Sexual coercion and the opportunity for sexual selection in guppies

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The operational sex ratio (OSR) is believed to play a major role in determining the opportunity for sexual selection. Most studies that investigate the effects of OSR on the opportunity for sexual selection, however, ignore the important effects that OSR has on sexual coercion. Sexually coercive behaviour by males, including forceful or subversive mating tactics and sexual harassment, may cause females to mate suboptimally and thus have important consequences for the opportunity for sexual selection. We investigated how variation in OSR affects sexual coercion in guppies, *Poecilia reticulata*, and examined the costs of this coercion to females. Males did not change mating tactics nor did individuals perform more coercive acts in the male-biased treatment, but the net rate of coercive intersexual interactions was higher simply because there were more males present. Increased sexual coercion did not affect direct fitness components (including number, weight and survival of offspring) or the proportion of courtship displays to which females responded positively.

Biases in the operational sex ratio (OSR) are expected to increase the opportunity for sexual selection of a population (Emlen & Oring 1977; but see Kokko & Monaghan 2001; Kokko & Johnstone 2002), because there is increased competition for mates by the more abundant sex (Kvarnemo & Ahnesjö 1996), and increased choosiness by the rarer sex (Berglund 1994; Jirotkul 1999). In measuring the effects of the OSR on the opportunity for sexual selection, however, many studies have neglected to take into account the possibility that the levels of sexual coercion that males impose on females may rise with increasing male bias in the OSR. Sexual coercion may arise from unsolicited mating attempts, harassment or intimidation.

In populations where OSRs are male-biased, females are likely to experience more sexual coercion (Clutton-Brock & Parker 1995). This may be because there are more males harassing females, or because competition between males injures females (e.g. Clutton-Brock et al. 1992) or interferes with their reproduction (e.g. Marchesan 2002). The use of alternative mating strategies by males when they are faced with increased competition (e.g. Crespi 1988; Shine et al. 2003; Byrne & Roberts 2004) may also increase the levels of sexual coercion experienced by females, for example if females thereby suffer more matings or are

more likely to be injured. Such is the case in green-winged teal, *Anas crecca carolinensis*, where forced extrapair copulations may be harmful to females as well as incite further matings from a female's partner (McKinney & Stolen 1982).

Sexual coercion is often costly to females (e.g. McKinney et al. 1983; Magnhagen 1991; Mesnick & Leboeuf 1991; Magurran & Seghers 1994; Watson et al. 1998; Schlupp et al. 2001), and as such may have important consequences that affect both female fitness and evolution by sexual selection. The opportunity for sexual selection is in part determined by female choosiness, and how choosy a female is depends primarily on the costs of choice (Johnstone et al. 1996). If sexual coercion is costly for females, then increased levels of sexual harassment could increase the costs of rejecting males and, in turn, cause females to mate indiscriminately to avoid further harassment (i.e. 'convenience polyandry') (Thornhill & Alcock 1983). Consequently the opportunity for sexual selection may decrease.

Our primary aim in this study was to examine the costs of sexual coercion to females and explore how these costs affect the opportunity for sexual selection. To do this we manipulated the adult sex ratio of a laboratory population of guppies, *Poecilia reticulata*. Previous studies on guppies have shown that in male-biased OSRs, males display less often and that these displays are more likely to be interrupted by other males (Jirotkul 1999). In addition, increased male attention decreases females' feeding opportunities in

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populations with male-biased OSRs (Magurran & Seghers 1994). Whether increased sexual coercion actually leads to increased costs for females and how these costs might affect the opportunity for sexual selection have not been investigated.

Several aspects of guppy breeding ecology predict intense male sexual coercion. First, males do not provide resources to females and can greatly enhance their reproductive success by mating many times, whereas females need to mate only a few times to ensure fertilization and are able to store sperm (Constantz 1989). Second, fertilization in guppies is internal and males may achieve matings either through solicited copulations following courtship displays or via unsolicited (sneak) copulations (in which a male approaches a female from behind and inserts its gonopodium into the female's gonopore). Sexual harassment in guppies may take a number of forms including excessive attention and/or courtship as well as sneak copulations which circumvent mate choice (Magurran & Seghers 1994).

Based on results of previous studies we predicted that in male-biased tanks males would experience increased competition and would thus alter their mating strategy to perform fewer courtship displays and attempt more sneak copulations than in female-biased tanks (Jirotkul 1999). We predicted that such changes in male behaviour would be costly to females, causing increased energy expenditure on avoiding male harassment and/or decreased time spent feeding (Magurran & Seghers 1994). The OSR may also affect the proportion of male displays that a female accepts, that is, their sexual responsiveness. Jirotkul (1999) suggested that in male-biased OSRs female sexual responsiveness will decrease as they become more choosy, whereas the convenience polyandry hypothesis predicts that sexual responsiveness will increase with increased sexual coercion (Thornhill & Alcock 1983).

METHODS

We used guppies from fourth-generation laboratory stock, which descended from 500 male and female wild-caught feral guppies at Alligator creek, near Townsville, Australia. Females came from a tank containing only virgin females, which were separated from males upon sexing at 30–40 days, after which females were reared separately from males. Males came from mixed-sex tanks and thus had sexual experience. All fish were returned to stock tanks after the study. The experiment was approved by The University of New South Wales animal care and ethics committee.

In the wild, guppies may experience a range of sex ratios that vary both spatially and temporally (Pettersson et al. 2004; M. Head, unpublished data). To examine the effects of OSR on harassment and fitness of females, we varied the adult sex ratios at which the guppies were housed. The female-biased treatment consisted of three male and six female guppies (OSR = 1:2) and the male-biased treatment contained six male and three female guppies (OSR = 2:1). These OSRs were within the range found in the field in both Australia (M. Head, unpublished data)

and their native streams of Trinidad (Pettersson et al. 2004).

Each treatment was replicated six times. Fish were kept in glass tanks (76 × 40 cm and 38 cm high). The bottoms of the tanks were covered with gravel and the water temperature was 22–24°C. Brine shrimp were added to each tank daily (9 ml/tank or 1 ml/fish, sufficient for normal growth). The guppies were maintained in these treatment tanks for 21 days.

Fish were placed in their respective OSR treatment the day before observations began, allowing them to settle in. We observed the fish for the first 2 days of the experiment and then weekly until the fish were removed (i.e. observations took place on days 1, 2, 7, 14 and 21 after the start of each treatment). On each day observations involved following each male in random order for 5 min and then repeating the process in a different random order. Observations began 10 min after lights came on and totalled 90 min per day. Males were identified by their individual colour patterns. We recorded the frequency of courtship behaviours including following, chasing, jockeying (where two males chase a female), nipping, sneak copulations and sigmoid displays (as described by Houde 1997). All of these behaviours, apart from sigmoid displays, can be classed as sexually coercive. Sigmoid displays were classified on a scale from 0 to 5 (Houde 1997), based on how far through the display process, towards a full mating, courtship proceeded. Males display continuously to females and a positive response is scored if the female moves towards the displaying male indicating sexual acceptance (Houde 1997). We calculated the proportion of displays rejected, interrupted by other males and eliciting a positive response (the same as the 'fraction of female responses' recorded in other studies; Endler & Houde 1995; Jirotkul 1999). The proportion of successful displays was calculated only from uninterrupted displays.

Females were weighed immediately before and after each treatment (i.e. on day 0 and day 21) to give an estimate of female weight gain. Once removed from the treatment tanks, females were housed individually in 5-litre plastic tanks until parturition. These tanks contained a gravel substrate and plastic plants to prevent offspring from being eaten. Females were kept until they had given birth or until 80 days after the treatment if they had no offspring. Tanks were checked for offspring daily. Upon parturition offspring were removed and we recorded the number of offspring and female gestation time. Four offspring from each brood (range 1–10 offspring) were housed individually in 500-ml tanks, so that we could measure offspring survival and weight at maturity without the confounding factor of offspring density. All offspring were fed 1 ml each of diluted brine shrimp daily, sufficient for normal growth. After 40 days offspring were sexed under a microscope and weighed; any offspring that was unable to be sexed at this stage was kept for later sexing. Offspring were moved to stock tanks after the study.

For analyses we used SPSS version 11.0 software (SPSS Inc., Chicago, IL, U.S.A.). The mean frequency of behaviours per male and female was analysed with a multivariate, repeated measures analysis of variance. When the assumption of sphericity was not met we used

Greenhouse–Geisser adjusted degrees of freedom (Quinn & Keough 2002).

To investigate the relation between the number of positive responses a male received and his sneak copulation rate we conducted a nested analysis of covariance. We included in our model: treatment, tanks within treatment, number of responses (covariate), the treatment by covariate and covariate by tank within-treatment interactions. Nonsignificant interaction terms ($P > 0.25$) were dropped from the model (Quinn & Keough 2002, page 260). Female weight gain and reproductive output measures within tanks were pooled to avoid pseudoreplication and were analysed with MANOVA.

RESULTS

Behavioural Observations

Females in the male-biased treatment were subject to more following, chasing, jockeying, nipping, attempted sneak copulations and displays (Table 1, Fig. 1). This was because of the greater number of males, not because of a difference in number of behaviours per male. The number of jockeys was an exception, with individual males in the male-biased treatment jockeying more (Table 2, Fig. 2). There were both significant time and time by treatment effects for the number of nips, sneak copulations and displays experienced per female (Table 1). However, these do not override the treatment effects (Fig. 1).

The proportion of interrupted displays was greater in the male-biased treatment. Neither the proportion accepted nor the proportion rejected differed between treatments. The outcome of displays changed significantly over the period of treatment: females were receptive only in the first 2 days of this experiment (Table 3, Fig. 3). The number of displays by a male that received a positive response was correlated with the sneak copulation rate ($F_{1,10.513} = 4.007$, $P = 0.052$, partial correlation coefficient = 0.253).

Fitness Components

We found no difference in female weight gain, gestation time, number of offspring, offspring survival to maturity/sexing or offspring weight at maturity/sexing between the treatments (Table 4).
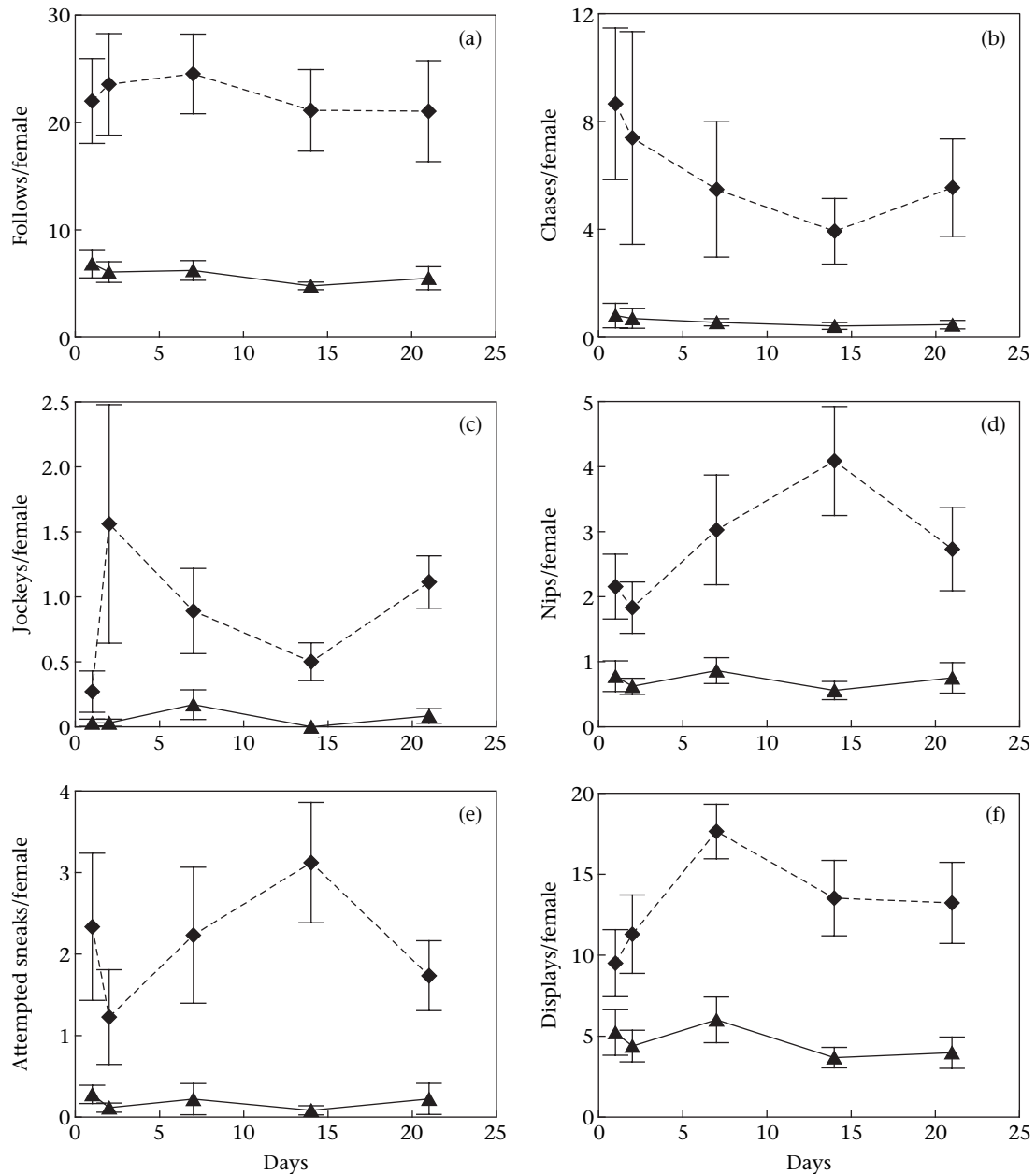
DISCUSSION

OSR and Sexual Selection

A bias in the OSR is thought to increase mate competition of the more numerous sex, and choosiness of the minority sex, thus leading to an increase in the opportunity for sexual selection (e.g. Emlen & Oring 1977; Clutton-Brock & Parker 1992). However, the importance of male–male interference competition, unsolicited copulations and sexual harassment has been ignored. Our results show that while male guppies did not alter their mating strategies in male-biased OSRs, they did experience more interference competition. Females were also subject to increased harassment and sneak copulations, simply because there were more males present. The effects that this may have on the opportunity for sexual selection are discussed below.

There is evidence for both an increase in the opportunity for sexual selection on males in male-biased populations (e.g. strawberry dart-poison frog, *Dendrobates pumilio*: Prohl 2002; guppies: Jirotkul 2000) and a decrease (e.g. European bitterlings, *Rhodeus sericeus*: Mills & Reynolds 2003). The reasons for the different effects of OSR on the opportunity for sexual selection may be that alternative mating tactics are used in some species and not others, and that these tactics vary with male phenotype and the use of conventional mating tactics (Jones et al. 2001).

For species with alternative mating tactics, males may alter their tactics in response to the sex ratio. For instance, males often switch from tactics that attract females, such as calling (e.g. quacking frogs, *Crinia georgiana*: Byrne & Roberts 2004) or courting (e.g. garter snakes, *Thamnophis sirtalis parietalis*: Shine et al. 2003) to tactics that bypass female choice. In such situations the variance in male mating success is expected to decrease (e.g. European bitterlings: Mills & Reynolds 2003).

In our study, and another similar study (Jirotkul 1999), male guppies did not abandon conventional mating tactics and invest more in sneak copulations in response to a male-biased sex ratio. Although Jirotkul (1999) did find a decrease in the number of solicited copulations she found no increase in the use of sneak copulations in the male-biased treatments of her study. The lack of response of male guppies to variation in the sex ratio is probably

Table 1. Repeated measures analysis of variance of the effect of operational sex ratio treatment and day on the frequency of courtship behaviours performed by males, per female

	Within-subjects contrasts (time)			Between-subjects contrasts (treatment)			Interactions (time*treatment)		
	df	F	P	df	F	P	df	F	P
Multivariate	24,152	2.14	0.003	6,5	7.10	0.024	24,152	1.68	0.033
Follows	2.39,23.93*	0.93	0.424	1,10	18.33	0.002	2.39,23.93*	0.38	0.721
Chases	1.12,11.21*	1.59	0.237	1,10	6.33	0.031	1.12,11.21*	1.13	0.319
Jockeys	1.31,13.08*	1.56	0.242	1,10	9.32	0.012	1.31,13.08*	1.41	0.268
Nips	4,40	3.42	0.053	1,10	13.43	0.004	4,40	3.98	0.008
Sneaks	4,40	2.83	0.067	1,10	9.57	0.011	4,40	3.01	0.029
Displays	4,40	3.26	0.048	1,10	21.95	0.001	4,40	2.17	0.090

*Greenhouse–Geisser approximation as sphericity could not be assumed.

Figure 1. Mean frequency of courtship behaviours performed by males, per female, ±SE for male-biased (- - -) and female-biased (—) treatments over a 3-week period. (a) Following female, (b) chasing female, (c) jockeying, where two males chase a female, (d) nipping female, (e) attempting a sneak copulation and (f) performing a sigmoid display.

Table 2. Repeated measures analysis of variance of the effect of operational sex ratio treatment and day on the frequency of courtship behaviours performed by males, per male

	Within-subjects contrasts (time)			Between-subjects contrasts (treatment)			Interactions (time*treatment)		
	df	F	P	df	F	P	df	F	P
Multivariate	24,152	1.69	0.030	6,5	4.29	0.066	24,152	0.92	0.572
Follows	4,40	1.72	0.165	1,10	0.05	0.836	4,40	0.72	0.582
Chases	1.41,14.07*	1.94	0.185	1,10	2.62	0.137	1.41,14.07*	0.47	0.567
Jockeys	1.99,19.88*	1.62	0.223	1,10	5.03	0.049	1.99,19.88*	1.17	0.331
Nips	2.43,24.29*	0.93	0.424	1,10	0.02	0.893	2.43,24.29*	1.50	0.242
Sneaks	4,40	1.79	0.164	1,10	3.39	0.095	4,40	2.21	0.085
Displays	4,40	2.25	0.121	1,10	2.25	0.165	4,40	1.11	0.367

*Greenhouse–Geisser approximation as sphericity could not be assumed.
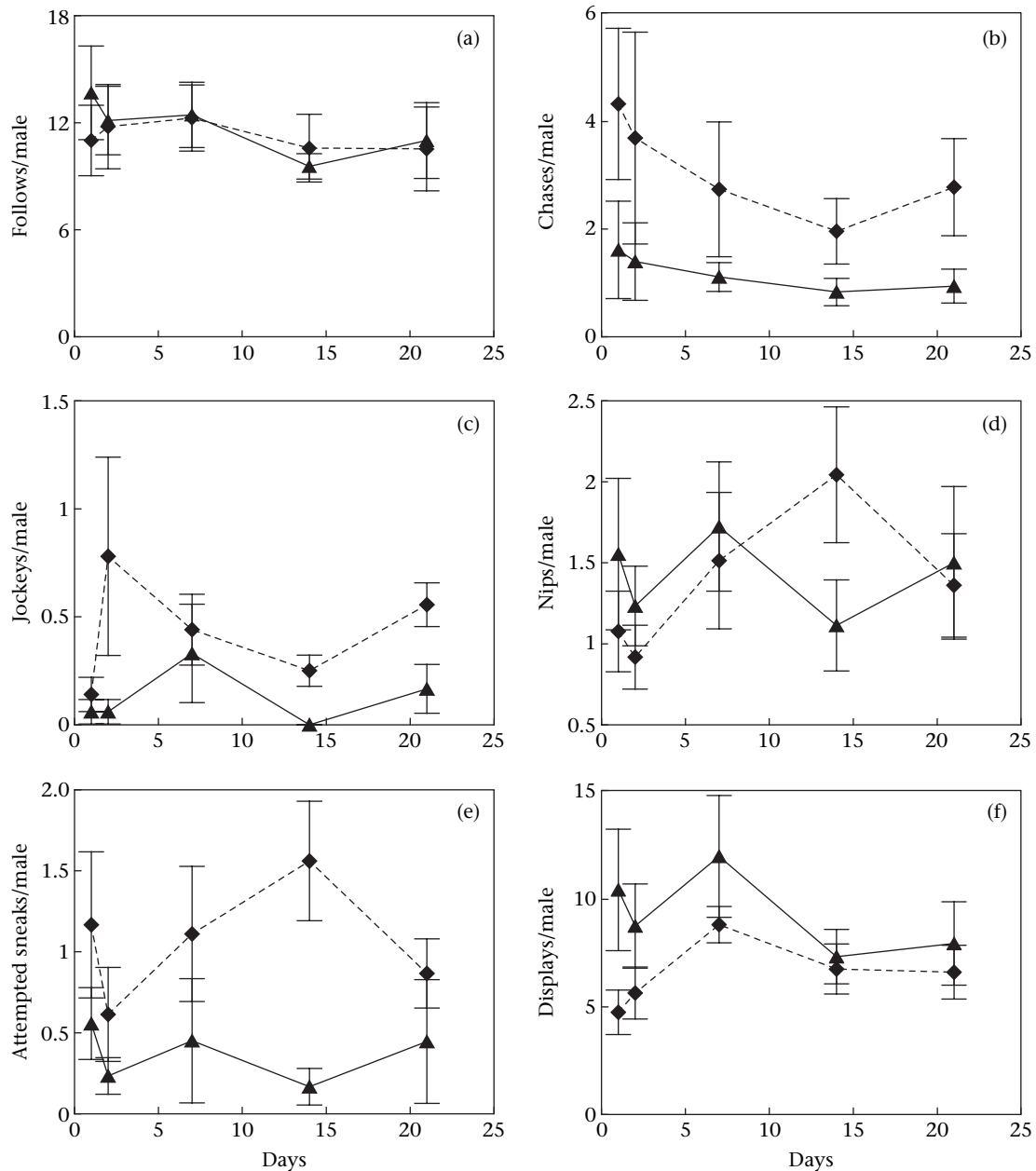
Figure 2. Mean frequency of courtship behaviours performed by males, per male, ±SE for male-biased (- - -) and female-biased (—) treatments over a 3-week period. (a) Following female, (b) chasing female, (c) jockeying, where two males chase a female, (d) nipping female, (e) attempting a sneak copulation and (f) performing a sigmoid display.

due to the relative costs and benefits of performing courtship displays and sneak copulations. If courtship is not costly and sneak copulations are rarely successful then it may not pay males to alter their mating strategies in response to increased sexual competition.

Despite no change in male behaviour in our experiment, females received more sneak copulations and more courtship displays in our male-biased treatment, simply because there were more males performing these. How this increase in both the number of sneak copulations and courtship displays experienced by females in the male-biased treatment affects the opportunity for sexual selection depends on how these behaviours are distributed in relation to each other and to male phenotype

(Jones et al. 2001). In many species, males that perform alternative mating tactics are different from those that obtain solicited copulations (e.g. spadefoot toads, *Pelobates fuscus*: Eggert & Guyetant 2003). In these cases the variance in male mating success in the population is expected to be lower than if males that use alternative mating tactics are the same males that receive solicited copulations. In our experiment, however, we found a marginally significant, positive, relation between the number of positive responses that a male received and his sneak copulation rate. Thus, even with alternative male mating tactics, the opportunity for sexual selection is predicted to increase slightly as a result of sneak copulations in this system.

Table 3. Repeated measures analysis of variance of the effect of operational sex ratio treatment and day on outcomes of displays

	Within-subjects contrasts (time)			Between-subjects contrasts (treatment)			Interactions (time*treatment)		
	df	F	P	df	F	P	df	F	P
Multivariate	12,120	2.16	0.018	3,8	8.15	0.008	12,120	0.71	0.743
Proportion interrupted	2.06,20.57*	0.43	0.664	1,10	24.28	0.001	2.06,20.57*	1.23	0.314
Proportion rejected	2.09,20.89*	3.42	0.050	1,10	0.99	0.344	2.09,20.89*	0.87	0.439
Proportion accepted	1.20,12.03*	8.71	0.010	1,10	1.75	0.216	1.20,12.03*	0.69	0.447

*Greenhouse–Geisser approximation as sphericity could not be assumed.
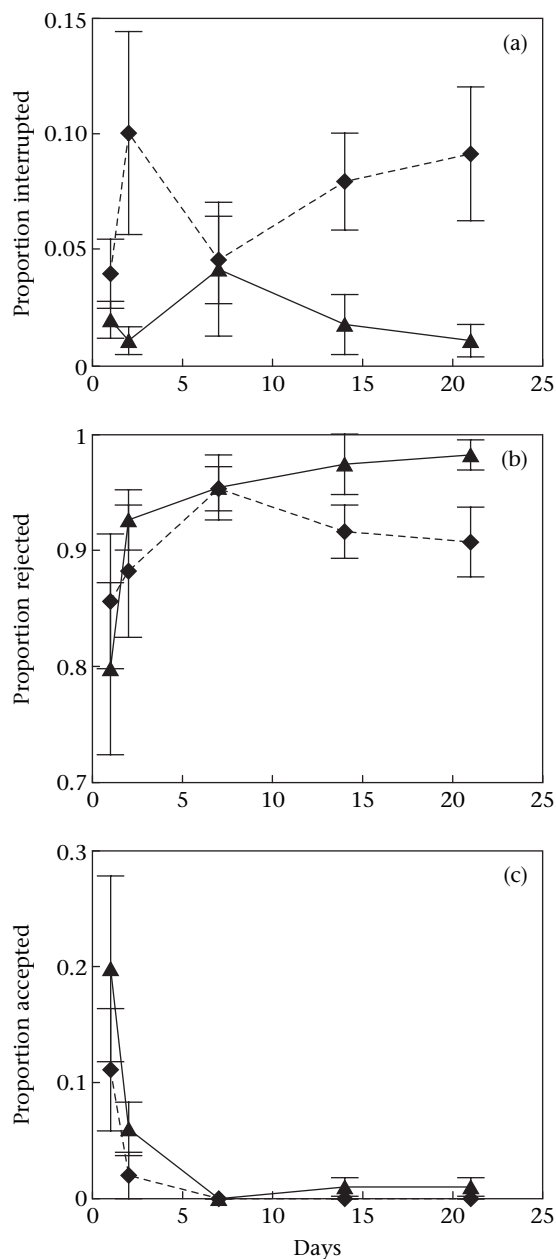
Figure 3. Mean outcome of courtship displays for male-biased (- - -) and female-biased (—) treatments over a 3-week period. (a) Proportion of displays that were interrupted, (b) proportion of displays that the females rejected and (c) proportion of displays that females accepted.

The importance of alternative mating tactics, such as sneak copulations, as an agent of sexual selection will depend on the relative fertilization success of males using these tactics compared to that of males using courtship displays. Recent studies suggest that the role of alternative mating tactics in increasing the reproductive success of males is not trivial. For instance, in guppies males deliver on average a third of the number of sperm in sneak copulations that they do in solicited copulations (Pilastro & Bisazza 1999). Increased levels of male–male interference, such as those in our experiment, may also increase the importance of sneak copulations relative to solicited matings. If females are soliciting copulations less often, because displays are being interrupted, then sneak copulations may contribute to a greater proportion of fertilizations.

Fitness Consequences of Sexual Coercion

Despite higher levels of chasing, jockeying, nipping and sneak copulations we found no effect of OSR and thus sexual coercion on any of the female fitness components we measured. This result was unexpected since sexual coercion is costly in many species (e.g. McKinney et al. 1983; Mesnick & Leboeuf 1991; Watson et al. 1998), although, in the wild, guppies may be subject to potential costs that we were unable to measure such as increased risk of predation or parasite infection.

There are numerous possible reasons why we did not find a cost of sexual coercion. First, since our male-biased treatment had fewer females present than our female-biased treatment decreased female–female competition may have counteracted increased costs of male coercion. Second, contrary to predictions from other studies that increased male harassment will lead to lower fitness (Magurran & Seghers 1994; Brewster & Houde 2003), the increase in male courtship behaviour that we see here may simply impose no cost. Magurran & Seghers (1994) found that sexual harassment in male-biased ponds led to a 25% decrease in time spent foraging compared to ponds with equal numbers of males and females. Since the opportunity for females to forage in our experiment was limited to a short period, if there was an increase in the energy expenditure of females avoiding males, we would have expected a decrease in offspring number. Hester (1964) found such a decrease when he manipulated food rations of female guppies. In his experiment both immediate and subsequent brood sizes were reduced for

Table 4. Female and offspring fitness components

	Male-biased	Female-biased	df	Wilk's λ	F	P
Multivariate			5,6	0.782	0.33	0.875
Female weight gain (g)	0.07±0.01	0.06±0.02	1,10		0.19	0.674
Female gestation time (days)	40.44±3.44	41.87±1.84	1,10		0.13	0.722
Number of offspring	4.50±0.60	4.07±0.48	1,10		0.31	0.591
Proportion of offspring surviving to maturity	0.91±0.04	0.93±0.03	1,10		0.09	0.765
Offspring weight at maturity (g)	0.05±0.00	0.06±0.01	1,10		1.92	0.197

Means are given ±SE.

females in low-food treatments; however, offspring size and gestation time did not differ. That there was no difference in female weight gain in our study also suggests that future investment in eggs would not differ between treatments, since larger females tend to have large broods (Hester 1964).

Although we found no direct costs of sexual coercion, there may be indirect costs for females in the form of decreased selectiveness for mates. The convenience polyandry hypothesis (Thornhill & Alcock 1983) predicts that if sexual harassment is costly, females will mate with males to avoid further unwanted attention, thus leading to a positive relation between harassment rate and female responsiveness to mating. Unlike in the water strider, *Gerris buenoi*, where female mating activity and male harassment rate were positively related (Rowe 1992), we found no difference in female responsiveness (measured as the proportion of accepted displays) under different levels of harassment. Similarly, Brewster & Houde (2003) found that female guppies flee when approached by multiple males, suggesting that, in this system, females try to avoid male harassment rather than alleviate it by accepting superfluous matings. This suggests that the cost of avoiding males is less than the cost of superfluous copulations in guppies, as is also the case in dung flies, *Sepsis cinerea* (Mulhauser & Blanckenhorn 2002).

In summary, we found no effect of OSR on male mating strategies; however, females did experience an increase in sexual coercion because of increased sexual harassment and attempted sneak copulations in male-biased treatments. We found no evidence that this increase in sexual coercion was costly to females, for any of the fitness traits that we measured.

Acknowledgments

References

Berglund, A. 1994. The operational sex ration influences choosiness in a pipefish. *Behavioral Ecology*, **5**, 254–258.

Brewster, J. & Houde, A. E. 2003. Are female guppies more likely to flee when approached by two males? *Journal of Fish Biology*, **63**, 1056–1059.

Byrne, P. G. & Roberts, J. D. 2004. Intrasexual selection and group spawning in quacking frogs (*Crinia georgiana*). *Behavioral Ecology*, **15**, 872–882.

Clutton-Brock, T. H. & Parker, G. A. 1992. Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, **67**, 437–456.

Clutton-Brock, T. H. & Parker, G. A. 1995. Sexual coercion in animal societies. *Animal Behaviour*, **49**, 1345–1365.

Clutton-Brock, T. H., Price, O. & MacColl, A. 1992. Mate retention, harassment, and the evolution of ungulate leks. *Behavioral Ecology*, **3**, 234–242.

Constantz, G. D. 1989. Reproductive biology of Poeciliid fishes. In: *Ecology and Evolution of Livebearing Fishes (Poeciliidae)* (Ed. by G. K. Meffe & F. F. J. Snelson), pp. 33–49. Upper Saddle River, New Jersey: Prentice-Hall.

Crespi, B. J. 1988. Alternative male mating tactics in a thrips: effects of sex ratio variation and body size. *American Midland Naturalist*, **119**, 83–92.

Eggert, C. & Guyetant, R. 2003. Reproductive behaviour of spadefoot toads (*Pelobates fuscus*): daily sex ratios and males' tactics, ages, and physical condition. *Canadian Journal of Zoology*, **81**, 46–51.

Emlen, S. T. & Oring, L. W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215–223.

Endler, J. A. & Houde, A. E. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution*, **49**, 456–468.

Hester, F. J. 1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). *Journal of the Fisheries Research Board of Canada*, **21**, 757–764.

Houde, A. E. 1997. *Sex, Color, and Mate Choice in Guppies*. Princeton, New Jersey: Princeton University Press.

Jirotkul, M. 1999. Operational sex ratio influences female preference and male–male competition in guppies. *Animal Behaviour*, **58**, 287–294.

Jirotkul, M. 2000. Operational sex ratio influences the opportunity for sexual selection in guppies. *Journal of Fish Biology*, **56**, 739–741.

Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, **50**, 1382–1391.

Jones, A. G., Walker, D., Kvarnemo, C., Lindström, K. & Avise, J. C. 2001. How cuckoldry can decrease the opportunity for sexual selection: data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proceedings of the National Academy of Sciences, U.S.A.*, **98**, 9151–9156.

Kokko, H. & Johnstone, R. A. 2002. Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philosophical Transactions of the Royal Society of London, Series B*, **357**, 319–330.

Kokko, H. & Monaghan, P. 2001. Predicting the direction of sexual selection. *Ecology Letters*, **4**, 159–165.

Kvarnemo, C. & Ahnesjö, I. 1996. The dynamics of operational sex ratios and competition for mates. *Trends in Ecology and Evolution,* **11**, 404–408.

McKinney, F. & Stolen, P. 1982. Extra-pair-bond courtship and forced copulation among captive green-winged teal (*Anas crecca carolinensis*). *Animal Behaviour,* **30**, 461–474.

McKinney, F., Derrickson, S. R. & Mineau, P. 1983. Forced copulation in water fowl. *Behaviour,* **86**, 250–294.

Magnhagen, C. 1991. Predation risk as a cost of reproduction. *Trends in Ecology and Evolution,* **6**, 183–186.

Magurran, A. E. & Seghers, B. H. 1994. A cost of sexual harassment in the guppy, *Poecilia reticulata. Proceedings of the Royal Society of London, Series B,* **258**, 89–92.

Marchesan, M. 2002. Operational sex ratio and breeding strategies in the feral pigeon (*Columba livia*). *Ardea,* **90**, 249–257.

Mesnick, S. L. & Leboeuf, B. C. 1991. Sexual behaviour of northern elephant seals 2. Female response to potentially injurious encounters. *Behaviour,* **117**, 262–280.

Mills, S. C. & Reynolds, J. D. 2003. Operational sex ratio and alternative reproductive behaviour in the European bitterling, *Rhodeus sericeus. Behavioral Ecology and Sociobiology,* **54**, 98–104.

Mulhauser, C. & Blanckenhorn, W. U. 2002. The costs of avoiding matings in the dung fly *Sepsis cynipsea. Behavioral Ecology,* **13**, 359–365.

Pettersson, L. B., Ramnarine, I. W., Becher, S. A., Mahabir, R. & Magurran, A. E. 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, *Poecilia reticulata. Behavioral Ecology and Sociobiology,* **55**, 461–468.

Pilastro, A. & Bisazza, A. 1999. Insemination efficiency of two alternative male mating tactics in the guppy (*Poecilia reticulata*). *Proceedings of the Royal Society of London, Series B,* **266**, 1887–1891.

Prohl, H. 2002. Population differences in female resource abundance, adult sex ratio, and males mating success in *Dendrobates pumilio. Behavioral Ecology,* **13**, 175–181.

Quinn, G. P. & Keough, M. J. 2002. *Experimental Design and Data Analysis for Biologists.* Cambridge: Cambridge University Press.

Rowe, L. 1992. Convenience polyandry in a water strider: foraging conflicts and female control of copulation frequency and guarding duration. *Animal Behaviour,* **44**, 189–202.

Schlupp, I., McKnab, R. & Ryan, M. J. 2001. Sexual harassment as a cost for molly females: bigger males cost less. *Behaviour,* **138**, 277–286.

Shine, R., Langkilde, T. & Mason, R. T. 2003. The opportunistic serpent: male garter snakes adjust courtship tactics to mating opportunities. *Behaviour,* **140**, 1509–1526.

Thornhill, R. & Alcock, J. 1983. *The Evolution of Insect Mating Systems.* Cambridge, Massachusetts: Harvard University Press.

Watson, P. J., Arnqvist, G. & Stallman, R. R. 1998. Sexual conflict and the energetic costs of mating and mate choice in water striders. *American Naturalist,* **151**, 46–58.