Visual Communication Behaviour as a Mechanism Behind Reproductive Interference in Three Pygmy Grasshoppers (Genus *Tetrix*, Tetrigidae, Orthoptera)

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Specific mate recognition systems should enable species to recognize conspecific mates correctly. However, heterospecific matings have been observed in a variety of taxa. One of these cases is the pygmy grasshopper genus Tetrix, *in which three species show sexual interactions.* T. ceperoi *males mount preferably females of* T. subulata, *but they are rejected as mates.* T. subulata *males prefer* T. undulata *females over conspecific females and heterospecific matings occur. Here, we study the underlying behavioural mechanisms of this pattern by analysing the visual courtship behaviour of the three species videographically. We test the hypothesis that the displays of* T. ceperoi *are highly differentiated from the other species, while the courtship of* T. subulata *and* T. undulata *is more similar. This is supported by our results: while* T. ceperoi *males perform a fast movement of high amplitude ("pronotal bobbing"), the other two species show only minor movements ("lateral swinging," "frontal swinging"). The first function of a discriminant analysis of the temporal dimensions of the displays explained 96% of the variance. 100% of the* T. ceperoi *displays were classified correctly, whereas only 50% of the* T. subulata *and 81% of the* T. undulata *displays were grouped accurately. A two-way ANOVA revealed no significant effects of the direction of the "swinging" movements (laterally or frontally) and no interactions between direction and species either, whereas each temporal parameter differed significantly between the three species. The highest degree of differentiation*

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was found between T. ceperoi *and* T. undulata*, while* T. subulata *and* T. un-dulata *only differed significantly in two of the six temporal parameters. Our results suggest that the mismatings between* T. undulata *and* T. subulata *are caused by an insufficient specificity of the courtship behaviour. Apparently, ecological segregation of these two species could impede sexual interactions in the field.*

INTRODUCTION

Communicative behaviour is of high significance for inter- and intraspecific, as well as for inter- and intrasexual interactions. Signal evolution is, therefore, believed to be selected by several forces, such as sexual selection (Andersson, 1994), interspecific interactions (Servedio and Noor, 2003), phylogenetic constraints (Ryan, 1998), and environmental factors (Endler, 1992). Premating isolation might either evolve in allopatry or in sympatry. Differing environmental conditions in allopatry, such as presence of predators, competitors or environmental noise could cause shifts in signal quality. Additionally, genetic drift or differences in female choice might lead to prezygotic isolation. In sympatry premating barriers may evolve through disruptive evolution or through reinforcement in response to disadvantages from mismatings or hybridization. Generally, courtship behaviour is thought to act as a specific mate recognition system, increasing the mating success of the individuals engaged (Paterson, 1978). Recent evidence, however, suggests that mismatings and hybridisation in animals are more common than usually thought (Mallet, 2005). In these cases, the question arises, whether incomplete premating isolation stems from an insufficiently distinct signalling system compared to taxa, which do not interbreed.

Insects utilise a variety of signals in communicative behaviour, such as acoustic, visual, olfactory, tactile or vibrational signals (Thornhill and Alcock, 2001). All of these signal types are also known to occur in Orthoptera (Faber, 1953; Otte, 1970; McVean and Field, 1996; Hassanali *et al.*, 2005). Although the study of acoustic communication in Orthoptera has a long tradition (Faber, 1953; Helversen and Elsner, 1977; Huber, 1992; Ragge and Reynolds, 1998), the majority of grasshoppers communicate visually (Otte, 1970), and visual traits are of particular importance in courtship behaviour (Riede, 1986). It is reasonable to suggest that the multiple mechanisms of sound production are derived from movements which originally evolved for visual signalling (Bailey, 1991).

The communicative behaviour of the genus *Tetrix* (pygmy grasshoppers) has not been studied in detail. Faber (1953) and Jacobs (1953) described movements of some *Tetrix* species, which they interpreted as visual signals, although sometimes erroneously (Lock and Durwael, 1999). Here, we present a videographic analysis of the visual courtship behaviour of *Tetrix subulata* (Linnaeus, 1758), *Tetrix undulata* (Sowerby, 1806) and *Tetrix ceperoi* (Bolívar, 1887). In a mate choice experiment (own data) between *T. subulata* and *T. undulata*, interspecific matings occurred frequently. *T. subulata* males preferred to copulate with heterospecific females, but *T. undulata* males favoured conspecific females (i.e. asymmetric mate preferences). In a second experiment between *T. ceperoi* and *T. subulata*, no heterospecific matings occurred, although males of *T. ceperoi* had asymmetric preferences for *T. subulata* females. We tested the hypothesis that the stronger degree of premating isolation of *T. ceperoi* is caused by a higher differentiation of its visual courtship behaviour compared to the other two species.

METHODS

The Study Organisms

Tetrigidae are small, short-horned Orthoptera with an elongated pronotum, which covers the abdomen and hind wings. Even among the well-studied fauna of Central Europe, Tetrigidae belong to the least-studied groups of Orthoptera. This is probably due to their small body size, their inconspicuous appearance, the lack of audible sound production and their unusual life cycle (Hochkirch *et al.*, 2000). Most Tetrigidae are terricolous and inhabit marshy places, some are even semi-aquatic and good swimmers and divers (Paranjape *et al.*, 1987). They feed on a variety of algae, mosses, small plants and detritus (Hochkirch *et al.*, 2000). While *T. subulata* has a holarctic distribution, *T. ceperoi* is a West-Mediterranean species, with the north-eastern edge of its range in Central Europe. *T. undulata* is distributed from Spain to the Baltic states (Kleukers *et al.*, 1997). All three species occur sympatrically in northern Germany and overlap in their general habitat preferences. They reproduce during the same period from April to June (Kleukers *et al.*, 1997). Tetrigidae do not posses any stridulatory or tympanal organs, but males are known to perform visual displays during courtship (Jacobs, 1953). Recent studies suggest that vibrational signals might also play a role in communication (Benediktov, 2005). Males of most grasshopper species are less choosy than females. Copulation trials of Tetrigidae males have been observed with almost any moving object of small size, including males, heterospecific individuals or even flies (Lock and

Durwael, 1999, own observations). Sexual size dimorphism is distinct and, as in all Caelifera, the females are considerably larger than the males due to an additional nymphal instar (Ingrisch and Köhler, 1998).

Videography

We examined three different types of behaviour, which were exclusively performed by males in close proximity to a female. These behaviour types were termed "lateral swinging," "frontal swinging" and "pronotal bobbing." A detailed description is given in the results. Video records were made with a digital Canon video camera (MV 600) in the field and in the laboratory from 21 April to 03 June 2004. All field records were obtained in Lower Saxony (Germany) on the East Frisian isles of Langeoog (53°45′N, 7°30′E) and Spiekeroog (53°45′N, 7°40′E), in the nature reserves "Renzeler Moor" (52°36′N, 8°44′E) and "Grasmoor" (52°23′N, 7°54′E). In the laboratory, one male and female of each species were transferred into a terrarium ($25 \times 40 \times 25$ cm) with a sand-covered floor and moss. All behaviour records were obtained at temperatures higher than 20°C, which is the optimal temperature for courtship. The insects were integrated in a breeding programme afterwards.

Pinnacle Studio 9.0 was used to cut courtship scenes from the 14 h of video material. The displays were analysed by videography, sequentially frame-by-frame (25 pictures/second). Provided that the movements exceed the duration of a half-frame scan, all movements will be captured on the video. The frame-by-frame analysis was made by JD on a flat panel computer monitor with the program Adobe Premiere 6.0. Spatial measurements were made by attaching a transparent film to the monitor and measuring the angle between the pronotum or the hind legs and their initial position. Movements of *T. subulata* and *T. undulata* consisted only of minor angles (maximum of 3°), which are difficult to measure. In these cases the temporal dimensions were noted. Temporal patterns are known to be of crucial importance in the acoustic signals of Orthoptera (Ragge and Reynolds, 1998). We distinguished the temporal parameters "time to maximum position of the movement" (T1), "duration of maximum position" (T2), and "total time of the movement" (T3). All of these parameters were measured for both, leg (L) and pronotal (P) movements.

Statistical Analysis

To illustrate the spatial dimensions of the "pronotal bobbing" display, we aligned our temporal data at the time of maximum elevation. Due to

the high qualitative differences in the spatial aspects of communication be-
haviour of *T. ceperoi* and the other two species, a statistical comparison of
the spatial dimensions was not possible (and not necessary). For the analy-
sis of temporal data we performed a two-way ANOVA, using the factors
"species" and "direction" (either lateral or frontal) as explanatory vari-
ables. Interactions were removed from the model, if they were not signifi-
cant. If necessary, data were Box-Cox-transformed. Significant results were
tested by multiple *t*-tests with Bonferroni correction in order to identify the
significantly different species pairs. All tests were carried out in "R 2.1.1"
(R Development Core Team, 2004) including the library MASS (Venables
and Ripley, 2002) to calculate Box-Cox-lambdas.

To examine the interspecific differentiation of the displays, we also
tested the temporal dimensions by a stepwise discriminant analysis and
subsequent classification statistics. The parameters were chosen stepwise
according to their contribution to the discriminant functions, significantly
minimizing Wilks' Lambda (an inverse measure). The significance of each
parameter measured was calculated by univariate *F* statistics based on
Wilks' Lambda. Records with missing data were excluded and thus 78 dis-
plays were included in the analysis. This sample consisted of 13 *T. ceperoi*,
31 *T. subulata*, and 34 *T. undulata*. The analysis was performed using SPSS
12.0.1 for Windows.

RESULTS

We observed three types of visual behaviour, which were identified as
courtship displays. "Pronotal bobbing" is a fast synchronous movement of
hind legs and pronotum with high amplitude (Fig. 1), which was exclusively
found in *T. ceperoi* (16 records). "Frontal swinging" and "lateral swinging"
are slow, horizontal movements of the insects body with minor spatial di-
mensions. At the beginning of the "frontal swinging" behaviour the insects
stretch their fore and mid legs. The maximum of the movement is reached
when femur and tibia of the mid legs form an approximately straight line, el-
evating the insects body. The frontal direction of the movement is achieved
by stretching the hind legs synchronously. During the "lateral swinging"
display, the direction of the movement is varied by stretching one hind leg
more than the other. Swinging displays were only performed by *T. subulata*
(23 records for "frontal swinging," 13 records for "lateral swinging") and *T.*
undulata (32 frontal, 12 lateral). Only minor differences in display quality
were found between those two species, whereas the display of *T. ceperoi*
was qualitatively distinct.

The mean maximum angle of the hind legs during "pronotal bobbing"
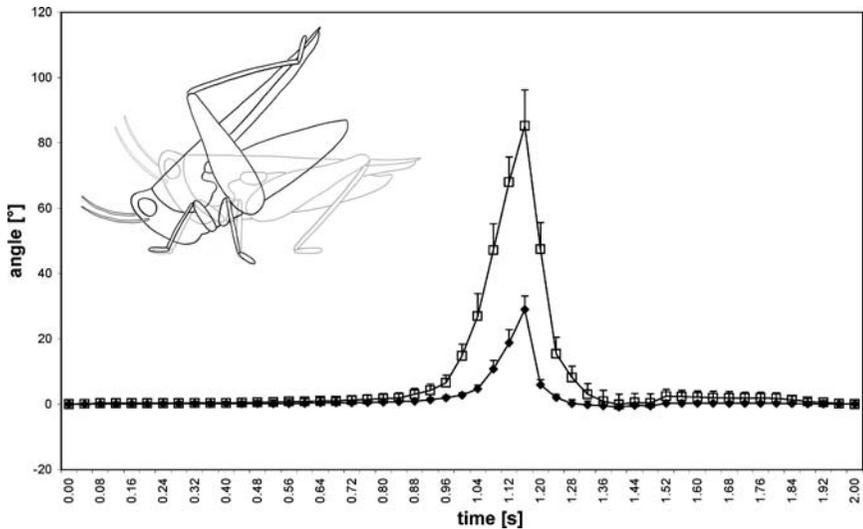of *T. ceperoi* males was 86° (± 10.2°), the mean angle of the pronotum was

Fig. 1. Spatio-temporal course of the hind legs (open squares) and pronotum (closed diamonds) of the visual display in *Tetrix ceperoi*. Data points represent means, error bars refer to standard errors.

28° ($\pm$ 4.1°). The mean duration of a display was 0.80 s ($\pm$ 0.12 s), while the maximum elevation was reached on average after 0.42 s ($\pm$ 0.08 s). However, the fastest recorded display only took 0.28 s. The mean maximum amplitude during the elevation was 250° per s for the pronotum and 625° per s for the hind legs. Both pronotum and hind legs were raised in synchrony, but the elevation of the legs started in a mean of 0.16 s sooner than the pronotum.

Comparing the two swinging movements, no significant temporal effects of the direction (lateral or frontal) and no significant statistical interactions between species and direction were detected. Therefore, both lateral and frontal movements are treated here together. In *T. subulata*, the mean duration of the swinging display was 1.13 s ($\pm$ 0.06 s), while the maximum elevation was reached on average after 0.28 s ($\pm$ 0.03 s). In *T. undulata*, the swinging display took in mean 0.98 s ($\pm$ 0.04 s), while the maximum elevation was reached after 0.16 s ($\pm$ 0.02 s).

The two-way ANOVA revealed significant differences between the three species for each temporal parameter (Table I), but no effect of direction or interactions between both factors occurred. *T. ceperoi* differed in all parameters from *T. undulata* and in four traits from *T. subulata*, whereas only two of the six factors differed significantly between *T. subulata* and *T. undulata* (time to maximum position of both, hind legs and pronotum).

Table I. Results of the ANOVA for the Six Temporal Parameters of the Displays

	ANOVA				Bonferroni posthoc-test		
Parameter	Lambda	DF	F	P	T. ceperoi - T. subulata	T. ceperoi - T. undulata	T. subulata - T. undulata
P-T1	− 0.10	2, 88	14.30	<0.001*	0.117	<0.001*	<0.001*
L-T1	− 0.05	2, 84	16.31	<0.001*	0.099	<0.001*	<0.001*
P-T2	− 0.62	2, 88	8.97	<0.001*	<0.001*	0.007*	0.293
L-T2	− 0.48	2, 86	8.66	<0.001*	<0.001*	0.001*	1.000
P-T3	− 0.16	2, 83	5.68	0.005*	0.004*	0.034*	0.768
L-T3	− 0.16	2, 79	7.97	<0.001*	<0.001*	0.017*	0.315

Note. In a two-way ANOVA, no significant effects of direction and no significant interactions between direction and species were found. Therefore, only differences between species are considered.

The discriminant analysis (Table II) revealed a strong overlap of the courtship displays of *T. undulata* and *T. subulata*, but a rather good discrimination of the *T. ceperoi* display (Fig. 2). The parameters L-T1, L-T3, P-T1 and P-T3 were highly correlated. A strong correlation was also found between the parameters L-T2 and P-T2. The first axis of the discriminant analysis accounted for 96% of the variance with an eigenvalue of 1.342. Wilks' Lambda was comparatively high ($\Lambda = 0.404$), indicating a high overlap of the analysed data. The classification phase of the discriminant analysis assigned only 72% of the displays correctly. However, the wrong assignments concerned only *T. undulata* and *T. subulata*, but never *T. ceperoi*. While 100% of the *T. ceperoi* displays ($n = 13$) were classified correctly, only 50% of the *T. subulata* displays ($n = 32$) and 81.1% of the *T. undulata* displays ($n = 37$) were assigned to the right species.

DISCUSSION

Our analyses revealed high qualitative and quantitative differences between the visual courtship displays of *T. ceperoi* compared with the other

Table II. Results of the Stepwise Discriminant Analysis for the Six Temporal Parameters of the Displays

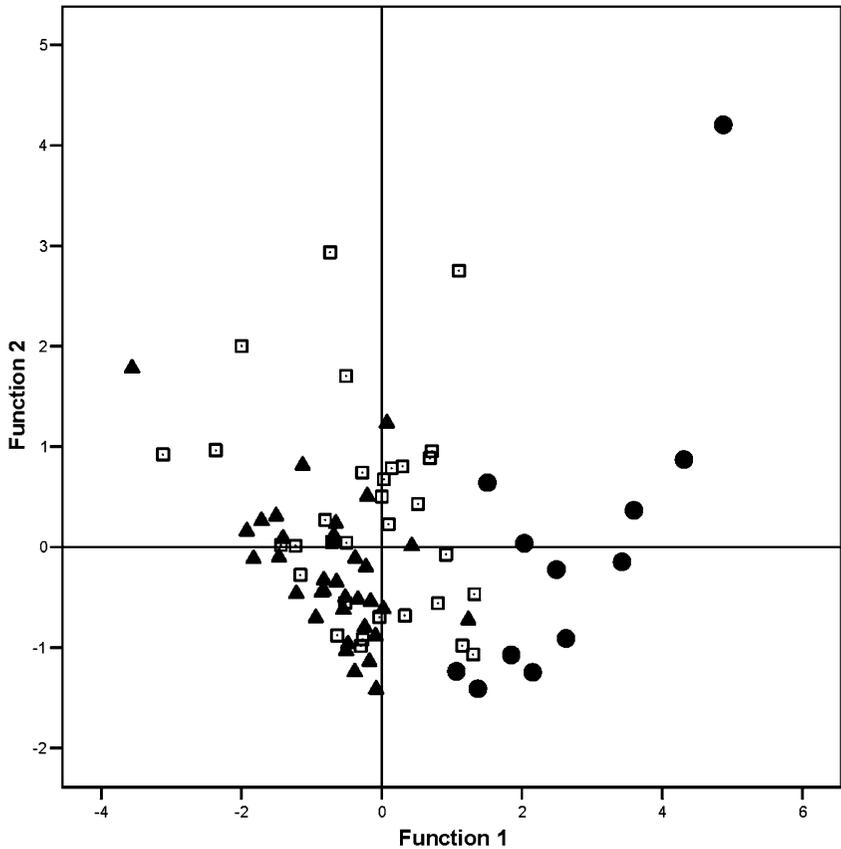|	Discriminant analysis			F Statistics		
Step	Parameter added	DF	Wilks lambda	DF	F	P
1	L-T1	1, 2, 75	.751	2, 75	12.452	<0.001*
2	L-T3	2, 2, 75	.470	4, 148	16.992	<0.001*
3	P-T1	3, 2, 75	.404	6, 146	13.947	<0.001*

Fig. 2. Plot of canonical functions 1 and 2 of the discriminatory topology, illustrating the high overlap between the temporal parameters of the displays of *Tetrix subulata* (open squares) and *T. undulata* (dark triangles). *T. ceperoi* (dark circles) is well separated from the two species on function 1, which explains 96% of the variance.

two species, whereas the displays of *T. subulata* and *T. undulata* are rather similar. These findings support the hypothesis that the mismatings between the two latter species are caused by an insufficient differentiation of the male displays. Since *T. subulata* occurs sympatrically throughout nearly the complete range of *T. undulata*, the question arises, which mechanisms enable these species to coexist. Apparently, sexual interactions can have rather similar consequences as competition, both decreasing the reproductive success of a species (Brown and Wilson, 1956). However, overlapping ranges do not necessarily imply that two species coexist in an ecological

sense (Hochkirch and Papen, 2001). Spatial, temporal or ecological segregation may impede the direct interaction of two species (Schoener, 1974), through differences in their reproductive periods (allochrony), occurrence at different sites or in different habitats within the same range. Secondly, dilution effects may decrease the negative effects of mismatings, since reproductive interference (like competition) is density dependent. These mechanisms could include aggregations (Hanski, 1981), lower abundance of the dominant species, or differences in the colonization rates (Amarasekare, 2003).

In the case of *T. undulata* and *T. subulata* ecological differentiation seems to be the main mechanism facilitating coexistence. *T. subulata* prefers marshy locations, such as river shores, stream valleys, sand pits, dune slacks, and ditches and seems to be confined to acid-free soils, whereas *T. undulata* inhabits a broader range of wet and dry habitats, such as heaths, forest edges and clearings, peat bogs, quarries, damp grassland and sand pits (Marshall and Haes, 1990). On study sites, where both species are found (e.g. sand pits), ecological segregation obviously occurs. In these cases, *T. undulata* prefers drier zones than *T. subulata* and *T. ceperoi* (Gröning *et al.*, 2005). Temporal niche partitioning can be completely ruled out as a mechanism of coexistence, since both species reproduce from April to June (Kleukers *et al.*, 1997), which is also indicated by the mate choice experiments. Aggregations may play a role in preventing heterospecific matings, but might be caused by the patchy distribution of the microhabitats (Gröning *et al.*, 2005).

In contrast to the other two species, *T. ceperoi* has rarely been reported to mate with heterospecific individuals, although *T. ceperoi* males have asymmetric preferences for *T. subulata* females (own data). Our data indicate that females of *T. subulata* are able to discriminate between conspecifics and *T. ceperoi* males, possibly due to the distinctive features of the courtship of *T. ceperoi*. However, another factor for female choice might be found in the male body size. *T. ceperoi* males are much smaller than *T. subulata* males (Kleukers *et al.*, 1997) and may, therefore, be rejected as mates. Size can also play a role for the asymmetric mate preferences of the males, since the males of many insects are known to prefer larger females (Bonduriansky, 2001). Hence, *T. subulata* males might not be interested in the females of *T. ceperoi* due to their small size, whereas *T. subulata* females possibly represent a superoptimal stimulus for *T. ceperoi* males. Our mate choice experiments indicate that these asymmetric mate preferences could decrease the reproductive success of *T. ceperoi* in sympatric situations, despite its high degree of reproductive isolation by its specific mate recognition system. From an ecological point of view, therefore, asymmetric mate preferences can have rather similar effects as hybridization. As in the case

of *T. subulata* and *T. undulata*, ecological segregation appears to impede the effects of reproductive interference between *T. ceperoi* and *T. subulata*. *T. ceperoi* is restricted to damp, warm habitats, like moist dune valleys, sand pits, drainage ditches or heath ponds (Marshall and Haes, 1990). On study sites with both species, *T. ceperoi* prefers more open patches than *T. subulata* (Gröning *et al.*, 2005).

Sexual selection (Andersson, 1994), interspecific interactions (Servedio and Noor, 2003), phylogenetic constraints (Ryan, 1998), and environmental factors (Endler, 1992) are discussed as potential selective forces driving signal evolution. All three species are known to prefer damp, open ground as microhabitat, and apparently the males have even a stronger preference for such patches (*T. subulata*: Forsman and Appelqvist, 1999; Hochkirch *et al.*, 2000, *T. ceperoi* and *T. undulata*: own data). It is reasonable to suggest that these sex-specific microhabitat preferences are caused by the higher suitability of bare ground for visual signal transmission (Endler, 1992). Visual signals are more subject to obstruction by physical barriers than chemical or acoustic signals and they are restricted to use during daylight (except for bioluminescence, Thornhill and Alcock, 2001). However, visual signalling on bare patches might also increase the predation risk, which is indicated by a higher percentage of autotomized individuals in males of *T. ceperoi* compared to females (own data). Hence, microhabitat choice seems to be influenced by a trade-off between sexual and natural selection. Moreover, first experimental data indicate a lower mating success of autotomized males, since they are not able to perform the "pronotal bobbing" display any more. Orthoptera are known to incur both direct and indirect fitness costs from autotomy (Bateman and Fleming, 2005).

Since *T. undulata* and *T. subulata* are sister species (own molecular data) with overlapping ranges, our results suggest that the similar structure of their displays is caused by phylogenetic constraints (Ryan, 1998). These results are in disagreement with the reinforcement hypothesis (Dobzhansky, 1937), which suggests that courtship displays of related species should diverge in areas of geographic overlap (Thornhill and Alcock, 2001). It is rather unusual that closely related Orthoptera species have similar courtship behaviour, failing to act as specific mate recognition system. In contrast, many examples exist in which the songs are known to be the most important characters for identification (Ragge and Reynolds, 1998). Presumably, correct mate recognition is much more important in species pairs with a high ecological overlap, such as *T. ceperoi* and *T. subulata*. Reinforcement models have shown that sexual interaction is a much more effective selective power in species pairs with a high degree of postzygotic isolation, than in subspecies with

hybridization (Servedio and Noor, 2003). Hence, reproductive character displacement could account for the high degree of differentiation of the *T. ceperoi* display.

CONCLUSIONS

Our data support our hypothesis that heterospecific matings between *T. undulata* and *T. subulata* are facilitated through an insufficient differentiation of the mate recognition system. Mismatings, as well as other types of reproductive interference (such as asymmetric mate preferences), seem to act as a powerful selective force by decreasing the mating success of at least one species. Several evolutionary solutions to the problems are possible. While shifts in the communicative behaviour through reproductive character displacement (or reinforcement) have often been discussed (Servedio and Noor, 2003), ecological effects (either segregative or dilutive) have rarely been taken into consideration, although extinction has been found in several reinforcement models (Paterson, 1978 Liou and Price, 1994). There is a strong need for more studies on ecological responses to reproductive interference. Moreover, both field experiments and long-term studies of mixed populations are necessary to examine the effect of sexual interactions on population dynamics.

ACKNOWLEDGMENTS

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