Group leadership depends on energetic state in a nomadic collective foraging caterpillar

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Abstract

Group living is a common strategy among animals and has arisen independently in over 300 species of Lepidoptera. Yet activity synchrony between individuals is necessary to derive the benefits that ensue from an aggregated lifestyle. Which individuals decide which activities to perform and when to perform them is therefore a fundamental question. In some species of social caterpillars and sawflies, the role of a potential behavioral polyethism between individuals has been suggested, whereby certain individuals are consistently more likely to initiate and lead a foraging event. However, in these cases, evidence in support of division of labor is lacking. This study was undertaken to determine if certain individuals of *Malacosoma disstria* are more likely to be consistent group leaders, or if transient leaders could be predicted by the differences in energetic states between individuals. The results of this study indicate that unfed caterpillars initiate foraging bouts and are more likely to lead locomotion. There was no size or sex-based bias in those individuals that acted as temporary leaders. Consistent behavioural differences between individuals, if they exist, are therefore not necessary to explain task allocation and synchronisation during foraging in this species.

Introduction

Animal groups on the move often need to make collective decisions about the initiation, speed and direction of travel in order to stay together and reap the benefits of group living. However, individuals often differ in their requirements and hence have different preferences of when and where to go. In these cases, consensus can be made by the entire group (Conradt and Roper 2005). Consensus decisions can be taken in an equally shared (all group members participate in the decision) or unshared (one individual decides for the whole group) manner, but most often are partially shared among group members (Conradt and Roper 2005; Conradt and List 2009; Sumpter and Pratt 2009). In heterogeneous groups making partially shared consensus decisions, the question of who initiates locomotion and who occupies frontal positions during travel is central to understanding group dynamics (Conradt and Roper 2005; Petit and Bon 2010). Leadership could depend on transient states such as energetic state or knowledge, or it could be based on stable traits such as temperament or sex.

Rands *et al.* (2003) suggested the spontaneous emergence of temporary “leaders” and “followers” in pairs of foragers, owing to the build-up of differences in energetic state. The individual with the lowest energy reserves emerges as the “leader”, whom the other individual imitates. Dostalkova and Spinka (2007) further demonstrated with a model that this was possible if individuals chose to forage before their ideal time in order to avoid being separated from the group. A higher probability to move as a result of low level energy reserves has been shown in many animals (Barton Browne 1993), and in collective displacements hungry individuals often initiate and lead movement (Petit and Bon 2010), as seen for example in meerkats and zebras (Holekamp *et al.* 2000; Fischhoff *et al.* 2007). The initiation of collective foraging is often preceded by increased restlessness associated with hunger in caterpillars (Long 1955; Fitzgerald and Costa 1999; Ruf 2002) and other animals, such as gorillas (Stewart and Harcourt 1994) and cattle (Ramseyer *et al.* 2009). In fish, the leadership position in a traveling school is often occupied by individuals that have been deprived of food (Krause *et al.* 1992; Krause 1993; Krause *et al.* 1998) and there appears to be a trade-off for these individuals between the benefit of a higher food intake (Krause *et al.* 1992) and the cost of an increased predation risk in the frontal position (Bumann *et al.* 1997). Similarly, Cornell *et al.* (1988) showed that leadership of traveling caterpillar colonies was not consistent over larval development, and suggested that temporary leaders emerge due to differences in individual digestive periods and hence energetic state.

In other cases, certain individuals are consistently more likely than others to assume the leadership role (Petit and Bon 2010). More generally, a polyethism is observed when certain individuals are more likely to lead group locomotion, as in sawfly larvae (Weinstein and Maelzer 1997) and in cattle (Ramseyer *et al.* 2009). This tendency to lead can be correlated with personality characteristics such as boldness, as in fish (Leblond and Reebs 2006; Harcourt *et al.* 2009) and birds (Beauchamp 2000), or with dominance, as in primates (King and Cowlishaw 2009). This division of labour can also be based on size or sex, for instance in fish (Krause *et al.* 1998; Reebs 2001) and in caterpillars (Underwood and Shapiro 1999; Fitzgerald 2003).

The present study investigates which individuals initiate collective locomotion and occupy frontal positions in travelling colonies of the nomadic foraging forest tent caterpillar *Malacosoma disstria* (Lasiocampidae: Lepidoptera). Wellington (1957) suggested that consistent individual differences in behaviour may play a role in group dynamics of *Malacosoma* caterpillars, but subsequent studies have failed to substantiate this (Laux 1962; Greenblatt and Witter 1976; Edgerly and Fitzgerald 1982). Edgerly & Fitzgerald (1982) found that activity of first instar caterpillars of *Malacosoma americanum* was not consistent and could not be generalized to subsequent instars. They observed only transient leaders of collective foraging and suggested that the first larvae to initiate a foraging bout might have been the hungriest. Yet Nemiroff and Despland (2007) found overall inter-individual differences in the activity of *M. disstria* caterpillars over 4 trial days, but it is not clear whether this has any impact on leadership of foraging bouts.

Malacosoma disstria is a nomadic collective forager: the 50-200 siblings from an egg mass stay together for most of their larval development. They spin silk mats as temporary bivouacs on their host tree and travel together en masse between bivouacs and feeding sites. Pheromone trails are used to maintain cohesion during locomotion, and caterpillars, particularly in the early larval stadia, are reluctant to advance without a trail. Locomotion becomes more independent in the fifth and final stadium (Fitzgerald 1995). The foraging schedule is flexible: foraging bouts can occur at different times of day and are highly synchronized all-or-nothing events, with the entire colony traveling together and feeding together on the same leaf (Peters and Despland 2006; McClure and Despland 2010). The present study examines which individuals initiate foraging bouts and occupy frontal positions during travel. We test the alternate hypotheses of energetic state *vs.* consistent individual differences in leadership via two experiments. Experiment 1 examines whether certain individuals are consistently more likely to lead collective locomotion over three days and if this depends on sex or size. Experiment 2 examines whether unfed caterpillars are more likely to lead and if the proportion of unfed individuals in a group influence its locomotion.

Material and Methods

M. disstria caterpillars were reared in the laboratory from egg masses collected on aspen trees in Northern Alberta, Canada (56°17.5N, 113°93.9W) and stored at 4ºC with 80% R.H. until use. To minimize mortality from pathogens, egg bands were sterilized by soaking in sodium hypochlorite as described by Grisdale (1985). Caterpillars were kept in a growth chamber at 21ºC, on a 16h light: 8 h dark photoperiod with 70% R.H. The caterpillars were fed *ad libitum* on a nutritionally balanced, standard wheat germ-based meridic artificial diet (Addy 1969). All experiments were conducted at temperatures ranging between 20-23°C and 50-60% R.H. and at approximately the same time each day.

Experiment 1: Consistency in leaders

Fifteen groups each of second and fourth instar caterpillars were used on the second day after molting to ensure that none of the caterpillars molted before the end of the trials. Both second and fourth instar caterpillars were studied during these experiments, as they exhibit differences in group behavior. Trials were repeated at 24 h intervals for three consecutive days for each group. Caterpillars were food deprived for three hours prior to the experiment to control for energetic state. Groups consisted of all caterpillars arising from a single egg mass (with the number of individuals varying between 37 to 64 caterpillars) and were placed on plastic bridges covered in brown paper and elevated by rubber stoppers over a tray of water to prevent caterpillars from leaving the arena (see Dussutour *et al.* 2007 for a schematic description of a similar set-up). The bridges were replaced after each trial to ensure that pheromone trails were not present. Bridges measured 36.5 cm x 3 cm for second instar caterpillars and twice that length for fourth instar caterpillars. This increase in arena size was necessary due to an increase in larval size and activity. The width of the bridge, however, was kept constant as there was plenty of space for there to be more than one caterpillar side by side.

Once the caterpillars were on the bridge, an empty glass beaker acting as a barrier was removed to commence the experiment. A caterpillar moving towards the end of the bridge at the front of the group was identified as a leader and any other individual whose head was more than one body length behind was considered a follower. If a second individual was less than one body length behind the first, however, then it was also considered a leader. This means that there were occasionally simultaneous leaders. Occasionally, individuals in the lead turned back and were replaced by other leaders, who were then also marked as leaders. Thus several individuals could act as leaders in each trip. All individuals that acted as leaders during a given trial were marked with a spot of nontoxic washable paint on the abdominal setae. The experiment was terminated when at least one caterpillar reached the end of the arena. Each group of caterpillars was tested on three consecutive days and three different paint colors were used, therefore enabling easy identification of leaders and followers for each day. If foraging did not begin after one hour of being placed on the bridge, the trial was discarded and the data was not used in the analysis. All fourth instar caterpillars used were individually weighed after the last trial. Second instar caterpillars were not weighed as they are too small to accurately weigh individually. For five of the fourth instar groups, caterpillars observed to be leaders at least once were separated from those who were always followers and were reared to maturity separately. Pupae of both leaders and followers were sexed when metamorphosis was complete (N=206 caterpillars; 99 males and 107 females).

Statistical Analysis

Observed frequencies were the number of times during the three days of observation that an individual was a leader, identified by the number of colored paint dots. A Poisson distribution was used to calculate expected frequencies based on the Naperian logarithm (Sokal and Rohlf 1981) and a Chi-square test was used to determine, for each group independently, if there was significant departure from the expected frequencies. The effect size (Chi-square values) was plotted as a function of group size for each larval instar and analysed using a linear regression analysis. One overall Chi-square test per instar was also used to determine if there was significant departure from the expected frequencies for pooled groups. The larval weight of leaders and followers were compared using a t-test. The sex ratio of both leaders and followers were compared to the frequencies of both sexes measured in our combined groups (48% males and 52% females) using a Chi-square test.

Experiment 2: Leadership and energetic state

Groups of 40 caterpillars with different ratios of fed to unfed individuals (35:5; 30:10; 20:20; 10:30; 5:35) were prepared for this experiment. On the day after they moulted to second instar, caterpillars were individually marked with dots of non-toxic washable paint on the abdominal setae using two different colors to indicate fed and unfed individuals. Caterpillars were fed *ad libitum* on artificial diet, but for the unfed group, the food was removed three hours before the experiment, a normal intermeal interval for this species (Peters and Despland 2006; McClure and Despland 2010). A wooden craft stick measuring 113 mm x 6 mm was placed between two overturned Petri dishes 90 mm in diameter. At the beginning of a trial, all marked individuals were placed on one of the overturned Petri dishes and a small square of fresh artificial diet was placed on the second Petri dish at the opposite end. The test area was arranged so that all arenas received comparable amounts of light, arenas were replaced after each trial to ensure that pheromone trails were not present and caterpillars were used only once. During each trial, interval scans were performed every 60 seconds, and the paint mark (indicating if it was fed or unfed) of the individual in the front of the group was recorded. A total of 12 replicates were done for every ratio of unfed individuals (87.5%; 75%; 50%; 25%; 12.5%). Trials were terminated when the group reached the food or after 200 minutes.

Statistical Analysis

To determine if unfed individuals were more likely to take the lead then expected, a Chi-square test for goodness of fit compared across group ratios was used to compare the proportion of observations in which an unfed individual was the leader with the proportion of unfed individuals in the group.

Cox survival analyses were used to compare proportion of unfed individuals (as a continuous variable) with the latency to start a foraging bout and the time to reach the food once they had started.

Results

Experiment 1: Consistency in leaders

On average (mean±SEM) 56.07±3.50% or 25.87±2.35 second instar caterpillars and 41.99±4.30% or 16.60±1.83 fourth instar caterpillars per group led at least once. Chi-square tests done for each group individually, both of second and fourth instar caterpillars, were all non-significant ($p>0.05$; df = 3), indicating that the number of times an individual led did not differ from that expected if all individuals had an equal tendency to lead. The effect size necessary to obtain statistical significance at $\alpha = 0.05$ is $\chi^2_3 = 7.815$ (Sokal and Rohlf 1981); the effect sizes in our tests are all well below this critical value (see Fig. 1). The effect size (chi-square values) was also not significantly affected by group size in both larval instars (second instar: R_2=0.039; F=0.521; df=1, 13; p=0.483); fourth instar: R_2=0.154; F=2.361; df=1, 13; p=0.148; Fig. 1). Chi-square tests of pooled groups within larval instars was also not significant (second instar: χ^2=0.78; df=3; p=0.854; fourth instar: χ^2=3.37; df=3; p=0.338).

There was no significant difference in larval weight (mean±SEM) between caterpillars who led the group at least once and those that never did (36.97±20.46 mg *vs.* 39.50±22.02 mg; equal variances t=-1.185; df=475; p=0.237; Levene's test: F=0.072; p=0.789; Shapiro-Wilk test: W=0.912; df=477; p=0.120). Caterpillars that had led the group at least once were just as likely to be males or females (χ^2=0.004; df=1; p=0.95), as were the followers (χ^2=0.03; df=1; p=0.86). Thus, caterpillars do not appear to exhibit consistent individual differences in their tendency to lead.

Experiment 2: Leadership and energetic state

Individuals in the front of the group were more likely to be unfed than expected from the ratio of fed to unfed individuals in the group (χ^2=42.68; df=4; p<0.001, Fig. 2). Overall, 82% of all forays (N=50) were led by unfed individuals.

The majority (93%; N=60) of groups with 25-87.5% unfed individuals started a foraging bout within 40 minutes; however, more than half of the groups with 12.5% unfed individuals did not initiate a foraging bout in the 200 minutes of the trial (Fig. 2 & 3). Cox survival analysis showed a significant effect of the proportion of unfed individuals within a group on the rate of initiation of foraging (Wald=3.964; df=1; p=0.046).

Most groups reached the food within 60 min after departure (total N=50, including only those groups which did initiate foraging) except for two groups with 87.5% unfed individuals which took more than 2 hours (Fig. 4). Also, none of the groups with 12.5% unfed individuals reached the food in less than 15 minutes, whereas in all the other treatments, some groups reached the food in less than 5 min (Fig. 4). Cox survival analysis showed no significant effect of the proportion of unfed individuals within a group on the duration of travel time (Wald=0.046; df=1; p=0.831).

Discussion

Synchrony of group activities can result from social facilitation when individuals match their behaviour to that of other animals in the group (Gautrais *et al.* 2007; Sumpter and Pratt 2009). In caterpillars, the initiation of collective foraging is often preceded by increased restlessness associated with hunger. Tactile cues are thought to transmit the signal to begin locomotion as group members imitate the movement of their neighbors (Long 1955; Fitzgerald and Costa 1999; Ruf 2002). Hence, cohesion in group locomotion emerges from local interactions between individuals. Our findings suggest that these interactions are not initiated consistently by the same individuals, but rather by those that are hungriest.

Nemiroff and Despland (2007) found that some caterpillars of *M. disstria* were consistently more active than others and showed a lower latency to reach a novel food source, indicating greater propensity to independent movement. However their study tested caterpillars individually, and may not be indicative of what occurs in a group. The present study demonstrates that consistent individual differences in behavior, if they exist, do not significantly contribute to determining leadership of foraging in *M. disstria*. A similar conclusion was reached in other species of *Malacosoma* (Laux 1962; Greenblatt and Witter 1976; Edgerly and Fitzgerald 1982) and other (Cornell *et al.* 1988) caterpillars (but see also Wellington (1957)).

Instead, it appears that transient differences in energetic state determine who leads caterpillar collective foraging, as suggested by Edgerly and Fitzgerald (1982) and Cornell *et al.* (1988). Indeed, we show that hungry and therefore temporarily active individuals take frontal positions during travel (Fig. 2) and that groups containing hungry individuals initiate foraging sooner (Fig. 3). Our results indicate that in colonies of *M. disstria*, collective dynamics are not based on the actions of a few highly active leaders but rather depend on fluctuations in energetic state of group members. A recent study with locusts shows how allomimetism of hungry neighbors not only synchronizes group feeding activity but also leads to entrainment of internal physiological rhythms (Despland and Simpson 2006) and hence decreases conflicts between individuals and further facilitates synchronization.

This experiment thus provides an empirical demonstration of the mechanism for the model proposed by Rands *et al*. (2003), where individuals with low energy reserves initiate locomotion. It would therefore be interesting to test, in a model, the mechanism described in Rands *et al.* (2003) with larger groups and compare it to the results of this study. In both Rands *et al.* (2003) and this study, movement is driven not by individuals with particular personality traits, status or knowledge, but by those with the highest need. Other group members follow because there is a cost to being separated (Rands *et al.* 2003). In *M. disstria*, the selection pressure to remain with the group is strong because caterpillars in groups have higher survival rates, develop faster and reach larger sizes than isolated individuals (Despland and Le Huu 2007), possibly due to improved thermoregulation and group defence (McClure and Despland 2010). Indeed, in the field, young *M. disstria* caterpillars demonstrate very high levels of cohesion, and fragmentation of colonies is rare (Fitzgerald and Costa 1986; McClure and Despland 2010).

For planktivorous fish, occupying a frontal position provides the highest food intake (Krause *et al.* 1992). However, this is unlikely to be the motivation for leading in *M. disstria* caterpillars, since a single leaf generally provides more than enough for a meal for an entire colony of young caterpillars. Instead, increased hunger likely makes caterpillars more likely to accept the risks associated with leading a moving group. Young *M. disstria* caterpillars are reluctant to advance at the head of a group (Despland and Hamzeh 2004; Colasurdo and Despland 2005), possibly due to an increase in predation risk in the frontal position (McClure and Despland 2010). Caterpillars with lower energetic states may be more likely to take that risk (Werner and Anholt 1993). In our experiment, leaders often turned back to be replaced by other leaders, suggesting that even hungry individuals are reluctant to remain in the leadership position for very long.

In consensus decision-making, action can often be driven by a minority of highly motivated individuals (Huse *et al.* 2002; Couzin *et al.* 2005), as for instance in cockroaches (Halloy *et al.* 2007) and humans (Dyer *et al.* 2009). Petit and Bon (2010) showed that the strength of the initiation signal (either as an absolute number or a proportion of individuals) may represent a quorum at the individual level triggering the subsequent movement. Figure 3 suggests that the initiation signal is fully present even in groups where fed individuals outnumber the unfed ones 3 to 1, as groups with only 25% unfed individuals initiated foraging as rapidly as groups with a higher proportion of unfed individuals. However, those groups with only 12.5% unfed caterpillars were less likely to initiate foraging within the duration of the trial. These results suggest that, as seen in cattle (Ramseyer *et al.* 2009) and humans (Dyer *et al.* 2009), a minimum number of motivated individuals is necessary for action to begin.

At the other extreme, groups with 87.5% unfed individuals initiated locomotion rapidly, but showed more variation in the amount of time required to reach the food than more balanced groups (Fig. 4). Their movement appeared scattered to the observer with many individuals leading in different directions, suggesting that Wellington (1957) may have been right in speculating that following caterpillars play an important role in keeping the group cohesive. It's possible that groups with many individuals forming separate pheromone trails independently of one another are less effective at advancing forward than groups where a smaller number of individuals take turns progressing a single trail. This raises the possibility that, at least in caterpillar colonies, there could be an optimal balance between leaders and followers for effective collective locomotion.

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Conflict of interest

The authors declare that they have no conflict of interest.

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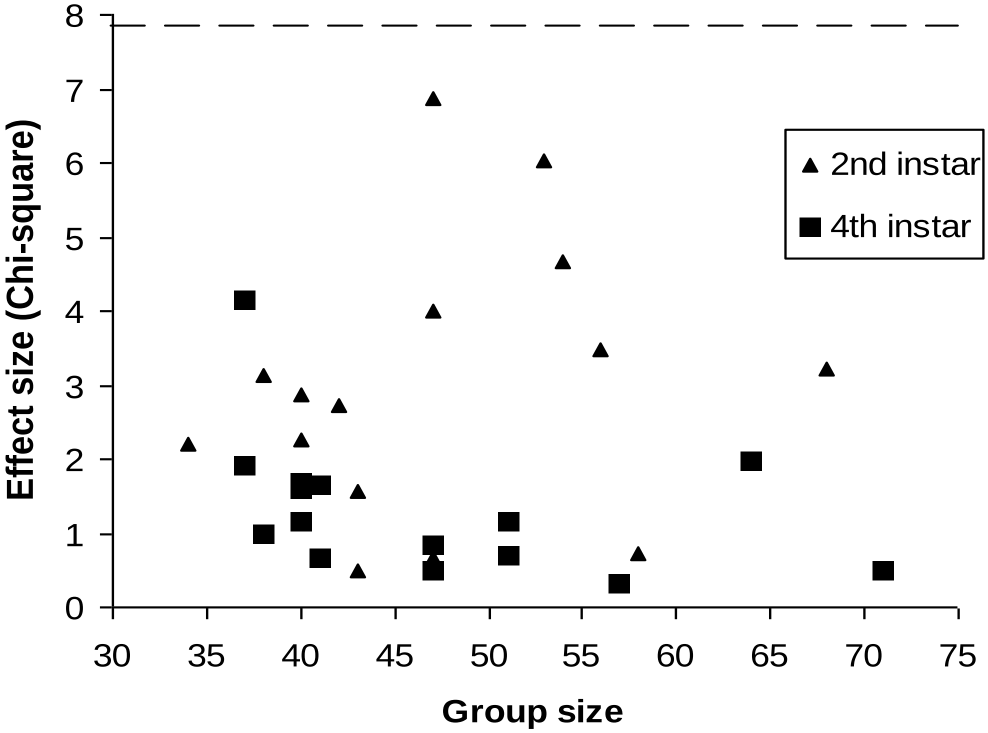
Fig. 1: The effect size (chi-square values) as a function of group size for both second and fourth instar *Malacosoma disstria* caterpillars. The dashed line represents the critical chi-square value (7.81) necessary to obtain p=0.05 with three degrees of freedom.

Fig. 2: The proportion of observations in which unfed *Malacosoma disstria* caterpillars are in the front of the group as a function of the percentage of unfed caterpillars in the group. The sample size (N) indicates the number of groups in each case which initiated foraging, out of a total of 12 tested.

Fig. 3: Survival curves showing the latency of *Malacosoma disstria* groups to start a foraging bout under the different fed: unfed ratios. The y-axis indicates the proportion of the groups that haven’t started foraging by the time indicated on the x-axis (in minutes). Curves that terminate above zero show the proportion of groups that did not initiate a foraging bout within 200 minutes.

Fig. 4: Survival curves showing, for all fed: unfed ratios, the time groups took to reach the food once they had started. The y-axis indicates the proportion of the groups that haven’t reached the food by the time indicated on the x-axis (in minutes).


Effect size (Chi-square)
0
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8
30
35
40
45
50
55
60
65
70
75
Group size
▲ 2nd instar
■ 4th instar

Fig. 1

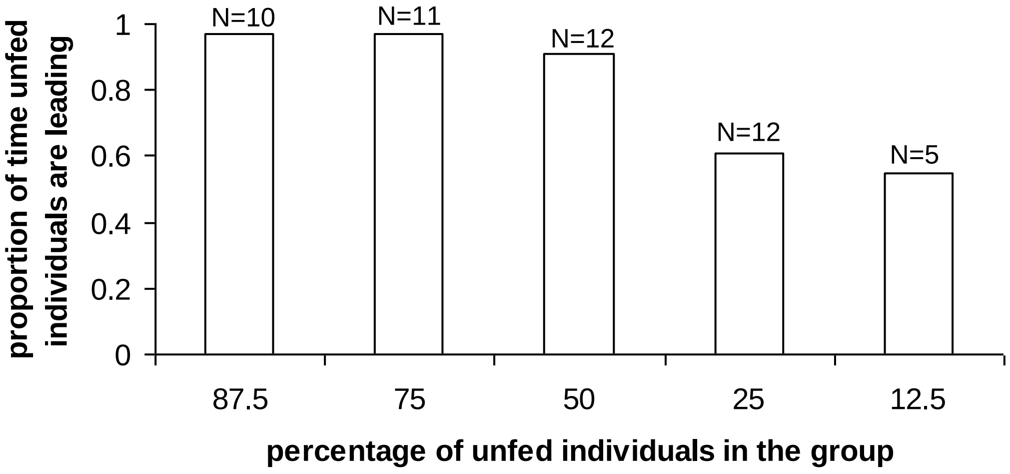
proportion of time unfed individuals are leading
1
0.8
0.6
0.4
0.2
0
N=10
N=11
N=12
N=12
N=5
87.5
75
50
25
12.5
percentage of unfed individuals in the group

Fig. 2

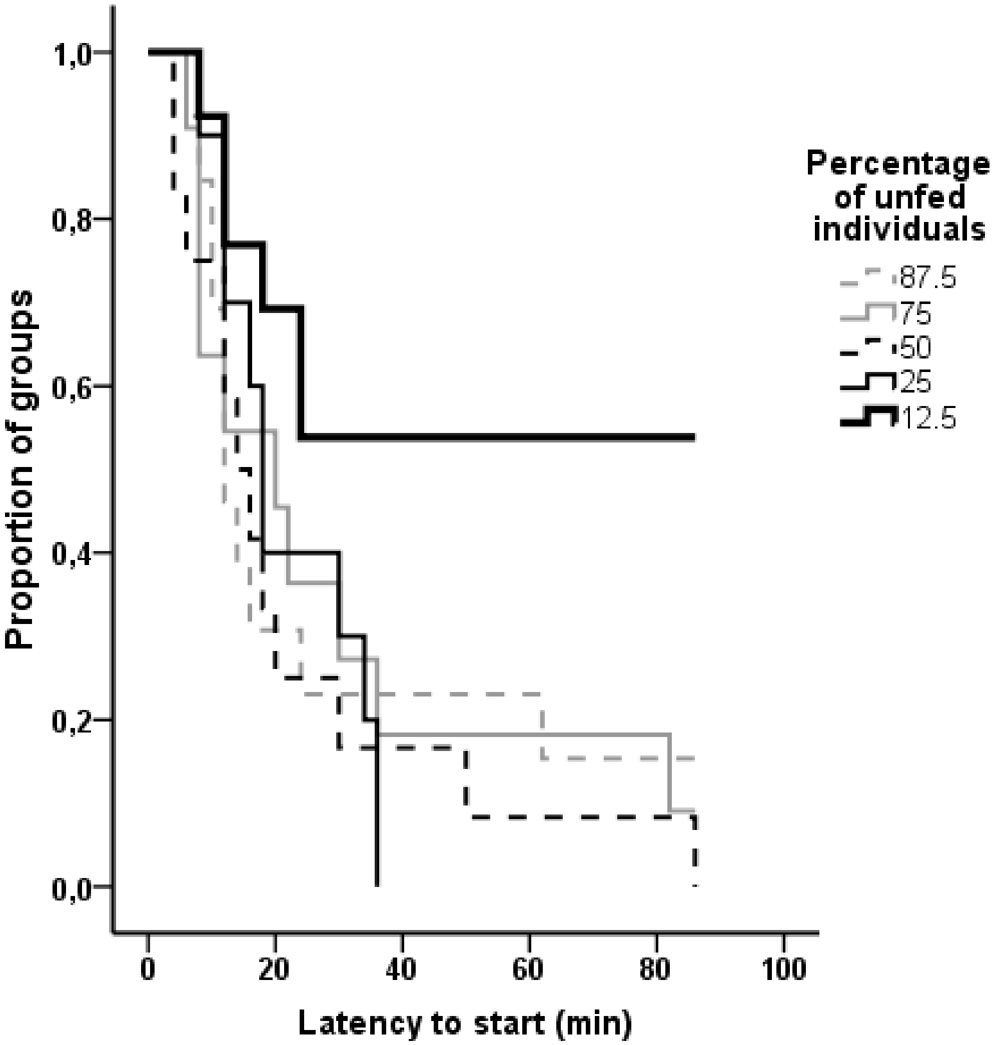
Proportion of groups
1,0
0,8
0,6
0,4
0,2
0,0
0
20
40
60
80
100
Latency to start (min)
Percentage of unfed individuals
87.5
75
50
25
12.5

Fig. 3

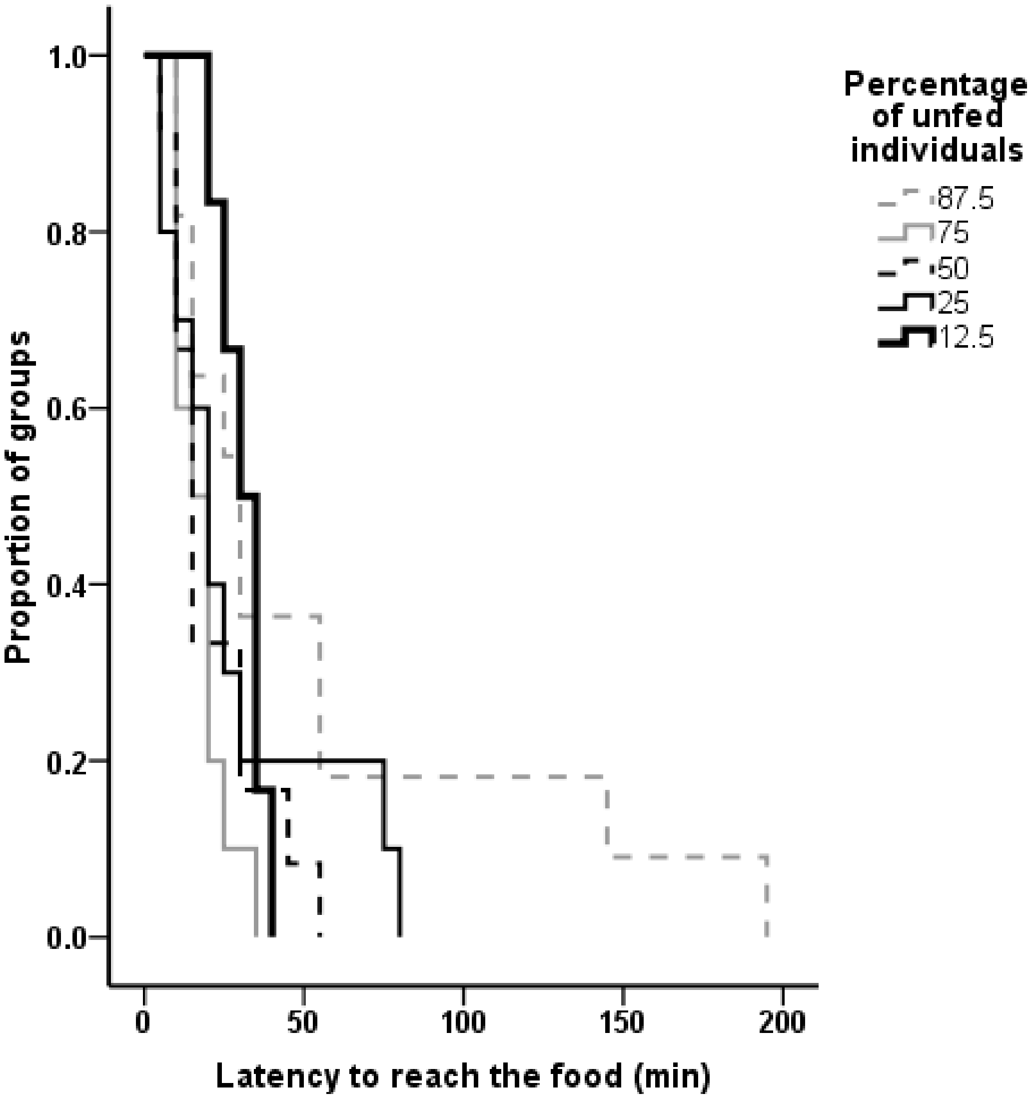
Proportion of groups
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
200
Latency to reach the food (min)
Percentage of unfed individuals
87.5
75
50
25
12.5

Fig. 4