

Female spadefoot toads compromise on mate quality to ensure conspecific matings

Karin S. Pfennig

Department of Ecology, Ethology, and Evolution, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA

When high-quality conspecifics resemble heterospecifics, females may be unable to engage effectively in both species recognition (identification of conspecifics) and mate-quality recognition (identification of high-quality mates). Consequently, females that engage primarily in mate-quality recognition may risk heterospecific matings, and females that engage primarily in species recognition may risk mating with low-quality mates. I examined the evolutionary consequences of this conflict between species and mate-quality recognition in spadefoot toads, *Spea multiplicata*. I compared mate preferences and the fitness consequences of these preferences in spadefoot toad populations that did and did not overlap with congeners. In non-overlapping populations, *S. multiplicata* females preferred an extreme call character resembling that of heterospecifics, and they had more eggs fertilized. In overlapping populations, *S. multiplicata* females preferred those call characteristics that were closest to the norm for their population, and they did not receive the benefit of enhanced fertilization success. Thus, *S. multiplicata* females appear to trade off species and mate-quality recognition, such that those co-occurring with heterospecifics forgo the benefits of high-quality matings to ensure conspecific matings. These results suggest that the interaction between species and mate-quality recognition may influence mate choice decisions in important and nonintuitive ways. *Key words*: mate choice, mate-quality recognition, species recognition, *Scaphiopus couchii*, *Spea bombifrons*, *Spea multiplicata*. [*Behav Ecol* 11:220–227 (2000)]

Mate choice often requires that individuals engage in both species recognition (identification of conspecifics) and mate-quality recognition (identification of high-quality mates) (Sherman et al., 1997). Because the types of traits used for each form of recognition potentially differ, a conflict may often exist between species and mate-quality recognition (Gerhardt, 1982; Pfennig, 1998; Ryan and Rand, 1993). This potential for conflict has important implications for the evolution of mate choice.

Females potentially face a conflict between species and mate-quality recognition whenever high-quality conspecifics resemble heterospecifics. To illustrate this conflict, consider that when engaging in mate-quality recognition, females often prefer those males with the most extreme secondary sexual characters (reviewed in Andersson, 1994; Ryan and Keddy-Hector, 1992). Because such traits are often costly to produce, they potentially serve as reliable signals that a male is of high quality in that he can provide either direct fitness benefits to the female or indirect fitness benefits to her offspring (reviewed in Andersson, 1994; e.g., Møller, 1990; Petrie, 1994; Reynolds and Gross, 1992). However, preferences for extreme traits may increase the likelihood that a female will mistakenly mate with heterospecifics, if heterospecifics resemble high-quality conspecifics (Gerhardt, 1982; Pfennig, 1998; Ryan and Rand, 1993). In contrast, when engaging in species recognition, females often prefer those males with secondary sexual characters closest to the population norm, presumably because such traits may best indicate species identity (Andersson, 1994; Gerhardt, 1991; Pfennig, 1998; e.g., Butlin et al., 1985; Gerhardt, 1991; Kyriacou and Hall, 1982; Waage, 1975). However, preferences for average traits may prevent females from identifying high-quality mates if these traits do not reli-

ably indicate quality. Thus, when high-quality conspecifics resemble heterospecifics, females that engage primarily in mate-quality recognition risk heterospecific matings, and females that engage primarily in species recognition risk matings with relatively low-quality males (Gerhardt, 1982; Pfennig, 1998; Ryan and Rand, 1993).

To mitigate this conflict between species and mate-quality recognition, selection should favor female preferences that minimize the costs and likelihood of mistakenly mating with heterospecifics or low-quality conspecifics (Pfennig, 1998). As a result, females may engage in one form of recognition at the expense of the other. For example, females that do not co-occur with heterospecifics may prefer extreme secondary sexual characters and benefit by selecting high-quality mates. Females co-occurring with heterospecifics, in contrast, may prefer typical values and therefore possibly forgo the fitness benefits of high-quality matings.

My study was designed to evaluate the above prediction in southern spadefoot toads (*Spea multiplicata*). I first asked whether secondary sexual characters (male calls) of *S. multiplicata* resembled those of two closely related sympatric species with which *S. multiplicata* occasionally mismates. I then compared mate preferences and the fitness consequences of these preferences in *S. multiplicata* populations that did and did not overlap with congeners. The results indicate that *S. multiplicata* females do indeed face a conflict between species and mate-quality recognition. The results further suggest that the interaction between these two processes may influence the evolution of mate choice in important and nonintuitive ways.

METHODS

Study species, field sites, and laboratory culture

Spea multiplicata co-occurs with the plains spadefoot toad, *Spea bombifrons*, and Couch's spadefoot toad, *Scaphiopus couchii*, in southeastern Arizona, USA, although *S. bombifrons* is restricted to lower elevations (Simovich, 1985). Mismatings occasionally occur between all three species (Pfennig KS, personal observation; Simovich, 1985). Matings between the *Spea*

Address correspondence to K. S. Pfennig at the Department of Biology, CB#3280, Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280, USA. E-mail: kpfennig@email.unc.edu.

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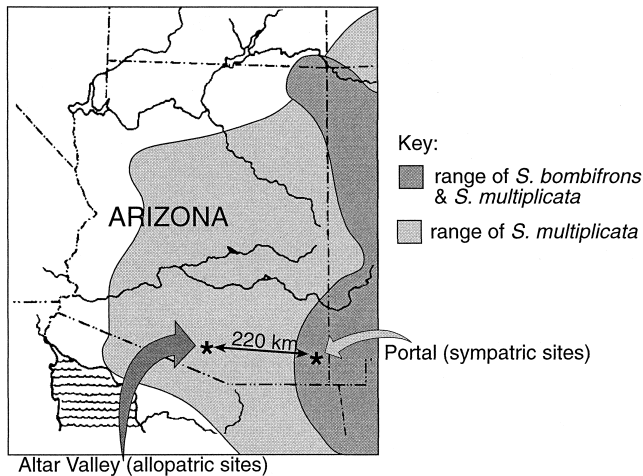


Figure 1
Map showing *Spea* ranges and collection sites. A third spadefoot species, *Scaphiopus couchii* (range not shown), occurs at both collection sites.

species are more common (10–30% of matings may be mismatches; Pfennig KS, personal observation; Simovich, 1985) because these species usually occur in the same breeding aggregations. Matings between the *Spea* species produce sterile males and females that are less fecund than either parent type (Simovich, 1985). Matings between *S. couchii* and *Spea* are rare (Pfennig KS, personal observation), in part because *S. couchii* does not always occur in the same breeding aggregations with *Spea*. When matings between *S. couchii* and *Spea* do occur, they produce inviable eggs (Tinsley RC, personal communication).

Female spadefoots have ample opportunity to choose mates (Pfennig KS, personal observation; Sullivan and Sullivan, 1985; Tinsley, 1990) and can use male call features to assess species identity and quality of potential mates. In other anuran species, females use species-specific values of call pulse rate (number of pulses within a call per second; Gerhardt, 1988, 1991) or call frequency (Gerhardt, 1988; Rand et al., 1992) to identify conspecific mates. They also use characters such as long call duration (Gerhardt, 1988; Taigen and Wells, 1985; Welch et al., 1998), fast call rate (Bevier, 1997; Cherry, 1993; Gerhardt, 1988; Grafe, 1996; Prestwich et al., 1989; Taigen and Wells, 1985) and frequency as indicators of male quality (Robertson, 1990; Ryan, 1980). Call frequency can be used to indicate body size (Robertson, 1990; Ryan, 1980), and both long call duration and fast call rate require greater investment of energy into calling (Bevier, 1997; Cherry, 1993; Grafe, 1996; Prestwich et al., 1989; Taigen and Wells, 1985), thereby potentially serving as reliable indicators of male quality (Cherry, 1993; Grafe, 1996; Welch et al., 1998).

I conducted field research near the American Museum of Natural History's Southwestern Research Station at Portal, Arizona, USA, where all three spadefoot species co-occur. In addition, *S. multiplicata* females were collected from the Altar Valley, Arizona, where *S. bombifrons* does not occur (area of allopatry; Figure 1).

Females used in phonotaxis experiments were transported to the University of Illinois or the University of North Carolina. There they were housed in 4-l buckets filled with dirt and fed nutrient-dusted crickets ad libitum. The animals were housed under a reverse light-dark cycle of 14 h light:10 h dark. During the fall months, the temperature in the room was cooled from a holding temperature of 25.6°C to approximately 17°C. The cooler temperatures were maintained for

approximately 3 months, then returned to 25.6°C. All phonotaxis experiments were conducted during the spring following this cool-down period.

Male call characters

Males of all three spadefoot species, along with several *S. bombifrons* × *S. multiplicata* hybrid males, were recorded in 2 separate years at four natural mixed-species ponds. I also recorded the pond temperature in which the males were calling because temperature can affect male call characters. I analyzed the recordings of the calls using sound analysis software to determine call rate, call pulse rate, call dominant frequency, and call duration for each species. Where temperature affected a call character, the characters were corrected to 20.4°C (the most common recording temperature) based on the regression relationship between temperature and the call character (Sokal and Rohlf, 1995; e.g., Gerhardt, 1991; Wagner and Sullivan, 1995).

Phonotaxis experiments

To determine what aspect (if any) of conspecific calls *S. multiplicata* females prefer, I collected females from both areas of sympatry and allopatry (i.e., where *S. bombifrons* is absent; Figure 1). Using these females, I then conducted two-speaker phonotaxis experiments in which females were presented alternative calls using standard procedures (e.g., Gerhardt, 1991; Wagner and Sullivan, 1995).

Each female was initially placed in the center of a wading pool equidistant between two speakers set 180° and 1.4 m apart. From each speaker I broadcast one of two stimuli (see below). Each female was initially placed in an opaque container for an acclimation period of 15 min. I began to play the stimuli at the start of this interval. At the end of the acclimation interval, the female was released and allowed to move freely about the pool, while the stimuli continued to play. Each female was watched continuously by a hidden observer for 30 min or until she approached within 10 cm (approximately two body lengths) of a speaker, whichever came first. Upon release, most females spent time orienting their head or body toward a speaker before actually approaching the speaker (i.e., females did not move randomly through the arena until they bumped into a speaker). I scored a female as preferring a stimulus when she approached the speaker broadcasting that stimulus (e.g., Gerhardt, 1991; Wagner and Sullivan, 1995). This is an appropriate bioassay of female mate preference because spadefoot females initiate amplexus by closely approaching and/or touching a male (Pfennig KS, personal observation). If a female had not approached a speaker within the 30-min observation interval, the female was considered nonresponsive and excluded from analysis.

In four separate experiments, I presented the sympatric *S. multiplicata* females with the following alternative call types differing in only one parameter: high versus low dominant frequency calls (see below for stimuli values used), long (1.26 s) versus short (0.91 s) duration calls, average (25.2 pulses/s) versus fast (26.4 pulses/s) call pulse rate, and average (31 calls/min) versus fast (37 calls/min) call rate. In each experiment, all call features (including volume) were kept constant at typical conspecific values, except for the character being manipulated.

To create the sound stimuli for each experiment (except dominant frequency, see below), I randomly chose 3–10 *S. multiplicata* calls from a collection of digitized recordings (from the recordings above). Each call was then manipulated using sound editing software to create the alternative stimuli given above. In the case of the dominant frequency experi-

ment, three sets of two calls (i.e., calls from six different males) were chosen from the digitized recordings. Two of these sets consisted of male calls at 1.25 kHz and 1.42 kHz, and a third set consisted of alternative male calls at 1.22 kHz and 1.38 kHz. These calls were then manipulated so that they consisted of typical species values for all other call characters. For each experiment (except for the call rate experiments), the manipulated calls were then repeated onto separate tracks of an audio tape at an average call rate. Thus, females presented a given tape heard alternative versions of the same male's call (except in the case of dominant frequency).

The females were randomly assigned to three to ten approximately equal-sized groups of 6–18 females. The number of groups and the number of females within groups depended on the experiment and the number of females available for testing when the experiment was conducted. I injected females with 0.1 ml 36.0 µg/ml luteinizing hormone-releasing hormone to bring them into reproductive condition (e.g., Semlitsch and Schmiedehausen, 1994). I tested the females in each experiment within 12 h of injection once they were in reproductive condition (eggs were readily visible through the skin of their abdomens). Each female within a group was tested on the same day and was presented the same tape. Thus, all females in a given experiment were presented the same stimuli sets (except dominant frequency; stimuli values are given above), but the male call that was used in making those stimuli differed between the groups. This procedure of presenting multiple representations of the stimuli ensured that females were responding to the values of the call stimuli *per se* rather than to an uncontrolled variable in a natural male recording (Kroodsmas, 1989).

All of the above stimuli values were within the natural range of variation for sympatric *S. multiplicata* males and were appropriate for the temperature (20.6°C) at which the females were tested. High and low values represented extremes within this range of variation for a given character. Females were used only once for a given set of stimuli. I switched the stimuli between speakers after each female to control for position effects.

I also tested 18 allopatric *S. multiplicata* females for their preferences of call rate. These females were presented the same average versus fast call rate stimuli as given above. They were not tested for any other stimuli.

I analyzed the preference data for each experiment by first determining if females could be pooled across groups using heterogeneity chi-square tests. Where there was no significant heterogeneity among groups, I pooled all of the females and, using log-likelihood ratio (*G*) tests, determined if female preferences deviated from 1:1 random expectation.

Benefits of female mate choice

To determine if *S. multiplicata* females benefited from mate choice when *S. bombifrons* were absent but not when they were present, I collected *S. multiplicata* pairs (before gamete release) from a high elevation, pure-species pond (~1650 m elevation) and from three lower elevation, mixed-species ponds (~1200 m elevation) within 10 km of each other near Portal, Arizona (*S. bombifrons* does not occur above 1500 m elevation; Simovich, 1985). The pairs were separated and the male designated as that female's "preferred" mate. Unmated calling males from the same breeding aggregation were collected and designated "nonpreferred" males.

I brought these animals into the laboratory and placed each female in 13.5-l dechlorinated water with either her preferred mate or a randomly chosen nonpreferred male from her breeding aggregation (order randomized). After each female released half her clutch (*Spea* have external fertilization), I

separated her from her first mate, rinsed her with water to remove residual sperm, and placed her with her second mate. Once mating was completed, I counted the proportion of fertilized eggs (the animal pole of fertilized eggs rotates upward and is easily identified with the unaided eye; Nace et al., 1974). I compared the proportions of each female's eggs fertilized by preferred and nonpreferred males using two-tailed paired *t* tests.

I removed a random subset of hatchlings from each clutch and reared them to metamorphosis in 1.8-m diameter wading pools (Pfennig et al., 1991). Within each wading pool, I placed two mesh-sided boxes (1 m × 0.7 m × 0.2 m) containing 25 offspring from the same female sired by either her preferred male or a nonpreferred male. This density fell within the range of densities in natural ponds (Pfennig et al., 1991). I fed tadpoles in each box rabbit chow three times for a total of 10.59 g, thereby simulating detritus on which tadpoles feed in natural ponds (Pfennig et al., 1991). This food amount was low and was meant to maximize potential differences between the offspring of preferred and nonpreferred males. I measured age, mass, and snout-vent length at metamorphosis and calculated mean values per box. These measures are important because age and size at metamorphosis correlate with adult survival in this species (Pfennig et al., 1991). I then compared these measures for the offspring of preferred males versus those of nonpreferred males using two-tailed paired *t* tests.

I measured the mass and snout-vent length of the preferred and nonpreferred males. I controlled for snout-vent length in these mass measurements by correcting mass to the average male snout-vent length using the regression relationship between mass and snout-vent length (Sokal and Rohlf, 1995). This technique allowed me to compare mass for a given body size between preferred and nonpreferred males and allowed me to assess male condition (heavier males for a given body size are likely to have greater energy stores, a potential indicator of male condition). Larger, heavier males may produce better quality offspring (Reynolds and Gross, 1992; Woodward, 1986), better quality sperm, or higher sperm counts (Berrigan and Locke, 1991; Pitnick and Markow, 1994).

I repeated the collection and pairing procedures with *S. bombifrons* from two mixed-species ponds where the *S. multiplicata* were collected. The proportion of fertilized eggs was counted for females paired with their preferred mates and with the nonpreferred males as for *S. multiplicata*. However, the offspring from these crosses were not reared to metamorphosis.

RESULTS

Male call characters

Spea multiplicata calls overlap with at least one other species for two call characters: call duration and call dominant frequency (Figure 2). Two other call characters, call pulse rate and call rate, are distinct among all three species and the hybrid males (Figure 2).

Phonotaxis experiments

Sympatric *S. multiplicata* females did not express any clear preference for an extreme value of either call duration (CD) or dominant frequency (DF). Of the 30 females presented the dominant frequency stimuli, 27 responded by approaching one of the two stimuli. There was significant heterogeneity among the three *S. multiplicata* female groups tested for dominant frequency ($\chi^2 = 7.24$, *df* = 2, *p* < .05), so that females could not be pooled across groups. One group of females (presented 1.25 kHz versus 1.42 kHz) showed significant pref-

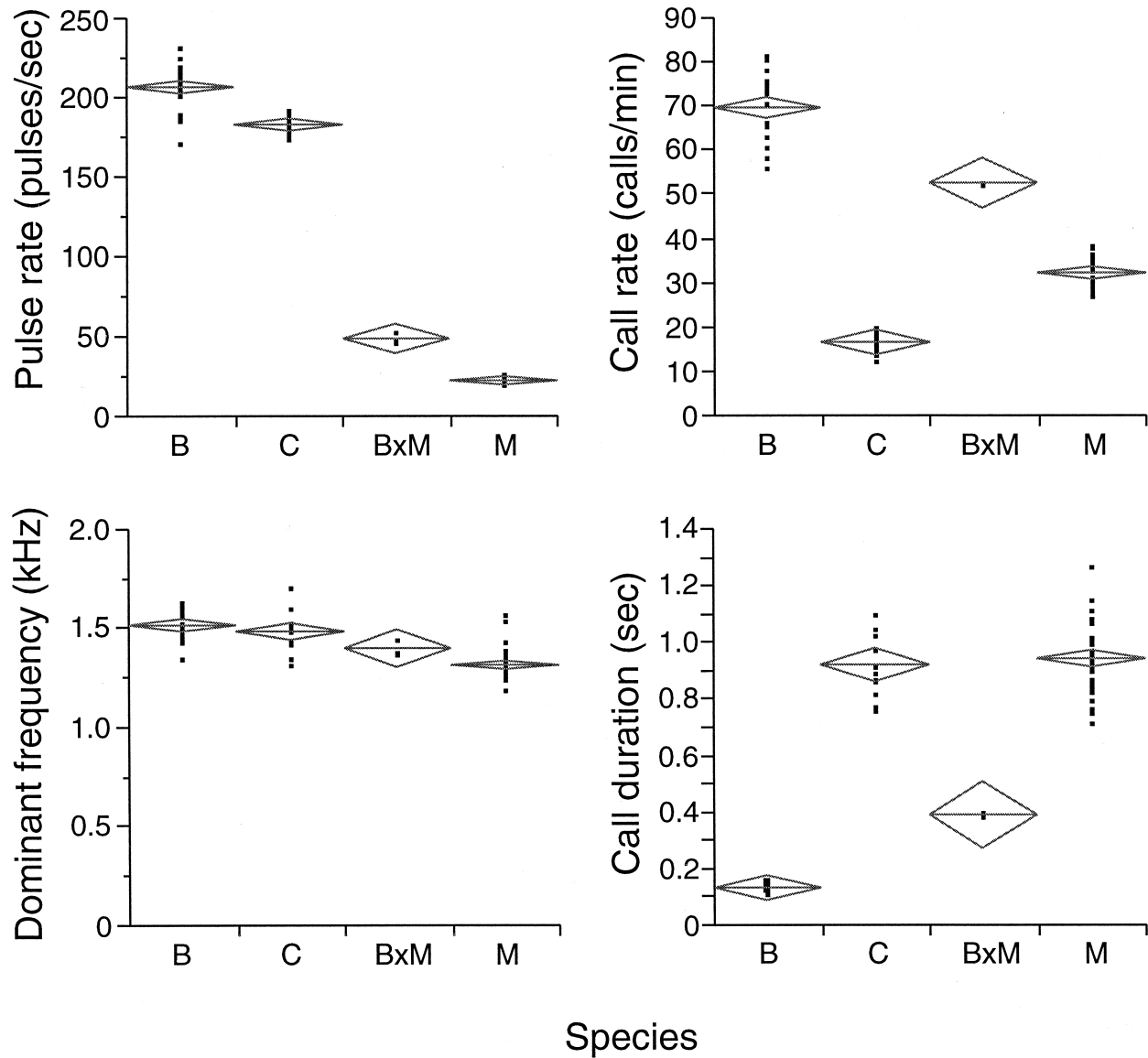


Figure 2

Distributions of male call characters for three sympatric species of spadefoot toad. Each point represents a single male *S. bombifrons* (B; $N = 16$), *S. couchii* (C; $N = 12$), *S. bombifrons* \times *S. multiplicata* hybrid (BxM; $N = 3$) or *S. multiplicata* (M; $N = 35$). Horizontal line inside diamond: mean; height of diamond: 95% confidence intervals. Corrected to 20.4°C.

erence for high DF (seven preferred high DF, whereas one preferred low DF; $G = 5.06$, $df = 1$, $p = .025$). However, the remaining groups did not show this tendency to prefer high DF. The second group (presented 1.25 kHz versus 1.42 kHz) was evenly split (five preferred high DF and five preferred low DF) and the third group (presented 1.22 kHz versus 1.38 kHz) showed the opposite trend (two preferred high DF and seven preferred low DF; $G = 2.94$, $df = 1$, $p = .086$).

Of the 31 sympatric *S. multiplicata* females tested for their preferences of call duration, 29 responded to the test. There was no significant heterogeneity among the female groups tested for call duration ($\chi^2 = 7.89$, $df = 4$, $p > .05$), so the groups were pooled for analysis. These females were nearly evenly split between the long and short call duration stimuli: 13 females preferred long CD and 16 preferred short CD.

In contrast to the results for dominant frequency and call duration, *S. multiplicata* females expressed clear preferences for values of pulse rate and call rate. Of the 42 sympatric *S.*

multiplicata females tested for their preferences of pulse rate, one female did not respond and was excluded from analysis. The females were pooled across groups for analysis (heterogeneity $\chi^2 = 2.02$, $df = 2$, $p > .25$). These *S. multiplicata* females preferred calls with an average pulse rate to those of a fast pulse rate (27 females preferred average pulse rate versus 14 that preferred fast; $G = 4.19$, $df = 1$, $p = .041$).

Spea multiplicata females also expressed a preference for call rate, but whether females preferred average or fast call rate depended on whether they were from populations in sympatry or allopatry with *S. bombifrons* (Figure 1). Of 18 allopatric *S. multiplicata* females presented the alternative call rate stimuli, all responded and were pooled across groups for analysis (heterogeneity $\chi^2 = 0.48$, $df = 2$, $p > .75$). These females showed a significant preference for conspecific calls at the faster than average call rate (Figure 3). In contrast, *S. multiplicata* females from sympatry significantly preferred the average call rate stimulus to the faster than average call rate

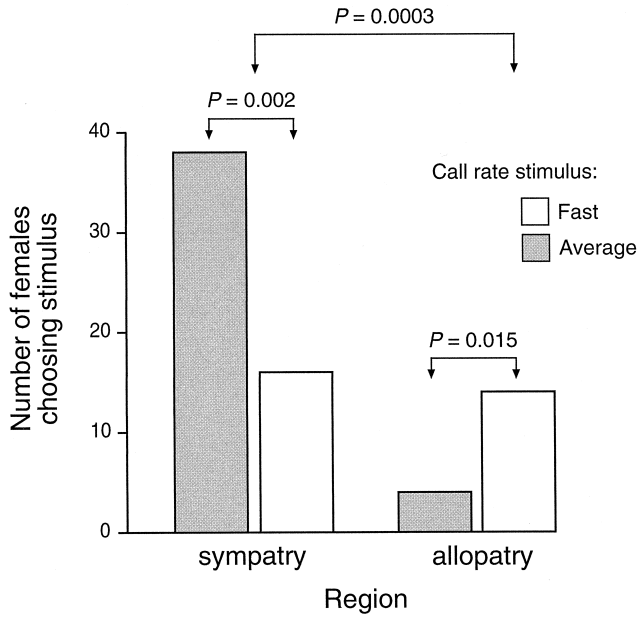


Figure 3
 Comparison of call rate preferences between *S. multiplicata* females from allopatry and sympatry with *S. bombifrons*. Sympatric preferences: $G = 9.23$, $df = 1$; allopatric preferences: $G = 5.88$, $df = 1$; comparison of preferences between sympatry and allopatry: $G = 13.10$, $df = 1$.

stimulus (Figure 3). Of the 67 sympatric *S. multiplicata* females available for testing, 54 approached one of the two call rate stimuli (13 were nonresponsive and excluded from analysis). These females were pooled across groups for analysis (heterogeneity $\chi^2 = 11.08$, $df = 9$, $p > .25$). Thus, preferences by *S. multiplicata* females for call rate significantly differed in sympatry and allopatry (Figure 3): females in allopatry preferred extreme values of call rate, whereas females in sympatry preferred average values of call rate.

Benefits of female mate choice

Preferred (P) *S. multiplicata* males did not sire larger or faster developing offspring than did nonpreferred (NP) males at either the pure- or mixed-species ponds (Table 1). However, in the pond where *S. bombifrons* was absent, *S. multiplicata*

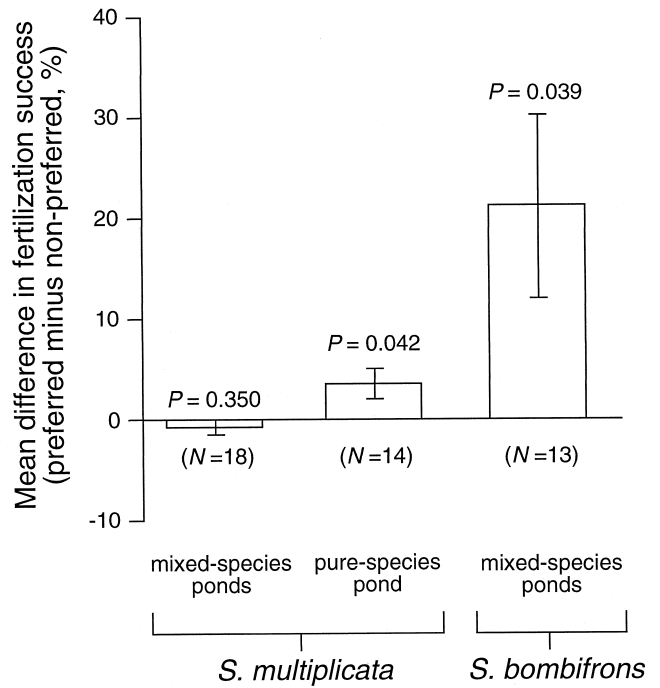


Figure 4
 Mean difference in fertilization success of preferred and nonpreferred males with *S. multiplicata* and *S. bombifrons* females (\pm SE). Numbers of males of each type tested given in parentheses. The p values are given for two-tailed paired t tests, $df = N - 1$.

females had significantly higher fertilization success with preferred males than with nonpreferred males (Figure 4), receiving 3.5% more offspring with their preferred mates. Moreover, these preferred males tended to be heavier for a given body size and were therefore likely in better condition than the nonpreferred males (Figure 5). In contrast, *S. multiplicata* females from the three mixed-species ponds did not receive this benefit; there was no difference between preferred and nonpreferred males in terms of ability to fertilize a female's clutch (Figure 4) or in terms of mass (Figure 5).

Contrary to the *S. multiplicata* females from the mixed-species ponds, *S. bombifrons* females had considerably higher fertilization success with their preferred mates as opposed to nonpreferred males (Figure 4). Moreover, preferred *S. bom-*

Table 1
 Comparison of age and size at metamorphosis for offspring of preferred males (P) versus nonpreferred males (NP) at pure-species (*S. bombifrons* absent) and mixed-species (*S. bombifrons* present) ponds

Pond type	Trait	Male type	Mean \pm SE	p
Pure	Snout-vent length	P	15.47 \pm 0.16 mm	.25
		NP	15.30 \pm 0.09 mm	
	Mass	P	0.564 \pm 0.02 g	.84
		NP	0.561 \pm 0.01 g	
Mixed	Age at metamorphosis	P	33.97 \pm 0.42 days	.31
		NP	34.33 \pm 0.45 days	
	Snout-vent length	P	15.14 \pm 0.23 mm	.91
		NP	15.16 \pm 0.12 mm	
Mixed	Mass	P	0.594 \pm 0.02 g	.70
		NP	0.585 \pm 0.01 g	
	Age at metamorphosis	P	31.09 \pm 0.27 days	.49
		NP	30.96 \pm 0.23 days	

All p values based on two-tailed paired t tests; $df = 13$.

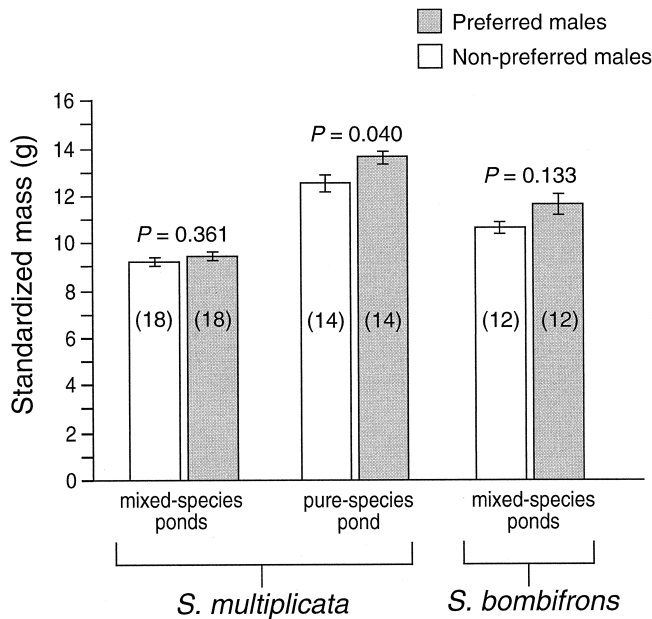


Figure 5

Standardized mass of preferred and nonpreferred *S. multiplicata* and *S. bombifrons* males (\pm SE). Mass is corrected to mean snout-vent length (SVL) for each group: *S. multiplicata* mean SVL from mixed-species ponds = 40.96 mm; *S. multiplicata* mean SVL from pure-species pond = 46.61 mm; *S. bombifrons* mean SVL from mixed-species ponds = 45.17 mm. Number of males measured given in parentheses. The p values are given for two-tailed t tests, $df = (N_1 + N_2) - 2$.

bifrons males tended to be heavier for a given body size than the nonpreferred *S. bombifrons* males (although the difference was not significant; Figure 5).

DISCUSSION

I compared mate preferences and the fitness consequences of these preferences in spadefoot toad populations that did and did not overlap with congeners. In non-overlapping populations, *S. multiplicata* females preferred an extreme call character resembling that of heterospecifics, and they had more eggs fertilized. In overlapping populations, *S. multiplicata* females preferred average call characteristics, and they did not benefit in terms of enhanced fertilization success.

The finding that sympatric *S. multiplicata* females prefer average call rate is unusual. Although anuran females often use species-typical values of pulse rate to identify conspecific males (Gerhardt, 1988), anuran females generally prefer faster call rates to slower values (e.g., Cherry, 1993; Dyson et al., 1998; Gerhardt, 1987; Lopez and Narins, 1991; Passmore et al., 1992; Sullivan, 1983; Wagner and Sullivan, 1995). Call rate is a condition-dependent character (i.e., the ability to call rapidly requires greater energy; Bevier, 1997; Grafe, 1996; Prestwich et al., 1989; Taigen and Wells, 1985) so that fast call rates are potentially reliable indicators of male quality (Cherry, 1993; Grafe, 1996).

Gerhardt (1991) suggested that anuran females may glean multiple messages from male calls, such that one trait (e.g., pulse rate) may indicate species identity and other traits (e.g., call duration or call rate) may indicate male quality. Moreover, females may weight the importance of this information differently depending on whether they are in sympatry or allopatry (e.g., Gerhardt, 1994). Why then do sympatric *S. multiplicata* females not use an average value of pulse rate to iden-

tify conspecific males and exaggerated values of call rate to identify high-quality mates (e.g., Gerhardt, 1994)? One possible explanation is that backcross hybrid males (which can occur in mixed-species ponds; Simovich, 1985) may possess calls that overlap with or are similar in pulse rate and/or call rate to calls of pure *S. multiplicata* males. Thus, sympatric *S. multiplicata* females may need to use species-specific values of both characters to identify conspecific mates. The need to avoid F_1 and backcross hybrid males may also explain female avoidance of a fast call rate (37 calls/min) that is still well below the average for *S. bombifrons*. To evaluate this hypothesis, it will be necessary to fully describe the call characters of F_1 and backcross hybrid males. It would also be interesting to determine how *S. multiplicata* females (both from sympatry and allopatry) react to simultaneous variation in both pulse rate and call rate (e.g., Gerhardt, 1994). Such experiments would provide a better understanding of how *S. multiplicata* females use the information in both characters.

In contrast to the call rate preferences of sympatric *S. multiplicata* females, allopatric *S. multiplicata* females preferred an exaggerated, faster than average value of call rate to the average value (Figure 3). Thus, *S. multiplicata* females appear to use exaggerated values of a condition-dependent trait when *S. bombifrons* is absent. These findings are based on females collected from one population in sympatry and one population in allopatry, however, so it will be necessary to compare female mate preferences from additional sympatric and allopatric populations to generalize beyond these two populations. Nevertheless, female mate preferences often differ between populations in sympatry and allopatry (e.g., Gerhardt, 1994; Markow, 1981; Márquez and Bosch, 1997; Noor, 1995; Ratcliffe and Grant, 1983; Waage, 1975), such that individuals in sympatry are more selective against heterospecifics than are individuals in allopatry.

By preferring an average call rate to a faster call rate, sympatric *S. multiplicata* females appear to sacrifice information on male quality to avoid mismating with *S. bombifrons* and sterile hybrid males, which possess fast call rates (Figure 2). Indeed, *S. multiplicata* females had enhanced fertilization success only when *S. bombifrons* were absent (i.e., in the pure-species pond; Figure 4). That *S. multiplicata* females benefited from mate choice when congeners were absent, but not when they were present, supports the prediction that females engaging primarily in species recognition forgo benefits of mate choice (Pfennig, 1998). Thus, *S. multiplicata* females apparently emphasize species recognition when risk of heterospecific matings is high and mate-quality recognition when such mismatings are unlikely. Note that, although *S. multiplicata* females from the Altar Valley co-occur with *S. couchii*, their preference for faster-calling conspecific males (Figure 3) potentially allows them to select against both low-quality conspecific mates and heterospecifics (i.e., *S. couchii*). This preference for an exaggerated value of call rate allows Altar Valley *S. multiplicata* females to select against heterospecifics because *S. couchii* males call more slowly than *S. multiplicata* males (Figure 2). Thus, in this situation, species and mate-quality recognition may reinforce one another (i.e., by selecting high-quality conspecifics, females also avoid heterospecifics).

Once a female is freed from having to engage primarily in species recognition, the benefits of mate-quality recognition can be substantial. For example, *S. multiplicata* females at the pure-species pond had 3.5% more offspring with preferred males versus nonpreferred males. Because this 3.5% is an increase in the number of offspring females receive, it is an estimate of the strength of selection on female preferences. Using the standard equation for the spread of a favorable allele (Ridley, 1996), an allele encoding a preference that yields

3.5% more offspring will go from being rare (1%) to common (>50%) in fewer than 200 generations.

The mechanism by which *S. multiplicata* females benefited from enhanced fertilization success with preferred males is unclear, but likely involves male condition. Females at the pure-species pond preferred mates that were heavier for a given body size than were nonpreferred males (Figure 5), suggesting that the preferred males were in better condition. In other species, larger males produce better quality ejaculate and higher sperm counts (Berrigan and Locke, 1991; Pitnick and Markow, 1994). Thus, spadefoot males that are heavier for a given body size may produce more or better quality sperm, thereby enabling them to better fertilize a female's clutch.

It might be contended that an unidentified environmental variable in the mixed-species ponds prevented *S. multiplicata* females from selecting high-quality mates. Yet, *S. bombifrons* females from these same ponds had substantially higher fertilization success with preferred males (Figure 4). This finding illustrates an important point: females that do not face a conflict between species and mate-quality recognition are not expected to compromise on mate quality, even when heterospecifics are present. Such is the case with *S. bombifrons* females that can potentially use extreme values of fast call rate to select high-quality conspecific mates without risking heterospecific matings (Figure 2).

It is possible that *S. multiplicata* females did not benefit in mixed-species ponds because *S. multiplicata* males at these ponds were unable to provide females with enhanced fertilization success. For example, mixed-species ponds, which are typically at lower elevations, may be in marginal habitat for *S. multiplicata* such that *S. multiplicata* males at mixed-species ponds are in poor condition and therefore unable to provide females with enhanced fertilization success. However, the mean fertilization success among males at each pond type is similar, thereby mitigating against this hypothesis (mean fertilization success at pure-species pond \pm SE = 90.29 ± 0.03 ; mean fertilization success at mixed-species ponds = 92.78 ± 0.01 ; $t = 0.92$, $df = 62$, $p = .36$). Moreover, although this hypothesis explains why *S. multiplicata* females would not receive benefits from males at the mixed-species ponds, it does not explain why sympatric (as opposed to allopatric) *S. multiplicata* females would prefer males with an average value of a condition dependent character (call rate).

It is also possible that a more complex acoustic environment at mixed-species ponds may have prevented *S. multiplicata* females (but not *S. bombifrons* females) from identifying high-quality mates (Gerhardt and Klump, 1988; Wollerman, 1999). However, this hypothesis also does not necessarily explain why sympatric *S. multiplicata* females prefer an average call rate. All else being equal, faster call rates contain more energy than slower values, so faster-calling males might be more easily detected against a background chorus sound. Thus, chorus noise per se potentially should select for preferences of fast call rates rather than average call rate.

Compromising on mate quality to ensure conspecific matings is not necessarily a long-term solution to a conflict between species and mate-quality recognition. Such a trade-off between species and mate-quality recognition may most likely occur when ranges of species that use similar secondary sexual signals have overlapped recently (as may be true of *S. multiplicata* and *S. bombifrons* in southeastern Arizona; Simovich, 1985). Ultimately, selection may favor females that use multiple characters that enable them to assess mate quality and species identity simultaneously, or selection may favor high-quality males that produce signals distinct from heterospecifics (Pfennig, 1998).

In general, females may engage in species recognition over

mate-quality recognition whenever sympatric species use similar secondary sexual signals. However, although this study has emphasized how species recognition may be expressed at the expense of mate-quality recognition, the converse may also hold. In particular, selection may favor an emphasis on mate-quality recognition over species recognition if the costs or risks of heterospecific matings are low (Pfennig, 1998). Such an emphasis on mate-quality recognition over species recognition may explain situations where mate preferences for exaggerated traits lead to preferences for traits of heterospecific males (Basolo, 1990; Jones and Hunter, 1998; McClintock and Uetz, 1996; Moodie, 1982; Morris and Fullard, 1983; Ryan and Wagner, 1987).

In sum, the interaction between species and mate-quality recognition can affect the evolution of individuals' abilities to detect mates, sexually selected characters, and, ultimately, mate choice behavior in important and seemingly nonintuitive ways. By establishing how these recognition processes interact, we will better understand why and how individuals choose certain mates.

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