use personal information that has already been acquired. For example, a foraging ant might search for a new honeydew source alone (explore), follow a pheromone trail (use social information), or revisit a patch where it has foraged previously (use personal information). Much effort has been devoted to understanding how individuals decide between the first two options (Rogers 1988; Boyd and Richerson 1988, 1995; Enquist et al. 2007), and contemporary theory suggests that acquiring information socially may frequently be the more adaptive strategy of the two (Rendell et al. 2010, 2011). Yet, a common theme to emerge from empirical studies is that often, neither social information use nor exploration is chosen because animals opt to use information that they have already acquired. Across the animal kingdom, foraging animals often fall back on social information only if personal information is unavailable, outdated, or proving unsatisfactory (e.g. van Bergen et al. 2004; Kendal et al. 2004, 2005; Grüter et al. 2008, 2010; Webster and Laland 2008; Grüter and Ratnieks 2011).

Why is personal information use such a popular option? Exploration may be time-consuming or risky (Boyd and

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Richerson 1985), and acquiring new information socially does not necessarily bypass such costs and may additionally incur others (Rieucau and Giraldeau 2011). For example, although honeybees might reduce exploration time by visiting feeders indicated by waggle dancers, the dance is a noisy signal (von Frisch 1967; Tanner and Visscher 2010; Couvillon et al. 2012), and individuals might invest time in extensive dance following (Grüter et al. 2013) and nonetheless fail to find the advertised patch (Seeley and Visscher 1988). In contrast, personal information, by definition, does not invoke acquisition costs. Accordingly, in a recent large-scale evolutionary simulation, agents that typically relied on information that they had already acquired (played “exploit”) did significantly better than those that invested more time in acquiring new information, either socially (played “observe”) or by trial and error (played “innovate”); Rendell et al. 2010).

A crucial caveat to emerge from the same simulation study is that personal information use is no longer likely to be the best option if the environment changes. How might animals assess whether personal information has become outdated? One possibility is simply to seek out social information only when they repeatedly fail to be rewarded for current behaviour (a “copy when established behaviour is unproductive” strategy; Laland 2004). Empirical evidence is beginning to suggest that social learning strategies such as this might underlie social information use in a wide range of taxonomic groups (Laland 2004; Kendal et al. 2005, 2009; Grüter et al. 2010, 2013), because they allow for flexible social information use that matches local circumstances (Laland 2004; Rendell et al. 2011). Here, we test whether personal information overrides a well-established form of social information use in a classic social insect model, the bumblebee (*Bombus terrestris*).

Foraging bumblebees face a temporally dynamic floral market, where new plant species frequently come into bloom and others quickly fade (Heinrich 1979). Like many eusocial insect colonies, bumblebee nests are microcosms of social information use, where individuals can learn about foraging options through a multitude of signals and social cues (Goulson et al. 1998; Seeley 1998; Dornhaus and Chittka 1999, 2004, 2001; Leadbeater and Chittka 2007a). Once they have left the colony to forage, bumblebees use additional social information to identify rewarding flowers and flower species, to learn flower-handling skills, and to avoid dangerous forage patches (Leadbeater and Chittka 2005, 2007a, b; Dawson and Chittka 2014; Dawson et al. 2013). Yet, bees also learn very quickly through their own personal experience, repeatedly revisiting flower patches and species that they have found to be rewarding (Chittka and Thomson 2001). In other words, all but the most naive foragers have personal information which might override, or at least bias, social information use.

We focus on nest-based social information about the scent of rewarding flowers. Foragers are known to

prefer floral scents that they have encountered in the nest, deriving from nectar collected by other foragers (Dornhaus and Chittka 1999). This phenomenon is also common in other social insects (Wenner et al. 1969; Farina et al. 2005, 2007; Taylor et al. 2010). As is the case for many classic examples of social information use (e.g. Terkel 1996 [rats], Thornton and McAuliffe 2006 [meerkats]), the actual presence of conspecifics is not required for learning to take place (Heyes 1994). Molet et al. (2009) found that even the artificial introduction of scents into the air of bumblebee nests from a glass vial, rather than by returning foragers, can increase the likelihood that foragers with no previous experience of scents choose similarly scented flowers on leaving the nest. Here, we hypothesize that bees with personal information about rewarding flower species will ignore contrasting floral scent information presented in the nest until they discover that their personal information has become outdated, adopting a “copy when established behaviour is unproductive” strategy.

Methods

Overview

Our experiment mimics a situation where the nectar rewards of one flower species start to dwindle, while a new species comes into bloom. All subjects initially foraged on an array of sucrose-filled geranium-scented flowers, acquiring personal information that geranium-scented flowers are rewarding. One group (scent group) subsequently experienced the scent of lavender flowers in the nest, acquiring social information that lavender flowers are rewarding, while the other encountered no scent (control). On returning to the arena, all bees encountered geranium-scented flowers and new lavender-scented flowers. We predicted that all bees, irrespective of their group, would initially ignore lavender-scented flowers, instead relying on their personal information that geranium-scented flowers are rewarding. Only when they subsequently discovered that their personal information was out of date, and geranium flowers no longer contained sucrose, did we expect an effect of treatment group: bees in the scent group should be quicker to switch from geranium- to lavender-scented flowers.

Subjects

Bees ($n=42$) came from four commercially bred *B. terrestris* colonies, housed in bipartite wooden nest boxes that were connected to a flight arena (120×70×30 cm) by a transparent plastic tunnel. Access to the arena could be controlled using

shutters. A 50-ml gravity feeder containing 30 % (v/v) sucrose was placed in the nest box every day after experiments had finished, and pollen was added directly into the nest three times per week. Individual bees were marked with coloured number tags.

Pretraining

The aim of this phase was to identify motivated foragers and allow bees to learn that geranium-scented flowers were rewarding. Bees had unrestricted access to the flight arena for 2 days, for approximately 5 h per day, before experiments began. During this time, the arena contained seven artificial flowers (circular yellow plastic foam discs, 45 mm in diameter, mounted on plastic cylinders 60 cm in height). Each flower was scented with 2 μ l of geranium (*Pelargonium graveolens*) essential oil (Calmer Solutions, Surrey, UK), placed directly onto the foam disc. A small well in the centre of each disc was filled with 50 μ l of sucrose solution and refilled immediately following foraging visits by bees. All flowers were cleaned with ethanol and water at the end of each day.

On the day of the experiment, a bee was selected from those that were attempting to leave the nest box to forage and permitted to enter the flight arena alone. Only bees that had previously been identified as motivated foragers (observed to feed from at least one flower, return to the nest, and then re-emerge and visit another flower within 10 min) were selected to participate. The arena contained the same array as before: seven rewarding, geranium-scented flowers that were refilled following each visit. Once the bee had collected sufficient sucrose, she returned to the nest box to empty her nectar stomach in preparation for the next foraging bout. Thus, all test subjects had up-to-date personal information that geranium-scented flowers contained sucrose.

Social information

Test subjects were randomly allocated to either the scent group or the control group. On returning to the nest box following individual pretraining, bees in the scent group encountered an unfamiliar lavender (*Lavandula angustifolia*) scent inside the nest. A piece of cardboard (10×10 mm) scented with 4 μ l lavender essential oil, suspended using a wooden skewer, was placed directly over the nest. A similar set-up, also using airborne odours, has previously been shown to elicit recruitment to scented flowers (Molet et al. 2009). The scented card remained in the nest only until the test subject left to return to the foraging arena, or for 10 min, whichever was the shortest. Bees in the control group experienced the same protocol, but no scent was presented. Thus, bees in the control group had personal information that geranium-scented flowers were rewarding, and bees in the scent group had the same personal

information, plus additional social information about a newly available lavender-scented species.

Testing

During the test phase, the flight arena contained seven familiar geranium-scented flowers alongside seven unfamiliar lavender-scented flowers of identical appearance, save for an inconspicuous black dot to allow differentiation between flowers by the observer. Geranium-scented flowers were all empty, and lavender-scented flowers each contained 50 μ l of sucrose solution. This design aimed to mimic a situation where the rewards of one flower species dwindle and another species comes into bloom. Flowers were placed arbitrarily around the arena to prevent bees from simply returning to floral locations that they recalled as being rewarding previously. We recorded every behaviour that a subject made to either type of flower, classifying behaviours as “visits” if a bee landed and probed the flower or “approaches” if she directly approached (<3 cm distance, orientated towards the flower) but did not land. The test ended when the bee attempted to return to the nest box to empty her nectar stomach, at which point she was removed from the colony. We tested 42 bees in total, divided evenly between the two groups. All flowers were cleaned with ethanol and water between tests.

Unlearnt preferences

To establish whether bees might have unlearnt preferences for one scent over the other that might bias their choices, we carried out a control treatment involving 20 bees from two additional colonies. These bees had the same pretraining experience as described above, but the flowers were never scented, and no social information about scent was provided in the nest. Thus, the bees had no personal information about the scent of rewarding flowers. Bees were tested individually. Each bee was offered the choice between seven geranium-scented flowers and seven lavender-scented flowers, all containing 50 μ l of sucrose solution, and all approach and landing behaviours were recorded. Three individuals never landed on either flower type during the test and were thus excluded from the analysis (thus $n=17$).

Analyses

We used separate binomial tests to establish whether bees in our “unlearnt preferences” test, in our “scent” treatment, and in our “control” treatment showed any significant preferences for geranium or lavender on their first flower visit during the test (i.e. “successes”=number of bees choosing lavender on their first flower visit, n =total number of bees, *probability of success under null hypothesis*=0.5). We also compared the number of bees

choosing lavender on their first flower visit between the scent and control groups using a simple Wilcoxon test.

We then tested whether bees in the scent group, on finding that geranium-scented flowers were now unrewarding, probed lavender-scented flowers more quickly than those in the control group. We created a generalized linear model (Poisson error structure), with “treatment” as the sole predictor and “number of geranium visits before the first lavender visit” as the response variable, for comparison with a null model containing only the intercept. p values are based on the difference in deviance between the two models, using ANOVA comparisons based on chi-squared statistics (Crawley 2007).

Finally, we tested preferences for lavender flowers following the first visit to a lavender-scented flower. Here, the response variable comprised two vectors bound together in the form (number of lavender visits, number of geranium visits), and we specified a binomial error distribution (Crawley 2007). Again, we compared this with a null model that contained only the intercept.

Results

Bees in our “unlearned preferences” test showed no significant preferences for geranium-scented flowers (mean preference for geranium=0.29, $p=0.14$), but bees in both the scent and control groups were more likely to visit geranium flowers on their first flower visit during the test period (mean preferences for geranium, 0.95 [control], 1.0 [scent], $p<0.0001$ in both

cases). This strong preference for geranium did not differ between the scent and control groups ($W=231$, $p=0.34$). Thus, bees relied heavily on personal information, and we found no evidence that social information influenced initial choice behaviour.

When bees subsequently found that geranium flowers were unrewarding, all but two individuals (one in each treatment group) began to visit lavender flowers. Bees that had experienced the lavender scent in the nest were no quicker to probe lavender flowers than control bees (Fig. 1, mean geranium acceptances before first lavender acceptance \pm s.e., 6.5 ± 1.6 , 7.2 ± 1.2 , respectively, $\chi=0.72$, d.f. = 1, $p=0.40$). They were also no more likely to approach lavender flowers without probing than control bees (mean approaches to lavender flowers before switching \pm s.e., 8.3 ± 1.8 , 7.19 ± 1.3 , respectively, $\chi=1.63$, d.f. = 1, $p=0.20$).

In contrast, as soon as they had probed lavender flowers, bees in the scent group visited a significantly higher proportion of lavender flowers than bees in the control group on subsequent flower visits (Fig. 2; mean preference for lavender flowers \pm s.e., 0.83 ± 0.02 , 0.59 ± 0.03 , respectively, $\chi=-72.36$, d.f. = 1, $p<0.001$). As a result, fewer flower visits were necessary to complete a foraging bout, so bees returned to the nest more quickly (mean flower visits \pm s.e., 24.0 ± 2.97 (scent group) and 31.43 ± 1.76 (control group)).

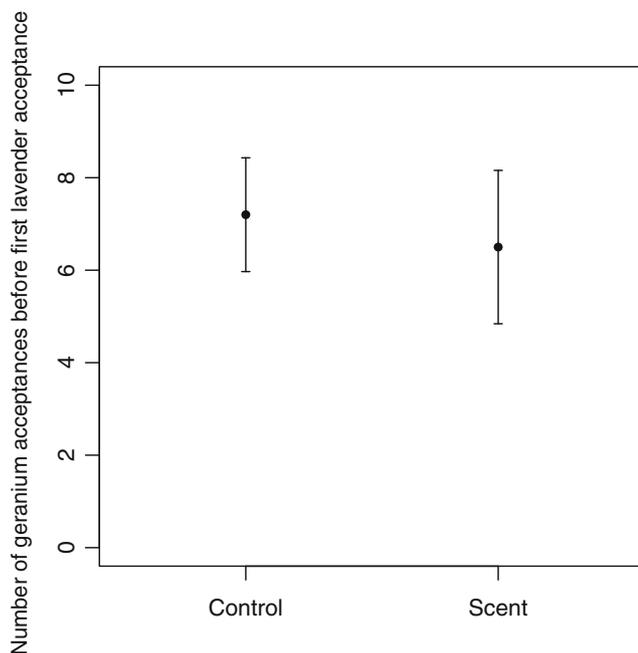


Fig. 1 Mean number of geranium acceptances before the first lavender acceptance ($n=42$ bees). Bees that had experienced lavender scent in the nest were no quicker to probe lavender flowers than controls. Bars indicate standard errors

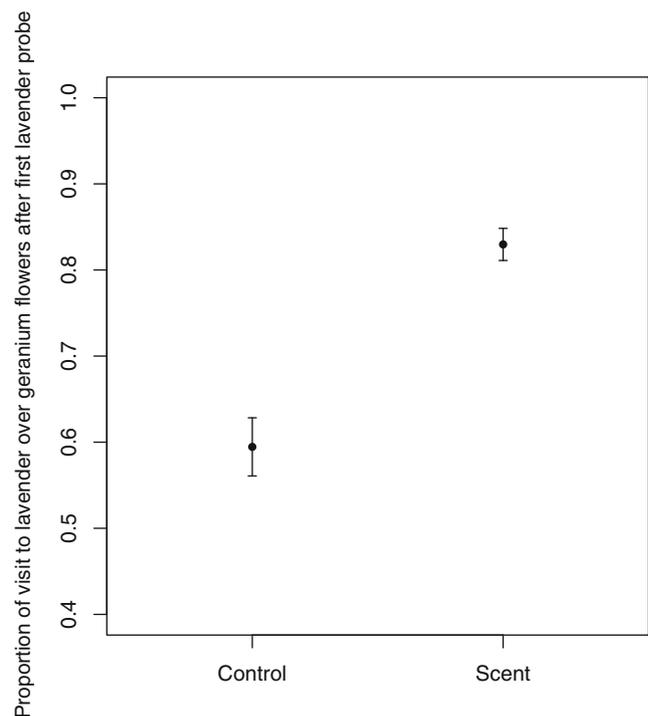


Fig. 2 The proportion of visits (acceptances) that were directed to lavender flowers following a bee’s first lavender acceptance. Bees in the scent group directed a significantly higher number of visits to the newly available lavender species than those in the control group. Bars represent standard errors; $n=42$ bees

Discussion

When bumblebees had recent personal information about one rewarding flower species, social information about a highly rewarding alternative did not influence their foraging preferences. On their first flower visit during the test period, our subjects in both the scent and control groups overwhelmingly chose the familiar geranium species that they knew to be rewarding, irrespective of the presence of an alternative scent in the nest. In other words, when personal information favoured one flower species but social information favoured the alternative, bees overwhelmingly used personal information.

Why did bees prioritize personal information? The most likely explanation is that up-to-date personal information involves little risk. If there is no reason to suppose that the environment has changed, reaping the benefits of information that has already been acquired rather than investing in learning makes sense. Yet, when the environment changes, personal information becomes out of date. Surprisingly, we found no evidence that social information affected bee behaviour even at this stage. Rather, our findings support the hypothesis that exploration of alternative options was driven by individual exploration, because bees with no social information were just as quick to switch flower species as their socially informed counterparts.

Although social information about an alternative, rewarding flower species did not make bees abandon their personal information more quickly, we did find an unexpected and strong effect of social information after bees had sampled alternative options for themselves. Once they had probed lavender flowers, bees in the scent group focussed their foraging effort more heavily upon the new species, while those in the control group were more likely to continue probing at least some geranium flowers. As a result, they collected a full load of sucrose more quickly, wasting less time on a flower species where rewards had dwindled to nothing. In other words, social information was important, but only when it complemented personal information (that lavender flowers were now rewarding). A similar phenomenon has been described in trail-following *Lasius niger* ants, whereby ants are faster and more direct when following a remembered trail if trail pheromone is also present (Czaczkes et al. 2011). In both cases, social information seems to act synergistically with personal information.

Our findings add strength to the hypothesis that animals may avoid investment in learning, either socially or through exploration, unless there is reason to abandon current behaviour (Kendal et al. 2009; Rendell et al. 2010; Grüter and Ratnieks 2011; Grüter et al. 2011). Traditionally, social information use has been considered a less-costly alternative to time-consuming exploration, but acquiring social information can also invoke specific time costs. Correspondingly,

honeybees that know of a rewarding food source often do not invest time in following dances before leaving the hive to forage (von Frisch 1967). Even when they do seek out dance information, bees frequently do so only to update information about known food sources rather than find new ones, which may require considerably more “runs” to be followed (Grüter et al. 2013). In other contexts, including our study, social information may be acquired at a relatively low cost. Ant foraging trails often commence at the nest entrance (Hölldobler and Wilson 1990), so a forager may pay little time cost to seek them out; likewise, exposure to a floral scent in the nest is unlikely to be costly. Our findings suggest that personal information is still the option of choice even in these circumstances, at least when it derives from recent experiences of the foraging environment.

In the wild, foraging bees and other animals will almost always have personal experience of their foraging environment. Although experiments with naive individuals are very useful in demonstrating whether animals *can* use social information (e.g. Dornhaus and Chittka 1999), the question of whether they actually *do* use it cannot be answered without taking into account the influence of personal experience. Our findings highlight that the most important role of social information may sometimes be to boost confidence in, rather than override, personal information.

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References

- Boyd R, Richerson P (1985) Culture and the evolutionary process. University of Chicago Press, Chicago
- Boyd R, Richerson P (1988) An evolutionary model of social learning: the effects of spatial and temporal variation. In: Zentall TR, Galef BG (eds) Social learning: psychological and biological perspectives. Lawrence Erlbaum Associates, Hillsdale, pp 29–48
- Boyd R, Richerson P (1995) Why does culture increase human adaptability? *Ethol Sociobiol* 16:125–143
- Chittka L, Thomson JD (eds) (2001) Cognitive ecology of pollination. Cambridge University Press, Cambridge
- Couvillon MJ, Riddell Pearce FC, Harris-Jones EL, Kuepfer AM, Mackenzie-Smith sJ, Rozario LA, Schürch R, Ratnieks FLW (2012) Intra-dance variation among waggle runs and the design of efficient protocols for honey bee dance decoding. *Biology Open*. ISSN 2046-6390
- Crawley MJ (2007) The R book. John Wiley & Sons, Ltd., Chichester
- Czaczkes TJ, Grüter C, Jones SM, Ratnieks FLW (2011) Synergy between social and personal information increases foraging efficiency in ants. *Biol Lett* 7(4):521–524. doi:10.1098/rsbl.2011.0067
- Dawson EH, Chittka L (2014) Bees use social information as an indicator of safety in dangerous environments. *Proc Roy Soc B* (in press)
- Dawson EH, Avargues-Weber A, Chittka L, Leadbeater E (2013) Learning by observation emerges from simple associations in an insect model. *Curr Biol* 23:727–730

- Dornhaus A, Chittka L (1999) Evolutionary origins of bee dances. *Nature* 401:38
- Dornhaus A, Chittka L (2001) Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications. *Behav Ecol Sociobiol* 50(6):570–576
- Dornhaus A, Chittka L (2004) Information flow and regulation of foraging activity in bumble bees (*Bombus* spp.). *Apidologie* 35(2):183–192
- Enquist M, Eriksson K, Ghirlanda S (2007) Critical social learning: a solution to Rogers's paradox of nonadaptive culture. *Am Anthropol* 109(4):727–234
- Farina WM, Gruter C, Diaz PC (2005) Social learning of floral odours inside the honeybee hive. *Proc R Soc Lond B* 272(1575):1923–1928
- Farina WM, Gruter C, Acosta L, Mc Cabe S (2007) Honeybees learn floral odors while receiving nectar from foragers within the hive. *Naturwissenschaften* 94(1):55–60
- Frisch V (1967) The dance language and orientation of bees. Harvard University Press, Cambridge
- Goulson D, Hawson SA, Stout JC (1998) Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. *Anim Behav* 55:199–206
- Grüter C, Ratnieks FLW (2011) Honeybee foragers increase the use of waggle dance information when personal information becomes unrewarding. *Anim Behav* 81(5):949–954. doi:10.1016/j.anbehav.2011.01.014
- Grüter C, Balbuena MS, Farina WM (2008) Informational conflicts created by the waggle dance. *Proc R Soc B* 275:1321–1327
- Grüter C, Leadbeater E, Ratnieks FLW (2010) Social learning: the importance of copying others. *Curr Biol* 20(16):R683–R685. doi:10.1016/j.cub.2010.06.052
- Grüter C, Czaczkes TJ, Ratnieks FLW (2011) Decision making in ant foragers (*Lasius niger*) facing conflicting personal and social information. *Behav Ecol Sociobiol* 65(2):141–148. doi:10.1007/s00265-010-1020-2
- Grüter C, Segers FHID, Ratnieks FLW (2013) Social learning strategies in honey bee foragers: do the costs of using personal information affect the use of social information? *Anim Behav* 85:1443–1449
- Heinrich B (1979) Bumblebee economics. Harvard University Press, Cambridge
- Heyes (1994) Social learning in animals: categories and mechanisms. *Biol Rev* 69:207–231
- Hölldobler B, Wilson EO (1990) The ants. Springer-Verlag, Berlin Heidelberg
- Kendal RL, Coolen I, Laland KN (2004) The role of conformity in foraging when personal and social information conflict. *Behav Ecol* 15(2):269–277
- Kendal RL, Coolen I, van Bergen Y, Laland KN (2005) Trade-offs in the adaptive use of social and asocial learning. *Adv Stud Behav* 35:333–379
- Kendal RL, Coolen I, Laland KN (2009) Adaptive trade-offs in the use of social and personal information. *Cognitive ecology II*
- Laland KN (2004) Social learning strategies. *Learn Behav* 32(1):4–14
- Leadbeater E, Chittka L (2005) A new mode of information transfer in foraging bumblebees? *Curr Biol* 15(12):R447–R448
- Leadbeater E, Chittka L (2007a) Social learning in insects: from miniature brains to consensus building. *Curr Biol* 17(16):R703–R713
- Leadbeater E, Chittka L (2007b) The dynamics of social learning in an insect model (*Bombus terrestris*). *Behav Ecol Sociobiol* 61:1789–1796
- Molet M, Chittka L, Raine NE (2009) How floral odours are learned inside the bumblebee (*Bombus terrestris*) nest. *Naturwissenschaften* 96(2):213–219. doi:10.1007/s00114-008-0465-x
- Rendell L, Boyd R, Cownden D, Enquist M, Eriksson K, Feldman MW, Fogarty L, Ghirlanda S, Lillicrap T, Laland KN (2010) Why copy others? Insights from the social learning strategies tournament. *Science* 328(5975):208–213. doi:10.1126/science.1184719
- Rendell L, Fogarty L, Hoppitt W, Morgan T, Webster M, Laland K (2011) Cognitive culture: theoretical and empirical insights into social learning strategies. *Trends Cogn Sci* 15:68–76
- Rieucou G, Giraldeau L-A (2011) Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philos Trans R Soc B* 366(1567):949–957. doi:10.1098/rstb.2010.0325
- Rogers AR (1988) Does biology constrain culture? *Am Anthropol* 90(4):819–831
- Seeley TD (1998) Thoughts on information and integration in honey bee colonies. *Apidologie* 29(1–2):67–80
- Seeley TD, Visscher PK (1988) Assessing the benefits of co-operation in honeybee foraging- search costs, forage quality and competitive ability. *Behav Ecol Sociobiol* 22(4):229–237. doi:10.1007/bf00299837
- Tanner DA, Visscher PK (2010) Adaptation or constraint? Reference-dependent scatter in honey bee dances. *Behav Ecol Sociobiol* 64(7):1081–1086. doi:10.1007/s00265-010-0922-3
- Taylor BJ, Schalk DR, Jeanne RL (2010) Yellowjackets use nest-based cues to differentially exploit higher-quality resources. *Naturwissenschaften* 97:1041–1046
- Terkel J (1996) Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In: Heyes CM, Galef BG Jr (eds) Social learning in animals: the roots of culture. Academic Press, San Diego, pp p17–p48
- Thornton A, McAuliffe K (2006) Teaching in wild meerkats. *Science* 313:227–229
- Van Bergen Y, Coolen I, Laland KN (2004) Foraging nine-spined stickleback exploit the most reliable source when public and private information conflict. *Proc R Soc Lond B* 271:957–962
- Webster M, Laland K (2008) Social learning strategies and predation risk: minnows copy only when using personal information would be costly. *Proc R Soc Lond B* 275(1653):2869–2876
- Wenner AM, Wells PH, Johnson DL (1969) Honeybee recruitment to food sources- olfaction or language? *Science* 164:84–86