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# Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*)

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**Abstract** Indicator or "good genes" models of sexual selection predict that mating preferences allow females to choose mates that are genetically superior. Female gray tree frogs (*Hyla versicolor*) prefer male advertisement calls of long call duration, which can be indicators of enhanced offspring growth performance. We tested the effects of father's call duration and the presence of a caged predator (dragonfly naiad) on tadpole activity and growth in a factorial experiment, controlling for maternal and environmental effects. The effect of food availability (a repeated measure) on tadpole activity was also examined. Tadpoles responded to predator presence and to high food availability by decreasing activity and feeding. Tadpoles exposed to a caged predator were smaller after 14 days than those exposed to an empty cage, suggesting that spending less time feeding carries the cost of reduced growth. Offspring of males with long versus short calls responded similarly to the presence of a predator. Nonetheless, offspring of long-calling males spent more time feeding than did offspring of short-calling males, except when a predator was present but no food was available. Increased time spent feeding may contribute to enhanced offspring growth and, therefore, to the indirect benefit that a female may realize by selecting a mate with long calls. However, because the behavioral differences depended on the environment, and because the fitness consequences of such behavioral differences should also vary with the environment, the benefit of mating with a long-calling male may depend on the conditions encountered by the offspring.

**Keywords** Activity · Anurans · Growth · Indicator trait · Mate choice

## Introduction

Indicator models of sexual selection by female choice predict that female mating preferences are based on some aspect of male behavior or morphology that indicates male quality (Zahavi 1975). The benefits of mating with a high-quality male can therefore act as selective factors in the evolution or maintenance of the female preference. Indicator traits can include behavioral displays (Borgia 1985; Parri et al. 1997), advertisement calls (Houtman 1992; Ritchie et al. 1995), bright coloration (Nicoletto 1993; Norris 1993), or other morphological features (von Schantz et al. 1989; Reynolds and Gross 1992). Although preferences for indicator traits can be favored by direct benefits to a female from her mate (e.g., food, protection, parental care, enhanced fertilization success), preferences can also be influenced by indirect benefits, which are genetic benefits realized by a choosy female's offspring (Moore 1994). The "good genes" model of sexual selection predicts that courtship displays signal heritable quality. By choosing males of high genetic quality, choosy females may enhance offspring viability and thereby increase the representation of their genes in future generations. Genetic benefits of mating with preferred males have been found in birds (Norris 1993; Petrie 1994; Sheldon et al. 1997), fish (Reynolds and Gross 1992; Nicoletto 1993), frogs (Mitchell 1990; Welch et al. 1998), and insects (Partridge 1980; Watt et al. 1986).

Good genes selection has been documented by demonstrating a positive statistical relationship between an indicator trait and a measure of offspring quality, such as viability (reviewed by Møller and Alatalo 1999), size (Mitchell 1990; Welch et al. 1998), and resistance to par-

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asites or pathogens (Hillgarth 1990; Potts et al. 1991). Although these studies show that good-genes selection can occur, we have little understanding of how indicator traits and offspring quality may be related functionally or genetically (but see Wilkinson et al. 1998).

We investigated the hypothesis that variation in offspring activity levels contributes to the relationship between an indicator trait and offspring quality in the gray tree frog (*Hyla versicolor*). Female gray tree frogs prefer synthetic calls of longer duration over alternatives of short duration in laboratory playback tests and in semi-natural enclosure experiments (Gerhardt et al. 1996; J.J. Schwartz, unpublished data). Females derive no direct benefits from mate choice because males do not provide resources, protection, or parental care (Fellers 1979), and there is no difference in fertilization success between clutches sired by males with long versus short calls (J.D. Krenz, R.D. Semlitsch, H.C. Gerhardt, unpublished data). In recent laboratory (Welch et al. 1998) and field (Welch 2000) experiments, offspring of males with long calls showed greater larval survival and growth and greater juvenile growth, and metamorphosed earlier or at a larger size than their half-siblings sired by males with short calls. Call duration, therefore, appears to advertise genetic quality in male gray tree frogs.

Tadpole activity levels can influence predator avoidance and growth, both of which can be important components of fitness. Many prey species reduce activity when confronted with visual, chemical, or tactile predator cues (Stauffer and Semlitsch 1993; Laurila et al. 1998). Reduced activity levels can help prey avoid detection by visually orienting predators (e.g., Lawler 1989; Azevedo-Ramos et al. 1992; Chovanec 1992; Skelly 1994). However, this reduction in activity can lead to reduced feeding (Horat and Semlitsch 1994; Anholt and Werner 1995; Koperski 1997; Ryer and Olla 1998), and can thereby inhibit growth (Semlitsch 1987; Skelly and Werner 1990; Peckarsky et al. 1993; Ball and Baker 1996). Activity levels can also be sensitive to the availability of food, with typically higher activity in the absence of food (Horat and Semlitsch 1994; Anholt and Werner 1995). Prey species are predicted to alter behavior to optimize their ability to exploit available food and to avoid predation, resulting in a potential trade-off between foraging and predator avoidance (Scrimgeour and Culp 1994; Anholt and Werner 1995, 1998; Ryer and Olla 1998).

We tested activity, in the presence and absence of a predator and in the presence and absence of food, of tadpoles sired by male gray tree frogs with long versus short calls. Our experiment was designed to address the following questions: (1) Do offspring of males with long calls show stronger predator avoidance responses than offspring of males with short calls? (2) Do the offspring of males with long versus short calls show differences in activity level? (3) Do offspring of males with long calls respond more strongly to food availability than offspring of males with short calls? (4) Do predation risk and parentage affect tadpole growth?

## Methods

### Selection of males

Between 19 May and 4 June 1999, we collected ten male *H. versicolor* from a natural population at the Baskett Wildlife Area, Boone County, Missouri, USA. Males were collected as five sets of two individuals calling simultaneously within 2 m of each other, one giving audibly longer calls than the other (hereafter long-calling and short-calling males, respectively). Males were collected in this manner because chorus density can influence calling effort and call duration (Wells and Taigen 1986), and therefore males' calls must be assessed in the same social context for a valid comparison. Short samples of each male's calls (approximately 25 calls per male) were recorded in the field with a professional cassette recorder (Sony Walkman WM-D6C) and a telescopic microphone (Audio-Technica ATR-55). All recordings were made between 1 h after sunset and midnight, when chorus activity was at its peak. Calls were analyzed for pulse number, call duration, and duty cycle (the proportion of time during which the individual was producing sound; a measure of calling effort) with a Kay DSP 5500 Sona-Graph and custom designed software (G. Klump, D. Polete, W. Cable). Male frogs were weighed to the nearest 0.01 g in the laboratory. Call duration and pulse number differed significantly between males regarded as long- and short-calling, but duty cycle and body mass did not differ (Table 1).

### Artificial crosses

Five gravid female *H. versicolor* were collected on 5 June 1999 from the same population as the males. Artificial crosses were performed later that night in which one female was mated with each set of males (i.e., one long- and one short-calling male that had been collected together). The testes were dissected from each euthanized male and were subsequently crushed in pond water in a petri dish to release the sperm. Small groups of ova were stripped from each female and were deposited into the two sperm suspensions, alternating between males to avoid confounding order of ovulation with effect of paternity. This procedure produced five maternal half-sibships (i.e., one mother, two fathers) for a total of ten full-sibships (i.e., one mother, one father). After 12 h, embryos were transferred to larger plastic containers and were maintained until the beginning of our experiment in a mixture of pond water and charcoal-filtered, UV-sterilized water.

### Experimental design

Tadpoles from each full-sibship were exposed to the presence or absence of a non-lethal predator (caged dragonfly naiad), begin-

**Table 1** Calling performance and body mass (mean±SD) of sires exhibiting long versus short calls. Parameters were compared with two-tailed paired *t*-tests (*df*=4)

| | Pulses per call | Call duration (s) | Duty cycle | Body mass (g) |
|---|---|---|---|---|
| Long-callers (*n*=5) | 22.5±4.3 | 1.03±0.34 | 0.179±0.037 | 7.3±0.6 |
| Short-callers (*n*=5) | 14.0±1.3 | 0.72±0.21 | 0.146±0.050 | 7.5±2.2 |
| Paired *t* | 3.52 | 2.57 | 1.09 | 0.21 |
| *P* | 0.004 | 0.03 | 0.30 | 0.84 |

ning on 22 June 1999. These 20 treatments (i.e., 10 full-sibships×2 predator treatments) were replicated in three randomized blocks for a total of 60 independent experimental units. Each experimental unit was a plastic tub containing three tadpoles from a single full-sibship and either a caged predator or an empty cage. Eighteen tadpoles from each full-sibship were assigned randomly to tubs. We selected tadpoles based on size similarity within each maternal half-sibship (i.e., two full-sibships). Water was changed every 2 days and tadpoles were fed finely ground and freeze-dried Tetra-Min fish flakes. At each feeding, all treatments received the same amount of food, but this amount was gradually increased from 5 to 15 mg per tadpole through the course of the experiment. Tadpoles and dragonflies were maintained in the experimental tubs until 6 July 1999, when tadpoles were individually weighed to the nearest 0.1 mg after blotting off excess water.

Dragonfly naiads (*Anax*) were collected from the same pond as the frogs. Each dragonfly was caged in a plastic cup (approximately 148 ml) with a square of fiberglass screen to provide substrate for the dragonfly; two pieces of screen were secured to the mouth of the cup with a rubber band to prevent the dragonfly eating tadpoles. Every other day, dragonflies were fed a fixed number of *H. versicolor* tadpoles just before behavioral observations. We fed dragonflies six tadpoles on the first day but fewer thereafter because we had a limited number of tadpoles. Dragonflies began eating immediately, and all tadpoles were consumed. Tadpoles respond most strongly to dragonflies that have recently consumed a tadpole, indicating that tadpoles sense a cue released when dragonfly naiads consume and defecate other tadpoles (Laurila et al. 1997, 1998; Leimberger and McCollum 1997).

### Behavioral trials

Each experimental unit was observed on 22, 24, 26, and 28 June 1999. Before each of the four observational periods, the water in the tubs was changed and predators were fed. Tadpoles were fed before the second and fourth observational periods, but were not fed until after the first and third observational periods. Thus, each tub was observed twice with food and twice without food to test the effect of food availability on behavior. Observations began 30 min after water was changed and predators were fed, allowing tadpoles to acclimate and predators to begin feeding.

During each observational period, the 60 tubs were observed sequentially 15 times. The observer recorded activities of the three tadpoles in each tub, for a total of 45 behavioral scores per tub. If a tadpole could not be located (i.e., it was hiding underneath the cup), no score was recorded for that tadpole. Three activities were categorized: feeding (repeated touching of an area with the mouth, coupled with tail undulations), swimming (any other movement), and resting (inactivity). The same observer conducted all behavioral observations and was unaware of the sibship to which tadpoles belonged.

### Statistical analysis

We calculated proportions of time spent swimming, feeding, and resting by the tadpoles in each tub during each observational period. A mixed-model multivariate analysis of variance (MANOVA) on angularly transformed proportions was used to test for main effects of predator presence, father's call duration (call), family identity (family), and food availability, and for interactions of predator with call, predator with food, call with food, and predator with call with food. All interactions with family identity were omitted, a priori, to simplify the model and because these interactions did not address our hypotheses. In all analyses, predator presence, call duration, and food availability were treated as fixed effects, while family identity was treated as a random effect because females were regarded as a random sample of the breeding population. Food availability was included as a repeated measure, nested within time (referring to the four observational periods). Only swimming and feeding were included in the MANOVA because the third response variable (resting) is uniquely defined by the first two. The MANOVA was followed with univariate analyses of variance (ANOVAs) on all three components of activity (swimming, feeding, and resting) to investigate how individual response variables contributed to multivariate effects. To compare behavior of offspring of long- and short-calling males under each of the four experimental conditions (i.e., predator absent, with food; predator absent, without food; predator present, with food; predator present, without food), we conducted *t*-tests of mean proportion of time spent in each activity, for each condition. Because each experimental unit was exposed to each food level twice in our repeated-measures design, *t*-tests were conducted using the mean squares for the experimental unit (tub, nested within father's call duration and family identity) as the error term. All analyses were performed using SAS (1990).

We also tested for main effects of predator presence, father's call duration, and family identity, and for a predator by call interaction on tadpole body mass with a mixed-model univariate ANOVA, using mean body mass of tadpoles in each tub. We were unable to test for effects of food on body mass because each tub of tadpoles was exposed to both food levels in our repeated-measures design. Tadpole body mass was normally distributed (Shapiro-Wilk's test, $P$=0.82) and therefore was not transformed. To investigate the relationship between tadpole activity and growth, we calculated Pearson correlation coefficients ($r_p$) between mean proportions of time spent swimming, feeding, and resting by tadpoles in each tub (averaged over the four observational periods) and mean body mass of the tadpoles in each tub at the end of the experiment. Because tadpoles exposed to different predator treatments differed significantly in mass at the end of the experiment, we calculated separate correlations for each predator treatment.

## Results

### Predator and food effects

Tadpoles responded to the presence of a predator by reducing activity (Tables 2, 3): tadpoles spent less time feeding and swimming and more time resting in the presence of the dragonflies than when no predator was present (Fig. 1). At the end of the experiment, tadpoles exposed to the presence of a predator were smaller than those in the no-predator treatment (predator: 0.2149±0.0735 g, no predator: 0.2763±0.0587 g; $F_{1,52}$=13.43, $P$=0.0006).

**Table 2** Repeated-measures multivariate analysis of variance for tadpole activity based on time spent feeding and swimming. Multivariate effects of predator, call, family, and predator×call were tested using the tub (predator×call×family) sum of squares and cross-products matrix as the error term. Multivariate effects of food, predator×food, call×food and predator×call×food were tested using the food×tub (predator×call×family) sum of squares and cross-products matrix as the error term

| Source | *df* | Wilks' λ | *F* | *P* |
|---|---|---|---|---|
| Predator | 2 | 0.0853 | 273.45 | 0.0001 |
| Call | 2 | 0.7637 | 7.89 | 0.0010 |
| Family | 8 | 0.6756 | 2.76 | 0.0084 |
| Predator×call | 2 | 0.8396 | 4.87 | 0.0116 |
| Food | 2 | 0.3818 | 44.53 | 0.0001 |
| Predator×food | 2 | 0.9321 | 2.00 | 0.1446 |
| Call×food | 2 | 0.9874 | 0.35 | 0.7058 |
| Predator×call×Food | 2 | 0.9635 | 1.04 | 0.3593 |
| Time (food) | 4 | 0.8636 | 4.45 | 0.0017 |

**Table 3** Repeated-measures univariate analyses of variance for time spent feeding, resting, and swimming. *F*-tests for univariate effects of predator, call, family and predator×call were constructed using the tub (predator×call×family) mean square as the denominator. *F*-tests for univariate effects of food, predator×food, call×food and predator×call×food were constructed using the food×tub (predator×call×family) mean square as the denominator

| Source | *df* | Type III MS | *F* | *P* |
|---|---|---|---|---|
| **Feeding** | | | | |
| Predator | 1 | 9.5097 | 476.05 | 0.0001 |
| Call | 1 | 0.2529 | 12.66 | 0.0008 |
| Family | 4 | 0.0650 | 3.26 | 0.0186 |
| Predator×call | 1 | 0.0341 | 1.71 | 0.1970 |
| Tub (predator×call×family) | 52 | 0.0200 | | |
| Food | 1 | 0.4724 | 38.75 | 0.0001 |
| Predator×food | 1 | 0.0489 | 4.00 | 0.0503 |
| Call×food | 1 | 0.0084 | 0.69 | 0.4094 |
| Predator×call×food | 1 | 0.0151 | 1.24 | 0.2712 |
| Food×tub (predator×call×family) | 56 | 0.0122 | | |
| Time (food) | 2 | 0.1028 | 6.20 | 0.0027 |
| **Resting** | | | | |
| Predator | 1 | 12.8949 | 485.78 | 0.0001 |
| Call | 1 | 0.1364 | 5.14 | 0.0276 |
| Family | 4 | 0.0404 | 1.52 | 0.2098 |
| Predator×call | 1 | 0.0004 | 0.01 | 0.9046 |
| Tub (predator×call×family) | 52 | 0.0265 | | |
| Food | 1 | 0.8695 | 68.64 | 0.0001 |
| Predator×food | 1 | 0.0120 | 0.94 | 0.3355 |
| Call×food | 1 | 0.0067 | 0.53 | 0.4694 |
| Predator×call×food | 1 | 0.0020 | 0.16 | 0.6906 |
| Food×tub (predator×call×family) | 56 | 0.0127 | | |
| Time (food) | 2 | 0.0569 | 2.56 | 0.0815 |
| **Swimming** | | | | |
| Predator | 1 | 2.9095 | 225.48 | 0.0001 |
| Call | 1 | 0.0069 | 0.53 | 0.4692 |
| Family | 4 | 0.0198 | 1.54 | 0.2050 |
| Predator×Call | 1 | 0.0719 | 5.57 | 0.0220 |
| Tub (predator×call×family) | 52 | 0.0129 | | |
| Food | 1 | 0.3322 | 47.60 | 0.0001 |
| Predator×food | 1 | 0.0002 | 0.03 | 0.8575 |
| Call×food | 1 | 0.0003 | 0.04 | 0.8483 |
| Predator×call×food | 1 | 0.0069 | 0.99 | 0.3238 |
| Food×tub (predator×call×family) | 56 | 0.0070 | | |
| Time (food) | 2 | 0.0252 | 1.93 | 0.1504 |

Tadpoles also showed decreased activity with increased food availability (Tables 2, 3): when food was present, tadpoles spent more time resting and less time feeding and swimming than when no food was present (Fig. 1). Although absolute activity levels depended on the availability of food in the environment, the predator avoidance response did not depend on food availability (Fig. 1), indicated by the lack of a significant multivariate interaction of food availability with predator presence (Table 2).

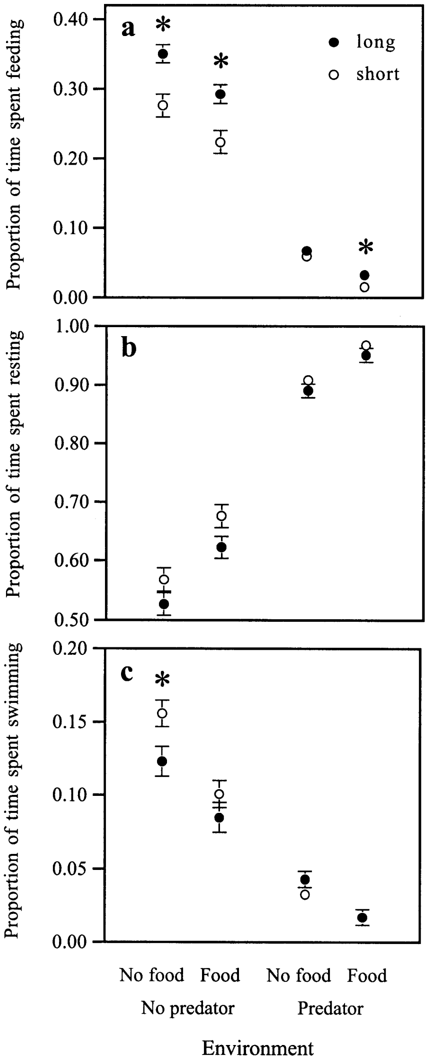

**Fig. 1** Mean proportion of time spent feeding (**a**), resting (**b**), and swimming (**c**), with and without food and with and without a predator, by the offspring of long-calling males (*filled circles*) and of short-calling males (*open circles*). Error bars represent ±1 SE. *Asterisks* indicate comparisons (*t*-tests) for which the offspring of long- and short-calling males differed significantly

## Genetic effects

Both aspects of genetic identity (father's call duration and family identity) influenced tadpole activity levels. Offspring of long-calling males spent more time feeding, overall, than did offspring of short-calling males (Table 3, Fig. 1). When no predator was present, offspring of long-calling males spent more time feeding than did offspring of short-calling males, regardless of the presence of food (with food: $t_{24}=2.42$, $P=0.023$; without food: $t_{24}=2.60$, $P=0.016$). In the presence of a dragonfly, however, offspring of long-calling males spent more time feeding than did offspring of short-calling males only when food was available ($t_{24}=2.16$, $P=0.041$); when no food was present, offspring of long- and short-calling males spent similar amounts of time feeding ($t_{24}$=0.52, $P$=0.609). Although offspring of long-calling males spent less time resting overall than did offspring of short-calling males (Table 3, Fig. 1), differences in time spent resting between offspring of long- and short-calling males were not significant under any of the four environmental conditions (predator absent, with food: $t_{24}$=–1.57, $P$=0.130; predator absent, without food: $t_{24}$=–1.15, $P$=0.262; predator present, with food: $t_{24}$=–1.57, $P$=0.129; predator present, without food: $t_{24}$=–1.00, $P$=0.326). Overall, offspring of long- and short-calling males spent similar proportions of time swimming (Tables 2, 3; Fig. 1). Differences in the activity levels of offspring of long- and short-calling males can be attributed to differences in paternal genetic contribution because we controlled for maternal effects by using maternal half-sibships and because rearing environment was controlled.

Offspring of long- and short-calling males showed similar predator avoidance responses in terms of the degree of reduction in activity and feeding. Feeding and resting were not significantly affected by the interaction of call duration and predator presence (Table 3). However, father's call duration and predator presence showed a significant multivariate interaction, attributable to the interactive effects of predator and call on time spent swimming (Tables 2, 3, Fig. 1). In the absence of a predator and without food, offspring of long-calling males spent less time swimming than did the offspring of short-calling males ($t_{24}$=–2.21, $P$=0.037). However, under the other three conditions, offspring of long- and short-calling males spent similar amounts of time swimming (predator absent, with food: $t_{24}$=–1.67, $P$=0.107; predator present, with food: $t_{24}$=0.39, $P$=0.701; predator present, without food: $t_{24}$=1.26, $P$=0.221).

Tadpole activity levels also depended on family identity, with significant variation among maternal half-sibships in time spent feeding (Tables 2, 3). The effect of family identity may represent genetic or non-genetic differences among mothers or genetic differences among sets of long- and short-calling males. Our experimental design does not allow us to distinguish between these possibilities because each male was crossed with only one female.

Tadpole size at the end of the experiment was related to activity levels during the experiment. In the predator treatment, tadpoles that spent more time feeding and less time resting were larger at the end of the experiment (feeding: $r_p$=0.38, $P$=0.035, $n$=30; resting: $r_p$=–0.40, $P$=0.030, $n$=30); time spent swimming was not significantly correlated with final mass ($r_p$=0.20, $P$=0.302, $n$=30). In the no-predator treatment, relationships between activity and final body mass were in the same directions, but were not significant (feeding: $r_p$=0.24, $P$=0.175, $n$=30; resting: $r_p$=–0.29, $P$=0.120, $n$=30; swimming: $r_p$=0.15, $P$=0.416, $n$=30). Although offspring of long-calling males tended to be larger at the end of the experiment than offspring of short-calling males (long: 0.2548±0.0739 g, short: 0.2364±0.0718 g), this difference was not significant ($F_{1,52}$=1.20, $P$=0.28). Tadpole body mass was not affected by family identity ($F_{4,52}$=1.94, $P$=0.12) or by the interaction of father's call duration and predator presence ($F_{1,52}$=0.04, $P$=0.84).

## Discussion

### Responses to predation threat and food availability

Tadpoles exposed to the presence of a caged dragonfly showed a marked reduction in time allocated to swimming and feeding. This reduction in time spent active was expected because similar behavioral responses have been observed in many prey species (e.g., Sih 1986; Semlitsch 1987; Skelly 1994). Although reduced activity decreases vulnerability to predators, it may also limit a tadpole's ability to forage, and therefore may be costly in terms of growth. (e.g., Skelly and Werner 1990; Peckarsky et al. 1993; Ball and Baker 1996). Such a growth cost was incurred by the tadpoles in the predator treatment, as reflected by their smaller size after 14 days (at the end of our study), relative to those tadpoles that were not exposed to a predator.

Tadpoles also reduced activity when resource (food) levels were high. This behavior is predicted because higher activity may result in higher mortality due to predation and the risk of starvation is relatively low at higher resource levels (Werner and Anholt 1993; Anholt and Werner 1995). Several previous studies have also documented decreased activity in response to higher resource levels (Horat and Semlitsch 1994; Anholt and Werner 1995, 1998).

### Call duration and offspring quality

In our experiment, offspring of long-calling males spent more time feeding than did offspring of short-calling males. Greater time spent feeding by the offspring of long-calling males may indicate an enhanced ability to acquire resources. Spending more time feeding is thus predicted to contribute to faster growth of tadpoles sired by long-calling males. This prediction is supported by the positive correlation between time spent feeding and tadpole size at the end of the experiment. The suggestion that spending more time feeding may have contributed to enhanced growth of offspring of long-calling males, relative to offspring of short-calling males, accords with evidence from previous laboratory experiments in which tadpoles sired by long-calling males showed higher growth rates – detected as larger mass at metamorphosis or earlier metamorphosis – than offspring of short-calling males (Welch et al. 1998). Both early metamorphosis and large size at metamorphosis are correlated with enhanced survival, larger adult size, and earlier reproductive maturity in anurans (Berven and Gill 1983; Smith 1987). Thus, increased feeding may be one mechanism underlying a growth advantage realized by the offspring of long-calling males. The differences between the offspring of long- and short-calling males in time spent feeding may therefore provide additional evidence that the preference of female gray tree frogs for males with long calls is a preference for good genes.

Although spending more time feeding should confer a benefit to tadpoles, the net fitness consequences of the activity differences observed between offspring of long- and short-calling males likely depends on the predation risk and the availability of resources in the environment. When the risk of predation is low, offspring of long-calling males are predicted to realize a net fitness benefit, relative to offspring of short-calling males, because we predict that spending more time feeding should enhance growth. However, when predatory dragonflies are abundant, the fitness advantage to offspring of long-calling males may be diminished in two ways. First, the difference in time spent feeding by offspring of long- and short-calling males in the presence of a dragonfly depended on the presence of food in the environment. With plentiful food, offspring of long-calling males spent more time feeding than did offspring of short-calling males; however, when food was absent, offspring of long- and short-calling males did not differ in time spent feeding. Second, in the presence of a predator, spending more time feeding may increase vulnerability to predation by increasing the likelihood of detection by the predator. Therefore, when predators are nearby and food is available, we predict that offspring of long-calling males may incur a cost in terms of predation risk, which would diminish, or possibly negate, the benefit of spending more time feeding. When predation is a threat and food is limited, we predict no difference between offspring of long- and short-calling males in either feeding or vulnerability and, hence, no difference in fitness. Our results suggest, therefore, that the indirect fitness consequences of mating with a long-calling male may depend on conditions in the environment encountered by the offspring.

In contrast to the present study, in which offspring of males with long calls spent more time feeding than did offspring of males with short calls, in a previous study using crayfish as predators, offspring of long- and short-calling males did not differ in time spent feeding (A,M, Welch, A.M. Winkeler, R.D. Semlitsch, H.C. Gerhardt, unpublished data). The difference in activity patterns between the two studies may be a function of environmental differences (e.g., in container size, hunger level, water temperature), ontogenetic differences (e.g., in tadpole size or stage), genetic differences (i.e., between the sets of females and males used as parents in the two studies), or some combination of these factors. Variation in time spent feeding is unlikely, therefore, to be the sole mechanism of good-genes selection in gray tree frogs. The genetic correlation between call duration and offspring performance may reflect different mechanisms, depending on the environment and the individual's genotype.

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