Egg size variation does not affect offspring performance under intraspecific competition in *Nasonia vitripennis*, a gregarious parasitoid

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Summary

1. As with many insects, egg size variation is correlated with body size in the gregarious parasitoid, *Nasonia vitripennis*. I use this feature to test the hypothesis that egg size differences among parents affects the ability of their larvae to compete for limited resources within a superparasitized host.

2. I show that egg size asymmetries in parents that oviposit into the same host have no detectable effect on relative offspring performance, even under conditions of resource limitation.

3. Broods within a host that were initiated earlier attained greater average size than competing broods in the same host that were initiated later.

4. Individuals in the more numerous brood emerged consistently larger than individuals in the less numerous brood.

5. The possibility that siblings cooperate in competing for limited resources within a host and the potential role of sibling cooperation on egg size evolution is discussed.

Key-words: competition, egg size, frequency–dependence, kin recognition, parasitoid.

Introduction

In many systems, parental investment is limited to the materials allocated by a parent to an individual propagule (i.e. an egg or a seed) to support its initial growth. Given fixed allocation to propagule production, high per-individual allocation levels occur at the cost of reduced numbers of propagules (Blackburn 1991; Roff 2002). Much theoretical and empirical research has focused on factors influencing propagule size (McGinley, Temme & Geber 1987; Fox 1994a,b; Bernardo 1996), and on the consequences of size variation (Fox 1994a; Fox & Mousseau 1996). Typically, propagule size is considered to be a genetically fixed, maternal trait that may vary due to environmental constraints operating on the parent (Perrins & McCleery 1994; Sheader 1996) or due to natural selection operating over several generations (McGinley *et al.* 1987; Lalonde 1991; Bernardo 1996; Roff 2002). Although different offspring environments can theoretically favour different optimal propagule sizes (Smith & Fretwell 1974), parents often have relatively poor information about the quality of the environment facing their offspring. Thus, in the case of

animals, we expect selection to produce either an egg of a constant size that shows the highest average fitness across offspring environments (McGinley *et al.* 1987), or a range of egg sizes within a brood that match the range of potential offspring environments (Kaplan & Cooper 1984; Poulin & Hamilton 2000). Egg size variation that does not conform to such explanations is more enigmatic.

An example of such an enigmatic pattern of egg size variation is the strong positive correlation between body size and egg size: a pattern that occurs in many animal taxa (reviewed in Bernardo 1996; Roff 2002). Given a tight correlation between egg size and offspring success, suboptimally reduced egg size in small adults imposes a reproductive cost to those adults.

A positive correlation between body size and propagule size may evolve when large females' offspring are more likely to experience food limitation through sibling competition. This occurs when large egg size increases offspring success and when large females lay more eggs in a given resource patch than small females. This last can occur despite large females' expectation of more oviposition opportunities because of increased lifespan (Ellers & Jervis 2003), because such females will always have more mature eggs at any given time (Blackburn 1991; Mayhew & Heitmans 2000) and thus have a greater tendency to be time, rather than egg-limited when foraging

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for oviposition sites (Parker & Begon 1986). However, when offspring of several females compete for limited resources in a scramble, offspring of all females must deal with resource limitation and theory predicts a constant egg size that is independent of female size (Parker & Begon 1986).

In this paper, I address the question of egg size variation and offspring fitness under interbrood competition in the gregarious parasitoid wasp, *Nasonia vitripennis* (Walk.). This wasp famously exhibits strong adaptations for optimizing the fitness of a superparasite (Werren 1980; King 1992) and has been shown to superparasitize hosts in the field (Werren 1983). Thus, *N. vitripennis* offspring will, at least occasionally, face strong interbrood competition, which should select for a large egg size that is invariant with respect to body size. However, *N. vitripennis* shows a strong positive correlation between female size and egg size (O'Neill & Skinner 1990; results below). I show here that although competing broods of *N. vitripennis* within a single host are resource-limited, small egg size associated with small body size in *N. vitripennis* does not measurably impair the ability of offspring to compete for limited resources. I then demonstrate that other factors such as relative age of competing broods and relative number of individuals in a given brood within a host are the strongest determinants of the competitive success of offspring.

Materials and methods

I replicated all experiments described below three times using three different wild-caught strains of *N. vitripennis* (C9, C15, LBII). My marker was a scarlet-eyed strain obtained from Carolina Biological Supplies. Strains were maintained in continuous culture on stocks of *Phaenicia sericata* (Meig.) (Diptera: Calliphoridae) obtained from the Simon Fraser University insectary. In all experiments, wasps were presented with host pupae that had pupated 2–4 days previously, well within the range of suitability for this parasitoid (Rivers & Denlinger 1994).

I dissected eggs from a range of females in all strains used, including the marker strain. All wasps were slide-mounted and their hind tibiae measured to the nearest 1/100 mm using an ocular micrometer in a compound microscope set at medium (100×) power. In addition to this, chorionated eggs were removed from the abdomen and egg length was measured in the same manner as for tibiae. In the majority of cases, the average length of five randomly selected fully mature eggs was calculated. If the abdomen of a dissected female did not contain five fully mature eggs the average length was calculated as the average of the total number of fully mature eggs in the abdomen.

In all treatment groups, each 2-day-old *P. serricata* pupa was exposed to one marker wasp (a red-eyed female) and one wild-type wasp simultaneously in an individual cage over 24 h. These trials were conducted at 24 °C in an 18 : 6 light : dark regimen. Immediately after exposure to wasps, pupae were weighed to the nearest 0·1 mg and placed individually in labelled gelatin capsules. All parent wasps were collected after the oviposition period, slide-mounted and their hind tibiae and remaining eggs measured in the manner described above. Progeny were then allowed to emerge and die inside the capsules. Any wasps that failed to emerge and any diapausing larvae were dissected from pupae after emergence was complete. Diapausing larvae were assumed to be wild-type, because the marker strain never produced diapausing offspring under the conditions used during the experiment (my unpublished data). I determined the sex of all mature offspring and measured their hind tibiae using the same protocol followed for the parents. Over the course of making my measurements it became obvious that offspring in the less numerous brood were smaller than the competing brood. Accordingly, I included relative size of competing broods in my analyses in this and the next experiment.

I exposed the progeny of wild-strain wasps to interbrood competition with three different time delays, relative to the marker brood. In the first treatment wild broods competed with conspecific markers laid at the same time. The second group competed against larvae that enjoyed a 24-h head start and the third faced conspecifics with a 48-h advantage. Wild-type wasps in the first treatment group were placed on the hosts at the same time as the marker strain, the second immediately after the markers were removed and the third were placed on hosts 24 h after the markers were removed. Wasps in all three treatment groups were exposed to hosts for 24 h. Hosts were prepared in the same manner as above and parents and progeny were processed as above, except that eggs were not dissected out of the parents. This last was because the strong correlation between parent size and egg size for all strains (marker; $r^2 = 0·72$; C15, $r^2 = 0·78$; C9, $r^2 = 0·63$; LBII, $r^2 = 0·60$; $P < 0·0001$ in all cases, Fig. 1) allowed me to use parental tibia length as a surrogate for egg size.

I calculated the relative success of wild strain wasps emerging from each host as the difference between
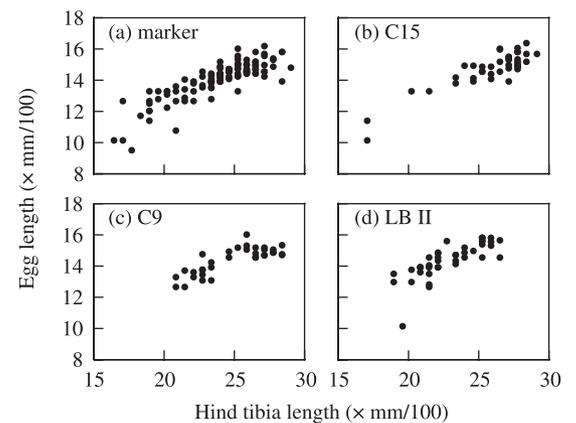

Fig. 1. Correlation between egg length and hind tibia length. (a) C15 strain; (b) C9 strain; (c) LBII strain; (d) red-eyed marker strain.

average standardized tibia length of wild and marker emergents. I standardized measures of tibia length for two reasons. First, to correct for differences between length of male and female tibiae and secondly to adjust for the effect of varying availability of food for developing larvae in individual hosts.

Average tibia length of male emergents was slightly larger than females across broods (paired *t*-test, 116 d.f., $t = 2 \cdot 647$, $P < 0 \cdot 0043$). Because of some variation in sex ratio among hosts and strains, this bias could have affected my results. To correct for this, I calculated average difference in tibia length between sexes for a given experiment, and added this difference to each female's tibia length before calculating average tibia length within a brood. I next adjusted tibia length estimates to correct for food availability. Mature size of all offspring was affected by the interaction between the size of the clutch and the mass of the host pupa such that the amount of host available to larvae strongly affected their average size within a host for both markers ($P = 0 \cdot 0004$, $r^2 = 0 \cdot 158$, Fig. 2a) and wild strain larvae ($P = 0 \cdot 0026$, $r^2 = 0 \cdot 11$, Fig. 2b). I corrected for this by regressing average sex-corrected tibia length against log-transformed host mass divided by number of competing parasitoid larvae. The log transformation was necessary in order to normalize these data. I used the residuals from these regressions as my estimate of standardized tibia length. All results reported below are for standardized tibia length, but analyses performed on raw data produced qualitatively identical results.
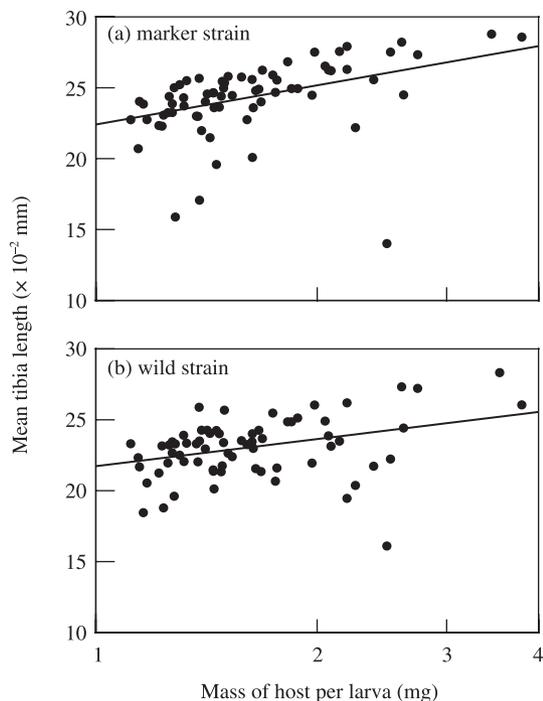
Table 1. Analysis of covariance on the effect of wild strain, log-transformed egg size ratio and log-transformed clutch size ratio between competing wild and marker strains within a host on relative brood success. Relative brood success was measured as the difference between the adjusted mean offspring size of the wild and marker broods within each host (whole model $r^2 = 0 \cdot 4133$, $P < 0 \cdot 0001$). S = wild strain, E = egg size ratio, C = clutch size ratio

Source	d.f.	F	P
Strain	2	0·2012	0·8184
Egg size ratio	1	0·4946	0·4849
Clutch size ratio	1	29·4459	< 0·0001
S × E	2	0·7754	0·4657
S × C	2	0·7319	0·4858
E × C	1	0·3540	0·1309
S × E × C	2	0·6286	0·5373

Results

I analysed the effect of strain, the log-transformed ratio of parental egg length and log-transformed clutch size ratio on the difference in average standardized offspring size among broods using an analysis of covariance. Log transformations were performed to normalize data. There was no detectable effect of egg length ratio on the success of offspring under competition (Table 1). Furthermore, there was no influence of strain type on the outcome of competition in this experiment (Table 1). Relative numbers of individuals in the two broods had the strongest effect on the outcome of within-host competition (Table 1). Relative offspring size showed direct frequency dependence, where the largest offspring in a given host were predictably members of the more numerous brood inside that host (Fig. 3). There was no significant interaction between any of the main effects in the model (Table 1).

I followed a slightly different procedure for the temporal effects experiment when I calculated standard tibia length for the wild strains. Here, I calculated deviations from the regression of tibia length against host
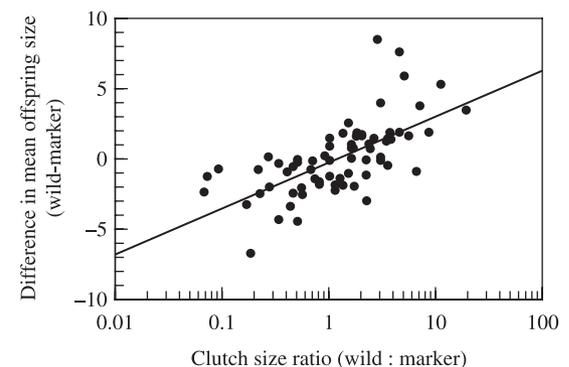

Fig. 2. Resource availability regressed against and mature size of offspring. Offspring size is indexed as within-brood average hind tibia length regressed against host mass, measured immediately after parental oviposition, divided by the total number of offspring in both competing broods that fed during development. (a) Marker strain; (b) wild strains.

Fig. 3. Effect of frequency on the outcome of competition. Difference in adjusted mean offspring size for the two competing broods (wild–marker), indexed as average hind tibia length, as affected by relative numbers of individuals in the competing broods (the clutch size ratio). The line is a least-squares regression fit.

Table 2. Analysis of covariance on the effect of time lag, log-transformed parent size ratio and log-transformed clutch size ratio between competing wild and marker strains within a host on relative brood success. Relative brood success was measured as the difference between the adjusted mean offspring size of the wild and marker broods within each host (whole model $r^2 = 0.4832$, $P < 0.0001$). L = lag, P = parental size ratio, C = clutch size ratio

Source	d.f.	F	P
Lag	2	4·0857	0·0207
Parental size ratio	1	1·6372	0·2046
Clutch size ratio	1	14·9174	0·0002
L × P	2	0·2131	0·8085
L × C	2	0·1383	0·8711
P × C	1	0·0565	0·8128
L × P × C	2	0·1120	0·8942

Fig. 4. Effect of frequency and timing on the outcome of competition. Difference in adjusted mean offspring size for the two competing broods (wild–marker), indexed as average hind tibia length, as affected by relative numbers of individuals in the competing broods (the clutch size ratio) and relative timing of brood initiation. Top plot, no lag; parents oviposited over the same 24-h period, middle plot, 24-h lag; wild-type parents had access to hosts for 24 h immediately after removal of marker females, Bottom plot, 48 h lag; wild-type parents had access to hosts for 24 h 1 day after the removal of the marker females. The lines are least-squares regression fits.

mass for the first (i.e. no time lag) treatment for all treatments. This was conducted to preserve size differences due to treatment that would have disappeared had separate within-treatment regressions been employed. I analysed the effect of strain, time elapsed between brood oviposition, the log-transformed ratio of parental tibia length ($\approx$ egg size, Fig. 1) on the difference in average standardized offspring size among broods using an analysis of covariance.

Strain type again had no main effect on brood success (ANCOVA, $P = 0.7335$) and this effect was removed from the model to preserve degrees of freedom in subsequent analyses. There was no effect of the logged ratio of tibia size of the ovipositing wild female to the marker female in determining the outcome of intraspecific competition (Table 2). Duration of time elapsed between the oviposition of the marker and the wild-type female parents did, however, have a significant effect on the relative size of offspring, where a long time penalty resulted in relatively smaller offspring (Table 2, Fig. 4). As in the preceding experiment, relative numbers of offspring in the two broods within a host had a strong and consistent effect on the outcome of competition. Here, success of a brood, relative to its competing brood, tended to be greatest when that brood was more numerous (Table 2, Fig. 4). There was no significant interaction between any of the main effects in the model.

Discussion

One underlying assumption of this study is that offspring size measures fitness adequately in parasitoids. Although I do not test this assumption here a number of studies of similar systems have demonstrated that this is reasonable (Visser 1994; West, Flanagan & Godfray 1996; Ellers, van Alphen & Sevenster 1998; but see Kazmer & Luck 1995). Furthermore, I assume that egg mortality will be constant across a range of egg sizes. This may not actually be the case as developmental mortality has been shown to be correlated with egg size in at least one system (Mayhew & Heitmans 2000).
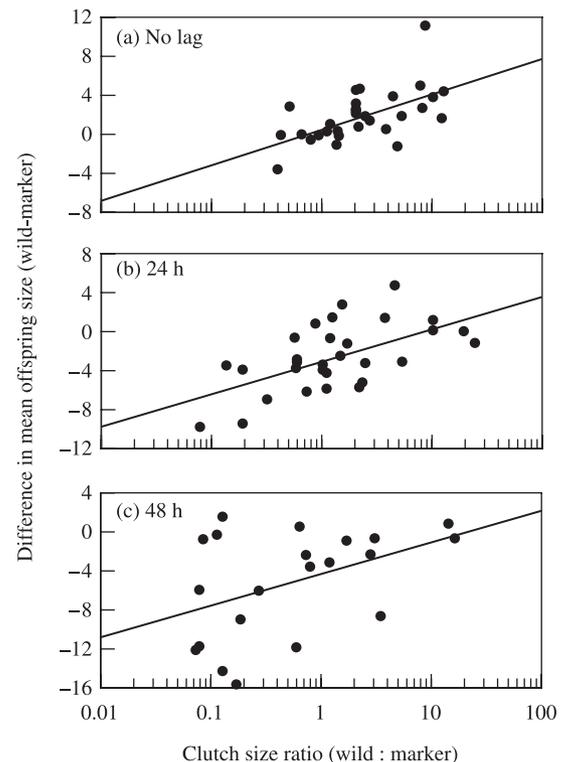
However, in this system it was not possible to evaluate developmental mortality. Given these caveats, I show here that the success of offspring of *N. vitripennis* under intraspecific competition can be affected by three factors: availability of food, relative age of broods and relative numbers of individuals in each brood. Finally, although there is strong variation in egg size with respect to body size in this species, I was unable to detect any fitness consequences of this variation under intraspecific competition.

It is not surprising that wasp offspring do better when they are supplied with abundant food, and when they are competing with younger (and therefore smaller) individuals. *Nasonia* offspring are gregarious (Whiting 1967) and evidently do not cannibalize (Wylie 1971). All other things being equal, older (and therefore larger) individuals can be expected to do better under conditions of scramble competition, because they are most able to process the limited resources at a rapid rate. These results are similar to those of Wylie (1971), who showed both differential mortality and reported qualitative size differences between first and second clutches of *N. vitripennis* laid into housefly puparia.

Positive propagule size effects have been demonstrated for both plant (Wulff 1986a, 1986b; Choe *et al*. 1988; Armstrong & Westoby 1993; Roff 2002), and animal systems (Tauber, Tauber & Tauber 1991; Fox 1994a,b; Fox & Mousseau 1996; Roff 2002), but the adaptive significance of propagule size variation remains obscure in a number of systems (Bernardo 1996). In particular, the relationship between egg size variation and competitive ability has been difficult to demonstrate in animals (Azevedo, French & Partridge 1997; but see Svensson & Sinervo 2000). However, large propagule size in plants has been shown to confer a competitive advantage under strong competition in a number of systems (Roff 2002).

In parasitoids, the role of egg size variation on offspring success is less clear. For example, there is some evidence that larger eggs can increase fitness via reduced mortality (Mayhew & Heitmans 2000), especially in ectoparasitic species (Mayhew & Blackburn 1999). However, small-egged species that engage in lethal fighting apparently enjoy an intrinsic advantage in interspecific contests, presumably because of shorter development time (Collier, Kelly & Hunter 2002). Under the kind of scramble competition exhibited by *N. vitripennis*, an egg size asymmetry may be assumed to confer an advantage to larger individuals if initial feeding rate determines the victors or towards smaller individuals if feeding commences sooner because of more rapid development. Either scenario should translate into size asymmetries in the adult stage whenever resources are limiting. The demonstrated effect of brood age, due presumably to enforced differences between onset of feeding across competing broods, suggests that egg size effects should be evident. However, my data do not demonstrate any effect of egg size variation on offspring success, even though there was demonstrable food limitation and strong variation in offspring size across broods. Estimating the fitness of eggs whose contents have been manipulated experimentally (Sinervo 1990; Emlet & Hoegh-Guldberg 1997; Svensson & Sinervo 2000), instead of employing the natural variation in egg size, is a definitive way to demonstrate any effect of egg size variation on performance, but is not a pragmatic approach for parasitoid systems.

Wasp larvae did best in competition with offspring of another strain when they and their siblings outnumbered the competition. This frequency–dependence was an unexpected result and suggests that siblings actively cooperate to outcompete unrelated rivals in superparasitized hosts. Although active intraspecific competition between offspring of solitary parasitoids is well documented (Godfray 1994; Rosenheim & Hongkham 1996), the general assumption has been that gregarious parasitoids only competed via individual scramble competition without cooperation among kin (Godfray 1987; Rosenheim 1993).

Within-brood facilitation in *N. vitripennis* implies that larvae are able to recognize and either cooperate with

kin or become aggressive to non-kin. Kin-recognition has been shown to reduce aggressive interactions between relatives in cannibalistic spadefoot toads (Pfennig, Reeve & Sherman 1993; Pfennig, Collins & Ziemba 1999) and nest-building *Polistes* wasps (Bura & Gamboa 1994) and is speculated to be a significant factor in non-social insect interactions (Fellowes 1998). Most recently kin recognition has been shown to direct larval aggression in a polyembryinic parasitoid (Giron *et al*. 2004). I should emphasize, however, that the mechanism underlying the frequency–dependent effect in this system is not known and may not involve any direct kin-recognition among larvae.

Finally, it is possible that the frequency–dependent effect may select for the allometric relationship between body size and egg size in *Nasonia vitripennis*. A female wasp's clutch size decision will probably be biased towards a higher number than would otherwise be optimal if relative clutch size determines her offspring's share of host resources under competition and superparasitism is a routine event. This phenomenon has been demonstrated in *Leptopilina heterotoma*, a contest-competing solitary parasitoid where eggs are essentially lottery tickets that determine which female's offspring is most likely to become the sole emergent (Visser, van Alphen & Nell 1990; Rosenheim & Hongkham 1996). This circumstance places a selective premium on larger egg loads. All other things being equal, selection for large egg loads (and therefore smaller eggs) will always be strongest on small females which are the most likely to be egg-limited at the time of oviposition. This may serve as a more general explanation for allometric egg size relationships if frequency–dependence affects success among competing broods of other gregarious species.

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