Fitness effects of group merging in a social insect

James T. Costa[1*] and Kenneth G. Ross[2]

[1]*Department of Biology, Western Carolina University, Cullowhee, NC 28723, USA*
[2]*Department of Entomology, University of Georgia, Athens, GA 30602, USA*

Animal social groups often consist of non-relatives, a condition that arises in many cases because of group merging. Although indirect fitness contributions are reduced in such groups compared with those in groups composed of close kin, the genetic-heterogeneity hypothesis suggests that these groups may benefit from increased intracolony genetic variation, which may boost group performance through increased task efficiency or parasite resistance. We confirm one prediction of the task-efficiency explanation by demonstrating a genetic basis for task thresholds of socially important behaviours in eastern tent caterpillars. However, we found no evidence that the expanded range of task thresholds in mixed colonies translates into improved individual or colony performance in the field. By contrast, increased group size, a less commonly considered correlate of group mixing, was found to enhance individual fitness through its effects on larval growth. We conclude that fitness benefits offsetting the dilution of relatedness in heterogeneous social groups may often stem from augmented group size rather than increased genotypic diversity.

Keywords: tent caterpillars; group effects; social behaviour; social evolution; *Malacosoma americanum*

1. INTRODUCTION

Animal societies are often composed of individuals that are not closely related, owing to the tolerance of surplus breeders, multiple mating or the merging of pre-existing social groups (Bernasconi & Strassmann 1999; Ross 2001; Clutton-Brock 2002). This observation has led to interest in the factors that promote cooperation when kinship is reduced or absent. Such factors are often assumed to confer fitness benefits via the elevated genotypic diversity characterizing heterogeneous groups—for instance, by improving colony performance through enhanced disease resistance or task efficiency. The disease-resistance hypothesis posits that genetic diversity better enables social groups to withstand parasites or pathogens through the increased likelihood that resistant genotypes will be present (Liersch & Schmid-Hempel 1998; Baer & Schmid-Hempel 1999). Genetic diversity plays a role in the task-efficiency hypothesis as well: colonies as a whole are posited to enjoy enhanced growth and reproductive benefits under diverse conditions through the specialization of colony members in the performance of key colony-maintenance or brood-rearing tasks (Kukuk *et al.* 1998; Cole & Wiernasz 1999; Page & Erber 2002). Performance specialization may simply be a by-product of variable stimulus-intensity thresholds required for the expression of particular behaviours among colony members; if such task thresholds have some heritable basis, then increasing genetic diversity in the group may enhance behavioural specialization.

While these ideas have been discussed primarily with reference to the eusocial insects, where the repertoire of social behaviours can be large and the composition of the group can be complex, they should apply equally to other social species with simpler repertoires and smaller societies. Indeed, such groups may be ideal for exploring these hypotheses because of the relative ease with which the factors that underlie colony-level performance can be disentangled. Demographically and behaviourally simpler societies are likely to be more easily observed and manipulated, and to have smaller ranges of interactions and colony parameters to control or explain, than eusocial groups.

This study explores the task-efficiency hypothesis using the eastern tent caterpillar, *Malacosoma americanum,* as a model. Eastern tent caterpillars form highly integrated social groups in which larvae coordinate their behaviour in tasks such as nest (tent) construction and group defence, and cooperate closely in foraging through trail-based recruitment communication (Fitzgerald & Peterson 1983; Fitzgerald & Willer 1983; Fitzgerald 1993, 1995). The performance of apparently altruistic acts, such as scouting for new food sources and laying odour trails to recruit nest-mates to them, probably incurs personal risks to individual caterpillars, so that such behaviours should be less likely to evolve under kin selection when the relatedness of group members is reduced. In the wild, colonies of this insect begin as simple families composed of full siblings, but unrelated colonies frequently merge to form mixed-family colonies during the course of their development (Costa & Ross 1993). Failure of caterpillars to exclude non-siblings from their colony means that nest-mate relatedness drops from 0.5 to an average of 0.25 by the end of the season, with the precise late-season value being dictated by the number of colonies foraging on the same tree. Colonies that are the sole occupants of a tree experience no dilution of relatedness, whereas those sharing a tree with four or more other colonies suffer a drop in average nest-mate relatedness to about 0.05 by late season (Costa & Ross 1993; J. T. Costa, unpublished data). Such pronounced relatedness drop-offs lead to concomitant falls in the indirect fitness benefits of cooperation among group members.

*Author for correspondence (costa@wcu.edu).

Proc. R. Soc. Lond. B (2003) **270**, 1697–1702
DOI 10.1098/rspb.2003.2422

1697

The observed failure of eastern tent caterpillars to exclude non-kin suggests that compensatory direct fitness benefits may be associated with the merging of groups. Such benefits may arise as a result of the increased genotypic diversity among caterpillars if, for instance, greater genotypic diversity leads to greater diversity in response thresholds for recruitment or defensive behaviours and consequent enhancement of colony performance. Alternatively, these benefits may arise simply as a result of increased group size if greater size confers better food acquisition or defensive abilities, a phenomenon observed in many social vertebrates (Stacey & Koenig 1990; Solomon & French 1997; Krause & Ruxton 2002) and invertebrates (Lawrence 1990; Vulinec 1990; Detrain *et al.* 1999). In this study, we first tested for an effect of genotype (family membership) on the execution of important colony tasks, a prerequisite for confirming the hypothesis that genotypic diversity influences colony performance through its effects on individual behaviour. We then manipulated the genetic makeup and size of tent caterpillar colonies to determine the relative importance of each on colony performance in the wild.

2. MATERIAL AND METHODS

Caterpillars were collected as overwintering egg masses from black cherry trees (*Prunus serotina*) in Jackson County, NC, USA, and maintained at 80% relative humidity at 4 °C until needed. To induce eclosion, egg masses were removed from refrigeration and placed in Petri dishes with fresh food (black cherry leaves).

(a) *Genotypic effects on task performance*
We tested for biases in behavioural-expression thresholds among caterpillars of different families using mixed-family colonies in three behavioural assays. First-instar caterpillars from each of 20 families were first genotypically profiled using three variable allozyme loci (*Gpi*, *Hbdh* and *Aat-1*) (Costa & Ross 1993, 1994). Sixteen of the families that were determined to be completely distinguishable on the basis of one or more loci were paired to create eight mixed-family colonies containing 200 same-age larvae, 100 from each of the two unrelated families. Once the caterpillars had moulted to the second instar, these mixed-family colonies were transferred to wood dowel tent stands, where they were permitted to construct silken tents.

After one week, larval behavioural tendencies for silk spinning, foraging and defensive displaying were assayed by randomly sampling individuals expressing these behaviours under standard conditions. The behavioural assays were conducted as follows:

(i) *Silk-spinning assay*. Prior to bouts of foraging, eastern tent caterpillars add fresh silk to their tent en masse by randomly walking over the tent surface while extruding silk (Fitzgerald & Willer 1983). We randomly sampled 30 larvae behaving in this manner.

(ii) *Foraging assay*. Following silk spinning, caterpillars typically leave the tent in search of new feeding sites, to which nest-mates are recruited (Fitzgerald & Peterson 1983; Fitzgerald 1993). We prevented caterpillars from leaving the tent to seek food until all caterpillars were actively walking on the tent surface, after which a bridge to food was provided. We sampled the first 22–33 caterpillars to cross this bridge.

(iii) *Defensive-display assay*. Eastern tent caterpillars exhibit group defence by synchronized rearing and flicking displays coupled with regurgitation of repellent compounds (Peterson *et al.* 1987; Fitzgerald 1995). We presented a high-frequency acoustic startle stimulus (Myers & Smith 1978) close to the tent during silk-spinning bouts and then randomly sampled 9–30 caterpillars that exhibited a sustained (20 s–1 min) rearing and flicking defensive display.

All caterpillars sampled in the behavioural assays were genotyped and assigned to family of origin, and the binomial probability of obtaining the observed numbers of caterpillars from each of the two families was computed for each assay.

(b) *Individual and colony performance*
We next explored the possible effects of colony merging on individual and colony performance in the field. We created 40 replicate three-colony sets (120 total colonies) using 80 unrelated families collected in the field as overwintering egg masses. In each set, there were two single-family colonies consisting of 100 first-instar caterpillars derived from a single egg mass and a mixed-family colony consisting of 50 caterpillars from each of the two egg masses. A parallel group of 40 smaller colonies was created in which each colony contained 30 first-instar caterpillars (all from a single family or 15 from each of two unrelated families); this latter group of colonies was used to study only the effects of colony size. Colony size in eastern tent caterpillars is highly variable (Stehr & Cook 1968; Fitzgerald 1995), with colonies of 30 and 100 young caterpillars falling within the naturally observed range.

All colonies were permitted to construct tents on branched wood dowel stands in the laboratory. After a 24 h establishment period, these were transported to an abandoned apple orchard where they were fixed one to a tree (to prevent merging) after removing any pre-existing natural colonies. The experimental colonies were permitted to develop under field conditions for one month, at which point all surviving larvae were collected, frozen and weighed (wet weight). Individual survivorship (the proportion of larvae recovered) and the mean and coefficient of variation (CV) of larval weight were taken as measures of individual larval performance. Whole-colony survivorship was estimated as the proportion of colonies in which at least 3% of the original colony occupants were recovered at the end of the experiment.

(i) *Comparison 1: single-family versus mixed-family colonies*
Larval weights in single-family and mixed-family colonies were compared using paired *t*-tests (one-tailed) of the means and CVs of matched 100-caterpillar colonies. The combined mean and CV for the single-family colonies in each replicate set were estimated as the unweighted arithmetic averages when both colonies in the replicate survived to the end of the experiment; unweighted averages were used because mean larval weight and individual survivorship in colonies were not correlated ($n = 55$, Spearman's $\rho = -0.05$, $p = 0.713$).

Larval weights in these single-family and mixed-family colonies were further compared by randomly sampling a single larva from each colony in a randomly selected three-colony set and ranking the larval weights. This procedure was repeated for 20 000 iterations and the proportion of times that individuals from mixed-family colonies were ranked highest in weight was compared with the null expectation that the top-ranking weight should occur by chance with a probability of 33% in such colon-
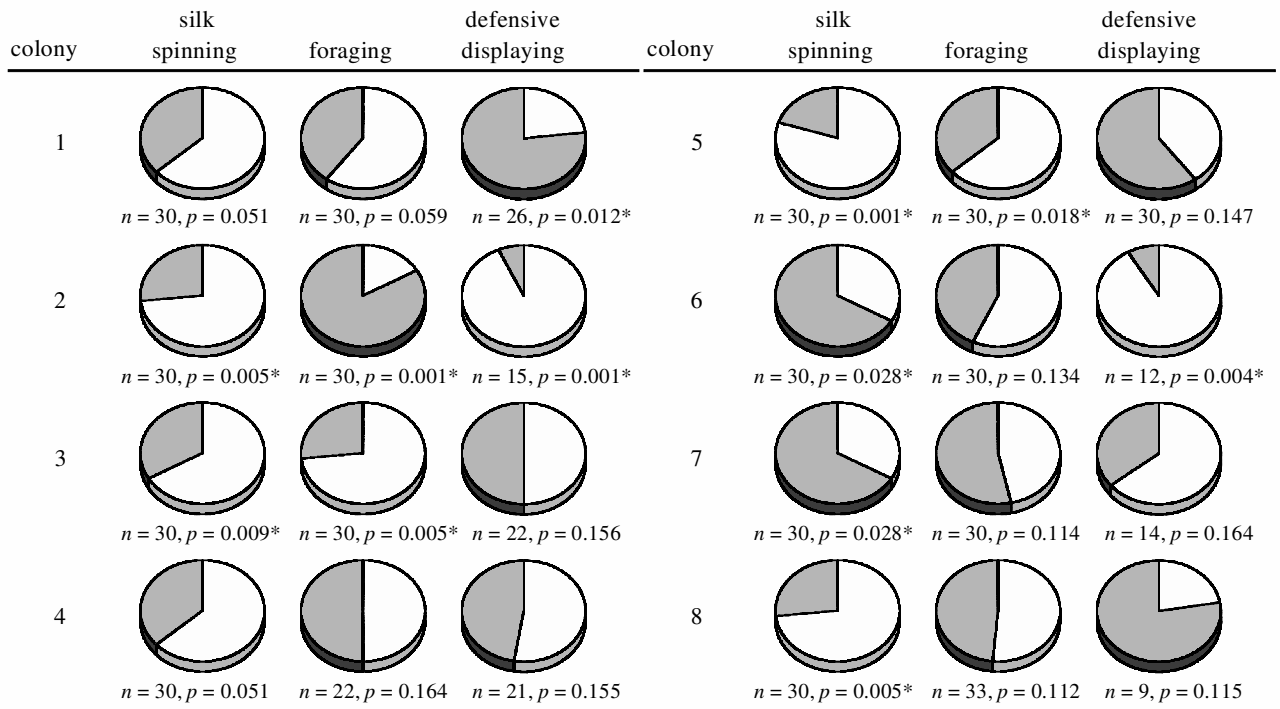
Figure 1. Relative numbers of members of different families expressing three behaviours in mixed-family eastern tent caterpillar colonies. Each colony contained 100 caterpillars from each of two full-sib families. The total number of caterpillars sampled in each assay is indicated by n, and the binomial probability that the two families are equally represented in the expression of a behaviour is indicated by p (probability values less than 0.05 are marked by asterisks).

ies. Colony sets for which only one of the two single-family colonies was recovered were analysed in the same manner, but using the null expectation that the top-ranking weight should occur by chance with a probability of 50% in mixed-family colonies.

Larval survivorships in these single-family and mixed-family colonies were compared by ranking the proportion of larvae surviving in the three colonies in each replicate set and testing the frequency of the occurrence of highest survivorship in the mixed-family colonies against the null expectation of 33%.

(ii) *Comparison 2: small versus large colonies*

Larval weights were compared between matched colonies consisting of 30 and 100 caterpillars ($n = 24$ pairs) using paired t-tests (one-tailed) of the means and CVs. One-tailed 95% confidence intervals (CIs) about the means and CVs were estimated for each colony by a bootstrapping procedure in which each colony of size n was reconstituted by randomly resampling n larvae (with replacement) over 800 iterations. The estimated means and CVs from each iteration were ranked and the 40 lowest (for the mean) or highest (for the CV) values were dropped to obtain the CI. Eight out of the 24 colony pairs in this experiment were pairs of mixed-family colonies in which each member of the pair was a mixture of the same source families; the remaining 16 pairs were formed from an original unique family.

Larval survivorships in these 30-caterpillar and 100-caterpillar colonies were compared by ranking the proportions of larvae surviving in each colony of a pair and testing the frequency of the occurrence of higher survivorship in each type against the null expectation of 50%.

3. RESULTS

(a) *Genotypic effects on task performance*

Six out of the eight replicate mixed-family colonies showed significant skew in family representation for silk spinning (binomial probabilities of less than 0.05; figure 1). In each of the tasks of foraging and defensive displaying, three colonies displayed significant family skew in task performance. Family skew was evident for more than one behaviour in half of the colonies, and in two of these colonies one family was over-represented for one behaviour and under-represented for another (figure 1). This fact, combined with the observation that three colonies showed family skew in only a single behaviour, suggests that the observed biases stem from heritable differences in specific task-performance thresholds rather than from between-family differences in general activity levels.

(b) *Individual and colony performance*

(i) *Comparison 1: single-family versus mixed-family colonies*

Larvae from mixed-family colonies failed to achieve greater weight gains than those from single-family colonies: mean weights in matched colonies of the two types did not differ significantly when both single-family colonies in a replicate survived ($t = 0.858$, $p = 0.203$, $n = 15$) or when only a single such colony survived ($t = -0.754$, $p = 0.769$, $n = 17$). A separate analysis of these data using a resampling procedure again failed to yield evidence for consistent differences in larval weight between matched single-family and mixed-family colonies (table 1). Variation in individual weights within colonies, as measured by the CV, also did not differ between the two types of

Table 1. Results of a resampling procedure for comparing larval weights in single-family and mixed-family eastern tent caterpillar colonies.

(Values are observed numbers (proportions in parentheses) of 20 000 resampling iterations in which randomly selected larvae from mixed-family colonies weighed more than those from matched single-family colonies, as well as the numbers (proportions) expected by chance if there is no difference in weights between the two types of colony. For (*a*), both original single-family colonies in a replicate set survived to the end of the experiment, whereas for (*b*), only one of the two single-family colonies survived. The number of replicate sets of each type is indicated by *n*. (See § 2b(i) for details of the resampling procedure.))

		observed	expected
(*a*)	three-colony comparisons	6012	6667
	(*n* = 15)	(0.301)	(0.333)
(*b*)	two-colony comparisons	10 416	10 000
	(*n* = 17)	(0.521)	(0.500)

colony ($t = 0.789$, $p = 0.778$ for replicates in which both single-family colonies survived; $t = 0.783$, $p = 0.777$ for replicates in which only one single-family colony survived).

Survivorship was similarly unaffected by colony genetic diversity. Mixed-family colonies had greater individual survivorship than both their matched single-family colonies in 5 out of 15 replicates, equal to the null expectation of 33% ($p = 0.469$, binomial test), and mixed-family and single-family colonies exhibited comparable whole-colony survivorships (92% and 90%, respectively). The results thus reveal no significant effects of increased genotypic diversity on the important fitness-related traits of growth and survivorship when colony size is standardized.

(ii) *Comparison 2: small versus large colonies*

Survivorship appeared not to be affected by group size. In 24 paired comparisons between small and large groups (colonies of 30 and 100 caterpillars from the same source families), exactly half of the large colonies exhibited higher larval survivorship than their smaller counterparts ($p = 0.581$, binomial test). Moreover, whole-colony survivorship did not differ significantly between small and large groups (85% and 91%, respectively; $p = 0.360$, Fisher's exact test).

By contrast, larval growth was strongly influenced by group size (figure 2). Caterpillars in large colonies displayed significantly greater weight gains than those in small colonies, both when mixed-family colonies alone are considered ($t = 7.06$, $p < 0.0001$, $n = 16$) and when single-family colonies are also included ($t = 6.81$, $p < 0.0001$, $n = 24$). Caterpillars in large colonies also experienced lower variation in growth than those in small colonies (mixed-family colonies only: $t = -1.59$, $p = 0.067$, $n = 15$; mixed- and single-family colonies combined: $t = -1.92$, $p = 0.035$, $n = 21$). On average, larvae in large colonies grew to 150% of the size of larvae in small colonies, while experiencing 19.3% less individual variation in growth.

4. DISCUSSION

This study reveals that increased genetic diversity stemming from colony merging has no apparent fitness effects
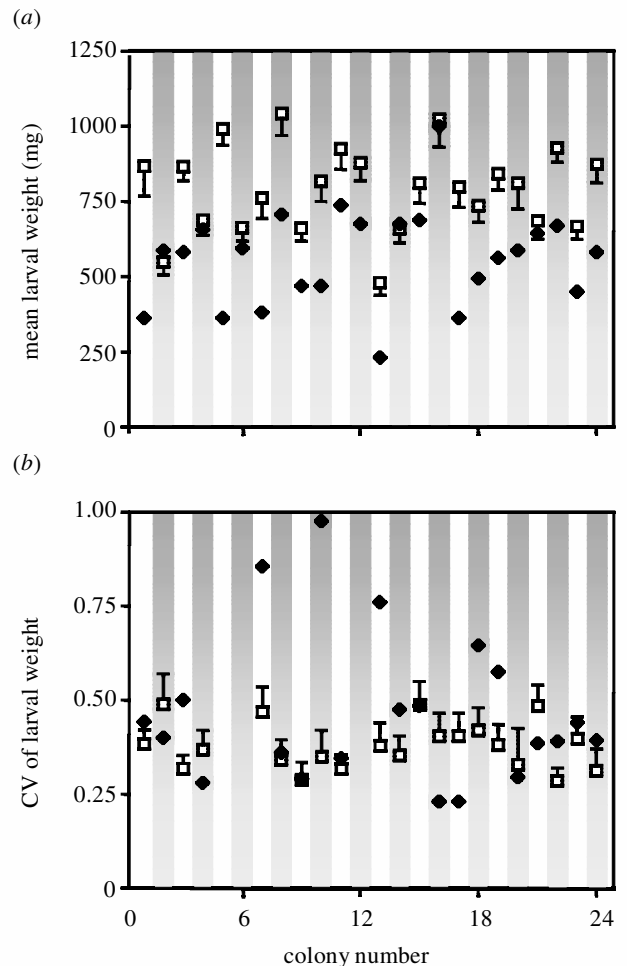
Figure 2. (*a*) Means and (*b*) CVs of larval weight in 24 paired large (100 caterpillars; open squares) and small (30 caterpillars; filled diamonds) eastern tent caterpillar colonies. One-tailed bootstrap 95% CIs are shown for the 100-caterpillar colonies (the upper tails for the mean and the lower tails for the CV for these colonies are omitted for clarity, as are both tails for the 30-caterpillar colonies). Replicates 1–8 are single-family colonies, while the remainder are mixed-family colonies. The small colonies of replicates 5, 6 and 12 contained too few surviving caterpillars to compute a CV for comparison with their matched large colonies.

in the eastern tent caterpillar. By contrast, the associated increase in group size has pronounced positive effects on the size attained by larvae, which is a trait highly correlated with adult reproductive success in this and other Lepidoptera with non-feeding adults (Shiga 1977; Stamp & Casey 1993). A number of features of eastern tent caterpillar feeding ecology and physiology might be expected to be affected by group size. Increased group size may facilitate larval growth by reducing the costs of predation and facilitating food acquisition, as has been reported in several other gregarious Lepidoptera (e.g. Tsubaki 1981; Lawrence 1990; Denno & Benrey 1997). Related to this, the amelioration of predator harassment (Stamp & Bowers 1988, 1991) and parasitism may be functions of group size, presumably because of the improved effectiveness of group displays in deterring predators and parasitoids as the number of group members increases (Vulinec 1990).

More specific to eastern tent caterpillars, increased group size may enhance larval growth through the joint effects of improved recruitment efficiency and improved group thermoregulation. Fitzgerald & Costa (1999) discussed how trail-mediated recruitment and group foraging in eastern tent caterpillars gain efficiency as the number of potential searchers and recruiters increases. Greater recruitment efficiency means faster location and consumption of high-quality food, which reduces the energy expenditures involved in foraging and the degree of exposure to predators. Thermoregulatory ability improves with increasing group size as a result of group basking: the hairy dark-bodied caterpillars experience less convective heat loss and greater thermal gains in larger groups of baskers (Casey *et al.* 1988; Joos *et al.* 1988). Moreover, the caterpillars may be able collectively to generate heat metabolically, as recently shown for the related European species *Eriogaster lanestris* (Ruf & Fiedler 2000), a feat also likely to be more efficient in larger groups. The ability to thermoregulate effectively may be especially important for the growth of eastern tent caterpillars because of the frequent cold periods larvae experience in the early spring when they are active.

Whatever the precise mechanisms involved, our study underscores the importance of accounting for the direct fitness-enhancing effects of increased group size in social species where colony merging or adoption of surplus breeders is common (Elmes & Keller 1993; Sundström 1995; Clutton-Brock 2002). Reduced inclusive fitness benefits caused by decreased genetic relatedness in such groups need not be offset by enhanced group performance stemming from the parallel increase in genetic diversity. Rather than direct positive fitness effects of increased genetic diversity, group-size effects may commonly cause the increased performance often reported in genetically heterogeneous social groups. With growing awareness of the low genetic relatedness in many animal societies (e.g. Bernasconi & Strassmann 1999; Clutton-Brock 2002), it is intriguing to consider that augmenting group size through group merging may be an effective strategy for some social species to meet better the diversity of the ecological challenges that they face, challenges that may favour grouping or cooperation regardless of genetic relationship.

REFERENCES

Baer, B. & Schmid-Hempel, P. 1999 Experimental variation in polyandry affects parasite loads and fitness in a bumblebee. *Nature* **397**, 151–154.

Bernasconi, G. & Strassmann, J. E. 1999 Cooperation among unrelated individuals: the ant foundress case. *Trends Ecol. Evol.* **14**, 477–482.

Casey, T. M., Joos, B., Fitzgerald, T. D., Yurlina, M. E. & Young, P. A. 1988 Synchronized group foraging, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate. *Physiol. Zool.* **61**, 372–377.

Clutton-Brock, T. 2002 Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72.

Cole, B. J. & Wiernasz, D. C. 1999 The selective advantage of low relatedness. *Science* **285**, 891–893.

Costa, J. T. & Ross, K. G. 1993 Seasonal decline in the intracolony genetic relatedness of eastern tent caterpillars: implications for social evolution. *Behav. Ecol. Sociobiol.* **32**, 47–54.

Costa, J. T. & Ross, K. G. 1994 Hierarchical genetic structure and gene flow patterns in macrogeographic populations of the eastern tent caterpillar (*Malacosoma americanum*). *Evolution* **48**, 1158–1167.

Denno, R. F. & Benrey, B. 1997 Aggregation facilitates larval growth in the Neotropical nymphalid butterfly *Chlosyne janais*. *Ecol. Entomol.* **22**, 133–141.

Detrain, C., Deneubourg, J. L. & Pasteels, J. M. (eds) 1999 *Information processing in social insects*. Basel, Switzerland: Birkhäuser.

Elmes, G. W. & Keller, L. 1993 Distribution and ecology of queen number in ants of the genus *Myrmica*. In *Queen number and sociality in insects* (ed. L. Keller), pp. 294–307. Oxford University Press.

Fitzgerald, T. D. 1993 Trail following and recruitment: response of eastern tent caterpillar *Malacosoma americanum* to 5β-cholestane-3,24-dione and 5β-cholestane-3-one. *J. Chem. Ecol.* **19**, 449–457.

Fitzgerald, T. D. 1995 *The tent caterpillars*. Ithaca, NY: Cornell University Press.

Fitzgerald, T. D. & Costa, J. T. 1999 Collective behavior in social caterpillars. In *Information processing in social insects* (ed. C. Detrain, J. L. Deneubourg & J. M. Pasteels), pp. 379–400. Basel, Switzerland: Birkhäuser.

Fitzgerald, T. D. & Peterson, S. C. 1983 Elective recruitment communication by the eastern tent caterpillar (*Malacosoma americanum*). *Anim. Behav.* **31**, 417–423.

Fitzgerald, T. D. & Willer, D. E. 1983 Tent building behavior of the eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae). *J. Kansas Entomol. Soc.* **56**, 20–31.

Joos, B., Casey, T. M., Fitzgerald, T. D. & Buttemer, W. A. 1988 Roles of the tent in behavioral thermoregulation of eastern tent caterpillars. *Ecology* **69**, 2004–2011.

Krause, J. & Ruxton, G. D. 2002 *Living in groups*. Oxford University Press.

Kukuk, P. F., Ward, S. A. & Jozwiak, A. 1998 Mutualistic benefits generate an unequal distribution of risky activities among unrelated group members. *Naturwissenschaften* **85**, 445–449.

Lawrence, W. S. 1990 The effects of group size and host species on development and survivorship of a gregarious caterpillar *Halisidota caryae* (Lepidoptera: Arctiidae). *Ecol. Entomol.* **15**, 53–62.

Liersch, S. & Schmid-Hempel, P. 1998 Genetic variation within social insect colonies reduces parasite load. *Proc. R. Soc. Lond.* B **265**, 221–225. (DOI 10.1098/rspb.1998.0285.)

Myers, J. H. & Smith, J. N. M. 1978 Head flicking by tent caterpillars: a defensive response to parasite sounds. *Can. J. Zool.* **56**, 1628–1631.

Page Jr, R. E. & Erber, J. 2002 Levels of behavioral organization and the evolution of division of labor. *Naturwissenschaften* **89**, 91–106.

Peterson, S. C., Johnson, N. D. & LeGuyander, J. L. 1987 Defensive regurgitation of allelochemicals derived from host cyanogenesis by eastern tent caterpillars. *Ecology* **68**, 1268–1272.

Ross, K. G. 2001 Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. *Mol. Ecol.* **10**, 265–284.

Ruf, C. & Fiedler, K. 2000 Thermal gains through collective metabolic heat production in social caterpillars of *Eriogaster lanestris*. *Naturwissenschaften* **87**, 193–196.

Shiga, M. 1977 Population dynamics of *Malacosoma neustria testacea* (Lepidoptera: Lasiocampidae): stabilizing process in a field population. *Res. Popul. Ecol.* **18**, 284–301.

Solomon, N. G. & French, J. A. 1997 *Cooperative breeding in mammals*. Cambridge University Press.

Stacey, P. B. & Koenig, W. D. 1990 *Cooperative breeding in birds*. Cambridge University Press.

Stamp, N. E. & Bowers, M. D. 1988 Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious larvae of the buckmoth, *Hemileuca lucina* (Saturniidae). *Oecologia* **75**, 619–624.

Stamp, N. E. & Bowers, M. D. 1991 Indirect effect on survivorship of caterpillars due to presence of invertebrate predators. *Oecologia* **88**, 325–330.

Stamp, N. E. & Casey, T. M. (eds) 1993 *Caterpillars: ecological and evolutionary constraints on foraging*. New York: Chapman & Hall.

Stehr, F. W. & Cook, E. F. 1968 A revision of the genus *Malacosoma* Hübner in North America (Lepidoptera: Lasiocampidae): systematics, biology, immatures, and parasites. *US Nat. Mus. Bull.* **276**.

Sundström, L. 1995 Sex allocation and colony maintenance in monogyne and polygyne colonies of *Formica truncorum* (Hymenoptera, Formicidae): the impact of kinship and mating structure. *Am. Nat.* **146**, 182–201.

Tsubaki, Y. 1981 Some beneficial effects of aggregation in young larvae of *Pryeria sinica* Moore (Lepidoptera: Zygaenidae). *Res. Popul. Ecol.* **23**, 156–167.

Vulinec, K. 1990 Collective security: aggregation by insects in defense. In *Insect defenses* (ed. D. L. Evans & J. O. Schmidt), pp. 251–288. Albany, NY: State University of New York Press.