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ORIGINAL PAPER

Social learning drives handedness in nectar-robbing bumblebees

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Abstract Bumblebees have been found to observe and copy the behaviour of others with regard to floral choices, particularly when investigating novel flower types. They can also learn to make nectar-robbing holes in flowers as a result of encountering them. Here, we investigate handedness in nectar-robbing bumblebees feeding on *Rhinanthus minor*, a flower that can be robbed from either the right-hand side or the left-hand side. We studied numerous patches of *R. minor* spread across an alpine landscape; each patch tended to be robbed on either the right or the left. The intensity of side bias increased through the season and was strongest in the most heavily robbed patches. We suggest that bees within patches learn robbing strategies (including handedness) from one another, either by direct observation or from experience with the location of holes, leading to rapid frequency-dependent selection for a common strategy. Primary robbing was predominantly carried out not only by a specialist robbing species, *Bombus wurflenii*, but also by *Bombus lucorum*, a widespread generalist. Both species adopted the same handedness within particular flower patches, providing the first evidence for social learning crossing the species boundary in wild insects.

Keywords *Bombus* · Foraging behaviour · Floral larceny · Learning · Apidae · Hymenoptera

Introduction

Social transmission of behaviours, sometimes known as social learning, is well known in vertebrates and can result in novel behaviours spreading rapidly through a population (Kawai 1965; Cavalli-Sforza and Feldman 1981). It may occur through direct observation of the behaviour of more experienced individuals or through individuals encountering the products of others' behaviour; for example, juvenile black rats only learn to extract seeds from pine cones if they encounter cones that have been partially stripped by adults (e.g. Terkel 1996). Although much of the literature on social learning focuses on vertebrates, it has recently become apparent that it is widespread in eusocial bees. Both Leadbeater and Chittka (2005) and Worden and Papaj (2005) demonstrated that bumblebees in flight arenas are more likely to visit novel artificial flowers if they observe another bee visiting them. More recently, Kawaguchi et al. (2007) found that wild bumblebees were more likely to land on novel, natural flowers if these had a dead bumblebee attached to them. These effects are not limited to conspecifics; bumblebees can learn to use the presence of honeybees on flowers as a cue when foraging (Dawson and Chittka 2012)

Darwin (1872) was amongst the first to describe nectar robbing, the removal of nectar from a flower by creating a hole in the side of the corolla. These holes may then be used to extract nectar by other individuals of the same or different species, known as secondary nectar robbery (Inouye 1983; Stout et al. 2000). Darwin was also the first to suggest that nectar robbery might be subject to social learning. In a letter to the Gardeners' Chronicle written in 1857, he observed:

> One day I saw for the first time several large humble-bees visiting my rows of the tall scarlet Kidney Bean; they were not sucking at the mouth of the flower, but cutting holes through the calyx, and thus extracting the nectar. … the very next day after the humble-bees had cut the holes, every single hive bee, without exception, instead of alighting on the left wing-petal, flew straight to the calyx and sucked through the cut hole …. I am strongly inclined to believe that the hive-bees saw the humble-bees at work, and well understanding what they

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> were at, rationally took immediate advantage of the shorter path thus made to the nectar.

More than 150 years later, Leadbeater and Chittka (2008) showed that *Bombus terrestris* workers that encounter robbed flowers are more likely to become robbers themselves, so that the behaviour can spread rapidly from one individual to many. Such behaviour could have significant impacts on plant fecundity, although the impact of robbing on reproductive success of plants is highly variable and not necessarily negative as Darwin presumed (reviewed by Maloof 2001).

Handedness (sometimes known as lateralization) is a side bias for motor output, perception and/or information processing, which has been widely studied in humans, but is also present in a range of animal species including bumblebees (Kells and Goulson 2001). In bumblebees, individual bees have a tendency to circle florets arranged in rings on a vertical raceme by either moving clockwise or counterclockwise, rarely switching between the two strategies (Kells and Goulson 2001). More recently, Anfora et al. (2011) described lateralization of learning in the brain of *B. terrestris*, whereby learned responses to olfactory cues are biased towards information from the right antennae.

Here, we study patterns of nectar robbing in bumblebee-visited yellow rattle, *Rhinanthus minor* L., in the Swiss Alps (Fig. 1). The calyx of this species is strongly flattened on each side, and robbing occurs via a hole cut into the side of the calyx and through the corolla. Preliminary observations in this region suggested that robbing holes within any one patch of *R. minor* tended to be on the same side. The bilateral symmetry of the calyx allows robbing to be characterized as occurring through either the right-hand side or left-hand side of the flower, hereafter considered to reflect visitor's handedness. To our knowledge, handedness in nectar robbery has not been previously described. Therefore, patterns of nectar robbing in *R. minor* offer a unique opportunity to (1) study the occurrence of handedness in natural populations, (2) establish the spatial and temporal variation in the pattern of handedness and (3) elucidate whether social learning plays a role in the establishment of site-wide bias in handedness of robbing bees. To address these issues, we carried out censuses of robbing patterns in 28 patches over 3 years and conducted bee observations to determine which species were responsible for nectar robbery and whether their behaviour exhibited handedness to match the distribution of robbing holes within a flower patch.

Methods

Study system

R. minor (Orobanchaceae) is an annual plant found in unimproved, species-rich grasslands throughout Europe (Westbury 2004). It is hemiparasitic, gaining nutrients from the roots of neighbouring grasses. It flowers from May to September, with peak flowering in June. Yellow zygomorphic flowers are produced on racemes up to 50 cm tall, with the lowest florets on the raceme flowering first. The calyx is flattened from side to side, inflated and bladder-like, surrounding all but the tip of the corolla (Fig. 1a). The flowers are deep, typically attracting long-tongued bumblebees such as *Bombus hortorum* and *Bombus pascuorum* (Kwak 1979; Kwak et al. 1985; Fig. 1b). In Switzerland, *R. minor* is frequent in unimproved alpine meadows, where it is subject to nectar robbing via holes cut into one or both sides of the calyx (Fig. 1c). Kwak (1979) describe nectar robbery by *Bombus lucorum*, with *Bombus lapidarius* and *Bombus pratorum* acting as secondary robbers. Robbing holes remain visible long after the floret has senesced, for the calyx dries and forms a case surrounding the seed capsule (Fig. 1a).

Patterns of robbing

Data were collected from 28 patches of *R. minor* within the vicinity of Mörlialp, Canton Obwalden, Switzerland, in June of 2009, 2010 and 2011, at altitudes ranging from 470 to 1,850 m (Fig. 2). Distances between patches ranged from 330 m to 15.2 km (mean, 5.6 km). Not all patches were present in every year, so that data were collected from 20, 16 and 22 patches in 2009, 2010 and 2011, respectively. In each patch, 20 racemes were chosen at random and each floret was scored according to whether it had been robbed on the left-hand side or the right-hand side, or on both sides. Scoring began with the highest, and hence youngest open floret, and worked downwards to the oldest floret, so that the score is correlated with the age of the floret. Approximate population size was estimated in each patch each year.

Observations of bee foraging behaviour

Bee behaviour was recorded in a subset of 13 patches in 2009 and 2011 (determined by suitability of weather for bee activity when visiting patches). Bees were followed until they had visited up to 20 florets or were lost from sight. Wherever possible, the bee was captured to confirm identity and to minimise the frequency with which the same bee was observed foraging more than once. Most bees were released after recording had finished for the day, although a small number of reference specimens were retained. It should be noted that some individual bees may have been observed on more than one occasion, but given the abundance of bees in the area, such records are likely to comprise a small proportion of our data. Foraging behaviour was recorded as:

(a) Legitimate foraging for nectar, which is only possible for long-tongued species.

Fig. 1 **a** An inflorescence of *R. minor*, showing robbing holes in the left-hand side of the calyces, clearly visible even on old florets (*bottom*) which have long since ceased to flower; **b** a primary nectar robber, *B. wurflenii*, biting a hole on the right-hand side of a floret; **c** a legitimate forager, *B. pascuorum*, collecting nectar

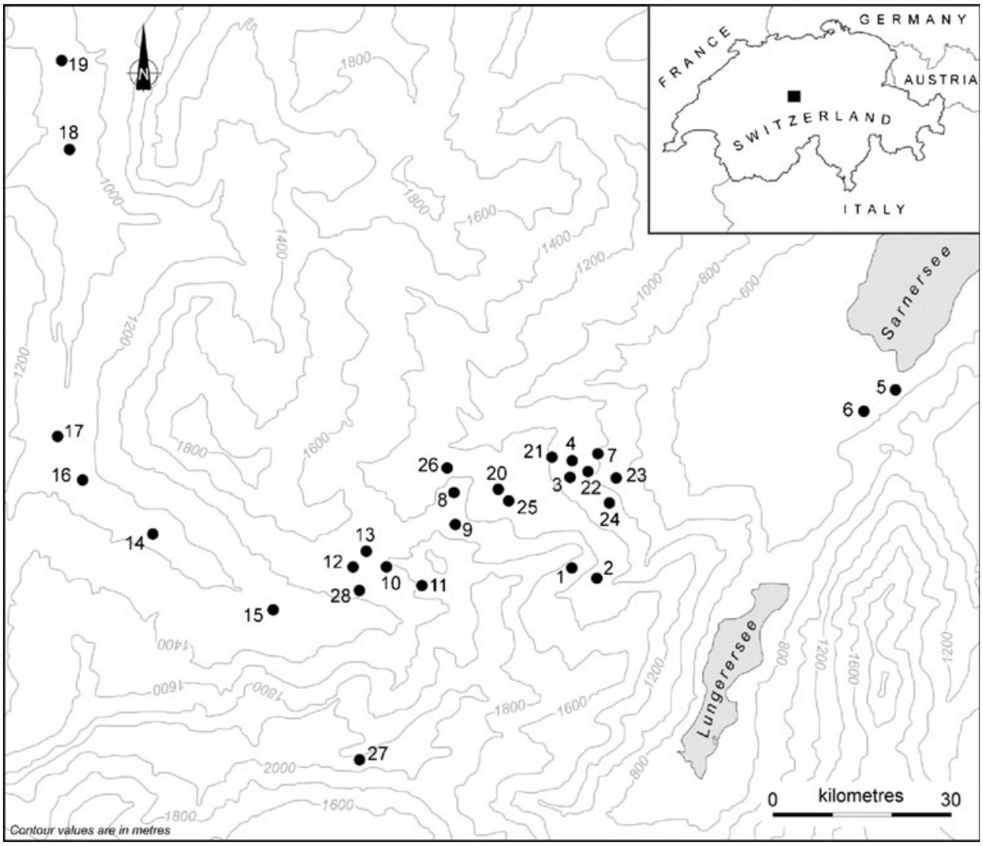

Fig. 2 Map of the sample patches

(b) Legitimate foraging for pollen. The anthers protrude slightly from the corolla and thus are readily accessible to all bee species.
(c) Primary robbing, involving the active use of mandibles to bite through one side of the calyx and corolla to access nectar.
(d) Secondary robbing, whereby an existing robbing hole is used to access nectar.

For c and d, the side of the floret that the bee first approached was recorded.

Analysis

The relationship between the proportion of florets robbed at least once in each patch and altitude was examined using a Generalized Linear Mixed Model (GLMM), with altitude as a covariate and year as a random factor. Departure from an expectation of an equal frequency of robbing to the left and right sides of florets was tested for each patch with a *t* test, using raceme as the unit of replication and the proportion of robbing holes which were on the left on each raceme as the dependent variable (the null hypothesis being that this proportion would be 0.5).

Relationships between the proportion of robbing holes on the left in each patch and altitude were examined with Spearman rank correlations, with separate analyses for each year. Relationships between patch-wide robbing bias (the absolute difference between the proportion of all holes on the left hand side and 0.5) and estimated patch size were also investigated using Spearman rank correlations, with separate analyses for each year.

To examine whether patches tended to exhibit robbing on the same side from year to year, the proportion of robbing holes within a patch that were on the left of florets was correlated between each pair of years using Pearson product moment correlations.

The difference in robbing strategy between a pair of patches was calculated as the absolute difference between the proportions of robbing holes on the left side of florets. This provides a value between 0 (identical strategy) and 1 (opposite strategy). A Mantel test was used to compare the difference in robbing strategy to the geographic distance between patches, since we might expect bees visiting adjacent patches to have similar strategies.

We built GLMMs implemented in the lme4 package (Bates et al. 2011) for R 2.14.1 (R Development Core Team 2011) to examine the binomial response of robbing side (coded as 0 for right, 1 for left). We treated each floret in our study as a replicate, fitting the random effects of patch (with each patch receiving a new code each year) and plant within patch. Including year as an additional random effect (within which patch and plant were nested) had no impact on our model selection, and because year accounted for a trivial (and non-significant [n.s.]) amount of variance, we present only the models without this random effect below. Florets, which were not robbed or which were robbed on both sides, were excluded from this model because they provide no information on characters that covary with left or right handedness. We included four fixed effects in the omnibus model: patch-wide robbing bias (proportion of robbed florets on the left-hand side excluding the focal floret), patch-wide robbing intensity (proportion of florets robbed out of the total in the patch), floret position (with the youngest open floret given the number 1, and older/lower florets assigned successively larger integers) and plant size (number of open florets on the plant). The last three of these (and their interactions with the first covariate) provide information on the likely role of learning on handedness. If social learning plays a role in robbing handedness, then learning might be more effective in more intensely robbed patches (where there are more opportunities to observe robbed florets), especially for later-opening florets (which are exposed to bees that have already learned the characteristics of a patch). In fact, this effect should be particularly strong in plants with many florets (which stretch further into the past, potentially to a time when the side bias of a patch had not yet been clearly established).

Our model selection procedure involved fitting the maximal model, including all main effects and interactions up to the third order, and iteratively removing terms that did not significantly reduce the model deviance, as indicated by likelihood ratio tests. Our model comparisons involve models estimated with maximum likelihood, but we report parameter estimates from models estimated using restricted maximum likelihood as recommended by Crawley (2007).

To visualize the interaction effects, we used the plotLMER.fnc function from the languageR library (Baayen 2011). We plotted the back-transformed fitted values of models built for the top and bottom quartiles of all combinations of continuous covariates, except patch robbing bias (proportion of florets robbed from the left, but excluding the focal floret), which is always plotted as the *x*-axis. Consequently, our figures illustrate the effect of other covariates on the predicted relationship between patch-wide bias and the probability of an individual floret being robbed on the left.

We studied the behaviour of individual bees when foraging to examine whether bees approached florets on the side that was most likely to be robbed within a patch. Using Pearson's correlation tests, we correlated the proportion of approaches by bees on the left-hand side of florets (pooled for bee species) with the proportion of existing holes on the left-hand side of florets within that patch. Separate correlations were carried out for primary and secondary robbers.

Results

Patterns of robbing

Population estimates varied from 25 to 250,000 flowering plants per patch and varied greatly between years; for example, patch 10 was estimated to contain 5,000, 250,000 and 500 plants in 2009, 2010 and 2011, respectively.

In total, robbing status was scored for 3,632, 3,483 and 4,187 florets in 2009, 2010 and 2011, respectively. Robbing was frequent, with 48.9, 36.1 and 53.7 % of florets subject to robbing on at least one side in 2009, 2010 and 2011, respectively. Moderate numbers of florets were robbed on both sides each year (11.1, 4.88 and 7.67 %, respectively). The frequency of robbing varied greatly between patches from 0 (patch 6 in 2009 and patch 7 in 2011) to 97.9 % of florets robbed at least once (patch 11 in 2011) (Table 1). The frequency of robbing tended to be higher at higher altitudes ($F_{1,54}=32.8$, $p<0.001$; Fig. 3), and there was no significant difference among years ($F_{2,54}=1.45$, $p=0.76$). At the two lowest patches, below 500 m (patches 5 and 6), robbing was rare or absent in all years.

Table 1 Frequency of robbing in 28 patches of *R. minor*

	Proportion of all florets robbed at least once		
Patch	2009	2010	2011
1	0.245	–	0.815
2	0.761	–	0.50
3	0.331	0.449	0.779
4	–	0.451	0.467
5	0.010	0.019	0.026
6	0	–	–
7	0.632	–	0
8	0.712	–	–
9	–	–	0.711
10	0.931	0.463	0.866
11	0.881	0.365	0.979
12	0.325	0.090	–
13	–	–	0.969
14	0.558	0.633	0.392
15	0.741	0.629	0.321
16	0.932	0.555	0.724
17	0.631	0.430	0.360
18	0.192	0.084	0.147
19	0.004	0.010	–
20	0.908	–	0.961
21	0.875	0.707	0.290
22	0.227	0.134	–
23	0.183	0.420	–
24	–	0.281	0.116
25	–	–	0.899
26	–	–	0.067
27	–	–	0.531
28	–	–	0.890

– the absence of the patch in that year (no flowering plants could be located)

The frequency of robbing on the left versus the right of the floret varied greatly between patches and years (Table 2). For example, in patch 20 in 2009, 169 of 171 robbing holes were on the left, while in contrast, in patch 28 in 2011, 154 of 161 robbing holes were on the right. Of 51 patch × year combinations for which sufficient robbing was present to test for a bias, 38 exhibited a significant bias to either left or right (14 biased to the left and 24 biased to the right). After sequential Bonferroni correction, 26 patch × year combinations exhibited a significant bias. There was no relationship between bias and altitude in any year (Spearman rank correlations, rho=−0.169, 0.332 and 0.272 for 2009, 2010 and 2011, respectively, all n.s.). There was no relationship between the degree of patch-wide robbing bias and patch size (Spearman rank correlations, rho=0.014, −0.277 and 0.158 for 2009, 2010 and 2011, respectively, all n.s.). Bias within patches was not correlated across any pair of years (Pearson correlation coefficients: $r=0.394$, $n=14$, $r=0.116$, $n=13$ and $r=-0.024$, $n=12$ for 2009–2010, 2009–2011 and 2010–2011, respectively). For example, patch 21 exhibited a strong bias towards robbing on the right in both 2009 and 2010, but switched to a strong bias to robbing on the left in 2011.

Interestingly, there was no evidence for spatial autocorrelation in robbing strategy, i.e. the pattern of robbing on the left or the right did not tend to be more similar in patches located nearer to one another (Mantel test, $r=0.037$, −0.069 and −0.098 in 2009, 2010 and 2011, respectively). For example, patches 7 and 23 were just 550 m apart, but 95 % of robbing holes in patch 7 were on the left, while

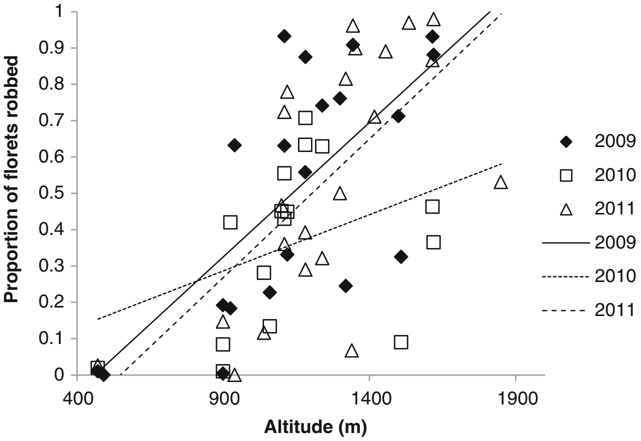

Fig. 3 The proportion of florets with at least one robbing hole according to altitude. Robbing frequency increased with altitude, but there was no significant difference between years

Table 2 Proportion of robbing holes which were on the left-hand side of florets

Patch	Altitude (m)	Proportion of all robbing holes on left hand side of calyx		
		2009	2010	2011
1	1,320	_0.889_***	–	_0.051_***
2	1,300	0.629*	–	_0.122_**
3	1,120	0.559 n.s.	0.333*	_0.280_***
4	1,100	–	0.245**	_0.755_***
5	472	1.00 n.a.	0.500 n.a.	0.600 n.s.
6	492	Unrobbed	–	–
7	940	_0.953_***	–	Unrobbed
8	1,500	0.278*	–	–
9	1,418	–	–	_0.726_***
10	1,616	0.527 n.s.	0.627*	_0.260_***
11	1,620	_0.952_***	0.591*	_0.187_***
12	1,509	0.588 n.s.	0.231 n.s.	–
13	1,536	–	–	_0.965_***
14	1,181	_0.281_***	0.317**	_0.217_***
15	1,239	0.469 n.s.	_0.657_***	0.600 n.s.
16	1,110	0.479 n.s.	0.503 n.s.	_0.118_***
17	1,110	0.366*	0.312*	_0.149_***
18	900	0.362 n.s.	0.083 n.s.	0.162*
19	900	1.00 n.a.	0.333na	–
20	1,344	_0.988_***	–	_0.902_***
21	1,182	_0.142_***	_0.155_***	_0.765_***
22	1,060	0.414 n.s.	_0_***	–
23	925	_0.106_**	0.371 n.s.	–
24	1,040	–	0.216**	_0.105_***
25	1,353	–	–	_0.222_***
26	1,340	–	–	0.222 n.a.
27	1,850	–	–	0.707*
28	1,456	–	–	_0.044_***

For all florets, departure from an expectation of an equal frequency of robbing to the left and right sides of florets in each patch was tested using a t test, using the proportion of robbing holes which were on the left on each raceme as the unit of replication (the null hypothesis being that this proportion would be 0.5). Numbers in italics indicate that the test remains significant after Bonferroni correction

n.a. test not applicable as three or fewer racemes had any robbed florets, – patch not present, *Unrobbed* no robbing in patch

$^{*}p<0.05$; $^{**}p<0.01$; $^{***}p<0.001$

89 % of robbing holes in patch 23 were on the right (2009 data).

Binomial probability of robbing on the left

Our minimum adequate model of covariates influencing robbing side probability included two three-way interactions (see Table 3 and Figs. 4 and 5). Both of these interactions involved the patch-wide robbing bias and the floret position: robbing side probability was closely related to patch robbing bias, but this effect was most evident in the most recently opened flowers, located at the top of the stem. In other words, the side on which a floret was robbed became more predictable over time.

In the first three-way interaction, this two-way interaction was further mediated by patch-wide robbing intensity: in heavily robbed patches, the predictive effects of patch bias and floret position were stronger than in very lightly robbed patches (Fig. 4). In other words, in heavily robbed patches, the florets which opened late in the season were very likely to all be robbed on the same side.

In the second, more modest three-way interaction, the two-way interaction between the patch-wide robbing bias and the floret position was moderated by plant size: the mediating influence of floret position was most important in plants with many florets and least important in plants with few florets (Fig. 5). Large inflorescences with many florets flower for a longer period and provide a robbing record that extends further back in time, and thus, they are more likely to provide evidence for temporal shifts in robbing behaviour.

Bee foraging behaviour

Observations were made on the foraging behaviour of 168 individual bumblebees, visiting a total of 906 florets of *R. minor* (Table 4). All bees observed were workers. Legitimate foraging for nectar was confined to the three longest-tongued

Table 3 Parameter estimates for the minimum adequate GLMM (fitted using REML) of the probability of a floret being robbed on the left as a function of patch-wide robbing bias (proportion robbed on the left in the patch), patch-wide robbing rate (proportion of florets robbed in the patch), plant size (number of florets on the plant) and floret position (numbered sequentially from the apex downward, indicating older flowers with higher integers)

Fixed effect	Estimate	SE	Likelihood ratio χ^2	P value
Intercept	−4.076	1.350		
Floret position (FP)	0.372	0.172	–	
Plant size (PS)	0.089	0.103	–	
Patch robbing intensity (PRI)	−6.639	1.828	–	
Patch robbing bias (PRB)	7.248	2.552	–	
FP/PS	−0.025	0.010	–	
FP/PRI	0.221	0.172	–	
FP/PRB	−0.644	0.369	–	
PS/PRI	0.055	0.109	–	
PS/PRB	−0.188	0.172	–	
PRI/PRB	13.557	3.264	–	
FP/PS/PRB	0.052	0.023	5.921	0.015
FP/PRI/PRB	−0.672	0.358	4.027	0.045

Parameter estimates are on a logit scale. Model random effects were patch (uniquely numbered every year; variance=0.225±SD 0.475) and plant nested within patch (2.007±1.417). Wald's likelihood ratio tests are based on analogous ML models

– the term cannot be removed for a likelihood ratio test because it features in a significant interaction

bumblebee species present, *B. hortorum*, *B. pascuorum* and *Bombus ruderatus*. The short-tongued *B. lucorum*, *B. pratorum*, *Bombus jonellus* and *Bombus wurflenii* visited florets for pollen. Primary and secondary nectar robbing were largely carried out by *B. wurflenii*, more rarely by *B. lucorum*.

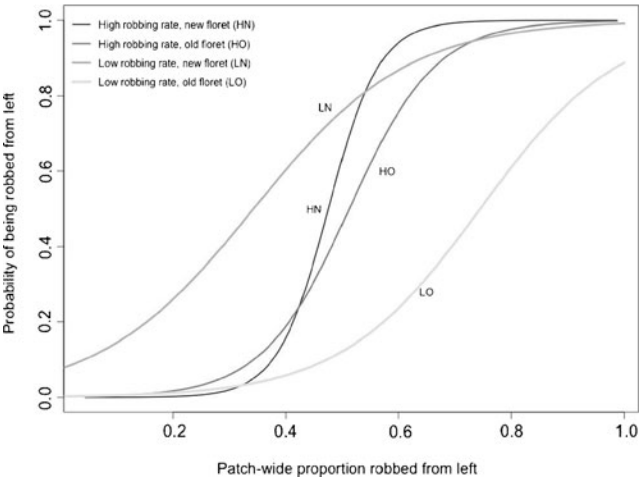

Fig. 4 The fitted effects of patch-wide robbing bias (on the *x*-axis), robbing rate and floral position (old flowers towards the base of the plant versus new flowers at its apex) on the binomial probability of a floret being robbed from the left. The curves come from separate GLMMs fitted for four separate datasets that include all combinations of the upper and lower quartiles of robbing rate and flower age

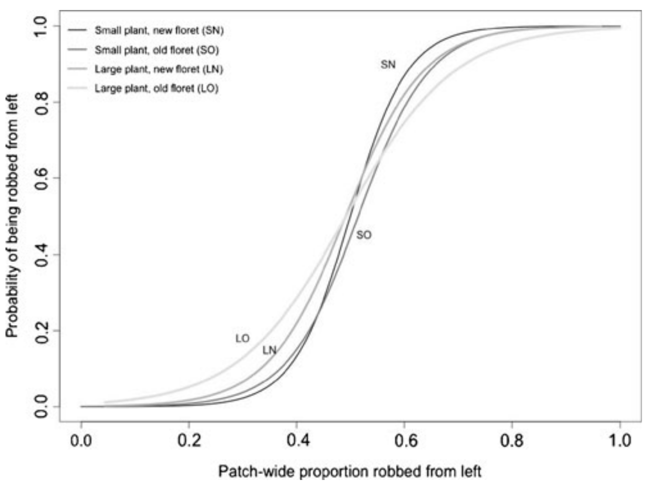

Fig. 5 The fitted effects of patch-wide robbing bias (on the *x*-axis), plant size and floral position (old flowers towards the base of the plant versus new flowers at its apex) on the binomial probability of a floret being robbed from the left. The curves come from separate GLMMs fitted for four separate datasets that include all combinations of the upper and lower quartiles of plant size and flower age

There was a strong correspondence between robbing behaviour and the distribution of robbing holes within patches. Bees within a particular patch tended to approach florets on the side which was most likely to have a hole, and this correlation was stronger for secondary robbers compared to primary robbers (bee species pooled, Pearson's product moment correlation coefficient, $r=0.678$, $p=0.045$ and $r=0.858$, $p=0.003$ for primary and secondary robbers, respectively). When acting as primary robbers, 91.7 % of *B. wurflenii* approached florets on the same side as the majority of existing holes (77 out of 84). For *B. lucorum*, all 20 observations of primary robbing involved an approach on the side of the majority of existing holes. Patterns were similar when acting as secondary robbers, with 97.0 % of approaches by *B. wurflenii* (261 out of 269) and 100 % of approaches by *B. lucorum* (20 out of 20) corresponding with the predominant location of existing holes. There was no significant difference between the two species in the likelihood that they would approach a floret on the 'correct' side when acting as either primary or secondary robbers (Fisher's exact tests, $p=0.213$ and $p=0.559$, respectively).

Discussion

R. minor is a common meadow plant in the study region, occurring in distinct patches with greatly varying population size. As an annual plant, population fluctuations are likely to be driven by the timing of cutting or grazing of the alpine

Table 4 Summary of the numbers of foraging observations obtained for each bee species

	wurflenii	*lucorum*	*hortorum*	*pascuorum*	*pratorum*	*monticola*	*jonellus*	*ruderatus*
Legitimate—nectar			69	62				2
Legitimate—pollen	40	290	1		29		4	
Primary robbing	84	20						
Secondary Robbing	269	20				1		
Total florets visited	393	330	70	62	29	1	4	2
Total individuals	59	56	25	16	9	1	1	1

meadows, for if they are cut before seeds have ripened, then the population is likely to experience a marked decline.

In the study area, these ephemeral patches are utilized by a guild of eight bumblebee species, including three long-tongued species that forage legitimately for nectar and three short-tongued species that collect pollen. The remaining two species, *B. wurflenii* and *B. lucorum*, are also short-tongued (Goulson et al. 2008) and are primarily nectar robbers, although both species also sometimes collect pollen. The majority of primary robbing was carried out by *B. wurflenii*, which is equipped with strongly toothed mandibles. *B. wurflenii* is an alpine species (Goulson et al. 2008) and was not observed visiting the two *R. minor* patches at lowest altitude (~480 m); correspondingly, these patches exhibited very low rates of robbing (between 0 and 2.6 % of florets). However, *B. lucorum* is a very widespread species occurring at all altitudes in the area, and this species was recorded as both a primary and secondary robber. It is notable that *R. minor* does not appear to be subject to widespread robbing in lowland parts of Europe where *B. lucorum* is frequent but *B. wurflenii* does not occur (in western France, England and Scotland; D.G., personal observation), although Kwak (1979) report low frequencies of robbing by *B. lucorum* in the Netherlands. It may be that *B. lucorum* have difficulty biting through the tough calyx of *R. minor*, since they lack the sharply toothed mandibles of a specialist nectar robber such as *B. wurflenii*, but that when many of the florets have already been robbed by another species, then they are encouraged to explore this route. Leadbeater and Chittka (2008) demonstrated that encountering robbed flowers renders bumblebees more likely to become primary robbers themselves. It is also conceivable that they observe and copy the behaviour of *B. wurflenii* wherever the latter are present, since bumblebees have been found to copy the behaviours of other foragers when choosing flowers (Worden and Papaj 2005; Leadbeater and Chittka 2005).

A marked feature of our data is the tendency for robbing holes to be largely on either the left or the right of the calyx in any particular patch, the observation that stimulated us to carry out this study. There was no spatial autocorrelation, with nearby patches showing no tendency to be robbed on the same side, and there was no correlation in the side on which any particular patch was robbed in successive years. For the smaller patches, it is conceivable that one bee could discover a patch first and make all of the robbing holes before any other bees came along and that this could explain robbing bias within patches. However, our data suggest strongly that robbing handedness spreads between bees in a patch. Firstly, even patches with very large numbers of flowers commonly showed high robbing bias, and it seems unlikely that a bee could discover and visit many thousands of florets before any other bees discovered the patch. Secondly, the behaviour of robbing bees within patches corresponded very closely to the distribution of existing holes, with bees generally approaching florets on the side that was most likely to already have a hole. This makes economic sense, for biting a hole takes time and energy, whereas using an existing hole is presumably much quicker. Given that some patches of flowers were small (with as few as 25 racemes) and that some patches were just a few 100 s of metres apart (well within the foraging range encompassed by worker bumblebees; Knight et al. 2005; Osborne et al. 2008), it seems likely that individual bees visit more than one patch. If this is so, and given that adjacent patches could have quite different robbing patterns, this suggests that bees may be able to learn that particular patches of flowers are likely to have holes on one side or another and adjust their behaviour accordingly. Of course, bees have long been known to be adept at learning handling skills appropriate for particular flowers (e.g. Menzel and Erber 1978; Chittka 1998), but to our knowledge, this is the first suggestion that bees might be able to switch between behaviours when visiting different patches of the same flower species. Further observations with marked bees could reveal whether this is indeed occurring.

It is interesting to note that robbing *B. lucorum* invariably approached florets on the side where the majority of holes were situated, whereas *B. wurflenii* appeared to be more likely to approach a floret on the ‘wrong’ side (9.2 % of visits), although this difference was not statistically significant. If *B. wurflenii* are more adept at primary robbing, then there may be less pressure on them to correctly identify the side of the floret that is most likely to have a hole.

An interesting question remains as to how patches come to be dominated by either left-handed or right-handed robbing. Some clues are provided by the three-way interactions that reveal several influences on the probability that a floret is robbed on the same side as the majority of other florets in the patch. In the first of these interactions (Fig. 4), the association between the side on which a floret is robbed and patch-wide side robbing bias is lowest in old florets coming from patches with a low overall robbing rate and, conversely, highest in the newest flowers from heavily robbed patches. In other words, bias accelerates through the season and more rapidly when robbing is frequent. In a similar way, the probability that a floret is robbed on the same side as the majority of other florets in the patch is lower in old flowers on large plants (Fig. 5). When *R. minor* begins to flower each year, the worker bumblebees present will have no previous experience in handling them. It seems likely that the first robbers to investigate florets of *R. minor* bite a hole in either the left side or the right side by chance, and having obtained a reward, they then repeat this behaviour on subsequent flowers. The first flowers to open will be the oldest and are likely to be on the largest plants which generally start flowering earlier (D.G., personal observation). Other bees may then copy this behaviour by direct observation (e.g. Worden and Papaj 2005) or, when investigating florets, they may discover the holes on one particular side and learn to associate that particular side with reward. We thus suggest that the behaviour spreads between bees visiting any particular patch, so that the large majority end up using the same strategy. Modelling approaches suggest that socially transmitted traits can spread rapidly via positive feedback, leading to much more rapid changes in behaviour at the population level than can occur through learning via personal experience (e.g. Giraldeau and Caraco 2000).

Both *B. lucorum* and *B. wurflenii* exhibited the same handedness within patches, providing evidence consistent with social learning across the species boundary. Indeed, without some mechanism for information transfer between species, it is very hard to explain the consistency of behaviour of the two species within patches. There is plentiful evidence that social learning occurs across species in vertebrates (reviewed by Sepp nen et al. 2007), and indeed, this is what Darwin first suggested in his observation that honeybees might copy the nectar-robbing behaviour of bumblebees (see quote from Darwin). To our knowledge, there is only one previous study demonstrating social learning across the species boundary in invertebrates; in a laboratory setting, Dawson and Chittka (2012) trained bumblebees to respond positively to the presence of a dead honeybee on artificial flowers.

Honeybees are well known for their recruitment of foragers to particular patches of flowers by exchange of information within the hive. With tens of thousands of workers in a colony, it is likely that all good food resources within the vicinity will be located and efficiently exploited using this strategy. In contrast, bumblebee colonies may have considerably fewer than 100 foragers (Goulson 2010). If they relied on information exchange between nestmates, then a colony may fail to detect the flowering of valuable food resources. There is much more information to be obtained from other foragers in the field, including non-nestmates and even other bee species (Leadbeater and Chittka 2005, 2009; Worden and Papaj 2005; Kawaguchi et al. 2007). Our study adds to the growing body of literature that suggests that bees are very adept at learning from other foragers in the field about new food sources and how best to efficiently extract rewards from them (Sherry 2008; Grueter et al. 2010).

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References

Anfora G, Rigosi E, Frasnelli E, Ruga V, Trona F, Vallortigara G (2011) Lateralization in the invertebrate brain: left–right asymmetry of olfaction in bumble bee, *Bombus terrestris*. PLOS ONE 6: e18903

Baayen RH (2011) languageR: data sets and functions with “Analyzing linguistic data: a practical introduction to statistics”. R package version 1.4. Available at http://CRAN.R-project.org/package=languageR

Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-42. Available at http://CRAN.R-project.org/package=lme4

Cavalli-Sforza L, Feldman MW (1981) Cultural transmission and evolution: a quantitative approach. Princeton University Press, Princeton

Chittka L (1998) Sensorimotor learning in bumblebees: long-term retention and reversal training. J Exp Biol 201:515–524

Crawley MJ (2007) The R book. Wiley, Chichester, p 942

Darwin C (1872) The effects of cross and self fertilisation in the vegetable kingdom. Murray, London

Dawson EH, Chittka L (2012) Conspecific and heterospecific information use in bumblebees. PLoS One 7:e31444

Giraldeau LA, Caraco T (2000) Social foraging theory. Princeton University Press, Princeton

Goulson D (2010) Bumblebees; their behaviour, ecology and conservation. Oxford University Press, Oxford, p 317

Goulson D, Lye GC, Darvill B (2008) Diet breadth, coexistence and rarity in bumblebees. Biodivers Conserv 17:3269–3288

Grueter C, Leadbeater E, Ratnieks FLW (2010) Social learning: the importance of copying others. Current Biology 20:R683–R685. doi:10.1016/j.cub.2010.06.052

Inouye DW (1983) The terminology of floral larceny. Ecology 61:1251–1252

Kawaguchi LG, Ohashi K, Toquenaga Y (2007) Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. Proc Roy Soc B 274:2661–2667

Kawai M (1965) Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. Primates 6:1–30

Kells AR, Goulson D (2001) Evidence for handedness in bumblebees. J Insect Behav 14:47–55

Knight ME, Martin AP, Bishop S, Osborne JL, Hale RJ, Sanderson RA, Goulson D (2005) An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. Mol Ecol 14:1811–1820

Kwak MM (1979) Effects of bumblebee visits on the seed set of *Pedicularis*, *Rhinanthus* and *Melampyrum* (Scrophulariaceae) in the Netherlands. Acta Botanica Neerlandica 28:177–195

Kwak MM, Holthuijzen YA, Prins HHT (1985) A comparison of nectar characteristics of the bumblebee-pollinated *Rhinanthus minor* and *R. serotinus*. Oikos 44:123–126

Leadbeater E, Chittka L (2005) A new mode of information transfer in foraging bumblebees? Curr Biol 15:R447–R448

Leadbeater E, Chittka L (2009) Bumble-bees learn the value of social cues through experience. Biol Lett. doi:10.1098/rsbl.2008.0692

Leadbeater E, Chittka L (2008) Social transmission of nectar-robbing behaviour in bumble-bees. Proc Roy Soc B 275:1669–1674

Maloof JE (2001) The effects of a bumble bee nectar robber on plant reproductive success and pollinator behavior. Am J Bot 88:1960–1965

Menzel R, Erber I (1978) Learning and memory in bees. Sci Am 239:102–110

Osborne JL, Martin AP, Carreck NL, Swain JL, Knight ME, Goulson D, Hale RJ, Sanderson RA (2008) Bumblebee flight distances in relation to the forage landscape. J Anim Ecol 77:401–415

R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at http://www.R-project.org/

Seppänen JT, Forsman JT, Mönkkönen M, Thomson RL (2007) Social information use is a process across time, space and ecology, reaching heterospecifics. Ecology 88:1622–1633

Sherry DF (2008) Social Learning: Nectar Robbing Spreads Socially in Bumble Beessource: Current Biol 18:R608–R610

Stout JC, Allen JA, Goulson D (2000) Nectar robbing, forager efficiency and seed set: bumblebees foraging on the self incompatible plant *Linaria vulgaris* Mill. (Scrophulariaceae). Acta Oecologia 21:277–283

Terkel J (1996) Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In: Heyes CM, Galef BG (eds) Social learning in animals: the roots of culture. Academic, San Diego, pp 17–47

Westbury DB (2004) *Rhinanthus minor* L. J Ecol 92:906–927

Worden BD, Papaj DR (2005) Flower choice copying in bumblebees. Biol Lett 1:504–507