Hiding behaviour in two cricket populations that differ in predation pressure

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Despite evidence that predators and parasitoid flies influence the evolution of song structure in crickets, much less is known about the influence of predators and parasitoids on crickets’ use of refuges. Individual field crickets, Gryllus integer, differ in the amount of time they spend hiding in refuges when placed into a novel environment. Here, we studied the hiding behaviour of crickets from two populations (Arizona and California, U.S.A.) that differ in predation pressure. Tethering experiments conducted at both habitats demonstrated that more predators occur in the Arizona population’s habitat than in the California population’s habitat. We also found more parasitoid flies, which are attracted to male song, in Arizona than in California. We tested hiding times of both male and female crickets from each of the two populations in the laboratory. Male Arizona crickets from the high-predation habitat hid longer when placed into a novel environment in the laboratory than male California crickets from a low-predation habitat, although females from the two populations did not differ. Since the crickets we tested were the first-generation laboratory population derived from field-caught mothers, differences in behaviour were due to either nongenetic maternal effects or genetic effects. These results suggest that hiding times of male crickets in these populations have been shaped by natural selection acting through predation pressure.

Differences between populations in antipredator behaviour are found in a variety of animals (e.g. insects: Lewkiewicz & Zuk 2004; spiders: Riechert & Hedrick 1990; amphibians: Chivers et al. 2001; fish: Giles & Huntingford 1984; Seghers & Magurran 1995; mammals: Oda & Masataka 1996). These differences often correspond to different levels of predation risk between habitats (Sparkes 1996; Wisenden et al. 1997; but see Seghers & Magurran 1995). Presumably, natural selection acts to favour stronger antipredator behaviour in habitats with higher predation risk (Riechert & Hedrick 1990; Chivers et al. 2001). Nevertheless, trade-offs between antipredator behaviour and other important activities such as foraging and mating may limit the degree of population differentiation (Endler 1980, 1983). For example, natural selection for predator avoidance may be countered by sexual selection for conspicuous mating displays (Andersson 1994; Zuk & Kolluru 1998), potentially limiting differences between populations in antipredator behaviour.

In crickets, as in other animals, male calls that attract females also attract predators (Bailey & Haythornthwaite 1998; Zuk & Kolluru 1998). In addition, cricket songs attract parasitoid flies (reviewed in Lehmann 2003). These flies lay their larvae on or near males; the larvae then burrow into the cricket’s body wall, feed on the cricket and kill it upon emergence (Adamo et al. 1995). Studies of numerous cricket populations strongly suggest that predators and parasitoids exert selection pressure on cricket populations for certain properties of male song (Zuk et al. 1993; Rotenberry et al. 1996; Bailey & Haythornthwaite 1998; Zuk et al. 1998; but see Müller & Robert 2002). Moreover, in some populations, male calls that are more attractive to females are also more attractive to parasitoid flies (Wagner 1996; Lehmann et al. 2001), suggesting a trade-off between sexual and natural selection.

Predators and parasitoids should influence not only the structure of male songs, but also more general antipredator tactics. However, relatively few studies have investigated general tactics used by crickets to avoid predation. In the field cricket Teleogryllus oceanicus, males prefer to
call from refuges, which protect them from bat predation (Bailey & Haythornthwaite 1998). In another field cricket, *Gryllus integer*, males within one population vary in their predator-avoidance behaviour (Hedrick 2000). Males of this species call to attract females, and males differ in their call durations (Hedrick 1986, 1988). In a previous study (Hedrick 2000), male field crickets with more conspicuous (longer) calls behaved more cautiously than males with short calls on two tests of predator avoidance. They took longer to emerge from a shelter in a novel, potentially dangerous environment, and ceased calling for a longer time when their calls were interrupted by a simulated predator cue (Hedrick 2000). These differences between males were consistent over time and thus potentially heritable. More recently, Lewkiewicz & Zuk (2004) examined the correlation between numbers of parasitoid flies and calling behaviour of male crickets among populations. They demonstrated that after disturbance, *Teleogryllus* crickets from populations with higher numbers of parasitoid flies ceased calling for longer times than males from populations with fewer flies.

Here we examine hiding behaviour (refuge use) in two populations (one in California (CA) and one in Arizona (AZ), U.S.A.) of the field cricket, *Gryllus integer*, that experience different levels of predation pressure. First, we assessed the relative numbers of cricket predators in each population using tethering experiments in the field at two times of year (spring and autumn), corresponding to the spring and autumn generations of *G. integer*. Second, we estimated parasitoid pressure by counting the number of parasitized crickets that we collected from each habitat over two consecutive years (2003, 2004). Finally, we measured hiding behaviour of individuals from each population in the laboratory. These laboratory tests were conducted on individuals reared in the laboratory from field-caught mothers, to control for environmental factors and thereby determine whether differences between populations were due to environmental effects, or alternatively, to environmental-maternal or genetic effects.

In both of our study populations, males call from cracks in the ground to attract sexually receptive females, and females travel above ground to find males. Males sing at the entrance of the crack with their heads outside the crack entrance, but abruptly stop calling and run further into the crack if they sense a predator approaching. Although they leave cracks to forage, they appear reluctant to leave cracks, presumably because this increases predation risk. Similar hiding behaviour occurs in many taxa and is generally recognized as an antipredator tactic (Dill & Fraser 1997; Hugie 2003, 2004; Jennions et al. 2003). Females are also sensitive to predation risk: they adjust their mate-choice decisions in response to perceived predation risk (Hedrick & Dill 1993).

Preliminary observations of crickets in each of the two habitats suggested that the populations differed in predation and parasitoid pressure. The Davis, California (north central California, Yolo County) population of *G. integer* occurs in irrigated and nonirrigated fields. In this population, calling sites of male *G. integer* are surrounded by low grasses and herbs 1–2 cm high and in

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<tr>
<th>Arizona</th>
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<td>Spadefoot toads (<em>Scaphiopus couchii</em>)</td>
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<td>Pocket mice (<em>Perognathus</em> spp., <em>Chaetodipus</em> spp.)</td>
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<td>and rats (<em>Dipodomys</em> spp.)</td>
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<td>Packrats (<em>Neotoma</em> spp.)</td>
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and therefore substantial gene flow between these populations is unlikely.

METHODS

Tethering Experiments

Tethering experiments were conducted in each study site once in the autumn (September) and once in the spring (May), to coincide with times of high cricket abundance. We conducted experiments in Arizona on 8 September 2003 and 15 May 2004 and in California on 13 September and 17 May 2004. For each experiment, we demarcated a study area of $45 \times 30$ m free of human disturbance and set out 17–22 (depending on availability in the laboratory) male crickets that had been reared in the laboratory (first generation of Davis, California crickets from field-caught mothers) evenly, 5–6 m apart within this area. The crickets were attached to the ground by lengths of fishing line (18 mm diameter, approximately 15 cm long) that were looped around their necks using an adjustable slip knot and then firmly tied around a wire flag that was inserted into the ground. Under these conditions, crickets behaved normally, even walking and calling, but could not escape predation. Pilot studies in the California habitat confirmed that crickets could not escape from these tethers over a 24-h period. Flags were numbered to aid us in finding each marker in the morning. We set crickets out in the field under flags in the evening (at ca. 2100 hours), and recovered flags and any remaining crickets 10 h later (at ca. 0700 hours). Occasionally, the line was cut when we returned in the morning, indicating that a predator had probably bitten through it. We also occasionally found crickets whose heads were attached to the tether but whose bodies were missing (probably eaten), and on one occasion the tether contained only the front half of the body of a cricket. Although crickets in these experiments could not escape from predators by jumping or hiding, the purpose of the experiments was to measure relative predator attack rates in different habitats, rather than actual risk, because we were interested here in predation pressure per se as a selective force.

We predicted that more crickets would disappear from our tethers in Arizona than in California, because of our observations of higher numbers and species of predators in Arizona compared to those in California.

Estimates of Parasitoid Pressure

We also estimated relative densities of parasitoid flies (Ormia ochracea), by counting the percentage of parasitized crickets that were collected from each of the two habitats during our field collections in 2003 and 2004. Prior to this study, no flies had been found in California despite many large collections of crickets spanning 15 years (A. V. Hedrick, unpublished data). During the study, we counted the number of parasitoids hatching from G. integer crickets that we collected in California ($N = 1029$) and in Arizona ($N = 126$). Sample sizes differed because we collected crickets over many more days in California than in Arizona.

Laboratory Experiments

In the laboratory, we measured the latency for each cricket to emerge from a shelter (translucent plastic vial, 4 cm diameter $\times$ 6.5 cm length) when placed into a novel, potentially dangerous environment. This method was used previously (Hedrick 2000) to assess the ‘cautiousness’ of individual crickets, and resembles methods that have been used extensively to measure ‘fearfulness’ in rodents (Boissy 1995). The crickets used in this experiment were the first laboratory generation derived from wild-caught females collected from Davis, California and Aguila, Arizona. Wild-caught females had been inseminated in the field before capture. Laboratory crickets were maintained at $25 \pm 1^\circ C$ with ad libitum food (Purina chick starter) and water (provided in vials stuffed with cotton) under a 12:12 h light:dark cycle. Experimental crickets were removed from bulk family boxes as nymphs (at approximately one-fourth of their adult size) and reared individually (also with ad libitum food and water) in waxed cardboard cups. Individuals of both sexes were physically (but not acoustically) isolated from other individuals. All trials were conducted at 26°C.

At the start of a trial, a cricket was placed inside a small clean plastic vial (dimensions given above). The vial with the cricket inside was then placed on its side in the centre of a small dimly lit (25-W red incandescent bulb, 60 cm distance) arena ($17 \times 17 \times 10$ cm), spatially and acoustically isolated from all other crickets. The red light was used to mimic nocturnal conditions. The bottom of the arena and the vial were carefully washed and dried between trials to guard against chemical cues. The arena was topped with a Plexiglas lid to attenuate sounds from outside the arena. The observer watched from above the arena. As soon as the vial had been placed in the arena, we began timing behaviours using a software program for behavioural measures (AV Bio-Statistics 4.4, available at http://www.cc.jyu.fi/~ansvain/avbs/). The time at which the cricket's head first emerged from the vial and the time at which its complete body was out of the vial were measured to the nearest 0.1 s. Values of 1 s or less were removed because these probably did not reflect hiding behaviour, but rather escape behaviour. If the cricket did not emerge in 10 min (600 s), the trial was stopped and the cricket was assigned a maximum latency to emerge of 10 min (600 s). Pilot experiments had shown that if a cricket did not emerge within 10 min, it often hid for another 10 min or more. Immediately after the trial, the cricket was weighed using an electronic analytical balance and its mass was recorded to the nearest 0.001 g.

During trials, the crickets often acted ‘cautiously’ when emerging (e.g. they moved carefully and slowly, sometimes poking their antennae out and pulling them in again several times before emerging). As in our previous study (Hedrick 2000), males never called from within the vial, suggesting that they did not treat it as a defendable resource. Therefore, our measurement of ‘latency to emerge’ apparently measured variation among crickets in predator-avoidance behaviour, as opposed to other kinds of behaviour, such as territoriality. Moreover, the test situation was not a completely artificial one for these crickets,
as they often fly to new habitats, where they land and then search for a safe shelter (Hedrick 2000).

Laboratory trials were conducted on 299 male and 280 female *G. integer* from Davis, California and on 44 male and 42 female *G. integer* from Aguila, Arizona.

In these experiments, we hypothesized that *G. integer* from the population with relatively more predators and parasitoids (AZ) would hide for longer times than crickets from the population with relatively fewer predators and parasitoids (CA). We also hypothesized that males would be more cautious than females. Male calls are conspicuous and are thought to increase the males’ risk of predation and parasitism (Zuk & Kolluru 1998). Although females travel above ground sampling male calls, we hypothesized that males would be more sensitive to predation/parasitoid pressure because of their calling behaviour (females do not call).

### Statistical Analysis

We analysed data from the tethering experiments and parasite abundance surveys using chi-square tests. To analyse data on latency to emerge from hiding, we used Kaplan–Meier survival analyses (Crowley & Breslow 1984). Specifically, we used Gehan–Breslow tests of survival data to compare survival curves. The Gehan–Breslow test is a nonparametric test that uses a chi-square statistic to reject the null hypothesis that two or more survival curves came from the same population. It assumes that the early survival times are known more accurately than later times and weights the data accordingly (SYSTAT 2004). These tests are appropriate for our data because we stopped trials after 10 min. We used the Gehan–Breslow tests to make planned comparisons between males and females of the two populations (AZ, CA), as well as comparisons of sexes within each population. Where the same data on survival times were used for more than one comparison, we adjusted our alpha levels using the Sidak method (Sidak 1967, SAS Institute online manual, available at http://v8doc.sas.com/sashtml/). Finally, we compared the body masses of crickets between populations and sexes using a two-way ANOVA with population and sex as factors. Our multiple comparisons of body weight were corrected for experiment-wise error rate using the Holm–Sidak method (SYSTAT 2004). We used Spearman rank correlation tests to look for statistically significant correlations between body mass and hiding time. All statistical tests were two-tailed.

### RESULTS

#### Tethering Experiments

As we expected, more individuals disappeared from our tethers in the Arizona habitat than from those in the California habitat, in both the spring and autumn experiments (Table 2). Overall, 95% of the crickets disappeared in the Arizona habitat, while only 40% were taken in the California habitat. These differences were statistically significant (chi-square test: $\chi^2 = 24.500, P = 0.001$).

### Numbers of Parasitoid Flies

The incidence of parasitoid flies (*Ormia ochracea*) hatching from AZ versus CA crickets was different, with more flies hatching from AZ crickets than from CA crickets. In Davis, California during the autumn of 2003, the spring of 2004 and the autumn of 2004, we found that 0% ($N = 464$), 0.50% ($N = 200$) and 0.27% ($N = 365$) of the crickets that we sampled were parasitized, respectively, giving an overall rate of 0.19% (total $N = 1029$) parasitism in this population. In contrast, in *G. integer* from the AZ population, we found that 10.00% ($N = 40$), 8.33% ($N = 12$) and 10.81% ($N = 74$) of the crickets that we sampled were parasitized in each of the three seasons, giving an overall rate of 10.31% (total $N = 126$) parasitism, significantly higher than the value for CA (chi-square test: $\chi^2 = 82.02, P < 0.001$). Of all of the crickets parasitized, we found only three harbouring a single fly larva, whereas the others each were carrying two or three larvae.

#### Latency Trials

Over all groups, the time at which the cricket’s head emerged (‘head out time’) was highly correlated with the time at which all of the body emerged (Pearson’s product-moment correlation: $r_{660} = 0.90, P < 0.001$), so hereafter we report only the head out times.

When we initially compared head out (hiding) times for all four groups of *G. integer* (male AZ, male CA, female AZ and female CA), we found that overall differences were not statistically significant, probably because a similar proportion of crickets from all of the groups spent at least 200 s hiding (Kaplan–Meier survival analysis: Gehan–Breslow test statistic = 3.61, df = 3, $P = 0.306$; Fig. 1). After 200 s of hiding, however, the survival curves diverged significantly (Gehan–Breslow test statistic = 10.08, df = 3, $P = 0.018$; Fig. 2). We conducted four planned comparisons on these latter data, including comparisons between AZ males and CA males, AZ males and AZ females, CA males and CA females, and AZ females and CA females. Our planned comparison between AZ males and CA males showed that a greater proportion of AZ male crickets remained hiding at each successive time point than CA males ($\bar{X} \pm SE$ hiding time: AZ males: 562.4 ± 16.3 s, $N = 32$; CA males: 480.8 ± 10.3 s, $N = 203$; Kaplan–Meier survival analysis: $P = 0.009$; Sidak-adjusted $\alpha = 0.013$).

| Table 2. Number of crickets in tethering experiments that disappeared (were eaten) versus those that survived for Arizona and California populations of *G. integer* |
|---|---|
| Eaten | Survived |
| Arizona | California |
| Spring | 21 | 12 |
| Autumn | 16 | 9 |
| Spring | 12 | 9 |
| Autumn | 4 | 15 |
Differences in hiding times between populations were not observed overall (Kaplan–Meier survival analysis: \( P = 0.367 \), Sidak-adjusted \( \alpha = 0.013 \)).

We also compared AZ females with CA females and found no difference overall in hiding times (Kaplan–Meier survival analysis: \( P = 0.386 \), Sidak-adjusted \( \alpha = 0.013 \)). Thus, male but not female G. integer showed differences in hiding times between populations.

Body mass of crickets (transformed to \( 1/\text{mass} \) to meet assumptions of normality) was related to population (two-way ANOVA: \( F_{1,660} = 106.25, P < 0.001 \)) and sex (\( F_{1,660} = 4.34, P = 0.04 \)), and there were significant interactions between population and sex (\( F_{1,660} = 20.82, P < 0.001 \)). Laboratory-reared males from AZ were heavier than CA males (AZ: \( 0.452 \pm 0.018 \) g; CA: \( 0.392 \pm 0.004 \) g; \( t_{623} = 4.08, P < 0.001 \), Holm–Sidak \( \alpha = 0.017 \)). However, in the laboratory-reared CA population, males were significantly heavier than females (males: \( 0.392 \pm 0.004 \) g; females: \( 0.344 \pm 0.003 \) g; \( t_{527} = 9.29, P < 0.001 \), Holm–Sidak \( \alpha = 0.017 \)). Body mass was not significantly correlated with hiding time in either population (Spearman rank correlation: CA: \( r_s = -0.0008, N = 579, P = 0.984 \); AZ: \( r_s = -0.066, N = 84, P = 0.551 \)), nor was body mass significantly correlated with hiding time for sexes within populations (CA males: \( r_s = 0.070, N = 280, P = 0.245 \); CA females: \( r_s = -0.057, N = 299, P = 0.323 \); AZ males: \( r_s = 0.079, N = 43, P = 0.615 \); AZ females: \( r_s = -0.114, N = 41, P = 0.477 \)).

**DISCUSSION**

Tethering experiments in the field clearly showed a difference in predation pressure in the two habitats we studied. When we tethered crickets in the Arizona habitat, many more crickets disappeared than when we tethered crickets in the California habitat. In the Arizona habitat, which holds a large array of potential predators (Table 1), we observed many tarantula and rodent burrows, and witnessed heavy predation by Colorado River toads and bats. In contrast, our tethering experiments and observations indicated that there are fewer predators in California (Table 1). Although bats were observed feeding on crickets in both habitats, their densities appeared to be higher in Arizona than in California.

The abundance of parasitoid flies also differed in the two habitats, with a relatively high incidence of parasitism in Arizona compared to a low incidence in California. Thus, both predation and parasitism by parasitoids appear to exert stronger selection on crickets in Arizona than in California. Reasons for the difference in abundance of flies between the habitats are not known. Previous estimates of parasitoid infestation in cricket populations range from a low of 3% for *Ormia ochracea* on the cricket *Gryllus* rubens (Walker & Wineriter 1991) to a high of 65% for the fly *Therobia leonidei* on the bushcricket *Poecilimon mariannae* (Lehmann & Heller 1998).
Although a prior study (Hedrick 2000) showed that lower body mass was correlated with longer hiding times within the CA population, we did not find a similar relationship here for body mass and hiding times within either the CA or AZ population. Moreover, in comparisons between populations, CA males had lower mean body mass than AZ males, but hid for shorter times than AZ males.

The Arizona and California habitats differ not only in predation and parasitoid pressure, but also in many other respects. Annual rainfall averages approximately two times higher in California (43.80 cm) than in Arizona (22.86 cm; Western Regional Climate Center, http://www.wrcc.dri.edu/CLIMATEDATA.html), affecting the kinds of vegetation and cover available. Maximum and minimum temperatures during times of cricket abundance (May–September) are higher in Arizona (average = 17.2–36.2°C) than in California (average = 11.3–31.6°C; http://www.wrcc.dri.edu/CLIMATEDATA.html). The substrates in the two habitats also differ, with sandier soil in Arizona. Therefore, numerous factors besides predator and parasitoid pressure could result in behavioural differences between the populations we studied. Also, crickets may be able to escape predation by other means, such as jumping, which we did not measure. Moreover, G. integer may be capable of behavioural compensation; for example, in the CA population, males with longer songs hide longer than males with shorter songs (Hedrick 2000), and immature crickets adjust their levels of activity in response to indirect chemotactile cues from spider predators (Kortet & Hedrick 2004). Thus, crickets within populations may have a variety of strategies for dealing with predators, which our behavioural trials in the laboratory did not measure.

In summary, our results show that male AZ crickets, which live in a relatively high-predation, high-parasitoid habitat, have longer latencies to emerge from hiding and are presumably more cautious regarding predation and/or parasitism risk than male CA crickets, which live in a lower-predation, very low-parasitoid habitat. Studies of additional populations and transplant experiments (Lehmann & Heller 1998), in which individuals are moved between habitats, should be conducted to support our conjecture that the differences in cautiousness are related to predation/parasitism risk. Also, studies in which hiding times longer than 10 min (600 s) are measured may reveal far more variation than we found here within and between populations. Nevertheless, our study suggests that despite the potentially large cost of failing to hide when a predator is nearby, male crickets in low-predator, low-parasitoid populations (e.g. Davis, CA) may not hide as long as their counterparts in high-predator, high-parasitoid areas, perhaps because of competing behavioural activities, such as calling for mates (Hedrick 1988, 2000), fighting with other males (Kortet & Hedrick 2005) or foraging (Hedrick 2005).

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References


