

# Effects of maternal diet and host quality on oviposition patterns and offspring performance in a seed beetle (Coleoptera: Bruchidae)

Marcia González-Teuber · Ricardo Segovia · Ernesto Gianoli

Received: 4 July 2007 / Revised: 25 November 2007 / Accepted: 12 February 2008 / Published online: 5 March 2008  
© Springer-Verlag 2008

**Abstract** In seed beetles, oviposition decisions may influence the offspring phenotype because eggs constitute the initial resources available for larval development. We tested the effects of host quality variations (small vs. large seeds of the host plant *Calystegia sepium*, Convolvulaceae) on oviposition patterns and offspring performance of the seed beetle *Megacerus eulophus*. We also manipulated the maternal diet: high diet quality vs. low diet quality to evaluate possible interactive effects of the maternal nutritional environment and host quality on oviposition patterns. We further assessed the consequences of egg size variation in offspring size. Female *M. eulophus* fed with high-quality diet (H-diet) laid more eggs and lived longer than females fed with low-quality diet (P-diet). Fecundity decreased under a low-quality host for both maternal diets. The occurrence of maternal environmental effects on egg size plasticity was detected. Under conditions of low-quality host, mothers fed with the high-quality diet produced bigger eggs in comparison with a high-quality host, whereas females fed with the low-quality diet produced smaller ones. Regardless of these differences observed in egg size depending on the maternal diet, progeny emerging from small seeds (low-quality host) showed a similar performance at emergence. Offspring traits were only significantly affected by host quality. Beetles emerging from large seeds had greater body weight and length than those reared on small seeds.

Variations in oviposition patterns in response to host quality are discussed.

**Keywords** Bruchidae · Egg size · Host quality · Maternal effects · Seed size · *Megacerus eulophus*

## Introduction

Maternal oviposition patterns in insects may significantly affect progeny phenotype because eggs determine the initial resource pool available for larval development. Larger eggs are generally associated with larger adults and greater survival of both larvae and adults (Fleming and Gross 1990; Fox 1994; Fox and Mousseau 1996). Females may modify their reproductive allocation, adjusting the number of eggs laid or egg size according to nutritional resources available in the maternal environment (Rotem et al. 2003; Kyneb and Toft 2006) or in response to host quality (Fox et al. 1997). Because the maternal reproductive effort should be divided optimally between the two fitness components, egg size and fecundity, the oviposition patterns may be affected by a trade-off between these two traits (Smith and Fretwell 1974; Messina and Fox 2001).

In seed beetles (Coleoptera: Bruchidae), oviposition decisions entirely determine the environment in which offspring will develop. On one hand, host quality may influence development rate, survival, and body size of progeny (Fox and Czesak 2000). Consequently, adaptive oviposition patterns in seed beetles should involve estimations of host quality (Cope and Fox 2003). For instance, if seed size is associated with host quality for larval development, females may use seed size as a cue for adjusting their oviposition pattern in such a way that resources are allocated optimally (Fox et al. 1997; Cope

M. González-Teuber (✉)  
Department of General Botany, University Duisburg-Essen,  
Essen, Germany  
e-mail: marcia.gonzalez@uni-due.de

R. Segovia · E. Gianoli  
Departamento de Botánica, Universidad de Concepción,  
Concepción, Chile

and Fox 2003; Yang et al. 2006). Plasticity in egg size in response to host quality has been described for the seed beetle *Stator limbatus*, where females lay larger eggs on seeds of the poor-quality host *Cercidium floridum* and smaller eggs on the high-quality host *Acacia greggii* (Fox et al. 1997; Fox et al. 1999). In *S. limbatus*, females respond adaptively to the available host by varying egg size to assure high larval survival (Fox et al. 1997). In the seed beetle *Bruchidius dorsalis*, egg size and the drilling ability of hatched larvae are positively correlated, and larger eggs are laid during the season in which the seeds of the host plant, *Gleditsia japonica*, show the greatest hardness (Takakura 2004). This suggests that females are able to detect and regulate egg size according to seed hardness. The environment experienced by mothers may influence life history traits (Møller et al. 1989; Bernardo 1996; Livnat et al. 2005). Such environmental maternal effects have been detected for oviposition patterns in seed beetles. Fed females show an increase in both egg size and fecundity in comparison with starved females (Fox and Dingle 1994; Gianoli et al. 2007); females mated with well-fed males lay larger eggs than those mated with poorly fed males (Takakura 2004), and multiple mating increases female longevity but only in starved females (Fox 1993). Few studies have manipulated as a whole different maternal diets and their effects on oviposition patterns to different host qualities. Such manipulations allow the assessment of restrictions in egg size plasticity and their further consequences.

*Megacerus eulophus* is a seed beetle associated with Convolvulaceae plant species. Adult individuals consume nectar and pollen on flowers of host plants (Suárez et al. 2004; Gianoli et al., personal observations), as has been described for other *Megacerus* species (Terán and Kingsolver 1977; Wang and Kok 1986a). For *M. eulophus*, nothing is known about the effects of host quality on oviposition decisions and offspring performance. In this study, we tested the effects of host quality variation at an intraspecific level (small vs. large seeds of the host plant *Calystegia sepium*, Convolvulaceae) on oviposition patterns and offspring performance of the bruchid beetle *M. eulophus*. We also manipulated the maternal diet (high-quality diet vs. low-quality diet) to evaluate possible interactive effects of the maternal nutritional environment and host quality on oviposition patterns.

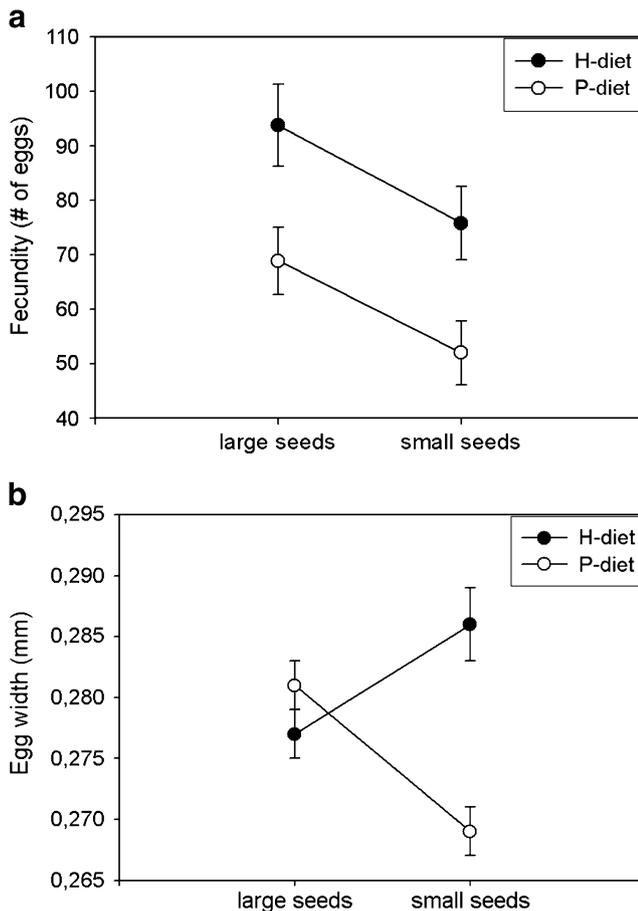
We hypothesized that fecundity would decrease and egg size would increase in the low-quality host (small seeds) in comparison with the high-quality host (large seeds). We also hypothesized that maternal effects on oviposition patterns would occur, leading to a greater overall fecundity in mothers fed with the diet of higher quality and, due to the egg size vs. egg number trade-off, also leading to a greater egg size in mothers fed with the diet of lower quality. Finally, we assessed the consequences of egg size variation on offspring performance.

## Material and methods

*M. eulophus* (Erichson; Coleoptera: Bruchidae) is a seed beetle associated with Convolvulaceae family (Terán and Kingsolver 1977). In Chile, plant species in the Convolvulaceae genera *Ipomoea*, *Calystegia*, and *Convolvulus* are known hosts (Barriga 1990). *M. eulophus* shows a broader host range than the North American species *Megacerus discooidus*, which also feeds on Convolvulaceae species (Wang and Kok 1986b). Females lay eggs on the external wall of mature fruits, on sepals, and even on isolated dispersed seeds. Egg hatching starts approximately 4–5 days after oviposition (at 24–25°C) and the first instar larvae burrow into the seed. The whole larval and pupal development is completed within a single seed. Adult emergence starts 25–30 days later (Pfaffenberger et al. 1984; Suárez, field and laboratory observations).

Experimental individuals of *M. eulophus* were obtained from a stock colony reared on *Convolvulus chilensis*. Beetles were reared for one generation more on seeds of *C. sepium* in laboratory conditions (20–22°C, 10 h L: 14 h D), and then virgin males and females were collected. Considering that individuals were reared for only one generation on seeds of *C. sepium*, we cannot discard possible environmental maternal effects of seeds of *C. chilensis* on this study. Each female was weighed and then paired with a single male (July 2005). Couples were confined in single Petri dishes (50 mm Ø) containing five seeds of *C. sepium*. Females oviposit directly onto seeds. Clean seeds continuously replaced seeds with eggs in such a way that oviposition was not limited by seed availability. Only one adult emerged from each seed in >95% of cases. To examine possible differential effects between diet qualities offered to parents, parental adults were fed with different relationships honey–pollen water solution (see below). Honey is highly rich in sugars, whereas pollen is a food highly rich in proteins. Considering that higher sugar availability in the diet has been related previously with higher individual fecundity and longevity (Hill 1989), we considered the honey-rich diet as the high-quality diet. The honey–pollen solution was delivered in each Petri dish on filter paper and was replaced daily.

To evaluate the effect of host quality on oviposition patterns and offspring performance, two groups of *C. sepium* seeds were used: (1) small seeds = 25.6 ± 0.29 mg (mean ± SE) and (2) large seeds = 37.8 ± 0.13 mg (mean ± SE; Mann–Whitney test,  $Z = -17.2989$ ,  $P < 0.01$ ). For each group, we chose the 200 smallest seeds and the 200 largest seeds from an extensive seed collection in natural populations of *C. sepium* in central Chile. All experimental seeds were healthy. To evaluate the effect of maternal diet on oviposition patterns, two treatments of diet based on honey–pollen solution were applied: (1) high-quality diet



**Fig. 1** Effects of host quality (large and small seeds of *C. sepium*) and maternal diet, high-quality (*H-diet*) vs. low-quality (*P-diet*), on lifetime fecundity (**a**) and egg width (**b**) of the seed beetle *M. eulophus*. Means±SE are shown

(*H-diet*), 80% honey:20% pollen, and (2) low-quality diet (*P-diet*), 80% pollen:20% honey. A relationship of 80:20 was used to assure nutritional differences between both diets. Honey and pollen were of commercial origin.

At the end of the experiment (January 2006), we recorded maternal and offspring traits. Maternal traits included fecundity (evaluated as the total number of eggs laid on seeds), egg size (egg width and length (millimeter)), and longevity (number of days). Offspring traits included ventral body length (millimeter), pronotum area (square millimeter), tibia length (millimeter), body weight at emergence (milligram), and longevity (number of days). Offspring longevity was evaluated in individuals without food provisioning. Measurements of body ventral length, pronotum area, tibia length, and egg width and length were made on digital images using Sigmascan software.

A two-way analysis of covariance (ANCOVA) was applied to evaluate the effects of maternal food (*H-diet* and *P-diet*) and host quality (small and large seeds) on maternal traits ( $N=25-29$  per treatment). Due to the fact that the offspring morphological traits measured were

highly correlated among them, a multivariate ANCOVA (MANCOVA) was done to evaluate the effects of host quality and maternal diet on them ( $N=20-25$  per treatment). Considering that sexual dimorphisms have been reported for other bruchidae species, and also for *M. eulophus* (Gianoli et al. 2007), the MANCOVA was done separately for females and males. Because offspring longevity was not correlated with other offspring traits ( $P>0.05$ ), it was not included in the MANCOVA analysis. A series of univariate ANCOVAs (main factors: maternal diet and host quality; covariate: mother biomass) were then performed to identify the effects of the factors on each trait. Because female and males showed the same tendency in the MANCOVA (see below), we pooled the data for the univariate ANCOVAs.

Pearson correlations between egg size (egg width) and fecundity were calculated both across and within each maternal diet to test for the occurrence of a trade-off. Offspring performance was expressed as body weight at emergence because it was highly correlated with all other body size traits (see below). All statistical analyses were performed with Statistica 6.0.

## Results

Female *M. eulophus* fed with *H-diet* laid significantly more eggs than females fed with *P-diet* (Fig. 1a; Table 1). Mothers laid significantly more eggs on large seeds than on small seeds (Fig. 1a; Table 1). No maternal diet  $\times$  host quality ( $D \times H$ ) interaction was found for fecundity (Table 1). Egg width was significantly affected by maternal diet but not affected by host quality (Table 1). There was a significant  $D \times H$  interaction on this trait (Table 1), which indicates the occurrence of maternal environmental effects on egg size plasticity. Whereas females fed with *H-diet* laid eggs of greater size in small seeds in comparison with large seeds ( $P=0.020$ , least significant difference (LSD) test), females fed with *P-diet* decreased egg size in response to small seeds

**Table 1** Two-way ANCOVA of the effects of maternal diet and host quality on life history traits of adult females of *M. eulophus* (covariate: body size)

|                   | Fecundity<br>(number<br>of eggs) | Egg<br>width<br>(mm) | Egg<br>length<br>(mm) | Longevity<br>(days) |
|-------------------|----------------------------------|----------------------|-----------------------|---------------------|
| Maternal diet (D) | 10.571*                          | 4.185**              | 1.755 ns              | 103.925***          |
| Host quality (H)  | 6.871**                          | 0.163 ns             | 0.001 ns              | 0.518 ns            |
| $D \times H$      | 0.372 ns                         | 10.248*              | 0.620 ns              | 2.035 ns            |

*F*-values are shown (*df* 1.109).

ns  $P>0.05$

\* $P<0.01$ ; \*\* $P<0.05$ ; \*\*\* $P<0.001$

**Table 2** Multivariate ANOVA for effects of maternal diet and host quality on morphological offspring traits in females and males of *M. eulophus*

|                   | <i>df</i> | Wilks's $\lambda$ | <i>F</i> | <i>P</i> |
|-------------------|-----------|-------------------|----------|----------|
| Females           |           |                   |          |          |
| Maternal diet (D) | 4.79      | 0.943             | 1.19     | 0.320    |
| Host quality (H)  | 4.79      | 0.718             | 7.72     | <0.001   |
| D×H               | 4.79      | 0.984             | 0.31     | 0.872    |
| Males             |           |                   |          |          |
| Maternal diet (D) | 4.76      | 0.937             | 1.26     | 0.293    |
| Host quality (H)  | 4.76      | 0.708             | 7.81     | <0.001   |
| D×H               | 4.76      | 0.981             | 0.35     | 0.839    |

The traits measured included body weight, body length, pronotum area, and tibia length

( $P=0.004$ , LSD test; Fig. 1b). Neither maternal diet nor host quality affected egg length (Table 1). Parental longevity was significantly affected by diet type: individuals fed with H-diet lived longer ( $103.5\pm 7.1$  days) than those fed with P-diet ( $48.9\pm 1.8$  days; Table 1). Given that females in the H-diet showed greater fecundity and lived much longer than those fed with the P-diet, the H-diet was considered of greater quality than the P-diet as food for *M. eulophus* adults.

A multivariate ANOVA showed that morphological traits in female and male offspring were not significantly affected by maternal diet but that there was a significant effect by host quality. No significant D×H interaction was detected (Table 2). Univariate ANCOVAs showed that none of the offspring traits was significantly affected by maternal diet and that only the morphological offspring traits were significantly affected by the host quality (Table 3). No significant D×H interaction was found for offspring body weight (Fig. 2; Table 3) or the other highly correlated morphological traits ( $P<0.0001$  for all Pearson correlations, data not shown). Offspring longevity was neither affected by maternal diet (C-diet= $39.56\pm 1.59$  days and P-diet= $39.07\pm 1.28$  days; mean±SE) nor by host quality (small

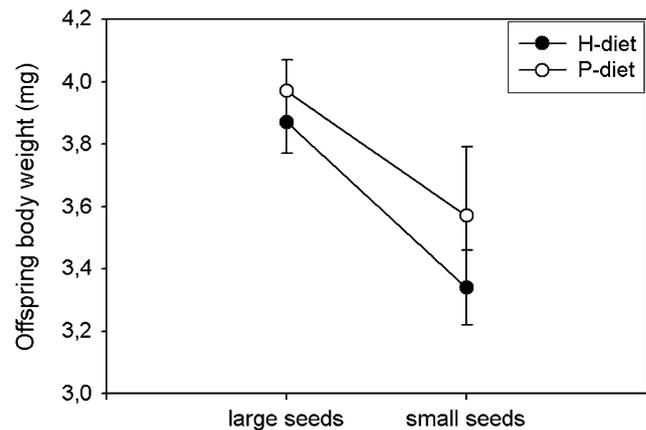
**Table 3** Two-way ANCOVA (covariate: mother biomass) for effects of maternal diet and host quality on progeny traits of *M. eulophus*

|                      | Longevity<br>(number<br>of days) | Body<br>weight<br>(mg) | Body<br>length<br>(mm) | Pronotum<br>area<br>(mm <sup>2</sup> ) | Tibia<br>length<br>(mm) |
|----------------------|----------------------------------|------------------------|------------------------|--|-------------------------|
| Covariable           | 2.060 ns                         | 2.321 ns               | 7.044*                 | 5.255**                                | 0.354 ns                |
| Maternal<br>diet (D) | 0.021 ns                         | 0.837 ns               | 0.638 ns               | 0.038 ns                               | 0.553 ns                |
| Host quality<br>(H)  | 0.221 ns                         | 9.758*                 | 24.348***              | 9.083*                                 | 6.878*                  |
| D×H                  | 2.628 ns                         | 0.09 ns                | 2.752 ns               | 1.290 ns                               | 0.835 ns                |

F-values are shown (*df* 1.104).

ns  $P>0.05$ ,

\* $P<0.01$ ; \*\* $P<0.05$ ; \*\*\* $P<0.001$

**Fig. 2** Effects of host quality (large and small seeds of *C. sepium*) and maternal diet, high-quality (H-diet) vs. low-quality (P-diet), on offspring body weight of the seed beetle *M. eulophus*. Means±SE are shown

seeds= $37.95\pm 1.26$  days and large seeds= $40.78\pm 1.59$  days; mean±SE; Table 3).

No evidence of a trade-off between egg size and fecundity was found either across treatments ( $r=0.06$ ,  $P=0.521$ ) or within each of the two maternal diet treatments (H-diet:  $r=-0.13$ ,  $P=0.355$ ; P-diet:  $r=0.11$ ,  $P=0.433$ ).

## Discussion

In general, it is predicted that females decrease their fecundity on smaller hosts because the amount of resources available to each larva would be reduced (Vinson and Iwantsch 1980; Bezemer and Mills 2003). This prediction was verified in *M. eulophus*, as has been shown for other seed beetles (Fox et al. 1996; Cope and Fox 2003). Maternal effects on fecundity were also detected: females fed with the high-quality diet showed greater overall fecundity. This might reflect a greater amount of resources allocated to reproduction due to a greater energetic budget in mothers fed with the high-quality diet (Mousseau and Dingle 1991). It was also observed that females fed with the H-diet lived much longer (double as much) than females fed with the P-diet. Therefore, a higher availability of sugars in the food is positively related with greater maternal fitness in *M. eulophus*. This last agrees with findings for other nectar-feeding species, where fecundity and longevity often increase with sugar availability in the diet (Karlsson and Wickman 1990; Boggs and Ross 1993).

In contrast, our prediction that egg size would increase in small seeds was only verified for females fed with the high-quality diet. Females from the low-quality diet laid smaller eggs on the low-quality host (small seeds). Both theoretical models and empirical studies indicate that egg size increases when conditions for juvenile development and

survival become poor (Parker and Begon 1986; Perrin 1988; Solbreck et al. 1989; Fox and Mousseau 1996). Larger eggs are associated with greater nutritional provisions and therefore larvae emerging from them may be better prepared for developing in restrictive environments (e.g., environments with lower nutritional resources). In seed beetles, egg size has been shown to increase in response to competition (Kawecki 1995) and host resistance (Fox et al. 1997). However, in the seed beetle *S. limbatus*, egg size was not affected by the size of the seeds of *C. floridum* (Savalli and Fox 2002). Although larger seeds provided a better environment for *M. eulophus* larvae (see below), only females receiving the high-quality diet supported our assumption that seed size could be considered a proxy of host quality. It is not clear why *M. eulophus* females fed with the low-quality diet did not show the expected increase in egg size in small seeds. A recent study has showed that maternal provisioning strategies (egg size and fecundity) are dynamic during the female's lifetime (Plaistow et al. 2007) and that these dynamic shifts can also be dependent of the food environment. Further studies are needed to understand in detail maternal plasticity on offspring provisioning strategies in *M. eulophus*.

Egg size variation is often correlated with offspring performance (Roff 1992; Fox et al. 1997), but this relationship may change with the environment (Parker and Begon 1986; Fox and Mousseau 1996; Czesak and Fox 2003) and with the total number of eggs laid (Bernardo 1996). In the present case, divergence in the pattern of egg size plasticity according to the maternal diet was accompanied with similar progeny performance in the low-quality host. Thus, body weight in small seeds was almost identical in progeny from high- or low-quality-diet mothers, which differed in their oviposition response to small seeds (increased egg size in high-quality-diet mothers, decreased egg size in low-quality-diet mothers). This suggests the existence of maternal diet effects on egg quality in *M. eulophus*, as has been described for other insect species and birds (Rossiter 1993; Jann and Ward 1999; Royle et al. 2003; McGraw 2006), which led to similar progeny performance in small seeds despite clear differences in egg size. Fox and Savalli (2000) reported for the seed beetle *S. limbatus* that maternal host effects on progeny survival in a novel host remained after accounting for variation in egg size, thus suggesting the occurrence of maternally mediated plasticity in egg composition. In *M. eulophus*, females experiencing a low-quality diet are constrained in their reproductive effort: they showed reduced overall fecundity and egg size in comparison with mothers in the high-quality diet. However, when facing a low-quality environment for their offspring (small seeds) it seems that they are able to modify egg composition in such a way that emerging progeny presented similar performance compared to off-

spring originated in eggs of greater size laid by females experiencing a better diet environment.

In general, regardless of the particular egg-to-larva-to-adult conversion process, results indicate that progeny size is largely determined by the environment experienced by larvae, i.e., the quantity of resources available within seeds of *C. sepium*. In other words, larger adults emerge from larger seeds. Fox and Dingle (1994) found that in the seed beetle *Callosobruchus maculatus* adult feeding had no effect on progeny body weight. Maternal effects usually vanish with progeny age (Bernardo 1996; Lindholm et al. 2006) and often are a less substantial influence on progeny performance than offspring environment (Beckerman et al. 2006). Offspring longevity was not affected by maternal diet or by seed size. Moreover, offspring longevity was nearly similar to the longevity of parents fed with the low-quality diet. This demonstrates that a diet with low sugar availability produces similar effects on longevity as the lack of diet. A recent study (Gianoli et al. 2007) and current results suggest that in *M. eulophus* adult feeding determines its longevity.

We do not have a clear explanation for the observed lack of trade-off between fecundity and egg size in *M. eulophus*. The detection of a trade-off can be confounded if there is a variation in resource acquisition among females (Tuomi et al. 1983; Jordan and Snell 2002) or if reproductive effort varies among mothers (van Noordwijk and de Jong 1986). Both of these might be the process underlying the observed pattern but we currently cannot distinguish the actual importance of them.

In conclusion, we observed maternal effects on oviposition patterns in response to host quality in the seed beetle *M. eulophus*. Variation in both fecundity and egg size in seeds of different size was influenced by the nutritional environment experienced by mothers. However, our estimate of progeny performance seemed to be determined by offspring environment. Considering that offspring provisioning strategies can be dynamic and that intergenerational effects may also be detectable in offspring traits more generations later (Plaistow et al. 2006, 2007), adaptive maternal effects for *M. eulophus* may not be discarded. Despite this apparent “reset” of conditions for offspring future fitness, the maternal effects on egg size plasticity and quality might play a crucial role in the evolutionary ecology of this seed beetle under more stressful environments, such as arid ecosystems (Gianoli et al. 2007) where food sources may be scant and host seeds are greatly reduced in size (Gianoli and González-Teuber 2005).

**Acknowledgments** We are grateful to Lorena Suárez for her help during data acquisition and analysis. We thank León Bravo for kindly sharing his photographic equipment. Comments by Miriam de Roman improved this manuscript. Financial support was provided by El Fondo Nacional de Desarrollo Científico y Tecnológico 1030702. All the experiments carried out comply with the current laws of Chile.

## References

- Barriga X (1990) Revisión de los brucos de importancia agrícola y cuarentenaria en Chile (Coleoptera: Bruchidae). Licentiate dissertation. Universidad de Chile, Santiago, 123 pp
- Beckerman AP, Benton TG, Lapsley CT, Koesters N (2006) How effective are maternal effects at having effects? Proc Royal Soc B 273:485–493
- Bernardo J (1996) The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. Am Zool 36:216–236
- Bezemer TM, Mills NJ (2003) Clutch size decisions of a gregarious parasitoid under laboratory and field conditions. Animal Behaviour 66:1119–1128
- Boggs CL, Ross CL (1993) The effect of adult food limitation on life history traits in *Speyeria mormonia* (Lepidoptera: Nymphalidae). Ecology 74:433–441
- Cope JM, Fox CW (2003) Oviposition decisions in the seed beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae): effects of seed size on superparasitism. J Stor Prod Res 39:355–365
- Czesak ME, Fox CW (2003) Evolutionary ecology of size and number in a seed beetle: genetic trade-offs differ between environments. Evolution 57:1121–1132
- Fleming IA, Gross MT (1990) Latitudinal clines: a trade off between egg number and size in Pacific salmon. Ecology 71:1–11
- Fox CW (1993) Multiple mating, lifetime fecundity and female mortality of the bruchid beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae). Funct Ecol 7:203–208
- Fox CW (1994) The influence of egg size on offspring performance in the seed beetle *Callosobruchus maculatus*. Oikos 71: 321–325
- Fox CW, Dingle H (1994) Dietary mediation of maternal age effects on offspring performance in a seed beetle (Coleoptera: Bruchidae). Funct Ecol 8:600–606
- Fox CW, Mousseau TA (1996) Larval host plant affects the fitness consequences of egg size variation in the seed beetle *Stator limbatus*. Oecologia 107:541–548
- Fox CW, Czesak ME (2000) Evolutionary ecology of progeny size in arthropods. Annu Rev Entomol 45:341–369
- Fox CW, Savalli UM (2000) Maternal effects mediate diet expansion in a seed-feeding beetle. Ecology 81:3–7
- Fox CW, Martin JD, Thakar MS, Mousseau TA (1996) Clutch size manipulations in two seed beetles: consequences for progeny fitness. Oecologia 108:88–94
- Fox CW, Thakar MS, Mousseau TA (1997) Egg size plasticity in a seed beetle: an adaptive maternal effect. Am Nat 149:149–163
- Fox CW, Czesak ME, Mousseau TA, Roff DA (1999) The evolutionary genetics of an adaptive maternal effect: egg size plasticity in a seed beetle. Evolution 53:552–560
- Gianoli E, González-Teuber M (2005) Environmental heterogeneity and population differentiation in plasticity to drought in *Convolvulus chilensis* (Convolvulaceae). Evol Ecol 19:603–613
- Gianoli E, Suárez LH, Gonzáles WL, González-Teuber M, Acuña-Rodríguez IS (2007) Host-associated variation in sexual size dimorphism and fitness effects of adult feeding in a bruchid beetle. Entomol Exp Appl 122:233–237
- Godfray H CJ (1987) The evolution of clutch size in parasitic wasps. Am Nat 129:221–233
- Godfray H CJ, Partridge L, Harvey PH (1991) Clutch size. Ann Rev Ecol Syst 22:409–429
- Hill CJ (1989) The effect of adult diet on the biology of butterflies. Oecologia 81:258–266
- Jann P, Ward PI (1999) Maternal effects and their consequences for offspring fitness in the yellow dung fly. Funct Ecol 13: 51–58
- Jordan MA, Snell HL (2002) Life history trade-offs and phenotypic plasticity in the reproduction of Galápagos lava lizards (*Microlophus delanonis*). Oecologia 130:44–52
- Karlsson B, Wickman PO (1990) Increase in reproductive effort as explained by body size and resource allocation in the speckled wood butterfly, *Pararge aegeria* (L.). Funct Ecol 4:609–617
- Kawecki TJ (1995) Adaptive plasticity of egg size in response to competition in the cowpea weevil, *Callosobruchus maculatus* (Coleoptera: Bruchidae). Oecologia 102:81–85
- Kyneb A, Toft S (2006) Effects of maternal diet quality on offspring performance in the rove beetle *Tachyporus hypnorum*. Ecol Entomol 31:322–330
- Lindholm AK, Hunt J, Brooks R (2006) Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. Biol Lett 2:586–589
- Livnat A, Pacala SW, Levin SA (2005) The evolution of intergenerational discounting in offspring quality. Am Nat 165:311–321
- McGraw KJ (2006) Dietary carotenoids mediate a trade-off between egg quantity and quality in Japanese quail. Ethol Ecol Evol 18:247–256
- Messina FJ, Fox CW (2001) Offspring size and number. In: Fox CW, Roff DA, Fairbairn DJ (eds) Evolutionary ecology: concepts and case studies. Oxford University Press, New York, pp 113–127
- Mousseau TA, Dingle H (1991) Maternal effects in insect life histories. Annu Rev Entomol 36:511–534
- Møller H, Smith RH, Sibly RM (1989) Evolutionary demography of a bruchid beetle. 1. Quantitative genetic-analysis of the female life-history. Funct Ecol 3:673–681
- Parker GA, Begon M (1986) Optimal egg size and clutch size: effects of environment and maternal phenotype. Am Nat 128:573–592
- Perrin N (1988) Why are offspring born larger when it is colder? Phenotypic plasticity for offspring size in the cladoceran *Simocephalus vetulus* (Müller). Funct Ecol 3:29–36
- Pfaffenberger GS, Muruaga S, Terán AL (1984) Morphological descriptions and biological and phylogenetic discussions of the first and final instars of four species of *Megacerus* larvae (Coleoptera: Bruchidae). Coleopt Bull 38:1–26
- Plaistow SJ, Lapsley CT, Benton TG (2006) Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. Am Nat 167:206–215
- Plaistow SJ, St. Clair JJJ, Grant J, Benton TG (2007) How to put all your eggs in one basket: empirical patterns of offspring provisioning throughout a mother's lifetime. Am Nat 170: 520–529
- Roff DA (1992) The evolution of life histories: theory and analysis. Chapman and Hall, New York
- Rossiter MC (1993) Initiation of maternal effects in *Lymantria dispar*: genetic and ecological components of egg provisioning. J Evol Biol 6:577–589
- Rotem K, Agrawal AA, Kott L (2003) Parental effects in *Pieris rapae* in response to variation in food quality: adaptive plasticity across generations? Ecol Entomol 28:211–218
- Royle NJ, Surai PF, Hartley IR (2003) The effect of variation in dietary intake on maternal deposition of antioxidants in zebra finch eggs. Funct Ecol 17:472–481
- Savalli UM, Fox CW (2002) Proximate mechanisms influencing egg size plasticity in the seed beetle, *Stator limbatus*. Ann Entomol Soc Am 95:724–734
- Smith CC, Fretwell DS (1974) The optimal balance between size and number of offspring. Am Nat 108:499–506
- Solbreck C, Olsson R, Anderson DB, Forare J (1989) Size, life history and response to food shortage in two geographical strains of the seed bug *Lygaeus equestris*. Oikos 55:387–396
- Suárez LH, Gonzáles WL, Gianoli E (2004) Biología reproductiva de *Convolvulus chilensis* (Convolvulaceae) en una población de Aucó (centro-norte de Chile). Rev Chil Hist Nat 77:581–591

- Takakura KI (2004) Variation in egg size within and among generations of the bean weevil, *Bruchidius dorsalis* (Coleoptera, Bruchidae): effects of host plant quality and paternal nutritional investment. *Ann Entomol Soc Am* 97:346–352
- Terán A, Kingsolver JM (1977) Revisión del género *Megacerus* (Coleoptera: Bruchidae). Ministerio de Cultura y Educación, Argentina, p 287
- Tuomi J, Hakala T, Haukioja E (1983) Alternative concepts of reproductive effort, costs of reproduction, and selection in life-history evolution. *Am Zool* 23:25–34
- Van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *Am Nat* 128:137–142
- Vinson SB, Iwantsch GF (1980) Host suitability for insect parasitoids. *Annu Rev Entomol* 25:397–419
- Wang R, Kok LT (1986a) Life history of *Megacerus discoidus* (Coleoptera: Bruchidae), a seedfeeder of hedge bindweed, in SW Virginia. *Ann Entomol Soc Am* 79:359–363
- Wang R, Kok LT (1986b) Host specificity of *Megacerus discoidus* (Coleoptera: Bruchidae) and its impact on hedge bindweed, *Calystegia sepium*. *Environ Entomol* 15:834–838
- Yang RL, Fushing H, Horng SB (2006) Effects of search experience in a resource-heterogeneous environment on the oviposition decisions of the seed beetle *Callosobruchus maculatus* (F.). *Ecol Entomol* 31:285–293