

Different mate preferences by parasitized and unparasitized females potentially reduces sexual selection

K. S. PFENNIG & R. C. TINSLEY

School of Biological Sciences, University of Bristol, Bristol, UK

Keywords:

male courtship;
mate choice;
parasites;
Pseudodiplorchis americanus;
Scaphiopus couchii;
sexual selection.

Abstract

Parasite-mediated models of sexual selection predict that females should avoid parasitized mates, thereby generating selection on male traits revealing health. The strength of this selection, however, may depend on the prevalence of parasitism among females if their infection status alters their mate preferences. We evaluated the effects of a socially transmitted parasite on male traits and female behaviour in spadefoot toads. Parasitized males were larger and in better condition than unparasitized males. Moreover, better condition males produced longer calls. Unparasitized females preferred longer calls indicative of good-condition males that are more likely parasitized. By contrast, parasitized females as a group possessed no preference for call duration. Presumably because of reduced selection by these parasitized females, male mating success was not associated with any measured traits. Thus, when females are parasitized, sexual selection on condition-dependent traits is potentially reduced.

Introduction

Indicator models of sexual selection predict that females will prefer mates that possess elaborate, condition-dependent characters that indicate male quality (reviewed in Andersson, 1994). By selecting such mates, females can enhance their reproductive fitness and exert directional selection on male traits, which potentially leads to the evolution of increasingly exaggerated male characters (reviewed in Andersson, 1994).

Parasites may facilitate sexual selection by affecting the expression and evolution of aspects of their hosts' phenotype used in courtship, mate attraction and mate choice. In particular, parasites can inhibit male courtship behaviour and depress the expression of characters used in mate attraction (Hamilton & Zuk, 1982; Møller, 1990; Zuk, 1992; Andersson, 1994; Møller *et al.*, 1999). By preferring males that advertise their health and freedom from disease (e.g. Clayton, 1990; Zuk *et al.*, 1990; Buchholz, 1995), females can avoid males that have

reduced fertility (e.g. Polak, 1998; Liljedal *et al.*, 1999) or poor-quality parenting abilities as a result of disease (e.g. Korpimäki *et al.*, 1995; Hakkarainen *et al.*, 1998). Moreover, by shunning parasitized males, females can avoid both becoming parasitized themselves (Able, 1996; Loehle, 1997) and passing on genes for parasite susceptibility to their offspring (Hamilton & Zuk, 1982; Møller, 1990). Such potential fitness benefits of avoiding parasitized males can selectively favour the evolution of female mate preferences for parasite-free males. Moreover, these preferences may lead to the evolution of male traits that reveal male health.

Parasite-mediated models of sexual selection generally do not consider that female responses to parasitized males may depend on the females' own infection status (Poulin, 1994; Simmons, 1994; Poulin & Vickery, 1996; Lopez, 1999). In studies that manipulated infection of females, female mating behaviour was altered (Simmons, 1994; Lopez, 1999; but see Clayton, 1990). A possible proximate cause of these alterations is that parasitized females may become less discriminating if pathogens depress their condition so that they invest less effort into their mate choice decisions (Poulin, 1994; Lopez, 1999; reviewed in Poulin & Vickery, 1996; for examples of

Correspondence: Karin S. Pfennig, Section of Integrative Biology, University of Texas, Austin TX 78712, USA.
Tel.: (512) 475-6164; fax: (512) 471-3878;
e-mail: kpfennig@uts.cc.utexas.edu

condition-dependent preference see also: Lesna & Sabelis, 1999; Hingle *et al.*, 2001a, b). By inhibiting a female's ability to discriminate among males, pathogen infection may alter the nature of sexual selection on, and subsequent evolution of, male traits (Poulin & Vickery, 1996).

We addressed these issues by examining the effects of parasites on male traits, female mate choice, and the potential for sexual selection in Couch's spadefoot toad (*Scaphiopus couchii*). Our goals were threefold. First, we ascertained whether male advertisement calls are associated with male size, aspects of condition, and infection status. By doing so, we sought to determine what male characters could be used by females to select better condition or unparasitized mates and are therefore potential targets of selection subject to evolutionary elaboration. Secondly, we evaluated female preferences for a male trait that was associated with male condition and infection status, and we compared preferences between parasitized and unparasitized females. Our purpose here was to evaluate the potential for sexual selection on male characters and assess how parasite infection of females might alter the strength of selection on male traits. Thirdly, we examined male mating success in a natural population in order to evaluate the potential strength of sexual selection in a critical component of male fitness. Our results suggest that parasite infection of females potentially reduces the strength of sexual selection on condition-dependent characters.

Materials and methods

Study system

Scaphiopus couchii ranges throughout the deserts of the southwestern USA. They hibernate underground for most of the year, emerging only to breed and forage following summer rains. Breeding takes place on a single night following a rainstorm (Bragg, 1965). Males aggregate in ephemeral pools and call to attract mates. Females initiate amplexus by closely approaching or touching the male, and they have ample opportunities to select mates at breeding aggregations (Tinsley, 1990; see also Pfennig, 2000).

Scaphiopus couchii suffers infection from *Pseudodiplorchis americanus* (Monogenea), a blood-feeding worm that resides in the bladder of adult toads (once intact in the host, the worms may live up to several years). *Pseudodiplorchis americanus* can cause chronic pathogenic effects in their hosts, especially when worm burdens are high, by depleting host packed cell volume of blood and lipid reserves necessary for survival during the toad's long hibernation period (Tocque, 1993; Tocque & Tinsley, 1994). Consequently, infection can reduce host survival, and potentially compromises the host's ability to invest energy into gonad development and the expression of secondary sexual characters such as male calls (Tocque, 1993; Tocque & Tinsley, 1994).

Release of the parasites' larvae (the infective stage) coincides with the hosts' breeding, so that the parasite can be transmitted both sexually and nonsexually among adults at breeding aggregations. Sexual activity by the host (e.g. male calling, amplexus) stimulates release of the larvae into the breeding pool where they infect nearby adult toads (reviewed in Tinsley, 1989, 1990; for details of infection and transmission route see Tinsley & Earle, 1983; Tinsley & Jackson, 1986). Infection of toads attending an aggregation is not uniform; the number of larvae, if any, that invade each host can be highly variable among members of a breeding aggregation (Tinsley & Jackson, 1988; K. S. Pfennig & R. C. Tinsley, unpublished data). Females could potentially avoid parasitized males, or areas where parasitized males are calling, to avoid those areas where parasite larvae are likely densest, thereby avoiding infection altogether or reducing the severity of new infection (*sensu* Able, 1996; Loehle, 1997). Moreover, males appear to vary in their resistance to the parasite (Tinsley, 1989), so by selecting unparasitized mates, females might choose males that pass on genes for resistance to their offspring (*sensu* Hamilton & Zuk, 1982).

In addition to evaluating male infection status, females also may assess other aspects of male quality. In anurans, females use calls as indicators of a male's size and ability to invest energy into calling (e.g. Ryan, 1980; Taigen & Wells, 1985; Gerhardt, 1988; Prestwich *et al.*, 1989; Robertson, 1990; Cherry, 1993; Grafe, 1996; Bevier, 1997). Similarly, *S. couchii* females might use calls to identify larger, better condition males that could possibly confer higher fertilization success to their mates or good genes to their offspring (as in other anuran systems; e.g. Ryan, 1985; Woodward, 1986; Robertson, 1990; Welch *et al.*, 1998; Pfennig, 2000).

Male calls, quality, and parasite infection status

To evaluate whether male calling behaviour indicates male phenotype or parasite infection status, we recorded 39 calling males at four natural breeding aggregations near Portal, Arizona, USA during July and August 1999. These aggregations were not significantly different in parasite prevalence. Water temperature at the time of recording was measured in the breeding pool where most males were calling. Within 24 h of their calls being recorded, each male was killed with an overdose of anaesthetic (males were placed in a 0.5 g L⁻¹ methanesulfonate salt solution for 15 min), patted dry, and then measured immediately for snout-vent length and weighed. This measure of mass prior to dissection is referred to as 'mass' henceforward. From dissections we determined each male's infection status, testes mass, fat body mass, and liver mass. Our sample also included 22 males that were collected and dissected as above, but no recordings were made of their calls. Of these 22 males, mass was not taken for one male, so for analyses

involving mass, our additional sample size consisted of 21 males.

Male calls were analysed using sound analysis software with a digitizing rate of 44.1 kHz. We measured call duration (length of call, s), call pulse rate (number of pulses in call s^{-1}), and call dominant frequency (the frequency in the call with the greatest energy) of at least six calls from each recording, then averaged these values for each male. For call rate, we measured the number of calls min^{-1} produced during the entire recording. (Three males did not call continuously during the recording period, so a reliable call rate could not be calculated for them. All other call characters were measured for these males, however.) We found no effect of temperature on male calling behaviour (temperature range of recordings: 20.5–22.5 °C), so temperature was not considered in subsequent analyses.

Prior to ascertaining whether calls indicated male size, we examined whether the observed variation in male mass was attributable to aspects of the males' growth and condition rather than features of the male not related to condition (e.g. urine held in the bladder). Specifically, we determined whether snout-vent length, fat body mass (an indication of lipid reserves), liver mass (an indication of glycogen reserves), and testes mass (an indication of investment into gonad development) were significantly correlated with our measure of male mass. To do so, we used partial correlation analysis to generate pair-wise partial correlation coefficients that measure the strength of association between two variables of interest while holding constant the other variables in the analysis (Sokal & Rohlf, 1995; Zar, 1999).

We next determined which call characters were correlated with male snout-vent length and mass using partial correlation analyses as above. Because mass was closely associated with snout-vent length (see Results), we controlled for snout-vent length in our measure of mass by computing the residuals of the cubic regression of mass (log-transformed) on snout-vent length. We refer to these residuals hereafter as standardized mass. This procedure allowed us to focus our attention on mass as a measure of energy reserves and investment in gonad development (see Results).

We found that one call character (call duration) was correlated with standardized mass (see Results). We therefore determined which particular features of the males' condition – liver mass, testes mass or fat body mass – best predicted male call duration. We performed a multiple regression in which call duration was our dependent variable and liver mass, testes mass and fat body mass were our independent variables.

Finally, we evaluated whether parasitized and unparasitized males differed in size and any of the variables associated with size and condition identified above. Sixteen males of our total sample of 61 males were parasitized, and of these males, the calls of only nine were recorded. Of the 16 males with parasites, five

males were infected with one worm. We therefore had insufficient variation in infection load and insufficient statistical power to examine the relationship between parasite load and male phenotype. Instead, we classified males as either parasitized or unparasitized and compared these groups for size and any correlated variables using two-tailed *t*-tests. Such categorization is biologically meaningful because, if given a choice between parasitized males and unparasitized males, females are expected to avoid parasitized males regardless of parasite load.

Where necessary, variables were transformed to meet parametric assumptions. Mass, liver mass, and testes mass were log transformed. Fat body mass was square root transformed.

Female preferences for call duration

We collected females near Portal, Arizona, USA, and returned them to the University of North Carolina. There they were housed according to methods in Pfennig (2000). To evaluate female mate preferences, we used a phonotaxis experiment in which females were presented alternative male calls that differed only in call duration. We tested females for their preferences of call duration because it was the only call character associated with both male condition and infection status (see Results).

Two alternative versions of synthesized male calls (see below) were presented to 31 sexually responsive females [females were injected with 0.1 mL $7.5 \mu g mL^{-1}$ luteinizing hormone releasing hormone (LHRH) to bring them into reproductive condition (e.g. Pfennig, 2000)]. Females were individually placed equidistant between two speakers set 180° and 1.4 m apart. Each speaker broadcast one of two alternative call duration stimuli (see below). The female was initially placed in an opaque container for an acclimation period of 15 min. Broadcasting of the stimuli began at the start of this period. Following acclimation, the female was released and allowed to move freely while the stimuli continued to play. A female was scored as preferring a stimulus when she touched the speaker broadcasting the stimulus. This behaviour is a reliable bioassay of female preference, because female spadefoot toads initiate pair formation when they closely approach or touch a male (Tinsley, 1990; Pfennig, 2000). The stimuli were switched between speakers after each female to control for position effects, and speakers were balanced for volume. No female was tested more than once.

To create the stimuli, we synthesized two alternative male calls: a long duration call (1.07 s) and a short duration call (0.88 s). These alternatives presented females with an unambiguous choice between a trait (long duration calls) indicative of larger, heavier males that are more likely parasitized vs. a trait (short duration calls) indicative of smaller, lighter males that are least

likely parasitized (see Results). Dominant frequency and pulse rate were the same in both stimuli (1.53 kHz and 169 pulses s^{-1} , respectively). The calls were repeated onto separate tracks of an audio tape at identical rates of 17 calls min^{-1} . Dominant frequency, pulse rate, and call rate were mean values for *S. couchii* derived from both the recordings above and an existing sample of male calls (see Pfennig, 2000).

Because parasites can affect female mate choice (Poulin, 1994; Simmons, 1994; Poulin & Vickery, 1996; Lopez, 1999), we assessed whether or not each female contained adult *P. americanus* parasites after her preference of call duration was evaluated (i.e. preference tests were blind with respect to each female's infection status). We determined each female's infection status by placing her against a fibre optic light source. The skin of *S. couchii* is transparent under light, so adult parasites are readily visible inside an illuminated live toad. This method is reliable for ascertaining infection status (R. C. Tinsley, unpublished data).

We used log-likelihood ratio χ^2 tests (Sokal & Rohlf, 1995) to determine whether female preferences for call duration deviated from 1 : 1 random expectation. Moreover, we used log-likelihood ratio χ^2 contingency table analysis (Sokal & Rohlf, 1995) to determine whether female preferences differed between parasitized and unparasitized groups. Finally, we tested the hypothesis that parasitized females invest less effort in mate choice. To do so, we used a two-tailed *t*-test to determine whether parasitized and unparasitized females differed in the time to selecting a stimulus. Time was log-transformed. If parasitized females invest less effort in mate choice, we expected them to take less time selecting a stimulus.

Male mating success in the field

Because male mating success is an important component of male fitness, we examined the potential strength of sexual selection on males by evaluating whether male mating success in the field was associated with any measured aspects of male phenotype.

We utilized data from 30 males (from our total sample size of 61; see above) that were collected from a single population. Of these 30, 15 were collected in amplexus with a female, and therefore designated 'preferred' mates. The remaining 15 of the 30 males were unmated calling males chosen randomly from throughout the breeding aggregation. These unmated males were designated 'nonpreferred' mates (see Pfennig, 2000 for a justification of this approach). Using two-tailed *t*-tests, we compared preferred and nonpreferred males for snout-vent length, standardized mass, testes mass and liver mass. Preferred males' calls were not recorded, so we could not compare call duration between preferred and nonpreferred males. Of the 30 males, mass was not measured for one male.

Results

Male calls, quality, and parasite infection status

Snout-vent length, testes mass, and liver mass were each significantly, positively correlated with male mass, when the other variables were controlled (Table 1). Moreover, the coefficient of determination (R^2 ; Zar, 1999) for the correlation of mass with these variables was 0.918, meaning that 91.8% of the observed variation in male mass was attributable to its correlation with snout-vent length, testes mass, liver mass and fat body mass (Table 1). Thus, mass largely reflects male growth and condition. Importantly, these findings reveal that heavier males for a given body length have relatively larger testes for their body length (indicating greater investment in gonad development) and relatively larger livers for their body length (indicating greater glycogen energy reserves).

Call duration was significantly, positively correlated with standardized mass when all other characters were controlled (Table 1). Thus, males that were heavier for their body size produced longer calls. When we examined which aspects of condition best predicted call duration, we found that only testes mass (not liver or fat body mass) predicted call duration (Table 2). Thus, females can use call duration to reliably assess testes size, which may indicate a male's ability to fertilize an entire clutch (for examples in other anurans see Ryan, 1985; Robertson, 1990; Pfennig, 2000). We also found that dominant frequency was significantly, negatively associated with male snout-vent length with all other call characters controlled (Table 1).

Table 1 Partial correlation analyses of: (A) mass with growth and condition measures (d.f. = 55); (B) standardized mass and snout-vent length (SVL) with call characters (d.f. = 30). First-order partial correlation coefficients are reported; some variables transformed prior to analysis (see text).

	Body mass	SVL	Liver mass	Testes mass	
(A)					
SVL	0.768***				
Liver mass	0.410**	0.022			
Testes mass	0.536***	-0.220	-0.068		
Fat body mass	0.045	0.053	0.317*	-0.164	
	Standardized mass	SVL	Call duration	Pulse rate	Call rate
(B)					
SVL	-0.254				
Call duration	0.491**	0.320			
Pulse rate	-0.091	-0.297	0.021		
Call rate	0.156	-0.007	-0.301	-0.151	
Dominant frequency	-0.219	-0.411*	0.134	0.012	-0.259

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2 Multiple regression of male call duration on testes mass, liver mass and fat body mass. All dependent variables were transformed prior to analysis (see text).

Source of variation	d.f.	SS	F-value	P-value
Model	3	0.040	3.576	0.024
Error	35	0.132		
Total	38	0.172		
$R^2 = 0.235$				
Parameter estimates:				
Term	Estimate	SE	P-value	Standard beta
Intercept	1.212	0.098	<0.001	0
Testes mass	0.181	0.073	0.019	0.426
Liver mass	0.034	0.073	0.645	0.097
Fat body mass	0.003	0.029	0.918	0.019

Table 3 Comparison of phenotypic characters between unparasitized and parasitized males.

Character	Male type	Mean \pm SE	t	P-value
SVL	Unparasitized	59.22 \pm 0.58	-4.316*	<0.001
	Parasitized	63.54 \pm 1.16		
Standardized mass	Unparasitized	-0.01 g \pm 0.00	-2.519**	0.015
	Parasitized	0.02 g \pm 0.01		
Liver mass	Unparasitized	0.69 g \pm 0.05	-2.723*	0.009
	Parasitized	0.97 g \pm 0.10		
Testes mass	Unparasitized	0.05 g \pm 0.00	-3.921*	<0.001
	Parasitized	0.07 g \pm 0.01		
Call duration	Unparasitized	0.96 s \pm 0.01	-0.049***	0.056
	Parasitized	1.01 s \pm 0.03		
Call dom. freq.	Unparasitized	1.54 kHz \pm 0.02	0.370***	0.713
	Parasitized	1.52 kHz \pm 0.04		

*d.f. = 59; **d.f. = 58; ***d.f. = 37.

Although parasites are generally expected to reduce male condition, parasitized males were actually significantly heavier for their body size than unparasitized males (Table 3). Moreover, parasitized males were larger in snout-vent length with significantly larger testes and livers than unparasitized males (Table 3). Parasitized males also had longer calls than unparasitized males, but call dominant frequency was not different between these groups (Table 3).

Female preferences for call duration

When data from all females were pooled, there was no statistically significant preference for either call duration stimulus (20 preferred long calls, 11 preferred short calls; log-likelihood ratio $\chi^2_1 = 2.651$, $P = 0.104$). However, female preferences depended on whether or not the female was infected with *P. americanus* (Fig. 1).

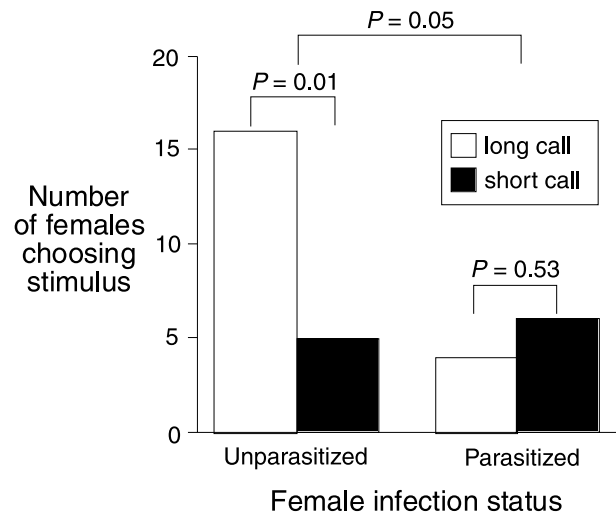


Fig. 1 Female preferences for male call duration compared both within and between unparasitized and parasitized female groups.

Unparasitized females significantly preferred longer duration calls (16 preferred long calls, five preferred the short calls; log-likelihood ratio $\chi^2_1 = 6.060$, $P = 0.014$). By contrast, parasitized females were random in their preferences of call duration (four preferred long calls, six preferred short calls; log-likelihood ratio $\chi^2_1 = 0.403$, $P = 0.526$). These patterns of female preferences tended to differ between the two female groups (log-likelihood ratio $\chi^2_1 = 3.811$, $P = 0.051$; Fig. 1), indicating that parasite infection is associated with differences in female mate preferences. Parasitized and unparasitized females did not differ, however, in time to selecting a stimulus [mean (\pm SE) log time to stimulus selection by: unparasitized females = 2.37 (0.10) s; parasitized females = 2.43 (0.17) s; $t_{29} = -0.364$, $P = 0.718$].

Male mating success in the field

Male mating success in the field was not associated with any features of the male's phenotype discussed above. Preferred and nonpreferred males were not significantly different in standardized mass, snout-vent length, testes mass, or liver mass (Table 4). Moreover, preferred and nonpreferred males did not differ in likelihood of being parasitized (five of 15 preferred males were parasitized; five of 15 males were not parasitized).

Discussion

Contrary to the predictions of parasite-mediated sexual selection models, parasitized males were larger in snout-vent length, heavier for a given body size, and had larger testes, larger livers, and longer calls than unparasitized males. These findings confirm similar results of Tocchio (1993), and are not unique to this system (e.g. Merilä &

Table 4 Comparison of phenotypic characters between nonpreferred and preferred males.

Character	Male type	Mean \pm SE	<i>t</i>	<i>P</i> -value
SVL	Non-preferred	60.03 \pm 0.93	-0.613*	0.545
	Preferred	61.05 \pm 1.38		
Standardized mass	Non-preferred	0.01 g \pm 0.01	-0.100**	0.921
	Preferred	0.01 g \pm 0.01		
Liver mass	Non-preferred	0.69 g \pm 0.06	-0.509*	0.615
	Preferred	0.81 g \pm 0.11		
Testes mass	Non-preferred	0.06 g \pm 0.01	-0.064*	0.950
	Preferred	0.06 g \pm 0.01		

*d.f. = 28; **d.f. = 27.

Sheldon, 1999). Such a pattern can occur when larger, older or good-condition males breed more often, and therefore have been exposed to parasites more often, than smaller, younger, or poor-condition males. Indeed, for parasites that are sexually or socially transmitted, males that successfully breed more often generally may be more highly parasitized than less promiscuous males. Males may therefore trade-off enhanced breeding opportunities with higher incidence of parasitism. Similarly, spadefoot females face a trade-off in that they must choose between males that are in good condition but that are more likely parasitized vs. males in relatively poor condition that are least likely parasitized. Understanding how females respond to this trade-off is critical to evaluating both the strength of sexual selection on male traits and the aspects of male phenotype that are the targets of selection.

That unparasitized females prefer long duration calls (Fig. 1) indicates that unparasitized females more likely choose a mate based on condition rather than infection status. Although mating with a parasitized male has potential costs (e.g. risk of acquiring infection or conferring genes for susceptibility to offspring), females may gain benefits that outweigh them. By preferring good-condition males, females can acquire mates with larger testes that are potentially better able to fertilize an entire clutch (e.g. in other spadefoot species, females that select heavier mates have higher fertilization success; Pfennig, 2000). Heavier males with longer calls may also sire better quality offspring [as in the anurans *Spea* (Woodward, 1986) and *Hyla* (Welch *et al.*, 1998)].

Contrary to unparasitized females, parasitized females did not express a preference for call duration (Fig. 1). Consequently, parasitized females may not receive the fitness benefits that unparasitized females receive from their mate choice decisions. Why should parasitized females forego the potential benefits of preferring good-condition mates?

At least three hypotheses explain why parasitized females as a group are less choosy. First, parasites may depress female condition so they do not invest effort into

mate choice (Poulin, 1994; Lopez, 1999; see review in Poulin & Vickery, 1996; see also: Lesna & Sabelis, 1999; Hingle *et al.*, 2001a, b). Although our data did not support this hypothesis, female motivation to select a mate might be expressed by means other than time to choose a stimulus, so we cannot rule out this hypothesis entirely. Secondly, individual females may assess whether the risk of selecting a potentially parasitized mate outweighs the potential benefits of selecting a relatively heavier mate. Females that are already parasitized may be more likely than unparasitized females to choose a mate based on infection status because female condition tends to decrease as parasite load increases (Tocque, 1993). Thirdly, parasites may manipulate female behaviour to enhance transmission to unparasitized males. Discriminating among these hypotheses is important for evaluating the selective pressures on female mate choice behaviours that ultimately affect sexual selection on male traits.

This study indicates that parasite infection of females can affect the nature of selection on traits that indicate male quality. Although unparasitized females' preferences for long call duration can exert directional selection on call duration (Fig. 1), the random preferences of parasitized females potentially diminishes the overall strength of sexual selection on this character. Indeed, male mating success in the field was not associated with our measures of size, condition, or infection status. Because male mating success is an important component of male fitness, our findings indicate that parasite infection of females potentially inhibits, rather than facilitates, sexual selection on male traits. Generally, as parasitism becomes more prevalent among females, sexual selection on male traits may be reduced.

The strength of sexual selection on male traits may not depend solely on the patterns of female preference and male mating success, however. For instance, reduced fecundity in parasitized females may diminish the impact of parasitized females' lack of preferences on the overall strength of sexual selection. Although males in better condition in our study did not have higher mating success, such males may sire more offspring and therefore be favoured by sexual selection if unparasitized females have higher fecundity than parasitized females (*sensu* Hingle *et al.*, 2001a). Moreover, selection should favour females that can best choose a fitness-enhancing mate, despite being parasitized. Thus, females may evolve enhanced resistance to parasites that depress their ability to choose such mates. Consequently, the dynamics of host-parasite coevolution ultimately may be critical to the outcome of sexual selection.

Acknowledgments

We are grateful to David Pfennig, Mike Ryan, Mark Kirkpatrick, Kern Reeve, Thomas Bataillon, Dave Hall,

Ham Farris, Bob Podolsky, Jon Allen, Ophelie Ronce, Peter Murphy, Mike Loeb, Laura Higgins, Sarah Joseph, and two anonymous reviewers for discussion and comments that improved the manuscript. Many thanks also to David Pfennig, William Harcombe, Peter Murphy, Serdar Dusen, Mike Westphal, Wade and Emily Sherbrooke, and the staff and volunteers at the American Museum's Southwestern Research Station for field assistance, Jay Marlowe for assistance in the lab, and the Arizona Game and Fish Department for collecting permits. This research was supported by a National Science Foundation–North Atlantic Treaty Organization postdoctoral fellowship to K. P.

References

- Able, D.J. 1996. The contagion indicator hypothesis for parasite-mediated sexual selection. *Proc. Natl. Acad. Sci. USA* **93**: 2229–2233.
- Andersson, M. 1994. *Sexual Selection*. Princeton University Press, Princeton.
- Bevier, C.R. 1997. Utilization of energy substrates during calling activity in tropical frogs. *Behav. Ecol. Sociobiol.* **41**: 343–352.
- Bragg, A.N. 1965. *Gnomes of the Night: The Spadefoot Toads*. University of Pennsylvania Press, Philadelphia.
- Buchholz, R. 1995. Female choice, parasite load and male ornamentation in wild turkeys. *Anim. Behav.* **50**: 929–943.
- Cherry, M.I. 1993. Sexual selection in the raucous toad, *Bufo ranganeri*. *Anim. Behav.* **45**: 359–373.
- Clayton, D.H. 1990. Mate choice in experimentally parasitized rock doves: lousy males lose. *Am. Zool.* **30**: 251–262.
- Gerhardt, H.C. 1988. Acoustic properties used in call recognition by frogs and toads. In: *The Evolution of the Amphibian Auditory System* (B. Fritsch, M.J. Ryan, W. Wilczynski, T.H. Hetherington & W. Walkowiak, eds), pp. 455–483. John Wiley and Sons, New York.
- Grafe, T.U. 1996. Energetics of vocalization in the African reed frog (*Hyperolius marmoratus*). *Comp. Biochem. Physiol. A* **114**: 235–243.
- Hakkarainen, H., Ilmonen, P., Koivunen, V. & Korpimäki, E. 1998. Blood parasites and nest defense behaviour of Tengmalm's owls. *Oecologia* **114**: 574–577.
- Hamilton, W.D. & Zuk, M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* **218**: 384–387.
- Hingle, A., Fowler, K. & Pomiankowski, A. 2001a. 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.
- Hingle, A., Fowler, K. & Pomiankowski, A. 2001b. Size-dependent mate preference in the stalk-eyed fly *Cyrtodiopsis dalmanni*. *Anim. Behav.* **61**: 589–595.
- Korpimäki, E., Tolonen, P. & Bennett, G.F. 1995. Blood parasites, sexual selection and reproductive success of European kestrels. *Ecoscience* **2**: 335–343.
- Lesna, I. & Sabelis, M.W. 1999. Diet-dependent female choice for males with 'good genes' in a soil predatory mite. *Nature* **401**: 581–584.
- Liljedal, S., Folstad, I. & Skarstein, F. 1999. Secondary sex traits, parasites, immunity and ejaculate quality in the Arctic charr. *Proc. R. Soc. Lond. B* **266**: 1893–1898.
- Loehle, C. 1997. The pathogen transmission avoidance theory of sexual selection. *Ecol. Model.* **103**: 231–250.
- Lopez, S. 1999. Parasitized female guppies do not prefer showy mates. *Anim. Behav.* **57**: 1129–1134.
- Merilä, J. & Sheldon, B.C. 1999. Testes size variation in the greenfinch *Carduelis chloris*: relevance for some recent models of sexual selection. *Behav. Ecol. Sociobiol.* **45**: 115–123.
- Møller, A.P. 1990. Effects of a haematophagous mite on the barn swallow (*Hirundo rustica*): a test of the Hamilton and Zuk hypothesis. *Evolution* **44**: 771–784.
- Møller, A.P., Christe, P. & Lux, E. 1999. Parasitism, host immune function, and sexual selection. *Q. Rev. Biol.* **74**: 3–20.
- Pfennig, K.S. 2000. Female spadefoot toads compromise on mate quality to ensure conspecific matings. *Behav. Ecol.* **11**: 220–227.
- Polak, M. 1998. Effects of ectoparasitism on host condition in the *Drosophila-Macrocheles* system. *Ecology* **79**: 1807–1817.
- Poulin, R. 1994. Mate choice decisions by parasitized female upland bullies, *Gobiomorphus breviceps*. *Proc. R. Soc. Lond. B* **256**: 183–187.
- Poulin, R. & Vickery, W.L. 1996. Parasite-mediated sexual selection: just how choosy are parasitized females? *Behav. Ecol. Sociobiol.* **38**: 43–49.
- Prestwich, K.N., Brugger, K.E. & Topping, M. 1989. Energy and communication in three species of hylid frogs: power input, power output and efficiency. *J. Exp. Biol.* **144**: 53–80.
- Robertson, J.G.M. 1990. Female choice increases fertilization success in the Australian frog *Uperoleia laevigata*. *Anim. Behav.* **39**: 639–645.
- Ryan, M.J. 1980. Female mate choice in a Neotropical frog. *Science* **209**: 523–525.
- Ryan, M.J. 1985. *The Túngara Frog*. University of Chicago Press, Chicago.
- Simmons, L.W. 1994. Courtship role reversal in bush crickets: another role for parasites. *Behav. Ecol.* **5**: 259–266.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*, 3rd edn. W. H. Freeman and Company, New York.
- Taigen, T.L. & Wells, K.D. 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *J. Comp. Physiol. B* **155**: 163–170.
- Tinsley, R.C. 1989. The effects of host sex on transmission success. *Parasitol. Today* **5**: 190–195.
- Tinsley, R.C. 1990. The influence of parasite infection on mating success in spadefoot toads, *Scaphiopus couchii*. *Am. Zool.* **30**: 313–324.
- Tinsley, R.C. & Earle, C.M. 1983. Invasion of vertebrate lungs by the polystomatid monogeneans *Pseudodiplorchis americanus* and *Neodiplorchis scaphiopodis*. *Parasitology* **86**: 501–517.
- Tinsley, R.C. & Jackson, H.C. 1986. Intestinal migration in the life-cycle of *Pseudodiplorchis americanus* (Monogenea). *Parasitology* **93**: 451–469.
- Tinsley, R.C. & Jackson, H.C. 1988. Pulsed transmission of *Pseudodiplorchis americanus* (Monogenea) between desert hosts (*Scaphiopus couchii*). *Parasitology* **97**: 437–452.
- Toçque, K. 1993. The relationship between parasite burden and host resources in the desert toad (*Scaphiopus couchii*), under natural environmental conditions. *J. Anim. Ecol.* **62**: 686–693.
- Toçque, K. & Tinsley, R.C. 1994. The relationship between *Pseudodiplorchis americanus* (Monogenea) density and host resources under controlled environmental conditions. *Parasitology* **108**: 175–183.

- Welch, A.M., Semlitsch, R.D. & Gerhardt, H.C. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science* **280**: 1928–1930.
- Woodward, B.D. 1986. Paternal effects on juvenile growth in *Scaphiopus multiplicatus* (the New Mexico spadefoot toad). *Am. Nat.* **128**: 58–65.
- Zar, J.H. 1999. *Biostatistical Analysis*, 4th edn. Prentice Hall, Inc, Upper Saddle River.
- Zuk, M. 1992. The role of parasites in sexual selection: current evidence and future directions. *Adv. Stud. Behav.* **21**: 39–68.
- Zuk, M., Thornhill, R., Ligon, J.D. & Johnson, K. 1990. Parasites and mate choice in red jungle fowl. *Am. Zool.* **30**: 235–244.

Received 26 November 2001; accepted 25 January 2002