



## Delay, avoidance and protection in oviposition behaviour in response to fine-scale variation in egg parasitism risk



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Organisms that do not provide parental care are challenged with multiple factors and risks in the selection of an oviposition site. Oviposition site selection greatly affects offspring fitness, but little is known about how females respond to fine-scale variation in environmental cues. The seed beetle, *Mimosstes amicus*, shows remarkable behavioural plasticity in response to variation in egg parasitism cues. When exposed to egg parasitoid adults, females superimpose eggs atop each other to protect bottom eggs from parasitism. Here, we examined egg protection behaviour in response to the microspatial distribution of parasitized eggs. We exposed females to treatments varying in the number and dispersion of parasitized eggs on seed pods. Our results showed that oviposition behaviour was influenced by the evenness of the distribution of parasitized eggs and suggest that *M. amicus* exhibits a conditional strategy on a highly localized 'pod-by-pod' basis. When pods bore no eggs or unparasitized eggs, beetles laid the greatest number of eggs, almost all singly. In contrast, stacking was greatest and oviposition most reduced when parasitized eggs were distributed across all of the five pods provided. Lastly, females avoided ovipositing on seed pods with parasitized eggs when other oviposition sites were available. In general, avoidance behaviour increased, stacking increased and oviposition decreased as the number of pods (one, three or five) with parasitized eggs increased. Our results provide novel evidence of an oviposition strategy that combines both risk avoidance and offspring protection. Avoidance behaviours and reductions in oviposition rate are likely to be obscure among animals and may be more common than has been documented to date.

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In terrestrial, egg-laying organisms that lack parental care, the choice of an oviposition site is a critical one, and mothers may weigh a complex set of factors and risks in deciding where to place their eggs. During oviposition, there are many different cues a female is exposed to; if the maternal environment is predictive of the offspring environment, we would expect that selection would produce mechanisms under maternal control that enhance offspring survival (Mousseau & Dingle 1991; Fox & Mousseau 1998; Mousseau & Fox 1998). These may include alterations to offspring size or development, in which females may impart cytoplasmic factors to eggs, based on the state of the environment and the mother's physiology (Ho & Burggren 2010). Given the importance of offspring survival in achieving reproductive success, the degree to which maternal environment, development and behaviour influence offspring fitness will determine the

likelihood that they will be shaped by natural selection (Mousseau & Fox 1998).

Various biotic and abiotic factors influence oviposition site selection in various taxa. Nest site or oviposition site preferences based on microclimate variables have been documented in birds (Lloyd & Martin 2004), nonavian reptiles (Shine & Harlow 1996; Wilson 1998) and insects (Pincebourde et al. 2007; Potter et al. 2009). Females among various animal taxa exhibit spatially or temporally sensitive egg dispersal mechanisms that guarantee a low probability of egg predation or parasitism, such as mites (Yanagida et al. 2001), mosquitoes (Kiflawi et al. 2003; Blaustein et al. 2004), hydrophilid beetles (Brodin et al. 2006), angelfish (Sakai & Kohda 1995) and treefrogs (Binckley & Resetarits 2002; Rieger et al. 2004). Specifically, herbivorous insects may choose to lay eggs on host plants that are less suitable for offspring development but provide a lower risk of predation or parasitism (e.g. enemy-free space: Jeffries & Lawton 1984; Denno et al. 1990; Berdegue et al. 1996; Mira & Bernays 2002; Heard et al. 2006).

Most studies, however, have not examined the finer spatial scale of variation in biotic risk on oviposition site selection. For example, females may discriminate among host species (Mira & Bernays

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2002) or pools (Blaustein et al. 2004) that harbour natural enemies, but there is also a selective advantage to choosing enemy-free areas within an individual location, such as certain leaves (Lucas & Brodeur 1999) or upper parts of a host plant (Gall et al. 2012), or at deeper depths within a single pool (Hirayama & Kasuya 2009). Furthermore, among herbivores that lay their eggs in fruits and seeds or insect parasitoids that oviposit in insects, opportunities for laying eggs are often constrained by the need to place their offspring in or on a discrete host resource of limited quantity (Diaz-Fleischer & Aluja 2003). The temporal and spatial variability in host resources is predicted to have a major effect on the evolution of egg load (Ellers et al. 2000; Harvey et al. 2001) and ovarian dynamics during a female's life span (Papaj 2000). Lastly, fine-scale oviposition decisions may be difficult to observe when resources of high and low value cannot be easily distinguished, but may bear larger-scale consequences, such as shifts in host population growth and species interactions within the community (Werner & Peacor 2003; Schmitz et al. 2004; Fill et al. 2012).

To examine the extent of fine-scale variation in parasitism cues on oviposition behaviour, we chose to study a beetle that deploys modified eggs as protective shields to reduce mortality by egg parasitism. *Mimosestes amicus* lays eggs on the outside of seed pods of legumes, and when exposed to parasitism cues, females superimpose eggs atop one another, shielding bottom eggs in the stack from parasitism by the trichogrammatid wasp, *Uscana semifumipennis* (Deas & Hunter 2012). In previous experiments, we discovered that parasitoid adults trigger the egg-stacking response (Deas & Hunter 2012), but, because these adults started to parasitize beetle eggs as soon as they were introduced, we could not determine whether beetles responded to the parasitoid adults or to the parasitized beetle eggs, or both. We predicted that parasitized eggs would be a reliable cue in nature (and in this experiment), because our casual observations of behaviours of both the parasitoid and the beetle suggested both the deposition of a cue by the parasitoid after parasitizing an egg and the reception of that cue by ovipositing beetles.

We tested whether parasitized eggs triggered the response and then compared oviposition behaviour across laboratory environments that varied in the probability of a female encountering parasitized eggs. We asked two specific questions. (1) Do beetles increase their stacking response (add proportionately more stacks to single eggs and more eggs per stack) when exposed to more parasitized eggs? (2) Do beetles increase their stacking response when parasitized eggs are more dispersed across pods? We predicted that a beetle's stacking response would increase when parasitized eggs were either more numerous or more widely dispersed across pods.

## METHODS

### Study System

Seed beetles are an ideal system for examining the fine-grained spatial scale of oviposition decisions because they lack parental care (J. B. Deas, personal observation) and thus selection of high-quality oviposition sites can have enormous consequences for offspring fitness (Gall et al. 2012). Additionally, seed beetles require legumes for oviposition that vary temporally and spatially in accessibility (J. B. Deas, personal observation). Finally, and notably, different seed beetle species exhibit ovipositional and egg size plasticity in response to different aspects of habitat quality (Prevedt 1966; Messina & Renwick 1985; Fox et al. 1997; Teixeira et al. 2009; Deas & Hunter 2012).

*Mimosestes amicus* is a seed beetle (Chrysomelidae: Bruchinae) distributed from the southwestern United States throughout

Mexico and Costa Rica (Kingsolver & Johnson 1978). *Parkinsonia florida* (blue palo verde), *Parkinsonia microphyllum* (foothill palo verde) and *Prosopis velutina* (velvet mesquite) are the host plants most commonly attacked by *M. amicus* populations in central Arizona, but we used *P. microphyllum* pods to maintain laboratory colonies and experiments because these pods confer higher beetle survivorship (J. B. Deas, unpublished data). *Mimosestes amicus* lay eggs and egg stacks directly on seed pods, placing eggs on pods containing seeds. Upon hatching, larvae burrow through the pod and into the seed below, where they develop, pupate and emerge as adults. Eggs may be laid in stacks of two or more eggs. Top eggs protect the bottom egg from parasitism in both laboratory and field settings (Deas & Hunter 2012). Mitchell (1977) observed the stacks and originally speculated that females were responding to risk of parasitism or desiccation of eggs, given his observations of parasitized eggs and unexplained embryonic mortality in top eggs. Our results supported the role of protection against parasitism but not against desiccation; even in the absence of parasitism, all top eggs are smaller and inviable, and larvae die before hatching (Deas & Hunter 2012). Desiccation is not ruled out as a selective pressure involved in the evolution of egg stacking behaviour, but our results suggest that the inviability of these eggs is not due to desiccation. *Uscana semifumipennis* (Trichogrammatidae) is a solitary egg parasitoid that co-occurs with *M. amicus* in southern Arizona and belongs to a genus that parasitizes the eggs of seed beetles (Fursov 1995).

### General Methods

During late June of 2010 and 2012, we collected apparently uninfested seed pods from *P. microphyllum* trees in Tucson, Arizona, U.S.A. All pods were used for rearing, but the newest pods (June 2012) were used for experiments. Seed pods were stored at  $-20^{\circ}\text{C}$  to exterminate larvae of *M. amicus*, and lethal, bruchid parasites such as the straw itch mite, *Pyemotes tritici* (Southgate 1979). Beetles and wasps used in experiments were descended from individuals collected in early to mid-August of 2010 and 2011 and were reared on stored seed pods. Laboratory populations were reared at  $30^{\circ}\text{C}$ , 50% relative humidity. Emerging female and male beetles were collected from laboratory populations and kept in breeding containers for 1–2 days before being used in experiments. Seed pods of *P. microphyllum* vary between one and three seeds per pod, so except for each of three replicates in which we had to use one two-seed pod and three one-seed pods, we used only one-seed pods in our experiments. The egg parasitoid *U. semifumipennis* used in experiments originated from parasitized eggs of *M. amicus* collected in the field, which were reared in the laboratory on eggs of *Callosobruchus maculatus*, which were, in turn, reared on cowpea seeds, *Vigna unguiculata*. After emergence, wasps were kept in 100 mm test tubes at  $12^{\circ}\text{C}$  and 65% relative humidity with drops of honey until needed for experiments.

### Do parasitized eggs alone trigger the stacking response?

To produce parasitized eggs for experiments, we collected adult beetles as they emerged, allowed the females to mate and lay eggs for 48 h, and then exposed approximately 75% of each female's eggs to 1–3-day-old *U. semifumipennis*. The remaining 25% of the eggs were untouched and used as a control for the female's response to the presence of conspecific eggs ( $N = 47$  sets). Seed pods bearing parasitized eggs were then split into two treatments. Parasitized eggs were either left intact ( $N = 23$  sets), or removed to control for the presence of cues left on the seed by the female ( $N = 46$  sets). Eggs were removed in this treatment in order to distinguish between the females' responses to parasitism cues associated with the eggs themselves and their possible responses to cues left by the

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