

Reproductive Compensation: A Review of the *Gryllus* spp.—*Ormia ochracea* Host-Parasitoid System

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Abstract Calling male field crickets (*Gryllus* spp.) are acoustically located and subsequently parasitized by the parasitoid fly, *Ormia ochracea* (Diptera: Tachinidae). Parasitism by *O. ochracea* results in cricket death. The reproductive compensation hypothesis posits that when a host's residual reproductive value decreases, it would be adaptive for that host to shift its resources into current reproduction. Reproductive compensation has not been observed in the cricket-fly system. Here we review the studies to date that have investigated reproductive compensation in the cricket-fly interaction, in an attempt to understand why crickets do not compensate for their future reproductive losses. We conclude that the cricket-fly interaction may not be an ideal system in which to investigate reproductive compensation and furthermore, that reproductive compensation has been poorly investigated in this system.

Keywords Parasitoid · reproductive compensation · *Ormia ochracea* · parasite · host

Introduction

Life history theory is founded on the premise that resources allocated to one aspect of life history (growth, maintenance, reproduction) cannot be simultaneously allocated to another; this results in a trade-off between an individual's life history traits (Stearns 1992). Given that individuals cannot simultaneously maximize all life-history traits,

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differential investment in each of these traits is expected over an individual's lifespan. The timing of investment in reproduction is expected to be largely dependent on the probability of future reproductive success and therefore, life expectancy (Williams 1966). As the probability of future survival decreases, investment in current reproduction is expected to increase.

Parasites are costly to their hosts and have been found to decrease their hosts' longevity, castrate the host and affect other aspects of host fitness (Lanciani 1975; Minchella and Loverde 1981; Smith 1988; Forbes and Baker 1991). Given the impact of parasitism on host fitness, hosts should be strongly selected to mitigate the costs of parasitism (Forbes and Baker 1991). Minchella and Loverde (1981) found that when exposed to a castrating trematode parasite, the snail *Biomphalaria glabrata* increased its reproductive effort by increasing the number of eggs laid soon after parasite exposure. This increase in reproductive effort was observed in individuals that were sham treated, that is, those that were exposed to the castrating trematode parasite, but not parasitized by it. These findings lead the authors to propose the reproductive compensation hypothesis, which predicts that when an individual perceives a threat to its future reproductive success, it increases its current reproductive effort. This hypothesis stems from the concept of residual reproductive value (Fisher 1958; Williams 1966) and assumes that when a host's residual reproductive value decreases, it would be adaptive for that host to increase its current reproductive effort. Reproductive compensation has been demonstrated in several invertebrate and vertebrate models (Minchella and Loverde 1981; Polak and Starmer 1998; Agnew et al. 2000; McCurdy et al. 1999; Schwanz 2008).

To date, reproductive compensation has not been observed in the host-parasite system of crickets, *Gryllus* spp. (Orthoptera: Gryllidae) and the parasitoid fly, *Ormia ochracea* (Diptera: Tachinidae). This is surprising because parasitism by *O. ochracea* unavoidably results in the loss of future reproductive success due to host death. Herein we (1) describe the dynamics of the cricket-fly system, (2) review the studies that have investigated reproductive compensation in this system, and (3) review the reproductive compensation hypothesis to evaluate whether its assumptions are met by the cricket-fly interaction. Our aim is to understand why neither male nor female crickets appear to reproductively compensate for their future reproductive losses resulting from parasitism by *O. ochracea*.

Natural History of the Cricket and the Fly

Male crickets produce long distance acoustic signals (calls) to attract sexually receptive female crickets (Alexander 1961). Female *O. ochracea* have a highly developed ear that results from the coupling of their two tympani (Robert et al. 1996). Gravid female flies locate their hosts by 'homing in' on the male's mating call. The fly then lays live larvae on and around the calling cricket. The planidia (1st instar *Ormia* larvae) burrow into the host's body (Cade 1975). During the first 3 days of infection, phase I, larvae occupy the flight muscles in the hosts' thorax. During the final 4 days of infection, phase II, larvae occupy the hosts' abdomen where they feed on host fat bodies and muscle (Adamo et al. 1995a). Parasitized crickets initiate an encapsulation response to kill the larvae before they have a chance to establish

themselves (Vinson 1990). However, encapsulation responses are often co-opted by the parasitoid larvae and used to form a trachea (Vinson 1990). Six to ten days after entering the cricket, the parasitoid larvae purge their guts and make an exit hole through which they exit the cricket's body (Adamo et al. 1995a). Crickets die shortly following parasitoid emergence (Cade 1975; Adamo et al. 1995a; Kolluru et al. 2004).

Ormia ochracea parasitizes several cricket species throughout the United States including the sand field cricket *Gryllus firmus* (Walker and Wineriter 1991), the southeastern field cricket *G. rubens* (Walker 1986), the Texas field cricket *G. texensis* (Cade 1975), the western stutter trilling cricket *G. integer* (Hedrick and Kortet 2006) and the variable field cricket *G. lineaticeps* (Wagner 1996). On the Hawaiian Islands, *O. ochracea* parasitizes the cricket *Teleogryllus oceanicus* (Zuk et al. 1993). Herein we evaluate investigations conducted in some of these cricket populations and discuss possible reasons that reproductive compensation was not observed.

Review of Cricket-fly Reproductive Compensation Research

Orozco and Bertram (2004) compared the time spent producing long distance mate attraction calls (calling effort) of parasitized and unparasitized *G. texensis* crickets. The authors found that male *G. texensis* did not increase their calling effort once parasitized compared to non-parasitized males. Instead, Orozco and Bertram (2004) observed the opposite; male cricket calling effort diminished during parasitization by *O. ochracea*. In Hawaii, where *O. ochracea* uses the cricket *T. oceanicus* as a host (Zuk et al. 1998), parasitized male *T. oceanicus* did not differ significantly in their calling activity: proportion of males calling, number of calling bouts, length of longest calling bout, or calling duration, from healthy males (Kolluru 1999). Furthermore, similar to Orozco and Bertram (2004), Kolluru et al. (2002) found that parasitized male *T. oceanicus* exhibited a reduction in reproductive effort, quantified by spermatophore production, calling, mating activity, and mass allocated to reproductive tissue. These results strongly suggest that, contrary to the reproductive compensation hypothesis, parasitized male crickets do not increase their reproductive efforts once parasitized by *O. ochracea*.

Despite the fact that parasitoid flies acoustically orient to calling males, several authors have observed parasitized females in the wild (Walker and Wineriter 1991; Zuk et al. 1993; Adamo et al. 1995b). Parasitism in female crickets is likely the result of female crickets acoustically locating to calling males, thus, coming into contact with any live planidia laid in the surrounding area (Cade 1975). Because females are parasitized in nature, we expect them to possess the ability to reproductively compensate once parasitized. Studies on the impact of *O. ochracea* on the reproductive success of female crickets have traditionally focussed on cricket egg laying behaviour (Adamo et al. 1995a; Adamo 1999).

Adamo et al. (1995a) found that parasitized female *G. texensis*, *G. rubens* and *G. bimaculatus*, did not increase egg laying behaviour when parasitized. In a similar study, Adamo (1999) found that 2-week-old *Acheta domesticus* females laid the same number of eggs per day as healthy females for the first 5 days following

parasitization. However, 1 day prior to emergence of the parasitoid larvae, egg laying rates of parasitized females decreased significantly. Therefore, similar to males, female crickets also fail to support the reproductive compensation hypothesis. It is important to note however, that *A. domesticus* is not parasitized by *O. ochracea* in the wild and therefore selection to evolve a response to parasitism by *O. ochracea* is absent. Consequently, we would not expect to observe reproductive compensation in response to *O. ochracea* in *A. domesticus* unless it was a general response to immune threats.

Reproductive Compensation Hypothesis—The Assumptions

The reproductive compensation hypothesis makes two fundamental assumptions. First, that the host is capable of *detecting that its residual reproductive value is at risk*. Second, that the host is capable of *increasing its reproductive effort*. Here we examine each of these assumptions in turn to determine whether they are satisfied in the cricket-fly system.

Assumption 1—Detection of Threat to Residual Reproduction Value

The immune-based encapsulation response initiated by crickets when parasitized by *O. ochracea* (Vinson 1990; Adamo et al. 1995a) provides strong evidence that crickets can detect an *O. ochracea* infection. Previous studies have assumed that because the parasite's presence is associated with host death or castration, the parasite poses a recognized threat to the host's reproductive value (Minchella and Loverde 1981; Adamo 1999; Kolluru et al. 2002).

Assumption 2—Increase Reproductive Effort

All evidence to date suggests that crickets do not increase their reproductive output once parasitized. Male crickets do not signal more often, produce more calling bouts, increase the length of their calling bout, produce more spermatophores, or alter their mating activity (Zuk et al. 1998; Kolluru et al. 2002; Orozco and Bertram 2004). Similar to males, female crickets do not increase their reproductive output (number of eggs laid) in response to an *O. ochracea* infection (Adamo 1999). These findings suggest that crickets may not be able to increase their reproductive effort following parasitism, even if it may be adaptive to do so. However, these studies measured reproductive *output* and used it as a proxy of reproductive *effort*. Reproductive output may not be a suitable indicator of reproductive effort because if crickets increase their reproductive effort following parasitism, this increase may not be reflected in their output because of the extra metabolic demands placed on the cricket by the parasite. Instead, the energetic costs of being parasitized could result in an overall reduction of cricket reproductive output.

To address the problem with measures of reproductive output representing the synergistic effect of both reproductive effort and host metabolism, Kolluru et al. (2002) quantified both the reproductive output and metabolic rate of parasitized crickets. Parasitized and unparasitized *T. oceanicus* did not differ in their resting

metabolic rates. Parasitized crickets did, however, exhibit reduced reproductive outputs. Because parasitized crickets did not experience increased metabolic costs relative to their unparasitized counterparts, their reduced reproductive output implies that their reproductive efforts decreased instead of increased following parasitism. In Kolluru et al.'s (2002) study it was impossible to distinguish between host metabolism and parasite metabolism. Thus, the possibility exists that the larval parasitoid's respiration contributed substantially to the observed metabolic rate of the host-parasitoid complex, thereby masking any potential change in host metabolic rate that may have occurred (Kolluru et al. 2002).

Host reproductive output is typically measured for the duration of the two-phase infection by *O. ochracea* (Zuk et al. 1998; Adamo 1999; Kolluru et al. 2002; Orozco and Bertram 2004; Shoemaker et al. 2006). Phase I of infection by *O. ochracea* is thought to be relatively benign (Adamo et al. 1995a). If reproductive compensation efforts are masked by the cost of parasitism, assessing host reproductive effort during both phases of infection may allow for reproductive compensation to be more easily observed as compensation in one phase (e.g. Phase I) will not be obscured by a lack of compensation or a reduction in reproductive effort in the other phase. In the studies for which the data collected during phase I and phase II of infection could be distinguished (Adamo 1999; Kolluru et al. 2002; Orozco and Bertram 2004), crickets were not reproductively compensating during either stage of infection by *O. ochracea*, thereby precluding the possibility that crickets are only compensating during one stage of infection.

Experimental Design: Testing the Reproductive Compensation Hypothesis

Although it appears that crickets do not reproductively compensate in response to parasitization by *O. ochracea*, it is debatable whether the experimental designs of the aforementioned studies were appropriate. The experiment that led Minchella and Loverde (1981) to formulate the reproductive compensation hypothesis consisted of three treatments: a control treatment where snails were neither exposed nor parasitized by the castrating trematode parasite, a parasitized treatment where the snails were both exposed to and parasitized by the trematode, and a sham treatment where snails were exposed to the castrating trematode, but not parasitized by it. The only individuals that exhibited reproductive compensation were those that were exposed to a parasite but were not themselves infected. This is an important detail to note: that only the sham treated individuals exhibited reproductive compensation. One possible explanation for this finding is that both the parasitized and unparasitized (sham treated) snails compensated by increasing their number of eggs laid, but this increase in parasitized individuals was counteracted by the costs associated with parasitism. In this scenario, if only reproductive output was quantified, only the unparasitized (sham treated) snails would exhibit reproductive compensation. Inclusion of a sham-treatment group allows researchers to resolve the difficulty in differentiating between effort and output in parasitized host individuals. To date, all but one of the studies examining reproductive compensation in the cricket-fly system have excluded a sham treatment. Had Minchella and Loverde (1981) neglected to include the sham treatment as all of the aforementioned cricket-fly studies have done, the reproductive compensation hypothesis may never have been conceived.

The one study in the cricket-fly system that included a sham-treatment was performed on *A. domesticus* crickets (Adamo 1999). In this study, female crickets were placed in one of the following treatments: handled/uninfected (control), infected with parasitoid larvae (parasitized), or ‘infected’ with sephadex beads (sham). Both sephadex bead and *O. ochracea* larvae treatments induced an encapsulation response in the host (Adamo 1999). Infected crickets did not differ in their egg output from the control or sham treatment until the final day of parasitism when egg output decreased in infected females. This approach provides preliminary evidence that suggests that *A. domesticus* females do not reproductively compensate by increasing their egg laying behaviour following parasitization (an expected outcome, given that *A. domesticus* is not a natural host for *O. ochracea*). However, because the sham treatment induced an encapsulation response in the host, any costs associated with launching an encapsulation response went unaccounted for. Thus, costs of an encapsulation response could explain why sham treated females did not lay more eggs than control females. The costs associated with parasite avoidance behaviours and immune response have been demonstrated in several invertebrate systems (Baker and Smith 1997; Moret and Schmid-Hempel 2000; Giorgi et al. 2001; Little and Killick 2007)

It is imperative that future tests of the reproductive compensation hypothesis include a sham treatment. The most obvious method for achieving this involves exposing crickets to parasitoid larvae, and then removing the larvae before they have the chance to enter the cricket host. Vincent and Bertram (2010) found that crickets increase grooming activity when in contact with *O. ochracea* larvae suggesting that crickets are capable of detecting the threat of parasitism. Thus, by placing parasitoid larvae on crickets and not allowing the larvae to enter the host, crickets will be exposed to a parasitic threat without enduring the costs associated with parasitism; any changes in reproductive output of these host individuals can then be quantified.

Discussion

Gryllus spp. do not appear to reproductively compensate in response to parasitization by *O. ochracea*. However, reproductive compensation has not been fully explored in the cricket-fly system. In order to convincingly show that crickets do not reproductively compensate in response to parasitism by *O. ochracea*, the ambiguity between effort and output must be discerned, preferably by including a sham treatment in the experimental design. Additionally, researchers should expand the range of potential compensatory mechanisms investigated in the cricket-fly system. For example, immune challenged mealworms (*Tenebrio molitor*) have been found to increase their investment in cuticular hydrocarbons (CHCs; Sadd et al. 2006). Crickets utilize CHCs to identify individuals and discriminate between potential mates (Tregenza and Wedell 1997; Ivy et al. 2005; Hedrick and Kortet 2006; Thomas and Simmons 2009); therefore, researchers should investigate whether parasitized crickets have different CHC expression and composition.

One possible problem with investigating reproductive compensation in the cricket fly system is that the interaction between crickets and their parasitoid flies represents a *parasitoid*-host interaction, yet the reproductive compensation is based on a

parasite-host interaction. Parasites compete with hosts for resources, potentially decreasing the amount of energy available to their hosts for reproduction, whereas parasitoids ultimately kill their hosts (Roberts and Janovy 2005). This contrast in the temporality of the relationships between parasite-host and parasitoid-host introduces one major problem in comparing the two; presumably, hosts with parasitoids do not live to pass on their genes, certainly not with the frequency that we would expect from hosts in a parasitic relationship. However, *B. glabrata* is castrated by its parasite *S. mansoni* (Minchella and Loverde 1981; Cooper et al. 1996). In terms of reproductive success, castration and mortality have the same impact, in that they both render the host incapable of passing on its genes. Since *B. glabrata* exhibits reproductive compensation, it is reasonable to ask whether crickets have also evolved compensatory mechanisms to parasitoid fly infection. Thus, formally investigating whether crickets may evolve compensatory strategies in order to mitigate the costs of parasitism by *O. ochracea* remains a worthwhile pursuit.

Finally, it is important to acknowledge that crickets may not reproductively compensate in response to parasitism by *O. ochracea*. Care should be taken to avoid creating a modern adaptationist paradigm (Gould and Lewontin 1979) where one not only anticipates the adaptive benefit of traits, but also suspects that adaptive traits exist even in the absence of empirical support. Once reproductive compensation is properly (quantifying effort), and thoroughly (across-populations) investigated, researchers must begin to formulate new theories as to whether crickets should be exhibiting any response to parasitism by *O. ochracea* at all, what these responses may be, and why the cricket-fly interaction is an exception to the reproductive compensation hypothesis.

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