

GENETIC BENEFITS OF A FEMALE MATING PREFERENCE IN GRAY TREE FROGS ARE CONTEXT-DEPENDENT

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Abstract.—“Good genes” models of sexual selection predict that male courtship displays can advertise genetic quality and that, by mating with males with extreme displays, females can obtain genetic benefits for their offspring. However, because the relative performance of different genotypes can vary across environments, these genetic benefits may depend on the environmental context; in which case, static mating preferences may not be adaptive. To better understand how selection acts on the preference that female gray tree frogs (*Hyla versicolor*) express for long advertisement calls, I tested for genetic benefits in two realistic natural environments, by comparing the performance of half-sibling offspring sired by males with long versus short calls. Tadpoles from twelve such maternal half-sibships were raised in enclosures in their natal pond at two densities. In the low-density treatment, offspring of long-call males were larger at metamorphosis than were offspring of short-call males, whereas in the high-density treatment, offspring of males with long calls tended to metamorphose later than offspring of males with short calls. Thus, although the genes indicated by long calls were advantageous under low-density conditions, they were not beneficial under all conditions, suggesting that a static preference for long calls may not be adaptive in all environments. Such a genotype-by-environment interaction in the genetic consequences of mate choice predicts that when the environment is variable, selection may favor plasticity in female preferences or female selectivity among environments to control the conditions experienced by the offspring.

Key words.—Genotype-by-environment interaction, “good genes,” *Hyla versicolor*, maternal half-sibships, metamorphosis, sexual selection, tadpoles.

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Mating preferences in some species may have evolved as adaptive mechanisms for assessing genetic quality in potential mates (Williams 1966; Zahavi 1975, 1977). Genetic indicator hypotheses propose that courtship display traits that are preferred by the choosing sex can function as signals of heritable genetic quality among individuals of the displaying sex (reviewed in Andersson 1994). A hallmark of these hypotheses is that the display trait covaries genetically with offspring fitness, leading to the explicit prediction that the offspring of individuals with the preferred display phenotype will have higher genetic quality than offspring of individuals with the less preferred phenotype. Important empirical support for genetic indicator hypotheses has come from tests of this critical prediction. Males with preferred traits have been shown to sire offspring with enhanced viability or growth (i.e., “good genes” benefits) in a variety of animals, including insects (Moore 1994; Jia and Greenfield 1997; Hoikkala et al. 1998; Iyengar and Eisner 1999), birds (Norris 1993; Møller 1994; Petrie 1994; von Schantz et al. 1994; Hasselquist et al. 1996; Sheldon et al. 1997), fish (Reynolds and Gross 1992; Barber et al. 2001), spiders (Alatalo et al. 1998; Watson 1998), and amphibians (Welch et al. 1998). These empirical tests provide evidence that female mating preferences may be under selection exerted by the indirect benefits of enhanced offspring viability.

Little is known, however, about whether such indirect benefits are consistent across environments and hence whether “good genes” selection acts consistently on mating preferences across environments (Sheldon 2000). Because genetic indicator models require that a display trait is associated with genes that promote fitness in the offspring, it is important to

consider how genotype-by-environment interactions can affect the relationship between a male display trait and offspring fitness and thereby influence selection on female preferences. Genotype-by-environment interactions—in which the performance of different genotypes varies across environments—are common (Falconer and Mackay 1996; Roff 1997), with the consequence that a genotype that is advantageous in one environment may be relatively unsuccessful in another environment. Because the performance of genotypes is inextricable from the environment in which performance is measured, a relationship between male display phenotype and offspring fitness may only be relevant to the environment in which this relationship was tested. Yet, the indirect benefits of mating preferences have seldom been tested under natural conditions, except in birds (e.g., Norris 1993; Hasselquist et al. 1996; Sheldon et al. 1997), or in multiple environments (but see Jia and Greenfield 1997; Blanckenhorn et al. 1998; Welch et al. 1998). If the expression of either the male trait (Qvarnström 1999; David et al. 2000; Jia et al. 2000; Kotiaho et al. 2001) or the correlated response in offspring fitness (Jia and Greenfield 1997; Sheldon 2000) is subject to genotype-by-environment interactions, the potential genetic benefit of mating with males bearing the trait may depend on the environment experienced by males and by their offspring. If the relationship between a male trait and offspring fitness varies among environments, then selection on the preference will also vary across environments (Qvarnström 2001). Therefore, it is important to test the genetic consequences of female mating preferences under natural conditions and in multiple environments. In the present study, I test the relationship between a male trait for which a female preference has been documented—long call duration in gray tree frogs—and offspring quality under two environmental conditions in the field.

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TABLE 1. Calling performance and body mass (mean \pm SD) of sires exhibiting long versus short calls. Parameters were compared with two-tailed paired *t*-tests (df = 11).

	Pulses per call	Call duration (s)	Duty cycle	Body mass (g)
Long-call males (<i>n</i> = 12)	31.3 \pm 4.9	1.80 \pm 0.49	0.207 \pm 0.025	8.1 \pm 0.7
Short-call males (<i>n</i> = 12)	19.4 \pm 4.1	1.09 \pm 0.32	0.172 \pm 0.031	7.4 \pm 1.0
Paired <i>t</i>	11.71	9.54	4.23	0.09
<i>P</i>	<0.0001	<0.0001	0.0014	0.0925

Female gray tree frogs (*Hyla versicolor*) prefer male advertisement calls of long duration to shorter alternatives in laboratory playback tests (Klump and Gerhardt 1987; Gerhardt et al. 1996; Gerhardt et al. 2000) and under more natural conditions (Schwartz et al. 2001). Some male gray tree frogs consistently produce longer calls than nearby males (Gerhardt 1991; Sullivan and Hinshaw 1992; Runkle et al. 1994; Gerhardt et al. 1996). Long calls are energetically more costly than short calls (Taigen and Wells 1985; Wells and Taigen 1986; Grafe 1997), and males that produce long calls spend less time calling per night (Wells and Taigen 1986) and attend fewer choruses per season (Sullivan and Hinshaw 1992) than males that produce short calls. Call duration may, therefore, be an honest indicator of male quality. Males do not provide resources, protection, or parental care (Fellers 1979; Sullivan and Hinshaw 1992), and there is no difference in fertilization success between clutches sired by males with long versus short calls (J. D. Krenz, unpubl. data). Genetic benefits of mate choice may therefore be the critical source of selection on mating preferences in this species. In laboratory experiments, the offspring of males with long calls showed higher larval survival and greater larval and juvenile growth, and metamorphosed earlier or at larger size than did their half-siblings sired by males with short calls (Welch et al. 1998). Large size at metamorphosis and early metamorphosis have been shown to enhance fitness in anurans (e.g., Smith 1987; Berven 1990; Goater 1994). Call duration thus appears to indicate heritable genetic quality in male gray tree frogs that can enhance the quality of their larval offspring.

Here, I test the relative genetic quality of offspring of male *H. versicolor* with long versus short calls under natural conditions in two environmental treatments. To compare the performance of offspring of long- and short-calling males while holding constant all maternal genetic and nongenetic effects, I generated a series of maternal half-siblings, using artificial fertilization and a split-clutch design. By completely controlling maternal investment, this experimental design circumvents the potential for confounding an effect of differential maternal investment with a genetic effect of male attractiveness (Burley 1986, 1988; Gil et al. 1999; Cunningham and Russell 2000; Kolm 2001). Larval offspring were allowed to develop in enclosures in the pond from which their parents had been collected. I gauged offspring performance in terms of survival through the larval stage, length of larval period, and mass at metamorphosis. Size at metamorphosis and length of larval period are important fitness correlates in amphibians, through their influence on future growth, survival, and reproductive success (e.g., Smith 1987; Semlitsch et al. 1988; Berven 1990; Scott 1994).

MATERIALS AND METHODS

Selection of Males

All frogs were collected from a large natural population at the Baskett Wildlife Area, Boone County, Missouri. Between 24 April and 13 May 1998, I collected 24 male *H. versicolor*. Males were collected as 12 sets of two individuals calling simultaneously within two meters of one another. One male in each set was exhibiting calls of audibly longer duration than the other (hereafter long-call and short-call males, respectively). Males were collected in this manner because chorus environment, particularly chorus density, can influence calling effort and call duration (Wells and Taigen 1986). Thus, males' calls must be assessed in the same social context to be validly compared. Samples of each male's calls (approximately 25 calls per male) were recorded in the field with a Sony (Tokyo, Japan) Walkman professional cassette recorder (WM-D6C) and an Audio-Technica (Tokyo, Japan) telescopic microphone (ATR-55). All recordings were made between approximately one hour after sunset and midnight, when chorus activity was at its peak. After recording calls in the field, males were brought back to the lab and body mass was measured to the nearest 0.1 g. I analyzed recorded calls for pulse number, call duration, and duty cycle with a Kay (Lincoln Park, NJ) DSP 5500 Sona-Graph and custom-designed software (G. Klump, D. Polete, and W. Cable; at gerhardth@missouri.edu). Pulse number is a temperature-independent measure of the length of a call, and call duration (measured in seconds) is the product of pulse number and pulse rate, which increases with temperature (Gayou 1984). Duty cycle, a measure of calling effort, is the ratio of call duration to the total duration of the call plus the following intercall interval. Duty cycle reflects the aerobic cost of calling in gray tree frogs (Taigen and Wells 1985; Wells and Taigen 1986; McLister 2001), whereas call duration (and pulse number) may reflect a separate cost of calling (Wells and Taigen 1986), perhaps in terms of depletion of lipid stores (Grafe 1997). Mean number of pulses per call, mean call duration, and mean duty cycle differed between males selected as exhibiting long versus short calls (Table 1). Mean pulse number for males recorded giving short calls was near the mean pulse number reported for this population in 1987 (Gerhardt et al. 1996), while mean pulse number for long call males was more than two standard deviations above the 1987 population average (Gerhardt et al. 1996). This comparison is not perfect, however, because males vary pulse number with chorus density (Wells and Taigen 1986; Schwartz et al. 2002): males in the current study were recorded in dense choruses (leading to higher pulse number),

whereas in 1987 males were recorded at varying chorus densities (Gerhardt et al. 1996).

Artificial Crosses

I collected 10 female *H. versicolor* on 16 May 1998 and two additional females on 17 May 1998; all females were collected in amplexus from the same population as the long- and short-call males. These females were used in a series of artificial crosses with the 12 sets of long- and short-call males. Because artificial crosses in *H. versicolor* must be performed on the night females are collected, the offspring of the first 10 females (maternal half-sibships 1–10) were one day older than the offspring of the other two females (maternal half-sibships 11 and 12). Each female was artificially crossed with a different set of two males (i.e., one long- and one short-call male that had been calling within 2 m of each other). Thus, within each maternal half-sibship, one full-sibship was sired by a male with calls of longer duration than the male that sired the other full-sibship. I made sperm suspensions for each male by double pithing the male, then crushing both testes in pond water in a petri dish. Ova from each female were deposited into the sperm suspensions of the two males. To avoid confounding order of ovulation with an effect of paternity, I placed a few ova at a time into each sperm suspension, alternating between the two (Semlitsch et al. 1996, 1997). I thus generated 12 maternal half-sibships, for a total of 24 families. After 12 h, embryos were transferred to larger containers.

Field Experiment

I tested for effects of maternal half-sibship, father's call duration, and density of tadpoles within field enclosures using a three-way fully factorial design. The 24 full-sibships represented 12 individual mothers, 24 fathers, and two levels of call duration. Tadpoles from each of these 24 families were reared in field enclosures at low and high densities, for a total of 48 treatments. I randomly assigned treatments to enclosures within three randomized blocks. Each block consisted of two adjacent rows of enclosures running parallel to the edge of the pond. The three blocks were positioned in three areas of the pond from which the parent frogs had been collected. On 29 May 1998, I introduced tadpoles from the artificial crosses into the enclosures. I haphazardly selected 60 tadpoles from each family for inclusion in the experiment. Because of insufficient numbers of tadpoles, there was no low-density enclosure for short-call family 8 in block 3. Thus, the experiment included 143 independent experimental units (enclosures) and 1435 tadpoles.

Field enclosures were cylindrical frames (49.5 cm high, 16.5 cm diameter) covered with fine mesh. Open-ended cylinders were shaped from plastic hardware cloth (2.5 cm × 2.5 cm mesh), secured with plastic cable ties. A mosquito net (1 mm × 1.5 mm mesh) sheath covered each cylinder and extended approximately 20 cm above the cylinder. Enclosures were held in position in the pond with wooden stakes. To each stake I secured four enclosures, using plastic cable ties inserted through slits cut in the seam of the mosquito net sheath. A clothespin suspended with wire from the wooden stake held the top of each mosquito net sheath closed,

thereby excluding predators and preventing the escape of newly metamorphosed frogs. The distance of enclosures from the edge of the pond was adjusted as necessary to maintain water level constant at approximately 47 cm. At this height, each enclosure contained approximately 10 L of water.

I used two densities to provide two distinct environments, characterized by different levels of competition, because intraspecific competition can have strong effects on tadpole populations under natural conditions (e.g., Brockelman 1969; Wilbur 1977; Smith 1983; Skelly 1995). Low density consisted of five tadpoles per 10-L enclosure, whereas high density consisted of 15 tadpoles per 10-L enclosure. The low density used in this experiment is within the range of natural densities typically observed for larval hylids (Morin 1983; Smith 1983). The high density in this experiment is higher than most reported natural densities for hylid larvae (Morin 1983; Smith 1983), although even higher densities of small gray tree frog (*H. chrysoscelis*) larvae have been reported (Petranka 1989). Although the conditions in the enclosures were natural with respect to temperature regime, food sources, and potential pathogens, restricting larvae to enclosures does not perfectly mimic natural conditions because predators are excluded, tadpole movement may be limited, and food availability may be altered. In particular, the pond used in this experiment naturally contains a diversity of predators (including dragonfly naiads [Aeschnidae], giant water bugs [Belostomatidae], newts [Notophthalmus], and salamander larvae [Ambystomatidae]; pers. obs.), which should reduce tadpole densities and thereby reduce levels of competition (e.g., Morin 1983, 1987; Wilbur and Fauth 1990). Hence, the low-density treatment used in this experiment may be more representative of conditions that tadpoles in this population would have encountered naturally.

To assess offspring quality, I used three response variables that are important determinants of fitness in anurans (e.g., Smith 1987; Berven 1990; Goater 1994): larval period, mass at metamorphosis, and survival to metamorphosis. Metamorphs naturally crawled out of the water when their tails were about two-thirds resorbed (stage 44; Gosner 1960). Enclosures were checked daily for metamorphs, which were collected and transported back to the laboratory in plastic containers. Larval period was defined as the number of days from the beginning of the experiment (stage 25) until the metamorph was collected. Metamorphs were held in the laboratory until tail resorption was complete (stage 46, 2 to 3 days), at which time mass at metamorphosis was measured to the nearest 0.1 mg after blotting with paper towels to remove excess water. Because the enclosure, rather than the individual, was the experimental unit, I calculated mean larval period and mean mass at metamorphosis for each enclosure. I calculated survival to metamorphosis for each enclosure as the proportion of individuals that survived to be collected upon crawling out of the water. The experiment ended when all tadpoles had either metamorphosed or died.

Statistical Analyses

I performed mixed-model analyses of covariance (ANCOVAs) for larval period and mass at metamorphosis. Using ANCOVA allowed me to compare the effects of father's call

duration while accounting for variation among maternal half-sibships, density treatments, or spatial blocks. Number surviving was included as a covariate in analyses of larval period and mass at metamorphosis because these response variables can depend on the realized density within enclosures. To account for correlations between larval period and mass at metamorphosis, each was used as a covariate in analyses of the other, such that larval period was corrected for mass at metamorphosis and vice versa. To allow for different relationships between the covariates and the response variable at each density, covariates were included in the model as their interaction with density. Larval period and mass at metamorphosis were log transformed (Sokal and Rohlf 1995), which improved normality and equality of error variances.

I tested for main effects of density, father's call duration (call), maternal half-sibship (half-sibship), and spatial block (block), as well as for interactions of density with call, half-sibship, and block, and of half-sibship with call and with block. Three-way interactions of call \times half-sibship \times density and half-sibship \times block \times density were also included in the model. In preliminary analyses, there were no significant interactions of call with block or of call \times block \times half-sibship or call \times block \times density, so these terms were excluded from the model. I was unable to test for the four-way interaction (call \times half-sibship \times density \times block) because there was no replication of combinations of call \times half-sibship \times density within blocks.

Density, block, and father's call duration were considered fixed effects. Maternal half-sibship was considered a random effect, representing the 12 maternal half-sibships and thereby encompassing effects of the 12 sets of long- and short-call males and the 12 mothers, which were regarded as a random sample of the population of breeding females. *F*-tests were conducted with the RANDOM statement in PROC GLM, using appropriate denominator mean squares (MS) for the unbalanced design (SAS Institute 1990). For the main effects of density, block, and call, the denominators were approximately MS(half-sibship \times density), MS(half-sibship \times block) and MS(call \times half-sibship), respectively. For the main effect of half-sibship, the denominator was a linear combination of the mean squares of all interaction terms including half-sibship. For the block \times density and call \times density interactions, the denominators were approximately MS(half-sibship \times block \times density) and MS(call \times half-sibship \times density), respectively. For the call \times half-sibship and half-sibship \times block interactions, the denominators were exactly MS(call \times half-sibship \times density) and MS(half-sibship \times block \times density), respectively. Finally, for the half-sibship \times density interaction, the denominator was a linear combination of the mean squares of the three-way interactions and the error.

For mass at metamorphosis and larval period, I followed the analyses of covariance (combining both densities) with separate analyses of covariance for each density treatment, in order to examine the effects of father's call duration and other factors in the model within each density. These models were analogous to those described above, including the same covariates and all of the main effects and interactions except those involving density. *F*-tests were conducted with the RANDOM statement in PROC GLM (SAS Institute 1990). For the main effects of call and block, the denominator was

approximately MS(call \times half-sibship) and MS(half-sibship \times block), respectively. For the main effects of half-sibship, the denominator was a linear combination of MS(call \times half-sibship), MS(half-sibship \times block), and MS(error).

I analyzed survival to metamorphosis using a binomial error structure because the data—proportion surviving from each enclosure—were binomially rather than normally distributed. This analysis was conducted as a generalized linear mixed model with a binomial error distribution and a logit link function, using the GLIMMIX macro in SAS (Littell et al. 1996). The model included the same fixed and random effects and interactions as the ANCOVA models for larval period and mass at metamorphosis, but included no covariates. Fixed effects (density, block, block \times density, call, and call \times density) were tested with Type-III *F*-tests, using denominator degrees of freedom calculated with the DDFM=Satterthwaite option (Littell et al. 1996). Each random effect (half-sibship, half-sibship \times density, call \times half-sibship, call \times half-sibship \times density, half-sibship \times block, and half-sibship \times block \times density) was tested with a likelihood-ratio χ^2 test by comparing the difference in scaled deviance between the full model and a model without the random effect against a χ^2 distribution with one degree of freedom (for the one parameter dropped from the model; Littell et al. 1996).

The low-density enclosure for short-call family 1 in block 1 was excluded from analyses because the mesh sheath developed a large hole through which tadpoles could escape and large predators could invade; no metamorphs were collected from this enclosure. No individuals metamorphosed from two adjacent enclosures in block 1 (low-density short-call family 8 and high-density long-call family 11), so these two outliers were also excluded from analyses. Including these outliers did not qualitatively change the results of the analysis of survival.

RESULTS

Father's call duration affected offspring larval performance, but this effect depended on the environmental conditions to which offspring were exposed. Mass at metamorphosis—corrected for larval period and survival within each density—was significantly affected by the interaction of father's call duration with density (Table 2). In the low-density treatment, mass at metamorphosis was significantly greater for offspring of males with long calls (hereafter, LC offspring) than for offspring of males with short calls (hereafter, SC offspring; Table 3; Fig. 1). In the high-density treatment, however, LC and SC offspring did not differ in mass at metamorphosis (Table 3; Fig. 1). Unlike mass at metamorphosis, the effect of father's call duration on offspring larval period did not depend on the density at which offspring were reared (no call \times density interaction; Table 2). LC offspring tended to metamorphose later than SC offspring, although this main effect of father's call duration was marginally nonsignificant (Table 2; Fig. 1). At both densities, LC offspring metamorphosed later (marginally nonsignificant) than SC offspring (Table 4; Fig. 1). Sensitivity analyses, conducted by sequentially dropping maternal half-sibships from the analyses, verified that the effects of call duration on mass at metamor-

TABLE 2. Mixed-model analyses of covariance for offspring mass at metamorphosis and larval period.

Response variable Source	df	MS*	F	P
Mass at metamorphosis				
Survival × density	2	0.274	2.13	0.1318
Larval period × density	2	1.105	8.60	0.0008
Density	1	0.625	4.86	0.0333
Block	2	0.992	2.96	0.0633
Block × density	2	0.012	0.07	0.9362
Call	1	1.031	3.42	0.0885
Call × density	1	0.286	5.04	0.0362
Half-sibship	11	0.659	1.63	0.2180
Half-sibship × density	11	0.162	1.17	0.4254
Call × half-sibship	11	0.325	6.93	0.0016
Call × half-sibship × density	11	0.047	0.36	0.9623
Half-sibship × block	22	0.193	0.86	0.6403
Half-sibship × block × density	22	0.225	1.75	0.0603
Error	40	0.129		
Larval period				
Survival × density	2	0.091	0.84	0.4373
Mass at metamorphosis × density	2	0.955	8.89	0.0006
Density	1	0.642	5.96	0.0191
Block	2	3.576	11.10	0.0004
Block × density	2	1.126	5.78	0.0090
Call	1	1.442	4.43	0.0594
Call × density	1	0.011	0.10	0.7552
Half-sibship	11	0.971	1.69	0.1676
Half-sibship × density	11	0.231	1.19	0.3795
Call × half-sibship	11	0.320	3.03	0.0396
Call × half-sibship × density	11	0.106	0.98	0.4777
Half-sibship × block	22	0.339	1.68	0.1152
Half-sibship × block × density	22	0.202	1.88	0.0411
Error	40	0.108		

* Type-III mean squares, multiplied by 100.

phosis and larval period were not attributable to deviations within a single maternal half-sibship (results not shown). Survival was unaffected by father’s call duration (Table 5).

Additional genetic effects on larval performance were revealed by significant interactions of father’s call duration with maternal half-sibship. Call × half-sibship interactions were a significant source of variation in mass at metamorphosis and larval period (Table 2). In particular, the call × half-sibship interactions affected mass at metamorphosis at high density (Table 3; Fig. 2) but not at low density (Table 3) and larval period at low density (Table 4; Fig. 2), but not at high density (Table 4). These interactions of call duration with maternal half-sibship indicate that the relative performance of LC versus SC offspring varied among maternal

half-sibships, with LC offspring outperforming SC offspring in some maternal half-sibships and vice versa in others. The call × half-sibship interaction, therefore, provides evidence that some of the genetic variation in larval performance was not predictable based on father’s call duration. This variation may represent genetic variation among fathers that was unrelated to call duration, variation in the genetic compatibility of individual females with long- and short-call males, or variation in the genetic compatibility of individual females and males, regardless of call duration. I cannot distinguish between these alternatives because each female was mated with only one representative of each call type, and each male was crossed with only one female.

Environmental variation between densities and among spa-

TABLE 3. Separate mixed-model analyses of covariance for offspring mass at metamorphosis at low density and high density.

Source	Low density				High density			
	df	MS*	F	P	df	MS*	F	P
Survival	1	0.402	1.92	0.1815	1	0.147	2.62	0.1203
Mass at metamorphosis	1	1.706	8.18	0.0100	1	0.504	9.01	0.0068
Block	2	0.277	0.93	0.4032	2	0.239	3.29	0.0491
Call	1	1.109	6.09	0.0244	1	0.126	0.71	0.4148
Half-sibship	11	0.346	1.15	0.4167	11	0.432	2.05	0.1103
Call × half-sibship	11	0.176	0.84	0.6038	11	0.195	3.48	0.0068
Half-sibship × block	22	0.342	1.64	0.1398	22	0.081	1.45	0.1981
Error	19	0.209			21	0.056		

* Type-III mean squares, multiplied by 100.

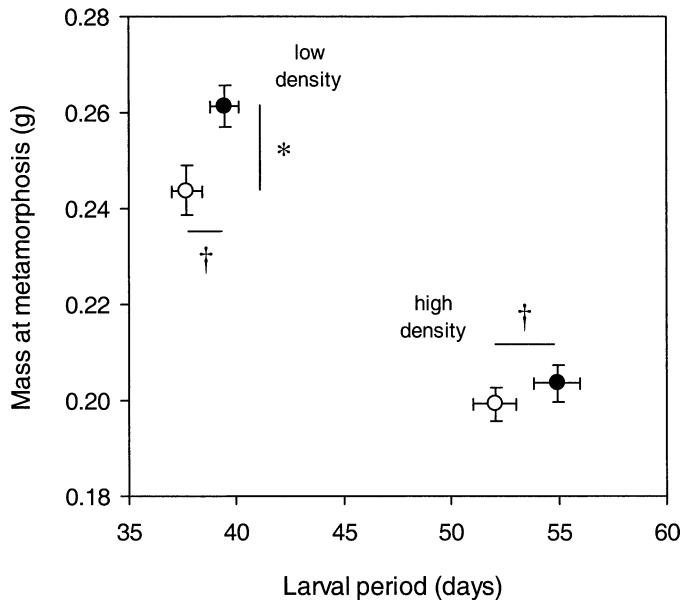


FIG. 1. Bivariate reaction norm showing least squares mean mass at metamorphosis and least squares mean larval period for LC offspring (filled symbols) and SC offspring (open symbols) under low- and high-density conditions. Error bars represent ± 1 standard error. Asterisk indicates $P < 0.05$, dagger indicates $P < 0.10$.

tial blocks also affected larval performance. Offspring reared under low-density conditions metamorphosed both larger and earlier than did offspring reared under high-density conditions (Table 2; Fig. 1). Larval period and mass at metamorphosis also varied among spatial blocks (Table 2), although the effect was marginally nonsignificant for mass at metamorphosis. The three spatial blocks were positioned in areas of the pond that received direct sunlight in differing amounts and at different times during the day, possibly affecting water temperatures, which can influence development rates in larval amphibians (Smith-Gill and Berven 1979; Leips and Travis 1994; Beachy 1995). Density interacted with spatial block to affect larval period (Table 2), further evidence of sensitivity of development rate to environmental differences. Variation among block \times density combinations also influenced the relative performance of maternal half-siblings (half-sibship \times block \times density interactions, marginally nonsignificant for mass at metamorphosis; Table 2), suggesting variation in the performance of genotypes among environments or an interaction of nongenetic maternal effects (e.g., egg size) with

environmental conditions. Survival to metamorphosis appears to have been affected by block and by the interaction of density with father's call duration and half-sibship (Table 5). These effects should be interpreted cautiously however, as the validity of inference statistics for generalized linear mixed models has not been well tested (Littell et al. 1996).

DISCUSSION

Under realistic natural conditions, offspring of gray tree frog males with a trait preferred by females—long call duration—realized an advantage over their half-siblings sired by males with shorter calls. At low density, LC offspring were larger at metamorphosis, for a given larval period, than their SC half-siblings. Large size at metamorphosis is generally indicative of enhanced future fitness in anurans: size at metamorphosis has been shown to be positively correlated with juvenile survivorship (Berven and Gill 1983; Berven 1990; Goater 1994; Beck and Congdon 1999; Morey and Reznick 2001; Altwegg 2002) and age at reproductive maturity (Smith 1987; Berven 1990), as well as with size at reproductive maturity (Clarke 1974; Berven and Gill 1983; Smith 1987; Berven 1990), which is predictive of female fecundity (Berven 1990; Ritke et al. 1990). The difference between LC and SC offspring in size at metamorphosis cannot be attributed to differences in maternal genetics, maternal investment, or environmental factors and should, therefore, be a consequence of genetic differences between the males categorized as long-calling and those categorized as short-calling. Previous laboratory experiments also revealed genetic differences between offspring of long- and short-calling males (Welch et al. 1998; Doty and Welch 2001). In male gray tree frogs, long calls—a trait preferred by females—thus appear to indicate heritable genetic quality that can benefit offspring under realistic natural conditions. This fitness benefit of mating with a long-calling male should, in turn, exert selection on the preference of females for long calls.

Although mating with a long-calling male may lead to genetic benefits under some natural conditions, the genes signaled by long calls are not necessarily beneficial to offspring in all environments. In the high-density enclosures, LC and SC offspring metamorphosed at similar size, for a given larval period. The difference between the two densities in the relative size at metamorphosis of LC and SC offspring suggests that the potential fitness benefits of mating with a long-calling male will only be accrued when offspring de-

TABLE 4. Separate mixed-model analyses of covariance for offspring larval period at low density and high density.

Source	Low density				High density			
	df	MS*	F	P	df	MS*	F	P
Survival	1	0.089	1.90	0.1841	1	0.093	0.57	0.4581
Mass at metamorphosis	1	0.432	9.25	0.0067	1	1.478	9.10	0.0066
Block	2	0.462	7.65	0.0024	2	4.205	9.50	0.0010
Call	1	0.550	3.45	0.0888	1	0.939	3.82	0.0784
Half-sibship	11	0.292	1.57	0.2264	11	0.866	1.65	0.1620
Call \times half-sibship	11	0.169	3.62	0.0068	11	0.242	1.49	0.2092
Half-sibship \times block	22	0.062	1.33	0.2668	22	0.470	2.89	0.0090
Error	19	0.047			21	0.163		

* Type-III mean squares, multiplied by 100.

TABLE 5. Generalized linear mixed model analysis of proportion of offspring surviving. For fixed effects, numerator and denominator degrees of freedom, Type-III *F*-statistics, and *P*-values are reported. For random effects, parameter estimates and standard errors, the change in scaled deviance between the full model and a model without the random effect of interest, and *P*-values are reported.

Fixed effect	Numerator df	Denominator df	Type-III <i>F</i>	<i>P</i>
Density	1	29.8	0.60	0.4434
Block	2	38.2	3.44	0.0422
Block × density	2	35.6	1.02	0.3726
Call	1	17.2	0.03	0.8653
Call × density	1	22.1	0.13	0.7250
Random effect		Parameter estimate (SE)	Δ in scaled deviance	<i>P</i>
Half-sibship		0	0	1.0
Half-sibship × density		0	0	1.0
Call × half-sibship		0.0435 (0.1629)	0.21	0.6443
Call × half-sibship × density		0.2174 (0.2037)	4.21	0.0403
Half-sibship × block		0.1924 (0.1666)	1.39	0.2385
Half-sibship × block × density		0.1217 (0.2033)	3.08	0.0792

velop under certain conditions in the larval environment, a type of genotype-by-environment interaction. Indeed, the significant interaction of larval density with father's call duration is evidence of a genotype-by-environment interaction affecting mass at metamorphosis.

Further support for a genotype-by-environment interaction affecting the fitness of offspring sired by LC and SC males comes from the marginally nonsignificant main effect of father's call duration on larval period. At high density, when LC offspring are not at a size advantage, their later metamorphosis may translate into somewhat reduced fitness. Later metamorphosis may diminish fitness in anurans by decreasing juvenile survivorship (Berven and Gill 1983) or by delaying reproductive maturity (Smith 1987). Hence, if anything, at high density, LC offspring are expected to be at a disadvantage relative to their SC half-siblings. For LC offspring at low density, however, any cost associated with slightly later metamorphosis is likely to be outweighed by the significant benefit of larger size at metamorphosis. Accordingly, the tendency of some anuran larvae to delay metamorphosis in order to attain larger size at metamorphosis (e.g., Alford and Harris 1988; Laurila and Kujasalo 1999; Morey and Reznick 2000; Kiesecker et al. 2002) suggests that large size may be more valuable than early metamorphosis when conditions in the larval environment are favorable for growth and survival (Wilbur and Collins 1973; Werner 1986). Thus, the present data suggest that the genetic consequences of mating with a long-calling male depend on the environment experienced by the offspring. Such context-dependent benefits of female mating preferences can have important implications for sexual selection, as discussed below.

While LC offspring benefited in only one experimental environment in the current study, in previous experiments, offspring of long-call males benefited under laboratory conditions of both high and low food (Welch et al. 1998). The environmental conditions provided in the field and in the laboratory are not directly comparable, however. The relatively small size of metamorphs from the present experiment, even at low density (Table 6), suggests that intraspecific competition, or other density-dependent factors such as disease or parasitism, was fairly intense in the low-density enclosures and extremely intense in the high-density enclosures. The

low-density treatment is probably more representative of conditions that tadpoles in this experiment would have encountered naturally, because predators naturally occurring in the natal pond are expected to reduce tadpole densities (e.g., Morin 1983, 1987). Hence, a benefit of mating with long-call males may be realistic in this environment and the observed female preference for long calls may be adaptive in this population.

Genetic variation that was not related to father's call duration also predicted some of the variation in larval performance. For larval period, particularly in the low-density treatment, and for mass at metamorphosis, particularly in the high-density treatment, there was a significant interaction of call duration with maternal half-sibship. This interaction may reflect either heritable variation among males that is not aligned with call duration or variation in the genetic compatibility of individual females with the long- and short-call males with which they were mated. Genetic compatibility has been suggested as a basis for mate choice in some species (e.g., Brown 1997; Johnsen et al. 2000; Tregenza and Wedell 2000; Wedekind et al. 2001). If genes indicated by long calls are more compatible with the genetic contributions of certain females, then the genetic consequences of mating with a long-call male are predicted to vary among females. Within populations, female gray tree frogs vary in the strength with which they prefer long calls (Gerhardt et al. 2000), and the strength of a female's preference for long calls could reflect the degree to which she can benefit by selecting a mate with long—rather than short—calls.

The most interesting finding of this study may be that the benefits of mating with a preferred (long-calling) male can depend on the environmental conditions experienced by the larval offspring. A similar genotype-by-environment interaction has been found in wax moths, in which the relationship between father's attractiveness and offspring performance varied depending on the environment experienced by the offspring (Jia and Greenfield 1997). And in collared flycatchers, the relationship between a male display trait and fledgling condition differed between two years, possibly because of differences in growth conditions between years (Sheldon 2000).

One implication of such genotype-by-environment inter-

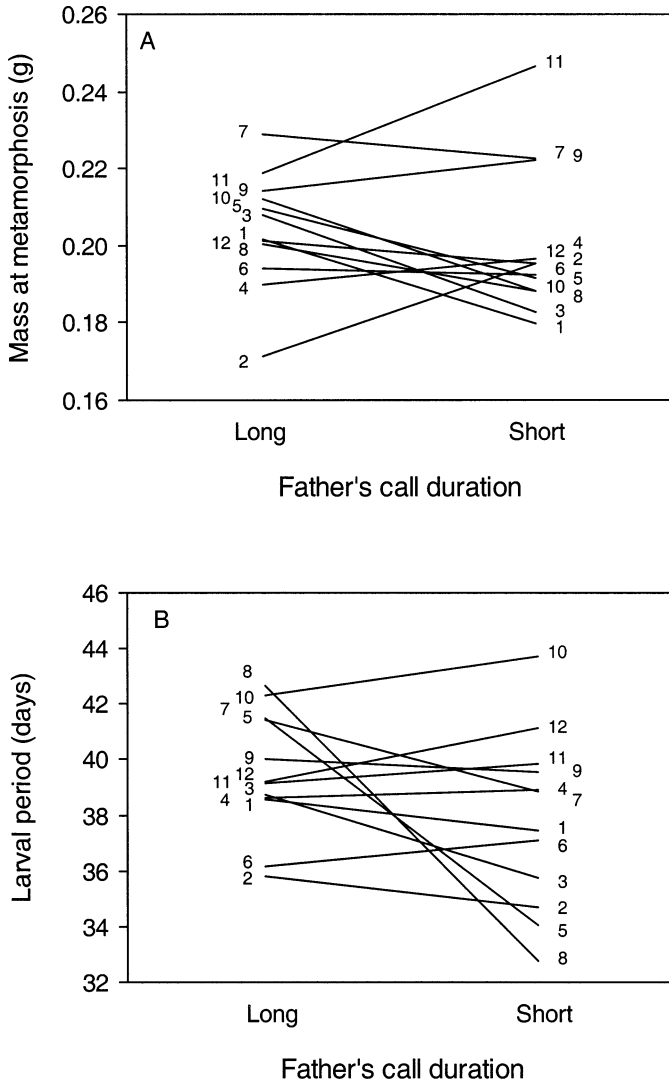


FIG. 2. Reaction norms showing larval performance for 12 maternal half-sibships sired by males with long and short calls. (A) Least-squares mean mass at metamorphosis, in high-density enclosures, was higher for LC offspring in eight half-sibships (1, 3, 5, 6, 7, 8, 10, 12) and for SC offspring in the other four half-sibships (2, 4, 9, 11). (B) Least-squares mean larval period, in low-density enclosures, was shorter for LC offspring in five half-sibships (4, 6, 10, 11, 12) and for SC offspring in the other seven half-sibships (1, 2, 3, 5, 7, 8, 9).

actions in the consequences of mating with a preferred male is that a static mating preference may not be adaptive for females in variable environments. If genes associated with an indicator trait are beneficial to offspring only in certain environments, selection on mating preferences will depend on the environment that offspring encounter. Female gray tree frogs choosing mates with long calls should realize a genetic benefit if the offspring develop under moderate intraspecific competition, but may not realize a benefit under more crowded conditions. Such variation in the genetic consequences of a mating preference could weaken selection on a female preference. Further, variation among environments in the fitness of offspring produced by males with preferred displays suggests that natural selection on male displays—

TABLE 6. Mean mass at metamorphosis for gray tree frogs in the present study and three previous studies.

Study	Treatment	Mass at metamorphosis
Present experiment	Low density	0.255 g
	High density	0.202 g
Laboratory experiment (Welch et al. 1998)	High food	0.253 g
	Low food	0.340 g
Field experiment (J. D. Krenz, unpubl. data)		0.325 g
Observational field study (Ritke et al. 1990)		0.330 g

acting via offspring fitness—can vary as a function of offspring environment. Thus, spatial or temporal variation in the relationship between male displays and offspring fitness may contribute to the maintenance of genetic variation in both male displays and female preferences.

If there are detectable cues to the environmental conditions that offspring will encounter, however, selection may favor plasticity in mating preferences (Qvarnström 2001). Adaptive plasticity in mate choice has been found in soil mites, in which mating preferences shift with diet composition, allowing females to equip offspring with genes for efficient use of the available prey resource (Lesna and Sabelis 1999); and in collared flycatchers, in which a female preference is expressed more strongly late in the breeding season, when the preferred trait is positively correlated with female reproductive success (Qvarnström et al. 2000). Differences in the strength or direction of mating preferences expressed in different environments may weaken selection on any one male phenotype (Pfennig and Tinsley 2002; but see Hingle et al. 2001).

Selection may also favor selectivity among oviposition sites when there are detectable cues to the environmental conditions that offspring will encounter. Oviposition site selectivity allows females of various taxa to provide favorable developmental environments for their offspring (Rauscher 1983; Bernardo 1996; Resetarits 1996). In several frog species, including gray tree frogs, females avoid ovipositing in sites with conspecific eggs or larvae (Banks and Beebee 1987; Resetarits and Wilbur 1989; Marsh et al. 2000), thereby reducing the level of intraspecific competition experienced by their larval offspring. With oviposition site selectivity to avoid highly competitive larval environments, the preference for long calls in gray tree frogs may be under consistent selection, as offspring are unlikely to encounter the crowded conditions in which the genes signaled by long calls are not adaptive. By allowing females some control over the developmental environment experienced by their offspring, oviposition site selectivity may allow a static mating preference to be adaptive in a variable environment, resulting in strong selection on both the female preference and the male display phenotype.

Alternatively, the preferred male phenotype may indicate different aspects of quality in different environments or individuals. Although the genes indicated by long calls among males in the present study were not beneficial to offspring in all environments, I cannot conclude that long calls indicate the same genes in all individuals or environments. Condition-

dependent models of intersexual selection predict that the preferred male phenotype is an indicator of general condition (Williams 1966; Zahavi 1977; Kodric-Brown and Brown 1984; Andersson 1986). Condition, as a composite of many distinct traits and processes, may reflect the contribution of many genes (Rowe and Houle 1996), and these genes may have different effects in different environments (Qvarnström 2001). If the genetic basis of condition differs across environments—a genotype-by-environment interaction—a single condition-dependent trait can reflect different genes in different environments. Evidence for genotype-by-environment interactions in the expression of condition-dependent traits has been found in collared flycatchers (Qvarnström 1999), wax moths (Jia et al. 2000), stalk-eyed flies (David et al. 2000), and dung beetles (Kotiaho et al. 2001). A genotype-by-environment interaction in condition-dependent trait expression means that the genes inherited by offspring of choosy females will depend on the environment. In such a case, the magnitude (Qvarnström 1999; David et al. 2000; Kotiaho et al. 2001) or direction (Jia et al. 2000) of the genetic consequences of mate choice should depend on the environment in which offspring develop (Qvarnström 2001), and a genotype-by-environment interaction should be detectable in the offspring. This prediction is consistent with the finding that the genetic benefits of mating with an attractive male can depend on the environment encountered by the offspring (in wax moths, Jia and Greenfield 1997; in gray tree frogs, this study; and possibly in collared flycatchers, Sheldon 2000). When a genotype-by-environment interaction affects condition, females that prefer the condition-dependent trait may realize genetic benefits (i.e., enhanced offspring condition) as long as offspring experience an environment similar to that of their father. The strength of selection on the female preference, in this case, should depend on the similarity of the environment encountered by males and their offspring.

Future studies should recognize that the potential for genetic benefits of mate choice can depend on the environmental context experienced by the offspring. When this is the case, environmental variability may affect the action of selection on the female preference and the male display trait. Predicting these effects will require understanding how environmental variation influences the expression of female mating preferences, other female behaviors such as selectivity among environments, and the condition-dependence of male traits, as well as the genetic benefits of mating preferences. Thus, the effects of genotype-by-environment interactions at all of these levels are important to address in future studies. Considering how environmental variation affects the relationships among “good genes,” male trait expression, offspring performance, and female behavior will yield a richer understanding of how sexual selection operates in real populations.

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LITERATURE CITED

- Alatalo, R. V., J. Kotiaho, J. Mappes, and S. Parri. 1998. Mate choice for offspring performance: major benefits or minor costs? *Proc. R. Soc. Lond. B* 265:2297–2301.
- Alford, R. A., and R. N. Harris. 1988. Effects of larval growth history on anuran metamorphosis. *Am. Nat.* 131:91–106.
- Altwegg, R. 2002. Trait-mediated indirect effects and complex life-cycles in two European frogs. *Evol. Ecol. Res.* 4:519–522.
- Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: sexual selection based on viability differences. *Evolution* 40:804–816.
- . 1994. *Sexual selection*. Princeton Univ. Press, Princeton, NJ.
- Banks, B., and T. J. C. Beebe. 1987. Factors influencing breeding site choice by the pioneering amphibian *Bufo calamita*. *Holarct. Ecol.* 10:14–21.
- Barber, I., S. A. Arnott, V. A. Braithwaite, J. Andrew, and F. A. Huntingford. 2001. Indirect fitness consequences of mate choice in sticklebacks: offspring of brighter males grow slowly but resist parasitic infections. *Proc. R. Soc. Lond. B* 268:71–76.
- Beachy, C. K. 1995. Effects of larval growth history on metamorphosis in a stream-dwelling salamander (*Desmognathus ochrophaeus*). *J. Herpetol.* 29:375–382.
- Beck, C. W., and J. D. Congdon. 1999. Effects of individual variation in age and size at metamorphosis on growth and survivorship of southern toad (*Bufo terrestris*) metamorphs. *Can. J. Zool.* 77:944–951.
- Bernardo, J. 1996. Maternal effects in animal ecology. *Am. Zool.* 36:83–105.
- Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology* 71:1599–1608.
- Berven, K. A., and D. E. Gill. 1983. Interpreting geographic variation in life-history traits. *Am. Zool.* 23:85–97.
- Blanckenhorn, W. U., T. Reusch, and C. Mühlhäuser. 1998. Fluctuating asymmetry, body size and sexual selection in the dung fly *Sepsis cynipsea*—testing the good genes assumptions and predictions. *J. Evol. Biol.* 11:735–753.
- Brockelman, W. Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. *Ecology* 50:632–644.
- Brown, J. L. 1997. A theory of mate choice based on heterozygosity. *Behav. Ecol.* 8:60–65.
- Burley, N. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* 127:415–445.
- . 1988. The differential-allocation hypothesis: an experimental test. *Am. Nat.* 132:611–628.
- Clarke, R. D. 1974. Postmetamorphic growth rates in a natural population of Fowler's toad, *Bufo woodhousei fowleri*. *Can. J. Zool.* 52:1489–1498.
- Cunningham, E. J. A., and A. F. Russell. 2000. Egg investment is

- influenced by male attractiveness in the mallard. *Nature* 404: 74–77.
- David, P., T. Bjorksten, K. Fowler, and A. Pomiankowski. 2000. Condition-dependent signalling of genetic variation in stalk-eyed flies. *Nature* 406:186–188.
- Doty, G. V., and A. M. Welch. 2001. Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*). *Behav. Ecol. Sociobiol.* 49:150–156.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4th ed. Longman Scientific, Essex, UK.
- Fellers, G. M. 1979. Mate selection in the gray treefrog, *Hyla versicolor*. *Copeia* 1979:286–290.
- Gayou, D. C. 1984. Effects of temperature on the mating call of *Hyla versicolor*. *Copeia* 1984:733–738.
- Gerhardt, H. C. 1991. Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim. Behav.* 42:615–635.
- Gerhardt, H. C., M. L. Dyson, and S. D. Tanner. 1996. Dynamic properties of the advertisement calls of gray tree frogs: patterns of variability and female choice. *Behav. Ecol.* 7:7–18.
- Gerhardt, H. C., S. D. Tanner, C. M. Corrigan, and H. C. Walton. 2000. Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behav. Ecol.* 11:663–669.
- Gil, D., J. Graves, N. Hazon, and A. Wells. 1999. Male attractiveness and differential testosterone investment in zebra finch eggs. *Science* 286:126–128.
- Goater, C. P. 1994. Growth and survival of postmetamorphic toads: interactions among larval history, density, and parasitism. *Ecology* 75:2264–2274.
- Gosner, K. L. 1960. A simplified table for staging anuran larvae and embryos with notes on identification. *Herpetologica* 16: 183–190.
- Grafe, U. 1997. Use of metabolic substrates in the gray treefrog, *Hyla versicolor*: implications for calling behavior. *Copeia* 1997: 356–362.
- Hasselquist, D., S. Bensch, and T. von Schantz. 1996. Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* 381:229–232.
- Hingle, A., K. Fowler, and A. Pomiankowski. 2001. The effect of transient food stress on female mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Proc. R. Soc. Lond. B* 268: 1239–1244.
- Hoikkala, A., J. Aspi, and L. Suvanto. 1998. Male courtship song frequency as an indicator of male quality in an insect species, *Drosophila montana*. *Proc. R. Soc. Lond. B* 265:503–508.
- Iyengar, V. K., and T. Eisner. 1999. Heritability of body mass, a sexually selected trait, in an arctiid moth (*Utetheisa ornatrix*). *Proc. Natl. Acad. Sci. USA* 96:9169–9171.
- Jia, F.-Y., and M. D. Greenfield. 1997. When are good genes good? Variable outcomes of female choice in wax moths. *Proc. R. Soc. Lond. B* 264:1057–1063.
- Jia, F.-Y., M. D. Greenfield, and R. D. Collins. 2000. Genetic variance of sexually selected traits in waxmoths: maintenance by genotype \times environment interaction. *Evolution* 54:953–967.
- Johnsen, A., V. Anderson, C. Sunding, and J. T. Lifjeld. 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. *Nature* 406:296–299.
- Kiesecker, J. M., D. P. Chivers, M. Anderson, and A. R. Blaustein. 2002. Effect of predator diet on life history shifts of red-legged frogs, *Rana aurora*. *J. Chem. Ecol.* 28:1007–1015.
- Klump, G. M., and H. C. Gerhardt. 1987. Use of non-arbitrary acoustic criteria in mate choice by female gray treefrogs. *Nature* 326:286–288.
- Kodric-Brown, A., and J. H. Brown. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *Am. Nat.* 12: 309–323.
- Kolm, N. 2001. Females produce larger eggs for large males in a paternal mouthbrooding fish. *Proc. R. Soc. Lond. B* 268: 2229–2234.
- Kotiaho, J. S., L. W. Simmons, and J. L. Tomkins. 2001. Towards a resolution of the lek paradox. *Nature* 410:684–686.
- Laurila, A., and J. Kujasalo. 1999. Habitat duration, predation risk and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles. *J. Anim. Ecol.* 68:1123–1132.
- Leips, J., and J. Travis. 1994. Metamorphic responses to changing food levels in two species of hylid frogs. *Ecology* 75:1345–1356.
- Lesna, I., and M. W. Sabelis. 1999. Diet-dependent female choice for males with “good genes” in a soil predatory mite. *Nature* 401:581–584.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. *SAS system for mixed models*. SAS Institute, Cary, NC.
- Marsh, D. M., A. S. Rand, and M. J. Ryan. 2000. Effects of inter-pond distance on the breeding ecology of tungara frogs. *Oecologia* 122:505–513.
- McLister, J. D. 2001. Physical factors affecting the cost and efficiency of sound production in the treefrog *Hyla versicolor*. *J. Exp. Biol.* 204:69–80.
- Møller, A. P. 1994. Male ornament size as a reliable cue to enhanced offspring viability in the barn swallow. *Proc. Natl. Acad. Sci. USA* 91:6929–6932.
- Moore, A. J. 1994. Genetic evidence for the “good genes” process of sexual selection. *Behav. Ecol. Sociobiol.* 35:235–241.
- Morey, S., and D. Reznick. 2000. A comparative analysis of plasticity in larval development in three species of spadefoot toads. *Ecology* 81:1736–1749.
- . 2001. Effects of larval density on postmetamorphic spadefoot toads (*Spea hammondi*). *Ecology* 82:510–522.
- Morin, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecol. Monogr.* 53:119–138.
- . 1987. Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. *Ecology* 68:675–683.
- Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits, *Parus major*. *Nature* 362:537–539.
- Petranka, J. W. 1989. Chemical interference competition in tadpoles: does it occur outside laboratory aquaria? *Copeia* 1989: 921–930.
- Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* 371:598–599.
- Pfennig, K. S., and R. C. Tinsley. 2002. Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection. *J. Evol. Biol.* 15:399–406.
- Qvarnström, A. 1999. Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). *Evolution*. 53:1564–1572.
- . 2001. Context-dependent genetic benefits from mate choice. *Trends Ecol. Evol.* 16:5–7.
- Qvarnström, A., T. Pärt, and B. C. Sheldon. 2000. Adaptive plasticity in mate preference linked to differences in reproductive effort. *Nature* 405:344–347.
- Rausher, M. D. 1983. Ecology of host-selection behavior in phytophagous insects. Pp. 223–257 in R. F. Denno and M. S. McClure, eds. *Variable plants and herbivores in natural and managed systems*. Academic Press, New York.
- Resetarits, W. J., Jr., 1996. Oviposition site choice and life history evolution. *Am. Zool.* 36:205–215.
- Resetarits, W. J., Jr., and H. M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* 70:220–228.
- Reynolds, J. D., and M. R. Gross. 1992. Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. *Proc. R. Soc. Lond. B* 250:57–62.
- Ritke, M. E., J. G. Babb, and M. K. Ritke. 1990. Life history of the gray treefrog (*Hyla chrysoscelis*) in western Tennessee. *J. Herpetol.* 24:135–141.
- Roff, D. A. 1997. *Evolutionary quantitative genetics*. Chapman and Hall, New York.
- Rowe, L., and D. Houle. 1996. The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* 263:1415–1421.
- Runkle, L. S., K. D. Wells, C. C. Robb, and S. L. Lance. 1994. Individual, nightly, and seasonal variation in calling behavior of the gray tree frog, *Hyla versicolor*: implications for energy expenditure. *Behav. Ecol.* 5:318–325.
- SAS Institute. 1990. *SAS/STAT user's guide*. Ver. 6. 4th ed. SAS Institute, Cary, NC.
- Schwartz, J. J., B. W. Buchanan, and H. C. Gerhardt. 2001. Female

- mate choice in the gray treefrog (*Hyla versicolor*) in three experimental environments. *Behav. Ecol. Sociobiol.* 49:443–455.
- . 2002. Acoustic interactions among male gray treefrogs, *Hyla versicolor*, in a chorus setting. *Behav. Ecol. Sociobiol.* 53:9–19.
- Scott, D. E. 1994. The effects of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75:1383–1396.
- Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma tadpoideum*. *Ecology* 69:184–192.
- Semlitsch, R. D., S. Schmiedehausen, H. Hotz, and P. Beerli. 1996. Genetic compatibility between sexual and clonal genomes in local populations of the hybridogenetic *Rana esculenta* complex. *Evol. Ecol.* 10:531–543.
- Semlitsch, R. D., H. Hotz, and G.-D. Guex. 1997. Competition among tadpoles of coexisting hemiclones of hybridogenetic *Rana esculenta*: support for the frozen niche variation model. *Evolution* 51:1249–1261.
- Sheldon, B. C. 2000. Environmental dependence of genetic indicator mechanisms. Pp. 195–207 in Y. Espmark, T. Amundsen, and G. Rosenqvist, eds. *Animal signals: signalling and signal design in animal communication*. Tapir Academic Press, Trondheim, Norway.
- Sheldon, B. C., J. Merilä, A. Qvarnström, L. Gustafsson, and H. Ellegren. 1997. Paternal genetic contribution to offspring condition predicted by size of male secondary sexual character. *Proc. R. Soc. Lond. B* 264:297–302.
- Skelly, D. K. 1995. Competition and the distribution of spring peeper larvae. *Oecologia* 103:203–207.
- Smith, D. C. 1983. Factors controlling tadpole populations of the chorus frog (*Pseudacris triseriata*) on Isle Royale, Michigan. *Ecology* 64:501–510.
- . 1987. Adult recruitment in chorus frogs: effects of size and date at metamorphosis. *Ecology* 68:344–350.
- Smith-Gill, S. J., and K. A. Berven. 1979. Predicting amphibian metamorphosis. *Am. Nat.* 113:563–585.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W. H. Freeman and Company, New York.
- Sullivan, B. K., and S. H. Hinshaw. 1992. Female choice and selection on male calling behaviour in the grey treefrog, *Hyla versicolor*. *Anim. Behav.* 44:733–744.
- Taigen, T. L., and K. D. Wells. 1985. Energetics of vocalization by an anuran amphibian *Hyla versicolor*. *J. Comp. Physiol. B* 155:163–170.
- Tregenza T., and N. Wedell. 2000. Genetic compatibility, mate choice and patterns of parentage: invited review. *Mol. Ecol.* 9:1013–1027.
- von Schantz, T., M. Grahm, and G. Göransson. 1994. Intersexual selection and reproductive success in the pheasant *Phasianus colchicus*. *Am. Nat.* 144:510–527.
- Watson, P. J. 1998. Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). *Anim. Behav.* 55:387–403.
- Wedekind, C., R. Müller, and H. Spicher. 2001. Potential genetic benefits of mate selection in whitefish. *J. Evol. Biol.* 14:980–986.
- Welch, A. M., R. D. Semlitsch, and H. C. Gerhardt. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science* 280:1928–1930.
- Wells, K. D., and T. L. Taigen. 1986. The effect of social interactions on calling energetics in the gray treefrog, *Hyla versicolor*. *Behav. Ecol. Sociobiol.* 19:9–18.
- Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. *Am. Nat.* 128:319–341.
- Wilbur, H. M. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. *Ecology* 58:196–200.
- Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. *Science* 182:1305–1314.
- Wilbur, H. M., and J. E. Fauth. 1990. Experimental aquatic food webs: interactions between two predators and two prey. *Am. Nat.* 135:176–204.
- Williams, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton Univ. Press, Princeton, NJ.
- Zahavi, A. 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.* 53:205–214.
- . 1977. The cost of honesty (further remarks on the handicap principle). *J. Theor. Biol.* 67:603–606.

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