Benefits and Mechanisms of Group Living in the Nomadic Social Forager *Malacosoma disstria*

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ABSTRACT

Benefits and mechanisms of group living in the nomadic social forager *Malacosoma disstria*

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The present work has two main objectives; to determine the benefits and the mechanisms of group-living in *M. disstria* caterpillars. A combination of laboratory and field experiments showed that groups of *M. disstria* caterpillars can thermoregulate, that body temperatures achieved while basking in a group coincided with temperatures at which development rate is maximal for this species, and resulted in higher growth rates in the laboratory. Not only is collective thermoregulatory behaviour possible and advantageous in this species, it also drives much of the colony's behaviour, in large part dictating temporal and spatial patterns of movement. The objective of the second section of the study was to determine if the gregarious habit of *M. disstria* caterpillars is advantageous against different invertebrate natural enemies as a function of group size and larval instar. We found that behavioural tactics in response to attacks were specifically tailored to the particular mortality agents acting on them and were more diverse and more effective for larger caterpillars. We also show that grouping benefits caterpillars through both the dilution of risk and group defences.

Synchronization of activity 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. The results of our study indicate that unfed caterpillars initiate foraging bouts and are more likely to lead locomotion. Consistent behavioural differences between individuals, if they exist, are therefore not necessary to explain task allocation and synchronisation during foraging in this species.

In conclusion, these findings suggest that group thermoregulation and protection from predation may be important selection pressures keeping larval colonies of *M. disstria* together. Like other groups of animals with self-organization, these caterpillars are able to make collective decisions as a result of individual behaviours in order to benefit from these advantages.

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Contributions of Authors

The four chapters within this thesis have resulted in high quality manuscripts published in international peer-reviewed journals. I was the principle investigator for all of the research work undertaken in this thesis, under the supervision of Dr. Despland, and I was the main author for all of the manuscripts. The other two co-authors of the papers, Elizabeth Cannell and Melissa Ralph, were undergraduate students completing small independent research projects. They both completed subsets of the experimental trials under my supervision and their results were pooled with the rest of the data.

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Chapter 1- General Introduction

Groups occurs in a wide range of taxa, including bacteria, arthropods, fish, birds and mammals, and depending on the species may be labelled as herds, shoals, flocks, schools or swarms, but is more broadly denoted as aggregations. Questions such as why animals aggregate, what are the ecological consequences and what proximate cues are used, are central ones in both ecological and evolutionary theory.

There are many potential advantages of animal aggregations, including an increased likelihood of food finding and/or acquisition (e.g., in beetles: Travers, 1993; and in chickens: Collins and Sumpter, 2007), increased growth rate and/or survivorship (e.g., in beetles: Breden and Wade, 1987; and in caterpillars: Denno and Benrey, 1997), increased predator defence and/or vigilance (e.g., in mammals: Hass and Valenzuela, 2002; in amphibians: DeVito, 2003; and in birds: Cresswell and Quinn, 2010), thermal benefits (e.g., in reptiles: Shah *et al.*, 2003).

But in order to stay together and reap the benefits of group living, animal groups need to make collective decisions about the initiation and direction of travel. However, individuals often differ in their requirements and hence have different preferences of when and where to go and so to coordinate foraging and travel, animal groups need to reach a consensus; that is, group members need to agree on the same option (Conradt and Roper, 2005; Sumpter *et al.*, 2008; Conradt and Roper, 2010; Sueur *et al.*, 2010). Consensus can either be unshared (one individual decides for the whole group) or shared (all group members participate in the decision), but most often are partially shared among group members (Conradt and Roper, 2005; Conradt and List, 2009; Sumpter and Pratt, 2009). For example, it has been suggested that the animal with the lowest energy reserves

(i.e., potentially having the highest consensus costs) in groups of two should always initiate activity changes from resting to foraging (Rands *et al.*, 2003). Similarly, Couzin *et al.* (2005) modelled large groups containing individuals that preferred one of two different travel destinations and when the differences in direction between the preferred goals were large, the whole group moved in the direction of the goal preferred by a majority of individuals. In the absence of centralized control (i.e., under self-organization), arriving at a consensus depends on local interactions in which each individual's likelihood of choosing an option increases with the number of other individuals already committed to that option. The selected option is then implemented through amplification and positive feedback.

These general principles of decision-making have been shown in a wide range of self-organized animal groups (ants, fish, ungulates, humans), though the group-level outcome may differ according to the environmental context, group size, the degree of sociality, etc. The future of collective behaviour research lies in identifying these principles, establishing the properties they produce at a group level and asking why they have evolved in so many different natural systems. To explain animal aggregations it is essential to investigate both the functional explanation as to why it has evolved through natural selection and the mechanistic explanation of how animals interact to produce group level patterns. Doing so in a variety of different social systems will further our understanding of the emergence of collective patterns and cooperation.

1.1 Sociality in insects

Most studies on sociality in insects have focused on eusocial species, such as ants and bees, yet they represent only one end of a broad spectrum of insect sociality. Although many other insect species are known to aggregate, the benefits and the grouping mechanisms are still poorly understood. Costa & Fitzgerald (1996) suggested that documenting the range and diversity of social forms and means of communication among group-living insect species is essential in order to gain a better understanding of extrinsically-selected contexts for cooperation. Herbivorous larvae, although they constitute a relatively small proportion of social insects, vary widely in their colony composition and social interactions, and are therefore interesting systems to study.

Although there are inherent disadvantages to group living such as, for example, increased competition for resources, increased pathogen transmission and conspicuousness that could attract predators, plant-feeding insects benefit in various ways from being in a group. As such, larvae of several groups of phytophagous insects-Lepidoptera, Symphyta (Hymenoptera), Acrididae (Orthopertera) and Chyrsomelidae (Coleoptera)-have converged on a lifestyle that includes group living. Direct benefits of group living in these species are sufficient that aggregation is favoured whether or not the individuals are genetically related, and in many species, groups that encounter each other merge together into multifamily, and occasionally multispecies, groups (Costa and Ross, 1993; Costa and Pierce, 1997 and references therein).

Proposed selective advantages of larval aggregation include increased feeding efficiency (Clark and Faeth, 1997; Denno and Benrey, 1997), enhanced group defence against predators (Stamp and Bowers, 1990; Vulinec, 1990), and improved

thermoregulation (Stamp and Bowers, 1990; Casey, 1992; Bryant *et al.*, 2000). However, the selection pressures that these different ecological factors exert and their adaptive value tends to change during larval development. As such, group living tends to be favoured in younger larvae and the majority of social larvae show a distinct waning in group fidelity as they age (e.g., Benrey and Denno, 1997; Clark and Faeth, 1997; Reader and Hochuli, 2003). Although larval societies are unique in that they are single-generation cohorts that dissolve when the larvae mature, these systems exhibit remarkably diverse social complexity, with considerable communication among group members.

1.2 Sociality in the Lepidoptera and in *Malacosoma disstria*

Although most species of Lepidoptera lay single eggs and develop as solitary caterpillars, sociality has arisen independently in as many as 27 families and over 300 species (Stamp, 1980; Fitzgerald and Peterson, 1988; Sillén-Tullberg and Leimar, 1988; Fitzgerald, 1995; Costa and Pierce, 1997). All known gregarious Lepidoptera larvae arise from egg clustering by females. Because an increased proportion of the energy reserves stored during larval life can be directed towards egg production if females engage in limited flight, Herbert (1983) argued that egg clustering is a consequence of energetic limitations on adult females (see also Stamp, 1980; Chew and Courtney, 1991). Courtney (1984) therefore suggested that adults of batch laying Lepidoptera evolved by selection for increased fecundity of adult females and accordingly gregarious larvae are more frequent in species that do not feed as adults (Hunter, 1991).

However, although synchronous hatching of a batch of larvae may provide the opportunity for aggregation, not all egg clusters give rise to aggregates of larvae (but see Stamp, 1980; Sillén-Tullberg and Leimar, 1988; Fitzgerald, 1995), as siblings arising from a common egg mass may either disperse after hatching or aggregate. In species that aggregate, prolonged association and cooperation among the larvae in a cohort may have been favoured in ancestral solitary species that experienced improved survivorship by virtue of grouping. So even though Courtney (1984) viewed the benefits accruing to aggregated larvae as consequences rather than as causes of the evolution of egg clustering, the evolutionary fitness-enhancing patterns of cooperating behaviour could be expected to contribute to the evolution of adult ovipositional patterns (Fitzgerald, 1993b). While the maximum size of a sibling cohort is ultimately limited by female fecundity, large multicolony assemblages have been reported for a number of species (Stamp, 1981; Fitzgerald and Willer, 1983; Costa and Fitzgerald, 1996; Costa and Pierce, 1997; Costa and Ross, 2003). As such, aggregates of social caterpillars vary in size from only a few individuals to assemblages containing hundreds or even thousands of larvae. The direct benefits of group living are likely sufficient that the evolution of sociality in these groups is favoured whether or not the individuals are genetically related. But because these social groups originate from a single egg mass, cooperation may also benefit closely related individuals, despite their inability to discriminate against non-kin.

Although the Lasiocampidae are only of moderate diversity (ca. 1500 species in 150 genera) as compared to other lepidopterous families, larval sociality seems to be surprisingly frequent. Members of the genus *Malacosoma* are among the most extensively studied, in large part because of their periodic abundance and dramatic

eruptive population dynamics (Fitzgerald, 1995). *Malacosoma disstria* Hübner, also known as the forest tent caterpillar, is one of the most ubiquitous forest insects in North America and is an economically important pest of deciduous forests. It occurs from southern Texas to northern Canada and from the Atlantic to the Pacific (Stehr and Cook, 1968). Across this vast range, *M. disstria* uses a taxonomically diverse array of host species, but its primary host in Canada is trembling aspen, *Populus tremuloides* Michaux, on which it also develops best (Lorenzetti, 1993; Nicol *et al.*, 1997).

As with other species of *Malacosoma*, *M. disstria* is univoltine throughout its range (Stehr and Cook, 1968), with all active stages present during the spring and summer months. The larvae go through five or six instars, with the entire life cycle taking approximately six weeks (Fitzgerald, 1995). The moths do not feed and it is therefore essential that they receive all necessary nutrients during the larval stage. Female moths lay their whole egg complement in a single egg mass and the pharate larvae pass the winter inside their eggs, which are aggregated into a single band on the tips of twigs. Like in other *Malacosoma* species, increasing ambient temperatures in the spring appear to induce hatching of the first instar larvae, which is generally synchronised with the bud burst of host trees and as a result most of their larval stage is spent feeding on highly nutritious spring leaves. Because budbreak usually occurs in early spring, these caterpillars are also active at a time of year when the average daily ambient temperature is often below the minimum temperature required for growth and development. Nevertheless, an early emergence is likely to also be advantageous because many predators and parasitoids will not be abundant until later in the season. Thermoregulation

and protection from predation may therefore be important advantages of sociality in this species.

Malacosoma disstria is unique amongst the *Malacosoma*, however, because it is the only nomadic forager, moving en masse in synchronised columns and using pheromone trails to stay cohesive (Fitzgerald and Costa, 1986). It does not construct a silk tent for shelter, but instead constructs temporary silk mats which are regularly abandoned as the colony searches for new feeding sites. Because the use of a shelter significantly affects the advantages (such as thermoregulation and protection from predation) and the mechanisms of group living, it can be expected that there will be important differences between *M. disstria* and other congener species.

1.3 Advantages of group living

Thermoregulation in larval aggregations

The behavioural response to temperature (thermoregulation: body temperatures are above or below ambient temperatures or thermoconformation: body temperature passively follows ambient temperatures) employed by different insects is a compromise shaped by biotic and abiotic components of their environment. Unlike some winged insects that are able to produce warmth by endogenous means (i.e., shivering of flight muscles: Heinrich, 1981; Bishop and Armbruster, 1999), most ectothermic insects that thermoregulate must utilize solar radiation, thereby exposing themselves to predators and parasitoids (Casey, 1976; Schultz, 1983; Knapp and Casey, 1986; Casey, 1993). So although thermoregulation is usually assumed to be advantageous as it enhances growth and consequently reduces the duration of the larval stage, many ectothermic insects are

forced to allow their body temperatures to passively follow the surrounding temperature. Because most physiological processes such as food intake, digestion, and assimilation are temperature dependent (Porter, 1982; Knapp and Casey, 1986), the foraging behaviour of these ectothermic insects is often less than nutritionally and physiologically ideal (Frears *et al.*, 1999).

As such, many insects that bask also possess an aposematic colouration advertising toxicity or hairs and/or spines which render them unpalatable to most species of vertebrate predators. Because they don't need to hide from most potential predators, they may be able to spend more time feeding and basking than cryptic caterpillars that must behave in ways that reduce their susceptibility to predation. Such insects often possess behavioural and physiological mechanisms that enable the regulation of body temperatures independently of passive thermoregulation processes, such as radiation, convection and evaporation (Heinrich, 1993b), and which enables them to maintain relatively stable ranges of body temperature, either above or below the prevailing ambient temperature (Heinrich, 1981; Heinrich, 1993b). This has been reported for a number of species in different orders, including Lepidoptera (e.g., Casey, 1976; Rawlins and Lederhouse, 1981; Porter, 1982; Knapp and Casey, 1986; Fields and McNeil, 1988; Joos *et al.*, 1988; Stamp and Bowers, 1990; Kukal, 1993; Bryant *et al.*, 1997; Frears *et al.*, 1997; Schultz, 1998), Orthoptera (Lactin and Johnson, 1996) and Coleoptera (May, 1982).

Microhabitat selection is probably the most common and effective mechanism of behavioural thermoregulation in insects (May, 1979) and consists of the short-term selection of thermally favoured microclimates. For example, Kührt *et al.* (2005) found

that codling moth larvae (Lepidoptera: Tortricidae) preferentially feed on the warmer side of apples (also called cryptic basking). Orientation and postural adjustments can also enable insects to maximize the body surface area exposed to radiation. Caterpillars of the white-lined sphinx (Lepidoptera: Sphingidae), for example, bask on the desert floor during cold periods enhancing heat gain by conduction and re-radiation from the warm substrate (Casey, 1976). The colour of the integument will also have important consequences for the thermal balance as darker colouration enhances the amount of radiation being absorbed, which is why many basking caterpillars are also darkly coloured (Casey, 1976; Porter, 1982; Knapp and Casey, 1986; Fields and McNeil, 1988; Stamp and Bowers, 1990). In some species, colouration may change in response to changing environmental conditions (Nice and Fordyce, 2006), enhancing body temperature during cool periods and reducing the temperature excess during the warmer season (Fields and McNeil, 1988). Additionally, surface structures such as setae provide selective insulation and reduce convective heat loss without affecting radiant heat gain (Kevan *et al.*, 1982; Fields and McNeil, 1988). Shaved arctic woolly bear caterpillars (Lepidoptera: Lymantriidae), for example, are able to maintain a body temperature excess of only 6.9°C, much lower than the 10°C measured for intact animals (Kevan *et al.*, 1982).

However, solitary caterpillars, even dark hairy ones, may only attain low gains of temperature by basking due to their small body mass and high surface-to-volume ratios (Casey, 1976; Rawlins and Lederhouse, 1981; Kevan *et al.*, 1982; Fields and McNeil, 1988; Karban, 1998). In social caterpillars, aggregations have been shown to reduce convective heat losses by reducing the relative body surface exposed and to enhance the

maximum achievable heat gain by increasing their effective body mass (i.e., decreasing their surface-to-volume ratio), (Casey, 1976; Rawlins and Lederhouse, 1981; Kevan *et al.*, 1982; Porter, 1982; Knapp and Casey, 1986; Joos *et al.*, 1988; Stamp and Bowers, 1990; Bryant *et al.*, 2000; Shah *et al.*, 2003) which results in much larger temperature gains than in solitary larvae (Seymour, 1974; Porter, 1982; Knapp and Casey, 1986; Stamp and Bowers, 1990; Casey, 1993; Klok and Chown, 1999).

Furthermore, in social caterpillars that build shelters (i.e., tents), these structures may enhance temperature gains ever further and may enable them to maintain high body temperatures throughout a wide range of ambient temperatures (Knapp and Casey, 1986; Casey *et al.*, 1988; Joos *et al.*, 1988; Bryant *et al.*, 2000; Ruf and Fiedler, 2002a). Tents provide a large boundary layer which reduces convective heat loss by blocking the wind and have also been shown to function as a greenhouse, trapping solar radiation and resulting in an additional heat gain (Knapp and Casey, 1986; Joos *et al.*, 1988). Also, the tent traps metabolic heat production when caterpillars are present, resulting in a slight increase (ca. 0.5-1.5°C) even in the absence of radiant heat (Breuer and Devkota, 1990; Ruf and Fiedler, 2000). In addition to allowing the caterpillars to heat up far above the levels they could achieve without it, the tent provides a range of temperatures which the caterpillars can utilize by microhabitat selection to actively regulate their body temperatures (Joos *et al.*, 1988; Fitzgerald and Underwood, 2000).

In general, the major benefit of behavioural thermoregulation in caterpillars is thought to be a reduction in the duration of the larval stage by enhancing growth rates (Heinrich, 1981; Rawlins and Lederhouse, 1981; Knapp and Casey, 1986; Casey *et al.*, 1988; Lactin and Johnson, 1996; Bryant *et al.*, 2000; Kingsolver, 2000; Levesque *et al.*,

2002). Although most caterpillars are capable of producing only modest increases in their body temperature, even small increments of temperature excess may cause large reductions in developmental time. Lance *et al.* (1987) demonstrated that in gypsy moth caterpillars (Lepidoptera: Lymantriidae), an increase of only 2°C during daytime leads to a reduction in developmental time by more than 1 week (13%). Similarly, monarch butterfly larvae (Lepidoptera: Nymphalidae) increase their body temperature by 3-8°C by basking and this behaviour significantly reduces development time, particularly at low ambient temperatures (Rawlins and Lederhouse, 1981). Consequently, the time period that the larvae are exposed to predators, parasites and pathogens is reduced (Heinrich, 1981). This is particularly important in species such as *M. disstria*; because the moths are non-feeding and short lived, predation is most important in the larval stage (Fitzgerald, 1995). And indeed, Evans (1982) and Porter (1983) show that when conditions are sunny but cool, basking tent caterpillars may have higher levels of activity and develop more rapidly than their non-basking predators and parasitoids. A reduced developmental time may be particularly important in spring caterpillar species as a fast development may further maximize the intake of high quality food, which is rich in nitrogen and water and available for only a short time after budbreak (Evans, 1982; Porter, 1982; Porter, 1983; Stamp and Bowers, 1990; Parry *et al.*, 1998).

Thermoregulation in *M. disstria* caterpillars

Thermoregulation has been studied extensively in *M. americanum* and both the tent and gregariousness appear to play an important role. I therefore hypothesize that *M. disstria* caterpillars are able to achieve temperatures above ambient while aggregated,

although it is unlikely that they thermoregulate independently of ambient temperature as do species that build tents. Although temperature gains are likely to be lower in this nomadic species, Levesque *et al.* (2002) have shown that relative growth rates of *M. disstria* caterpillars increase almost linearly with increasing temperatures up to 30°C. As such, caterpillars spent less time in the vulnerable instars at higher temperatures. Because growth rates were found to plateau at temperatures above 30°C, it is unlikely that they continue to behaviourally thermoregulate by basking at these temperatures. In fact, *M. disstra* caterpillars have been shown to be photopositive until heated sufficiently (at ambient temperatures between 30.5 and 35.5°C), at which time they reverse their orientation preference (Wellington, 1951; Sullivan and Wellington, 1953). In the early larval instars, these caterpillars move between the sunlit and shaded side of the leaves depending on their internal temperatures. Because trees are heterogeneous varying in available temperatures and basking opportunities, it is likely that these caterpillars select microhabitats conducive for basking.

The number of caterpillars within the group is also likely to influence the temperature gain, with group sizes below a certain threshold unable to effectively thermoregulate by basking. Later instars of *M. disstria* caterpillars have been shown to forage more independently and basking is likely to be less important because ambient temperatures at the end of their development are likely to approximate temperatures required for optimal growth and they may achieve sufficient thermal gains due to their larger size. It is therefore possible that group dispersal is partly facilitated by the loss of this thermal advantage.

Predation in larval aggregations

Group living may enhance defence against natural enemies, given that larger larval aggregations reportedly have lower mortality rates from natural enemies than do smaller groups or solitary individuals (Lawrence, 1990; Fitzgerald, 1993b). For example, gregariousness in aposematic insects is thought to increase the strength of the warning signal (Guilford, 1990; Bowers, 1993; Fitzgerald, 1993b; Gamberale and Tullberg, 1996) and the presence of other unpalatable individuals in the immediate vicinity of the attacked individual is thought to reinforce avoidance learning in predators (Sillén-Tullberg and Leimar, 1988; Guilford, 1990).

Although not all unpalatable species are gregarious (Sillén-Tullberg and Leimar, 1988; Nilsson and Forsman, 2003), phylogenetic studies have shown that distastefulness invariably preceded gregariousness for lineages in which both distastefulness and gregariousness have evolved and where the two evolutionary events could be separated (Sillén-Tullberg and Leimar, 1988). Beatty *et al.* (2005) suggested that profitable prey would tend to survive better on a per capita basis when solitary rather than in aggregated form for the simple reason that aggregations of profitable prey represent rich sources of prey that are preferentially exploited. Because there are benefits to gregariousness not related to prey defence (such as thermal enhancement, increased growth and faster development, and protection from desiccation: e.g., Clark and Faeth, 1997; 1998; Klok and Chown, 1999; but see Krause and Ruxton, 2003 for a review), Nilsson and Forsman (2003) suggested that unprofitable prey tend to be aggregated because they can avail themselves of these benefits, while profitable prey cannot. This could explain why some, but not all, aposematic species are aggregated and why so few palatable species are found

in aggregations (Nilsson and Forsman, 2003). The observed association between gregariousness and aposematism might not be a function of prey defence in itself, but a case where selection against aggregation has been relaxed in unprofitable prey. In other words, the advantages of aggregation in these species outweigh the disadvantages.

Aggregation itself may also be a defence, even in some insects that are palatable. For instance, increased group defence may be through the enhancement of chemical (regurgitate) and behavioural (twitching) defences against predators (see Montllor and Bernays, 1993), and has been well documented in both sawfly larvae (Lindstedt *et al.*, 2006) and caterpillars (Evans, 1983; Vulinec, 1990; Fitzgerald, 1993b; Costa, 1997; Poirier and Borden, 2000) which sequester host-derived allelochemicals. For example, eastern tent caterpillars (Lepidoptera: Lasiocampidae) have been shown to incorporate host-derived benzaldehyde into regurgitated enteric fluid, which was found to be repellent to ants (Peterson *et al.*, 1987).

Larger group sizes may also facilitate early detection of predators (Vulinec, 1990; Uetz *et al.*, 2002), with larger groups able to detect predators from further away than small groups (Watt and Chapman, 1998). Another benefit that may accrue from gregariousness is the dilution effect, in which an individual is less likely to be attacked when in a group than when alone once it has been detected by a predator (Hamilton, 1971; Sillén-Tullberg and Leimar, 1988; Vulinec, 1990; Pérez-Contreras *et al.*, 2003). A predator encounter may result in one or very few individuals being taken, either through the escape of non-attacked prey or through predator satiation. This is purely statistical and does not require any complex or cooperative behaviour. However, individuals may only benefit from such passive defences if predators are not attracted to grouped prey

disproportionately and the rate of attack by an individual predator is independent of colony size (e.g., Lawrence, 1990; but see Vulinec, 1990 for a review). Individuals may also gain protection from predators by surrounding themselves with others (Hamilton, 1971). Tostowaryk (1971), for example, found that sawfly larvae that lie on the periphery of the aggregate are approximately twice as likely to be attacked as those toward the centre.

These group defences against natural enemies are often not exclusive, as insects may display an aposematic signal to escape predation from vertebrates, but which may be largely ignored by invertebrate predators. Because invertebrate predators are restricted in terms of the size of insects that they can attack, predation pressures often change with ontogenetic development (Sullivan and Green, 1950; Iwao and Wellington, 1970; Bernays and Montllor, 1989; Montllor *et al.*, 1991). The decreased tendency to aggregate of later larval instars in many species may therefore be related to their increased ability to defend themselves against arthropod enemies (e.g., Cornell *et al.*, 1987; Reader and Hochuli, 2003).

Predation in *M. disstria* caterpillars

Moths of *M. disstria* are short lived as they do not feed, often mating and ovipositing on the same day as they emerge (Fitzgerald, 1995). And although the eggs are known to be parasitized by various species of Hymenoptera and Diptera, they are not considered to be very important natural enemies (Hodson, 1939). As such, predation pressure is strongest during the larval stages.

Bird predation is considered to have little effect on population dynamics of *Malacosoma* caterpillars in North America (Witter and Kulman, 1972). Most species find any but the smallest tent caterpillars unpalatable, and even when they are surrounded by huge numbers of potential prey, these caterpillars are likely to constitute only a fraction of their food intake. Most authors attribute this avoidance by birds to their hairiness, and unprofitability of this prey likely acts as a satiation mechanism in the sense that it limits the number of prey taken (Gamberale and Tullberg, 1996). The impact of birds is also lessened by the habit of tent caterpillars to have mostly completed their larval development before their eggs hatch (see Fitzgerald, 1995).

A lot less is known on the advantages of aggregation against predation by invertebrate predators. The entomophagous insects associated with *Malacosoma* caterpillars occur in the orders Coleoptera, Hemiptera, Diptera and Hymenoptera (Green and Sullivan, 1950). Within the Coleoptera, beetles in the genus *Calosoma* (Carabidae) are well-known predators of caterpillars. These are likely to be important predators of all larval instars, as their powerful jaws enable them to subdue even the largest of caterpillars. The most important hemipteran predators of tent caterpillars are stinkbugs (Hemiptera: Pentatomidae). They are timid predators and the most common species were found to limit their predation of caterpillars 20 mm or less in length, though they are occasionally able to kill larger prey. Social hymenopterans, such as the large wasps in the family Vespidae, are likely to be formidable predators as they have the ability to subdue large numbers of caterpillars. However, most species are seasonal nesters and therefore have only incipient colonies at the time tent caterpillars are present (Witter and Kulman, 1972; Casey *et al.*, 1988; Fitzgerald *et al.*, 1988). All other hymenopterans are parasitoids

and although many species only parasitize the egg or pupal stage, a few families frequently attack the larval stage (Williams *et al.*, 1996). All the known Diptera associated with these caterpillars function as ecto- or endoparasitoids with most species attacking the pupal stage or laying microtype eggs on foliage which are then ingested by the larvae, so they are unlikely to elicit any behavioural response from the caterpillars.

Congregation itself could be an adaptive defence against these invertebrate predators and parasitoids, because predators don't often congregate to the same degree as their prey, which means many prey can escape predation by hiding in a group. There are also possibly individual or group defences that come into play against invertebrate predators, and they may differ among predator types. *Malacosoma* larvae are known for flicking the anterior portion of their body from side to side when attacked, and this behaviour quickly propagates through the group into a synchronised behaviour. This behaviour is presumably a defence against ichneumoid parasitoids, such as *Aleiodes malacosomatus*, which like to oviposit behind the head (Myers and Smith, 1978). Although head-flicking might also be a dissuasive response to the buzzing sound of tachinid parasitoids and may ward off entomophagous predators (Costa, 1997).

However, *M. disstria* caterpillars, like many other species, disperse as they grow suggesting that group-living is particularly important during the early larval stadia (Fitzgerald, 1995). The shift from group to solitary living may be the result of a delicate interplay between the costs and benefits of group living (Despland and Hamzeh, 2004). As caterpillars grow, fourth instars may experience more intraspecific competition because they are much larger and need to consume more food. This may cause caterpillars to abandon their colony mates and engage in solitary foraging. It therefore

becomes apparent that disadvantages of group living may become more important with ontogenetic development, but few studies have looked at how advantages of group living may also change.

1.4 Behavioural mechanisms necessary for group living

Mechanisms of gregariousness in larval aggregations

Of particular interest regarding larval societies is how the members maintain group cohesion and coordinate their activities in order to benefit from advantages of sociality (Conradt and Roper, 2007). This is especially relevant for the synchronous behaviour of all the individuals, which, for example, is crucial for social foraging and recruitment (e.g., caterpillars: Ruf *et al.*, 2001; and cockroaches: Jeanson and Deneubourg, 2007; Lihoreau *et al.*, 2010), nest construction (e.g., caterpillars: Ruf and Fiedler, 2002a). Studies seeking to understand the foraging ecology of gregarious species must therefore address the mechanisms by which animals maintain cohesion.

Tactile contact promotes grouping or foraging in many social caterpillar and sawfly species (e.g., Costa *et al.*, 2003; Flowers and Costa, 2003). This is particularly important in species that exhibit processionary behaviour, a coordinated form of locomotion in which cohorts of insects travel single file in head-to-tail contact (e.g., Weinstein and Maelzer, 1997; Fitzgerald and Pescador-Rubio, 2002; Fitzgerald, 2003; Costa *et al.*, 2004). Acoustic cues appear to be less common but have also been reported to occur in some species (e.g., see references in Costa *et al.*, 2004). But in most social species, contact with group members is maintained via trail pheromones (e.g., Fitzgerald and Underwood, 1998; Costa and Louque, 2001; Ruf *et al.*, 2001; Costa *et al.*, 2003).

Fitzgerald & Peterson (1988) classified social larval communities as patch-restricted, nomadic, or central-place foragers (or a combination of these) depending on whether they feed within their home webs, travel between different resource patches, or use a communal nesting site which they leave periodically to forage. Trail pheromones are central components of the communication systems of these societies and as such their properties, like fade-out time, can be expected to be fine-tuned to the needs of the colonies. For example, trails of shelter-building central place foragers have long-lived components that facilitate the colony's return to profitable feeding sites for days after their initial discovery (e.g., Fitzgerald and Underwood, 1998; Ruf *et al.*, 2001; Ruf and Fiedler, 2002b; Fitzgerald, 2003). They avoid the confusion that might occur if their foraging arenas became cluttered with long-lived trails by incorporating into the trails a labile component (i.e., these components have different evaporative rates) that allows them to ascertain relative trail age. In these species, there is a strong preference for younger trails over older trails (Fitzgerald and Webster, 1993).

The complexity of information encoded in the trails also varies; in caterpillars described as being either nomadic or patch-restricted foragers, chemical cues often only serve as a cohesive device and contain little or no foraging information and fail to elicit recruitment (Fitzgerald and Costa, 1986). This is because caterpillars living near their food have no need to assist one another in finding food sources. In contrast, successful foragers encode foraging information in their pheromone trails and direct unfed group members to the most profitable food finds in many species of central-place foragers (Fitzgerald and Peterson, 1983; Peterson, 1988; Fitzgerald and Costa, 1999).

Synchronised foraging schedules of gregarious species are highly variable (see Ruf and Fiedler, 2002b and references therein). The plasticity of foraging schedules in the face of environmental variability also differs between species: those that exhibit a fixed circadian foraging schedule, like eastern tent caterpillars (Fitzgerald, 1980; Fitzgerald *et al.*, 1988; Fitzgerald and Underwood, 2000), are constrained by the occurrence of synchronising cues and does not necessarily reflect, or meet, individual requirements. For instance, if daybreak rather than hunger level triggers foraging, the timing of foraging will be synchronous among individuals but not necessarily in line with their feeding requirements. Other species, however, can undertake foraging bouts at different times of day and foraging is highly influenced by temperature (Ruf and Fiedler, 2002b; Peters and Despland, 2006). This plasticity can improve the group members' ability to meet their requirements in different environments.

Little is known on how members of such groups reach a consensus on the timing of foraging bouts. Long (1955) demonstrated that in larval groups of the large white butterfly(Lepidoptera: Pieridae) and of the silver-Y moth (Lepidoptera: Noctuidae), movement of an individual together with a sense of its direction was conveyed to adjacent larvae. In this manner, the consensus on group activity emerges from interactions between individuals, and between individuals and their environment. Self-organization has often been shown to generate synchronised group activity without external triggering cues (see Peters and Despland, 2006). Rands *et al.* (2003) suggested the spontaneous emergence of temporary "leaders" and "followers" owing to the build-up of differences in energetic state. The individual with the lowest reserves emerges as the "pace-maker" and determines when the pair should forage. Most species that forage in

groups do so en masse and this reluctance to forage individually has been suggested to serve in maintaining colony cohesion during exploration of new territory (Colasurdo and Despland, 2005). If the individuals with the lowest reserves determine when the group should forage, one might expect that as the number of hungry individual increases, so does the level of restlessness within the group, and that above a certain threshold, the group goes on a foraging bout. This appears to be the case in cows and gorillas, whereby a phase of preparation characterized by an increase in activity and vocalizations respectively, precedes departures (Stewart and Harcourt, 1994; Ramseyer *et al.*, 2009). In which case, one might wonder which individuals take the lead. In fish, food-deprived individuals were significantly more likely to be in the front of the group where they benefited from a higher feeding rate (Krause *et al.*, 1992; Krause, 1993), but at an increased predation risk (Krause *et al.*, 1998).

For larval groups, not only is trail laying during exploratory foraging costly, but the leader is more likely to be at risk of succumbing to small predators that lie in wait, such as spiders, since the leader would likely be the first to move within striking distance of the predators and it is unprotected from frontal attack. In the pine processionary caterpillar (Lepidoptera: Thaumetopoeidae), Fitzgerald (2003) found that leaders of over-the-ground processions expend more energy in locomotion than other caterpillars in the processions, and thus followers enjoy an economy of movement at the expense of the leader. Interestingly, laboratory studies showed that females of the pine processionary caterpillar lead processions more often than males, indicating that the colonies may have a gender-based division of labour (polyethism) with females predisposed to expend more energy and to expose themselves to more risk than males. In colonies of the madrone

caterpillar (Lepidoptera: Pieridae), Underwood & Shapiro (1999) also reported a gender-based division of labour in which the male caterpillars were more likely to spin silk than the females and laid down most of the foraging trails. However this doesn't appear to be the norm and Flowers & Costa (2003), for example, found that movement by the red-headed pine sawfly (Hymenoptera: Diprionidae) was not consistently led by any particular subset of larvae. Although polyethism was reported in *Malacosoma* caterpillars by Wellington (1957), who argued that colonies consisted of a mixture of siblings with different activity levels, subsequent studies (Edgerly and Fitzgerald, 1982) have failed to substantiate these earlier studies and cast doubt on the occurrence of polyethism in *Malacosoma* species.

Mechanisms of group foraging in *M. disstria* caterpillars

Malacosoma disstria has been shown to use a complex system of relatively non-volatile pheromone trails for communication (Fitzgerald and Webster, 1993). Although the congener species *M. americanum* reinforce successful trails and recruit colony mates to feeding sites, satiated *M. disstria* caterpillars don't appear to recruit other individuals as the latter do not select trails of satiated over starved individuals (Fitzgerald and Costa, 1986; McClure *et al.*, submitted). Instead, the chemical trails are believed to be used in communication with colony mates and are thought to be important in maintaining colony cohesion during synchronous foraging bouts (Fitzgerald and Costa, 1986). Indeed, previous studies have shown that larvae always start foraging en masse, and individual caterpillars do not explore a new substrate individually. Exploration is done by caterpillars in the vanguard advancing only a short distance, then turning back and being

replaced by another that extends the explored trail slightly farther, and so on. As colony mates move onto the newly marked trail, they reinforce it, encouraging the group to advance. This effectively pushes forward the end of the trail, allowing the group to slowly progress (Fitzgerald and Costa, 1986). Colasurdo & Despland (2005) have shown that both young and older larvae discriminate between fresh and older trails. In addition to trail following, young caterpillars tend to maintain close contact with a conspecific in the absence of trails, whereas the older caterpillars are more independent and are more likely to explore new territory by themselves. This leader following behaviour likely provides a way for young caterpillars to explore new areas without losing contact with colony mates and might play an important role in maintaining group cohesion during nomadic foraging.

Although studies have shown that being in the front of the group is more costly and that individuals are more at risk of predation (Fitzgerald, 2003), in *M. disstria* little is known about which individuals are in the front of the group. Hungry individuals, however, may be expected to modify their positions relative to neighbours as a function of their internal state and may tend to occupy positions toward the front of the group, being more willing to risk dangerous positions if that will benefit their resource intake. In which case turning back towards the group might be a trade-off between being the first to encounter a food source and the risk of encountering predators. Also, the lack of a permanent resting site matched with no active recruitment to food sources suggests that synchronization of foraging decisions in the forest tent caterpillar is imperative. In this situation, the probability that a caterpillar foraging alone would lose the group becomes significant. But little is known about the mechanisms used by the group to determine

when to forage. We also predict that an increase in the number of hungry individuals will increase the number of physical contacts between individuals due to restlessness and may be an important cue to determine when the group should forage.

1.5 Objectives of this thesis:

The aim of this thesis is to investigate the benefits of cooperation and coordination of movement in a social living organism. Doing so using different social systems should improve our understanding of the emergence of collective patterns and cooperation, in addition to assessing the importance of various extrinsic ecological factors for the evolution of social systems. The present work has two main objectives:

Determine the advantages resulting from sociality in *M. disstria*, specifically in relation to their ability to thermoregulate and to defend themselves against invertebrate predators.

The specific objectives in relation to thermoregulation are:

1. Determine if larvae of *M. disstria* are capable of efficient thermoregulation by basking and if this is enhanced by grouping.
2. Determine if behavioural thermoregulation changes during ontogenic development.
3. Determine the role of thermoregulation in driving the colony's temporal foraging patterns and spatial habitat use.

This is discussed in both Chapter 2 and Chapter 3.

The specific objectives relating to predation are:

1. Determine if the gregarious habit of these caterpillars is advantageous against different invertebrate natural enemies, and whether it is through dilution, increased vigilance or group defences.
2. Determine if the advantages of aggregation against invertebrate predation and parasitism changes as a function of group and larval size, possibly due to increased handling time or decreased success rate.

Both these questions are addressed in Chapter 4.

Determine the mechanisms of group synchronization in *M. disstria*, specifically:

1. Determine which individuals decides which activities to perform and when.
2. Determine which individuals act as leaders when foraging, and if this is the result of consistent individual differences or the result of temporary differences in energetic states.
3. Determine if energy state affects efficiency of foraging.

Results regarding these questions are addressed in Chapter 5.

Chapter 2- Collective foraging patterns of field colonies of *Malacosoma disstria* caterpillars

The following chapter is based on the published manuscript: McClure, M. and Despland, E. (2010) Collective foraging patterns of field colonies of *Malacosoma disstria* caterpillars. Canadian Entomologist 142: 473-480

2.1 Abstract

We monitored 12 colonies of the nomadic social caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), on trembling aspen, *Populus tremuloides* Michx. (Salicaceae), under field conditions in spring 2007. We examined cohesion and synchronization of colonies and spatio-temporal activity patterns to compare foraging in the field with the results of laboratory studies and with foraging of central-place foragers. All colonies were highly cohesive; fragmentation was only observed 3 times. Activity was highly synchronous within colonies, with clear alternation between periods of activity and quiescence. Colonies averaged 4.25 ± 0.12 (S.E.) activity bouts per day and foraging was more likely to occur in the early morning than at mid-day. Colony activity was weakly correlated with temperature. In contrast to *M. americanum* (F.), foraging schedule was flexible: foraging was observed at all recorded times and temperatures. Colonies searched for a new feeding site on average every 2.54 ± 0.37 days, after a food source was depleted. Time spent at a food source decreased with colony size and distance travelled between food sources increased with instar. On aspen, *M. disstria* caterpillars do

not exhibit much food choice; rather they minimize movement, decreasing potential contacts with predators.

2.2 Introduction

The forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), is the only known nomadic forager in the genus; caterpillars move together in synchronised columns between feeding sites (Fitzgerald and Costa, 1986). Many other species of *Malacosma* Hübner are central-place foragers and build silk tents for shelter. *M. disstria* constructs temporary silk mats (bivouacs) that are regularly abandoned as the colony searches for new feeding sites using pheromone-laden silk trails to direct group locomotion (Fitzgerald and Costa, 1986). Similar to other tent caterpillar species, early instar larvae of *M. disstria* are highly gregarious (Fitzgerald, 1995) and grouping is essential to survival (Despland and Le Huu, 2007). Because they do not build tents to serve as rallying points and shelter between foraging bouts, *M. disstria* are expected to show a different spatio-temporal foraging structure from central-place foraging social caterpillars.

Although both *M. disstria* and the central-place foraging species *M. americanum* (F.) exhibit synchronized collective foraging, the plasticity of foraging schedules in the face of environmental variability differs between these two species, according to differences in their social organization. *M. americanum* maintains a fixed schedule under varying temperatures, foraging at dawn, mid-afternoon, and dusk (Fitzgerald, 1980; Fitzgerald *et al.*, 1988; Fitzgerald and Underwood, 2000). Under constant lab conditions, *M. disstria* colonies exhibit continuous alternation between foraging and basking bouts

irrespective of photoperiod, and the rhythm of alternation accelerates at higher temperatures (Peters and Despland, 2006). This is likely because locomotion and digestion rates increase at higher temperatures and both tasks can be accomplished faster (Stamp and Bowers, 1990).

Nomadic foraging also implies different use of space from that seen in central place foragers. *Malacosoma americanum* and other social caterpillars have a fixed tent and foragers return to this central point after each meal (Fitzgerald and Peterson, 1988). The only previous study examining the spatial pattern of nomadic foraging in the field showed that *M. disstria* colonies on sugar maple, *Acer saccharum* Marsh. (Aceraceae), remained cohesive and used several different feeding sites during a larval instar (Fitzgerald and Costa, 1986). Foraging sites were often abandoned before available foliage was entirely consumed, possibly because of induced chemical defences in the tree (Fitzgerald and Costa, 1986).

Our objectives were to provide a basic understanding of the foraging activity of field colonies of *M. disstria* and investigate the effects of daily temperature variations on colony cohesion and synchronization and on spatio-temporal activity patterns. We examined foraging patterns of *M. disstria* on trembling aspen, *Populus tremuloides* Michx. (Salicacae), a more favourable host plant than is sugar maple (Lorenzetti, 1993; Abou-Zaid *et al.*, 2001; Barbehenn *et al.*, 2005). We expected colonies to remain cohesive as they moved between feeding sites and bivouacs and be synchronous in their foraging activities. Based on lab experiments (Peters and Despland, 2006), we expected to observe foraging at all times of day when temperature permitted rather than on a fixed schedule as in *M. americanum*. We also expected colonies on trembling aspen to move

less often between feeding sites than has been observed on sugar maple, as the latter contains half the soluble sugar (Panzuto *et al.*, 2001) and mobilizes feeding deterrents in response to herbivory (Lorenzetti, 1993; Abou-Zaid *et al.*, 2001; Barbehenn *et al.*, 2005).

2.3 Methodology

Insects and study site

Unhatched egg masses were obtained from a declining population on aspen trees in northern Alberta, Canada (56°17.5'N, 113°93.9'W). Twelve egg masses were removed from dormancy on 16 May 2007 during local bud flush (when eggs of *M. disstria* normally hatch) in the Lac Brome region near Knowlton, Quebec, Canada (45°13.3'N, 72°30.3'W). Although natural populations occur in the region, none were observed at the time of the experiment. Egg masses were attached on 12 small trembling aspen trees (average height 1.20 ± 0.27 m) with Tanglefoot® at the base. Trees were at the western edge of the forest and were selected for ease of observation (i.e., smaller trees were selected). The site received direct sun through the afternoon from ~1330 hrs but was fully shaded until noon.

Observations

Data were collected at 1h intervals from 700-2100 hrs Eastern Daylight Time. Occasional observations (N=28) were also made after sunset to check for nocturnal foraging. *Malacosoma disstria* caterpillars are not active in the absence of a radiant heat source and do not develop at ≤10 °C (Hodson, 1941) and nocturnal foraging was not expected to be an important activity. Ambient temperature was measured 1 m above

ground and 30 cm from caterpillars using a hand-held digital thermometer (Fisher Scientific; MA, USA).

We conducted observations during two initial rain events and found that colonies remained inactive on their bivouacs; therefore observations were not made during subsequent rain events (9 in total). The young colonies were monitored daily for 19 days during which development progressed from first to early fourth larval instars. Instar stage was recorded by counting moults and monitoring size and other visible characteristics. Observations were terminated after 19 days following colony predation by wasps, *Polistes* Latreille (Hymenoptera: Vespidae).

Colony cohesion and synchronisation

For each observation, we monitored cohesion by recording whether the colony fragmented. We also measured caterpillar behaviour, characterized as active (feeding or locomotion) or resting. Synchronization of group activity was assessed by calculating the proportion of individuals in each colony engaged in the same activity.

Temporal pattern of foraging

A colony was considered to be engaged in a foraging bout if the majority of caterpillars were active. Logistic regression was used to determine factors influencing when a colony forages.

Logistic regression allows simultaneous testing of effects of different types of predictors (including scalar and categorical variables) on a binary dependent variable (Hosmer and Lemeshow, 1989). The predictors included in the model were: temperature,

hour (time of day coded as a categorical variable), colony (categorical variable), instar, and day (N = 609 observations). The Wald chi-square was used to determine if a predictor was significant; the βeta coefficient shows whether the effect was positive or negative.

Spatial pattern of foraging

The mean distance between feeding sites (defined as a cluster of leaves on the same twig) was determined by measuring petiole-to-petiole distance between exhausted and new sites. The effect of colony size on time spent at a feeding site was analysed using linear regression. Multiple linear regression was used to determine whether colony size and instar influenced distance traveled between feeding sites.

2.4 Results and Discussion

Performance

On average, egg masses took 5.75 ± 0.97 days to hatch (SEM); the first 4 days were rainy and cold with temperatures of 2-13 °C (average 8.1 °C). Colony size ranged from 24-137 caterpillars (average 69 ± 9.32 caterpillars). The first, second, and third instars lasted 4.75 ± 0.46, 5.75 ± 0.63 and 5.9 ± 1.1 (n=12) days respectively.

First instar colonies suffered the greatest rates of mortality, with 17.57% of larvae disappearing between observations (Table 2.1). This frequently occurred after rain showers or cold nights; likely those caterpillars fell off the trees. Less than 3% of individuals died because of pathogens or predation until the end of our observations when *Polistes* wasps destroyed all the colonies (Table 2.1).

When attacked by wasps, caterpillars thrashed vigorously and sometimes fell off the trees. Only caterpillars that fell off survived attack. Unattacked caterpillars in close proximity to attacked individuals also thrashed. After an attack, the entire colony relocated to a new site. However, the wasps eventually destroyed all the colonies. Wasp destruction of experimental colonies has been previously documented (Shiga, 1979; Casey *et al.*, 1988; Fitzgerald *et al.*, 1988).

Table 2.1: Number of *Malacosoma disstria* caterpillars that died in the field during each instar due to various causes of mortality (total number of caterpillars at the start of the experiment was 825). "Missing" caterpillars disappeared between observations.

	Instars			
Mortality	**1**	**2**	**3**	**4**
unknown (missing)	145	2	5	0
nuclear polyhedrosis virus (NPV)	0	5	10	0
ant	0	0	1	0
spider	0	5	2	0
wasp	0	0	0	653

Colony cohesion and synchronisation

Caterpillar colonies basked in tight groups on warm sunny days. When temperatures exceeded 30 °C, caterpillars moved to the underside of leaves or hung from their prolegs.

In spite of being nomadic, field colonies were highly cohesive. Colony fragmentation was only observed 3 times in 122 colony-days of observation. Fragmentation occurred during moulting when freshly moulted individuals departed before their unmoulted colony mates; colony fragments always rejoined after 1-2 days apart.

Colonies always fed together on the same leaf cluster (N = 513 feeding bouts). For the first two instars, the caterpillars spent all inter-meal intervals resting together on the blade or the petiole of the leaf upon which they were feeding. During the third and fourth instars they also sometimes rested on the twig.

Moulting was generally synchronized, occurring mostly within the same day, and occurred at the current bivouac site (N = 34 moulting events). Moulted caterpillars always moved from moulting sites to new leaf clusters to feed and set up new bivouacs. These post-moult bivouac changes gave rise to the only occasions when feeding sites were abandoned before depletion (see below).

Activity was highly synchronous, with clear alternation between periods of activity or quiescence of all or most colony members within a group (Figure 2.1). Foraging bouts were initiated with an average of 92% of individuals becoming active between observations (N = 513 foraging bouts). Similar synchronization has been observed in previous lab studies (Fitzgerald and Costa, 1986; Peters and Despland, 2006). Based on this synchrony, colonies were scored as either active or inactive.

Temporal pattern of foraging

Average temperature measured at the study site during observation hours was 22.0 ± 0.8 °C. In the region, daily temperatures ranged from 2-32.5 °C and averaged 16.9 ± 0.8 °C (Environment Canada, Lac Brome 2007). Optimal temperature for development of *M. disstria* is approximately 25 °C (Levesque *et al.*, 2002).

There were 4.25 ± 0.12 (S.E.) foraging bouts per day, starting early in the morning (Figure 2.1). Our first observations were made approximately one hour after

sunrise; most colonies were already active then, irrespective of ambient temperatures which ranged from 10-19.7 °C. Some foraging was observed after dusk, when temperatures were favourable (approximately 18 °C after sunset).

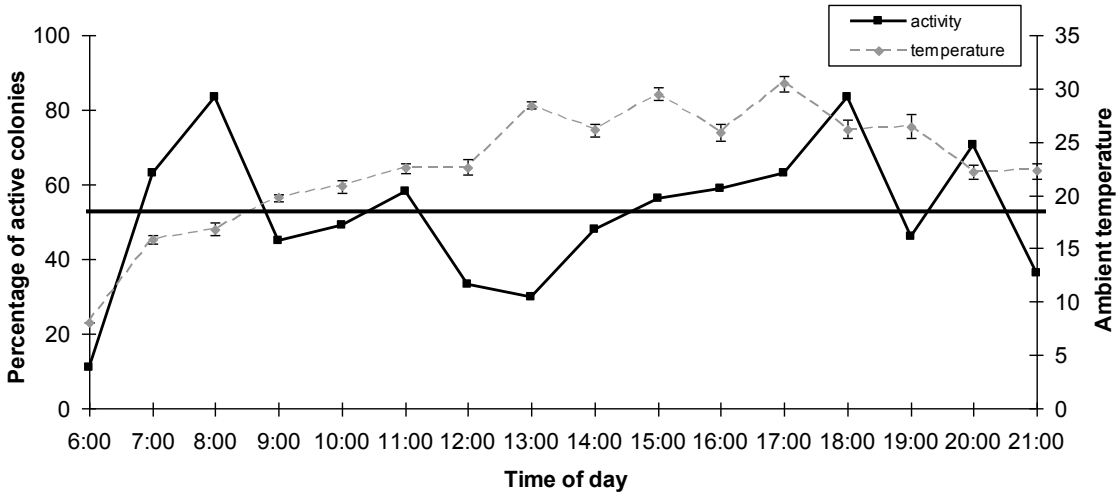


Figure 2.1: Mean (and SE) percentages of colonies of *Malacosoma disstria* active (when more than half the group was involved in either feeding or moving) relative to time of day in spring 2007 in the Lac Brome region, Quebec. Bold line indicates average proportion of active colonies for all observations. Sunrise occurred at approximately 600 hours and sunset at 2000 hours.

When logistic regression was used, similar results were obtained for both forward and backward stepwise models, with hour (Wald $\chi^2_{15} = 49.5$; $p < 0.001$) and temperature (Wald $\chi^2_1 = 5.22$; $p = 0.02$) as the only significant variables. Colonies were significantly more likely to be active at 0700 (β regression coefficient = 0.75, Wald $\chi^2_1 = 5.42$; $p = 0.02$), 0800 (β = 1.88, Wald $\chi^2_1 = 19.66$; $p < 0.001$), and 1800 hrs (β = 1.21, Wald $\chi^2_1 = 6.19$; $p = 0.01$) and significantly less likely to be active at 1200 (β = -0.70, Wald $\chi^2_1 = 5.25$; $p = 0.02$) and 1300 (β = -1.19, Wald $\chi^2_1 = 6.00$; $p = 0.01$) hrs (Figure 2.1). Colonies were also more likely to be active at higher temperatures (β regression coefficient = 0.05). However, the model including these two variables classified only 62 % of colony

observations correctly as either active or inactive (compared to the 50% obtained with a null model). Indeed, foraging was observed at all times of day and under all temperatures recorded (Figures 2.1, 2.2). The other variables were not retained in the model because they did not significantly improve prediction of activity (day: Wald $\chi^2_1 = 0.062$; $p = 0.80$; colony: Wald $\chi^2_{11} = 17.5$; $p = 0.09$; instar: Wald $\chi^2_1 = 0.20$; $p = 0.66$).

Thus, high temperature increases colony activity of *M. disstria* as expected from lab studies (Peters and Despland, 2006). The effect of time of day, however, was contrary to that of ambient temperature: colonies were more likely to be active in early morning and less likely to be active at mid-day (Figure 2.1). This is unlike the continuous alternation between foraging and resting bouts irrespective of time of day observed in *M. disstria* colonies reared under constant lab conditions (Peters and Despland, 2006). The early morning activity peak could be due to increasing hunger caused by interruption of feeding during the pre-dawn hours when temperatures are at their lowest. The dip in mid-day foraging activity is particularly intriguing as it occurs when solar radiation is strongest, but temperature is not necessarily at its daily high (Figure 2.1). Possibly it is linked to patterns of polarized light when the sun is at its zenith making synchronized movement more difficult. *M. disstria* caterpillars are sensitive to variations in the plane of polarization and have been shown to use polarization patterns of the sky in their orientation (Wellington, 1951).

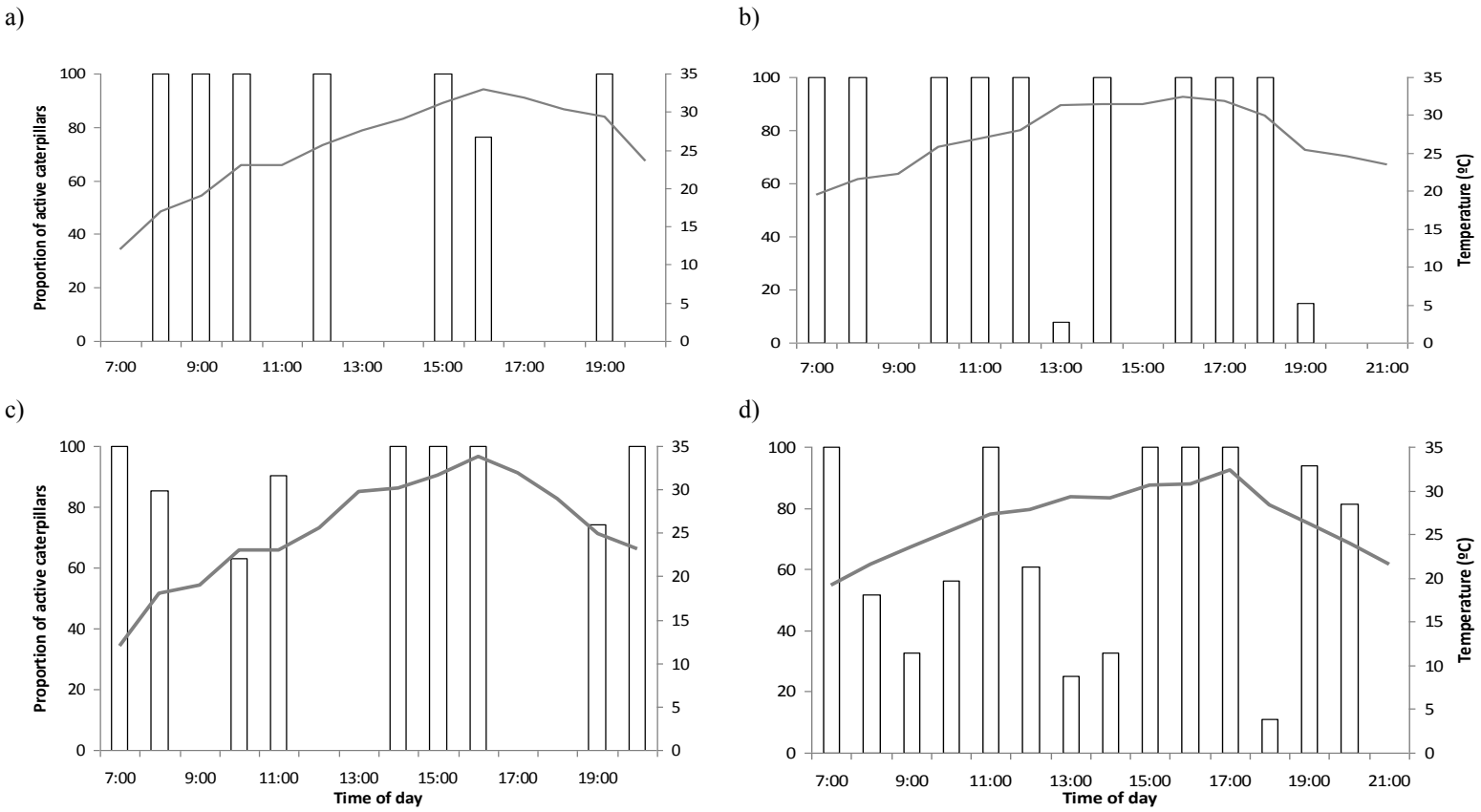


Figure 2.2: Examples of activity of colonies of *Malacosoma disstria* in spring 2007 in the Lac Brome region, Quebec, measured as the proportion of active caterpillars within colonies (bars), and air temperature recorded at the study site (lines) for two different colonies during the first (a and c) and third (b and d) instars. Sunrise occurred at approximately 600 hours and sunset at 2000 hours.

Nonetheless, *M. disstria* demonstrated a flexible foraging schedule (i.e., caterpillars foraged at different temperatures and times of day) with a variable number of foraging events occurring at different times of day, unlike shelter-building, central-place foragers, such as *M. americanum* and *Eucheira socialis* Westwood (Lepidoptera: Pieridae), which exhibit fixed foraging schedules (Fitzgerald, 1980; Fitzgerald *et al.*, 1988; Fitzgerald and Underwood, 2000). In fact, *M. americanum* forages only at dawn, mid-afternoon, and dusk, regardless of temperature (Fitzgerald, 1980; Fitzgerald *et al.*, 1988; Fitzgerald and Underwood, 2000). The temporal pattern of foraging we observed in *M. disstria*, with feeding occurring throughout the daylight hours, is similar to that documented in *Eriogaster lanestris* (L.) (Lepidoptera: Lasiocampidae) (Ruf and Fiedler, 2002b), a shelter building central-place forager. Like *M. disstria*, *E. lanestris* has a flexible foraging schedule that varies with ambient temperature. In both *E. lanestris* and *M. disstria*, the duration of foraging and resting bouts decreases with temperature, resulting in colonies foraging more frequently at higher temperatures (Ruf and Fiedler, 2002b).

Spatial pattern of foraging

As they matured, field colonies travelled increasingly long distances when moving to new food patches, averaging 270 ± 63mm during the first and second instars *vs*. 695 ± 175mm during the third and fourth instars. Multiple linear regression showed that colony size did not significantly affect distance travelled between food patches ($t = -0.692$; $p = 0.494$), but that instar did ($t = 8.667$; $p < 0.001$). A model containing only developmental stadium showed R^2=0.70.

Colonies generally ate all leaves at a feeding site before abandoning it: of 84 feeding sites observed, only 7 were abandoned by the colony before foliage was completely consumed. In those 7 cases, abandonment occurred immediately after a moulting event, when the colony was relocating to a fresh bivouac. Colonies averaged 2.54 ± 0.37 days at a feeding site before moving on, with smaller colonies taking longer to deplete a patch (linear regression between colony size and time spent at the feeding site: $R^2 = 0.18$; $p = 0.014$).

Fitzgerald and Costa (1986) observed *M. disstria* colonies on sugar maple trees and recorded a similar duration spent at each feeding site, but they also observed frequent abandonment of non-depleted feeding sites. This host-related difference is likely due to host plant quality.

Sugar maple is a less favourable host for *M. disstria* than is trembling aspen: caterpillars do not develop as well on it (Lorenzetti, 1993) and it is less preferred in choice tests (Etilé, 2008). Sugar maple mobilizes feeding deterrents in response to herbivory (Lorenzetti, 1993; Abou-Zaid *et al.*, 2001; Barbehenn *et al.*, 2005) and contains half the soluble sugar found in trembling aspen (Panzuto *et al.*, 2001). Etilé (2008) observed that *M. disstria* caterpillars in a laboratory assay took fewer but longer meals on trembling aspen leaves, whereas feeding activity on sugar maple was interrupted by frequent switching. Despite this difference in the pattern of feeding, there was no difference in the time spent feeding or the amount of food ingested in Etilé's (2008) experiment. Therefore, in lab experiments, individual caterpillars sampled multiple sources when presented with sugar maple, but fed consistently on the first leaf they encountered when presented with trembling aspen. In the field, this difference appears to

result in colonies abandoning a sugar maple feeding site before it is depleted (Fitzgerald and Costa, 1986), but consuming aspen leaves entirely before moving to a new site.

These results suggest that, when feeding on aspen, *M. disstria* colonies exhibit very little food choice or sampling: colonies completely consume whatever leaves they first encounter. Others have shown that *M. disstria* are not very selective of food sources (Despland and Noseworthy, 2006; Noseworthy and Despland, 2006): in lab assays with aspen leaves of varying quality, the first and second feeding bouts of fourth instar *M. disstria* caterpillars were generally on the same leaf and they seldom switched leaves (Noseworthy and Despland, 2006).

These differences in foraging behaviour on different host trees can lead to significant differences in colony activity with possible implications for predation rate. On sugar maple, the more frequent movements of colonies between feeding sites likely places them at a stronger risk of predation than are colonies on aspen (Montllor and Bernays, 1993; Fitzgerald, 2003). Prior to the destruction of our colonies by wasps, we observed 8 predation events, all by invertebrates and when the colony was in transit to a new feeding site (Table 2.1). Predated caterpillars were always ones leading individuals in the colony, no defensive behaviours were observed, and no predated caterpillar survived. Bivouacking close to the feeding site and minimizing movement between sites could therefore be advantageous to young *M. disstria* colonies.

2.5 Conclusion

Our study in a natural field setting confirmed laboratory work showing high cohesion and synchronicity of *M. disstria* caterpillar behaviour. It also demonstrated a

flexible pattern of activity very different to that previously observed in central-place foraging species such as *M. americanum*. In addition, this study further suggests that *M. disstria* caterpillars avoid invertebrate predators by minimizing movement when feeding on a preferred high-quality host plant.

Chapter 3- Thermal ecology and behaviour of the nomadic social forager, *Malacosoma disstria*

The following chapter is based on the published manuscript: McClure, M., Cannell, E. and Despland, E. (2011) Thermal ecology and behaviour of the nomadic social forager, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). Physiological Entomology 36: 120-127

3.1 Abstract

This study examines, both in the laboratory and in the field, whether the nomadic social caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), can thermoregulate despite the lack of a tent, and evaluates the role of thermoregulation in directing the colony's behaviour. The presence of a radiant heat and light source (a lamp in laboratory experiments, the sun in the field observations) enables caterpillar colonies to increase body temperature by basking (remaining still under a heat source) and this is only effective when caterpillars cluster in groups. Body temperatures achieved while basking in a group coincide with temperatures at which development rate is maximal for this species. Indeed, in the laboratory experiments, the presence of a lamp results in higher growth rates, confirming that thermoregulation is an advantage to group living. When a radiant heat/light source is provided at a distance from the food in the laboratory, caterpillars behave in order to maximize thermal gains: colonies move away from the food to bivouac (group together and remain still on a silk mat) under the lamp, spend more time on the bivouac and cluster in a more cohesive group. Thermal needs thus

influence habitat selection and colony aggregation. *Malacosoma disstria* relies on developing rapidly, despite low seasonal temperatures, in order to benefit from springtime high food quality and low predation rates; however, unlike others in its genus, it does not build a tent but instead exhibits collective nomadic foraging (i.e., the whole colony moves together between temporary resting and feeding sites). In this species, collective thermoregulatory behaviour is not only possible and advantageous; it also drives much of the colony's behaviour, in large part dictating temporal and spatial patterns of movement. These findings suggest that thermoregulation may be an important selection pressure keeping colonies together.

3.2 Introduction

Like other ectotherms, caterpillars are normally unable to elevate their body temperature, which therefore tracks ambient temperature. However, most physiological processes are temperature-dependent and caterpillars may experience ambient temperatures inadequate for growth and/or development (Knapp and Casey, 1986; Casey *et al.*, 1988). Species that experience suboptimal temperatures should therefore exploit the heterogeneity in their environment by selecting favourable microhabitats and by changing their orientation to the sun for basking (remaining still under a radiant heat source). These behaviours have been shown to regulate body temperature within an optimum range in several caterpillar species (e.g., Knapp and Casey, 1986; Joos *et al.*, 1988; Frears *et al.*, 1997; Bryant *et al.*, 2000; Fitzgerald and Underwood, 2000; Ruf and Fiedler, 2000; Kuhrt *et al.*, 2005).

Many species that thermoregulate by basking have a black colouration that enhances radiant heating and are thickly covered with setae that reduce convective heat

loss (Joos *et al.*, 1988; Bryant *et al.*, 2000; Ruf and Fiedler, 2000). But, due to their small size, solitary caterpillars can only achieve small temperature gains (e.g., Rawlins and Lederhouse, 1981; Bryant *et al.*, 2000), and so many caterpillar species increase their body temperature by living communally (e.g., Stamp and Bowers, 1990; Klok and Chown, 1999; Bryant *et al.*, 2000), and some even build silk tents that trap solar heat (e.g., Casey *et al.*, 1988; Joos *et al.*, 1988; Ruf and Fiedler, 2000; 2002a).

The relationship between thermoregulation and the timing of foraging events has been investigated in *Malacosoma americanum* (Fitzgerald *et al.*, 1988) and *Eriogaster lanestris* (Ruf and Fiedler, 2002b), both tent-building central-place foragers. These two species show different strategies for conciliating tent-based thermoregulation and foraging needs, since *E. lanestris* has a flexible foraging schedule that varies with temperature whereas *M. americanum* has a fixed foraging schedule.

Like both *M. americanum* and *E. lanestris*, *M. disstria* Hübner hatches in early spring when temperatures are below optimal, in order to maximize the intake of the high quality foliage that is only available for a short time after budbreak (Parry *et al.*, 1998; Jones and Despland, 2006). However, *M. disstria* is a nomadic forager, travelling between temporary resting sites and feeding sites, and does not build a tent (Fitzgerald, 1995). Like the shelter-building *E. lanestris* (Ruf and Fiedler, 2002b), *M. disstria* is opportunistic in response to the thermal environment with a flexible foraging schedule that varies with ambient temperature (Peters and Despland, 2006; McClure and Despland, 2010). As such, the duration of foraging and resting periods decreases with temperature and colonies forage more frequently at higher temperatures (Ruf and Fiedler, 2002b; Peters and Despland, 2006). However, nomadic foraging implies a different use of space

and little is known of how thermal requirements influence habitat selection, colony cohesion or spatial foraging patterns.

The present study includes field and laboratory experiments to confirm that, similar to other early spring species, *M. disstria* is able to behaviourally thermoregulate, that grouping improves their ability to do so and that group thermoregulation confers an advantage. Finally, and most importantly, whether thermoregulatory considerations dictate habitat selection and spatial patterns of nomadic collective foraging is investigated.

3.3 Methodology

Egg masses were collected from trembling aspen trees, *Populus tremuloides* Michx. in Northern Alberta Canada (56^{o}17.5N, 113^{o}93.9W) and stored at 4ºC with 80% RH until use. To minimize mortality from pathogens, egg masses were sterilized by soaking in sodium hypochlorite (Grisdale, 1985).

Thermoregulation in the field

Twelve egg bands were removed from dormancy on May 16 2007 shortly after local bud flush in the Lac Brome region (Knowlton; Quebec, Canada; N 45°13.323' W 72°30.317') and attached on 12 selected *P. tremuloides* (average height of 120.62±27.24 cm) in the field with pre-coated sticky tree bands (Tanglefoot, Canada) at the base. The site received direct solar radiation during the afternoon hours from ~13.30 h Eastern Daylight Time but was fully shaded by a nearby building until noon. Data were collected at 1-h intervals (when weather permitted) from ~07.00-21.00 h. On each occasion,

location in the habitat (classified as either "in the sun" or "in the shade"), the developmental stage of the larvae, the size of the colony with which it was associated and the behaviour of caterpillars, characterized as active (feeding or moving) or bivouacking (remaining quiescent on a silk mat) were recorded. The young colonies were monitored daily for 19 days during the first-, the second-, the third- and the beginning of the fourth-larval instars, when colonies were decimated by paper wasps (*Polistes* spp.).

Field body temperatures of caterpillars were recorded on second-instar caterpillars (from May 29 to June 2 2007) and fourth-instar caterpillars (from June 9 to June 12 2007). Body temperature of individual caterpillars at the centre of the colony, on the outskirt of the colony and of solitary caterpillars isolated from the colony was measured to the nearest 0.1 °C by cautiously pressing a miniature coated thermocouple (NiCr-NiAl) attached to a hand-held digital thermometer (Fisher Scientific) onto the back of the caterpillar for approximately 3 s. Knapp & Casey (1986) reported no significant difference between this non-invasive method and piercing the cuticle of larvae to directly measure internal body temperature. Ambient temperature was measured in the open, 1 m above the ground and 30 cm away from the caterpillars. Wind speed was also measured, using a 4-in-one professional measuring instrument (Mannix DLAF8000, Fisher Scientific Traceable®; accuracy of the anemometer is of ±0.6 m s^{-1}), 1 m away from the caterpillar group. An electronic digital calliper (0.03 mm accuracy) was used to measure larval lengths and diameters of larval clusters. Cohesion of larval clusters was calculated by estimating the surface area occupied by the caterpillar colony and dividing by the number of individuals present.

To determine whether caterpillars exhibited any form of behavioural

thermoregulation, a linear regression analysis of body temperature on ambient temperature was undertaken for caterpillars both in the sun and in the shade, and for second- and fourth-instars. A slope of 0 indicates complete independence (or regulation) of body temperature, a slope of 1 indicates dependence of body temperature on ambient temperature, and a slope of 1 with an intercept of 0 represents complete thermal conformance (May, 1982). Regressions for isolated and grouped caterpillars were compared to test if grouping improves thermoregulation.

Multiple linear regressions by the complete simultaneous method (called ENTER in SPSS) were used to determine which independent variables (ambient temperature, position in the sun or the shade presented as a dichotomous variable, activity or quiescence presented as a dichotomous variable, number of individuals, group cohesion and wind speed) significantly influenced larval body temperature for each instar.

Thermoregulation in the laboratory

Colonies each arising from a single egg mass were kept in translucent plastic rearing containers. During the first-instar, all caterpillars were reared on a nutritionally balanced, standard wheat germ-based meridic artificial diet (Addy, 1969) under a controlled light and temperature regime of 21 °C, 70% RH and LD 16:8 h. Once caterpillars moulted to the second-instar, colonies were fed trembling aspen foliage collected from multiple trees in Montreal, Canada. Leaves were sterilized using 1% hypochlorite solution and rinsed with tap water against the possible presence of pathogens and were kept in water to maintain their turgor. Experiments were started on May 14th 2007, such that colonies could receive appropriate age foliage. Colonies that

hatched after mid-June when the leaves were of poorer quality were reared on an artificial diet throughout their development and were only used during the fourth-instar.

All experiments were conducted in growth chambers at controlled temperatures of 17 and 27 °C and 70% RH. A video camera was mounted above the setup and all experiments were recorded one frame per 2 s for 6 h. The experimental set-up (Figure 3.1) consisted of a Perspex plastic bridge 43 cm long x 3 cm wide covered with brown paper. Increments of 1 cm were marked along the edge of the paper. The bridge was balanced on rubber stoppers covered in acetate, placed in a tray containing 2 cm of water in order to prevent caterpillars from escaping. The caterpillar colonies were placed at the start of the bridge either with or without a radiant heat source, and a food source consisting of fresh aspen foliage was placed at the other end of the bridge. The heat source was provided by an incandescent lamp (desk lamp E101956 model 1260, China; Sylvania light bulb, Canada, type R14 with 25 W, 120 V, 60 Hz and colour temperature of 2850 K) 35 cm above the surface of the bridge.

Four bridges were filmed simultaneously in an incubator between 09.00 and 17.00 h; two with and two without the lamp. An upright divider constructed of aluminum foil and craft sticks was placed between the bridges with and without the lamp (see Figure 3.1). The temperature of bivouacking caterpillar groups and of the substrate was measured at the start of the bridge (end without the food supply) for all 4 treatments (two temperature regimes, each with or without the lamp heat/light source). Preliminary observations showed that the ambient temperature directly under the lamp increased by 5°C and that the neighbouring bridge was not affected. A group of 40 siblings originating from a single colony was used for each trial. Experimental insects were used within 2

days of moulting to the second- and fourth-instars and each individual was only used once. Colonies of fourth-instar caterpillars were weighed to within 0.01 mg before and after each trial.

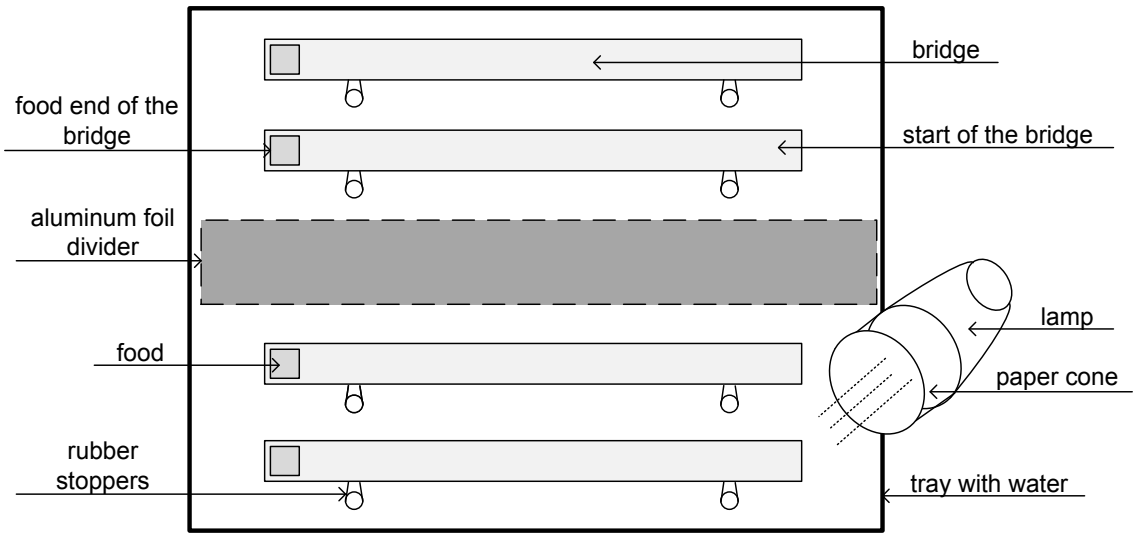


Figure 3.1: Top view of experimental set-up for thermoregulation experiments in the laboratory.

Each experimental condition was repeated 20 times. Colonies were allowed to settle for approximately 30 min before the start of the experiment. For experiments using second-instar larvae, a thin line of artificial trail pheromone (5β-cholestane-3,24-dione) diluted in hexane to obtain 10^{-9} g of pheromone per mm of trail (Fitzgerald, 1993a) was painted from one end of the bridge to the other to accelerate the initiation of foraging in second instar caterpillars. Videos were used to determine the number of individuals either active (walking or eating) or bivouacking. For bivouacking groups, the location and approximate size of the aggregates were measured. Cohesion of bivouacking groups was calculated as above (i.e. by estimating the surface area occupied by the colony and dividing by the number of individuals present). The experiment was conducted in two

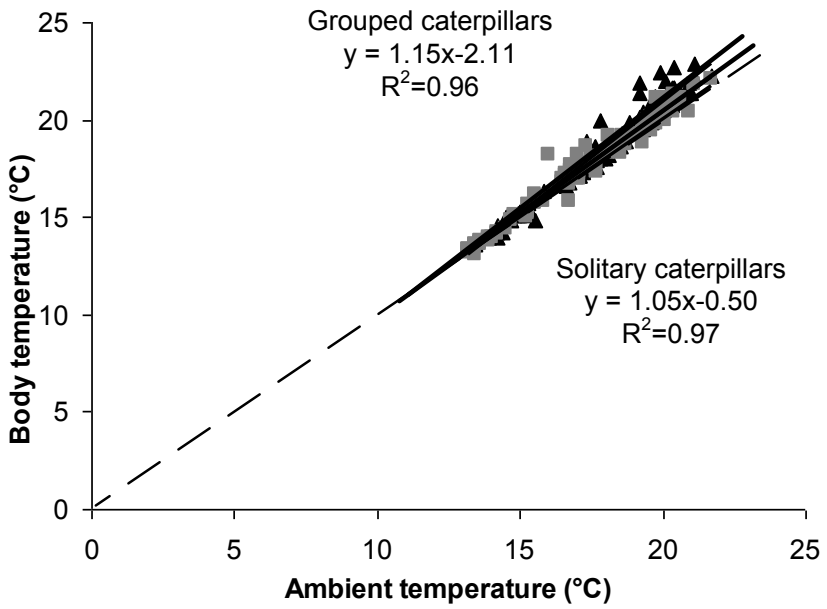
factorial ANOVAs, one for each stadium, with the factors being temperature (17 and 27 °C), and the presence or absence of the lamp. Factorial analyses of variance tested effects on the following dependent variables: cohesion, the number of quiescent and active periods, the total amount of time spent quiescent (or bivouacking) or active and the amount of weight gained. Frequencies with which groups selected a bivouac site at the start of the bridge or near the food were compared between treatments using a cross-tabulation Chi-square. For each treatment, average body temperature was compared with average ambient temperature using a Student *t*-test.

3.4 Results

Thermoregulation in the field

Colony size varied between 24 and 137 caterpillars, with a mean ± SE of 69±9.32 caterpillars. Groups of *M. disstria* exposed to solar radiation were often observed remaining still in tight groups. Body temperature of groups in the shade tracked ambient temperature (i.e., demonstrated by an expected slope approaching or close to being equal to 1; Figures 3.2a, 3.3a, intercept close to 0), as did that of isolated caterpillars. However, caterpillar colonies remaining still in the sun were not thermoconformers (i.e., an expected slope <1, intercept> 1; Figures 3.2b, 3.3b). In fact, groups of second-instar larvae in the sun achieved body temperatures 4.2±1.1 °C (mean±SE) in excess of ambient temperature (Figure 3.2b). Fourth-instar caterpillar groups in the sun continue to gain a thermal advantage and achieve on average body temperatures 6.2±1.3 °C above ambient (Figure 3.3b). For both instars, temperature excesses decrease at higher temperatures.

a) Shade



b) Sun

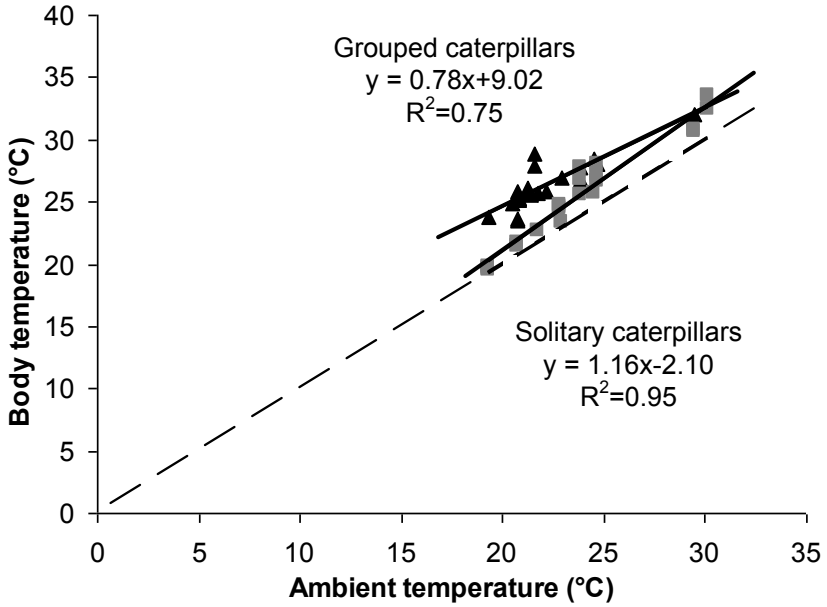
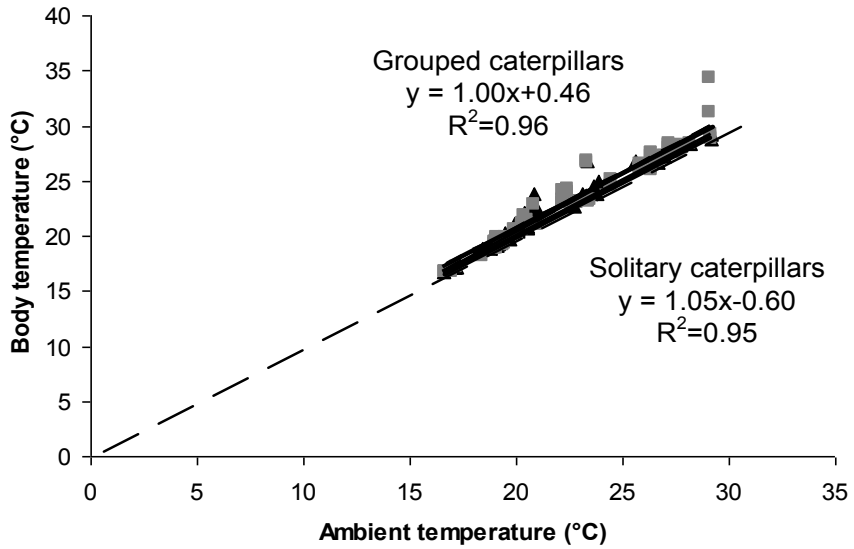


Figure 3.2: Relationship between ambient temperature and larval body temperature of solitary and grouped second-instar caterpillars of *Malacosoma disstria* during a) periods of cloud cover and b) periods of sun. Solid lines were fitted by the method of least-squares linear regression, dashed lines represent body temperature = ambient temperature (thermal conformance). Black triangles are temperatures of caterpillars within groups and grey squares are temperatures of solitary caterpillars.

a) Shade



b) Sun

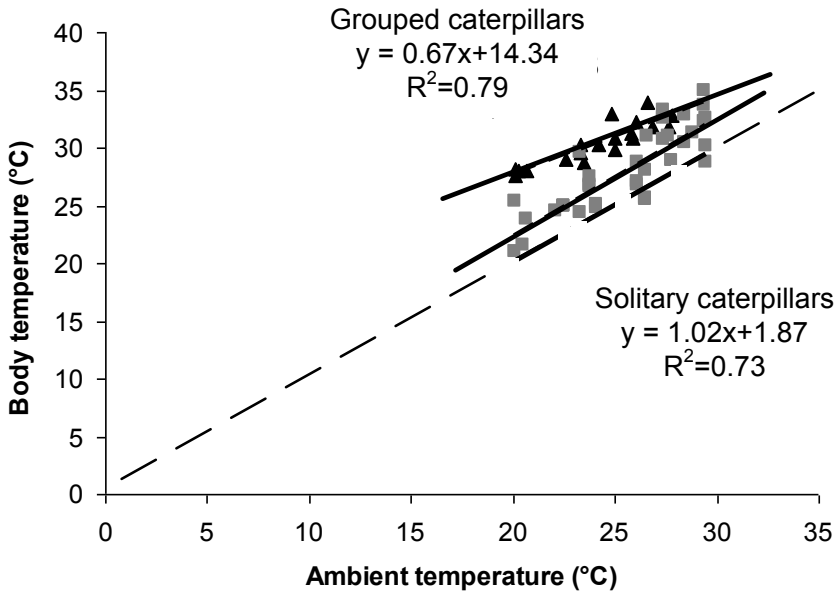


Figure 3.3: Relationship between ambient temperature and larval body temperature of solitary and grouped fourth-instar caterpillars of *Malacosoma disstria* during a) periods of cloud cover and b) periods of sun. Solid lines were fitted by the method of least-squares linear regression, dashed lines is where body temperature equals ambient temperature (represent body temperature = ambient temperature; thermal conformance). Black triangles are temperatures of caterpillars within groups and grey squares are temperatures of solitary caterpillars.

Colonies bivouacked on the petiole of the leaf on which they had been feeding or on the nearest branch (McClure and Despland, 2010). At high temperatures, caterpillars were often seen feeding on the underside of the leaves, and above 32 °C they displayed hanging behaviour (i.e., the caterpillars let go of the branch with the front two-thirds of the body) and/or moved to the underside of the leaves.

For second-instar caterpillars, ambient temperature (t=37.358, P<0.001), position in the shade or in the sun (t=7.782, P<0.001) and activity (t=4.380, P<0.001) influenced larval body temperature significantly, but cohesion, number of individuals and wind speed did not (adjusted R^2= 0.940; Table 1a). For fourth-instar caterpillars, ambient temperature (t=20.861, P<0.001) and position in the shade or in the sun (t=6.935, P<0.001) significantly influenced body temperature, but cohesion, number of individuals, activity and wind speed did not (adjusted R^2= 0.899; Table 1b). For both instars, ambient temperature was the major predictor for larval body temperature, and was responsible for 85% of the variance in body temperature observed in second-instar caterpillars and for 80% of the variance observed in fourth-instar caterpillars.

Table 3.1: Results of the multiple linear regression using the enter method for a) second-instar and b) fourth-instar caterpillars of *Malacosoma disstria*.
a) Adjusted R square= 0.940; $F_{6,163}$= 440.584, P<0.001. Significant variables are shown below.

Predictor variable	βeta	*P*
Ambient temperature	0.852	*P*<0.001
Position in the shade or the sun	0.182	*P*<0.001
Group activity	0.088	*P*<0.001

(Number of individuals, group cohesion and wind speed were not significant predictors in this model.)

b) Adjusted R square=0.899; $F_{6,110}$=173.141, P<0.001. Significant variables are shown below.

Predictor variable	βeta	*P*
Ambient temperature	0.800	*P*<0.001
Position in the shade or the sun	0.255	*P*<0.001

(Group activity, number of individuals, group cohesion and wind speed were not significant predictors in this model.)

Thermoregulation in the laboratory

In the laboratory, colonies of caterpillars remaining still under a lamp achieved temperature gains between 6 and 13 °C above ambient temperature. Gains were higher at 17 than at 27 °C, but were similar for second- and fourth-instar caterpillars (Table 3.2). The presence of a lamp increased the cohesion of groups of second-instar caterpillars (F=6.547; d.f.=1, 116; P=0.012), but temperature had no significant effect (F=0.261; d.f.=1, 116; P=0.611). A significant interaction (F=8.461; d.f.=1, 116; P=0.004; Figure 3.4) showed that the effect of the lamp on cohesion was much stronger at 17 than at 27 °C. Groups of fourth-instar caterpillars did not change their cohesion based on temperature (F=2.547; d.f.=1, 176; P=0.112) or the presence of a lamp (F=0.577; d.f.=1, 176; P=0.449). Differences in body size preclude comparison between instars.

Table 3.2: Mean±SE temperature gains for bivouacking groups of second- and fourth-instar larvae of *Malacosoma disstria* at ambient temperatures of 17 and 27 °C with and without a lamp. Numbers in bold signify statistical significance at $P < 0.05$

Instar	Lamp	*n*	Ambient temperature (°C) Mean±SE	Body Temperature (°C) Mean±SE	Temperature gain (°C) Mean±SE	*t*-test	d.f.	*P*
2nd	**no**	20	17.4±0.2	18.7±0.1	1.3±0.2	-4.756	30.416	0.051
2nd	**yes**	20	17.4±0.2	27.3±0.2	9.9±0.4	-31.371	38	**>0.001***
2nd	**no**	20	25.3±0.4	24.9±0.3	-0.2±0.4	0.861	38	0.394
2nd	**yes**	20	25.3±0.4	34.0±0.4	8.6±0.4	-9.551	38	**>0.001***
4th	**no**	20	18.0±0.5	20.0±0.5	2.0±0.5	-2.852	38	**0.011***
4th	**yes**	20	17.4±0.5	29.9±0.5	12.6±0.9	-10.796	38	**>0.001***
4th	**no**	20	27.2±0.2	26.5±0.3	-0.7±0.1	3.090	38	0.067
4th	**yes**	20	27.2±0.2	34.3±0.5	7.2±0.3	-6.038	20.553	**>0.001***

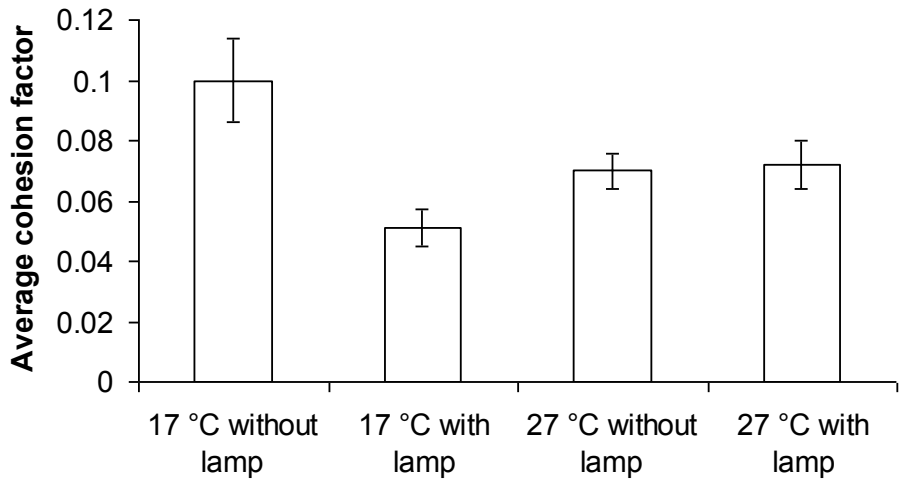


Figure 3.4: Average (±SE) cohesion factors of bivouacking second-instar caterpillars of *Malacosoma disstria* (measured by dividing the area occupied by caterpillar groups by the number of caterpillars) at both temperature conditions (17 and 27 °C), with or without access to a lamp. Lower values are indicative of a more tightly bivouacking group.

For colonies of second-instar caterpillars, ambient temperature significantly influenced bivouac site selection (χ^2=20.19; d.f.=1; P<0.001) but the presence of a lamp did not (χ^2=1.81; d.f.=1; P=0.179). At ambient temperatures of 17 °C, colonies bivouacked at the start of the bridge most of the time regardless of the presence of a lamp. At 27 °C, colonies that did not have access to a lamp bivouacked more often at the food end, whereas colonies that had access to a lamp bivouacked sometimes at one end, and sometimes at the other (Figure 3.5). For colonies of fourth-instar caterpillars, temperature did not significantly influence the location of the bivouac (χ^2=1.55; d.f.=1; P=0.213), but the presence of a lamp did (χ^2=66.14; d.f.=1; P<0.001). At both ambient temperatures, the majority of colonies of fourth-instar caterpillars that had access to a lamp bivouacked at the start of the bridge and the majority of colonies without access to a lamp bivouacked near the food (Figure 3.5).

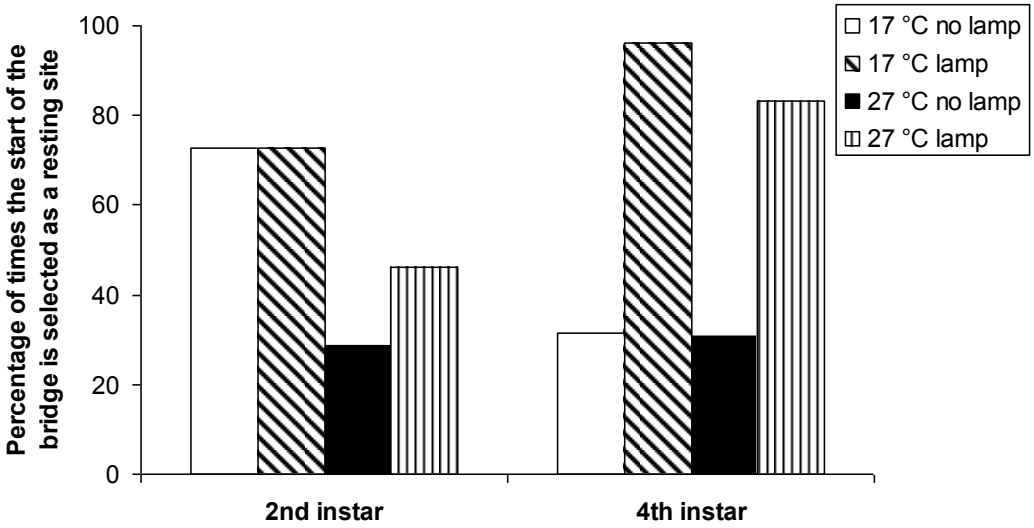


Figure 3.5: Relative frequency with which groups of second-instar larvae and fourth-instar larvae of *Malacosoma disstria* select the start of the bridge (i.e., the opposite end from the food) as a bivouac site at two ambient temperatures, with or without access to a lamp.

All colonies showed a clear alternation between quiescent and active periods, and colonies consistently remained together. No clear differences in aggregation or synchronization were observed between the treatments. Colonies of both second (F=2.711; d.f.=3, 89; P=0.050) and fourth-instar (F=4.864; d.f.=3, 65; P=0.004) caterpillars spent less time quiescent at low temperature without a lamp than in any other treatment (Figure 3.6). Fourth-instar colonies spent significantly more time quiescent when a lamp was present, but none of the factors were significant in determining the time spent quiescent for second-instar caterpillars (Table 3.3).

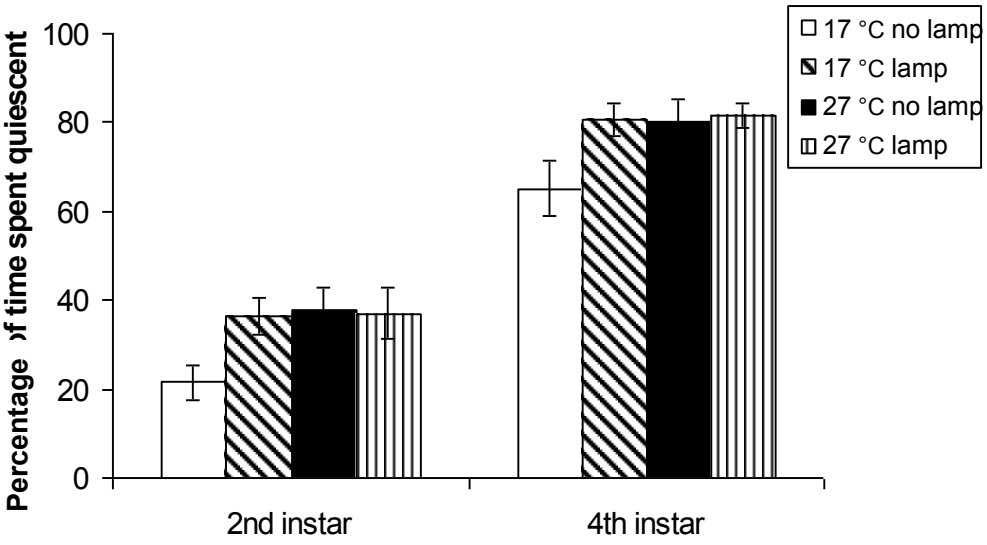


Figure 3.6: Average percentage of time (±SE) spent bivouacking for second- and fourth-instar caterpillars of *Malacosoma disstria* at both temperature conditions (17 and 27 °C) with and without a lamp.

Table 3.3: Statistical results for the total amount of time spent quiescent for groups of a) second (F=2.711; d.f.=3, 89; P=0.050) and b) fourth-instar (F=4.864; d.f.=3, 65; P=0.004) caterpillars of *Malacosoma disstria* at ambient temperatures of 17 and 27 °C with and without a lamp. Number in bold signifies statistical significance at $P < 0.05$

a)

Measured variable	Experimental factor	*F*-value	d.f.	*P*
Amount of time spent quiescent	ambient temperature	1.91	1, 89	0.178
Amount of time spent quiescent	presence of a lamp	2.59	1, 89	0.111
Interaction	lamp*temperature	3.67	1, 89	0.059

b)

Measured variable	Experimental factor	*F*-value	d.f.	*P*
Amount of time spent quiescent	ambient temperature	0.92	1, 65	0.342
Amount of time spent quiescent	presence of a lamp	11.19	1, 65	**0.001***
Interaction	lamp*temperature	2.48	1, 65	0.120

The mass gained by fourth-instar caterpillars significantly increased with temperature (F=11.289; d.f.=1, 52; P= 0.001) and in the presence of a lamp (F=8.388; d.f.=1, 52; P=0.006; Figure 3.7) with no interaction between these two factors (F=0.374; d.f.=1, 52; P=0.543).

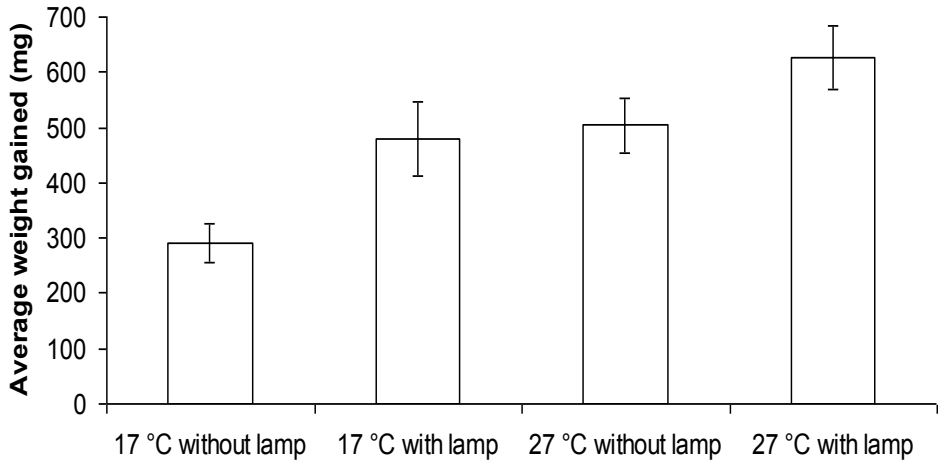


Figure 3.7: Average (±SE) amount of weight that groups of fourth-instar caterpillars of *Malacosoma disstria* gained (mg) for each treatment.

3.5 Discussion

Malacosoma disstria colonies are able to behaviourally thermoregulate, grouping is important for achieving thermal gains and thermoregulatory considerations influence both temporal and spatial patterns of collective foraging. This suggests that thermoregulation may be an important selection pressure shaping group living in this social nomadic forager.

In the field, aggregations of *M. disstria* are often observed in full sunlight and are thus able to achieve higher body temperatures than solitary individuals. They also demonstrate mechanisms to cope with elevated temperatures, consistent with observations by Sullivan & Wellington (1953) that *M. disstria* becomes photonegative above 30 ºC. Wind speed was not observed to influence body temperature in the field, but this may be due to the low wind speeds encountered during the present study (mean ± SE, 1.21±0.081 m s^{-1}). Joos *et al.* (1988) only observed an effect of wind speed on body

temperature of caterpillars in the laboratory at wind speeds of 2.8 m s^{-1}.

The main benefit of thermoregulation for ectotherms is improvement in behavioural and physiological performances, the most important ones generally being locomotion and food uptake (rate of eating and absorption), and food processing (digestive efficiency) (Dubois *et al.*, 2009). In caterpillars, the benefits of thermoregulation can lead to an increase in growth and development rates and has been shown in the consgeneric tent-dwelling *M. americanum* (Casey *et al.*, 1988). For *M. disstria*, Levesque *et al.* (2002) show relative growth rate increases almost linearly with increasing temperatures up to 30 °C, via increases both in food consumption and in the proportion of food converted to biomass. These increases in rates of locomotion and food processing at higher temperature lead to shorter active and quiescent periods, respectively, and hence acceleration of behaviour and higher food consumption (Peters and Despland, 2006). The present study confirms that these behavioural and physiological advantages allow *M. disstria* to grow faster with access to a basking spot.

Thermoregulation thus has clear benefits for *M. disstria*, and could therefore be a key factor directing colony behaviour, as it is known that thermoregulation can determine habitat use by ectotherms (e.g., Bouaïchi *et al.*, 1996; Dubois *et al.*, 2009). The present results show that caterpillars' use of both time and space are driven in part by the use of thermal resources.

Previous studies show that caterpillars of *M. disstria* exhibit a plastic temporal foraging/activity pattern that is strongly influenced by temperature. *Malacosoma disstria* colonies in the field alternate between active and quiescent periods when temperatures are above 10 ºC, with no consistent daily pattern of foraging (McClure and Despland,

2010). Peters & Despland (2006) found that these synchronized activity patterns are accelerated at higher temperature, due to a decrease in the duration of both active and quiescent periods. In the present experiment, the time spent quiescent significantly increases when a lamp is present, suggesting that caterpillars make use of this thermal resource to maximize food processing and achieve the higher efficiency of food conversion documented by Levesque *et al.* (2002).

Caterpillars further increase thermal gains by selecting a bivouac site according to thermal resources present in the environment and by clustering in a cohesive group when a radiant heat source is present. When groups of fourth-instar caterpillars are given access to a lamp in the laboratory, they move away from the food to bivouac under the lamp. In the absence of a basking site, colonies are more likely to bivouac right by the food source. This decreases both energy expenditure and encounters with invertebrate predators (see McClure and Despland, 2010), suggesting a trade-off between the physiological benefits of thermoregulation and its ecological costs (Dubois *et al.*, 2009). As expected, caterpillars are more likely to remain still under the lamp at the cooler temperature, when thermal needs are greatest. Second-instar caterpillars return to bivouac at the start of the bridge at low temperature, even when a lamp is not present. It is possible that the start of the bridge is slightly warmer than the end with the food even without the lamp due to spill over heat from the next bridge, although no difference is detected beyond ±1°C. Second-instar caterpillars may be sensitive to such a slight temperature gradient. On *M. disstria* host trees, fresh palatable foliage occurs in the sun, and hence good food sources tend to be close to good basking sites. Field colonies therefore probably do not often need to risk the ecological cost of travel to achieve the

physiological benefits of thermoregulation; however, the insects' positioning in the laboratory studies testifies to the importance of those benefits.

Another behaviour by which *M. disstria* maximizes thermal gains is clustering in groups to bask (i.e., resting while exposed to a heat source). In the laboratory, second-instar caterpillars at 17 °C bivouac in tighter groups when a lamp is present. In the field, caterpillars are always observed bivouacking in tight groups, except at temperatures above 30 °C. These groups achieve higher temperatures than isolated caterpillars. Cohesion can be an important factor in reducing convective heat loss by minimizing the relative body surface exposed. Grouping to bask therefore appears to be an important advantage to group living in *M. disstria* and could indeed be an important selection pressure favouring gregariousness in this species.

Malacosoma disstria caterpillars become increasingly independent as development progresses (Fitzgerald, 1995; Despland and Hamzeh, 2004). Fourth-instar caterpillars increasingly forage independently but return to bask with the group, and by the fifth-instar, caterpillars seldom aggregate. Continued thermal gains may not be sufficient for strong aggregative behaviour to persist if the costs of grouping, such as increased intraspecific competition, become more important later in development (Knapp and Casey, 1986; Despland and Le Huu, 2007). This may be especially true if ambient temperature during the later instars approaches optimal temperature and thermal gains by basking are not essential. Indeed, in the present field observations, fourth-instar caterpillars experienced temperatures in the shade (without basking) similar to those achieved by basking second-instar colonies and which approach optimal temperatures for this species (~25 °C; Levesque *et al.*, 2002). In *M. americanum*, late-instar caterpillars

regulate their temperature to only slightly above ambient, but they nonetheless continue to use the tent. In *M. disstria*, caterpillars gradually forage more independently as they get larger, but the present study shows that they nonetheless continue to use collective basking to achieve thermal gains.

The relative importance of different factors promoting group living likely varies among gregarious caterpillar species (Costa, 2006). For *M. disstria* caterpillars, which rely on developing fast despite low seasonal temperatures to benefit from springtime high food quality and low predation rates, thermoregulation is likely to be an important factor contributing to group living. Indeed, low spring temperatures and unsynchronized phenology with host plants can affect *M. disstria* caterpillar population dynamics (Parry *et al.*, 1998 and references therein) and hence thermal requirements appear to be an important selection pressure for aggregation in these temperate early spring feeders. As such, spatial and temporal patterns of foraging in the nomadic forager *M. disstria* are, at least in part, shaped by these thermal requirements.

The present study confirms that collective thermoregulation can be advantageous for tent-less social larvae, and is the first to show that thermoregulatory behaviour drives much of the colony's activity, including habitat selection, cohesion, as well as spatial and temporal foraging patterns.

Chapter 4- Defensive responses by a social caterpillar are tailored to different predators and change with larval instar and group size

The following chapter is based on the published manuscript: McClure, M., and Despland, E. (2011) Defensive responses by a social caterpillar are tailored to different predators and change with larval and group size. Naturwissenschaften 98: 425-434

4.1 Abstract

Gregariousness in animals is widely accepted as a behavioural adaptation for protection from predation. However, predation risk and the effectiveness of a prey's defense can be a function of several other factors, including predator species and prey size or age. The objective of this study was to determine if the gregarious habit of *Malacosoma disstria* caterpillars is advantageous against invertebrate natural enemies, and whether this is through dilution or cooperative defenses. We also examined the effects of larval growth and group size on the rate and success of attacks.

Caterpillars of *M. disstria* responded with predator-specific behaviours, which led to increased survival. Evasive behaviours were used against stinkbugs, while thrashing by fourth instar caterpillars and holding on to the silk mat by second instar caterpillars was most efficient against spider attacks. Collective head flicking and biting by groups of both second and fourth instar caterpillars were observed when attacked by parasitoids.

Increased larval size decreased the average number of attacks by spiders but increased the number of attacks by both stinkbugs and parasitoids. However, increased

body size decreased the success rate of attacks by all three natural enemies and increased handling time for both predators.

Larger group sizes did not influence the number of attacks from predators but increased the number of attacks and the number of successful attacks from parasitoids. In all cases, individual risk was lower in larger groups. Caterpillars showed collective defenses against parasitoids but not against the walking predators.

These results show that caterpillars use different tactics against different natural enemies. Overall, these tactics are both more diverse and more effective in fourth instar than in second instar caterpillars, confirming that growth reduces predation risk. We also show that grouping benefits caterpillars through dilution of risk, and, in the case of parasitoids, through group defenses. The decreased tendency to aggregate in the last larval instar may therefore be linked to decreasing predation risk.

4.2 Introduction

Many animals live in groups, and gregariousness has been shown to provide protection from predation in a variety of taxa such as anuran larvae (DeVito, 2003; Smith and Awan, 2009), fish (Krause and Godin, 1995), invertebrates (Clark and Faeth, 1997; Uetz *et al.*, 2002; Lemos *et al.*, 2005), small mammals (Hass and Valenzuela, 2002; Rogovin *et al.*, 2004), ungulates (Mooring and Hart, 1992), and many others. Predation risk and the effectiveness of a prey's defense can be a function of several variables, including prey group size and individual prey size as a function of age (Botham *et al.*, 2006; Smith and Awan, 2009). Although larger groups of prey may be more easily discovered and may suffer more frequent attacks due to increased conspicuousness,

hunting success of predators and per capita predation risk of prey have also been shown to decrease in larger groups (Lawrence, 1990; Clark and Faeth, 1997; Hunter, 2000; Botham *et al.*, 2005). Group members may suffer a lower risk of capture because of cooperative defense, enhanced advertisement of unprofitability in aposematic species, shared and more effective vigilance and a reduced probability of predation by virtue of a dilution effect when a predator can take only a limited number of individuals from the group (Seyfarth *et al.*, 1980; Peterson *et al.*, 1987; Vulinec, 1990; Mooring and Hart, 1992; Uetz *et al.*, 2002; DeVito, 2003). In addition, animals in the center of a group can decrease their risk of predation by surrounding themselves with others (Tostowaryk, 1971; Mooring and Hart, 1992; Krause *et al.*, 1998), which Hamilton (1971) termed the selfish herd effect.

As prey individuals grow, their vulnerability to predators can also change. Smaller predator species may not be physically capable of handling large prey or the costs of subduing them may be too great (Peters, 1983; Warren and Lawton, 1987; Cohen *et al.*, 1993), whereas larger predator species may avoid small prey because they are too costly to handle for the energy gains. Gaston *et al.* (1997) found that the body masses of the bird species feeding on successive instars of the mopane worm were strongly correlated with the larvae's mass. The ability of pentatomid predators to subdue caterpillars also depends on the larvae's size and behaviour (Iwao and Wellington, 1970).

Most prey is subject to predation from multiple predators, and different defenses are thought to have evolved in response to selective pressures from different types of predators. As such, different predators may elicit different responses or a prey species may adopt a general response which provides protection from many different types of

predator (Botham *et al.*, 2006). Generalized responses that are successful against many different predators, rather than species-specific responses, may benefit prey in species that co-occur with multiple similar predators (Webb *et al.*, 2010); hence the importance of testing the effectiveness of a prey's defensive mechanisms against different predators. Yet many studies investigating behavioural responses in predator-prey interactions have focused on single predators, and experimental evidence that prey benefit in terms of survival by adopting different responses to different predators appears to be lacking (Botham *et al.*, 2006; Castellanos and Barbosa, 2006).

We examined the responses of *Malacosoma disstria* caterpillars against three natural enemies and tested the effects of larval growth and gregarious behaviour on the rate and success of attacks. Caterpillars of *M. disstria* are gregarious until the final larval stadium, and decreased predation risk is often listed among the benefits of group living for this (Parry *et al.*, 1998) and other gregarious caterpillar species (Reader and Hochuli, 2003). *M. disstria* caterpillars are collective nomadic foragers and use pheromone trails to travel as a cohesive group between feeding sites. These caterpillars hatch in early spring when food quality is high and they develop rapidly to escape predation (Parry *et al.*, 1998), as predation risk is thought to decrease with increasing larval size (Costa, 1993; Reavey, 1993). The importance of predation in shaping the gregarious and fast-developing life history traits is not known, nor is the identity of the predators exerting the selection pressure. Caterpillars of *M. disstria* are unpalatable to most vertebrates (Heinrich, 1983; 1993b), but little is known of the defensive mechanisms against invertebrate predators (see Fitzgerald, 1995). Synchronous flicking of the body has been described for many social caterpillars (see Fitzgerald and Costa, 1999 and references

therein), and some, such as the closely related *Malacosoma americanum*, also combine these displays with defensive regurgitation of enteric fluid containing host-derived benzaldehyde when attacked by predatory ants (Peterson *et al.*, 1987).

The objective of this study was to determine if the gregarious habit of *M. disstria* is advantageous against invertebrate predation, and whether it is through dilution or cooperative defenses. We also hypothesized that the rate and success of attacks would decrease with increasing group size and caterpillar size (as a function of larval instar), but that these could vary between the three natural enemies tested, depending on the behavioural response exhibited in each case.

4.3 Methodology

Unhatched egg masses of *M. disstria* were collected from Southern Ontario, Canada (44°33.5N, 76°24.1W) in March 2009 and stored at 4ºC with 80% relative humidity (RH) until use. To minimize mortality from pathogens, egg bands were sterilized by soaking in 5% sodium hypochlorite as described by Grisdale (1985). Caterpillar colonies arising from a single egg mass were kept in plastic -rearing containers and kept in a rearing chamber under a controlled light and temperature regime of 21°C, 70% RH and 16L: 8D. Caterpillars were fed ad libitum on a nutritionally balanced, standard wheat germ-based meridic artificial diet (Addy, 1969). Although *M. disstria* caterpillars have never been observed to regurgitate, gut content may affect predation and so caterpillars were given fresh leaves of their primary host, trembling aspen (*Populus tremuloides*), 24 h before being used in experiments with the walking predators. Leaves were collected from multiple trees in Montreal, Quebec and were

sterilized using 1% hypochlorite solution and rinsed with tap water against the possible presence of pathogens. All experiments were conducted at temperatures ranging between 20-23°C and 50-60% RH.

Fifteen species of hemipteran stinkbugs are known to prey on tent caterpillars, but *Podisus maculiventris* Say is one of the most common and it is distributed over most of the USA and southern part of Canada. Stinkbugs overwinter as adults and are active in early spring, searching for prey and responding within a short distance or after physical contact (Evans, 1982). When a prey is detected, stinkbugs stretch out their proboscis before eventually attacking by inserting their stylets. Stinkbugs appear limited to attacking caterpillars of 20 mm or less (Evans, 1982). Beetles in the genus *Calosoma* are also well-known predators of tent caterpillars, which are grasped and cut in half with sharp mandibles (Fitzgerald and Costa, 1999 and references therein). Spiders are also important generalist predators, especially of earlier instars (McClure and Despland, 2010; Ronnas *et al.*, 2010). Although many species of parasitoids attack the eggs or pupae of *Malacosoma*, a few families also attack the larval stage (see Fitzgerald, 1995 and references therein; Williams *et al.*, 1996). *Malacosoma* caterpillars are known for flicking the anterior portion of their body when attacked by parasitoids, and this behaviour quickly propagates through the group into a synchronized behaviour. Prop (1960) found that such group displays in gregarious sawflies deterred oviposition by an ichneumonid parasitoid.

Three invertebrate predators, which co-occur with *M. disstria*, were therefore initially selected: stinkbugs (*P. maculiventris*) were obtained from The Bug Factory (Canada), and carabid beetles (*Calosoma* sp.) and spiders (*Thanatus vulagaris*) were

collected in Montreal (Quebec, Canada). However, in preliminary trials (*N*=6) carabid beetles were found to be too mobile, with beetles escaping the setup often without contacting the group of caterpillars (*N*=4), and were subsequently not used. A generalist parasitoid wasp (*Hyposoter fugitivus*) was also selected and was obtained from Dr. Stoltz's rearing colony (Dalhousie University in Halifax, Canada). All walking predators were starved 24h before use and a predator used in a test was not used again until it had fed and again been deprived of food. The predators were fed larvae of the greater wax moth, *Galleria mellonella,* and were supplied with moisture via a soaked paper towel. The parasitoids were fed with honey droplets. All walking predators were maintained in rearing chambers under a controlled light and temperature regime of 21°C, 70% RH, and 16L: 8D, and parasitoids were stored at 10°C until use.

Tested group sizes were of 2, 10 and 30 second or fourth instar caterpillars. Only second and fourth instar caterpillars were studied during our experiments as they reflect distinct differences in both body size and group behaviour (older caterpillars exhibit more independent locomotion). The experimental setup consisted of a plastic arena (43 cm long x 3 cm) covered in brown paper. The arena was balanced on rubber stoppers covered in acetate, placed in a tray containing 2 cm of water in order to prevent caterpillars from leaving. Caterpillars were placed at one end of the arena 20 min before the introduction of a predator or two parasitoids to allow them to acclimatize, and caterpillars were only used once. When using parasitoids, the experimental setup was placed in a mesh cage.

All group size, instar, and natural enemy combinations were repeated 20 times. Experiments were terminated after 20 min for predators and 40 min for parasitoids. This was considered enough time to observe an attack, as on average predators attacked in less

than 1 min (mean ± SE of 49.22±11.49 s), and parasitoids did so in less than 8 min (mean ± SE of 7.96±1.10 min). A video camera was mounted above the arena and all experiments were recorded for further analysis. The likelihood of attack in each treatment was analyzed using chi-square. A multivariate analysis of variance (MANOVA) was used for each natural enemy to determine if the number of caterpillars attacked and the number of those attacks that were successful was significantly affected by group size and/or larval instar. The MANOVA for both walking predators also included the latency to attack (i.e., the time from the moment the predator is introduced into the arena to the first attack observed) and the handling time (i.e., the time required for a predator to subdue its prey) as dependent variables. In addition, the MANOVA for the stinkbugs also included the time needed to perceive the caterpillars (determined as when the proboscis was raised). The MANOVA for the parasitoids included the time caterpillar groups spent head flicking after an attack as a dependent variable. Behavioural descriptions of predator or parasitoid attacks and escape responses of caterpillars were also noted for every predator-prey combination. Parasitizing success was determined by rearing some of the groups (a minimum of seven replicates per group size-instar combination was used for a total of N=45) until parasitoid emergence. Mortality risk per caterpillar from each natural enemy was also calculated by dividing the number of individuals within a group by the number of successful attacks and averaging them for all larval instar and group sizes.

4.4 Results

Although these caterpillars are covered in setae, especially in the later instars, observations during this study gave no indication that they played any role in defense

against the predators and parasitoids that were used. Because spiders and stinkbugs are only capable of predating one individual at a time and require time to consume it, there could not be more than one successful attack per given trial. However, when unsuccessful, multiple attacks by these predators could be made within a single trial. *M. disstria* caterpillars were never observed to regurgitate. Group activity (defined as either active or resting) was never a significant predictor of either attacks or the success of these attacks for any of the natural enemies.

Carabid beetles

Preliminary trials with carabid beetles (*N*=6) were done with groups of 30 fourth instar caterpillars, but proved to be difficult as the carabid beetles were large and too mobile for the chosen experimental setup. In four of the trials, the beetle repeatedly escaped the setup without making contact with the caterpillars. In two trials, the beetle attacked one caterpillar within the group and quickly devoured it. Predated individuals thrashed vigorously, but were never successful at escaping. The group's response consisted of all caterpillars walking away and relocating at the opposite end of the bridge setup while the predator was occupied with its prey. Although carabid beetles have been described as being aggressive predators which often attack multiple caterpillars within a group, only one individual was observed to be attacked (*N*=2). Both beetles subsequently escaped the setup shortly after the predation events.

Spiders

Spiders attacked by pouncing on the caterpillars and rapidly piercing them with their chelicerae. Responses of caterpillars attacked by spiders were different for second

and fourth instars, but did not change for different group sizes (Table 4.1). Although 42% of second instar caterpillars thrashed when grasped and a small number bit the spiders (5%), this was never successful. Surprisingly, 52% of the attacked caterpillars responded by gripping onto the silk mat: when spiders were unable to dislodge the caterpillar from its silk mat, they abandoned it. This tactic was successful in evading a predation event 80% of the time and bitten caterpillars that were abandoned always survived. Although this is not a group response per se, a group is needed to build a silk mat and this response was therefore not possible for individuals in groups of two. The larger fourth instar caterpillars were more aggressive in their responses. All individuals that were attacked thrashed vigorously. When not combined with any other behaviour, this was successful in only 37% of attacks. Survival was similar when thrashing was combined with biting, but increased if caterpillars dropped off the bridge, which was always an effective evasive tactic. This would also be advantageous in the field as larger caterpillars can survive in the absence of conspecifics (Fitzgerald and Costa, 1999).

For spiders, the time to attack (i.e., the latency for the spider to attack from the moment it is introduced) was not significantly influenced by group or larval size, but handling time was much longer for fourth instar caterpillars than for second instar caterpillars (162.00±33.87 vs. 2.58±0.33 s; Table 4.2). The probability of at least one attack occurring during the trial decreased with larval instar (χ^2=4.805, *df*=1, *p*=0.028) but was not affected by group size (χ^2=1.669, *df*=2, *p*=0.434). The number of attacks per trial increased with group size for second but decreased for fourth instar caterpillars (Figure 4.1). Attacks on fourth instar caterpillars were less likely to be successful than on second instar caterpillars. Attack success rate was not affected by group size (Table 4.2),

and therefore the per capita mortality risk decreased in larger groups (Figure 4.2). Position within the group was also found to be important, as the center of the group sustained fewer attacks.

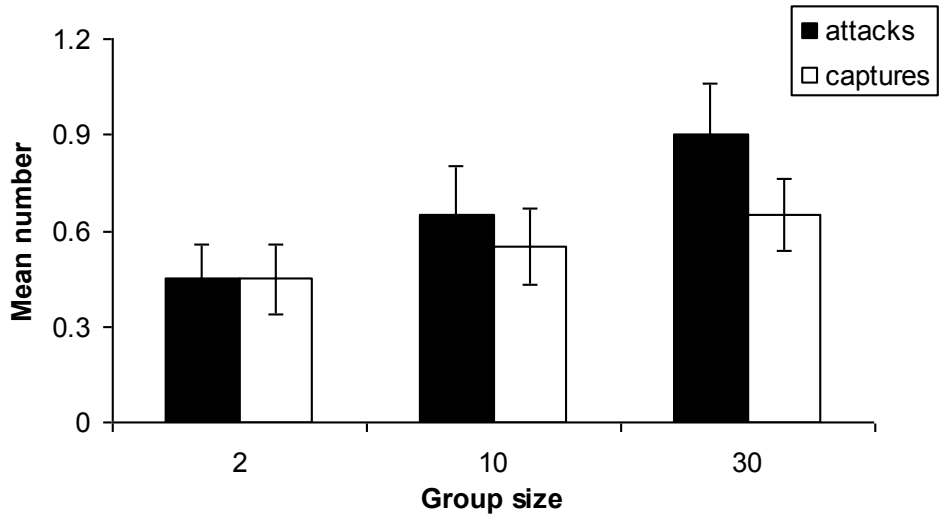
Table 4.1: The behavioural response (when one was observed) elicited by an attack by an invertebrate predator or parasitoid, the proportion of *M. disstria* caterpillars responding and the proportion of those that were successful in escaping predation or parasitism.

Type of predator	Instar	Behavioural response	Percent responding	Percent surviving an attack
Spider	2	thrashing	42	0
		biting	5	0
		holding the silk mat	53	80
	4	thrashing	37	38
		thrashing & biting	30	38
		thrashing & falling	33	100
Stinkbug	2	jerking back	11	100
		thrashing	61	0
	4	walking away	12	100
		jerking back	26	100
		thrashing	56	17
		thrashing & biting	5	0
		thrashing & falling	2	100
Parasitoid	2	head flicking	70	9
		head flicking & biting	30	30
	4	head flicking	66	32
		head flicking & biting	34	66

Table 4.2: Statistical results for three separate MANOVAs done for each natural enemy as a function of group size and larval instars of *M. disstria* caterpillars (*N*=120 groups per analysis). Asterisks indicates statistical significance at p<0.05

Type of predator	Measured variable	Experimental factor	*F* value	*df*	*p* value
Spider	Number of attacks	Caterpillar instar	2.7	1, 114	0.103
		Group size	0.36	2, 114	0.701
		Interaction	3.77	2, 114	**0.026***
	Number of captures	Caterpillar instar	12.26	1, 114	**0.001***
		Group size	0.27	2, 114	0.768
		Interaction	1.02	2, 114	0.36
	Time to attack (s)	Caterpillar instar	0.15	1, 59	0.698
		Group size	0.08	2, 59	0.923
		Interaction	0.93	2, 59	0.402
	Handling time (s)	Caterpillar instar	86.38	1, 40	**>0.001***
		Group size	0.81	2, 40	0.453
		Interaction	0.85	2, 40	0.434
Stinkbug	Number of attacks	Caterpillar instar	7.94	1, 114	**0.006***
		Group size	0.37	2, 114	0.695
		Interaction	0.16	2, 114	0.851
	Number of captures	Caterpillar instar	0.31	1, 114	0.58
		Group size	1.27	2, 114	0.286
		Interaction	4.42	2, 114	**0.014***
	Time to perceive (s)	Caterpillar instar	1.6	1, 78	0.214
		Group size	0.3	2, 78	0.741
		Interaction	0.23	2, 78	0.798
	Time to attack (s)	Caterpillar instar	15.96	1, 78	**>0.001***
		Group size	2.63	2, 78	0.087
		Interaction	1.8	2, 78	0.181
	Handling time (s)	Caterpillar instar	14.28	1, 53	**>0.001***
		Group size	0.01	2, 53	0.994
		Interaction	0.02	2, 53	0.984
Parasitoid	Number of attacks	Caterpillar instar	4.16	1, 114	**0.042***
		Group size	4.75	2, 114	**0.009***
		Interaction	1.47	2, 114	0.232
	Successfully parasitized	Caterpillar instar	16.69	2, 39	**>0.001***
		Group size	20.02	1, 39	**>0.001***
		Interaction	3.22	2, 39	0.051
	Time to attack (s)	Caterpillar instar	6.29	1, 72	0.594
		Group size	0.002	2, 72	0.998
		Interaction	0.33	2, 72	0.719
	Time spent flicking (s)	Caterpillar instar	0.6	1, 72	0.441
		Group size	26.03	2, 72	**>0.001***
		Interaction	1.32	2, 72	0.276

a)



b)

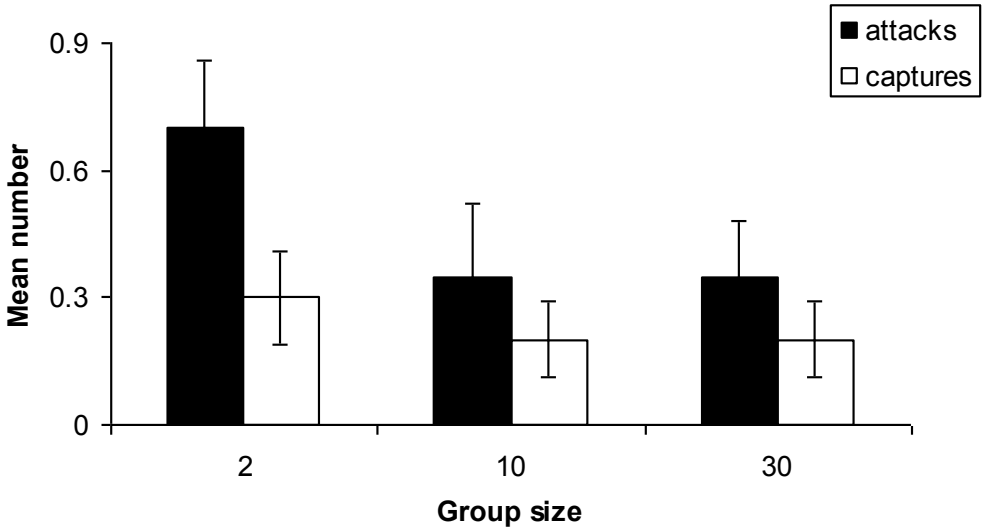
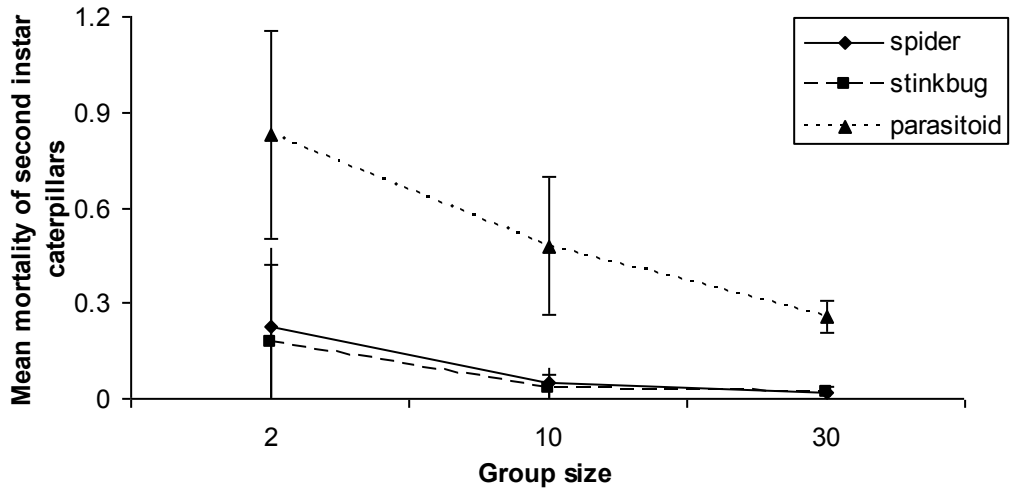


Figure 4.1: Spiders: the mean number of attacks (including both successful and failed attempts) and successful attacks (±SEM) for different group sizes of a) second and b) fourth instar caterpillars of *M. disstria* (*N*=20 caterpillar groups per treatment combination of instar and group size)

a)



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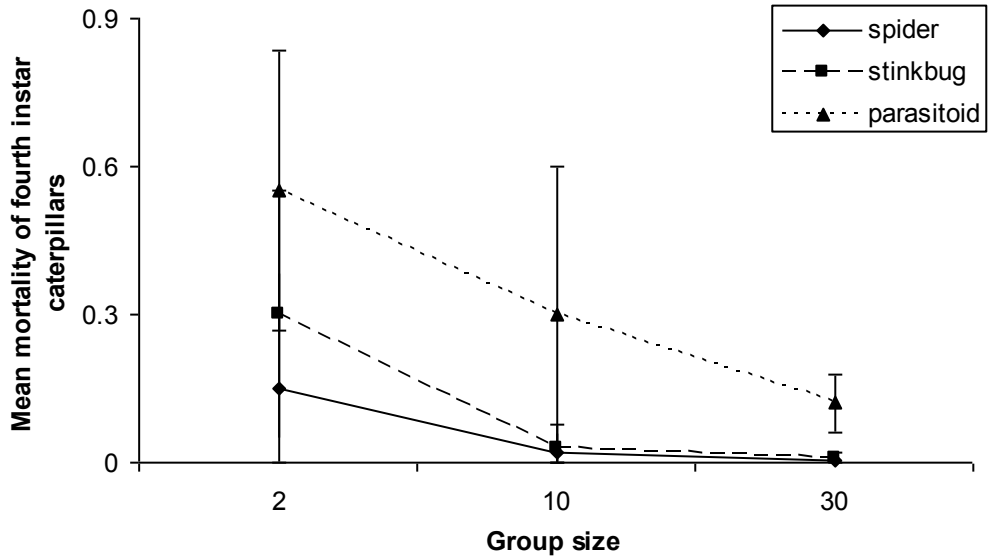


Figure 4.2: The mean mortality (±SEM) per capita of *M. disstria* caterpillars in different group sizes, for both a) second and b) fourth larval instar, for different invertebrate predators and parasitoids (*N*=20 caterpillar groups per treatment combination of instar and group size)

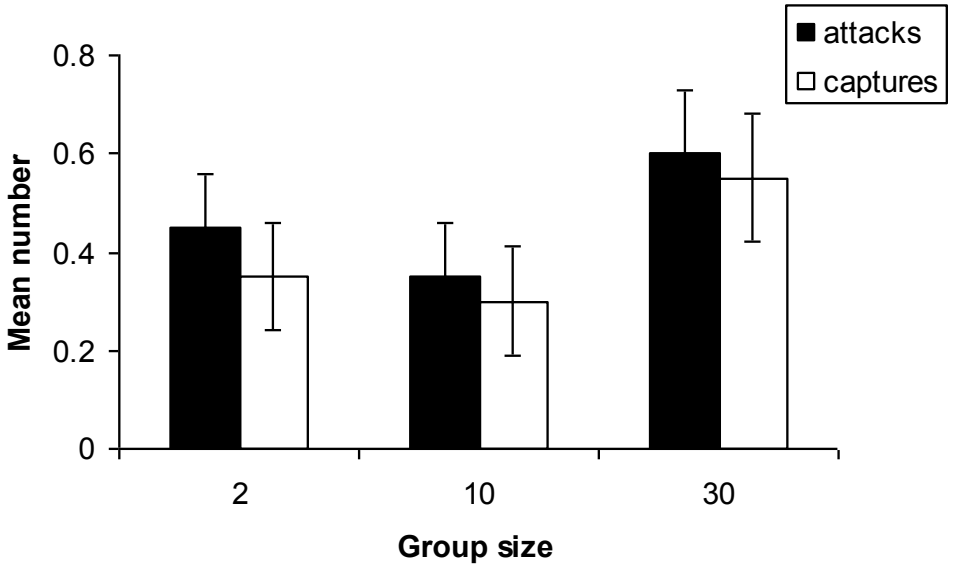
Stinkbugs

Caterpillars responded differently to stinkbugs, which after detecting the caterpillars raised their proboscis and approached them slowly, than they did to spiders. When second instar caterpillars detected the stinkbug before an attack (which occurred in

10% of cases), they took evasive responses by jerking away (Table 4.1). This was always successful as stinkbugs retreated. Once the predator had inserted its stylets into the caterpillar, none succeeded in escaping despite 60% of caterpillars thrashing in response to the attack. Fourth instar caterpillars showed a larger range of behavioural responses to stinkbugs, which occurred either singly or in various combinations. Caterpillars took evasive measures in 37% of cases, either by walking quickly out of the predator's path or by jerking away, and this was always successful in evading an attack. Predators were sometimes seen pursuing an escaping caterpillar with extended proboscis, but they never succeeded in catching them and quickly gave up the chase. Caterpillars responded to the stylets being inserted into their body by thrashing 56% of the time, but this was only effective in 17% of cases, even when combined with biting. Although only very few attacked caterpillars were able to both thrash and fall off the bridge (2%), this was always a successful tactic and these caterpillars always survived the piercing of their cuticle. Caterpillar responses, however, did not change with group size.

Whether stinkbugs attacked at least once was not significantly affected by either instar (χ^2=1.634, *df*=1, *p*=0.201) or group size (χ^2=2.467, *df*=2, *p*=0.291). Stinkbugs launched more attacks per trial against fourth instar caterpillars, but were more successful in capturing second instar caterpillars (Figure 4.3).

a)



b)

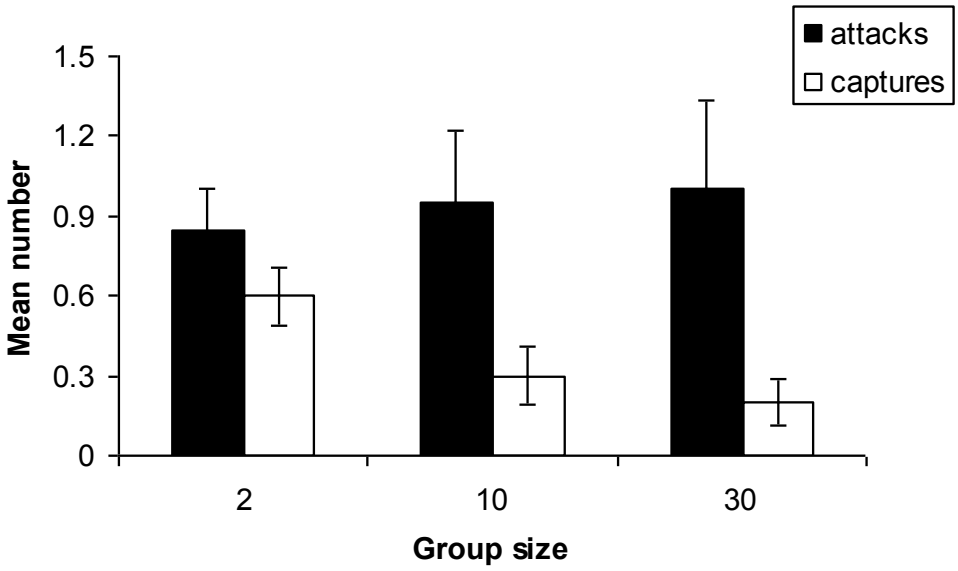


Figure 4.3: Stinkbugs: the average number of attacks (including both successful and failed attempts) and successful attacks (±SEM) for different group sizes of a) second and b) fourth instar caterpillars of *M. disstria* (*N*=20 caterpillar groups per treatment combination of instar and group size)

Again, because the number of successful attacks was not affected by group size, the mean mortality risk decreased with group size (Figure 4.2). The time needed for stinkbugs to perceive the caterpillars (i.e., the time between introducing the stinkbug to

the arena and the first moment they raised their proboscis) was not affected by either larval instar or group size (Table 4.2), but both the amount of time required to attack (35.68±10.43 vs. 200.57±43.29 s; Table 4.2) and to subdue the prey (i.e., for the attacked caterpillar to stop moving; 25.58±3.64 vs. 168.95±32.15 s; Table 4.1) was significantly longer for fourth instar caterpillars. Position within the group was again found to be important, as the center of the group did not sustain any attack for either the second or fourth instar caterpillars.

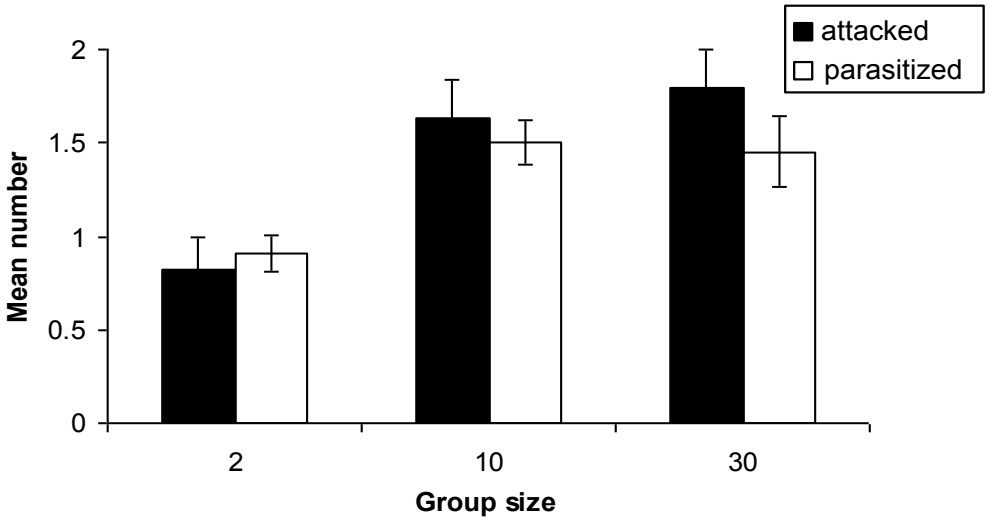
Parasitoid wasps

Caterpillars reacted to parasitoids, which stung the caterpillars with their ovipositor, both individually and as a group by flicking their heads, and in some cases, head flicking was accompanied by biting, which made it a far more effective tactic (Table 4.1). Groups of two second instar caterpillars almost never reacted to being attacked. However, for both second and fourth instar caterpillars, groups of 30 were more likely to use biting along with flicking than groups of 10 caterpillars. Indeed, on several occasions the larger groups of caterpillars succeeded in grasping the wasp with their mandibles and proceeded to rip it to shreds. This would always severely injure the wasp and occasionally even killed it.

The probability of at least one attack by a parasitoid per trial significantly increased with group size (χ^2=9.872, *df*=2, *p*=0.007) but was not affected by larval instar (χ^2=0.573, *df*=1, *p*=0.449). The number of attacks increased with caterpillar instar (Figure 4.4), but the number of successful attacks (i.e., determined by the subsequent emergence of a parasitoid from the caterpillar) decreased with instar (Table 4.2). The number of

attacks and of successful attacks increased with group size (Figure 4.4), but the individual mortality risk still decreased with group size (Figure 4.2).

a)



b)

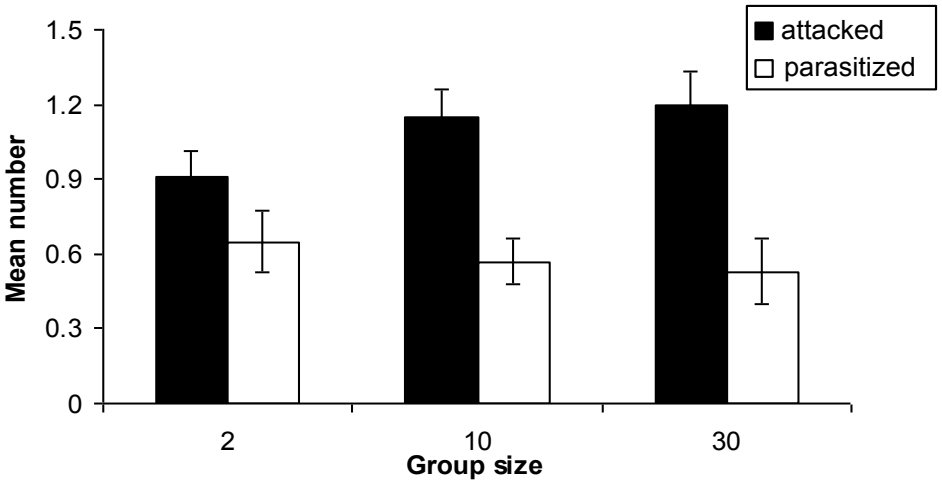


Figure 4.4: Parasitoids: the average number of attacks (including both successful and failed attempts) and successful attacks (±SEM) for different group sizes of a) second and b) fourth instar caterpillars of *M. disstria* (*N*=20 caterpillar groups per treatment combination of instar and group size)

The time before an attack (i.e., time elapsed between the start of the experiment and the first attack observed) was not influenced by either caterpillar instar or group size, but the amount of time caterpillars spent head flicking after an attack significantly increased with group size (Table 4.2). Position within the group was again found to be important as the center of the group sustained fewer attacks.

4.5 Discussion

Caterpillars of *M. disstria* responded to attacks with predator-specific behaviours, which in many cases were successful in warding off attacks. When stinkbugs were used as predators, evasive behaviours were the most efficient in increasing survival, as has also been observed for *Nezara viridula* (De Clercq *et al.*, 2002) and *Bombyx mori* (Lemos *et al.*, 2005) caterpillars. These behaviours were never observed against spiders. Many fourth instar caterpillars thrashed when attacked by either spiders or stinkbugs, but this behaviour was most successful when used against spiders. Second instar caterpillars that were attacked by spiders sometimes responded by holding onto the silk mat. This behaviour was never observed with stinkbugs, and it would not likely have been successful, as shriveled caterpillar carcasses are often found still attached to naturally occurring tents and silk mats of *Malacosoma* colonies attacked by *Podisus* stinkbugs. Head flicking and biting were observed in both second and fourth instar caterpillars when attacked by parasitoids, but not when attacked by walking predators. Predator-specific responses of *M. disstria* groups were also observed during preliminary trials using *Calosoma* beetles: attacked individuals thrashed vigorously, but unsuccessfully as even fourth instar caterpillars are much smaller than the beetles. But while the beetle was busy

with one prey, the rest of the caterpillar group moved away together and relocated to a new bivouac elsewhere, which is important because a single beetle can eradicate an entire colony (Fitzgerald and Costa, 1999). Other studies (e.g., Clark and Faeth, 1997) have shown that, if predators are not satiated by a single prey item, or if they show a strong and very rapid numerical response, they can annihilate entire groups and group relocation may be beneficial. Indeed, groups of *M. disstria* caterpillars have also been shown to relocate their bivouac in response to attacks by *Polistes* wasps (McClure and Despland, 2010). However, relocation of the entire group before a food patch is depleted is likely costly, and it makes sense that this response would only be observed when caterpillar groups are attacked by predators capable of successfully predating most, if not all, of the group.

Although different responses to different predators are believed to be adaptive and has previously been suggested, little experimental work has been done to empirically demonstrate this (Botham *et al.*, 2006).

The escape responses of *M. disstria* caterpillars to predator attacks also varied with larval instar. Smaller caterpillars had fewer defensive behaviours and never dropped off the bridge, probably because the cost of being separated from the group is much higher for younger caterpillars (Despland and Le Huu, 2007). Although second instar caterpillars were at times aggressive against parasitoids, biting their legs and antennae, they never successfully bit either the spiders or the stinkbug predators, both of which are larger than the parasitoids. The larger fourth instar caterpillars, however, were more likely to defend themselves with aggressive retaliation such as biting against all

predators, as the value of this defense increases with the size of the prey relative to its predator.

As such, the number of caterpillars successfully predated or parasitized decreased with increasing body size, and the time required to subdue the prey increased for both spiders and stinkbugs. However, stinkbugs and parasitoids did attack fourth instar caterpillars more often. Because stinkbugs are cautious predators that slowly approach their prey, failed attempts often occurred before any physical contact was made. As such, attempting to attack a larger caterpillar was possibly less costly for stinkbugs than for spiders and, in fact, stinkbugs were more likely to try again. However, this is likely to change with continued growth of the caterpillars and more aggressive defensive behaviours (Morris, 1963), and in fact Evans (1983) observed that stinkbugs experienced increasing difficulty in capturing *Malacosoma* caterpillars as the season advanced. As the caterpillars grew, they rapidly gained the ability to defend themselves from attacking adult stinkbugs by thrashing vigorously and forcing the timid stinkbugs to retreat and abandon the attack.

Although parasitoids can develop in second instar caterpillars, they face a higher risk of the host dying before the parasitoid larvae can complete its development (personal observation). Therefore, fourth instar caterpillars are better hosts and this is most likely why parasitoids preferentially attacked more of the fourth instar caterpillars. Yet the proportion of caterpillars successfully parasitized decreased with increasing larval size, which suggests a trade-off for parasitoids. This may be due to both an increasing difficulty in successfully parasitizing the caterpillars due to defensive behaviours such as biting, and a stronger immune system in older caterpillars. As such, successful parasitism

is likely to continue decreasing with increasing growth of the caterpillars. Thus, overall increased body size lowers likelihood of successful attack for all three natural enemies but, at least for parastioids, larval body size appears to increase attractiveness of prey.

Grouping appeared to lower individual risk from all three natural enemies via dilution and the selfish herd effect. In all three cases, individual risk decreased with increasing group size and individuals in the center of the group were at a lesser risk of sustaining attacks than individuals situated at the periphery.

For spiders and stinkbugs, group size had no effect on the number of attacks or the number of successfully captured caterpillars. Because the number of prey successfully attacked was never more than one per trial, mortality risk always decreased with group size. There were no group responses for either second or fourth instar caterpillars attacked by either of the walking predators and therefore, against these predators, dilution of risk appears to be the only group benefit. Presumably, larger aggregations would be beneficial in the field if they do not attract more predators. For the gregarious caterpillar *Halisidota caryae* (Lawrence, 1990), larger aggregations did not attract more invertebrate predators than did smaller ones, and so the likelihood of being taken was lower in a larger group. For *Malacosoma* species, Evans (1983) found that the density of caterpillars in a group was always high enough that the functional response of a pentatomid predator was independent of larval density.

By contrast, collective defense was observed against parasitoids. The parasitoids attacked more than one caterpillar once a group was located. However, despite multiple attacks and a higher attack success rate, mean mortality still decreased for individual caterpillars living in larger groups. The number of individuals successfully parasitized did

not increase as rapidly as the number of individuals within a group. This may in part be because the optimal foraging time spent at a patch for parasitoids is limited by a diminishing return (Wajnberg, 2006), but may also be due to the increasing difficulty in attacking defensive groups.

Indeed, although there was no evidence for group vigilance in trials done with spiders or stinkbugs, caterpillars appeared to benefit from the warning of a parasitoid's presence, possibly through the wing vibrations of parasitoids, vibrations in the silk mat generated by flicking caterpillars, and/or through the direct physical contact with flicking caterpillars, although they do not appear to respond to vibrations caused by approaching predators or by thrashing conspecifics. Caterpillars attacked by the parasitoids usually aggregated as tight flicking groups and displayed cooperative defenses such as simultaneous biting of the wasps' legs and antennae. Individuals who started flicking before having sustained an attack themselves therefore appear to be benefiting from the signaling of other individuals, but those who have already been attacked also benefit as they may be attacked more than once (personal observation). Although groups of two caterpillars occasionally displayed these behaviours, they occurred less often, at a lower intensity and for a shorter time. The time spent flicking by groups after the first attack also increased with group size, which suggests that the effectiveness of this behaviour increases for larger groups.

In conclusion, we show that *M. disstria* exhibit different behaviours in response to different predators and at different larval stadia. Like guppies (Botham *et al.*, 2006) and monkeys (Seyfarth *et al.*, 1980), these caterpillars are able to discriminate between different predators, likely as a result of very different modes of attack, and respond

appropriately. Indeed, this study shows experimentally that prey benefit in terms of survival by adopting different responses, although how these caterpillars are able to identify the predator and decide which response to take has yet to be determined.

In general, fourth instar caterpillars showed more varied defensive responses, including falling off the bridge and biting the aggressor, and were more successful against all three natural enemies. Our results confirm that larval vulnerability is greatest in the early larval instars, supporting the idea that rapid growth constitutes a defensive benefit. An extended development time in herbivorous insects increases larval exposure to natural enemies, termed the slow-growth high-mortality hypothesis, and has been shown in many species (Schultz, 1983; Benrey and Denno, 1997). For example, Parry *et al.* (1998) found that survivorship of later hatching *Malacosoma* caterpillars was drastically reduced by invertebrate predation and Evans (1982) observed that during unfavorable weather in the spring, the activity of predatory stinkbugs was temporarily suppressed and enabled the tent caterpillars to escape predation by growing to sizes too large to be subdued by the predators. We show that increased size is advantageous for caterpillars against three very different modes of attack, due not only to the predator's difficulty in handling larger prey, but also to the caterpillar's broader range of defensive behaviours. Our results also show a lower per capita predation risk in larger groups. In the case of spiders and stinkbugs, the benefits of grouping could only be attributed to dilution of risk, but against parasitoids, caterpillars also exhibited group defenses. Improved anti-predator defense has been suggested as a benefit to group living in a wide range of taxa (e.g., Hass and Valenzuela, 2002; Uetz *et al.*, 2002; DeVito, 2003; Rogovin *et al.*, 2004; Lemos *et al.*, 2005; Smith and Awan, 2009), including many caterpillars (see

Vulinec, 1990). We confirm that grouping does indeed protect *M. disstria* caterpillars against predation and that they use group defenses in some contexts. Aggregations of early instars of *M. disstria* have also been shown to benefit from group thermoregulation (McClure *et al.*, 2011) which enhances larval growth rates (Levesque *et al.*, 2002), and thus the aggregated larval lifestyle may also indirectly reduce predation by decreasing exposure to predators. Grouping thus appears to protect *M. disstria* against predation via several simultaneously acting mechanisms: predator dilution, group defenses, faster development, and possibly aposematism (Heinrich, 1993a). Hunter (2000), who compared the shapes of published survivorship curves of gregarious and solitary Lepidoptera and Symphyta, concluded that there was something in addition of the possession of defenses that explains the higher larval survival of gregarious species. This study further supports their suggestion that dilution of risk, possibly in concert with increased group defense behaviours, and reduced duration of exposure to enemies because of rapid development time may explain the survival advantage of gregariousness.

Finally, the decreased tendency to aggregate of later instars of *Malacosoma* species has been tied to an increase in food competition (Despland and Le Huu, 2007) and a reduced need for thermoregulation (McClure *et al.*, 2011); our results suggest that it may be further enabled by caterpillars' increased ability to defend themselves against invertebrate predators.

Chapter 5- Group leadership depends on energetic state in a nomadic collective foraging caterpillar

The following chapter is based on the published manuscript: McClure, M., Ralph, M. and Despland, E. (2011) Group leadership depends on energetic state in a nomadic collective foraging caterpillar. Behavioral Ecology and Sociobiology 65: 1573-1579

5.1 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 behavioural 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 labour 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 synchronization during foraging in this species.

5.2 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 some caterpillars (Underwood and Shapiro, 1999; Fitzgerald, 2003).

The present study investigates which individuals initiate collective locomotion and occupy frontal positions in traveling 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 interindividual differences in the activity of *M. disstria* caterpillars over four trial days, but it is not clear whether this has any impact on leadership of foraging bouts.

M. 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 3 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.

5.3 Methodology

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 16-h 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 colonies each of second and fourth instar caterpillars were used on the second day after moulting to ensure that none of the caterpillars moulted before the end of the trials. Both second and fourth instar caterpillars were studied during these experiments, as they exhibit differences in group behaviour. Trials were repeated at 24-h intervals for three consecutive days for each colony. Caterpillars were food-deprived for 3 h prior to the experiment to control for energetic state. Colonies consisted of all

caterpillars arising from a single egg mass (with the number of individuals varying between 37 and 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 setup). The bridges were replaced after each trial to ensure that pheromone trails were not present. Bridges measured 36.5 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 colony 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 colony 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 1 h 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, due to their small size, we could not accurately weigh them individually. For five of the fourth instar colonies, 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 3 days of observation that an individual was a leader, identified by the number of coloured 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 colony independently, if there was significant departure from the expected frequencies. The effect size (chi-square values) was plotted as a function of colony size for each larval instar and analyzed 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 colonies. 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 colonies (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 nontoxic 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 3 h before the experiment, a normal intermeal interval for this species (Peters and Despland, 2006; McClure and Despland, 2010). A wooden craft stick measuring 113 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 s, 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 treatment of unfed individuals (87.5%, 75%, 50%, 25%, 12.5%). Trials were terminated when the group reached the food or after 200 min.

Statistical Analysis

To determine if unfed individuals were more likely to take the lead than expected, a chi-square test for goodness of fit compared across ratio treatments 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.

5.4 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 colony led at least once. Chi-square tests done for each colony individually, both of second and fourth instar caterpillars, were all nonsignificant (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 α = 0.05 is χ^2_3 = 7.815 (Sokal and Rohlf, 1981); the effect sizes in our tests are all well below this critical value (see Figure 5.1). The effect size (chi-square values) was also not significantly affected by colony size in either larval instar (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; Figure 5.1). Chi-square tests pooling all 15 colonies together were not significant either (second instar, χ^2=0.78; df=3; p=0.854; fourth instar, χ^2=3.37; df=3; p=0.338).

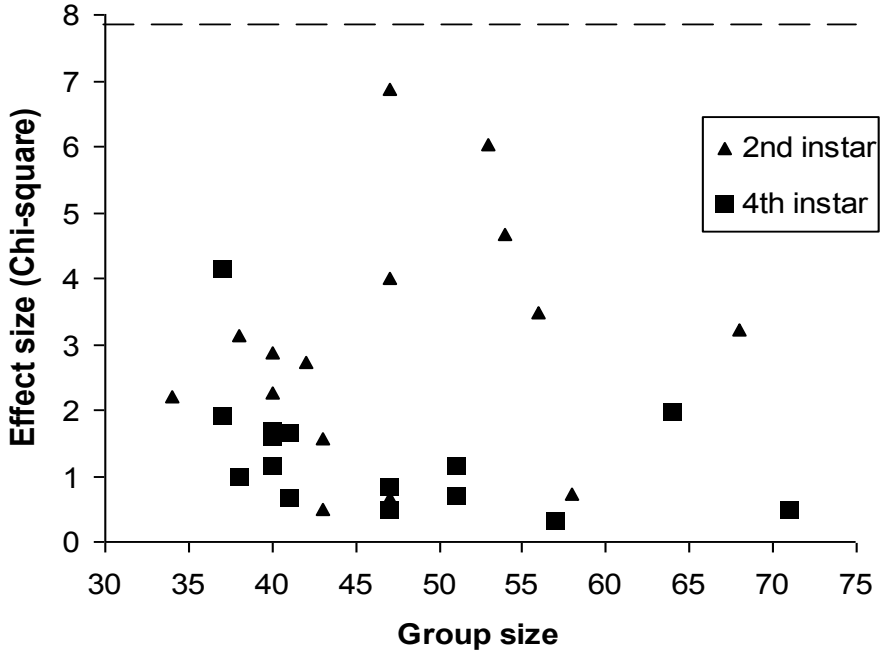


Figure 5.1: The effect size (chi-square values) as a function of group size for both second and fourth instar *M. disstria* caterpillars. The *dashed line* represents the critical chi-square value (7.81) necessary to obtain p=0.05 with three degrees of freedom.

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, Figure 5.2). Overall, 82% of all forays (N=50 groups that initiated foraging) were led by unfed individuals.

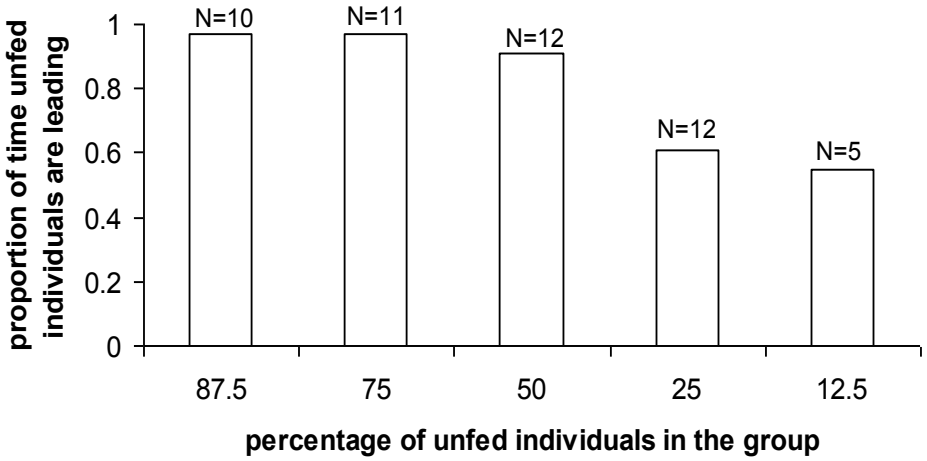


Figure 5.2: The proportion of observations in which unfed *M. disstria* caterpillars are in the front of the group as a function of the percentage of unfed caterpillars in the group. The sample size (N) indicates the number of groups in each case which initiated foraging, out of a total of 12 tested.

The majority (93%; N=48) of groups with 25-87.5% unfed individuals started a foraging bout within 40 min; however, more than half of the groups (N=12) with 12.5% unfed individuals did not initiate a foraging bout in the 200 min of the trial (Figures 5.2, 5.3). 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).

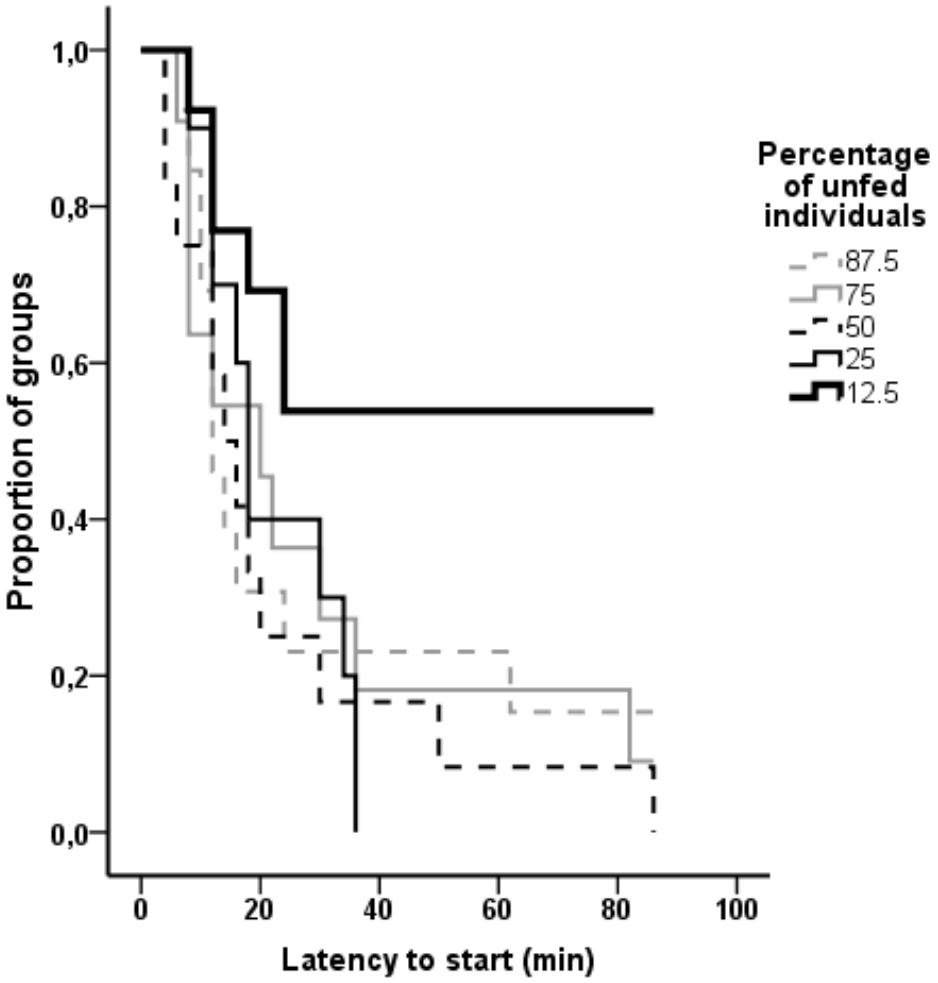


Figure 5.3: Survival curves showing the latency of *M. disstria* groups to start a foraging bout under the different fed/unfed ratios. The *y*-axis indicates the proportion of the groups that have not started foraging by the time indicated on the *x*-axis (in minutes). Curves that terminate above zero show the proportion of groups that did not initiate a foraging bout within 200 min.

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 h (Figure 5.4). Also, none of the groups with 12.5% unfed individuals reached the food in less than 15 min, whereas in all the other treatments, some groups reached the food in less than 5 min (Figure 5.4). 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).

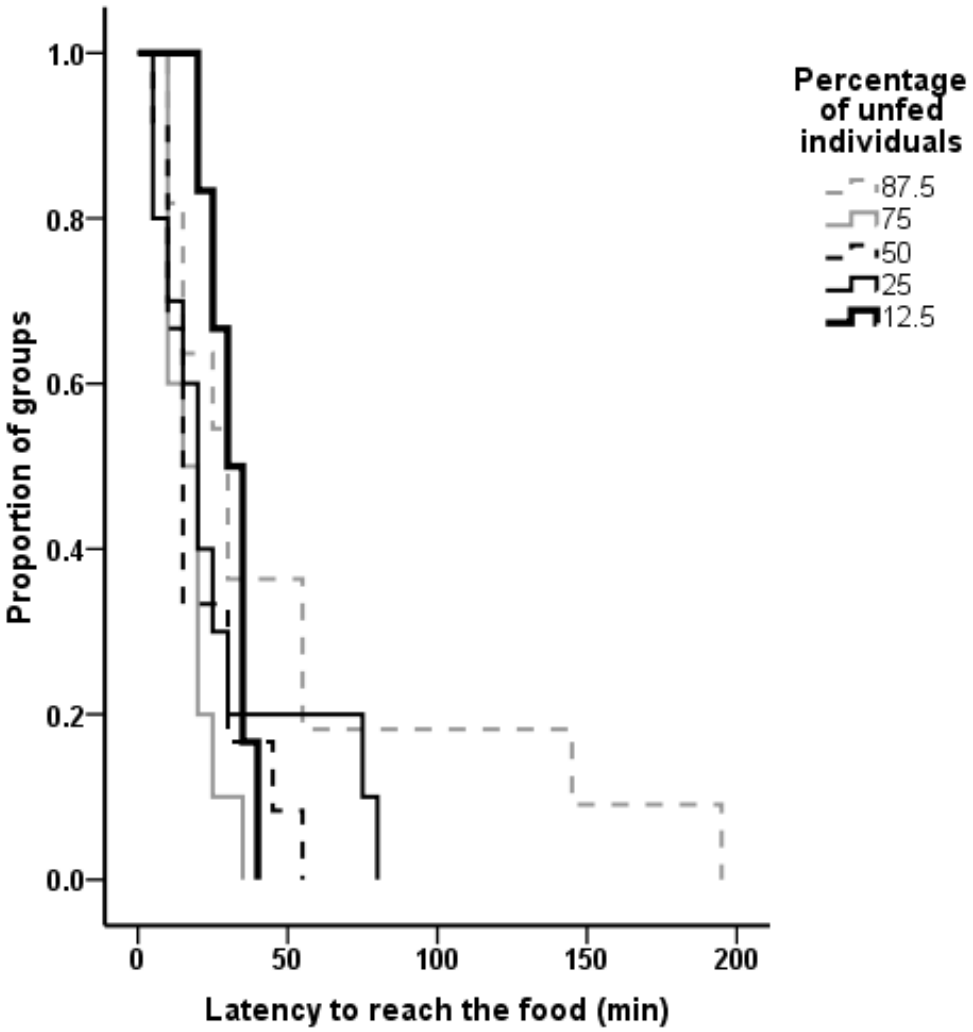


Figure 5.4: Survival curves showing, for all fed/unfed ratios, the time groups took to reach the food once they had started. The *y*-axis indicates the proportion of the groups that have not reached the food by the time indicated on the *x*-axis (in minutes).

5.5 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. Indeed, tactile cues are thought to transmit the signal to begin locomotion as group members imitate the movement of their neighbours (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 behaviour, 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 caterpillars (Cornell *et al.*, 1988), 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 (Figure 5.2) and that groups containing hungry individuals initiate foraging sooner (Figure 5.3). 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 neighbours 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 defense (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 5.3 suggests that the initiation signal is fully present even in groups where fed individuals outnumber the unfed ones three to one, 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 (Figure 5.4). 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 is 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.

Chapter 6- General Conclusion

The objective of this study was to determine the benefits of grouping and the mechanisms for staying together in the nomadic social forager, *M. disstria*. This species relies on developing rapidly despite low seasonal temperatures, benefiting from springtime high food quality and low predation rates. As such, behavioural thermoregulation and protection from invertebrate predators are likely to be important advantages of larval aggregations in this species.

Our study shows that collective thermoregulatory behaviour is not only possible and advantageous in this species, but it also drives much of the colony's behaviour, in large part dictating the temporal (chapter 2; chapter 3) and spatial patterns (chapter 3) of movement. Colonies were able to increase their body temperature by basking when a radiant heat source (i.e., a lamp in the lab and the sun in the field) was present, although this was only effective when caterpillars clustered in groups. Body temperatures achieved when basking in a group coincided with the temperatures at which the development rate is maximal for this species and resulted in higher growth rates in the lab, suggesting that thermoregulation is an advantage to group living. Colonies moved away from the food to bivouac and bask when a radiant heat source was provided, but colonies were more likely to bivouac right by the food when there were no basking opportunities. This is likely a trade-off between the physiological benefits of thermoregulation and its ecological costs (Dubois *et al.*, 2009), as it likely reduces energetic costs and potentially fatal encounters with invertebrate predators (chapter 2).

This study also shows that grouping of *M. disstria* caterpillars confers protection from invertebrate predation mostly through dilution of risk, and, in the case of

parasitoids, also through group defences. We also show that growth to larger body sizes is advantageous for caterpillars against three different natural enemies with very different modes of attack, due not only to a difficulty in handling larger prey, but also to the caterpillar's broader range of defensive behaviours. Because an extended development time in herbivorous insects has been shown to increase larval exposure to natural enemies (Evans, 1982; Schultz, 1983; Benrey and Denno, 1997; Parry *et al.*, 1998; 2000; Despland and Le Huu, 2007), these results lend further credence that larval vulnerability is greatest in the early larval instars and that rapid growth constitutes a defensive benefit. As suggested by Hunter (2000), this study shows that dilution of risk, increased group defensive behaviours, and reduced duration of exposure to enemies because of rapid development, likely all act in concert to explain the increased survival advantage of gregarious larvae.

Therefore, in *M. disstria* the selection pressure to remain within a group in the early larval stages is strong because caterpillars in groups have higher survival rates, develop faster and reach larger sizes than isolated individuals (Despland and Le Huu, 2007), likely as a result of improved thermoregulation and group defence (Chapter 2, 3 & 4). Yet, in order to stay together and reap the benefits of group living, animal groups on the move need to make collective decisions about the initiation, speed and direction of travel. Activity of *M. disstria* colonies is highly synchronous with clear alternations between periods of activity and quiescence, likely as a result of social facilitation. In larvae, tactile cues from increasingly restless individuals are believed to initiate collective foraging. The signal to begin locomotion is then transmitted to the group as individuals

imitate the movement of their neighbours (Long, 1955; Fitzgerald and Costa, 1999; Ruf, 2002).

Our findings suggest that these interactions are not initiated consistently by the same individuals, but rather by those that are hungriest. Rands *et al.* (2003)'s model suggests, and the data in Chapter 5 confirms, that 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 from the group. Indeed, as suggested by Conradt *et al.* (2009), group movements are led by those members for whom it is most crucial to reach a particular destination, and they likely do so by changing simple behavioural parameters, such as movement speed, assertiveness, or their range of social attraction – or in this case willingness to move off trails (i.e., assertiveness). Termed leading according to need, this has also been demonstrated in fish, whereby food-deprived individuals position themselves in the front of shoals and have a stronger influence on movement direction, whereas well-fed fish, which are predicted to have a stronger interest in group cohesion, follow behind (Krause *et al.*, 1992; Krause, 1993). The consensus decision to initiate foraging in *M. disstria* caterpillars appears to be partially shared among group members. Indeed, the strength of the initiation signal (as an absolute number or a proportion of individuals) represents a quorum at the individual level triggering the subsequent departure of the group (Petit and Bon, 2010). Our results suggest that this initiation signal is driven by the highly motivated and hungry individuals, but that a minimum number is necessary for action to begin.

In conclusion, the results of this study have shown that, for the nomadic and social caterpillars of *M. disstria*, group thermoregulation and protection from predation

are important selection pressures keeping larval colonies together. These advantages dictate both the temporal and spatial patterns of foraging in this nomadic species. In order to benefit from these advantages, *M. disstria* caterpillars are able to stay cohesive and make collective decisions as a result of individual interactions. However, a gregarious lifestyle is affected by the complex balance between both costs and benefits. Therefore, in this thesis we have also examined how protection from predators and thermal benefits, using both field and laboratory experiments, influence the social structure of groups during ontogenic development. Indeed, the decreased tendency to aggregate of later instars has been tied to an increase in food competition, and our results suggest that it may be further affected by the caterpillars' reduced need for thermoregulation (chapter 3) and increased ability to defend themselves against invertebrate predators (chapter 4).

As a result, group living in this species is favoured in the earlier part of development, when its adaptive value is strongest. Indeed, because the costs of becoming separated from the group (i.e., reduced predation risk and loss of thermal opportunities) decrease with age, older caterpillars are increasingly more independent. As such, the behavioural mechanism to this waning group fidelity can be linked to older caterpillars being capable of more independent locomotion and being more likely to explore new territory on their own (Colasurdo and Despland, 2005). Just as individuals acting as temporary leaders are likely do so as a result of changes in their behavioural parameters, the greater independence of older caterpillars is likely the result of greater assertiveness and a decrease in their attraction to other individuals. As group cohesion becomes less important and as activity asynchrony increases, the likelihood of group fragmentation increases (Conradt, 1998; Conradt and Roper, 2000; Conradt *et al.*, 2009).

Like other examples of self-organization, groups of *M. disstria* caterpillars share similar behavioural mechanisms by which group members maintain cohesion and coordinate their activities. It is therefore possible to establish general principles or to test the generality of behavioural rules existing in other species. However, general conclusions across species regarding the advantages accruing from sociality in general are difficult to make as they are both numerous and various even within gregarious caterpillars (Costa, 2006). Because the relative importance of different factors promoting group living varies greatly among different social animals, it is essential to search for common patterns, both among phylogenetically close species and those that experience similar environmental conditions. Similarly, investigating different social systems exhibiting a diversity of cooperative traits will improve our understanding of the emergence of collective patterns and cooperation. As such, there are still many questions that can be answered by further studying the collective foraging of *M. disstria* caterpillars. For example, in order for animal groups to move cohesively, group members need to reach a consensus not only on the timing, but also on the spatial direction/destination of the collective movement. However, amplification can be sensitive to initial conditions (Sumpter, 2006 and references therein) and strong amplification of the initial choice can lead to the group becoming 'trapped' on the first source that is contacted (Beckers *et al.*, 1990; Beckers *et al.*, 1992; Schmidt *et al.*, 2006; Dussutour *et al.*, 2007). A recent study (McClure *et al.*, submitted) has shown that, in *M. disstria*, a reduction in the trail following behaviour enables caterpillars to abandon a poor food source and allows the formation of new trails which are preferentially followed by the group, despite a lack of recruitment by either chemical or physical means like in eusocial

insect species. However, the efficiency with which they do so varies as a function of the type of quality variation between the patches. How this may relate to the collective food choices of these caterpillars remains to be seen.

Similarly, much of the previous literature has looked at host acceptability of individual caterpillars because individual preferences are often amplified at the group level in social animals. Yet the collective decision to exploit a food source may differ from the individual decision to do so because of differing foraging strategies. Because abandoning a suboptimal food source in the hopes of discovering a new and better one is costly (in energy expenditure and predation risks, but also in loss of feeding opportunities), availability is likely to be an important factor. This may be especially important in these caterpillars which can reach very high densities during outbreaks, and where excess choosiness could lead to a loss of feeding opportunities during scramble competition. Studies on these principles of collective food choices are presently ongoing in *M. disstria* caterpillars.

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