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Reproductive character displacement between the closely related freshwater snails *Lymnaea peregra* and *L. ovata*

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ABSTRACT

Theory predicts that enhanced assortative mating, favouring intraspecific mating, should evolve together with reproductive character displacement. Assortative mating may be involved directly in the evolution of species barriers in the case of sympatric speciation, and may strengthen species barriers after secondary contact. If hybrids are at a selective disadvantage, interspecific mating leads to wasted reproductive effort and enhanced assortative mating is predicted to be favoured, while in allopatric populations of the same species, selection for assortative mating does not take place. Here, we assessed whether sympatric and allopatric populations of the two closely related freshwater snails species *Lymnaea peregra* and *L. ovata* mate assortatively. More specifically, we tested populations from several allopatric and one sympatric location for discrimination against interspecific versus intraspecific matings in a series of non-choice mating trials. We found, as predicted by the theory, that snails from the sympatric location avoided mating with the opposite species, while allopatric snails showed less discrimination against the opposite species. In a broader perspective, our results support the view that reproductive isolation may commonly be reinforced by selection when two closely related taxa occur in sympatry.

Keywords: assortative mating, *Lymnaea*, reinforcement, reproductive character displacement, speciation.

INTRODUCTION

Reproductive isolation between two populations can evolve as a by-product of ecological divergence, or as a response to selection acting directly on reproductive traits (recent reviews include Butlin, 1987; Diehl and Bush, 1989; Schluter and Nagel, 1995; Schluter, 1998; Dieckmann and Doebeli, 1999). If hybrids are at a disadvantage, natural selection on reproductive traits should lead to enhanced avoidance of interspecific matings (positive assortative mating) in sympatric locations compared with allopatric locations (Dobzhansky,

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1940; Blair, 1955). Individuals mating assortatively would be favoured because they avoid maladaptive hybridization and wasted reproductive effort (Loftus-Hills and Littlejohn, 1992; Noor, 1999). This process, known as reinforcement of pre-mating isolation, may lead to reproductive character displacement. Reproductive character displacement has been documented on an intraspecific level and may be involved in the sympatric formation of species barriers (for examples, see Coyne and Orr, 1989; but see Ritchie *et al.*, 1992; Noor, 1995; Coyne and Orr, 1997; Gregory *et al.*, 1998; Rundle and Schluter, 1998; Higgie *et al.*, 2000).

Here, we use a system of two closely related freshwater pulmonate snails to study reproductive character displacement. We used the species pair *Lymnaea ovata* and *L. peregra* because this system presents a potential example of early divergence and possible incipient speciation. The taxonomic status of these snails is unresolved and they are often considered as morphs of one species (Hubendick, 1951; Økland, 1990). These snails are simultaneous hermaphrodites and have the capability of self-fertilization. Although they appear to be frequent outcrossers, variation among populations in outcrossing rate can be significant (Jarne and Delay, 1990; Coutellec-Vreto *et al.*, 1997).

In our experiments, we examined whether mating is generally assortative by species or whether assortative mating is reinforced in sympatry. The first possibility would indicate that the two taxa had diverged sufficiently to be effectively reproductively isolated at secondary contact. The second possibility would indicate that natural selection had reinforced pre-mating isolation in sympatry, thus reducing the fitness costs of hybrid matings.

Our study system does not allow us to determine whether reproductive isolation in sympatry has been evolving primarily in sympatry or during secondary contact. In the first case, reproductive character displacement may have been involved in species formation. If significant gene flow between the two species of snail is still possible, the first scenario may be more likely. It is unclear whether hybridization takes place in natural populations of these snails, but several factors suggest that it is uncommon. Even if the shell form and life-history traits of these species are highly plastic, the species have a habitat-specific spatial distribution (Wullschleger and Ward, 1998; Wullschleger and Jokela, 1999) and express genetically based ecological divergence in some life-history traits (Wullschleger and Jokela, in press). Moreover, allozyme data on a diagnostic locus suggest no hybridization in our sympatric site (unpublished data). Evidence of ecological and life-history divergence makes it plausible that these snail species have diverged recently, or are still in a stage of incipient speciation. Our results support this view by showing that pre-mating isolation is enhanced in sympatry.

METHODS

Study sites

We wished to examine individuals in several allopatric and sympatric populations, but extensive sampling (more than 100 locations visited) revealed only one sympatric site with sufficient sample sizes for both snail species (Wullschleger and Jokela, 1999). This site (Seealpsee, eastern Switzerland) is composed of a shallow, vegetated mudflat, which may become dry several times during the summer season. Apparently, at high water level, *L. ovata* migrates continually into this habitat from a neighbouring steep and stony shore, which sustains a stable population (E.B. Wullschleger, personal observation).

Mate-choice experiments

We conducted a series of nine non-choice mating trials during the summer (May to August) of 1999. We collected the snails for the experiments from 10 allopatric field sites and one sympatric field site in eastern Switzerland. In the first six mate-choice experiments, we tested individuals from allopatric *L. ovata* and *L. peregra* populations from different sites against each other. In the last three experiments, we tested sympatric *L. peregra* and *L. ovata* populations from Seealpsee against each other (Table 1).

After collection in the field, the snails were brought to a climate chamber (20°C; 12:12 h, dark:light). Before the experiments, the snails were kept in isolation in glass jars for about 2 days. During this time, the snails were fed with lettuce *ad libitum*. Individuals that were infected by trematodes and produced cercariae were excluded from the experiment. For the experiments, we placed pairs of snails in the required combinations in small containers (0.2 litre of water, no food) and left them unobserved for about 1 h to familiarize them with their new environment and the mate offered to them. We formed both intraspecific (*L. peregra–L. peregra*, *L. ovata–L. ovata*) and interspecific (*L. peregra–L. ovata*) pairs and observed matings every 30 min for 5 h. We recorded the occurrence, duration and time of the onset of copulation for each pair. In interspecific pairs, the species acting as the 'male' was also recorded. Each individual was used only once in the experiments and all experiments were conducted during daytime.

Statistical analysis

We analysed the results of the non-choice mating trials using a logit analysis. We used the frequency of observed matings as a response variable and 'mating combination' and

Table 1. Non-choice mating trials between allopatric and sympatric *L. peregra* and *L. ovata* individuals

	Origin of *L. peregra*	Origin of *L. ovata*	Date
Experiments with allopatric populations			
1	Dietikon 1	Dietikon 2	2 May 1999
2	Lufingen	Freiweid	11 May 1999
3	Länggenbach	Surb	22 May 1999
4	Erlenmoos	Surb	11 July 1999
5	Einsiedeln	Volketswil	18 July 1999
6	Chälenhof	Surb	25 July 1999
Experiments with sympatric populations			
1	Seealpsee	Seealpsee	31 July 1999
2*	Seealpsee	Seealpsee	14 August 1999
3*	Seealpsee	Seealpsee	18 August 1999

Note: In each experiment, both intraspecific (*L. peregra–L. peregra*, *L. ovata–L. ovata*) and interspecific (*L. peregra–L. ovata*) mating combinations were tested simultaneously. The results are presented in Fig. 1.

* The experiments in which the number of pairs per mating combination was 10. In all other experiments, the number of pairs per mating combination was 20.

'experiment' as factors. We then assessed the significance of each factor by comparing the reduced model (omitting the factor of interest) with a model in which this factor was included (McCullagh and Nelder, 1989; Crawley, 1993). The full model contained the main effects of the factors and their interaction. We analysed the experiments with allopatric and sympatric populations separately. As our main aim was to compare the mating frequency in the different mating combinations, we also tested each mating combination against the others with pairwise contrasts using the GENLOG procedure available in SPSS 6.1.1 (Norušis, 1990). As an additional test of the difference between sympatric and allopatric combinations, we contrasted the observed sympatric interspecific mating frequency with the mating frequency observed in each allopatric interspecific mating combination using pairwise contrasts.

We expected the 'males' involved in matings to be drawn equally from the two species; this was tested in a subsample of interspecific matings using a χ^2-test. Male role is regarded as indicating which individual initiates mating; 'male' individuals attempt mating with no specific courtship behaviours (Dillon, 2000) and copulation begins when 'females' accept the mating attempt.

Furthermore, we analysed the duration of copulations, contrasting the interspecific copulations with the intraspecific ones. We chose a subsample of experiments in which a sufficient number of matings in each group was observed, and analysed differences in duration of copulation using a two-way mixed-model analysis of variance. Three of the six experiments with allopatric population combinations were included in this analysis. 'Experiment' was treated as a random factor and 'mating combination' as a fixed factor in the analysis.

RESULTS

Mate choice

Analysis of the allopatric population combinations indicated a strong interaction between experiment and mating combination (Table 2). Our prediction was that, if assortative mating takes place, the interspecific mating combination would result in a lower frequency of matings than either of the intraspecific combinations. In three of the experiments (Experiments 1, 4 and 6; Fig. 1), this was indeed the case. However, in the remaining three experiments, we observed an intermediate interspecific mating frequency when compared with the intraspecific combinations (Experiments 2, 3 and 5; Fig. 1). As each of these experiments represents an independent combination of populations (Table 1), this suggests that evidence for assortative mating between the morphs may be found between some, but not all, allopatric populations.

This result was further clarified when we considered the results of the pairwise contrasts (Table 2). When we contrasted the two intraspecific combinations, the mating frequency was significantly higher in *L. peregra* pairs (Table 2, Fig. 1). Similarly, when we contrasted the *L. peregra* pairs with interspecific pairs, *L. peregra* pairs had a significantly higher mating frequency (Table 2, Fig. 1). However, we found no significant difference in mating frequency between *L. ovata* pairs and the interspecific pairs (Table 2, Fig. 1). Because the mating frequency of interspecific pairs was not lower than the mating frequency in one of the intraspecific combinations, the support for general assortative mating between allopatric snail species has to be considered weak.

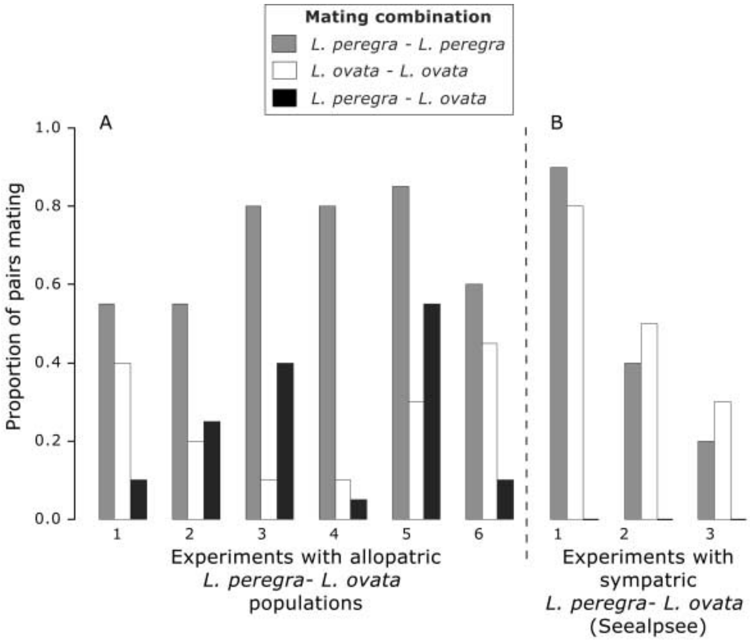

Fig. 1. Number of matings observed in no-choice mating experiments with *Lymnaea peregra* and *L. ovata.* (A) In the first set of experiments (Table 1), individuals from one allopatric *L. peregra* and *L. ovata* population were tested in pairs. A different population combination was used in each of the six experiments. (B) In the second set of experiments, *L. peregra* and *L. ovata* individuals from the sympatric Seealpsee population were tested in pairs. Note that none of the interspecific pairs of sympatric snails mated, although several interspecific matings were observed in experiments conducted with allopatric populations. Values reported are proportion of pairs mating.

Table 2. Results of logit-analysis for the effect of 'experiment' and 'mating combination' on the observed mating probability

Effect	χ^2	d.f.	*P*
Mating combination (M)	68.04	2	<0.00001
Experiment (E)	13.04	5	0.02300
M × E	30.35	10	0.00075
Contrast	**GLOR**	**Wald**	***P***
p-p *vs* o-o	11.66	41.25	<0.0001
o-o *vs* p-o	1.12	0.31	0.5795
p-p *vs* p-o	12.77	43.48	<0.0001

Note: This analysis includes the six experiments conducted with allopatric *L. peregra* and *L. ovata* populations (Table 1). We further contrasted the three mating combinations using pairwise contrasts. Each of the contrasts reports the generalized log-odds ratio (GLOR), Wald test statistic and the corresponding significance value. 'p-p' = *L. peregra–L. peregra* pairs, 'o-o' = *L. ovata–L. ovata* pairs and 'p-o' = *L. peregra–L. ovata* pairs. See Fig. 1 for results.

Analysis of the three experiments that we conducted with the sympatric *L. peregra* and *L. ovata* of Seealpsee yielded a different result. Here, we found strong support for assortative mating between the snail morphs (Table 3, Fig. 1). Analysis of pairwise contrasts indicated that the intraspecific pairs did not differ in mating frequency, but both intraspecific combinations had a higher mating frequency than the interspecific pairs (Table 3, Fig. 1). In fact, although we found a high frequency of matings in the intraspecific mating combinations, we observed no matings between the two sympatric snail species (Fig. 1).

Contrasting the results of these two sets of experiments supports the view that assortative mating between the snail species is reinforced in sympatry. Note that even in the experiments with allopatric populations where assortative mating was supported (Experiments 1, 4 and 6; Fig. 1), we always observed some interspecific matings. This is in strict contrast to the complete absence of interspecific matings in the sympatric case. In fact, when we compared the mating frequency in each interspecific allopatric combination (six experiments) with the mating frequency in the sympatric interspecific combinations, the mating frequency of sympatric combinations was significantly lower in each case (Table 4, Fig. 1). As a general test of reproductive character displacement, we tested if the mean mating frequency in the six allopatric *L. ovata–L. peregra* experiments ($\bar{x} = 0.24$) deviated significantly from that of the sympatric combination (Table 1, Fig. 1). The test had low power because there was only one sympatric population and because the mating frequency in the allopatric combinations was expected to vary. However, the result was marginally significant (one-way *U*-test, $Z = 1.51$, $P = 0.065$). Therefore, with some caution due to marginal significance, the result of the general test supports the view that reproductive character displacement did indeed take place.

Sexual role and duration of matings

Lymnaea peregra functioned as a male in 24 (75%) of the 32 interspecific copulations in the dataset ($\chi^2_1 = 8.00$, $P = 0.0047$), suggesting that *L. peregra* was more likely to initiate

Table 3. Results of logit-analysis for the effect of 'experiment' and 'mating combination' on the observed mating probability

Effect	χ^2	d.f.	*P*
Mating combination (M)	97.12	8	<0.00001
Experiment (E)	23.85	2	0.00001
M × E	1.27	4	0.86673
Contrast	**GLOR**	**Wald**	***P***
p-p *vs* o-o	−0.13	0.01	0.9348
o-o *vs* p-o	10.34	14.64	0.0001
p-p *vs* p-o	10.21	13.75	0.0002

Note: This analysis includes the three separate experiments conducted with the sympatric *L. peregra–L. ovata* population from Seealpsee (Table 1). We further contrasted the three mating combinations using pairwise contrasts as presented in Table 2.

Table 4. Results of pairwise contrasts in which each of the six allopatric interspecific mating combinations was contrasted against the sympatric interspecific combination

Contrast	GLOR	Wald	P*
Experiment 1 *vs* Sympatric	7.80	9.09	0.0026
Experiment 2 *vs* Sympatric	8.77	11.85	0.0006
Experiment 3 *vs* Sympatric	9.42	13.78	0.0002
Experiment 4 *vs* Sympatric	7.24	7.53	0.0061
Experiment 5 *vs* Sympatric	9.99	15.53	<0.0001
Experiment 6 *vs* Sympatric	7.80	9.09	0.0026

Note: 'Experiment' refers to allopatric experiments and 'Sympatric' to sympatric experiments illustrated in Fig. 1. Data from the three experiments with the sympatric populations were combined because they were replicates of the same experiment.

* Significance before sequential Bonferroni correction (Rice, 1989). When the correction is applied, all P-values remain significant at the 5% level.

interspecific matings. Intraspecific *L. peregra–L. peregra* copulations lasted significantly longer in all three experiments where sample size was sufficient to allow analysis of copulation duration (Fig. 2). The main effect of mating combination was significant in the analysis of variance ($\mathrm{MS} = 29.20$, $F_{2,4} = 14.43$, $P = 0.015$; error $\mathrm{MS} = 2.02$), while the main effect of the experiment and the interaction between experiment and mating combination were not significant (experiment: $\mathrm{MS} = 12.23$, $F_{2,88} = 1.80$, $P = 0.171$; interaction: $\mathrm{MS} = 2.02$, $F_{4,88} = 0.30$, $P = 0.879$; error $\mathrm{MS} = 6.79$). Together, these results suggest that *L. peregra* initiated interspecific copulations, but their duration was more similar to the duration of intraspecific copulations between two *L. ovata* individuals and clearly shorter than the duration of copulations between two *L. peregra* (Fig. 2).

DISCUSSION

Our results indicate that assortative mating may occur between allopatric populations of *L. peregra* and *L. ovata*, but the magnitude of discrimination appears to depend on the identity of the populations tested and, therefore, discrimination against the opposite species cannot be considered as a general rule. The sympatric study site was the only one where we found complete assortative mating, suggesting that pre-mating isolation is considerably enhanced in sympatry, as predicted by the hypothesis of reproductive character displacement.

The results also reveal differences in mating behaviour between the two species of snail. In particular, the frequency of mating was higher and the duration of copulation longer in the *L. peregra–L. peregra* combinations than in the other two mating combinations. This suggests that the two species differ in the total resources that are allocated to mating – that is, they differ in their basic reproductive behaviour. *L. peregra* acted as the male in 75% of the interspecific copulations, further supporting the view that 'mating drive' is higher in *L. peregra*. However, the mean duration of copulations in the interspecific combinations was more similar to the duration of copulations in *L. ovata–L. ovata* pairs, suggesting that although *L. peregra* was able to initiate copulations, these may not have lasted long

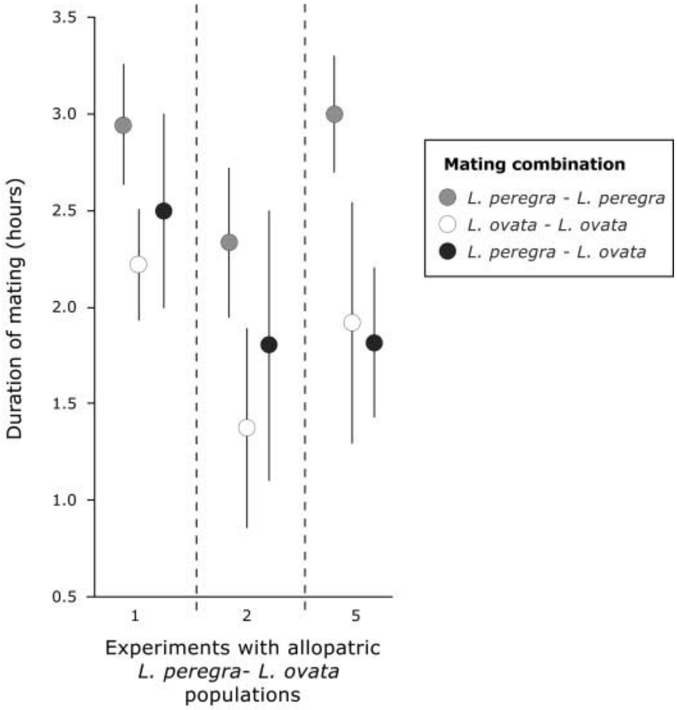

Fig. 2. Duration of mating in three experiments with allopatric *L. peregra–L. ovata* populations. Values given are mean ± 1 standard error. The experiments are numbered as in Table 1 and Fig. 1.

enough for *L. peregra* to complete the transfer of sperm. This also suggests that copulation duration is behaviourally determined by the individual acting as the 'female'. Hence, the available evidence points to rather complete reproductive isolation between the two species of snails. Even if interspecific copulations take place between allopatric snails, we were unable to find hybrids at the sympatric site or in laboratory crossings between snail morphs (unpublished data). That sympatric populations between these two species of snail appear to be exceedingly rare (Wullschleger and Jokela, 1999) suggests further that the species represent genetically isolated units with a very low ecological opportunity for gene flow. A parsimonious explanation for the enhanced assortative mating in sympatry (i.e. reproductive character displacement) is the waste of reproductive effort in interspecific matings.

Occasional copulations between closely related, but distinct snail species have been observed in other cases (e.g. Burla and Speich, 1971; Saur, 1990; Porter and Ribi, 1994; Ribi and Katoh, 1998), suggesting that mate choice errors may be common in these organisms with low differentiation of mating signals. For example, *L. ovata* have been found occasionally in copula with a more distantly related species, *L. auricularia*, in Lake Zürich, Switzerland, although intraspecific copulations were overall more common (Burla and Speich, 1971). In that case, no hybrids between the two species were found (Burla and Speich, 1971). These two species apparently have occurred sympatrically in Lake Zürich over a longer period, which would argue for the evolution of stronger mate choice barriers if interspecific matings were costly. However, *L. auricularia* has been much less abundant than *L. ovata* in Lake Zürich in recent years (J. Jokela, personal observation), so selection for mate recognition at present should be higher in *L. auricularia*. Unfortunately, it is unclear whether *L. ovata* or *L. auricularia* functioned more often as a male in the interspecific copulations that Burla and Speich (1971) reported.

High species specificity in mate discrimination may be expected if efficient conspecific recognition systems have low costs. An interesting example of potential costs of the conspecific recognition system is reported for spadefoot toads. In sympatric populations, female spadefoot toads were found to engage more in species recognition but to be less able to assess male quality, while the females of allopatric populations were less accurate in species recognition but very accurate in recognizing high-quality males (Pfennig, 2000). In our system, mating certainly has fitness costs, for example with respect to loss of energy, loss of foraging opportunities and increased predation risk (Dillon, 2000). Therefore, the evolution of mate recognition should not be easily constrained by possible costs of the recognition system.

The occurrence of reproductive character displacement in sympatry has been reported in some cases (e.g. Marquez and Bosch, 1997; Fishman and Wyatt, 1999), but it has also been reported to be absent in some other potential systems (Veech *et al.*, 1996; Castellano *et al.*, 1998). In this paper, we have reported on a case that supports reproductive character displacement in a hermaphroditic snail that does not appear to have highly differentiated mating signals (Dillon, 2000). Our results support the view that evolution of reproductive character displacement is likely even in systems without conspicuous mating signals (Hewitt *et al.*, 1989; Gregory and Howard, 1994; Higgie *et al.*, 2000). In this particular system, mate recognition may be based on cryptic behavioural or biochemical traits.

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REFERENCES

Blair, W.F. 1955. Mating call and stage of speciation in the *Microhyla olivacea–M. carolinensis* complex. *Evolution*, **9**: 469–480.

Burla, H. and Speich, C. 1971. *Lymnaea auricularia* und *Lymnaea ovata* im Zuerichsee. *Rev. Suisse Zool.*, **78**: 549–556.

Butlin, R. 1987. Speciation by reinforcement. *Trends Ecol. Evol.*, **2**: 8–13.

Castellano, S., Giacoma, C., Dujsebayeva, T., Odierna, G. and Balletto, E. 1998. Morphometrical and acoustical comparison between diploid and tetraploid green toads. *Biol. J. Linn. Soc.*, **63**: 257–281.

Coutellec-Vreto, M.-A., Madec, L. and Guiller, A. 1997. Selfing and biparental inbreeding: a mating system analysis in *Lymnaea peregra* (Gastropoda: Lymnaeidae). *Heredity*, **79**: 277–285.

Coyne, J.A. and Orr, H.A. 1989. Patterns of speciation in *Drosophila. Evolution*, **43**: 362–381.

Coyne, J.A. and Orr, H.A. 1997. 'Patterns of speciation in *Drosophila*' revisited. *Evolution*, **51**: 295–303.

Crawley, M.J. 1993. *Glim for Ecologists*. Oxford: Blackwell.

Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**: 354–357.

Diehl, S.R. and Bush, G.L. 1989. The role of habitat preference in adaptation and speciation. In *Speciation and Its Consequences* (D. Otte and J.A. Endler, eds), pp. 345–365. Sunderland, MA: Sinauer Associates.

Dillon, R.T. 2000. *The Ecology of Freshwater Molluscs*. Cambridge: Cambridge University Press.

Dobzhansky, T. 1940. Speciation as a stage in evolutionary divergence. *Am. Nat.*, **74**: 312–321.

Fishman, L. and Wyatt, R. 1999. Pollinator-mediated competition, reproductive character displacement, and the evolution of selfing in *Arenaria uniflora* (Caryophyllaceae). *Evolution*, **53**: 1723–1733.

Gregory, P.G. and Howard, D.J. 1994. A postinsemination barrier to fertilization isolates two closely related ground crickets. *Evolution*, **48**: 705–710.

Gregory, P.G., Remmenga, M.D. and Howard, D.J. 1998. Patterns of mating between two closely related ground crickets are not influenced by sympatry. *Entomol. Exp. Appl.*, **87**: 263–270.

Hewitt, G.M., Mason, P. and Nichols, R.A. 1989. Sperm precedence and homogamy across a hybrid zone in the alpine grasshopper *Podisma pedestris*. *Heredity*, **62**: 343–354.

Higgie, M., Chenoweth, S. and Blows, M.W. 2000. Natural selection and the reinforcement of mate recognition. *Science*, **290**: 519–521.

Hubendick, B. 1951. Recent Lymnaeidae: their variation, morphology, taxonomy, nomenclature and distribution. *Kungl. Svenska Vetenskaps Akad. Handl.*, **3**: 1–223.

Jarne, P. and Delay, B. 1990. Population genetics of *Lymnaea peregra* (Müller) (Gastropoda, Pulmonata) in Lake Geneva. *J. Mollusc. Stud.*, **56**: 317–321.

Loftus-Hills, J.J. and Littlejohn, M.J. 1992. Reinforcement and reproductive character displacement in *Gastrophryne carolinensis* and *G. olivacea* (Anura: Microhylidae): a reexamination. *Evolution*, **46**: 896–906.

Marquez, R. and Bosch, J. 1997. Male advertisement call and female preference in sympatric and allopatric midwife toads. *Anim. Behav.*, **54**: 1333–1345.

McCullagh, P. and Nelder, J.A. 1989. *Generalized Linear Models*. London: Chapman & Hall.

Noor, M.A. 1995. Speciation driven by natural selection in *Drosophila*. *Nature*, **375**: 674–675.

Noor, M.A.F. 1999. Reinforcement and other consequences of sympatry. *Heredity*, **5**: 503–508.

Norušis, M.J. 1990. *SPSS Advanced Statistics User's Guide*. Chicago, IL: SPSS Inc.

Økland, J. 1990. *Lakes and Snails*. Øgstgeest: Universal Book Services.

Pfennig, K.S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behav. Ecol.*, **11**: 220–227.

Porter, A. and Ribi, G. 1994. Population genetics of *Viviparus* (Mollusca: Prosobranchia): homogeneity of *V. ater* and apparent introgression into *V. contectus*. *Heredity*, **73**: 170–176.

Ribi, G. and Katoh, M. 1998. Weak preference for conspecific mates in the hybridizing snails *Viviparus ater* and *V. contectus* (Mollusca: Prosobranchia). *Ethol. Ecol. Evol.*, **10**: 383–392.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.

Ritchie, M.G., Butlin, R.K. and Hewitt, G.M. 1992. Fitness consequences of potential assortative mating inside and outside a hybrid zone in *Chorthippus parallelus* (Orthoptera: Acrididae): implications for reinforcement and sexual selection theory. *Biol. J. Linn. Soc.*, **45**: 219–234.

Rundle, H.D. and Schluter, D. 1998. Reinforcement of stickleback mate preferences: sympatry breeds contempt. *Evolution*, **52**: 200–208.

Saur, M. 1990. Mate discrimination in *Littorina littorea* (L.) and *L. saxatilis* (Olivi) (Mollusca: Prosobranchia). *Hydrobiologia*, **193**: 261–270.

Schluter, D. 1998. Ecological causes of speciation. In *Endless Forms, Species and Speciation* (D.J. Howard and S.H. Berlocher, eds), pp. 114–129. Oxford: Oxford University Press.

Schluter, D. and Nagel, L.M. 1995. Parallel speciation by natural selection. *Am. Nat.*, **146**: 292–301.

Veech, J.A., Benedix Jr., J.H. and Howard, D.J. 1996. Lack of calling song displacement between two closely related ground crickets. *Evolution*, **50**: 1982–1989.

Wullschleger, E. and Jokela, J. 1999. Does habitat-specific variation in trematode infection risks influence habitat distribution of two closely related freshwater snails? *Oecologia*, **121**: 32–38.

Wullschleger, E.B. and Jokela, J. in press. Life-history divergence between two closely related freshwater snails, *Lymnaea ovata* and *Lymnaea peregra*. *J. Mollusc. Stud.*

Wullschleger, E.B. and Ward, P.I. 1998. Shell form and habitat choice in *Lymnaea*. *J. Mollusc. Stud.*, **3**: 402–404.