Potential lifetime reproductive success of male bushcrickets parasitized by a phonotactic fly

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Males of the bushcricket *Poecilimon mariannae* are parasitized by the acoustically orienting fly *Therobia leonidei*. Developing fly larvae reduce male bushcricket survival and reproductive effort. We estimated potential lifetime reproductive success (PLRS) of male bushcrickets to investigate the likely costs of this parasitism. Our analysis explored the relative reduction in PLRS caused by parasitoid infection by examining effects on survival, calling attractiveness and spermatophylax size. We also incorporated nonparasitoid-related mortality. Parasitized males lost 42% of their PLRS compared to nonparasitized males. The shortened life span after parasitism accounted for half of the PLRS reduction. Decreased spermatophylax production also had a major effect on PLRS, while decreased calling attractiveness had a smaller effect. This fitness loss was context dependent and changed with extrinsic nonparasitoid-related mortality. If nonparasitoid-related mortality was high, the selection on host males to avoid parasitism was weak; if it was low, parasitized males lost a considerable amount of reproductive opportunities compared with unparasitized males.

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Host–parasite relationships are important for our understanding of fundamental issues in evolutionary biology, for example parasitism can alter host life history patterns (Forbes 1993; Agnew et al. 2000). The ultimate effect of parasitism on an individual host in general is an early death and a decreased contribution to the next generation compared with unparasitized individuals (Godfray 1994).

Most parasitoid species attack the immature stages of their hosts, but some attack reproductive adults (Godfray 1994). These interactions between parasitoids and adult hosts have rarely been studied or modelled (Taylor 1996; Sparato & Bernstein 2000). Acoustically orienting parasitoid flies attack singing adults of cicadas (Soper et al. 1976; Lakes-Harlan et al. 2001), crickets and bushcrickets (reviewed in Lehmann 2003). For example, the parasitoid fly, *Therobia leonidei* Mesnil, 1964 (Diptera: Tachinidae) infects a broad range of bushcricket species in southern Europe (Leonide 1969; Lehmann 2003). In our study species, the bushcricket *Poecilimon mariannae* Willemse & Heller, 1992, adult males suffer high levels of parasitism, whereas females and larval instars have never been found

to be infected (Lakes-Harlan & Heller 1992; Lehmann & Heller 1998). None the less, parasitism is not immediately fatal and males can reproduce to a limited extent (Adamo et al. 1995; Kolluru et al. 2002). Parasitized *P. mariannae* males transfer less spermatophylax material at mating (Lehmann & Lehmann 2000a), which decreases the female's refractory period and reduces the number of eggs laid during this period (Lehmann & Lehmann 2000b). Reduced calling after infection has been cited (Burk 1982) or suggested (Allen 1995a) for bushcrickets, but until now has been quantified only for gryllid species (Cade 1984; Kolluru et al. 2002). This reduction in calling and any changes in calling quality induced by parasitoid infection may alter the attractiveness of male songs. The multiple costs of parasitoid infection on reproduction and survival are assumed to constrain the evolution of conspicuous signalling (Zuk & Kolluru 1998; Haynes & Yeargan 1999). But how costly is it to host such a parasitoid?

Fitness obviously depends on multiple traits, so we analysed the costs of parasitism in terms of survival, calling attractiveness and spermatophylax size. Potential lifetime reproductive success (PLRS) also depends on nonacoustic predators, which are a major threat in closely related *Poecilimon* species (Heller & von Helversen 1990; Heller 1992), especially for moving individuals (Heller 1997). Therefore, to analyse the potential for reproduction of parasitized and unparasitized individuals, we also

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measured other causes of mortality. Combining the reduction in fitness with the field-measured risk of parasitism results in an estimate of the selection strength imposed on *P. mariannae* by the acoustically hunting parasitoid.

METHODS

We first quantified the costs of parasitoid infection for individual males and measured reproductive activities. We have no clear evidence of adaptation to parasitism in *P. mariannae* yet, so we also hypothesized that parasitism has a less pronounced influence on PLRS than nonparasitoid-related mortality.

Measuring Parasitism Costs

We collected last-instar nymphs from a roadside at Vrissiá, central Greece (22°19′E, 39°15′N) within a radius of 50 m, to reduce ecotype variability, and reared them to adulthood in self-made gauge cages (1×0.5 m and 0.3 m high) close to the experimental locality. The in-house temperature fluctuated from 25°C during the day to 15°C at night and the natural light:dark cycle was approximately 14.5:9.5 h in June). Adult males were then placed individually into plastic 200-ml vials. Data from an enclosure experiment done in June 1995 at the same site were included where appropriate (Lehmann & Heller 1998; Lehmann & Lehmann 2000a, b).

Survival

After having located a singing male bushcricket, the female parasitoid fly deposits planidium larvae on the abdomen of the male. The larvae then burrow inside and feed on the host for several days before emerging and pupating. A few days after infection, the larvae make a connection with the air outside the host through a chitinized breathing funnel. Parasitized males can then be identified by having a brown dot on the ventral surface of the abdomen (Leonide 1969).

To expose bushcrickets to the parasitoids, we marked 100 adult males with reflecting tape on the hind femora and released them overnight into the field. We collected them the next morning and put them in 200-ml vials. They received protein-rich flowers of gorse, *Spartium junceum*, ad libitum. We checked them daily for parasitoid infection and recorded the time from the day of release to the day of appearance of the fly breathing funnel (t_p), and the time from visible parasitism to death (t_d). A further sample of 22 individuals from the same site with a single breathing funnel of known age from the enclosure experiment (Lehmann & Heller 1998) were included for measurement of the time from visible parasitism to death (t_d). All males were checked twice daily for mortality and pupal emergence. The nonparasitized males were held under identical conditions for comparison.

Calling

To quantify a possible effect of parasitism on calling ability, we recorded the singing activity of 19 males with

and 19 without parasites. Experimental males were placed into 200-ml jars (*Drosophila* rearing boxes, Greiner Bio-one GmbH, Frickenhausen, Germany), which were acoustically isolated in the field station to prevent interference between males. Electret-Condensator microphones were integrated into the plug of these jars, with a maximum sensitivity at 25 kHz (*P. mariannae* produces a broadband ultrasonic signal with a main component between 20 and 40 kHz and a peak frequency around 25 kHz; Heller 1988; Lehmann & Heller 1998). Microphone sensitivity was adjusted to the song of the males. A six-channel event recorder sampled the microphones sequentially and a relay reset every channel 1 s after the onset of a verse. The multisyllable song (verse) of unparasitized *P. mariannae* lasts a mean ± SE of 600 ± 30 ms and is repeated every 2.5 ± 0.3 s ($N = 12$). To store the data, we used the Quick Base program (Zirelco AG, Dulliken, Switzerland), adjusted to the song of *P. mariannae*, on a laptop and we evaluated the data with a computer program written by K. Reinhold (University of Erlangen, Germany). We thus obtained the number of verses per night for individual males.

Visibly parasitized males, bearing a single fly larva, were obtained from the enclosure experiment (Lehmann & Heller 1998). Control males were matched for age and size to the parasitized males in a paired design. After the parasitized male in a pair died, the unparasitized individual was recorded for another 2 days, to evaluate any possible changes in calling over time. To estimate the calling activity of the two groups, we assigned the day of death of the parasitized male as day zero for the infected and the paired control males.

In a phonotactic experiment, we investigated whether 19 pairs of unparasitized and parasitized males attracted similar numbers of females. Control males were matched for age and size to the parasitized males in a paired design. We placed 25 phonotactically reacting virgin females on the bottom of a cage (1.20×0.80 m and 0.60 m high) in the centre and two small boxes ($7 \times 7 \times 7$ cm) containing, respectively, a parasitized singing male and an unparasitized singing male on top of the cage at either end. The normal separation distance between singing males is 0.3–2.0 m in the field (unpublished data). Before starting a trial, we checked the singing activity of both males visually (by their wing movement) and acoustically. After 10 min we counted the females that had approached each of the two boxes within a radius of 10 cm. After each trial we replaced females on the bottom of the cage. The positions of singing males were changed between trials. We calculated the mean number of females attracted from five trials to avoid pseudoreplication (Machlis et al. 1985).

Survival rate in the field

In an enclosure of 50 m² (Lehmann & Heller 1998) we observed 50 marked males per night over 12 nights. Females were removed from the enclosure several days earlier to avoid matings affecting the predation rate. By marking males with reflecting tape (Heller & von Helversen 1990) we were able to find all surviving individuals. In some cases, the causes of death were directly
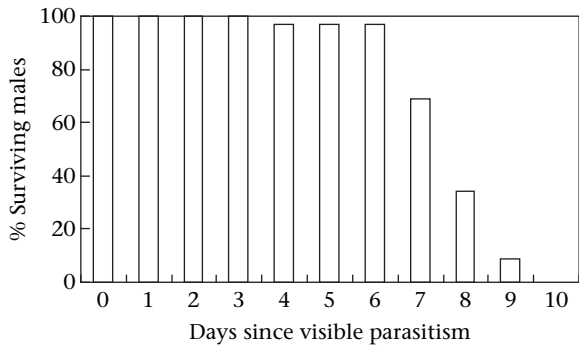
Figure 1. Relative number of males surviving after the appearance of the parasitoid breathing funnel. $N = 32$.

observed, and in others the remains of killed males were detected by their reflecting tapes. The survival rate for each night was calculated as the number of males found alive, divided by the number of males released the previous night. Males in the population outside the enclosure experiment were checked daily for occurrence to estimate the length of the adult male season.

Calculating PLRS

As outlined above, we compared a range of variables between parasitized and unparasitized males, but to measure the likely costs of parasitism it is necessary to link these factors to the PLRS. We calculated the PLRS for parasitized and unparasitized males, analogous to survivorship curves. For simplification, we assumed that unparasitized males are subject to a constant daily death rate by nonparasitoid-related mortality. In addition, the population dies out under natural conditions after a maximum time span (T_{max}). Parasitized males showed reduced survival, call rate, acoustic attractiveness to females and spermatophylax size. Call rate and call attractiveness might be tightly coupled, so we used only call attractiveness as a factor in our analysis. Spermatophylax size is an important component of reproductive success (Lehmann & Lehmann
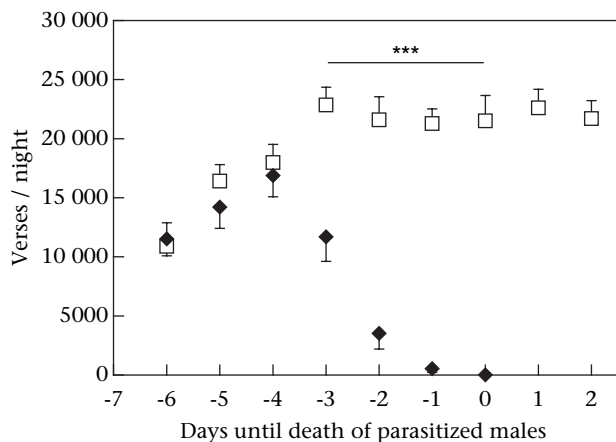
Figure 2. Mean calling activity ± SE in unparasitized (□) and parasitized (◆) males. Each point represents data derived from 15 individuals. *t* test: ***P < 0.001.
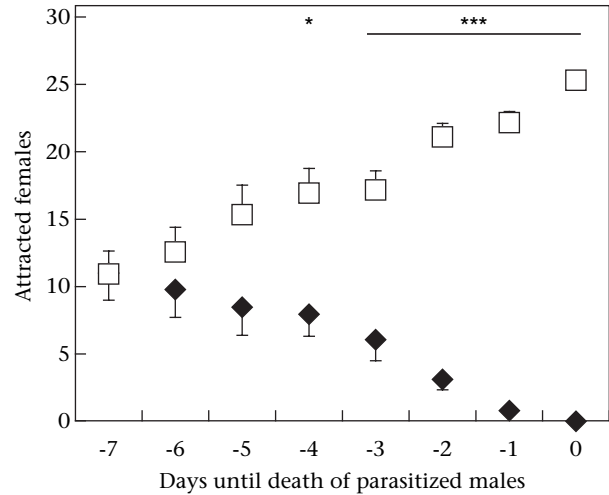
Figure 3. Mean number ± SE of females attracted to unparasitized (□) and parasitized (◆) males. Each point represents data derived from 13–19 pairs. Paired *t* test: *P < 0.05; ***P < 0.001.

2000a), determining the remating interval in females and the number of eggs laid during this refractory period (Lehmann & Lehmann 2000b). Parasitized males showed a correlated reduction in spermatophylax size and sperm number (Lehmann & Lehmann 2000a). In general, in the genus *Poecilimon* the last male to mate sires the offspring (Achmann et al. 1992; Achmann 1996; Achmann & Heller 2000), so we ignored sperm number in our analysis. The mortality of parasitized males, call attractiveness and spermatophylax size were multiplied by the nonparasitoid-related mortality. The resulting PLRS curves were resolved by numerical integration (daily summation of the values).

We predicted that the reduction in PLRS for parasitized males compared to unparasitized males would depend on the survival rate calculated to take into account nonparasitoid-related mortality. Even so, the relative importance of factors in the analysis responsible for any reduction in the PLRS might change with the survival rate in the field. We therefore repeated the analysis varying the constant daily survival rate from 100 to 75%. In addition, the day of parasitism in the season might affect PLRS, so we conducted the analysis with T_{max} decreasing to zero. Segregation of reproductive behaviours shows under which conditions their relative importance changes for parasitized males.

RESULTS

Parasitism Costs

Survival

Of the 100 released males, 10 were found to be infected in a single night, each by a single fly larva. The breathing funnels of the larvae were visible a mean ± SE $3.9 ± 0.2$ days ($N = 10$) after parasitism. Parasitoid larvae emerged 7–10 days after the appearance of the breathing funnel (with one exception where emergence was after 4 days). Parasitized males died within minutes of this emergence. The mean survival time from appearance of the breathing

Table 1. Survival probability, calling attractiveness and spermatophylax size in parasitized males relative to unparasitized control males

	Day													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Survival probability (%)	100	100	100	100	100	100	100	**97**	**97**	**97**	**69**	**34**	**9**	**0**
Calling attractiveness (%)	100	100	100	100	100	100	100	**78**	**55**	**47**	**35**	**15**	**4**	**0**
Spermatophylax size (%)	100	100	100	**80**	**80**	**60**	**50**	**50**	**50**	**50**	**50**	**50**	**0**	**0**
All three factors (%)	100	100	100	80	80	60	50	38	27	23	12	3	0	0

Percentages in bold are significantly lower in parasitized males (survival, spermatophylax: t test; call attractiveness: pairwise t test). Data for spermatophylax size were calculated after Lehmann & Lehmann (2000a).

funnel $\pm$ SE was 7.0 ± 0.2 days ($N = 32$), including a further sample of 22 individuals from the same site with a single breathing funnel of known age from the enclosure experiment (Fig. 1). Combining the time from parasitism until appearance of the breathing funnel with the time from visible parasitism to death, we found that the probability of survival for parasitized males was reduced to zero within 14 days of being attacked (compare Fig. 4 below). The 90 unparasitized males recaptured from the field were all still alive at the end of this 14 days, giving a significant difference in the survival analysis between parasitized and unparasitized males (log-rank test: $\chi_1^2 = 147.75$, $P < 0.001$).

Calling

The number of verses per night increased from 10000 to 18000 per individual over the first 3 days regardless of parasitism. For unparasitized males, calling stabilized at around 22000 verses per night. In contrast, calling activity of parasitized individuals declined drastically within the last 3 days of their lives (Fig. 2). Both day (repeated measures ANOVA: days -6 to 0: $F_{6,28} = 9.5$, $P < 0.001$) and parasitism ($F_{1,28} = 159.8$, $P < 0.001$) significantly influenced the number of verses. The decline in verses was specific to infected individuals (interaction: $F_{6,28} = 25.1$, $P < 0.001$; Fig. 2).

Parasitized males with freshly burrowed breathing funnels attracted the same numbers of females as unparasitized males did. However, the mean number of females attracted decreased over time and was zero on the day the parasitized male died (Fig. 3). The influence of parasitism on the number of females attracted is significant (repeated measures ANOVA on the difference in numbers of attracted females (unparasitized minus parasitized males): $F_{7,18} = 15.1$, $P < 0.001$). The tendency for parasitized calling males to attract fewer females than their unparasitized rivals reached a significant level 4 days before the death of parasitized males (paired t test: day -4: $t_{17} = 2.67$, $P = 0.02$; days, -3 to 0: $t_{19} = 3.99$–49.32, $P < 0.001$). Up until 4 days before the death of the parasitized males, they attracted similar numbers of females as unparasitized males did (Fig. 3).

Survival rate in the field

The mean daily survival rate for males $\pm$ SD was $87.4 \pm 4.6\%$ (range 79.2–95.6%) in the enclosure experiment. We directly observed insectivorous bushcrickets (*Tettigonia viridissima*, *T. caudata*), spiders (*Hogna* cf. *radiata* (Lycosidae), *Xystinus* cf. *cristatus* (Thomisidae)) and carabid beetles predating marked males during the experiment. The time span between the observation of the first and the last surviving unparasitized male outside the enclosure experiment was 35 days, and this was used as an estimate for maximum unparasitized adult male life span (T_{max}).
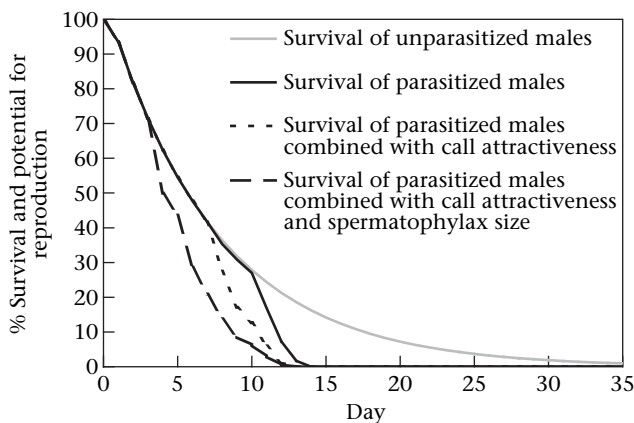
Figure 4. Probability of survival and potential for reproduction of parasitized and unparasitized males. Mean survival rate in the field enclosure was used as a constant daily background mortality rate.
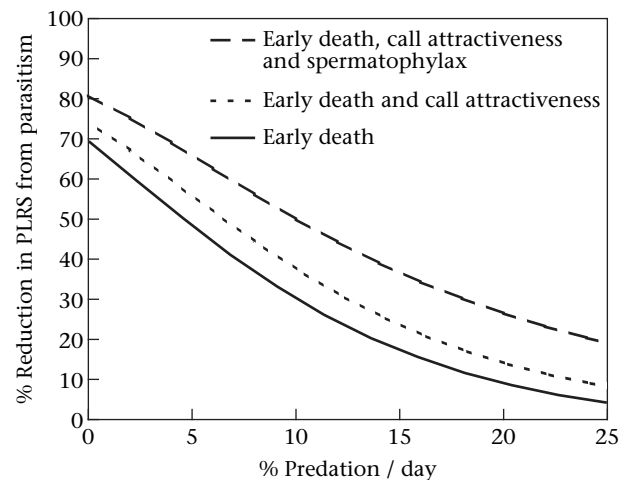
Figure 5. Reduction in potential lifetime reproductive success (PLRS) in parasitized males in relation to the daily predation rate by nonacoustic predators.

PLRS

The parasitoid significantly reduced survival and reproductive behaviour in parasitized males. In comparison to unparasitized males, parasitized males had a lower survival probability, their calling was less attractive and they produced smaller spermatophylaces (Table 1). Calling activity was not included here, as it might be confounded in part with call attractiveness.

This reduction in survival and reproductive behaviour was combined in the PLRS curves (Fig. 4). Numerical integration of these curves showed that parasitized males lost 42% of their PLRS relative to unparasitized males. The largest influence was the reduced survival probability of parasitized males (22%). The loss in PLRS caused by the reduction in calling attractiveness was less severe and added a further 7%. Spermatophylax size was smaller in parasitized males, resulting in a 13% reduction in PLRS.

Parasitism had a substantial effect on the expected PLRS. However, PLRS was also greatly influenced by nonparasitoid-related mortality (Fig. 5). When mortality from nonacoustic predators was high, the decrease in PLRS of parasitized males was less severe. If background survival was 75% per day, parasitism resulted in a PLRS reduction of only 20% (Fig. 5). In our enclosure experiment the measured survival rates were between 96 and 80% daily, equal to a PLRS reduction of 69–27%. A variable nonparasitoid-related mortality rate not only affected the summed costs of parasitism, but also changed the importance of the single factors early death, call attractiveness and spermatophylax size. When the background mortality was low, males suffered most from parasite-induced early death, because it restricted their reproduction potential later in life. Conversely, when the background mortality was high, the main factor affecting PLRS was the smaller spermatophylax produced by parasitized males.

Parasitism in the field takes place over the whole adult life span but it is intuitive that the reduction in PLRS must be smaller if parasitism occurs at the end of the season. The reduction thus follows a negative exponential function over time. We found no PLRS reduction if parasitism occurred after the 30th day of the adult season, as males live for at most 35 days, and spermatophylax reduction was not seen until 4 days after visible parasitism. The PLRS reduction induced by early death dropped to zero on the 22nd day of the season.

DISCUSSION

The attraction of female parasitic flies to male bushcricket songs represents a cost of sexual behaviour (Burk 1982; Sakaluk 1990; Zuk & Kolluru 1998; Kotiaho 2001). In our study species males inevitably die when the fly larva emerges. If adults are parasitized shortly after their final moult their life span is substantially decreased. The reproductive behaviour of these parasitized males (calling activity, call attractiveness and spermatophylax size) was distinctly inferior to that of unparasitized males.

Parasitism by *T. leonidei* reduced the number of songs of *P. mariannae* males (Fig. 2). This finding agrees well with results from other parasitized crickets, which all decreased their song activity after parasitoid infection. In two gryllid species infected by the same fly species, the song reduction was either gradually (Cade 1984) or drastically (Kolluru et al. 2002) reduced 2 days after infection. Males of *P. mariannae* showed a gradual decline in song production similar to that found by Cade (1984). Earlier data on bushcrickets were unquantified (Burk 1982) or extrapolated from the reduced number of singing males with old parasitoid larvae found in the field (Allen 1995a), which might indicate a decline in singing activity over the final days before death.

Females reacted differently to the songs of parasitized and unparasitized males. This is a clear example of males being handicapped in a secondary sexual character through a parasitoid (Zahavi 1975; Zahavi & Zahavi 1997). Song seems to be a reliable character for the choosing females, as it reflected the health of males. None the less, spermatophylax size had decreased before calling was affected (Lehmann & Lehmann 2000a), which means that females cannot determine the size of the nuptial donation from song alone.

Despite its importance for sexual selection theory (Andersson 1994; Johnstone 1995; Kotiaho 2001), no other data on female choice on parasitized orthopterans exist to date. Female choice is easily understandable when it provides material (direct) benefits to the female. Females might discriminate against parasitized males for direct benefit reasons: infected males transfer a smaller spermatophylax during copulation (Lehmann & Lehmann 2000a), so there are fewer resources for female nutrition and egg production (Gwynne 1997). Although avoiding parasitized males is obviously an advantage for females, how they detect the differences in calling or song pattern between healthy and parasitized males is unknown, especially because they discriminate significantly against parasitized males before the number of verses is reduced.

Contrary to the reproductive compensation hypothesis (Minchella & Loverde 1981), there is a net decrease in reproductive effort in response to parasitism because of the nutritional drain and/or pathology caused by the parasitoid. This is in accordance with all available data on Ormiini-infected crickets (Cade 1984; Adamo et al. 1995; Adamo 1999; Kolluru et al. 2002) and bushcrickets (Lehmann & Lehmann 2000a). However, parasitized males are not totally excluded from contributing to the next generation. The quantified loss in PLRS in parasitized males compared to unparasitized males was 42%. This was mainly due to the shortened life span and the smaller spermatophylax transferred at mating (Fig. 4). The influence of the reduced song production in parasitized males on PLRS was small compared to that of survival and spermatophylax size, even though parasitized males invest heavily in song production since calling is essential for mate attraction in bushcrickets (reviewed in Gwynne 2001).

The costs of parasitism in this study were variable and depended largely on nonparasitoid-related mortality. An increasing predation rate reduced the negative influence of parasitism on the PLRS. Relative costs of parasitism

changed considerably with the nonacoustic predation rate. The higher the nonacoustic predation rate, the lower the relative loss in PLRS of parasitized males. When nonacoustic predation was high, the effect of the reduced spermatophylax size in parasitized males was greater than that of the reduction in survival or calling (Fig. 5). Under a low predation regime, the reduction in PLRS was greater, mainly because of the shortened life span. Costs of parasitism decreased over the restricted adult season.

Our analysis made several simplifying assumptions that may not be supported by additional study. First, the probability that a male bushcricket is taken as prey by nonacoustic predators was assumed to be the same regardless of its parasitism status. However, the predation rate may in some way be connected to behavioural alterations (Adamo 1997) or song differences induced by parasitism. Nevertheless, predation on bushcrickets was unaffected by calling behaviour, as nonacoustically orienting predators consumed similar numbers of artificial mute or singing males in cage experiments (Heller 1997). Reproductive success of males may depend on the sex ratio. If the parasitism rate is high (compare Allen 1995a for an Australian bushcricket species) the sex ratio becomes female biased, relaxing male–male competition and increasing mating opportunities for parasitized males. Population density and the number of competitors for mates may also influence the relative PLRS of parasitized males.

As well as limiting the potential for reproduction, Ormiini parasitism of singing orthopterans differs fundamentally from predator–prey systems in the selection regime. In predation, where, for example, singing bushcrickets (Belwood 1990; Belwood & Morris 1987) and calling frogs (Tuttle & Ryan 1981; Ryan et al. 1982) are caught by acoustically hunting bats, the prey is killed immediately with no chance for any reproductive success after the attack. With even a chance of reproduction for parasitized males, the selection pressure of a parasitoid is less severe and might produce fewer counteradaptations in the hosts than predators. Given a higher risk of being eaten (mean daily risk: 12.6%, this study) than of being parasitized (mean daily risk: 5.7%, Lehmann & Heller 1998) and a 2.5-times higher cost in terms of PLRS reduction in our experiment, males suffered fivefold greater reduction in PLRS from predation than from parasitism. As a consequence, predation appears to exert greater selection pressure on males than parasitism.

The difference in selection strength might explain why bushcrickets show a wide range of behavioural adaptations against bat predation (Gwynne 2001; Robinson & Hall 2002). In contrast, no adaptation to parasitism is found in the Greek *Poecilimon propinquus*-group (Lehmann 1998, unpublished data) or the Australian *Sciarasaga quadrata* (Allen 1995b, 1998, 2000). Low-frequency calling at 5 kHz in *Sciarasaga* males might have evolved to shift the frequency from the best hearing range of its fly enemy (Römer & Bailey 1998; discussed in Lehmann 2003), but alternative explanations cannot be ruled out. The suggestion that the unusually short adult season (in general 4 weeks) of the Greek *Poecilimon* bushcrickets might be a reason for an apparent absence of counteradaptation against parasitism (Heller 1997; Gwynne 2001) is not supported

by the differences in costs quantified here. The adult season of the Australian *S. quadrata* is much longer, lasting up to 3 months (Allen 1995a), but there is no evidence supporting behavioural adaptation towards parasitism (Allen 1995a, 1998, 2000).

Several adaptations linked to parasitism risk have been reported for crickets (Cade 1981; Cade & Wyatt 1984; Zuk et al. 1993; Rotenberry et al. 1996; Lewkiewicz & Zuk 2004). The costs of infection in gryllids seem to act as a selection force. Reported parasitism rates are higher in bushcrickets than in crickets (Lehmann 2003), so the lack of apparent adaptation in the former seems incongruous. However, parasitism rates need to be converted into parasitism risk and the daily parasitism rates may be even higher in gryllids. Individuals of *Gryllus* are produced continuously because moulting is asynchronous, thereby diluting the number of adults in samples. In contrast, the life history of *Poecilimon* bushcrickets shows a high synchronicity with 50% of the population moulting into adults within 3 days and a short protandry phase of 2–3 days (unpublished data for several species and populations). Estimates of daily parasitism rates in gryllids and calculations of PLRS will help resolve this issue.

A further systematic difference between bushcrickets and crickets is found in the sexes that suffer from parasitism. In bushcrickets only calling individuals (males) are infected (Lakes-Harlan & Heller 1992; Lehmann & Heller 1998; review in Lehmann 2003). However, in three *Gryllus* species in North America, noncalling females as well as calling males also suffer from parasitism (reviewed in Lehmann 2003). As shown in one species, the parasitic fly deposits its eggs not only on, but also around, a calling male, and the larvae can crawl to any passing female attracted to the singing male (Adamo et al. 1995). The larvae of two different fly species survive on wet sand (Adamo et al. 1995; Allen et al. 1999), but the absence of parasitism of female *Poecilimon* bushcrickets suggests that, with these species, the flies do not lay eggs outside of males, or if they do the larvae do not survive well. Therefore, selection by parasitism might be more pronounced in crickets than in bushcrickets.

Acknowledgments

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