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Individual differences influence collective behaviour in social caterpillars

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(Received 28 August 2007; initial acceptance 29 November 2007;
final acceptance 15 December 2007; published online 8 May 2008; MS. number: 9502)

The expression of individual differences within a population often depends on environmental conditions. We investigated, first, whether there are differences between individual group-living forest tent caterpillars, *Malacosoma disstria*, that are expressed only in nutritionally unbalanced environments, and second, to what extent these individual behavioural differences influence the strategies used by the group to exploit food resources. We offered groups of caterpillars a binary choice between two equal food sources, either containing a balanced ratio of protein and carbohydrate or lacking digestible carbohydrate. Individual caterpillars responded to the diet treatment by becoming either inactive or active. The existence of these two behavioural categories was evident under dietary imbalance but not when foods were nutritionally balanced. At a collective level, the individual differences in behaviour led to colony decisions that were dependent upon the ratio of the two behavioural categories present in the group. Colonies comprising a majority of active caterpillars ('active biased') were less cohesive than inactive-biased colonies. Under dietary imbalance, active-biased groups did not focus their activity on one food source but split and exploited two sources at the same time. Since both food sources were nutritionally unbalanced, these groups grow less well than inactive-biased groups that remained on one food source. The coexistence of two foraging strategies may provide a compromise between maintaining colony cohesion and optimizing food location and diet balancing.

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Keywords: alternative phenotypes; collective decision; feeding behaviour; forest tent caterpillar; *Malacosoma disstria*; nutrition

Group-living animals have special importance for the study of decision making, because they make choices not only as individuals, but also collectively. Researchers have frequently assumed that all individuals within

a group behave the same (Camazine et al. 2001), and consequently the contribution of individual differences to collective behaviour has remained largely unexplored. However, even slight differences in the tendency of individual animals to show a given behaviour may be at the heart of decision-making processes and may have consequences for the ecology and evolution of populations (Camazine et al. 2001; Dussutour et al. 2005).

A special case of individual differences is behavioural polymorphism, where individuals within a population can be categorized into types or strategies according to their behaviour (West-Eberhard 1989). Behavioural polymorphism is most evident in the castes of eusocial insects (Oster & Wilson 1978), but less extreme examples are

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found elsewhere, often in the context of food acquisition behaviour where explorative and sedentary foraging strategies coexist (rodents: Kotler & Brown 1988; Benus et al. 1991; marine and freshwater snails: Wilson et al. 1999; Chase et al. 2001; nematodes: de Bono & Bargmann 1998; de Bono 2003; fruit flies: Sokolowski 1980). For example, in the fruit fly, *Drosophila melanogaster*, natural variants in foraging behaviour occur, in large part a result of a single gene, *foraging* (*for*) (Sokolowski 1980; de Belle et al. 1989, 1993; Pereira & Sokolowski 1993; Osborne et al. 1997). Rover larvae have longer foraging trails than sitter larvae; they move significantly more from food patch to food patch while feeding, whereas sitters tend to remain within a patch (Sokolowski et al. 1983). This variation in foraging behaviour may influence a larva's ability to exploit food resources (Sokolowski 1985) and thereby its fitness by affecting development (Robertson 1963), the time to reach the critical weight for pupation (Bakker 1961), and adult emergence (Ohnishi 1979).

A similar situation may occur in social caterpillars, involving distinct active and sluggish insects (Wellington 1957; Laux 1962; Greenblatt & Witter 1976). Wellington (1957) claimed that, in the absence of food, colonies of the social tent caterpillar, *Malacosoma californicum pluviale*, contained a mixture of 'type I' caterpillars, capable of independent movement away from the group, and more sluggish 'type II' caterpillars, which remained within the aggregation. Type I larvae were said to stir the colony to activity and to establish trails to new food sources, whereas type II caterpillars were proposed to be responsible for maintaining colony cohesiveness. Some authors have shown in other species of social caterpillars and sawflies that certain individuals are more likely than others to assume the leadership role in processions (Weinstein & Maelzer 1997; Fitzgerald 2002). However, other studies failed to substantiate Wellington's assertion and cast doubt on the occurrence of distinct behavioural forms in social caterpillars (Edgerly & Fitzgerald 1982; Papaj & Rausher 1983; Fitzgerald 1995).

The expression of individual differences within a population often depends on environmental conditions (West-Eberhard 2003; DeWitt & Scheiner 2004; Pigliucci & Preston 2004; Jablonka & Lamb 2005), and so behavioural differences within a group may sometimes appear difficult to detect. For example, in *Drosophila*, rover larvae can be made to behave as sitters by a short period of food deprivation (Graf & Sokolowski 1989), so that the group appears to be composed only of sitters. Conversely, sitters can be made to behave like rovers by altering other environmental variables (Sokolowski 2001). Similarly, in social caterpillars, local search duration (the time spent within a food patch before moving away) decreases with resource quality (Dussutour et al. 2007). When caterpillars encounter a nutritionally balanced source they cease to explore, and therefore differences in foraging strategy between individuals may be impossible to detect.

In the present study we investigated, first, whether there are pronounced differences between individual social caterpillars that are expressed only in nutritionally unbalanced environments, and second, to what extent these individual behavioural differences, if they exist, can

influence the strategies used by the group to exploit food resources. We carried out a laboratory experiment within a simple environment, consisting of a bridge offering a group of forest tent caterpillars, *Malacosoma disstria*, a binary choice between two equal food sources, either containing a balanced ratio of protein and carbohydrate (nutritionally balanced environment) or lacking digestible carbohydrate (nutritionally unbalanced environment). The forest tent caterpillar is a common pest of deciduous trees in North America. As larvae, they are social foragers that build silk mats as temporary bivouacs between feeding sites. They spin silk threads as they travel and mark them with a trail pheromone, much in the same manner as ants. These pheromone trails maintain colony cohesion and allow caterpillars to feed together at the same site (Fitzgerald 1995). Colonies alternate between periods of quiescence and activity, and move between feeding and resting sites as a group (Fitzgerald 1995; Dussutour et al. 2007). Consequently, any differences in the foraging pattern between individuals are likely to influence the foraging behaviour and the cohesiveness of the group.

METHODS

Experimental Insects

We obtained larvae from egg masses collected in March 2005 in Alberta, Canada. The egg masses were stored at 4°C for a maximum of 3 months. To eliminate any potential contamination with nuclear polyhedrosis virus (NPV), we washed egg masses in a 6% solution of sodium hypochlorite for approximately 2 min, until most of the spumaline coat was dissolved (Fitzgerald 1995). They were then rinsed thoroughly with running water, set out to dry, and left to hatch at room temperature in 300 ml paper cups with plastic lids. Hatching occurred about 5 days after removal from the refrigerator. Larvae from the egg masses were individually reared on a standard semidefined synthetic diet (Addy 1969) under a 12:12 h photoregime at 22°C. Experimental insects were removed from the culture within 24 h of ecdysis to the second instar. We found no evidence of disease among cohorts of experimental caterpillars.

Experimental Set-up and Protocol

We used artificial foods because they enabled us to manipulate and standardize nutrient content. Moreover, caterpillars initially reared on the standard artificial diet (Addy 1969) prefer this diet to host leaves (Colasurdo 2006). Forest tent caterpillars grow well on artificial diet compared to natural foods (N. Colasurdo & E. Despland, unpublished data). We manipulated the carbohydrate content of the Addy diet as follows: nutritionally balanced food = 20% dry weight protein and 20% dry weight digestible carbohydrate; unbalanced food = 20% dry weight protein and 0% digestible carbohydrate. The protein consisted of casein, and dextrose was the carbohydrate component. Other ingredients 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, comprised the remaining proportion. The food was presented to the insects in a 2% agar solution at a 6:1 ratio of agar solution to dry mass of ingredients.

For each replicate, we placed an experimental group of 40 caterpillars, belonging to the same egg mass, in the centre of a cardboard bridge (20 cm long and 3 cm wide; see Dussutour et al. 2007), henceforth termed the bivouac area. This area was marked with artificial pheromone (5 β -cholestane-3,24-dione) diluted in hexane to obtain 10⁻⁹ g of pheromone per mm of trail (Fitzgerald 1993a) to encourage the caterpillars to come back to the centre of the bridge after each foraging period. In nature, the bivouac is up to 50 cm from the food source in groups of second-instar caterpillars and colonies use the same bivouac for several days (Fitzgerald 1995). The caterpillars were confined in the bivouac area by a plastic barrier coated with Fluon and deprived of food for 2 h, after which the barrier was removed, providing access for 24 h to two nutritionally identical food sources; these were presented as blocks (3 \times 2 cm and 2 cm high) on a plastic square at each end of the bridge. The experimental arena was surrounded with white cardboard walls 50 cm high. All replicates were filmed (time lapse: 1 image/s) for 24 h by a video camera (Canon GL1 miniDV camera; Canon Canada Inc., Mississauga, Canada) placed over the bridge and connected to a computer. Video data were captured with Virtualdub (Free Software Foundation, Cambridge, MA, U.S.A.).

We conducted two treatments: one with two nutritionally balanced food sources and the other with two nutritionally unbalanced food sources. For each treatment we conducted 20 replicates with 20 different egg masses. Each replicate group comprised 40 caterpillars belonging to the same egg mass. We analysed the experiments at both the group level, to determine collective foraging decisions, and at the individual level, to quantify how individual caterpillars in a group responded to food quality.

Data Collection

Effect of food quality on group activity patterns

In our experiment, 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 quality on the activity rhythm of the colony, we recorded the number of foraging and resting periods, and their duration, for all replicates for each treatment. A colony was considered to be in a foraging state when there were more than five caterpillars walking. All 40 caterpillars were rarely active at the same time and about 50% of the group was active most of the time. A foraging period was defined to include both walking and feeding, beginning when activity was initiated in the resting group and ending when the group settled again at the bivouac.

We chose the maximum level of activity observed during each foraging period within a replicate, that is, the highest number of active caterpillars, for comparison between treatments. This gave us a measure of recruitment strength as a function of food quality.

We used a repeated measure ANOVA to compare the durations of foraging and resting periods and the levels of activity between treatments. We considered only the first 10 foraging periods, because not each replicate had equal numbers of foraging and resting periods. In this and all other parametric analyses, data normality and homoscedasticity were checked with a Kolmogorov–Smirnov test and a Levene's test, respectively. All statistical tests were conducted in SPSS for Windows, version 14 (SPSS Inc., Chicago, IL, U.S.A.). All means in the text are given \pm SE. The probabilities given in the text are always two tailed.

Effect of food quality on collective decisions

To investigate group decision making for each colony, we counted the caterpillars resting at the bivouac and foraging at each food source every 10 min for 24 h. 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 chose both sources with equal probability (Siegel & Castellan 1988). We considered that a food source was selected when the binomial test showed significantly more foragers on that food source than on the other.

Effect of food quality on individual behaviour

All caterpillars were weighed (\pm 0.1 mg) on an electronic balance (HM-202-C, DEBAC Electronic Scale Supply) before and after each replicate to determine their mass change during the 24 h experimental period. The initial mass of the caterpillars was not significantly different between the two treatments (nested ANOVA: food effect: $F_{1,1560} = 0.18$, $P = 0.669$; mean weight \pm SE = 1.25 \pm 0.006 mg and 1.26 \pm 0.006 mg for the unbalanced and balanced foods, respectively) or between egg masses (egg mass (food): $F_{38,1560} = 1.17$, $P = 0.222$).

For the individual behavioural responses, caterpillars were observed from the video recordings during the first foraging period, that is, during the establishment of the trail. Behavioural data were collected for a total of 50 individuals, randomly selected caterpillars observed across five randomly selected replicates (egg masses) for each treatment (10 caterpillars out of 40 per replicate). First, we recorded for the focal caterpillars the duration of the first meal, which gives an approximation of the amount eaten during this meal (Simpson 1995). A meal consisted of multiple periods of ingestion, between which caterpillars paused or moved around, either on or near the food (Dussutour et al. 2007). It was considered to have ended when the caterpillar returned to the bivouac to rest. Second, we recorded the time spent moving during the

first foraging period, providing a measure of 'exploratory behaviour' (Dussutour et al. 2007).

We compared the individual response to food quality by applying a nested ANOVA to test for an egg mass (replicate) effect. The nested design allowed us to test (1) the difference between unbalanced and balanced diet treatments, and (2) variability among egg masses within a food type. We investigated the relation between meal duration and the time spent moving by using curve estimation procedures. Finally, we conducted two cluster analyses to attempt to identify the presence of relatively homogeneous types of caterpillars. The first cluster analysis was based on caterpillar mass and the second on time spent moving and feeding. We adopted a procedure called 'two-step cluster', provided by the SPSS statistical package, version 14. This procedure is an exploratory tool designed to reveal natural groupings (or clusters) within a data set. Caterpillars were sequentially merged into a decreasing number of clusters until the conjoint set contained all caterpillars. The choice of

a similarity measure and the determination of the number of clusters were based on the log likelihood distance and Schwarz's Bayesian information criterion, respectively.

RESULTS

Effect of Food Quality on Group Activity Patterns

The number of foraging excursions over 24 h was not different when the groups were offered either two unbalanced or two balanced food sources (Student's t test: $t_{38} = 1.31$, $P = 0.197$; mean number = 8.95 ± 0.62 and 7.95 ± 0.43 , for the unbalanced and balanced foods, respectively). However, foraging excursions were significantly longer when the sources were nutritionally unbalanced (two-way ANOVA with repeated measures on foraging time: food effect: $F_{1,38} = 44.08$, $P < 0.001$; mean duration of a foraging period = 5301 ± 253 s and

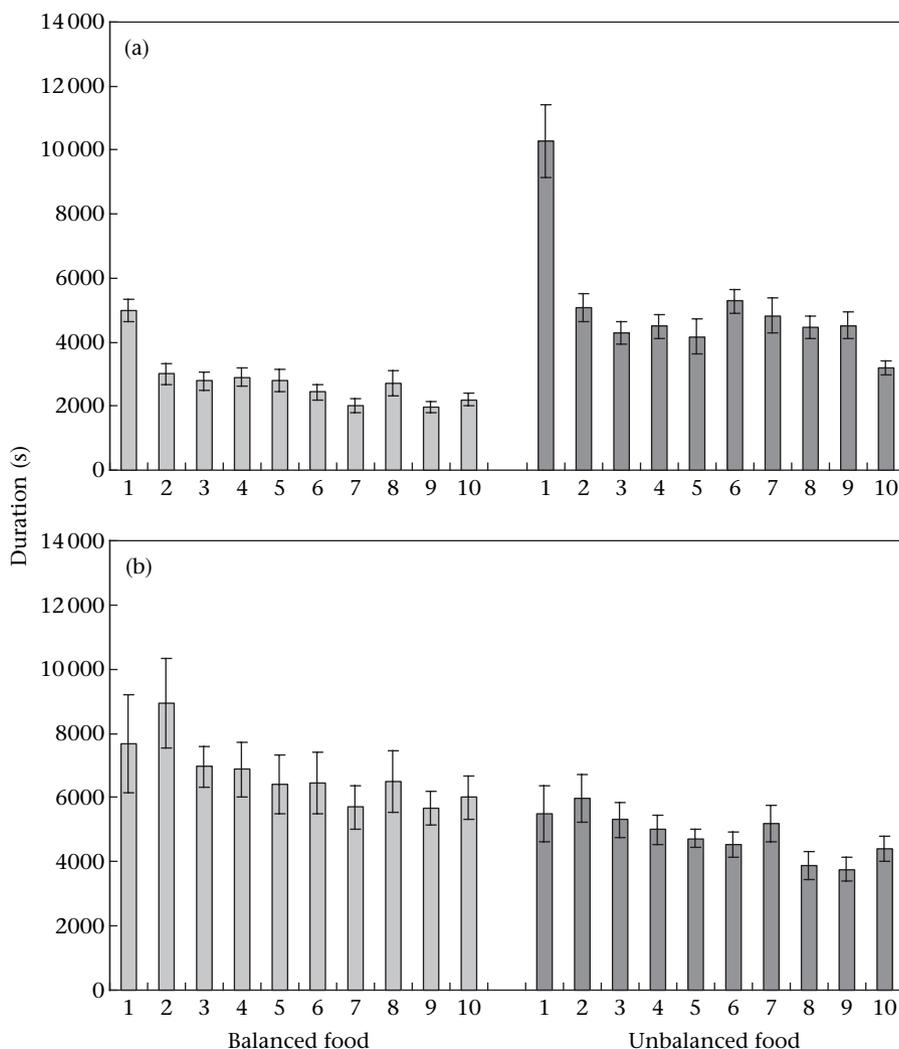


Figure 1. Mean duration \pm SE of (a) the first 10 foraging periods and (b) the first 10 resting periods for each treatment (nutritionally balanced and unbalanced foods; $N = 20$ replicates per treatment). Foraging periods were separated by resting periods.

2737 ± 116 s for the unbalanced and balanced foods, respectively; Fig. 1a). The first foraging period was longer than subsequent ones (time effect: $F_{4,152} = 27.79$, $P < 0.001$; mean duration of the first feeding period = 10290 ± 1146 s and 4980 ± 351 s for the unbalanced and balanced foods, respectively; Fig. 1a) for both diet treatments (interaction time*food: $F_{4,152} = 2.48$, $P = 0.094$), owing to exploration and trail formation. Resting periods at the bivouac between foraging excursions were significantly shorter when the food sources were nutritionally unbalanced than when they were balanced (two-way ANOVA with repeated measures on resting time: food effect: $F_{1,38} = 4.527$, $P = 0.040$; mean duration of a resting period = 5259 ± 213 s and 6418 ± 364 s for the unbalanced and balanced foods, respectively; Fig. 1b). The duration of the resting periods did not change significantly over time (time effect: $F_{4,152} = 1.85$, $P = 0.122$) for either of the two diet treatments (interaction time*food: $F_{4,152} = 0.21$, $P = 0.934$).

The maximum level of activity during each foraging period was significantly higher when the food sources were nutritionally balanced than when they were unbalanced (two-way ANOVA with repeated measures on foraging time: food effect: $F_{1,38} = 12.24$, $P < 0.001$; proportion of foraging caterpillars = 0.47 ± 0.02 and 0.59 ± 0.02 for the unbalanced and balanced foods, respectively; Fig. 2), suggesting a higher recruitment when the caterpillars were offered two nutritionally balanced food sources. The proportion of active caterpillars during the first foraging period was significantly higher than during subsequent foraging periods (time effect: $F_{4,152} = 6.20$, $P < 0.001$; mean proportion of active caterpillars = 0.62 ± 0.04 and 0.73 ± 0.03 for the unbalanced and balanced foods, respectively) for both treatments (interaction time*food: $F_{4,152} = 1.868$, $P = 0.120$), owing to exploration and trail formation.

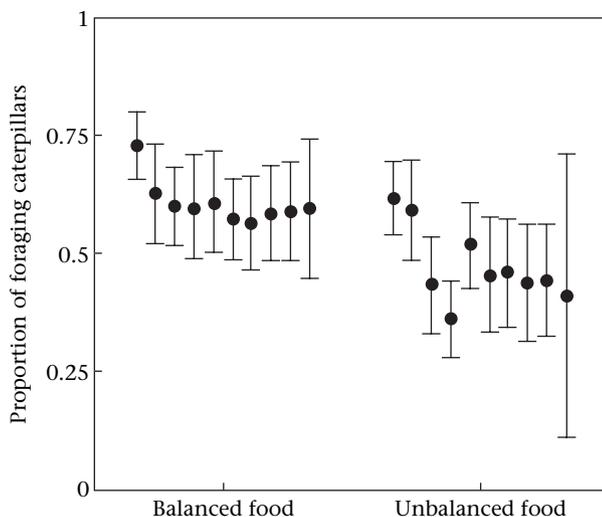


Figure 2. Mean proportion of foraging caterpillars for each foraging period ($N = 10$) for each treatment (nutritionally balanced and unbalanced foods; $N = 20$). Error bars show 95% confidence intervals of the mean.

Effect of Food Quality on Collective Decisions

The latency to come into contact with one of the two food sources was not significantly different when the groups were offered either two unbalanced or two balanced food sources (Student's t test: $t_{38} = 0.21$, $P = 0.832$; 984 ± 154 s and 1035 ± 178 s for the unbalanced and balanced foods, respectively). The groups of caterpillars foraged on the same food source during the 24 h in all 20 replicates in the balanced food treatment and in 13 of the 20 replicates in the unbalanced treatment (binomial test: $P < 0.05$ in these cases; Fig. 3). When two balanced food sources were offered, the left food source was chosen by 10 groups and the right by the other 10 groups. When the food sources offered were nutritionally unbalanced, seven groups fed solely from the one on the left, six ate only the one on the right, and seven exploited both food sources.

In both treatments several groups of caterpillars moved their bivouac from the centre of the arena towards the chosen food source (in 12 of 20 replicates in the balanced treatment, and in six of 20 replicates in the unbalanced treatment). The latency to move the bivouac was significantly longer when the food sources offered were nutritionally unbalanced (Student's t test: $t_{16} = 4.2$, $P = 0.001$; 23 800 ± 2756 s, about 6.5 h, and 9600 ± 1891 s, about 2.75 h, for the unbalanced and balanced foods, respectively).

Effect of Food Quality on Growth

As expected, caterpillars grew significantly better when they were offered two nutritionally balanced food sources (food effect: $F_{1,1526} = 570.88$, $P < 0.001$; mean weight = 1.56 ± 0.011 mg and 1.85 ± 0.006 mg for the unbalanced and balanced foods, respectively; Fig. 4a, b). Egg mass had a significant effect on the weight reached by caterpillars (egg mass (food): $F_{38,1526} = 1.76$, $P = 0.003$). The final mass distribution was strongly bimodal when caterpillars were offered two nutritionally unbalanced foods

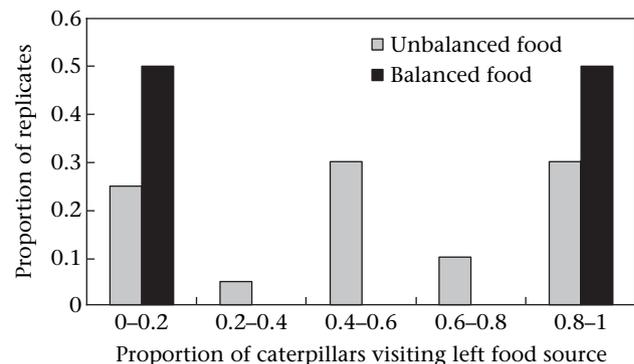


Figure 3. Collective decisions made by groups of 40 caterpillars: frequency distribution of the proportion of caterpillars visiting the food source on the left ($N = 20$ for each treatment) during the experiment (24 h). The proportion of caterpillars visiting the food source on the left was calculated from the sum of the 10 min periods during the experiment (see text).

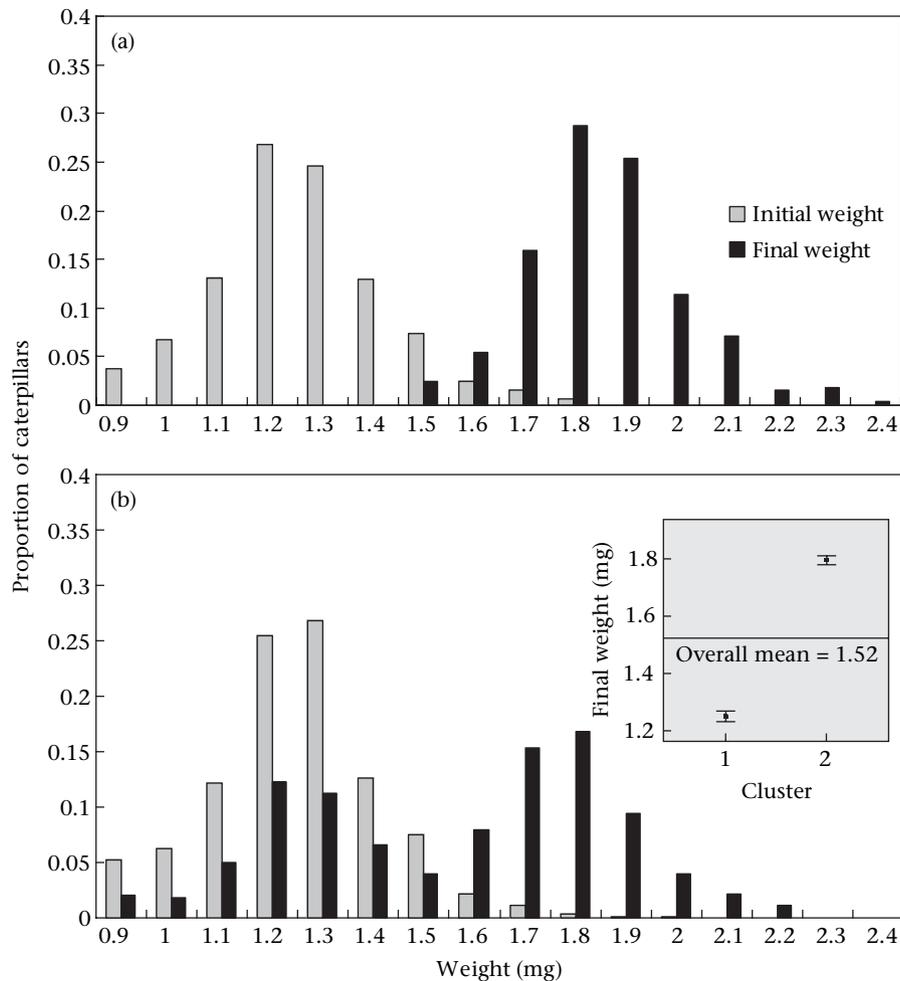


Figure 4. Body mass frequency distribution when caterpillars were offered (a) two nutritionally balanced food sources ($N = 800$ and $N = 794$, before and after the experiment, respectively) and (b) two nutritionally unbalanced food sources ($N = 800$ and $N = 772$, before and after the experiment, respectively). The inset shows the results of the cluster analysis and indicates the mean final weight \pm the 95% confidence intervals for each cluster.

(Fig. 4b), in contrast to the normal distribution observed for the balanced diet treatment and this was true for each of the 20 groups used (Fig. 5). A two-step cluster analysis revealed two clusters of individuals with the unbalanced treatment. The first cluster (category 1, small caterpillars) contained 43.1% of all the caterpillars (mean mass = 1.25 ± 0.008 mg) and the second (category 2, large caterpillars) the remaining 56.9% (mean mass = 1.79 ± 0.005 mg; see inset in Fig. 4b). Category 1 caterpillars on average remained the same mass after 24 h (time effect: $F_{1,1093} = 0.14$, $P = 0.906$; egg mass (time): $F_{38,1093} = 0.84$, $P = 0.740$). Caterpillars in category 2 gained mass significantly (time effect: $F_{1,1199} = 3195.93$, $P < 0.001$; egg mass (time): $F_{38,1199} = 0.99$, $P = 0.493$), but not as much as the caterpillars that were offered two balanced foods (food effect: $F_{1,1193} = 42.21$, $P < 0.001$; egg mass (food): $F_{38,1193} = 0.99$, $P = 0.488$; mean mass = 1.79 ± 0.005 mg and 1.85 ± 0.006 mg for category 2 caterpillars and for caterpillars offered two balanced foods, respectively).

The proportions of 'small' (0.431) and 'large' (0.569) caterpillars within each egg mass differed significantly from the overall proportion (chi-square test: $\chi^2_{19} = 40.9$,

$P = 0.002$). Eight of the 20 egg masses had more than 50% of caterpillars that did not grow. These included the six egg masses in which caterpillars foraged on the two unbalanced food sources (Fig. 6). A quadratic model investigating the relation between the proportion of category 1 caterpillars and collective decisions on food choice reached by the group was highly significant (ANOVA for the whole model: $F_{2,17} = 67.98$, $P < 0.001$; Fig. 6) and accounted for 88.9% of the variance. The proportion of category 1 caterpillars and the collective decision reached by the entire group were significantly correlated (quadratic model: $t_{17} = 11.33$, $P < 0.001$), that is, a high proportion of category 1 caterpillars was associated with collective exploitation of both food sources (Fig. 6).

Effect of Food Quality on Individual Response

As predicted by Dussutour et al. (2007), caterpillars fed for longer when they were on the nutritionally balanced food than when the food lacked carbohydrate (food effect: $F_{1,90} = 3.53$, $P < 0.001$; egg mass (food type): $F_{8,90} = 0.88$,

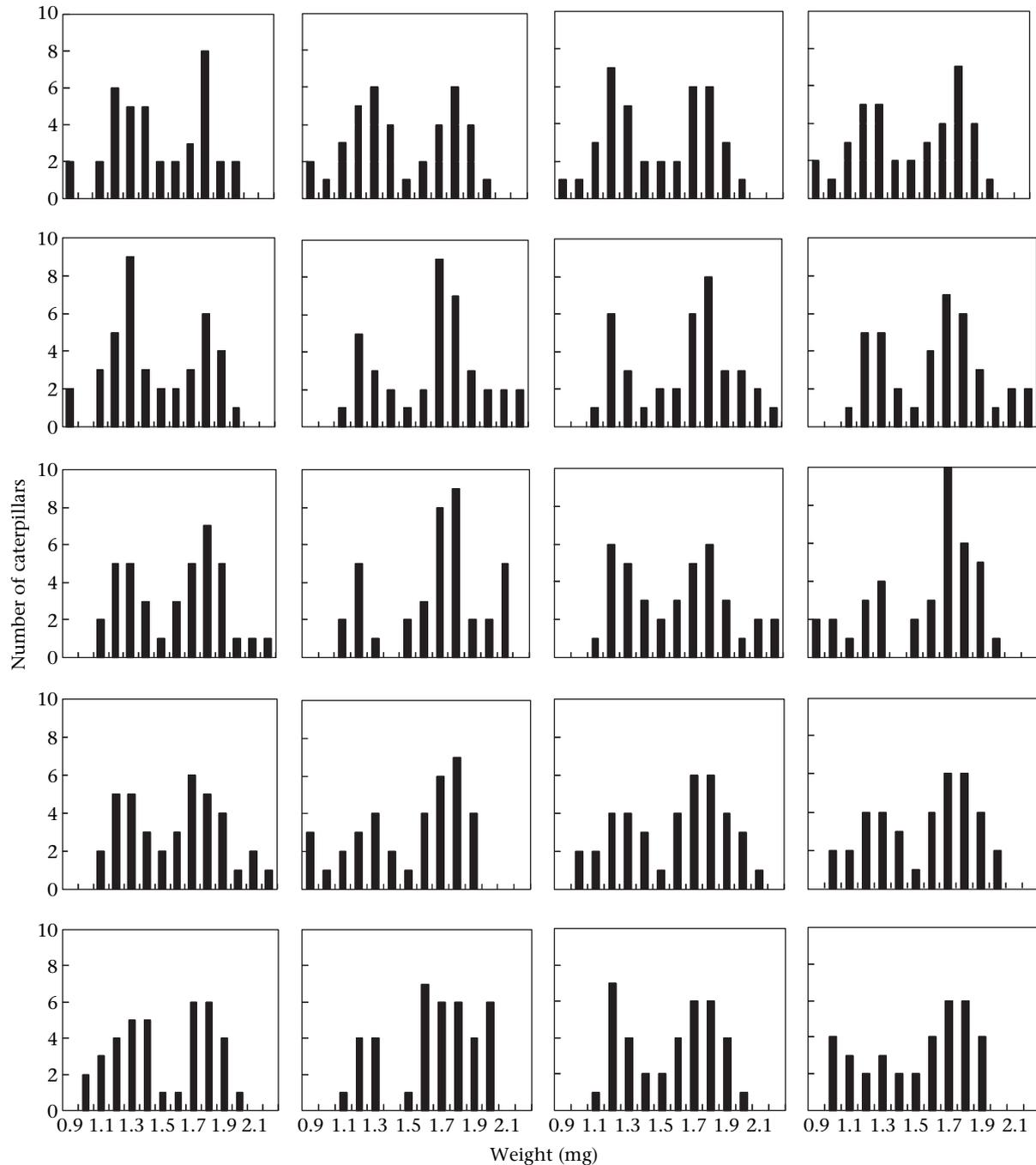


Figure 5. Distribution of the body mass reached at the end of the experiment when caterpillars were offered two nutritionally unbalanced food sources for each of the 20 colonies. Each panel represents one of the 20 replicate colonies.

$P = 0.537$; mean first meal duration = 206 ± 20 s and 437 ± 24 s for the unbalanced and balanced foods, respectively). More time was spent moving within the foraging period (in 'exploration') when the caterpillars were offered two unbalanced food sources than two nutritionally balanced foods (ANOVA with egg mass nested within food type: food effect: $F_{1,90} = 40.34$, $P < 0.001$; egg mass (food type): $F_{8,90} = 0.32$, $P = 0.956$; mean exploration time = 1351 ± 131 s and 464 ± 35 s for the unbalanced and balanced foods, respectively).

A negative exponential model investigating the relation between meal duration and the time spent moving was highly significant (ANOVA for the whole model: $F_{1,98} = 541.69$, $P < 0.001$; Fig. 7) and accounted for 84.7% of the variance. The time spent moving and meal duration were negatively correlated for the two treatments (negative exponential model: $t_{98} = 23.27$, $P < 0.001$), that is, longer meals were associated with less time moving. As was the case with growth, two different categories of caterpillars were evident when offered two unbalanced food

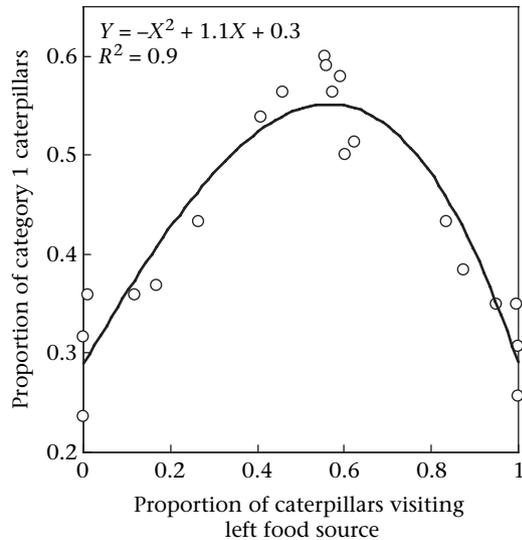


Figure 6. Relation between the proportion of category 1 (small) caterpillars in an egg mass and the proportion of caterpillars visiting the food source located on the left end of the bridge when the caterpillars were offered two unbalanced food sources ($N = 20$ replicates).

sources (Fig. 7). A two-step cluster analysis indicated two clusters. The first cluster contained 46% of caterpillars ('active' caterpillars: mean meal duration = 78 ± 6 s; mean exploration time = 2227 ± 131 s) and the second cluster the remaining 54% ('inactive' caterpillars: mean meal duration = 315 ± 20 s; mean exploration time = 604 ± 30 s). Hence, the time spent feeding was four times less in the first category than in the second, and the time spent exploring was four times greater.

DISCUSSION

Our study shows the existence of individual differences in social caterpillars, which become evident under dietary

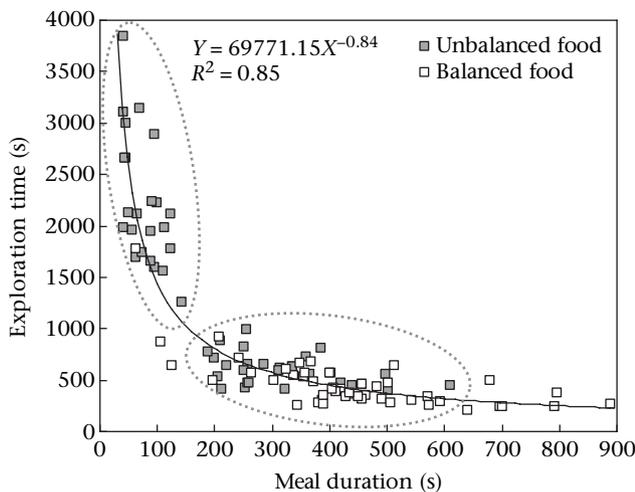


Figure 7. Relation between the time a caterpillar spent exploring and the time it spent feeding for each treatment ($N = 50$ caterpillars for each treatment). The dotted lines highlight the clusters identified when the caterpillars were offered two nutritionally unbalanced food sources.

imbalance but are not apparent when foods are nutritionally balanced. When available food sources lacked carbohydrate, caterpillars within a group fell into two clearly distinguishable behavioural categories, inactive and active, and ended up in two size categories, small and large. The active caterpillars spent considerable time exploring the environment and relatively little time feeding. These observations strongly suggest that the active caterpillars were those that became the small caterpillars, which failed to grow over the 24 h, whereas the inactive caterpillars that had longer meals were the large ones that grew. This would indicate that individuals remained consistent in their behavioural phenotypes across the experiment. Consistency of individual differences over time was recently confirmed in another experiment where the caterpillars were followed individually over 60 h (A. Dussutour, S. C. Nicolis & S. J. Simpson, unpublished data). Our results support the observations of Wellington (1957), who claimed that food-deprived *M. c. pluviale* larvae can be divided into two main categories: active and sluggish. Our data also confirm earlier work (Despland & Noseworthy 2006; Noseworthy & Despland 2006; Dussutour et al. 2007), in which caterpillars within a group ate more and spent less time moving when they found themselves on a nutritionally balanced than on an unbalanced food.

Why should these individual differences appear only under low-quality nutritional conditions? It is well known from other insects that feeding on nutritionally balanced foods reduces levels of locomotion and promotes remaining near the food source (Despland & Simpson 2000; Simpson & Raubenheimer 2000; Behmer et al. 2003; Simpson et al. 2006). In contrast, increased locomotion in response to nutrient deprivation is commonly observed as a functional strategy to find something better, in caterpillars (Morris & Kareiva 1990; Barton-Brown 1993; Dussutour et al. 2007), *Drosophila* (Tortorici et al. 1986; Tortorici & Bell 1988) and other insects (e.g. Simpson et al. 2006). Hence, when caterpillars of either the inactive or the active category encountered a nutritionally balanced source they were nutritionally replete and did not show 'exploratory' behaviour, which would enhance the probability of finding a better source. As a consequence, it would have been difficult to observe any individual differences under nutritionally balanced conditions. When faced with nutritionally unbalanced foods, however, active caterpillars took a short meal and continued to explore their environment, whereas sluggish caterpillars remained and made the best of the unbalanced food source.

The decision whether to stay on a nutritionally unbalanced food source or to leave will reflect the balance of the costs and benefits of the two strategies. The costs of leaving are (1) failure subsequently to locate a nutritionally superior food source, and (2) costs associated with being active, which include increased apparency to natural enemies, risk of dehydration and starvation. Studies of Lepidoptera have shown that an increase in feeding activity may increase the risk of predation substantially (den Boer 1971; Marston et al. 1978; Bergelson & Lawton 1988). For example, Bernays (1997) compared the predation risks of lepidopteran larvae in natural conditions

when they were feeding and resting, respectively. She showed that feeding was three times more dangerous in one species (*Manducta sexta*), while it increased the risk of predation 100 times in another species (*Uresiphita reversalis*).

Regarding the costs of remaining on an unbalanced food, these are threefold: (1) costs associated with eating too little of deficient nutrients; (2) costs of incidentally consuming too much of nutrients present in excess (Simpson et al. 2004; Raubenheimer et al. 2005; Boersma & Elser 2006); and (3) costs of missing a better balanced food located elsewhere. A diet entirely deficient in carbohydrate, as we used in the present study, is deleterious to fitness in caterpillars (Harvey 1974; Clancy 1992; Lee et al. 2002, 2003; *M. disstria*: Colasurdo 2006; Despland & Noseworthy 2006). Such a diet affects adult fecundity (Honek 1993; *M. disstria*: Colasurdo 2006) and first-instar survival of the progeny (Carisey & Bauce 2002). The amount of a nutritionally unbalanced food that an animal eats ought to reflect the probability that it will subsequently encounter an oppositely unbalanced food (Raubenheimer & Simpson 1999). This principle has been used to explain different nutritional strategies in specialist and generalist feeders (Simpson et al. 2002; Lee et al. 2003, 2006; Raubenheimer & Simpson 2003; Raubenheimer & Jones 2006). Kause et al. (1999) found a significant trade-off between staying on unbalanced food and dispersing according to environmental conditions, in caterpillars feeding on mountain birch foliage. These authors showed that early-season species disperse when the canopy is of heterogeneous quality, offering opportunities for mixing an optimal diet. In contrast, late-season species stay and show compensatory consumption to deal with the low nutritional quality of the old leaves that dominate the canopy at that time.

As social caterpillars live in groups, the existence of individual differences may have important consequences for the behaviour of the colony as a whole. The group-level consequences of increased activity in nutrient-deprived individuals may be profound, as shown recently for the Mormon cricket, *Anabrus simplex*, in which deficiencies in protein and salt drive mass migration, both directly through increasing locomotion and indirectly through cannibalistic attacks (Simpson et al. 2006). Wellington (1957) showed in *M. c. pluviale* that the proportions of the various types of larvae in a colony directly affect the activity of the group. In our experiment, when the food sources were nutritionally unbalanced, colonies either fed on only one source over the 24 h, as was also observed with nutritionally balanced food sources, or exploited both sources. This result is novel and intriguing because previous work on social insects faced with a choice between two equal food sources has found either the selection of one alternative only (ants: reviewed in Detrain et al. 1999) or the exploitation of both alternatives (honeybees, *Apis mellifera*: Visscher & Seeley 1982), but never the two options simultaneously.

We showed that the individual differences in behaviour led to colony decisions that were dependent upon the ratio of the two categories present in the group. Active caterpillar-biased colonies were less cohesive than colonies comprised

of proportionately fewer active caterpillars: the colonies did not focus their activity on one source but split and exploited two sources at the same time. Since both food sources were nutritionally unbalanced, these groups grew worse than inactive-biased groups that remained on one food source, but they would have grown better if complementary alternative foods (sensu Raubenheimer & Simpson 1999) had been available. In contrast, the inactive caterpillar-biased groups focused their activity on only one source over the 24 h. These caterpillars even moved the bivouac closer to the food source chosen after one or two foraging periods, and stayed there until the end of the experiment. Taking up residence close to a rare, high-quality food source (a high-protein food patch in an environment otherwise containing low-protein, high-carbohydrate patches) has been observed in locusts, *Locusta migratoria* (Behmer et al. 2003).

We showed in a previous study (Dussutour et al. 2007) that caterpillar colonies with access to both an unbalanced and a balanced food source initially chose one of the two food sources at random. Those groups that went first to the unbalanced food often became trapped there: even when individual caterpillars did escape the group and located the balanced food source, they were unable to recruit the rest of the group. However, in a few cases, groups of caterpillars that had initially arrived at the unbalanced food source succeeded in shifting to the balanced food source. We would predict from our present results that such colonies had a higher proportion of active caterpillars than those groups that failed to escape the unbalanced food.

According to Wellington (1957), colonies with many active members feed often and develop rapidly through their larval stage, and this may lead to population increases and outbreak. Conversely, Wellington (1957) suggested that egg masses with a greater proportion of sluggish individuals may be associated with population decline, implying that they are somehow adaptively 'senescent'. However, sluggishness at the group level, which results in groups persisting on a nutritionally suboptimal diet, may be the most appropriate strategy in degrading environments where better alternative foods are rare or unavailable, as reported by Kause et al. (1999) for mountain birch caterpillars. In addition, an active colony is less cohesive and consequently has a greater chance of splitting into more vulnerable small groups, as we observed in some of our replicates with the emergence of two bivouacs. Wellington (1957) found that colonies with a high proportion of active larvae were too active to stay together in their first stadium, so that many individuals wandered away from the protection of the communal tent (Wellington 1960). In high-density conditions, a high proportion of sluggish individuals can be adaptive because it decreases contact between colonies and hence decreases competition and disease transmission (Wellington 1960). It is well known in tent caterpillars (Fitzgerald 1993b; Costa & Ross 2003; Despland & Le Huu 2007), as in other gregarious animals (Krause & Ruxton 2002), that survivorship and the growth rate of individuals in colonies are influenced by the size of the group. Individuals gain protection from predators by surrounding themselves with others (reviewed in Fitzgerald 1993b; Sword et al. 2005). In addition to its direct effect on predation, being in a big group may also enhance larval

growth rates because of the joint benefits of group thermoregulation (Porter 1982; Bryant et al. 2000) and cooperative foraging (Denno & Benrey 1997). As a consequence, the coexistence of the two foraging strategies may provide a balance between maintaining colony cohesion and optimizing food location and diet balancing.

The existence of individual differences within a colony of caterpillars is strongly suggested by this study and their consistency over time is confirmed by results obtained recently (A. Dussutour, S. C. Nicolis & S. J. Simpson, unpublished data). A question remains: what could be the mechanisms responsible for these two behavioural categories? At least four possibilities suggest themselves. First, variation in foraging behaviours may be caused by different genes, as shown in fruit flies (reviewed in Reaume & Sokolowski 2006), honeybees (Ben-Shahar et al. 2002) and ants (Ingram et al. 2005). Second, variation in environmental conditions may elicit expression of alternative suites of genes within the same genotype, which manifest themselves as different behavioural phenotypes. For example, phenotypic plasticity has been identified in locusts in response to changes in rearing density (Simpson et al. 1999, 2002). Third, individual differences may result from an amplification process, in which slight differences in the tendency of individual animals to show a given behaviour are amplified in particular environments (reviewed in West-Eberhard 1989); for example, the social environment can amplify slight differences in the activity level of ants (Meudec 1979) and generate two categories of individual, active and inactive. Hence, if the acceptance threshold for foods lacking carbohydrates varies continuously among caterpillars, such that feeding was activated by the imbalanced diet in one subset of the population but not another, then the result would be a relatively immobile group (which fed) and a more mobile nonfeeding group, for which the imbalanced food did not provide sufficient stimulation to elicit feeding. In social insects such response threshold reinforcement leads to division of labour (Theraulaz et al. 1998). Fourth, the individual differences we observed may be sex related. Recent studies reported a gender-based division of labour in colonies of the caterpillar *Eucheira socialis*, in which males were more likely to spin silk than females (Underwood & Shapiro 1999), and in colonies of *Thaumetopoea pityocampa*, in which females were more likely to lead processions than males (Fitzgerald 2002).

Whatever the mechanisms underlying the two behavioural categories of caterpillar, our results highlight the importance of individual variation in the nutritional decisions of groups, adding a new aspect to the burgeoning field of nutritional ecology.

Acknowledgments

A.D. was supported by postdoctoral grants from foundation Fyssen and from Singer-Polignac. S.J.S. was supported by an ARC Federation Fellowship. We thank Natural Sciences and Engineering Research Council and Canadian Fund for Innovation for funding and Dr Barry Cooke of the Canadian Forest Service for collecting the egg masses.

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