The influence of past experience with flower reward quality on social learning in bumblebees

Patricia L. Jones [a, *], Michael J. Ryan [a], Lars Chittka [b]

[a] Department of Integrative Biology, University of Texas, Austin, TX, U.S.A.
[b] Biological and Experimental Psychology, School of Biological and Chemical Sciences, Queen Mary University of London, London, U.K.

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Foraging decisions can be influenced by innate biases, previous individual experience and social information acquired from conspecifics. We examined how these factors interact to affect flower colour preference in the large earth bumblebee, *Bombus terrestris dalmatinus*. Individual bees with no experience foraging on coloured flowers were first tested for innate colour biases on an unrewarded array of blue and yellow artificial flowers. Depending on treatment, bees then acquired individual experience foraging on a colour (either blue or yellow) associated with high-quality sucrose rewards, or a colour with low-quality sucrose rewards, or they did not acquire any individual experience. Bees were then exposed to the alternative colour associated with conspecific demonstrator bees (social information) or the alternative colour with no social information. Bees that had no individual experience visited flower colours that were associated with conspecific demonstrators (social information) but only significantly if the socially demonstrated colour was one for which bees had an innate bias. When bees had individual experience foraging on a colour with high-quality rewards they continued foraging on that colour, and generally did not visit the socially demonstrated alternative colour, regardless of innate colour bias. Alternatively, when bees had individual experience foraging on colours with low-quality rewards, they made more visits to the socially demonstrated alternative flower colour, but only when the alternative colour was the colour for which they had an innate bias. Bees that had no access to social information continued to forage on low-reward coloured flowers. Thus we show that reward quality of resources with which bees have individual experience affects the use of social information but with an important role of innate biases.

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When animals make decisions about which resources to consume they can be influenced by a number of different factors. Animals often have innate preferences, or biases, for particular foods (Birch, 1999). They also have previous individual experience with certain resources (Birch, 1999; Sclafani, 2007), and they often have access to information from other individuals, or social information (Avarguès-Weber & Chittka, 2014; Galef & Laland, 2005; Sherwin, Heyes, & Nicol, 2002). The use of social information in foraging decisions is taxonomically widespread, probably because social learning avoids the potentially costly mistakes of individual trial-and-error learning (Galef & Giraldeau, 2001). Social information, however, may not necessarily be relevant or accurate because it is acquired from others rather than by sampling the environment directly (Giraldeau, Valone, & Templeton, 2002). The costs and benefits of social information have led to the prediction that animals should use social information selectively in combination with information acquired from individual experience (Laland, 2004). Empirical research has confirmed that animals use social information only under certain conditions, following particular 'social learning strategies' (Kendal, Coolen, & Laland, 2009). For example, guppies (*Poecilia reticulata*) are more likely to use social information when they are uncertain (Kendal, Coolen, & Laland, 2004) and when acquiring individual information is costly (Laland & Williams, 1998); and nine-spined sticklebacks, *Pungitius pungitius*, are more likely to use social information when information acquired from individual experience is outdated (van Bergen & Coolen, 2004). These studies have provided important insights into how animals use social information when making foraging decisions.

Acquisition of information about novel foods has been proposed as a key advantage of social learning because testing novel foods carries inherent risks (Galef & Giraldeau, 2001). A substantial body

* Correspondence and present address: P. L. Jones, Department of Ecology & Evolutionary Biology, Cornell University, Corson Hall, Ithaca, NY 14853, U.S.A.
    E-mail address: plj6@cornell.edu (P. L. Jones).

of research on when animals use social information to learn about novel foods has been conducted in Norway rats, *Rattus norvegicus*; in which satisfaction, predation risk, uncertainty and environmental stability influence the use of social information about novel foods (Galef, 2009). This research is crucial to predict when foraging innovations will spread through social groups. One of the social learning strategies demonstrated in Norway rats is that of 'copy when dissatisfied' (Laland, 2004), in which rats that are fed on a low-quality diet are more likely to use social information than rats fed on a high-quality diet (Galef, Dudley, & Whisken, 2008). This social-learning strategy has also been demonstrated in the frog-eating bat, *Trachops cirrhosus*, for which individuals foraging using poorly rewarded prey cues are more likely to use social information to learn novel prey cues than bats foraging on well-rewarded cues (Jones, Ryan, Flores, & Page, 2013). 'Copy when dissatisfied' is a relatively simple social-learning strategy that is likely exhibited by many taxa. We tested whether large earth bumblebees, *Bombus terrestris dalmatinus*, exhibit this strategy.

Bumblebees can rapidly learn to associate particular colours (Menzel, 1985; Raine & Chittka, 2008) and scents (Guerrieri, Schubert, Sandoz, & Giurfa, 2005; Molet, Chittka, & Raine, 2009) with rewards, and to differentiate between flowers with different reward qualities (Heinrich, 2004; Waddington, 2001). Bumblebees also use social information in a variety of different contexts. Bumblebees are attracted to the presence of other bees on flowers (Leadbeater & Chittka, 2005, 2009), and they can even learn to associate flower colours with rewards by observing other bees through a screen (Avarguès-Weber & Chittka, 2014; Dawson, Avarguès-Weber, Chittka, & Leadbeater, 2013; Worden & Papaj, 2005). Bumblebees also learn to make nectar-robbing holes in flowers after encountering flowers in which other bees have made holes (Goulson, Park, Tinsley, Bussière, & Vallejo-Marin, 2013), and bumblebees learn to avoid flowers that have been scent-marked by previous visitors (Leadbeater & Chittka, 2011). Bumblebees additionally learn floral scents that they have been exposed to in the hive from nectar collected by other foragers (Dornhaus & Chittka, 1999). Bumblebees therefore have access to a wide range of social information with the potential to influence foraging decisions.

Recent studies have asked when bees use social information or rely on information from individual experience. One such study showed that bumblebees are more likely to associate with conspecifics when they are exposed to predation risk than when they are in predator-free environments (Dawson & Chittka, 2014). In addition, bumblebees are more likely to use scent marks from other bees as indicators that a flower's nectar has been depleted when the flowers are complex, and therefore individual sampling is more costly (Saleh, Ohashi, Thomson, & Chittka, 2006). In honeybees, individuals are also more likely to use social information when errors in individual experience are more costly (Wray, Klein, & Seeley, 2011). In both honeybees and bumblebees, however, use of social information is not ubiquitous (Grüter & Leadbeater, 2014). Bumblebees that have foraging experience with one rewarding floral scent do not use social information to switch to foraging on alternative scents encountered in the hive, even when the experienced scent is no longer rewarding (Leadbeater & Florent, 2014). Similarly, honeybees with experience foraging at feeders that become unrewarding are slow to switch to socially demonstrated rewarding alternatives, repeatedly revisiting the unrewarding feeders before switching (Grüter & Ratnieks, 2011). These studies emphasize the facultative but not obligate use of social information by bees.

Bees foraging in the wild have access to an array of different flower types with sucrose concentrations ranging from 10% to 75% (Kevan & Baker, 1983). To test whether bumblebees exhibit the social learning strategy of 'copy when dissatisfied' (Laland, 2004), we examined how variation in reward quality affects bumblebee social information use. We trained bees to associate a flower colour with either a low (20%) sucrose concentration or a high (50%) concentration. We then provided bees with social information about an alternative flower colour. We predicted that bees foraging on flowers with low sucrose concentrations would use social information to visit alternative, more highly rewarded, flower colours. In contrast, we predicted that bees already foraging on a flower colour associated with high sucrose rewards would continue to forage on that colour and not visit socially demonstrated alternatives.

Bumblebees also have adaptive innate biases for particular flower colours (especially in the violet–blue range; Chittka, Ings, & Raine, 2004; Gumbert, 2000; Lunau, Wacht, & Chittka, 1996; Raine & Chittka, 2007), but these biases are variable at the individual and colony level (Ings, Raine, & Chittka, 2009). The terms 'innate colour biases' or 'innate colour preferences' are used widely in the pollinator literature to refer to preferential approaches to certain colours by foraging-naïve individuals (Lunau & Maier, 1995). Even after learning, approaches to novel flower colours can be influenced by innate biases (Gumbert, 2000). There has been little investigation of the role of innate biases in the use of social information in any taxa, but one study with Norway rats showed that social transmission chains are more stable when they provide information about a preferred flavour (cinnamon) than a less preferred flavour (cocoa) (Laland & Plotkin, 1993). Many animals show innate foraging biases, but how they are integrated with acquired individual and social experience is not well understood. We therefore additionally investigated the role of innate colour biases in the use of social information by bumblebees.

METHODS

Experimental Overview

For each bee we first tested innate bias for two colours, blue and yellow, in an unrewarded initial test. Bees were then randomly assigned to one of four treatments, which differed in the availability of individual experience with a coloured flower, the quality of rewards acquired during this individual experience, and access to social information about an alternative flower colour (Fig. 1, Table 1). The four treatments were as follows: (1) No training – Social, in which bees had no individual experience and were provided with social information about a flower colour; (2) Training to high-quality flower – Social, in which bees acquired individual experience with a coloured flower with high-quality (50% v/v sucrose solution) rewards and social information about an alternative
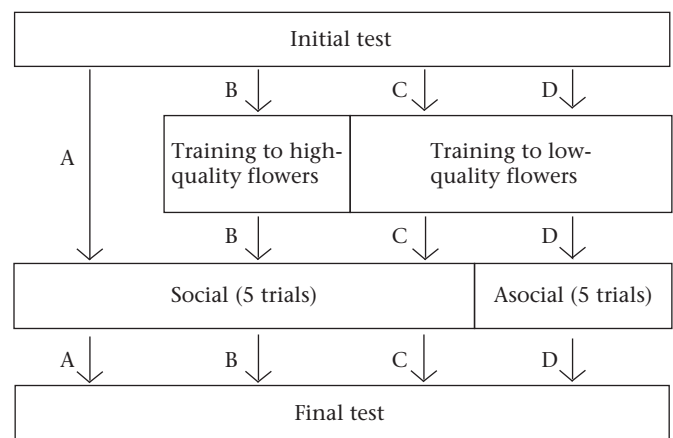

Figure 1. Experimental procedures for each of the four treatments are indicated by letters. A: No training – Social; B: Training to high-quality flower – Social; C: Training to low-quality flower – Social; D: Training to low-quality flower – Asocial.