

For a few males more: do changes in sex ratio predict reproductive success and offspring survival?

Thierry Lodé

Ethologie-Evolution-Ecologie, Université de Rennes 1, Rennes, France

ABSTRACT

Background: Sexual selection theory predicts that if the operational sex ratio is male-biased, females will be choosy, whereas males, for the most part, will compete with each other for mates. However, the influence of the operational sex ratio on reproductive success and offspring survival has rarely been studied.

Question: Does the operational sex ratio influence reproductive success and offspring survival?

Methods: I surveyed the sex ratio and reproductive success of agile frog (*Rana dalmatina*) populations at 19 breeding sites in western France. I assessed reproductive success using ratios among the number of clutches, the number of froglets, and the daily number of adult frogs. I also determined the survival rate of offspring.

Conclusions: Males dominated in 90% of ponds; the mean adult sex ratio and operational sex ratio ranged from 0.84 to 3.14 and from 2.84 to 13.71 respectively. The number of post-metamorphic froglets per clutch averaged 9.37 (S.D. = 2.37). Variations in the adult sex ratio and operational sex ratio did affect reproductive success. Froglet survival was diminished in populations with higher proportions of males. Furthermore, although each female produced a single clutch regardless of sex ratio, higher proportions of males depressed the average number of clutches per male. Evidently, adult male competition and sexual conflict reduce the fitness of both males and females.

Keywords: fitness, mating success, operational sex ratio, survival.

INTRODUCTION

Stochastic sex ratio variation is an important parameter in determining the intensity of sexual selection. The adult sex ratio is the ratio of the total number of adult males to the total number of adult females. Caswell (2001) stated that intrasexual competition regulates the adult sex ratio. In breeding sites, however, the sex ratio changes day by day, which Emlen and Oring (1977) call the operational sex ratio (i.e. the ratio of fertilizable females to active males at a given time). Variation in the operational sex ratio arises mainly from the

Correspondence: T. Lodé, UMR-CNRS 6552, Ethologie-Evolution-Ecologie, Université de Rennes 1, Campus de Beaulieu, 35042 Rennes, France. e-mail: thierry.lode@univ-rennes1.fr

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asynchrony of receptivity between the sexes. One of the hypotheses of sexual selection theory is that a bias in the operational sex ratio affects mating success because competition limits access to mates (Kodric-Brown, 1988; Clutton-Brock and Vincent, 1991).

Operational sex ratios might predict which sex will compete for mates and thereby might influence sexual competition and mate choice. Many studies have noted that, with a male-biased operational sex ratio, males are the predominant competitors and females are the choosy sex (Krupa and Sih, 1993; Pröhl, 2002). However, a female-biased operational sex ratio can lead to role-reversal. Experiments on sand gobies by Kvarnemo *et al.* (1995) and on certain katydids by Gwynne and Simmons (1990) showed that a female-biased operational sex ratio results in competition among courting females, whereas males become more selective of their mates (Gwynne and Simmons, 1990; Vincent *et al.*, 1994).

In this study, I investigate variations in the operational sex ratio of the agile frog *Rana dalmatina*, a species with no parental care. I address two questions: Do variations in the operational sex ratio affect reproductive success? And do these variations influence the survival rate of the offspring?

METHODS

Organism

The agile frog, *Rana dalmatina*, is widely distributed throughout Europe. Agile frogs are mainly terrestrial and nocturnal. They breed from February to March in small aggregations at night (Lodé and Lesbarrères, 2004). Males arrive a few days before females, spend more time in the ponds, and use low-intensity calls, often underwater, to attract their mates. Males are territorial, so that amplexing pairs and clutches are distant from each other. Each female lays a single clutch per breeding season (Lodé and Lesbarrères, 2004). The tadpoles metamorphose approximately 2 months after hatching.

Field study

I studied 19 sites in western France, separated from each other by a minimum of 20 km. I surrounded each pond with plastic sheets (height 1.5 m) to serve as a barrier to frog movement. I supported sheets with wooden stakes, deeply embedded into the soil, to protect barriers against unfavourable weather conditions. I buried traps (plastic buckets of diameter 30 cm; height = 30 cm) every 3 m on the outer and the inner side of each barrier. I covered the traps with a semi-rigid, transparent plastic film, cut in such a way that an individual frog could fall in but not escape.

I measured, weighed, and sexed the trapped individuals. Males were identified by the rough, grey patch close to the thumb on the forelimb and females by the presence of eggs in the oviduct. I toe-clipped trapped individuals for identification purposes.

Sex ratio and reproductive success

At each site, the total number of individuals (N) included the total numbers of males (N_m) and of females (N_f). I surveyed each site twice daily and noted the numbers of males and females arriving daily (N_{md} and N_{fd} respectively). I calculated the adult sex ratio (ASR) and the operational sex ratio (OSR) as follows: $ASR = N_m$ (total males)/ N_f (total females);

$OSR = N_{md}$ (daily number of males)/ N_{fd} (daily number of females). I categorized adult sex ratios as follows:

- female-biased ($ASR < 1$)
- moderately male-biased ($1.4 < ASR < 1$)
- strongly male-biased ($2.5 < ASR < 1.4$)
- severely male-biased ($ASR > 2.5$)

Likewise, I categorized operational sex ratios as follows:

- moderately male-biased ($4 < OSR < 2$)
- strongly male-biased ($9 < OSR < 5$)
- severely male-biased ($OSR > 11$)

(operational sex ratio was never female biased).

I categorized the ponds into early, medium, and late reproductive periods according to the mean arrival time of breeders. I measured the duration of each mating period from the time of the first adult frog's arrival to the time of the last adult frog's departure. I counted the number of clutches per day and marked each clutch with natural colouring to avoid recounting it. Towards May/June, I counted the total number of emergent post-metamorphic froglets (N_{te}) all around each pond. Thus, I determined reproductive success as: (1) the ratio between N_c (number of clutches) and N_m (males) and N_f (females) respectively; and as (2) the ratio between N_{te} (number of froglets) and N_m and N_f respectively.

The number of offspring surviving to dispersal should be an accurate estimate for fitness (Wiegmann *et al.*, 1997; Cunningham and Birkhead, 1998). I assessed the survival rate of offspring by relating the number of emergent froglets to the number of eggs per clutch as follows. I selected six clutches at random from each pond and weighed them. Next, I took a sample from each clutch, counted the number of eggs and accurately weighed them. Using these measurements I calculated the average number of eggs per clutch. I then determined the survival rate as the average number of emergent froglets divided by the average number of eggs.

I tested for differences between the period of reproduction and the different sex-ratio categories using the Kruskal-Wallis (KW) non-parametric test with Tukey *post hoc* tests. I obtained correlations using Pearson coefficients (r_p).

RESULTS

Population structure and breeding period

The 19 sites averaged 44 adults each (range 12–111; s.d. = 24.5; $n = 836$). Males predominated at 90% of ponds. The number of males ranged from 7 to 82 and averaged 27.5 males per pond (s.d. = 18.7; $n = 523$); the number of females ranged from 5 to 29 and averaged 16.5 females per pond (s.d. = 7.6; $n = 313$).

The adult sex-ratio ranged from a low of 0.76 to a high of 3.32 (mean 1.68; s.d. = 0.70) (Table 1). Ten percent of the ponds studied had a female-biased adult sex-ratio, 37% were moderately male-biased, 37% were strongly male-biased, and 16% were severely

Table 1. Reproductive success with respect to the different categories of the adult sex ratio

Sex-ratio category	Breeding sites	Adult sex ratio	No. of clutches per female	No. of clutches per male	No. of froglets per female	No. of froglets per male
Female biased	14	0.760	1.00	1.32	10.0	13.1
	16	0.913	1.00	1.10	11.0	12.1
	Mean	0.837	1.00	1.21	10.5	12.6
	s.D.	0.108	0.00	0.16	0.8	0.7
Moderately male biased	8	1.214	0.93	0.76	12.0	9.9
	3	1.261	1.00	0.79	10.5	8.3
	7	1.333	1.00	0.75	10.2	7.6
	13	1.385	1.00	0.72	9.1	6.6
	1	1.389	1.00	0.72	12.7	9.1
	2	1.400	1.00	0.71	9.9	7.0
	4	1.400	1.00	0.71	13.6	9.7
	Mean	1.340	0.99	0.74	11.1	8.3
	s.D.	0.075	0.03	0.03	1.7	1.3
Strongly male biased	19	1.474	1.00	0.68	12.4	8.4
	17	1.484	1.00	0.67	7.8	5.3
	9	1.579	1.00	0.63	8.3	5.3
	6	1.625	1.00	0.62	9.1	5.6
	5	1.667	1.00	0.60	6.7	4.0
	12	1.800	1.00	0.56	6.9	3.8
	14	1.800	1.00	0.56	7.2	4.0
	Mean	1.633	1.00	0.62	8.3	5.2
	s.D.	0.134	0.00	0.05	2.0	1.6
Severely male biased	18	2.828	1.00	0.35	7.0	2.5
	11	3.273	1.00	0.31	6.2	1.9
	10	3.316	0.95	0.29	6.3	1.9
	Mean	3.14	0.98	0.31	6.5	2.1
s.D.	0.27	0.03	0.03	0.5	0.3	

male-biased (Fig. 1). The operational sex ratio ranged from 2.14 to 16.04 (mean 8.23; s.D. = 4.12, Table 2). Twenty-one percent of ponds were moderately male-biased, 52% were strongly male-biased, and 26% were severely male-biased (Fig. 1).

The numbers of male and female frogs did not differ significantly with respect to their precocious arrival at spawning ponds (KW test for males: $H_{df=2} = 3.4$, $P > 0.05$; KW for females: $H_{df=2} = 1.6$, $P > 0.05$). Neither the adult nor the operational sex ratio (KW test for adult sex ratio: $H_{df=2} = 1.1$, $P > 0.05$; KW test for operational sex ratio: $H_{df=2} = 2.1$, $P > 0.05$) showed a significant difference over the periods I defined for this study (i.e. early, medium, and late).

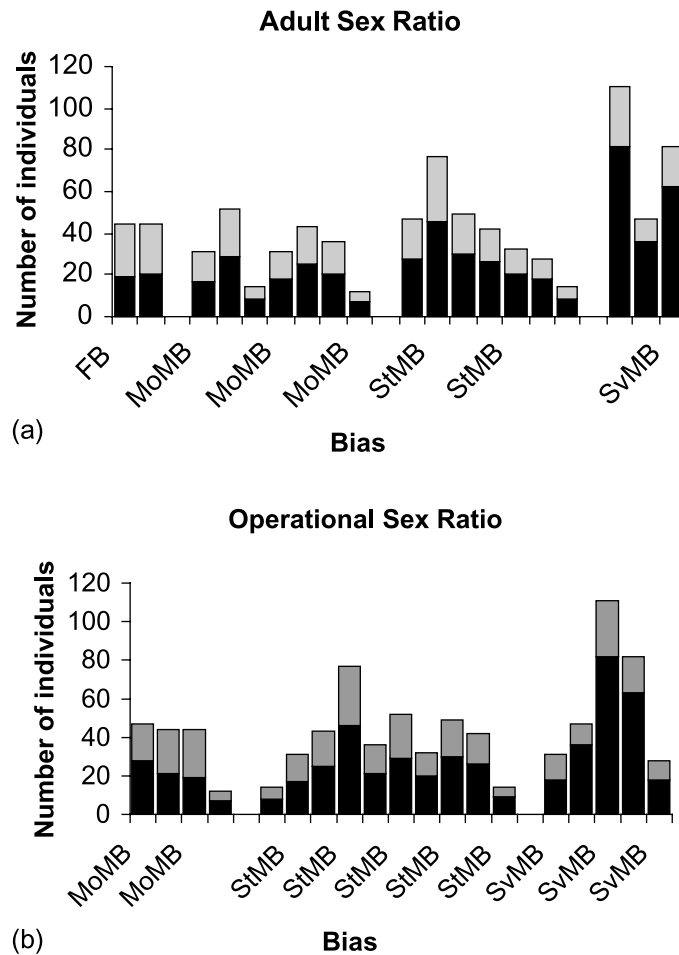


Fig. 1. (a) Variations in the different categories of the adult sex ratio. (b) Variations in the different categories of the operational sex ratio (mean per site). FB = female biased; MoMB = moderately male biased; StMB = strongly male biased; SvMB = severely male biased. Black = males, grey = females.

Reproductive success

The number of clutches averaged 16.4 (s.d. = 7.58; range 5–31; $n = 311$) and the number of post-metamorphic froglets averaged 152.2 per breeding pond (s.d. = 75.2; range 36–254; $n = 2891$). Unsurprisingly, the number of clutches correlated with the number of adult frogs ($r_p = -0.814$, $P < 0.001$). However, the number of clutches was not related to pond size ($r_p = -0.250$, $P > 0.05$), although one might have expected a positive relationship between them.

The number of clutches per male present on a pond averaged 0.68 (s.d. = 0.24; range 0.268–1.316). This ratio correlated significantly and inversely with the number of males ($r_p = -0.659$, $P < 0.002$). It was not possible to calculate the number of clutches fathered by any individual male because I did not conduct a parentage analysis. My results do agree with the premise that agile frog females lay a single clutch per season because the value of

Table 2. Reproductive success with respect to the different categories of the daily operational sex ratio

Sex-ratio category	Breeding sites	Operational sex ratio	No. of clutches per female	No. of clutches per male	No. of froglets per female	No. of froglets per male
Moderately male biased	19	2.135	1.00	0.68	12.4	8.4
	16	2.446	1.00	1.10	11.0	12.1
	15	3.112	1.00	1.32	10.0	13.1
	4	3.679	1.00	0.71	13.6	9.7
	Mean	2.843	1.00	0.95	11.8	10.8
	s.d.	0.690	0.00	0.31	1.6	2.1
Strongly male biased	7	5.590	1.00	0.75	10.2	7.6
	8	6.124	0.93	0.76	12.0	9.9
	1	6.625	1.00	0.72	12.7	9.1
	17	6.672	1.00	0.67	7.8	5.3
	2	6.989	1.00	0.71	9.9	7.0
	3	7.590	1.00	0.79	10.5	8.3
	5	8.926	1.00	0.60	6.7	4.0
	9	9.284	1.00	0.63	8.3	5.3
	6	9.286	1.00	0.62	9.1	5.6
	14	9.443	1.00	0.56	7.2	4.0
	Mean	7.653	0.99	0.68	9.4	6.6
		s.d.	1.461	0.02	0.08	2.0
Severely male biased	13	11.683	1.00	0.72	9.1	6.6
	11	12.537	1.00	0.31	6.2	1.9
	18	12.682	1.00	0.35	7.0	2.5
	10	15.590	0.95	0.29	6.3	1.9
	12	16.038	1.00	0.56	6.9	3.8
	Mean	13.706	0.99	0.44	7.1	3.3
	s.d.	1.97	0.02	0.19	1.2	2.0

N_c per female averaged 0.99 (s.d. = 0.02; range 0.929–1.0), with a significant correlation between the number of clutches and the number of females ($r_p = 0.999$, $P < 0.0001$).

The total number of froglets per clutch averaged 9.37 (s.d. = 2.37; range 6.18–13.60), although one cannot assign froglets to particular clutches. The average number of eggs per clutch was 771. The number of post-metamorphic emergent froglets per male (N_{te}/N_m) was 6.64 (s.d. = 3.28; range 1.89–13.11), while the number of post-metamorphic emergent froglets per female (N_{te}/N_f) was 9.30 (s.d. = 2.33; range 6.18–13.60). The number of post-metamorphic emergent froglets correlated significantly with the number of females ($r_p = 0.871$, $P < 0.0001$) but not with the number of males ($r_p = 0.325$, $P > 0.05$).

Neither the number of clutches (KW test: $H_{df=2} = 1.0$, $P > 0.05$) nor the number of post-metamorphic emergent froglets (KW test: $H_{df=2} = 1.45$, $P > 0.05$) was significantly related to the period of reproduction. Moreover, the duration of larval development (until metamorphosis) did not significantly affect adult reproductive success (number of clutches: $r_p = -0.359$, $P > 0.05$; number of froglets: $r_p = -0.377$, $P > 0.05$).

Sex ratios, reproductive success, and survival rate

Total male reproductive success, as revealed by the number of clutches, varied significantly with the different categories of the adult and operational sex ratios (KW test for adult sex ratio: $H_{df=3} = 16.2$, $P < 0.001$; KW test for operational sex ratio: $H_{df=2} = 6.9$, $P < 0.03$). Male reproductive success was negatively correlated with both the adult sex ratio ($r_p = -0.878$, $P < 0.0001$) and operational sex ratio ($r_p = -0.750$, $P < 0.0001$). Female reproductive success, however, did not correlate with either the adult or operational sex ratio (KW test for adult sex ratio: $H_{df=3} = 2.5$, $P > 0.05$; KW test for operational sex ratio: $H_{df=2} = 0.8$, $P > 0.05$) (see Tables 1 and 2).

In contrast, both the number of post-metamorphic froglets per female and the number of post-metamorphic froglets per male differed significantly with respect to the different categories of the adult and operational sex ratios (KW test for females: adult sex ratio, $H_{df=3} = 14.4$, $P < 0.002$; operational sex ratio, $H_{df=2} = 9.2$, $P < 0.01$; KW test for males: adult sex ratio, $H_{df=3} = 16.4$, $P < 0.001$; operational sex ratio, $H_{df=2} = 11.5$, $P < 0.003$) (Fig. 2).

Offspring had a low survival rate (1.21%, s.d. = 0.31). The rate depended significantly (Fig. 3) on both the adult sex ratio ($r_p = -0.647$, $P < 0.003$) and the operational sex ratio ($r_p = -0.769$, $P < 0.0001$). Similarly, survival rates of offspring varied significantly with respect to the different categories of the adult sex ratio (KW_{df=3} = 11.8, $P < 0.008$; Table 3). Although female-biased populations showed a slightly lower survival rate, no differences were observed between the female-biased populations and the moderately male-biased populations (Tukey post tests: $P > 0.05$). However, strongly male-biased populations were characterized by very low offspring survival rates, rates significantly lower than those in moderately male-biased populations (Tukey post tests: $P < 0.05$).

DISCUSSION

The reproductive output of agile frogs depended mainly on the number of females. Nevertheless, reproductive success was strongly influenced by the operational sex ratio. The variance in male reproductive success was high in strong male-biased and low in female-biased operational sex ratios, demonstrating that males were limited by females. That the number of females determined the number of clutches and offspring, whereas the number of males did not, supports the theory that operational sex ratios increase the opportunity for sexual selection. Furthermore, the more the sex ratio swings towards a male bias, the poorer the breeding success, which suggests that a male-biased sex ratio reduces the survival rate of the offspring. However, a female-biased operational sex ratio did not improve reproductive success.

A skewed operational sex ratio intensifies the competition for mates and alters reproductive behaviour, as suggested by Emlen and Oring (1977). The ratio of males was approximately three males for a single clutch. Perhaps that helps to explain why females do not interfere with each other's amplexus attempts, whereas males exhibit aggressive interactions. Furthermore, while breeding, male agile frogs are territorial. Territoriality might reduce the average reproductive success of males when male densities are high or breeding sites are small. Both high density and the operational sex ratio were reported to be factors promoting an increase in mate guarding (Yamamura, 1987). In agile frogs, territorial breeding behaviour could be regarded as prolonged mate guarding because territorial males prevent females from further mating.

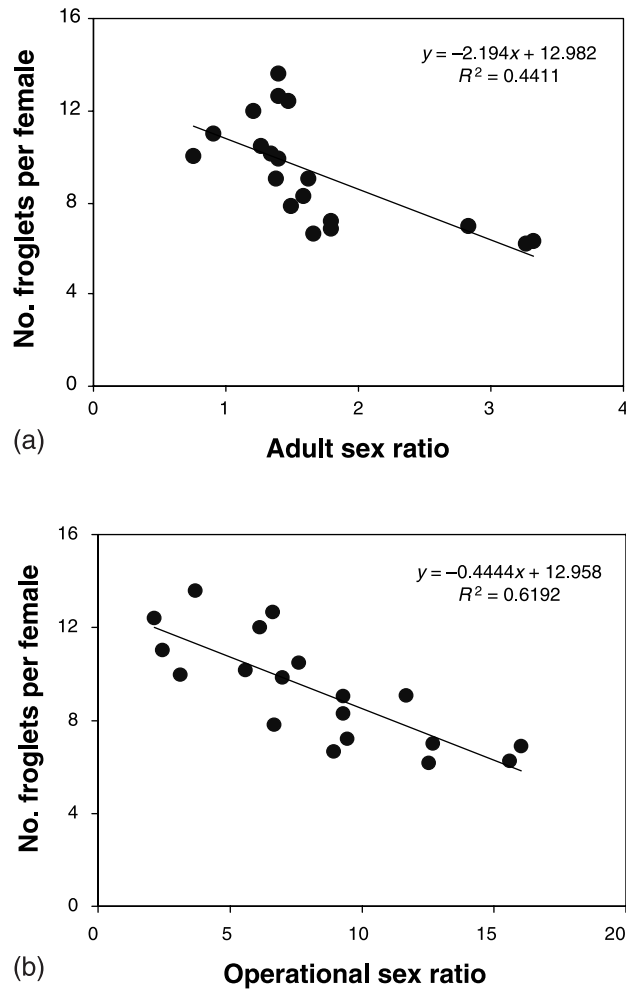


Fig. 2. The influence of the adult sex ratio (a) and operational sex ratio (b) on female reproductive success with respect to the number of post-metamorphic emergent froglets.

A large number of studies have focused on changes in frog reproductive behaviours, especially choosiness and competition (see review in Kvarnemo and Ahensjö, 1996). The potential effect of sex ratio on reproductive success and on offspring survival, although poorly documented to date, is not pure speculation. Lodé *et al.* (2005) reported that in *Rana dalmatina*, a biased sex ratio increased the cost of reproduction when estimated by clutches, froglets, and survival rates, especially in extremely male-biased sex ratios.

Reproductive effects of sex ratio: some non-exclusive hypotheses

More males means more fertilization. Perhaps a large number of males increases fertilization. Levitan *et al.* (1992) suggested that a surplus of males is more efficient for external fertilization. But my results showed that increasing male-biased sex ratios led to a significant

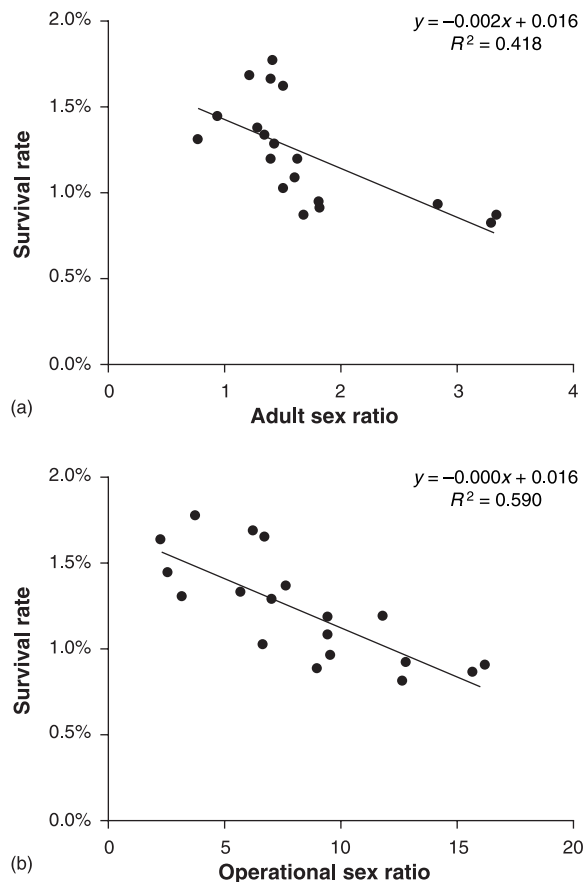


Fig. 3. Correlations of the survival rates of the offspring with (a) the adult sex ratio and (b) the operational sex ratio.

decrease in the number of froglets per clutch. Either more males reduced fertilization success or reduced froglet survival. Byrne and Roberts (1999) noted reduced fertilization in the females of the myobatrachid *Crinia georgiana* when mated with multiple males. And, in the presence of male-biased adult sex ratios, lizard females could be harassed by males and suffered reduced fertility (Le Galliard *et al.*, 2005).

More males, more female choice. Stringency of mate choice was the focus of operational sex ratio theory. According to the theory of sexual selection, the predominant sex (commonly males) would compete for mates while the other (commonly females) chose its mates (Burglund, 1994; Souroukis and Murray, 1995). A study of St. Peter's fish *Sarotherodon galilaeus* showed that female selectivity of mates increased due to greater availability of possible mates (Balshine-Earn, 1996). My results, however, show that female mating success was lowest in male-biased populations, suggesting that female mate choice played no role (or no more than a weak one) in enhancing the reproductive success of this frog species.

A corollary of this hypothesis is that a highly male-biased sex ratio will diminish male mating success (Halliday and Tejedó, 1995). Indeed, Pröhl (2002) reported that the intensity of sexual

Table 3. Survival rates of offspring with respect to the different categories of the adult sex ratio

Sex-ratio category	Breeding sites	Adult sex ratio	Survival rate
Female biased	15	0.760	0.0129
	16	0.913	0.0143
	Mean	0.837	0.0136
	s.d.	<i>0.108</i>	
Moderately male biased	8	1.214	0.0168
	3	1.261	0.0136
	7	1.333	0.0132
	13	1.385	0.0118
	1	1.389	0.0164
	2	1.400	0.0128
	4	1.400	0.0176
	Mean	1.340	0.0146
s.d.	<i>0.075</i>		
Strongly male biased	19	1.474	0.0161
	17	1.484	0.0101
	9	1.579	0.0108
	6	1.625	0.0118
	5	1.667	0.0086
	12	1.800	0.0089
	14	1.800	0.0093
	Mean	1.633	0.0108
s.d.	<i>0.134</i>		
Severely male biased	18	2.828	0.0091
	11	3.273	0.0080
	10	3.316	0.0086
	Mean	3.139	0.0086
s.d.	<i>0.27</i>		

selection in *Dendrobates pumilio* was higher when the operational sex ratio was male-biased. The *Rana dalmatina* results also supported the prediction – strongly male-biased operational sex ratios reduced the mating success of males. However, Klemme *et al.* (2007) reported the opposite.

A female-biased operational sex ratio can provide an opportunity for males to enhance their reproductive success (Jones *et al.*, 2005). For instance, the level of polygyny could increase, especially if reproduction were resource dependent (Davies and Lundberg, 1984). Yet sexual selection on male *Clethrionomys* was strongest with female-biased operational sex ratios.

More males, more competition. Sand gobies experience more male–male aggressive interactions per individual when the sex ratio is male-biased (Kvarnemo *et al.*, 1995). This increased intraspecific competition could reduce reproductive success in males. Excessive competition among males might also restrict female choice (but see Candolin, 1999; Jirotkul, 1999). Females might

also be directly affected. In lizard populations, an excess of adult males led to increased aggression of males towards adult females, whose survival and fecundity were reduced (Le Galliard *et al.*, 2005).

In addition, a biased operational sex ratio might result in alternative mating behaviours [guppies (Jirotkul, 1999); water striders (Krupa and Sih, 1993); sand gobies (Kvarnemo *et al.*, 1995)], leading to a larger range in mating variance rather than increasing sexual selection. Jones *et al.* (2001), for instance, showed that some individuals specialized in alternative behaviours, while others employed the more common breeding tactic. When the operational sex ratio was male-biased, water strider males augmented the number and the duration of copulations as if to compensate for the extra male competition (Arnqvist, 1992; Vepsäläinen and Savolainen, 1995). The more skewed the sex ratio, the more male alternative behaviours occurred (Kvarnemo *et al.*, 1995, Jones *et al.*, 2005). Nonetheless, my results showed that reproductive success diminished if the sex ratio was male-biased. So, at least in agile frogs, if there were such alternative or compensatory behaviours, they did not compensate fully for the male bias.

More males, more sexual conflict. By intensifying the competition and the sexual conflict among males (see Rice, 2000), a severe bias in the operational sex ratio should reduce reproductive success. Perhaps conflict between the sexes – in particular male harassment – also increases in a male-biased population (see Cordero, 1999, Lodé, 2006). Presumably, harassment evolved because it increased the number of matings when male abundance reduced an individual male's chances of being chosen as a mate (Clutton-Brock and Parker, 1995). But harassment costs females their ability to choose and coerces them into copulation (see Le Galliard *et al.*, 2005). Female fitness might also decline (Rowe *et al.*, 1994; Yasui, 1998).

Where males predominate, they do cause dramatic damage to females. Some studies have shown that a serious male-biased sex ratio even results in a rise in female mortality, such as in *Crinia georgiana* (Byrne and Roberts, 1999) and in *Ovis aries* (Reale *et al.*, 1996). But females of some species do consent to forced matings, in effect endorsing convenience polyandry because it is less harmful to them than the alternative (Cordero-Rivera and Andrés, 2002).

I observed coercion regularly in my study sites. The conflict of interest between the two sexes was the focus for the alteration in reproductive success. Although the number of females determined both the number of clutches and the number of offspring in *Rana dalmatina* populations, the response of the females could be attributed to the varying sex ratios. Low reproductive success and survival rates of agile frogs might result from females being unable to resist male harassment when the sex ratio is male-biased. The results of the present study support the conclusion that mate conflict imposes a severe mating cost on females, and that reproductive success and offspring survival rates were indeed influenced by variations in the sex ratio.

ACKNOWLEDGEMENTS

I thank Michael Rosenzweig and two anonymous referees for many suggestions that improved the manuscript. Thanks also to Mira Krishnakumar for her assistance.

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