

Chales W. Fox · John D. Martin · Monica S. Thakar
Timothy A. Mousseau

Clutch size manipulations in two seed beetles: consequences for progeny fitness

Received: 21 June 1995 / Accepted: 30 March 1996

Abstract Seed beetles (Coleoptera: Bruchidae) lay their eggs on discrete resource patches, such that competition among larvae for food is an important component of their biology. Most seed beetles, including *Stator limbatus*, lay eggs singly on individual seeds and avoid superparasitism except when seeds are limiting. In contrast, *S. beali*, a closely related congener, lays eggs in clutches on a single seed. We tested the hypothesis that natural selection on larval life history characters favors small clutches (selection against large clutches) in *S. limbatus*, but that selection against large clutches is relaxed in *S. beali* because of the large size of its host's seeds. We manipulated clutch size and examined its relationship to offspring fitness. Clutch size affected the survivorship of *S. limbatus* larvae ($r^2=0.14$), but had no detectable effect on the survivorship of *S. beali* larvae ($r^2=0.04$). Also, clutch size had a large effect on development time and body weight of *S. limbatus*, but not of *S. beali*. We discuss the implications of this result for the evolution of clutch size in *S. limbatus* and *S. beali*.

Key words Bruchidae · Resource patches · Clutch size · Larval survival · Larval development

Introduction

Many insects lay their eggs in clutches on discrete resource patches (Godfray et al. 1991). These patches are often the only food available for progeny, which makes competition for food among siblings an important aspect of their biology. Optimally models predict that females should lay smaller clutches on poorer-quality and/or smaller resource patches (Godfray 1987; Godfray et al.

1991) because sibling competition increases, and thus progeny fitness decreases, with decreasing resource quality and size. Studies of parasitic insects generally support this prediction (Hardy et al. 1992; Vet et al. 1993). For most parasitoids, small hosts produce fewer and smaller offspring than large hosts (Hardy et al. 1992; Vet et al. 1994), and females preferentially oviposit on large hosts. When forced to lay on specific hosts, females lay smaller clutches on small hosts (Hardy et al. 1992; Vet et al. 1993).

Seed beetles (Coleoptera: Bruchidae) lay their eggs on seeds (or fruits) of their host plants. In most species, larvae subsequently complete their life cycle inside the seed selected by their mothers, emerging only after pupation. Thus, these larvae develop on discrete resource patches, and larval competition structures their behavior and life history (Messina 1991). Most seed beetles, such as *Stator limbatus*, lay a single egg in each oviposition bout, and usually visit several seeds between successive ovipositions. These beetles generally avoid superparasitism or multiple ovipositions on the same host (Fox and Mousseau 1995a) except when seeds are limiting (e.g. Messina et al. 1992). However, some seed beetles, such as *S. beali*, lay multiple eggs in each oviposition bout (i.e. clutches) without leaving their host between each egg (Fox and Mousseau 1995a, b; Nilsson and Johnson 1993).

Differences in the degree of resource competition among larvae may explain why *S. limbatus* females lay eggs individually, while *S. beali* females lay clutches. In *S. limbatus* there is intense competition among larvae within a seed resulting from the small size of its host's seeds. In *S. beali*, however, there is likely less competition among sibling larvae within the seed and thus relaxed selection against laying clutches, because of the large size of its host's seeds. *S. beali* is a specialist on *Chloroleucon ebano* (= *Pithecellobium flexicaule*) (Fabaceae; Mimosoideae) (Johnson and Kingsolver 1976; Nilsson and Johnson 1993) which produces seeds that are large relative to the size of an adult *S. beali* (natural seed weight range: ≈ 0.3 – 1.2 g; beetle weight range:

C.W. Fox (✉)¹ · J.D. Martin · M.S. Thakar · T.A. Mousseau
Department of Biology of Biological Sciences,
University of South Carolina, Columbia, SC 29208, USA

Present address:

¹ The Louis Calder Center of Fordham University, Box K,
Armonk, NY 10504, USA
Fax: 914-273-2167; E-mail: Fox@murray.fordham.edu

≈2.5–5.9 mg; Fox and Mousseau 1995b) and large relative to most other legumes (Fabaceae; e.g., Fox et al. 1995a). *S. limbatus*, on the other hand, is a generalist seed parasite that uses seeds of >50 plant species in the Fabaceae (Johnson and Kingsolver 1976; Johnson et al. 1989), each of which produces substantially smaller seeds than *C. ebano* (e.g., Fox et al. 1995a).

We speculate that this small size of *S. limbatus* hosts results in intense larval competition within seeds bearing more than one egg, such that the fitness gain associated with increasing clutch size is low or negative. The large size of *C. ebano*, on the other hand, likely allows large *S. beali* clutches with little or no cost to progeny. In this manuscript, we test the hypothesis that increasing the number of eggs per seed has a negative effect on growth and development of *S. limbatus* but has little effect on the growth and development of *S. beali* by manipulating the number of eggs laid per seed and examining the consequences of artificial clutch size on progeny survivorship and development.

Materials and methods

The biology of *S. limbatus* and *S. beali*

S. limbatus is a widespread, generalist seed parasite that occurs from northern South America to the southwestern United States (Johnson and Kingsolver 1976; Johnson et al. 1989). It is an unusual member of the genus *Stator* because it has been collected from >50 host species, in at least nine genera of the Fabaceae; specialization (on one host, one genus, or closely related genera) is more typical among bruchids, and particularly *Stator*. In the United States, and particularly in Arizona, *S. limbatus* is abundant on many species of *Acacia* (Fabaceae: Mimosoideae) and two species of *Cercidium* (*C. floridum* and *C. microphyllum*, palo verdes; Fabaceae: Caesalpinioideae), although only one or a few hosts may be available in any single locality. *S. beali* is a more typical example of the genus *Stator* in its pattern of host use; it is a specialist on a single species (*C. ebano*; Nilsson and Johnson 1993), and thus limited to the geographic distribution of this plant.

Both *S. limbatus* and *S. beali* oviposit directly onto mature, dry host seeds, and are thus restricted to fruits for which they have access to the seeds (e.g., fruits that have either dehisced or been damaged by other organisms). Upon hatching, larvae burrow into the seed, where they complete development, pupate, and emerge as adults. Adults are the only dispersing stage; larvae are restricted to the host their mother has chosen for them. In the laboratory, mating and egg laying begin approximately 24–48 h post-emergence. Beetles require only a single seed to complete development and reproduce. Thus, neither food nor water supplementation was necessary for the following laboratory experiments.

Mean clutch size of *S. beali* is 7.6 ± 0.9 eggs/clutch in nature, with clutches ranging in size between 1 and 19 eggs, and 6.4 ± 0.2 eggs in the laboratory, ranging between 1 and 12 eggs/clutch (Fox and Mousseau 1995b).

Study populations

S. beali were collected from infested pods of Texas ebony (*C. ebano*) in Mont Meta Memorial Park, San Benito, Texas. Approximately 400 adults emerged from seeds collected in the field, and were used to initiate the laboratory population. *S. limbatus* were collected from infested pods of *Cercidium floridum* (Fabaceae: Caesalpinioideae) along Scottsdale Highway, 1.7 miles (2.7 km) north of Bell Road (behind the Scottsdale Well), in Scottsdale, Ar-

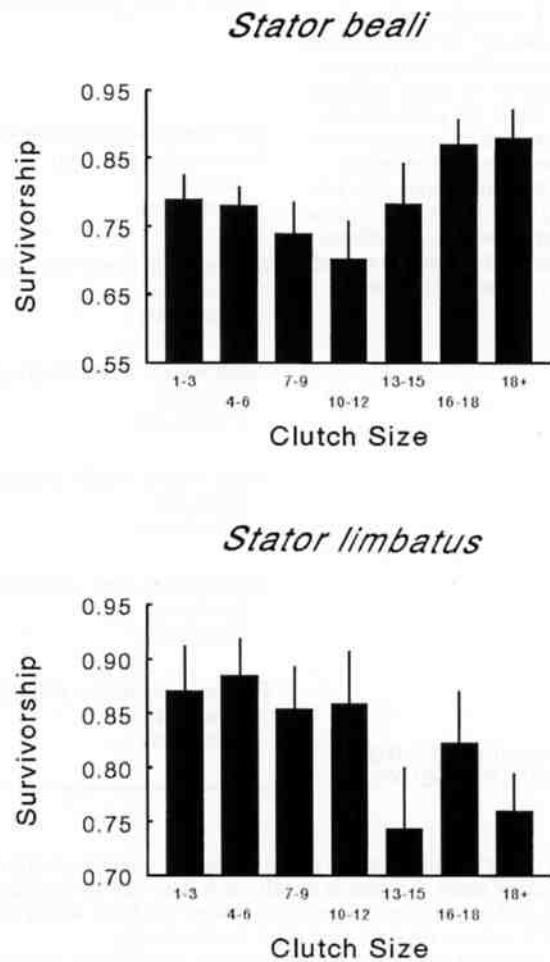


Fig. 1 The effect of manipulated clutch size on egg-to-adult survivorship of *Stator limbatus* and *S. beali*. Means for each class of clutch sizes were calculated from all clutches in this class (including clutches with zero survivorship). See Table 1 and text for details of statistical analyses)

izona. Approximately 500 adults emerged from seeds collected in the field, and were used to initiate the laboratory population.

Beetles of each species were maintained in laboratory growth chambers at large population sizes (more than 300–400 individuals per generation), at 30–31°C, L:D 15:9, before and during this experiment (*S. limbatus* reared on *Acacia greggii*, *S. beali* reared on *C. ebano*). The experiment was initiated with beetles reared in the laboratory two or three generations. Virgin beetles collected within 24 h after adult emergence from an isolated host seed were used to initiate this experiment.

The manipulation of clutch size

To create artificial clutches of variable sizes, a single virgin female, collected from her emergence seed within 24 h of adult emergence, was confined with a virgin male of the same species (also collected within 24 h of adult emergence) and a single host seed in a 60-mm petri dish. Although beetles were collected on *C. floridum*, *S. limbatus* pairs were confined with a single seed of *A. greggii* for these experiments, on which host-associated mortality is very low at densities of one beetle per seed (mortality generally <5%; Fox et al. 1994, 1995c). In contrast, host-associated mortality is very high on *C. floridum* (generally >50%; Siemens and Johnson 1992; Fox et al. 1994, 1995c) due to difficulty penetrating the seed coat, severely complicating the detection of clutch size

Table 1 Partial correlations and t-statistics for seed size and clutch size effects on progeny life histories in *Stator limbatus* and *S. beali*. All probabilities are corrected for multiple comparisons using a Bonferroni multiple comparisons test (following Rice 1989). The sign on the partial correlation reflects the sign on the regression coefficient; n =number of families

	Stator limbatus		Stator beali	
	Squared partial		Squared partial	
	r^2	t	r^2	t
Survivorship (all data)				
Seed size	0.01	1.42 ns	-0.00	-0.96 ns
Clutch size	-0.02	-1.92 ns	0.00	0.28 ns
	$n=203$		$n=222$	
Survivorship (zeros excluded)				
Seed size	0.00	1.02 ns	-0.01	-0.81 ns
Clutch size	-0.16	-6.05***	-0.04	-2.87 ns
	$n=194$		$n=207$	
Adult weight – female progeny				
Seed size	0.05	4.11***	0.00	0.72 ns
Clutch size	-0.41	-10.50***	-0.01	-1.35 ns
	$n=159$		$n=141$	
Adult weight – male progeny				
Seed size	0.03	2.93**	0.02	2.00 ns
Clutch size	-0.31	-8.52***	-0.02	-1.81 ns
	$n=168$		$n=151$	
Development time – female progeny				
Seed size	-0.00	-0.53 ns	0.00	0.83 ns
Clutch size	-0.13	-4.76***	-0.02	-1.70 ns
	$n=154$		$n=139$	
Development time – male progeny				
Seed size	-0.01	-1.30 ns	0.01	1.22 ns
Clutch size	-0.16	-5.47***	-0.02	-1.61 ns
	$n=165$		$n=149$	

ns not significant ($P>0.05$),
** $P<0.01$, *** $P<0.001$

effects on larval life histories on this host (the number of eggs that successfully enter the seed is usually less than half of the number of eggs laid on the seed). *S. beali* pairs were confined with a single seed of *C. ebano*, the only host plant for this beetle.

So that seed weight could be used as a covariate in all analyses, all seeds were weighed before mated pairs were added. Only seeds from approximately the middle 60% weight quartile were used for this experiment; the smallest $\approx 20\%$ and the largest $\approx 20\%$ of seeds were thrown out. The mean weights of seeds used in this experiment were 0.227 g for *A. greggii* (SD 0.039 g) and 0.735 g for *C. ebano* (SD 0.151 g).

Dishes were checked at 24-h intervals until eggs were found on the seed. Seeds were then randomly assigned to an artificial clutch size of less than or equal to the number of eggs laid on the seed (excess eggs were scraped from the seed). Note that because female *S. limbatus* generally lay only 1 egg per oviposition bout, and female *S. beali* generally lay <12 eggs per clutch in the laboratory manipulated clutches were created by forcing females to superparasitize seeds (lay eggs on a seed they had already laid on). To control for maternal age effects on larval survivorship and development, in which later laid offspring of many insects develop from smaller eggs, have lower survivorship, and develop longer (e.g., Fox 1993), only eggs laid during the first 24 h of egg-laying were included in this experiment.

This method of generating artificial clutches resulted in 203 *S. limbatus* and 221 *S. beali* clutches. Clutches were subsequently reared to adult at 29–30°C, L:D 15:9. Egg-to-adult development time and adult body weight at emergence were recorded for all surviving progeny. Because we were interested in the effects of larval competition, for all statistical analyses clutch size represented the number of eggs that hatched, rather than the number of eggs laid on a seed (hatched eggs are easily identified because larvae are visible under a dissecting scope and can be observed entering the seed). For most females, all eggs hatched. However, some females laid one or more apparently unfertilized eggs. Also, seed weight was included in all regression analyses, along with clutch size, to control for (a) effects of variable seed size on progeny life histories, and (b) effects of seed size on female behavior (i.e.,

more eggs laid on larger seeds, and thus larger artificial clutches on larger seeds).

Results

Average manipulated clutch size was 7.6 (SD 6.1) and 5.0 (SD 4.0) eggs for *S. limbatus* and *S. beali*, respectively. Both natural and manipulated clutch size was independent of seed size for *S. limbatus* (linear regression, $r^2=0.00$, $P>0.05$), but there was a weak positive relationship between clutch size and seed size in *S. beali*; natural and manipulated clutches were slightly larger on larger seeds ($r^2=0.03$ for each, $P<0.05$), resulting from a tendency of female *S. beali* to lay larger clutches on larger seeds (see also Fox and Mousseau 1995b).

Larval egg-to-adult survivorship from manipulated clutches averaged $0.85 \pm \text{SE } 0.02$ for *S. limbatus* and 0.78 ± 0.02 for *S. beali* larvae (Fig. 1). In initial analyses, in which survivorship of all clutches was included in a linear regression analysis, manipulated clutch size had no effect on survivorship of either *S. limbatus* or *S. beali*; progeny developing from large clutches survived just as well as progeny developing from small clutches (Table 1). However, this result appeared inconsistent with the patterns evident in Fig. 1, possibly due to zero-survivorship clutches anchoring the regression analysis at the small-clutch end of the distribution. Nine *S. limbatus* and 14 *S. beali* clutches failed to produce any adult progeny. When these zero-survivorship clutches were deleted from the linear regression analysis, survivorship was

Fig. 2 The effect of manipulated clutch size on adult body weight of *S. limbatus* and *S. beali*. Separate figures are presented for each sex because males are on average larger than females (Fox et al. 1994)

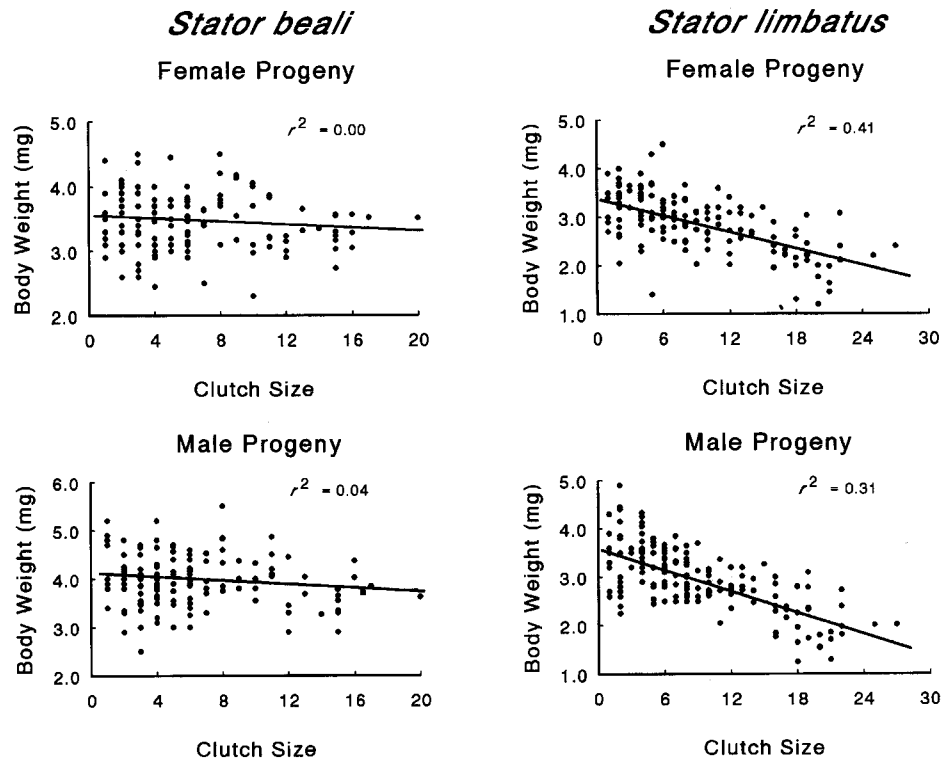
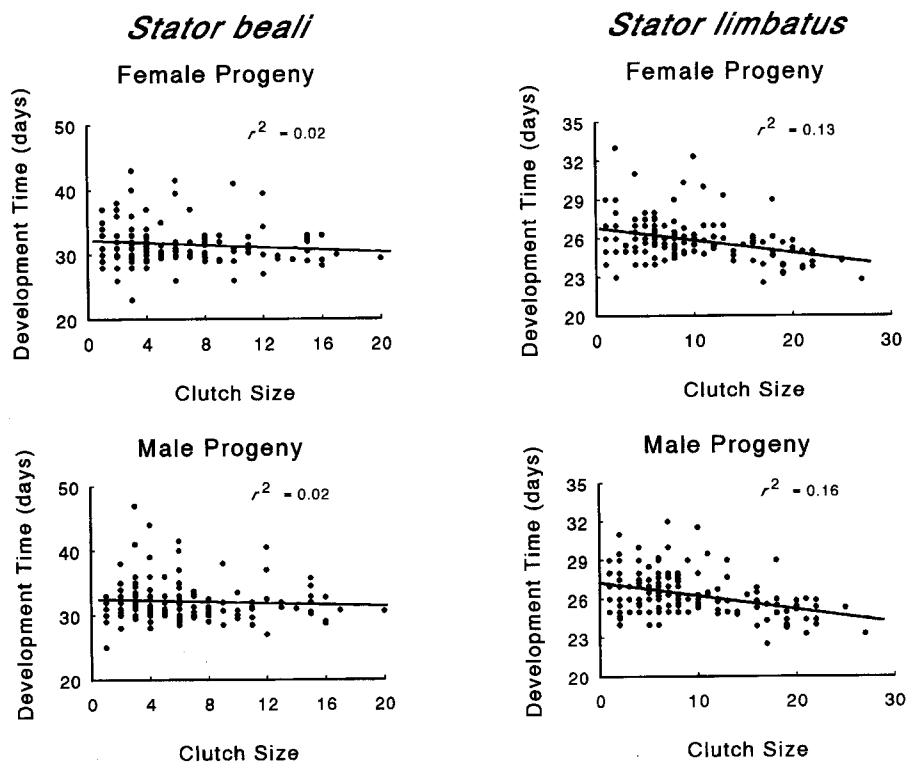


Fig. 3 The effect of manipulated clutch size on egg-to-adult development time of *S. limbatus* and *S. beali*. Separate figures are presented for each sex because females on average develop faster than males (Fox et al. 1994)



negatively correlated with clutch size in *S. limbatus* (partial $r^2=0.16$; larvae from larger clutches had lower survivorship; Table 1) but not in *S. beali* ($r^2=0.04$; not significant following a Bonferroni multiple comparisons test to correct for multiple analyses).

Body weight and development time of *S. beali* were unaffected by increasing clutch size (Figs. 2 and 3; Table 1). However, as predicted, clutch size affected both development time and adult emergence weight of *S. limbatus*; beetles developing from large clutches emerged

sooner, but at much lower body weight, than beetles developing from small clutches (Figs. 2 and 3; Table 1).

Body weight of emerging *S. limbatus* (both male and female progeny) was also affected by seed size; larger seeds produced larger beetles than small seeds (Table 1), consistent with our hypothesis that seed size is a factor selecting against large clutches in *S. limbatus*. However, there was no detectable effect of seed size on survivorship or development time of *S. limbatus*, nor on any measured life history character in *S. beali*.

One potential complication with this experiment is that, because "clutches" are only artificially reduced in size (by scraping eggs) and not also artificially augmented (eggs added), the maximum manipulated clutch size is determined by the number of eggs laid on a seed by a female. If some component of female oviposition behavior and/or female fecundity is correlated with progeny life history in *S. limbatus*, but not in *S. beali*, we might observe a correlation between manipulated clutch size and progeny life history mediated through female behavior rather than competition among progeny. However, that this is not the case is suggested by regression analyses in which the effects of natural clutch size (the number of eggs laid on a seed prior to manipulation) on progeny life history characters (survivorship, body size, and development time) is first removed and then the effect of manipulated clutch size on the residuals is examined. In these analyses, the effect of manipulated clutch size is still significant for each life history character (except survivorship) in *S. limbatus* ($P < 0.05$), and none are significant for *S. beali*.

Discussion

Here, we tested the hypothesis that the small size of *S. limbatus* hosts selects against large clutches in this beetle, while the large size of *S. beali*'s host results in relaxed selection against large clutches. Our data support this hypothesis. Manipulated clutch size had an effect on egg-to-adult survivorship of *S. limbatus* larvae (larvae developing from larger clutches had lower survivorship; Table 1) but not on egg-to-adult survivorship of *S. beali* larvae. Also, clutch size had a large effect on development time and body weight of *S. limbatus*, but not of *S. beali* (Figs. 2 and 3). This observed clutch size effect on body weight of *S. limbatus* likely has a substantial effect on subsequent reproductive success. Fecundity and egg size are positively correlated with both female body size and the size of her mate (Fox et al. 1995b). Egg size subsequently affects progeny survivorship on some host plants; larvae developing from large eggs survive better than larvae developing from small eggs (Fox and Mousseau 1996). Thus, large females produce more eggs than small females, and these eggs have higher survivorship than eggs produced by small females. Similarly, large males sire more offspring than small males (Fox et al. 1995b), and these offspring likely also have higher survivorship than offspring of small males.

Theoretical models of clutch size evolution predict that when resource patches are unlimited, females should disperse their eggs among the available patches to minimize competition between siblings (Mangel 1987). However, when resources are limiting, females must increase clutch size to insure against low realized fecundity resulting from adult mortality before the full complement of eggs can be laid (Courtney 1984; Parker and Courtney 1984; Messina et al. 1992; Wilson and Lessells 1994). Seeds of both *S. limbatus* and *S. beali* hosts are likely a limited resource for ovipositing females; despite an aversion to superparasitism in laboratory experiments, most seeds are superparasitized in nature (Siemens and Johnson 1992; Fox and Mousseau 1995b). This limitation in oviposition substrates theoretically selects for females laying multiple eggs per oviposition bout. Our data also indicate intense selection against females laying clutches in *S. limbatus*, such that when multiple host seeds are available, females should spread their eggs among them. Laboratory experiments indicate that this is what *S. limbatus* females do; in laboratory experiments in which seeds were abundant beetles spread their eggs among seeds by laying approximately 1 egg/seed (Siemens and Johnson 1992; C.W. Fox, personal observation). However, when seeds are limiting, as in the manipulations presented above, females revisit and superparasitize seeds (Siemens and Johnson 1992). Thus, selection against large clutches in *S. limbatus* appears to have resulted in a strategy in which females distribute eggs relatively evenly among seeds when seeds are in excess, and resort to superparasitism only when seeds are limiting.

Although superparasitism in *S. limbatus* is selected against when seeds are in excess (data presented here demonstrate that there is a clear advantage to evenly dispersing eggs when possible), when seeds are limiting the cost to superparasitizing a seed is relatively minor compared to the cost of withholding an egg and dying without realizing full potential fecundity. Even if females exclusively superparasitize seeds bearing their own eggs, increasing competition among their own progeny and thus reducing subsequent body size of their progeny, it is better to superparasitize than to withhold eggs. For example, adding five eggs to an *A. greggii* seed already bearing one egg only reduces the expected body size of emerging female *S. limbatus* offspring by ≈ 0.3 mg (based on data in Fig. 2). These slightly smaller females would suffer a reduction in fecundity relative to an individually reared female of $\approx 10\%$ each (calculations based on the body size/fecundity relationships reported in Fox et al. 1995b). Adding five more eggs, for a total of 11, would result in a total decrease in expected female size of ≈ 0.6 mg, for a total reduction in expected fecundity of $\approx 20\%$ for each female progeny.

Although selection favors small clutches in *S. limbatus* when seeds are not limiting, our experiment indicates relaxed selection against large clutches in *S. beali*. This difference in clutch size effects on progeny between species is likely due to a difference in the size of their host seeds; *S. limbatus* host seeds are smaller than *S. beali*

host seeds, such that scramble competition is more intense among *S. limbatus* larvae than among *S. beali* larvae developing inside the same seed. That seed size can be a major determinant of clutch size is indicated by research on another seed beetle, *Callosobruchus maculatus* (F.). *C. maculatus* females tend to distribute their eggs uniformly among seeds to reduce competition among larvae. However, populations associated with larger seeds more readily superparasitize and/or lay larger clutches than populations associated with small seeds (Messina and Mitchell 1989).

Also consistent with the hypothesis that seed size is an important factor in the evolution of clutch size is the result that seed size affected emergence weight of *S. limbatus* (large seeds produced larger beetles), but not of *S. beali*. This is further evidence that resources are extremely limited inside an *A. greggii* seed, but that even a small *C. ebano* seed contains enough resources to support a large clutch of *S. beali* eggs. However, this appears inconsistent with our previous observation that *S. beali* females lay smaller clutches on small seeds (Fox and Mousseau 1995b). That females lay smaller clutches on smaller seeds suggests that seed size and clutch size affect progeny life histories in this beetle and that females have responded to this selection by altering clutch size. Possibly, females lay smaller clutches on small seeds as a precaution against superparasitism, or some other unpredictable environmental effect, although sufficient resources are present inside a seed to support progeny of a large clutch.

In *S. limbatus*, increasing the number of eggs per seed resulted in decreased development time of larvae. This suggests that the reduced resources available under intense competition associated with multiple larvae per seed result in early pupation, rather than development to a target body size as expected under non-stressful conditions (Fox 1993). In some bruchids, increasing the number of eggs per seed causes substantially reduced survivorship of larvae (Wilson 1994 and references cited therein). The ability of *S. limbatus* to pupate early in response to resource limitation possibly explains the modest effect ($r^2=0.16$) of clutch size on mortality. However, the response of larvae to increased competition likely varies among populations, possibly due to variable tolerance of competition. For example, increasing the number of eggs per seed resulted in substantially decreased survivorship in another *S. limbatus* population ($r^2=0.59$; Siemens and Johnson 1992). Similar among-population variation in the effects of egg number on survivorship have been demonstrated for *Callosobruchus maculatus*; in highly competitive populations survivorship is affected by the number of eggs laid per seed (e.g., in Messina's S-strain, two eggs never produced more than one surviving adult) while in less competitive populations survivorship was less affected by clutch size (in Messina's I-strain, two eggs produced two adults 54% of the time), although emergers pupated smaller than when reared alone (Messina 1991). It will be interesting to examine among-population variation in the tolerance of *S.*

limbatus larvae to large clutches, and the relationship between this tolerance and host use patterns, host availability, and larval density.

One problem with studying the fitness consequences of clutch size is the difficulty of obtaining large clutches from a single female. To obtain large clutches, beetles were forced to superparasitize, resulting in abnormal patterns of egg distribution on a seed. For example, in clutches of *S. beali*, eggs within a single clutch are laid in contact with each other and larvae burrow away from their siblings when entering the seed, likely reducing sib competition. However, when multiple clutches are laid on a seed, the extra eggs are laid in a second group and enter the seed from a different location. Seed use by the two clutches is thus uncoordinated; larvae may subsequently encounter larvae from other clutches within the seed, resulting in larval interactions not typical of *S. beali* clutches, and possibly resulting in the detection of inflated clutch size effects. While the weak effects of clutch size on *S. beali* larval development, even for large artificial clutches (i.e., those requiring superparasitism), suggest this bias is not substantial for this species, such bias may be significant for *S. limbatus* since all *S. limbatus* clutches result from superparasitism. Also, because competing *S. limbatus* larvae within a seed in nature are often non-kin, siblicide and aggressive interference competition are likely selected for, resulting in large effects of manipulated clutch size on larval life history. However, kin selection likely reduces the aggressiveness of *S. beali* larvae, subsequently reducing the magnitude of clutch size effects on larval life history. Thus, the detected clutch size effects in *S. limbatus* may overestimate the actual effects detected if this species naturally laid coordinated clutches.

Acknowledgements We thank P. Kareiva, F.J. Messina, J.A. Rosenheim, C.P. Yeager, and two anonymous reviewers for helpful comments on earlier versions of this manuscript. We also thank C.D. Johnson for his advice on collecting and rearing beetles. Financial support was provided in part by NSF Grant no. DEB-9409004 to T.A. Mousseau and an NSF post-doctoral fellowship in environmental biology (DEB-9403244) to C.W. Fox.

References

- Courtney SP (1984) Evolution of egg clustering by butterflies and other insects. *Am Nat* 123:276–281.
- Fox CW (1993) The influence of maternal age and mating frequency on egg size and offspring performance in *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Oecologia* 96:139–146
- Fox CW, Mousseau TA (1995a) Experimental hybridizations between two seed beetle species (Coleoptera: Bruchidae): asymmetrical reproductive isolation between *Stator limbatus* and *S. beali*. *Coleopt Bull*, in press
- Fox CW, Mousseau TA (1995b) Determinants of clutch size and seed preference in a seed beetle (*Stator beali*). *Environ Entomol* 24:1557–1561
- Fox CW, Mousseau TA (1996) Larval host plant affects the fitness consequences of egg size in the seed beetle *Stator limbatus*. *Oecologia* (in press)
- Fox CW, Waddell KJ, Mousseau TA (1994) Host-associated fitness variation in a seed beetle (Coleoptera: Bruchidae): Evi-

- dence for local adaptation to a poor quality host. *Oecologia* 99:329–336
- Fox CW, Harbin AD, Mousseau TA (1995a) Suitability of a non-host palo verde for development of *Stator limbatus* (Coleoptera: Bruchidae) larvae. *Pan-Pac Entomol*, in press
- Fox CW, McLennan LA, Mousseau TA (1995b) Male body size affects female lifetime reproductive success in a seed beetle. *Anim Behav* 50:281–284
- Fox CW, Waddell KJ, Mousseau TA (1995c) Parental host plant affects offspring life histories in a seed beetle. *Ecology* 76:402–411
- Godfray HCJ (1987) The evolution of clutch size in parasitic wasps. *Am Not* 129:221–233
- Godfray HJC, Partridge L, Harvey PH (1991) Clutch size. *Annu Rev Ecol Syste* 22:409–429
- Hardy ICW, Griffiths NT, Godfray HCJ (1992) Clutch size in a parasitoid wasp: a manipulation experiment. *J Anim Ecol* 61:121–129
- Johnson CD, Kingsolver JM (1976) Systematics of *Stator* of North and Central America (Coleoptera: Bruchidae). *USDA Tech Bull* 1537:1–101
- Johnson CD, Kingsolver JM, Teran AL (1989) Sistemática del género *Stator* (Insecta: Coleoptera: Bruchidae) en Sudamérica. *Op Lilloana* 37:1–105
- Mangel M (1987) Oviposition site selection and clutch size in insects. *J Math Biol* 25:1–22
- Messina FJ (1991) Life-history variation in a seed beetle: adult egg-laying vs. larval competitive ability. *Oecologia* 85:447–455
- Messina FJ, Mitchell R (1989) Intraspecific variation in the egg-spacing behavior of the seed beetle *Callosobruchus maculatus*. *J Insect Behav* 2:727–742
- Messina FJ, Kemp JL, Dickinson JA (1992) Plasticity in egg-spacing behavior of a seed beetle: effects of host deprivation and seed patchiness (Coleoptera: Bruchidae). *J Insect Behav* 5:609–621
- Nilsson JA, Johnson CD (1993) Laboratory hybridization of *Stator beali* and *S. limbatus*, with new host records for *S. limbatus* and *Mimosestes amicus* (Coleoptera: Bruchidae). *Southwest Nat* 38:385–387
- Parker GA, Courtney SP (1984) Models of clutch size in insect oviposition. *Theor Popul Biol* 26:27–48
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:203–208
- Siemens DH, Johnson CD (1992) Density-dependent egg parasitism as a determinant of clutch size in bruchid beetles (Coleoptera: Bruchidae). *Environ Entomol* 21:610–619
- Vet LEM, Datema A, Welzen K van, Snellen H (1993) Clutch size in a larval-pupal endoparasitoid. I. Variation across and within host species. *Oecologia* 95:410–415
- Vet LEM, Datema A, Janssen A, Snellen H (1994) Clutch size in a larval-pupal endoparasitoid: consequences for fitness. *J Anim Ecol* 63:807–815
- Wilson K (1994) Evolution of clutch size in insects. II. A test of static optimality models using the beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae). *J Evol Biol* 7:365–386
- Wilson K, Lessells CM (1994) Evolution of clutch size in insects. I. A review of static optimality models. *J Evol Biol* 7:339–363