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LESS GROWTH WITH MORE FOOD: HOW INSECT-PREY AVAILABILITY CHANGES COLONY DEMOGRAPHICS IN THE ANT, *CAMPONOTUS FLORIDANUS*

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Abstract—Colonies of *Camponotus floridanus* were maintained on diets with three levels of access to insect prey. More insects always had linear effects on queen-influenced traits, such as increasing egg number, total egg clutch biomass and larval number, or decreasing the mean weight of individual eggs. Queens responded consistently to insect protein and nutrients and appeared to be relatively invariant in behaviour. However, worker-influenced traits, such as larval and total brood biomass and pupal numbers, were more complicated in that colonies grew fastest on intermediate levels of insect protein. Similar results in an ant/lycaenid mutualism, where colonies tending fewer amino acid-producing caterpillars grew larger as well as other social insect examples suggest that larvae serve multiple functions in a colony, one of which may be as nutrient storage vessels to be cannibalized when needed. From a survey of social insect data, cannibalism appears to be more prevalent in colonies than previously appreciated. However, for a multiple-function hypothesis to explain observed colony growth phenomena, it implies that adult workers pay a survival cost to maintain extra brood. Whether such trade-offs do occur should be of considerable interest for future research.

Key Word Index: Ants; *Camponotus floridanus*; cannibalism; colony growth; demographics; egg size; larvae; prey availability; pupae

INTRODUCTION

Social insect colony growth is physically constrained by environmental factors, the amount and type of food available, and the mortality rate of workers during foraging. However, within these fundamental constraints, growth is also a function of the reproductive strategy adopted by a colony in terms of the numbers and rate at which offspring are raised. Strategies could be inflexible, in that workers behave similarly under all conditions, with brood demographics varying quantitatively depending only upon the success rate of actual foraging. Conversely, workers could change brood size and therefore colony growth trajectories based on their perceptions of their environment. An example of behavioural flexibility affecting colony demographics is the response to the presence of competitors. *Camponotus floridanus* colonies reduce the number of larvae and their total brood biomass when the workers simply perceive the presence of conspecific ants even if food remains over-abundant (Nonacs and Calabi, unpublished). The value of such a response is that the presence of competitors likely increases forager mor-

talities per unit effort, so that a smaller brood would require adults to take fewer risks.

In addition to foraging risks, colonies may react to the type and amount of food available. For example, protein and/or other nutrients associated with captured prey items can be an important limiting factor for colony growth (Dlussky and Kupianskaya, 1972; Sorensen *et al.*, 1983; Buschinger and Pfeifer, 1988; Porter, 1989). However, dead prey items cannot be kept for long without spoiling and the only possible method of “storing” their valuable contents is rapidly to convert them into living biomass (e.g. eggs, larvae and pupae).

Prey are also likely to vary in abundance so that colonies experience periods of limited availability or reduced capture rates (see Dlussky and Kupianskaya, 1972). Episodic shortages may force cannibalism of some offspring so that others can survive. Therefore, the amount and size of a colony's brood may be a reflection not only of the present availability of nutrients, but also of a colony's perception of future availability. If brood can serve as nutrient storage vessels, then colonies with an unreliable prey supply may raise extra brood during the occasional time of plenty. Consequently, increasing prey availability may not always translate into more brood if colonies view the supply as having become both plentiful and

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stable. Such is the case in the ants *Myrmica lobicornis* (Dlussky and Kupianskaya, 1972) and *M. rubra* (Brian, 1973) where either larvae number or larval growth rates are, at least initially, higher in treatments where less protein is available. Although total biomass productivity increases with protein consumption in *Formica polyctena*, *M. rubra*, *M. scabrinodis* and *M. lobicornis*, the relationships are all curvilinear such that relative productivity (production/consumption) declines with increasing protein consumption (Ayre, 1960; Dlussky and Kupianskaya, 1972).

To examine how a social insect colony responds to availability of nutrients from prey, I provided *C. floridanus* ant colonies various levels of access to insect prey and measured the rate at which colonies grew. Worker number was held constant, so that colony size effects would not affect observed growth patterns.

MATERIALS AND METHODS

Mature *C. floridanus* colonies are always single-queened with a polymorphic worker caste composed of majors and minors. The species is opportunistic and omnivorous in its feeding habits: the diet routinely contains both plant products and insect prey. In the genus *Camponotus*, workers have egg-laying potential, but worker-laid eggs are rare if not entirely absent in the presence of a healthy queen (Suzzoni *et al.*, 1986; Carlin N. F., personal communication). For the experiments, I placed the queen and 30 minor workers in a 13 × 18 × 9 cm plastic box with a glass tube half full of water behind a cotton plug as a nest site. All the source colonies from which the queen and workers were removed had 200–300 workers plus eggs, larvae and pupae indicating that they were healthy and actively growing. No larvae or eggs were initially provided to the test colonies.

I measured growth of six colonies with three levels of insect-prey/protein availability. The low level was simply an excess of fresh Bhatkar and Whitcomb (1970) diet presented to the colonies every day. This diet is carbohydrate-rich and vitamin-supplemented, but does not contain a high level of protein. Buschinger and Pfeifer (1988) found that slave-making species consume many more captured larvae when kept on Bhatkar and Whitcomb diet that is not insect-prey supplemented. Therefore, they concluded that species which normally collect insect prey would incur a protein shortage on the Bhatkar and Whitcomb diet alone. To simulate a medium and ephemeral level of prey availability, one cricket (cut in half) was presented to the colony for 24 h, every fourth day. The cricket halves were stacked to a rubber stopper by insect pins so that they could not be retrieved into the nest tube. After 24 h I removed the cricket. To simulate a stable, high level of prey availability, a cut-up cricket was presented as described above, every single day. In addition to

crickets, all colonies also received an excess of fresh Bhatkar and Whitcomb diet every day. Therefore, treatments varied only in how often insect prey were supplemented. (Hereafter I will refer to the three treatments as: NEVER, 4TH and EVERY.)

A treatment consisted of a 6-week period of being maintained on one of the three diets. At the end of every week, I counted the number of eggs, larvae and pupae and weighed each component. Five colonies experienced all diet levels once and the sixth colony experienced only the 4TH and EVERY treatments. Prior to a treatment, I kept all the source colonies (from which queens and 30 workers would be removed) for 8 days on the same diet regime as the upcoming treatment. This pretreatment period is likely to be of sufficient length for physiological changes to have begun in colonies. In particular, oviposition rates of ant queens have been shown to respond to colony manipulation within 48 h (Tschinkel, 1988). After a 6-week treatment, the queens were returned to their original colonies and the pretreatment period began for the next scheduled diet level. The sequence of diet-level presentations was varied across colonies to control for order effects. While source colonies were without their queens during a treatment period, they were fed Bhatkar and Whitcomb diet every day and a cricket every third day.

For each test colony's first 6-week treatment I selected 15 workers doing outside tasks and 15 workers doing brood care. In this way I was assured of getting a representative sample of the workforce in terms of (older) foragers and (younger) nurses. In three of the six colonies, I killed all the workers at the conclusion of a treatment and returned only queens to their original colonies. To begin the next 6-week treatment, I selected another 30 workers as described above. Therefore, these colonies were age-controlled in that test workers were of approximately the same age distribution across diet level presentations. In the other three colonies, I marked all the initial test workers with a spot of paint on the abdomen and returned them with the queen to their source colony after each treatment. They would then be removed with their queens to begin the next treatment (a few new workers would have to be added in each new treatment because of mortality). Therefore, for these colonies each successive treatment had an older workforce, but served as individual-worker controls in that it was mostly the same workers taking care of broods across the three diet levels.

RESULTS

Queens always produced eggs by the end of the first week and all colonies had larvae by the third week. Pupae first appeared at the end of the fifth week, but all colonies in all treatments did not produce pupae by the end of 6 weeks. (However, all colonies did have large larvae at the end of the treatments,

indicating that pupae maturation was imminent.) All pupae produced were of the minor worker caste, except for three majors, which were about 2.5 times heavier than the minors. These three (all from 4TH treatments) were included in comparing pupae numbers and total biomass investments, but not in calculating mean pupal size.

I first analysed the data from the five colonies which experienced all three diets with a series of ANOVAs, using independent variables of whether the same or different workers were used across treatments, the diet treatment, and the week of measurement. The latter two variables were recorded as repeated measures. The dependent variables were divided into two categories of colony traits, defined as predominantly queen or worker influenced.

Predominantly queen-influenced traits were considered to be egg number, egg size, total egg biomass, larvae number and total brood biomass in weeks 1–3 (because during this period, brood biomass was composed primarily of eggs). Obviously workers can secondarily influence these colony traits through behaviour such as reducing egg or larvae number by cannibalism. However, all these traits depend initially upon the size and number of viable eggs the queens produce and so may directly indicate the queen's response to her diet.

Predominantly worker-influenced traits were considered to be larval size, total larval biomass, pupal number, pupal size, pupal biomass and total brood biomass in weeks 4–6 (when brood biomass was dominated by larvae and pupae). Because queens do not forage or tend brood in the presence of workers, they would appear to have little direct influence on these traits which depend on the rate of provisioning and the amount of care given to the larvae.

The age of the workers had neither a significant main effect nor was it involved in any significant interactions for all traits measured. Therefore, I dropped this factor from the ANOVAs and used only treatment and week as independent variables (Table 1).

For queen-influenced traits, the week of the experiment had a significant main effect for all traits except total biomass. The availability of insect prey also had a significant treatment effect for all traits except mean egg weight. No interaction between treatment and week was significant. For worker-influenced traits, the week of the experiment had a significant main effect for all traits except mean pupal weight. Prey availability had a significant treatment effect on larval biomass, pupal numbers and pupal biomass. There were significant interactions between treatment and week for mean larval weight, larval biomass and total brood biomass. The significant interaction terms indicated that the workers in the three treatments were rearing their larvae at different rates.

To define the relationships between the three levels of prey availability better, I examined the above results, along with the data from the sixth colony, by a series of matched-pair *t*-tests (Table 2). The effects of diet always produced a consistent ordering in queen-influenced traits. Egg number and egg biomass both increased, while mean egg weight decreased with more prey availability (Fig. 1). Larval number [Fig. 2(A)] and total brood biomass (Table 3) also increased with greater access to dead crickets.

Worker-influenced colony traits were not always affected linearly by prey availability (Table 2). Mean pupal weight did increase with increasing access to crickets [Fig. 3(B)], but pupal number and pupal biomass [Fig. 3(A) and (C)] were highest in 4TH, with both 4TH and NEVER being significantly greater

Table 1. The *F*-values in the repeated measures ANOVAs for predominantly queen-influenced or worker-influenced colony traits

Traits	ANOVA main effects		
	Week	Protein level	Interaction
Queen-influenced			
Egg number	$F_{3,20} = 16.36^{***}$	$F_{2,8} = 14.80^{**}$	$F_{10,40} = 1.73$
Mean egg weight	$F_{5,20} = 30.14^{***}$	$F_{2,8} = 1.57$	$F_{10,40} = 0.58$
Total egg biomass	$F_{5,20} = 15.86^{***}$	$F_{2,8} = 15.63^{**}$	$F_{10,40} = 1.95$
Larvae number	$F_{3,12} = 37.80^{***}$	$F_{2,8} = 36.43^{***}$	$F_{6,24} = 1.57$
Total brood biomass (week 1–3)	$F_{2,8} = 4.08$	$F_{2,8} = 17.06^{***}$	$F_{4,16} = 2.18$
Worker-influenced			
Mean larval weight	$F_{3,12} = 27.70^{***}$	$F_{2,8} = 1.28$	$F_{6,24} = 6.08^{***}$
Total larval biomass	$F_{3,12} = 47.14^{***}$	$F_{2,8} = 7.01^*$	$F_{6,24} = 12.60^{***}$
Pupal number	$F_{1,4} = 9.41^*$	$F_{2,8} = 4.50^*$	$F_{2,8} = 4.27$
Mean pupal weight	$F_{1,4} = 4.57$	$F_{2,8} = 0.34$	$F_{2,8} = 2.37$
Total pupal biomass	$F_{1,4} = 8.88^*$	$F_{2,8} = 4.50^*$	$F_{2,8} = 4.05$
Total brood biomass	$F_{2,8} = 65.03^{***}$	$F_{2,8} = 2.92$	$F_{4,16} = 8.63^{***}$

Total brood biomass was analysed by two ANOVAs: the first 3 weeks (mostly eggs) and the last 3 weeks (mostly larvae and pupae). The ANOVAs for egg-related traits used data from all 6 weeks. Larvae-related ANOVAs used data from the last 4 weeks and pupae-related ANOVAs used data only from the last 2 weeks (all colonies had no larvae or pupae before week 3 and 5, respectively). Significance levels are * $P < 0.05$, ** $P < 0.01$ and *** $P \leq 0.001$.

Table 2. Summary of the matched-pair *t*-tests with the diet treatments ranked from highest to lowest for a given colony trait value

Traits	Treatment ranking				
	Highest		Middle		Lowest
Queen-influenced					
Egg number	EVERY	**	4TH	***	NEVER
Mean egg weight	NEVER	**	4TH	*	EVERY
Total egg biomass	EVERY	*	4TH	***	NEVER
Larvae number	EVERY		4TH	***	NEVER
Total brood biomass (week 1-3)	EVERY	*	4TH	*	NEVER
Worker-influenced					
Mean larva weight		No consistent relationship			
Total larval biomass		No consistent relationship			
Pupal number	4TH		NEVER	*	EVERY
Mean pupa weight	EVERY	*	4TH	**	NEVER
Total pupal biomass	4TH		NEVER	*	EVERY
Total brood biomass (week 4-6)	4TH	*	EVERY		NEVER

The *t*-tests were comparisons across all weeks where non-zero data values were available (see Table 1). For all traits the relationships were the same in any given single week, except for total brood biomass in which NEVER exceeded EVERY in week 5 and for mean larva weight and total larvae biomass in which order differed from week to week depending on the rate at which larvae became pupae. (Significant differences between treatments are denoted as * < 0.05, ** < 0.01 and *** ≤ 0.001.)

than EVERY. Total brood biomass (Table 3) was significantly greater in 4TH than in EVERY or NEVER. The three treatments had no consistent relationship in mean larval size or larval biomass from week to week [Figs 2(B) and (C)]. Larval size and biomass increased more rapidly in 4TH and NEVER than in EVERY, but at the end of the sixth week, larval biomass was greater in EVERY than at any week in the other two protein-level treatments. The latter fact suggests that the EVERY treatment would have eventually overtaken the 4TH treatment in colony biomass. This extrapolation, however, is highly speculative because both the 4TH and NEVER treatments would have had more adults enclosing earlier and thus a greater capability for raising more numerous subsequent broods. Therefore, it remains unclear as to whether measurements over longer time periods would have had a similar biomass hierarchy across the three treatments.

DISCUSSION

As the insect prey available to a colony increased, *C. floridanus* queens made smaller eggs, but because they made significantly more of them, total egg biomass increased. Dlussky and Kupianskaya (1972) found that egg production also increases in *M. lobicornis* with increasing protein availability, but did not measure mean egg weight. In *M. rubra* and *Solenopsis invicta*, queens that lay fewer eggs do produce larger eggs (Brian and Hibble, 1964; Fletcher and Blum, 1983). In a detailed study on *S. invicta*, Tschinkel (1988) found a negative correlation between volume and egg-laying rate, such that queens

produce more eggs per unit of investment. It is not clear what *C. floridanus* queens gain by varying egg size because size does not appear to affect when the eggs hatch (all colonies had larvae by week 3). Fletcher and Blum (1983) proposed that such a relationship could be simply a byproduct of egg-laying rate (i.e. producing more eggs means increasing laying rate, which forces egg size to decline).

It is clear that the initially greater egg production in the high-protein treatment did not translate into immediately higher brood biomass or more rapid production of pupae. The linear effects of more insect prey in queen-influenced traits were generally not found in worker-influenced traits, except that the mean pupal weight was greatest in the EVERY treatment [Fig. 3(B)]. It may be that colonies with more protein favoured higher "quality" offspring in that, among ants, larger workers tend to have intrinsically longer lifespans (Calabi and Porter, 1989). However, both total biomass and production of pupae were maximized when crickets were available only every fourth day. Moreover, worker age or experience made no difference across diet treatments and, thus, cannot explain the results. Instead, workers appeared to be adopting differing strategies of brood rearing based on their perception of the available supply of crickets. It must be noted that the larvae themselves may not be totally passive in this situation and could favour their own faster growth. However, since ant larvae cannot collect their own food, workers must play a pivotal role regardless of whether or not larvae are willing collaborators.

The results of this experiment with *C. floridanus* bear great similarity to those found by D. R. Nash

(unpublished) with ants (*Iridomyrmex vicinus*) tending lycaenid caterpillars (*Jaimesia evagoras*). The caterpillars exude a variety of amino acids for the ants to collect (Pierce and Young, 1986) and Nash showed that ant colonies that tend caterpillars, will produce more larvae and grow faster than those that do not (over a measured period of 120 days). However, among colonies associating with caterpillars, those tending only one caterpillar produce larger colonies than those tending five. Proposed explanations of why more does not always seem better in

this system are that multiple caterpillars are manipulating their ant tenders by scaling back the quality of their secretions in response to their own density or that one caterpillar provides 100% of the colony's needs and colony size declines with more than one because of the energy lost in tending a non-optimal number of caterpillars (Nash and Pierce, unpublished).

However, the first of the above explanations cannot be valid for the responses of *C. floridanus* because dead crickets cannot be manipulating the ants. The

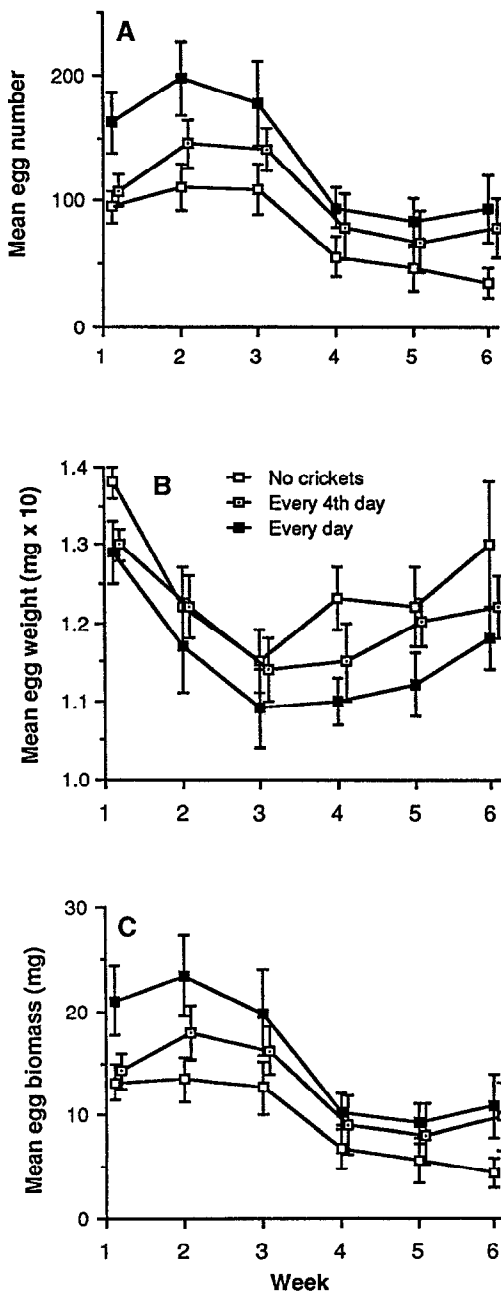


Fig. 1. The mean egg number (A), egg weight (B) and total egg biomass (C) per week ($\pm$ SE) for the three diet-level treatments.

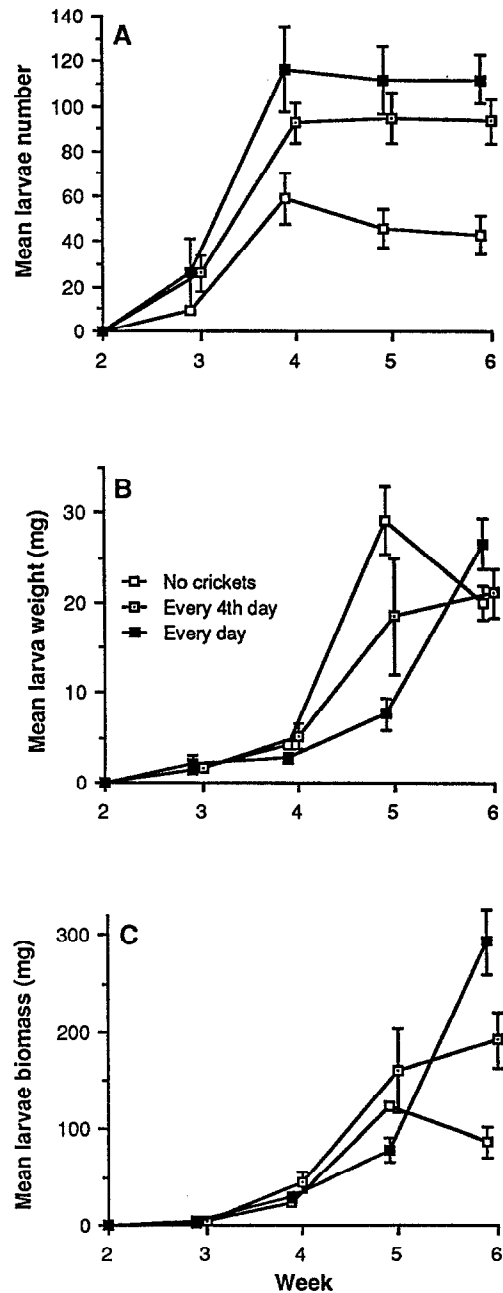


Fig. 2. The mean larva number (A), larva weight (B) and total larva biomass (C) per week ($\pm$ SE) for the three diet-level treatments.

Table 3. Mean total brood biomass (mg) per week for each diet treatment

		Treatment		
Week		NEVER	4TH	EVERY
1	Mean	13.14	14.21	21.02
	SE	± 1.75	± 1.77	± 3.31
2	Mean	13.44	17.95	23.38
	SE	± 2.16	± 2.58	± 3.94
3	Mean	14.05	21.88	23.56
	SE	± 2.56	± 3.43	± 3.07
4	Mean	30.41	54.78	39.41
	SE	± 5.41	± 12.53	± 5.67
5	Mean	136.29	209.33	89.90
	SE	± 17.97	± 53.20	± 13.65
6	Mean	197.58	400.42	317.86
	SE	± 25.04	± 69.09	± 34.97

second explanation is also very unlikely in both cases. For example, if a cricket every fourth day provided 100% of a limiting resource, then the EVERY treatment should have resulted in approximately equal, but not significantly less, growth in *C. floridanus*. Foraging in ants is energetically an extremely cheap activity (Fewell, 1988; Baroni-Urbani and Neilsen, 1990). Therefore, the minimal amount of extra work required in dealing with crickets every day (or five caterpillars instead of one) cannot by itself explain why colonies of *C. floridanus* or *I. vicinus* keep significantly less biomass with increased food.

As an alternative explanation for these growth patterns, one might consider that larvae have other roles in a colony than being potential adult workers. One of these multiple functions may be that larvae are vital protein or nutrient storage vessels. This idea was first put forth by Dlussky and Kupianskaya (1972), who proposed that cannibalism is a regular feature of the colony growth of many ant species and an adaptation to irregular protein availability. In a more general treatment, Alexander (1974) suggested that parents can produce surplus offspring in times of plenty, so that highly perishable nutrients are "iceboxed" for later use via cannibalism. Certainly, environmental variance in food availability has potential for disastrous consequences on offspring survival, such that one brief period of shortage in an otherwise plentiful season can cause entire broods to fail [for a discussion on the problems posed by variance, see Kozłowski and Stearns (1989) and Wenzel and Pickering (1991)]. In social insects, therefore, excess larvae that will be facultatively cannibalized may be a mechanism for reducing susceptibility to this variance.

In this study, *C. floridanus* colonies that find a cricket only every fourth day may view them as ephemeral. By working harder, workers may transfer cricket biomass (which will rapidly rot) into storable larval biomass as insurance against failure of the next cricket to appear. If protein food sources are stable (i.e. appear regularly every day), then no great benefit is gained in transferring biomass from dead prey to

storage in living larvae—only the costs (see below) of the associated work would remain. Similar forces may drive the ant/lycaenid interaction (Nash, unpublished). Fewer caterpillars to tend may decrease the perceived stability of the resource and thus increase tendencies to shift amino acids from caterpillars to ant larvae, resulting in greater numbers of larvae in the short term. Nash's finding that *I. vicinus* colonies grow larger when tending fewer lycaenids was based on counting all the individuals in a colony. However,

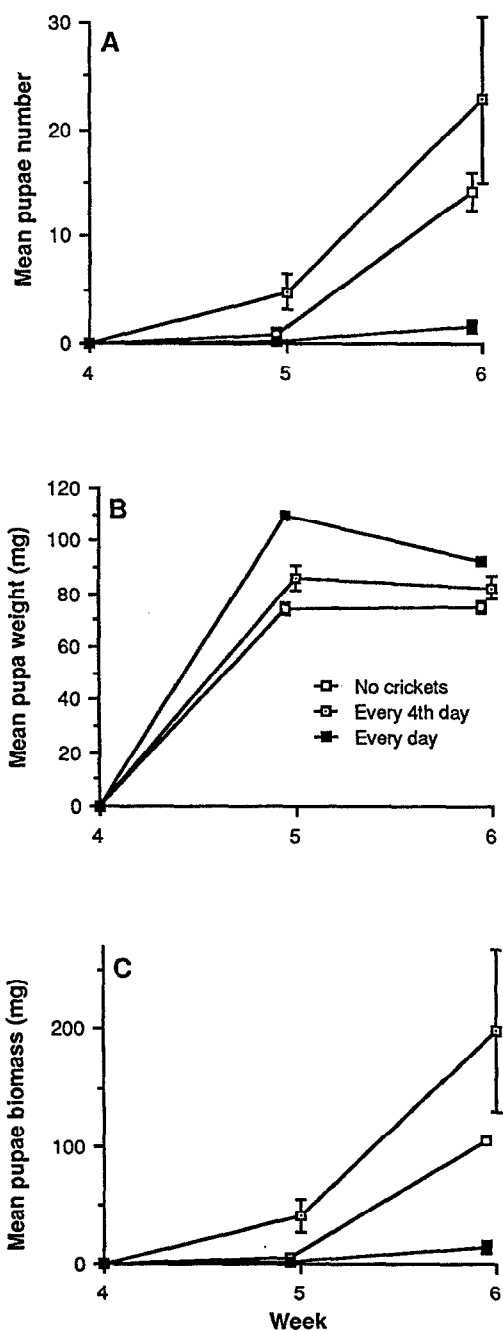


Fig. 3. The mean pupae number (A), pupa weight (B) and total pupal biomass (C) per week ($\pm$ SE) for the three diet-level treatments.

the greatest difference between the colonies was in the number of larvae maintained. Adult worker number was more similar across the treatments.

The hypothesis of larvae as storage vessels for dealing with variable food availability predicts that: (1) larvae are indeed routinely cannibalized in social insect colonies and (2) colonies may pay a cost for keeping extra, "insurance" larvae.

Concerning the first prediction, the eating of eggs is certainly common [see Crespi (1992) for a review] and cannibalism of later developmental stages, although more sparsely documented, appears to be more widespread than previously appreciated in the social Hymenoptera. Examples from ants include *C. floridanus*, where workers cannibalize larvae when larvae/worker ratios are too high, or in reaction to perceptions of increasing danger in foraging (Calabi and Nonacs, unpublished). *S. invicta* vigorously cannibalize larvae when colonies are food stressed, but some cannibalism may also be common in relatively unstressed colonies (Sorensen *et al.*, 1983). Brian (1951) found that only 33% of all eggs in *M. ruginodis* reach adulthood with mortality occurring in all developmental stages, and not attributable to obvious disease or physical injury. In Nash's (unpublished) experiment, *I. vicinus* colonies initially had larvae, but no eggs. Despite plentiful food, larvae numbers declined until new eggs began to hatch and adult number did not increase enough to account for all the missing larvae. Therefore, some must have been eaten.

Cannibalistic behaviour is by no means restricted to ants. Honeybees, although they do not collect insect prey, do eat their own larvae and pupae, particularly under periods of social stress (Winston *et al.*, 1979), or when pollen supply (the main source of protein) decreases (Newton and Michl, 1974). In wasps, larvae seem to function as a vital protein sink in that they regularly regurgitate protein and amino acid-rich droplets to adults upon solicitation (Hunt *et al.*, 1982, 1987). Hunt (1988) has proposed that this larval behaviour doubles also as an appeasement to prevent adults from eating them. Workers in many species do cannibalize apparently healthy larvae (Hunt, 1991), even under conditions when food is available *ad libitum* (Hunt, 1988). However, unlike honeybees or ants, most wasps are reproductively potent, and therefore cannibalism may reflect both a colony-level ergonomic strategy and reproductive competition between individuals (Crespi, 1992; Hunt, 1991).

The second prediction that maintaining insurance larvae has a cost must be true in at least a trivial manner: producing more brood must require more effort in brood care and food gathering. However, recent research suggests that these costs are demographically meaningful, too. When honeybees adopt higher work loads, their lifespan decreases such that brood-biomass/adult-longevity trade-offs are possible (Schmid-Hempel and Wolf, 1988). In and above a

physiological cost to working harder, maintaining more brood requires foraging more often and thus more exposure to possible predation. *C. floridanus* colonies are sensitive to the predation risks involved in foraging and reduce brood biomass when they perceive the presence of competing colonies, despite *ad libitum* food availability (Nonacs and Calabi, unpublished). Therefore, colonies that perceive insect prey to be always available (the EVERY treatment) may not maximize larval biomass as a trade-off for maximizing adult survivorship. If the above experimental foraging conditions had included predation, such a response may have actually maximized total colony biomass in the EVERY treatment.

In summary, the results from this experiment raise more questions than they answer. *C. floridanus* colony growth strategies are dependent upon insect prey availability. For some traits like egg production, larvae number, or mean pupal size, access to insects has consistent effects in that the trait consistently increases or decreases with more prey. Such ordered responses to prey availability seem most prevalent with queen-influenced traits, which may indicate that queen behaviour is relatively inflexible and only varies quantitatively by the amount of protein or nutrients they are fed. Worker-influenced traits, however, like pupal maturation and larval biomass, are more complicated with intermediate levels of protein producing the greatest response. Therefore, workers may react to prey availability with behaviourally flexible brood rearing strategies. The changes in colony demographics seem consistent with an explanation that some larvae are intended to be living storage vessels for ephemeral resources and that adult workers incur survival costs in relation to how much they forage and how many larvae they tend. These interesting hypotheses need to be further tested.

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