When the group denies individual nutritional wisdom

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In social insects, decisions are usually predicted to be more accurate than individual decisions, because individual preferences are amplified at the group level. Although social caterpillars, as individuals, possess considerable ‘nutritional wisdom’ and have the capacity to regulate their nutrient intake: does this mean that the collective nutritional decisions made by colonies are better? We investigated individual feeding responses and collective decisions when caterpillar colonies were faced with different food sources. Forest tent caterpillars, Malacosoma disstria, had to choose between nutritionally balanced and unbalanced food sources placed at opposite ends of a bridge. At the individual level, caterpillars showed a clear preference for the balanced food source. In contrast, at the collective level, colonies of caterpillars randomly chose one of the two, and then became trapped for at least 24 h as a result of trail following behaviour. If the first caterpillar found the unbalanced food, it was followed by the others and the colony was unable to reverse this choice. This study provides evidence for a novel potential cost to group living, and shows that group feeding behaviour cannot always be simply predicted from individual preferences.

In social insects, many group tasks lead to collective decisions, which are reliant on interactions having taken place between individuals which have access only to local information (Camazine et al. 2001). Collective decisions occur when a colony is faced with several opportunities, such as food sources with different qualities. Information about these opportunities is gathered by individuals and relayed to nestmates. The by-product of this distributed information transfer is, most of the time, the collective choice of the best alternative, without any individual necessarily being aware of all the available alternatives (reviewed in Detrain et al. 1999).

The most common mechanisms leading to accurate collective decisions in social insect are allelomimesis (roughly speaking, do what my neighbour is doing; see e.g. Sudd 1963; Altmann 1985; Deneubourg & Goss 1989) and differential signalling. Allelomimesis, by definition, leads to amplification, or a snowball effect: that is, I imitate others, others imitate me, and we all end up doing the same thing. Amplification is an essential component of many collective decisions observed in eusocial insects, such as recruitment to a single food source (ants: Pasteels et al. 1987; honeybees: Seeley et al. 1991; social caterpillars: Fitzgerald 1995). An individual that has discovered a profitable food source conveys a signal leading to the source. This signal is attractive to congeners and triggers the onset of a recruitment process. Recruited individuals follow the signal to the food source and in turn reinforce it. After a certain amount of time the majority of the foragers exploit the same food source. A decision emerges because an individual behaviour is amplified by the action of many other individuals.

Foraging in groups is assumed to be adaptive because it can involve information sharing and better nutritional choices (e.g. see Giraldeau & Caraco 2000; Krause & Ruxton 2002). When faced with different food sources, foragers need first to assess the nutritional quality of the sources and then to adjust the intensity of the signal conveyed in relation to food source quality (ants: Beckers et al. 1990, 1992, 1993; Mailléux et al. 2000; honeybees: Seeley et al. 1991; Seeley 1995; social caterpillars: Fitzgerald
This difference in signalling can be amplified by the group and lead to the selection of the nutritionally better food.

Since in social insects it has been shown that collective decisions are usually more accurate than individual decisions because individual preferences are amplified at the level of the group (e.g. Couzin et al. 2005; Dussutour et al. 2005), does this mean that the collective nutritional decisions made by social species between different food sources would automatically reflect and amplify the ‘nutritional wisdom’ of the individuals? Our aim was to address this question using the forest tent caterpillar Malacosoma disstria, a gregarious, outbreaking forest pest species that uses recruitment through scent trails to exploit food sources. In referring to caterpillars as social species in this paper, we are using the term in its broader sense as it applies to aggregates of individuals in which there is ‘reciprocal communication of a cooperative nature’ (Wilson 1971).

Using the forest tent caterpillar allowed us to build upon an extensive literature on nutrient regulation in other, nonsocial caterpillars, as well as recent work on isolated individuals of this same species (Despland & Noseworthy 2006; Noseworthy & Despland 2006). It is well established for many caterpillar species that individuals have the capacity to regulate their intake of both protein and carbohydrate to obtain an optimal balance of nutrients from nutritionally varied foods (e.g. Heliothis zea; Friedman et al. 1991; Heliothis virescens: Telang et al. 2001; Manduca sexta: Thompson & Redak 2000; Spodoptera littoralis: Simpson et al. 1988, 2004; Lee et al. 2002; Spodoptera exempta: Lee et al. 2003).

Isolated forest tent caterpillars respond to the nutritional quality of their diet (Noseworthy & Despland 2006), preferentially feeding from carbohydrate-enriched and untreated trembling aspen leaves over 24-h periods and avoiding protein-enriched leaves. Using synthetic diets, Despland & Noseworthy (2006) found that individual forest tent caterpillars had a less marked ability to regulate intake of protein and carbohydrate than other caterpillar species, but are substantially more of a nutritionally balanced diet than one deficient in either protein or carbohydrate. When in groups, caterpillars lay down a chemical trail that stimulates and orients others in the group (Fitzgerald 1995). In second instars, the distance between the bivouac and the food source never exceeds 50 cm. After feeding to repletion, the caterpillars set off together in search of a suitable temporary resting site to digest their meal. Colonies display an alternation between feeding and resting periods and use the same bivouac for several days (Fitzgerald 1995).

Forest tent caterpillar egg masses collected in Alberta were individually hatched and reared on a nutritionally standard meridic artificial diet (Addy 1969) under controlled light and temperature regimes: 12:12 h photoperiod and 22°C. Experimental insects were removed from the culture within 24 h of moulting to the second instar.

Experimental Set-up and Protocol

Artificial foods were used because they enabled us to manipulate and standardize nutrient content. The experimental foods were based on the Addy diet, but carbohydrate content was manipulated: nutritionally balanced food: 20% dry weight protein and 20% dry weight carbohydrate; unbalanced food: 20% dry weight protein and 0% dry weight carbohydrate. The protein content of the food consisted of casein, while the carbohydrate portion was made up of dextrose. Other components of the food were Wesson’s salt (5.7%), cholesterol (1%), sorbic acid (0.7%), methyl paraben (0.4%), choline chloride (0.6%) raw linseed oil (1.9%), ascorbic acid (2.9%), sodium alginate (2.9%), antibiotic (1%) and Vanderzant vitamin mixture (8.2%). Cellulose, a non-nutritive bulk agent, was added to fill the remaining part of the food. The food was presented to the insects in a 2% agar solution.

For each replicate, an experimental group of 40 caterpillars belonging to the same egg mass was placed in the centre of a cardboard bridge (20 × 3 cm; Fig. 1). The caterpillars were confined by a plastic barrier coated with Fluon and food deprived for 2 h. After the barrier was removed they had access to the two food sources positioned at the ends of the bridge. Each diet was presented as a block
of food (3 × 2 cm and 2 cm high) placed on a plastic square at each end of the bridge (Fig. 1).

The bivouac area was marked with artificial pheromone (5b-cholestan-3,24-dione) diluted in hexane to encourage the caterpillars to come back to the centre of the bridge after each foraging period. The whole experimental set-up was isolated from sources of disturbance by surrounding it with white cardboard walls. All replicates were filmed (time lapse: one image per second) for 24 h by a video camera placed over the bridge connected to a computer. Twenty replicates were achieved with 20 different egg masses.

The data were first collected at the individual level, to quantify how individual caterpillars in a group responded to the two food sources, and then at the collective level, to determine the group decision.

**Data Collection**

**Individual preference**

For the individual responses, we followed individuals chosen at random from within the group and observed them until they completed a meal. If a focal individual was interrupted by another during the course of the meal (which happened in fewer than 20% of cases), it was disregarded and another caterpillar was chosen. This procedure allowed us to be sure that feeding responses reflected the nutritional quality of the food and not disturbance by other caterpillars. Given the stochastic nature of disturbance by others, and the fact that fewer than 20% of individuals were, in fact, disturbed during the observation, there is no reason to suspect that the dietary responses of the focal, undisturbed larvae were not representative of all individuals within the group.

Caterpillars were observed at the beginning of the experiment and after 24 h. Variables recorded for focal caterpillars were the duration of the first contact with the food (Fig. 2), which reflects taste responses to the food (Simpson & Raubenheimer 2000), and the duration of the first and the last meals eaten over the 24-h recording period (Fig. 2) for each food source, which gives an approximation of the amount eaten during those meals (Simpson & Raubenheimer 2000). A meal consisted of multiple contacts during a foraging period, which ended when the caterpillars returned to the bivouac to rest (see Fig. 2). Moreover, the time locomoting during the first foraging period for each food source was noted (Fig. 2), providing an indication of ‘exploratory behaviour’.

Behavioural data were collected for a total of 40 individual caterpillars observed across six replicates (egg masses) for each food source (six or seven caterpillars out of 40 per replicate; Table 1). Since caterpillars were not individually marked, the probability that we observed the same caterpillar for the first and the last meal of the 24-h period was less than 0.025, hence they were treated as statistically independent. We conducted statistical tests (nested ANOVA) to be sure that there was not an egg mass (replicate) effect. The nested design allowed us to test two things: (1) difference between unbalanced and balanced food and (2) the variability of the egg masses within food type.

**Collective decision**

To investigate the group decision for each colony, the number of caterpillars at the bivouac and at each food source was measured every 10 min for 24 h for all replicates. Ten minutes was chosen because caterpillars could not leave the bivouac, visit a food source and walk back to the bivouac in this time. To test whether caterpillars preferred one food source over the other (asymmetric distribution) or whether they showed no preference (symmetric distribution), we used a binomial test on the number of caterpillars on each food source in each replicate. The null hypothesis was that caterpillars choose both sources with equal probability (Siegel & Castellan 1988). We arbitrarily assumed that a food source was selected when the binomial test showed a significantly higher number of foragers on one food source.

**Group activity pattern**

In our experiments, as in their natural environment, forest tent caterpillars left the bivouac in search of food and moved back to the bivouac to rest. We thus observed an alternation between foraging and resting periods throughout the 24 h. To investigate the effect of food...
type on the activity rhythm of the colony we measured the number of foraging and resting periods, and their duration for all experiments for each replicate. A colony was considered to be in a foraging state when there were more than five caterpillars walking. A foraging period was defined to include both walking and feeding from the time activity was initiated in the resting group until the time the group settled again at the bivouac. It was extremely rare that the 40 caterpillars were active at the same time. Most of the time, 50% of the group was active (mean number of active caterpillars during a foraging period 18.23 ± 2.11).

All statistical tests were conducted with SPSS for Windows (version 12, SPSS Incorporated, Chicago, IL, U.S.A.). Results are given in the text as mean ± SE and all the probabilities are two tailed.

RESULTS

Individual Preference

As expected, caterpillars fed more readily (ANOVA with egg mass nested within food type, food effect: $F_{1,68} = 65.79$, $P < 0.001$; Fig. 3a and see Fig. 2b for an example) and for longer when they were on the nutritionally balanced food than when the food lacked carbohydrate (food effect: $F_{1,146} = 69.94$, $P < 0.001$, egg mass (food type): $F_{10,146} = 0.27$, $P = 0.991$; Fig. 3c and see Fig. 2b for an example). This difference in response to the balanced versus unbalanced food persisted until the last meal (Fig. 3c), although caterpillars ate more in the last than in the first meal (time (food type): $F_{2,146} = 139.95$; Fig. 3c).

The time spent locomoting (in ‘exploration’) was significantly longer for the unbalanced food than for the balanced food (ANOVA with egg mass nested within food type, food effect: $F_{1,68} = 45.74$, $P < 0.001$, egg mass (food type): $F_{10,68} = 0.36$, $P = 0.987$; Fig. 3b and see Fig. 2c for an example).

Collective Decision

The groups of caterpillars foraged on only one source during the 24 h in 18 out of 20 replicates (binomial test: $P < 0.05$ in these cases; Fig. 4). In 11 out of the 20 replicates caterpillars initially chose the unbalanced food (Fig. 4). When the first caterpillar moved towards the unbalanced food it was followed by the rest of the group in nine out of these 11 cases and a trail emerged. If the first caterpillar moved towards the balanced source, it was also followed by the rest of the group (seven out of nine cases). The caterpillars were then trapped in their own trail and, over the 24-h trial, were incapable of reversing the choice made during the first feeding period (two reversals were seen out of 11 initial choices for the unbalanced food). Figure 5 illustrates one experiment where the caterpillars chose the unbalanced food source. Some caterpillars reached the balanced source during the first feeding periods but failed to bring the group to it. Hence, the collective choice observed during the first feeding period was random ($\chi^2 = 0.89$, $P = 0.346$) and in most cases determined the pattern for the remainder of the experiment (Fig. 4).
The number of foraging excursions over 24 h was significantly higher when the group concentrated its feeding on the unbalanced than the balanced food source ($t_{20} = 3.05$, $P = 0.007$, 9.50 ± 0.68 and 6.62 ± 0.53 for the unbalanced and balanced food, respectively). Moreover, the duration of each foraging excursion was significantly longer when the source was nutritionally unbalanced (two-way ANOVA with repeated measures on foraging time: food effect: $F_{1,18} = 7.54$, $P = 0.013$, mean duration of a foraging period: 5800 ± 351 s and 4275 ± 430 s for the unbalanced and balanced food, respectively). Since individual caterpillars actually took shorter meals on the unbalanced food (see above), the difference in foraging time was due to the substantially higher level of locomotion when foraging from the unbalanced than the balanced food source. The first foraging period was longer than subsequent ones (time effect: $F_{4,72} = 17.44$, $P < 0.001$, mean duration of the first feeding period: 11 850 ± 1323 s and 7650 ± 1621 s for the unbalanced and balanced food, respectively) for both of the two food sources (interaction time*food: $F_{4,72} = 2.48$, $P = 0.094$), due to exploration and trail formation.

**DISCUSSION**

As expected from earlier work (Despland & Noseworthy 2006; Noseworthy & Despland 2006), individual forest tent caterpillars within a group ate more and spent less time locomoting when they found themselves on the nutritionally balanced than the unbalanced food. In light of these results and previous studies conducted with ants (see e.g. de Biseau et al. 1991; Beckers et al. 1993), we supposed that we would observe the same preference for the balanced food at a collective level. However, our experiments
showed that, in spite of a high level of preference for balanced food at an individual level, groups of caterpillars that had initially arrived at the unbalanced food source did not move to the balanced food, but rather became trapped at that site for the next 24 h. This entrapment occurred despite markedly enhanced levels of locomotion when on the unbalanced food, which, if caterpillars were alone, would presumably have substantially increased the likelihood of encountering the balanced food. Even when individual caterpillars did escape the group and located the balanced food source, they were unable to recruit the rest of the group.

This result is contrary to studies conducted on eusocial insects, where individual nutritional preferences were considerably amplified through interactions between individuals, leading to more accurate collective decisions (ants: see e.g. Verhaeghe 1982; de Biseau et al. 1991; Beckers et al. 1993; Maillieux et al. 2000; honeybees: Seeley et al. 1991; Seeley 1995; termites: Andara et al. 2004). To achieve a decision when faced with several alternatives, bees and ants assess the profitability of food sources and adjust the intensity of the signal conveyed. Bees modulate the strength of the waggle dance and ants modulate the quantity of pheromones deposited. The collective decisions observed in our experiments showed that caterpillars are not able to transmit the information about food quality to their congeners even if they are able to assess it. During exploration, the first individual left the bivouac area and randomly chose a direction while laying down a trail. It was then followed by the other caterpillars, which in turn, reinforced the trail. If the first caterpillar found the unbalanced food, it was joined by the rest of the group. After feeding, the group came back to the bivouac, reinforcing the trail. During subsequent feeding periods the caterpillars followed the trail and the group was not able to reverse its choice even if individuals were able to find the balanced source. Caterpillars seem to lack flexibility in trail laying and trail following behaviour, which usually allows the formation of new trails (Deneubourg et al. 1983; Fitzgerald & Costa 1986). The difference observed between individual preference and group choice in caterpillars resulted from an excessively strong group cohesive mechanism. In a famous essay, Fabre (1899) reported that processional caterpillars could be trapped in their own trail for more than 8 days. In social caterpillars, trail laying and trail following promote individuals remaining together, which contribute significantly to individual fitness (Robison 1993). The price of such high group cohesion is suboptimal diet choices, because individuals are unable to use this system to transmit information about food quality.

Lack of flexibility during foraging was also shown in ants when the food sources were not offered at the same time. When the richer source is discovered after the poorer one, the richer source is only weakly exploited (Pasteels et al. 1987; Beckers et al. 1990; Traniello & Robson 1995). However, in ants experiments were conducted with less extremely biased diet, that is, the poor food source still contained carbohydrate, which is an essential nutrient. Also, these experiments were conducted over short periods of time (2 h), and after a few more hours ants were able to reverse their choice (A. Dussutour, personal observations). Collective behaviour needs a balance between efficiency in making group decisions and flexibility which allows reversal of decisions. Contrary to eusocial insects, caterpillars lack such flexibility.

It was evident, therefore, that forest tent caterpillars could become trapped on a nutritionally unbalanced food source, but two key questions remain. First, does becoming trapped constitute a fitness cost; and second, are groups of caterpillars more readily trapped than individual caterpillars? Regarding the first of these issues, there is little doubt that a diet entirely deficient in carbohydrate is deleterious to fitness. In caterpillars, as for other phytophagous insects (Raubenheimer & Simpson 1999), the role of carbohydrates as essential nutrients has been emphasized in numerous studies. Survival rate, survival time and development rate are low for caterpillars reared with diets

![Figure 5. Number of caterpillars visiting the unbalanced food (grey lines) source and the balanced (black lines) source every 10 min during one experiment (24 h).](image-url)

Regarding the second question, there is little doubt that being in a group impedes individual caterpillars from locating the balanced food once the initial choice had been made for the unbalanced food source. Increased exploration in response to nutrient deprivation is commonly observed as a functional strategy to find something better (Morris & Kareiva 1990; Barton-Brown 1993). Caterpillars in our study showed increased locomotory (‘exploratory’) activity when on the suboptimal food. As a result, a number of individuals did, in fact, locate the balanced food (e.g. Fig. 5), as compared to none on the unbalanced food in cases where the group arrived initially at the balance food source. But in our experiment even if an individual was able to find the balanced source, it was unable to bring the other caterpillars because they remained trapped in the first trail formed. Thus, even when the group spent more time locomoting, it did not find the balanced food source within 24 h. It should also be mentioned that, in nature, feeding more frequently and increasing exploratory behaviour increases predation risk, providing another cost to being restricted to an unbalanced food in addition to those discussed above (Krebs & Davies 1993; Bernays 1997). Consequently, the selective foraging on certain parts of the tree observed by Lévesque et al (2002) could be the result of a difference in survival rate and not the expression of a group preference.

The feeding behaviour of colonies that were trapped on the unbalanced food suggested a vain attempt to compensate for their incorrect choice by feeding more frequently on the nutritionally unbalanced food. Compensation in response to being restricted to nutritionally poor food has been extensively shown in insects (e.g. Simpson & Simpson 1990; Simpson & Raubenheimer 2000; Lee et al. 2004).

**CONCLUSION**

Our results emphasize the difference between individual behaviour and group decisions. They underline the fact that it is the information transmitted by individuals combined with the amplification phenomena that govern the group choice and not the individual preference. Previous work shows that using group decisions to infer individual preference often overestimates individual selectivity (Dussutour et al. 2005). We show here that the opposite can also be true: individuals can be more selective than groups. Together these findings emphasize that a direct relationship between individual preference and group choice cannot always be assumed. These findings could be relevant for the study of other group-living species, including not only social insects like ants, wasps and termites, but also cockroaches, other gregarious caterpillars, locusts, sawflies, and bark beetles. Animals’ feeding preferences are often studied as a means of predicting population distribution or feeding damage. In many experiments individuals are tested alone and the effect of amplifying mechanisms through the exchange of chemical, visual, tactic or acoustic signals between individuals are rarely considered (caterpillars: Simmonds et al. 1992; Stamp & Casey 1993; Alborn et al. 1996; Showler 2001; Lazarevic et al. 2003; Ghumare & Mukherjee 2005; Miles et al. 2005; cockroaches: Carrel & Tanner 2002; Jones & Raubenheimer 2002; Peterson et al. 2002; sawflies: Mansfield & Mills 2002; beetles: Poland et al. 2003). As a consequence, the level of selectivity of group feeding can be underestimated (if communication amplifies individual preferences) or overestimated (if, as in our study, communication traps groups following random initial discoveries). It is consequently important to understand how the group chooses between different resources, and not solely base our knowledge on individual preference.

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