Reproductive Costs to Heterospecific Mating Between Two Hybridizing Katydids (Orthoptera: Tettigoniidae)

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ABSTRACT   Animal taxa meeting in hybrid zones often exhibit partial reproductive isolation. This isolation may result from a variety of causes both before mating (e.g., incompatibilities in courtship behaviors) and subsequent to mating. Understanding the factors effecting reproductive isolation in hybrid zones can offer important insights into the process of speciation and the maintenance of species boundaries. The katydids *Orchelimum nigripes* Scudder and *O. pulchellum* Davis (Orthoptera: Tettigoniidae) form 2 hybrid zones in the eastern United States. I carried out breeding studies in the laboratory using animals from pure *O. nigripes* and *O. pulchellum* populations in the vicinity of one of these hybrid zones to examine possible modes of postmating reproductive isolation. The number of eggs produced by females mated to heterospecific males was dramatically lower than that of females mated conspecifically, but there was no evidence of any differences in hatch rate or offspring viability between egg clutches from heterospecific and conspecific crosses. Hatch rate, offspring viability, development time, and adult weight of hybrid progenies were all intermediate relative to corresponding values for progenies resulting from the 2 types of conspecific matings, although most of the differences between hybrids and each of the 2 classes of nonhybrid progenies were not statistically significant. The reduced oviposition of heterospecifically mated females suggests that females mated to heterospecific males do not receive the necessary stimulation to trigger oocyte maturation or oviposition behavior. The results reported here show that although some females will mate with heterospecific males, these matings tend to result in substantially reduced reproductive success relative to conspecific matings.

KEY WORDS   Tettigoniidae, fecundity, hybridization, postmating isolation, reproductive isolation

HYBRID ZONES PROVIDE evolutionary biologists with opportunities to study a variety of fundamental questions about the nature of species and speciation. By analyzing interactions between taxa that exchange genes in hybrid zones, we can gain critical insight into the evolution of reproductive isolation. I report here on an analysis of reproductive costs of heterospecific mating between *Orchelimum nigripes* Scudder and *O. pulchellum* Davis, 2 closely related, but morphologically and genetically distinct, conocephaline katydids that are widespread and abundant in the eastern United States. These insects are found on woody and herbaceous vegetation in swamps and freshwater marshes, and around the edges of lakes, ponds, and rivers. *O. nigripes* is found west of the Appalachians to Nebraska, from the Great Lakes to the Gulf Coast; *O. pulchellum* is found along the Coastal Plain from New York to Florida (Morris and Walker 1976). The 2 taxa meet in a broad and very old hybrid zone in the Deep South (in Alabama and Mississippi) (Shapiro 1998). In addition, *O. nigripes* became established in the Potomac River basin above Washington, DC, some time within the last 75 yr and is currently very abundant, having

completely replaced *O. pulchellum* along the river corridor east of the Appalachians and north of the city. These 2 katydids now form a narrow upstream–downstream hybrid zone where they meet along the Potomac River in the vicinity of Washington, DC (Shapiro 1998).

In recent years, theoretical models of hybrid zones have been developed that suggest that many zones may be stable for hundreds or even thousands of years. One model that has received a great deal of attention is the dynamic equilibrium, or tension zone, model of hybrid zone maintenance, in which hybrid zone stability results from a balance between dispersal of parental types into the zone and intrinsic selection against hybrids (Barton and Hewitt 1985). Thus, in conjunction with studies of premating isolation between *O. nigripes* and *O. pulchellum* (unpublished data), the current study compares the oviposition rates of conspecifically and heterospecifically mated females, as well as egg hatch rate, offspring viability, development time, and adult weight for egg clutches and progenies resulting from conspecific and heterospecific crosses. I use these data to identify potential sources of intrinsic selection against hybridization that may be important in shaping the dynamic interactions between these 2 katydids.

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Materials and Methods

All females used in this study were wild-caught virgins (collected as late instar nymphs) from pure *O. nigripes* and *O. pulchellum* populations in the vicinity of Washington, DC. Female *O. nigripes* and *O. pulchellum* were offered a choice between a male of each species and were allowed to mate just once. In addition, for a small number of *O. nigripes* females, single-male no-choice trials were carried out instead of choice trials. Four types of matings resulted from these trials: conspecific *O. nigripes* matings (NN), conspecific *O. pulchellum* matings (PP), *O. nigripes* female × *O. pulchellum* male matings (NP), and *O. pulchellum* female × *O. nigripes* male matings (PN). Mating trials were carried out in both 1994 and 1997, resulting in a total of 69 matings. Data on hatch rate, development time, viability, and adult weight were collected from the 1994 egg clutches; oviposition data were collected in both 1994 and 1997.

After a female was used in a mating trial that resulted in a copulation and transfer of a spermatophore, she was placed individually in an oviposition cage. The oviposition cage consisted of an expanded polystyrene foam base and a window screen enclosure (20 high by 10 cm diameter). *Orchelimum* females normally oviposit in plant stems (e.g., Feaver 1977), but females readily accepted the foam cage bases as oviposition sites. The cage base was replaced with a fresh piece of foam after 2 wk. The total number of eggs laid over a 4-wk period was recorded for each female.

To collect eggs, foam was submerged in a bowl of water and carefully broken up into small pieces. Eggs were gently excavated from the surrounding foam beads and removed using a pair of soft forceps. Each batch of eggs from a foam base was transferred to a petri plate lined with several Kimwipes (Kimberly-Clark, Roswell, GA) soaked with water, because tettigoniid eggs must absorb considerable amounts of water during development (Hartley 1990). Following a protocol suggested by J. C. Hartley (University of Nottingham), I kept harvested eggs at room temperature ($\approx$23°C) for 4–6 wk, then transferred them, all at once, to an environmental chamber at a temperature of 8°C for 6 mo. After this cooling period, the eggs were removed from the chamber to room temperature to complete development.

The date of egg hatch was recorded for each egg, and upon hatching each individual was housed separately in a 40-dram plastic vial with a fine mesh top. Animals were fed a mixture of commercial fish food and wheat germ, periodically supplemented with bee pollen and occasional sliced fruit or green leafy vegetables. Water was supplied in cotton-stoppered vials, or by regular misting. Both food and water were available at all times. Because maintaining katydid hatchlings individually is extremely labor intensive, only hatchlings up to a maximum of 30 per female were retained for rearing. Excess hatchlings were thus included in analyses of hatch rate, but not viability, development time, or adult weight. The date of the final molt was recorded for each katydid. Each individual was weighed at 23 and 25 d after the final molt and the mean of these 2 weights was used in analyses.

Results

The frequency distribution of the number of eggs produced by females for each type of cross is shown in Fig. 1. There was a significant difference in egg production between conspecific and hybrid crosses (Wilcoxon two-sample test, $P < 0.0001$). The 2 largest size classes included 37 of the 42 conspecific clutches (88%), but only 2 of the 8 hybrid clutches (25%). In contrast, the 2 smallest nonzero size classes included 5 of the 8 hybrid clutches (63%), but none of the 42 conspecific clutches. Furthermore, no eggs were produced by 11 of 19 (58%) heterospecifically mated females, but only 8 of 50 (16%) conspecifically mated females. PN crosses, in particular, tended to produce no eggs.

I tested hatch rate and viability data for normality and homoscedasticity and found no significant deviations from analysis of variance (ANOVA) assumptions. There was no significant effect of the type of cross on either the proportion of eggs that hatched (ANOVA, $F = 1.89$; df = 2, 25; $P = 0.17$; Table 1), or on the proportion of offspring surviving from hatching to the final molt (ANOVA, $F = 0.30$; df = 2, 20; $P = 0.74$; Table 1) (PN crosses were excluded from these analyses, as well as from the comparisons of development time described below, because there were only 2 PN clutches, including just 4 and 2 eggs, which produced 3 and zero hatchlings, respectively; only one of these hatchlings survived to maturity). The power of these tests, however, is relatively low because of the unavoidably small hybrid sample sizes. More data are available for conspecific crosses both because *O. nigripes* females (although not *O. pulchellum* females) mated almost exclusively with conspecific males when given a choice (unpublished data) and because (as noted above) both *O. nigripes* and *O. pulchellum* females showed dramatically reduced fecundity when mated heterospecifically, often producing no eggs at all.

Because development times were clearly not normally distributed and included a very large number of ties (which may lead to inaccurate results when rank-based nonparametric tests are applied), I used the permutation statistics package *P*-test (written by William Engels, University of Wisconsin at Madison) to carry out permutation tests to compare development times. Development time from hatching to final molt was significantly shorter for pure *O. nigripes* than for pure *O. pulchellum* (with NP hybrids intermediate), and shorter for females than for males (Fig. 2). (For these data, the same conclusions are reached by applying separate Kruskal–Wallis tests for sex and type of mating or by applying the Scheirer–Ray–Hare two-way extension of the Kruskal–Wallis test [Sokal and Rohlf 1995].) The differences in median development time, however, were small: 60, 61.5, and 63 d for NN,
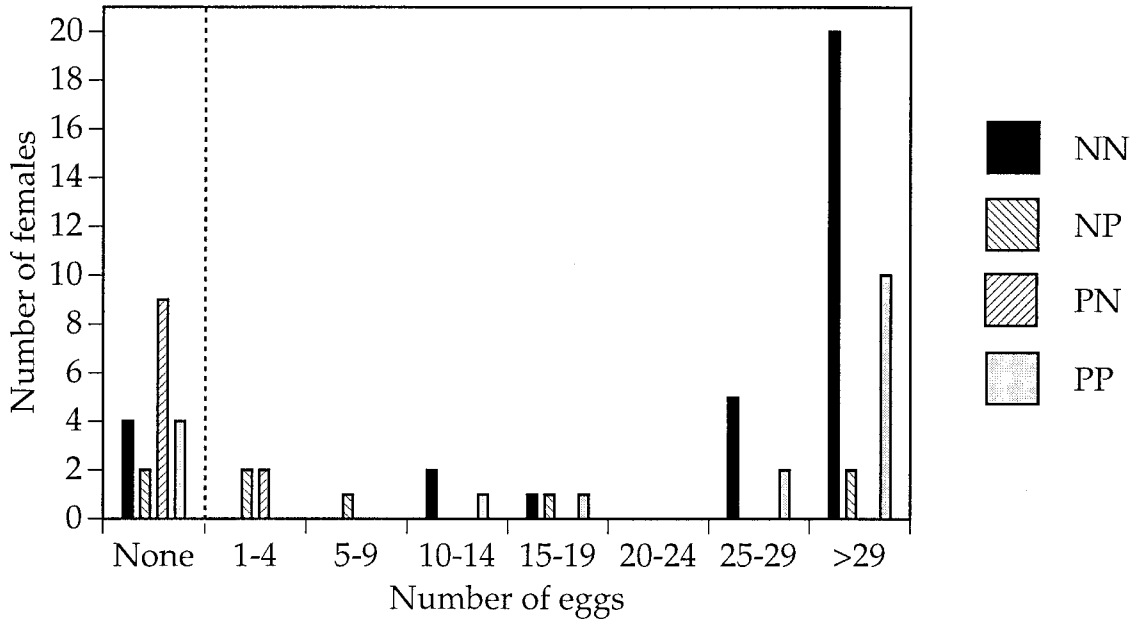
Fig. 1. Frequency distribution of the number of eggs produced by females (*n* = 69) for *O. nigripes* females mated conspecifically (NN), *O. pulchellum* females mated conspecifically (PP), *O. nigripes* females mated to *O. pulchellum* males (NP), and *O. pulchellum* females mated to *O. nigripes* males (PN). Note that not all eggs in excess of 30 were harvested from each female, so the largest size class is >29. Conspecifically mated females produced more eggs than did heterospecifically mated females (Wilcoxon two-sample test, *P* < 0.0001; if zero-eggs size class is excluded, *P* < 0.0007). Comparing only NP and PN crosses (zero-eggs size class included), PN crosses were far less productive because of the large number of females that produced no eggs at all (Wilcoxon two-sample test, *P* < 0.01).

NP, and PP, respectively; 61 and 63 d for females and males, respectively. I compared adult weights using a two-way ANOVA and found a dramatic effect of cross type (with pure *O. pulchellum* significantly larger than pure *O. nigripes*, and NP hybrids intermediate in size; ANOVA, *F* = 11.16; df = 2, 89; *P* < 0.0001), as well as sex (with females larger; ANOVA, *F* = 119.88; df = 1, 89; *P* < 0.0001) (Table 1). Hatch rate, offspring viability, development time, and adult weight of animals

Table 1. Hatch rate, viability, and adult progeny weight for conspecific and heterospecific crosses between *Orchelimum nigripes* and *O. pulchellum*

Cross	Hatch rate	Viability	Adult wt, g
NN	0.60 ± 0.049 (13)	0.48 ± 0.056 (12)	320.09 ± 15.390 (22)
NP	0.65 ± 0.153 (5)	0.47 ± 0.190 (2)	334.28 ± 10.950 (32)
PP	0.76 ± 0.048 (10)	0.40 ± 0.087 (9)	367.87 ± 13.850 (41)
Males	—	—	304.76 ± 5.871 (63)
Females	—	—	425.67 ± 11.743 (32)

Means ± SEM (*n*) for hatch rate (proportion of eggs in a clutch that hatched), viability (proportion of hatched offspring surviving to the final moult), and weight of adult progeny are shown for conspecific *Orchelimum nigripes* crosses (NN), conspecific *O. pulchellum* crosses (PP), and crosses between *O. nigripes* females and *O. pulchellum* males (NP). There were too few crosses available between *O. pulchellum* females and *O. nigripes* males to be included in these analyses (see text). Weights are also shown for pooled males and pooled females. Neither hatch rate nor viability showed a significant effect of the type of cross, but progeny from conspecific *O. pulchellum* crosses were significantly larger than those from conspecific *O. nigripes* crosses, and females were larger than males (see text).

from heterospecific crosses were all intermediate relative to corresponding values from the 2 types of conspecific crosses, although most of the differences between hybrid crosses and conspecific *O. nigripes* and *O. pulchellum* crosses were not statistically significant.

Discussion

The reduced fecundity of hybrid crosses between *O. nigripes* and *O. pulchellum* relative to conspecific crosses is striking. Heterospecifically mated females were far more likely than conspecifically mated females to produce no eggs at all, and when they did produce eggs they tended to produce far fewer, although once produced these eggs appeared to be equally likely to hatch and develop normally as those produced by conspecifically mated females. Such a finding of reduced oviposition for heterospecifically mated females has rarely been reported in the literature, although it appears that few workers have explicitly compared the number of eggs oviposited resulting from conspecific and heterospecific matings. Among the few examples in the literature, Tanaka (1991) and Gregory and Howard (1993) both found reduced oviposition rates for at least one of the reciprocal crosses between the ground crickets *Allonemobius fasciatus* (DeGeer) and *A. socius* (Scudder). A similar result was obtained in a study of
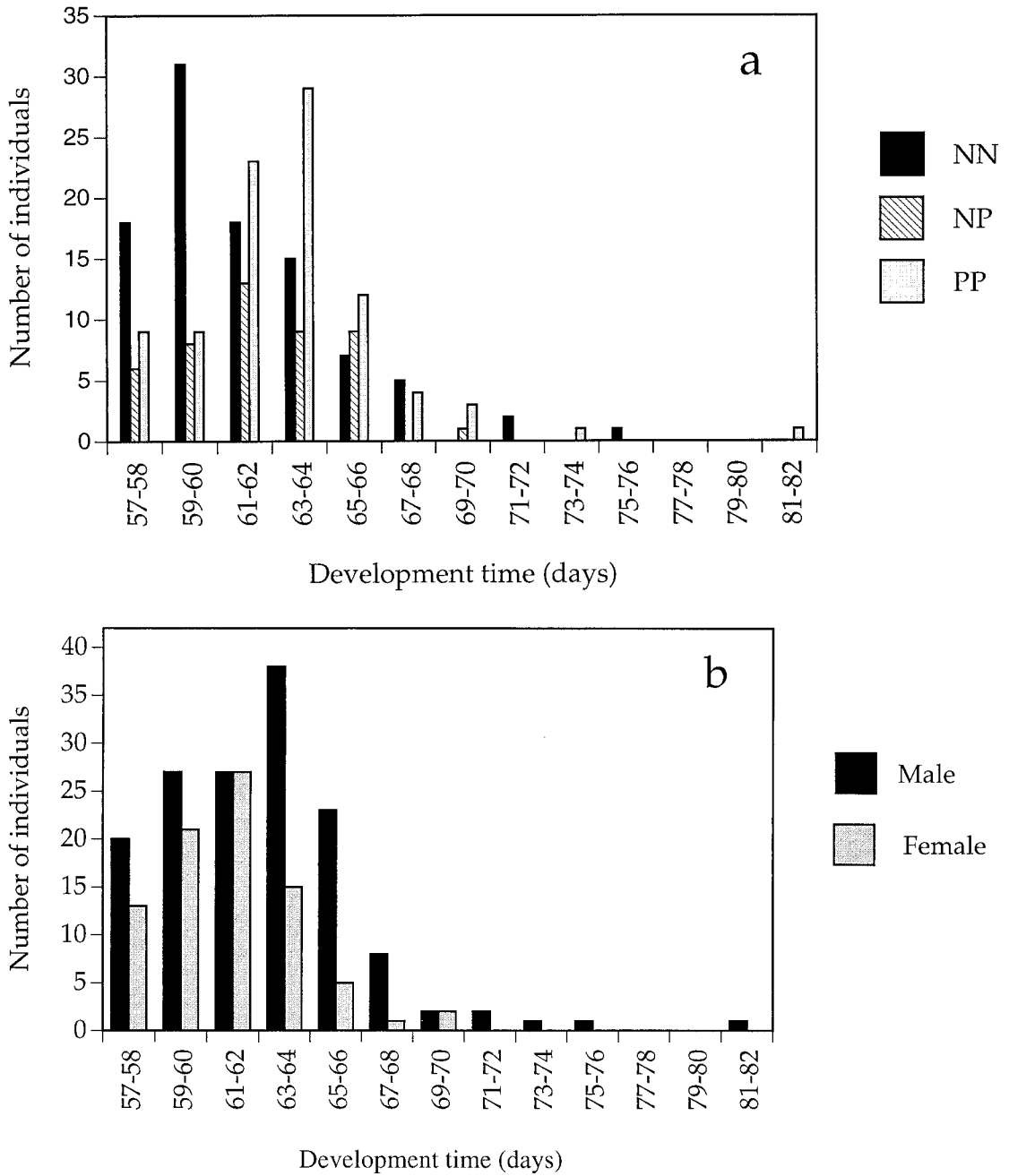
Fig. 2. Development time from hatching to final molt for (a) hatchlings from NN, NP, and PP crosses, and (b) males and females. Development time was significantly shorter for pure *O. nigripes* than for pure *O. pulchellum* (Monte Carlo sum test [1,000,000 permutations], $P = 0.0015$, two-tailed), and for females than for males (Monte Carlo sum test [1,000,000 permutations], $P = 0.0032$, two-tailed). Only 1 of the 2 very small PN clutches produced any hatchlings (3 hatchlings, only 1 of which survived to maturity). The sole maturing PN individual took 67 d to reach adulthood and is not included in this analysis.

postmating, prezygotic isolation between 2 flour beetles, *Tribolium castaneum* (Herbst) and *T. freemani* (Hinton), in which *T. castaneum* females mated to 2 heterospecific males showed reduced oviposition relative to *T. castaneum* females mated to 2 conspecific males (although this effect was not evident for the reciprocal cross) (Wade et al. 1994). A significant reduction in oviposition rate associated with het-

erospecific mating has also been documented for crosses between females of *Drosophila simulans* Sturtevant and males of *D. mauritiana* Tsacas & David; this effect is not seen in the reciprocal cross, although inefficiency in sperm use by females in this cross results in a rapidly declining proportion of fertile eggs beyond 48 h after copulation (C.S.C. Price and J. Coyne, personal communication).

Recently, there has been a surge of interest in postmating, prezygotic fertilization barriers leading to homogamy, or positive assortative fertilization, in animals (e.g., Eberhard 1996, Markow 1997, Price 1997, Howard et al. 1998), but the difficult work of identifying the proximal explanations for this phenomenon has only just begun. In some insects, heterospecific sperm are apparently not transferred effectively to the sperm storage organ, or are transferred but do not retain normal function, resulting in few fertilized eggs being produced from heterospecific matings (e.g., Katakura 1986a, Katakura and Sobu 1986, Albuquerque et al. 1996). The mechanisms responsible for the reduced oviposition effect reported here for *Orchelimum* are unknown. It may be that the factors leading to reduced oviposition by heterospecifically mated *Orchelimum* and to assortative fertilization in multiple-mating studies of other organisms are in fact similar. The very same reduced oviposition effect seen in the current study (in which females were singly mated to heterospecific males) may have simply been masked by the effect of the conspecific male in recent investigations of postmating, prezygotic isolation that have focussed only on looking for assortative fertilization by sequentially mating females to heterospecific and conspecific males. Alternatively, the reduced oviposition by heterospecifically mated *Orchelimum* females may indeed be an unusual phenomenon, and the mechanisms causing it may be quite distinct from the mechanisms (such as assortative sperm transport) that lead to assortative fertilization.

Oocyte maturation and oviposition behavior are known to be stimulated by mating in many insects (Gerber 1967, Pickford et al. 1969, Chapman 1982, Davey 1985, Eberhard 1985, Markow 1997), including some ensiferan Orthoptera (e.g., Loher and Edson 1973, Destephano et al. 1982, Murtaugh and Denlinger 1985). The mechanical or chemical stimulation of *Orchelimum, Allonemobius,* and *Tribolium* females by heterospecific males may be relatively weak, leading to reduced oviposition. Certainly, in these cases there is some behavioral or physiological interaction between males and females that does not proceed normally in heterospecific matings. An obvious potential explanation for this phenomenon is that heterospecific couplings are too brief for adequate transfer of sperm or accessory proteins. However, in laboratory mate choice trials using *O. nigripes* and *O. pulchellum* neither latency to copulation nor duration of copulation differed between conspecific and heterospecific matings (unpublished data) (although this information is available only for NN, PP, and PN crosses).

In the current study, females from all crosses were strikingly larger and heavier than males, a very com-mon pattern in insects (Darwin 1874, Hoňek 1993). More interestingly, Potomac *O. pulchellum* are significantly larger than Potomac *O. nigripes* (a pattern not apparent in the Deep South [unpublished data]), and offspring from pure *O. nigripes* crosses matured more quickly than those from pure *O. pulchellum* crosses. These differences in size and development time may be related, because a longer developmental period tends to result in larger size at maturity for univoltine insects (Masaki and Walker 1987); although the difference in development time observed in these laboratory studies is too slight to account for the considerable difference in size, it is possible that the difference found in the laboratory could be more substantial under natural conditions. Because both adult size and development time presumably have some genetic basis (a supposition supported by the fact that both size and development time of hybrids were intermediate relative to nonhybrid offspring) and may be shaped by geographically varying selection (Mousseau and Roff 1989), it is interesting to speculate that Potomac *O. nigripes* may be much smaller and slightly quicker to mature than Potomac *O. pulchellum* simply because *O. nigripes* in the Midwest (the likely source of Potomac *O. nigripes*) are similarly small (unpublished data) and quick to mature. Thus, it is possible that the smaller size and more rapid development of Potomac *O. nigripes*, relative to *O. pulchellum*, are the result of its genetic legacy rather than the current selective regime. However, these characteristics could nevertheless give *O. nigripes* a competitive advantage that might partially explain its spread along the Potomac River (Shapiro 1998). A better understanding of the importance of differences in development time between *O. nigripes* and *O. pulchellum* will require more detailed studies of development under a wide range of controlled conditions.

The data reported here suggest that female *O. nigripes* and *O. pulchellum* that mate with heterospecific males pay a high cost in reduced fecundity. There is also evidence suggesting that hybrid males may be sterile (Cabrero et al. 1999), providing another substantial cost for females accepting a heterospecific mate. It is possible, however, that if females mate with multiple males in nature, the cost in reduced fecundity of occasional heterospecific mating might be more than offset by the nutritional benefit of consuming the large gelatinous spermatophylax transferred by nearly all male katydids (including *Orchelimum*) along with the sperm-containing portion of the spermatophore (Gwynne 1990, Simmons and Bailey 1990, Burpee and Sakaluk 1993). If a heterospecifically mated female that subsequently mates with a conspecific male achieves normal fecundity, as appears to be the case for some insects, such as some coccinellid beetles (Nakano 1985; but see Katakura 1986b), then mating with heterospecific males might, in fact, result in little or no fitness cost to females. The frequency of multiple mating for *Orchelimum* in nature is not known, but both sexes will mate multiply in the laboratory, and multiple mating in both the laboratory and in nature has been documented for several other katydids and

crickets (e.g., Gwynne 1984, Simmons and Bailey 1990, Gregory and Howard 1996).

In the work reported here I have documented a severe reduction in oviposition associated with heterospecific mating between 2 hybridizing katydids. This form of postmating reproductive isolation has been reported only very rarely in the literature, but this rarity may represent an artifact of investigator focus and experimental design rather than its actual frequency in nature. Further investigation of this phenomenon in a variety of taxa will improve our understanding of the role of postmating reproductive isolation in hybrid zones.

Acknowledgments

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