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No Male Preference for Large Females in the Asian Common Toad (*Duttaphrynus melanostictus*): Effect of the Sex Ratio and Breeding System

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Abstract Mating preferences are common in natural populations of animals. Numerous studies have shown that male mate choice can occur in a wide range of taxa. However, male mating preferences are still poorly understood in anurans. Sexual selection theory predicts that male mate choice is not expected to arise if 1) adult population exhibited a highly male-biased sex ratio which will diminish male mating success; 2) males provide less parental care; 3) mating success of males is associated with chorus tenure in which males would maximize their fitness by mating with multiple mates. We tested these predictions in the Asian common toad *Duttaphrynus melanostictus* from southeastern Tibet, China. Our field experimental results indicated that, the breeding population exhibited a highly male-biased sex ratio, called males did not defend sites which contain significant resources required by females and offspring, both sexes provided no parental care after egg-laying, and the toad species was characterized with prolonged breeding season chorus attendance. In male mate choice experiment, males did not show preferences for a larger gravid female over a smaller gravid female. We suggest that male mating success in the Asian common toad is likely determined by the number but not the quality of mates. Future research should focus on how sexual selection on male acoustic signaling and how female preference exert different types of selection pressure on male call traits in this Tibet toad.

Keywords Asian common toad, chorus attendance, *Duttaphrynus melanostictus*, male mating preference, parental care, sex ratio

1. Introduction

A key question in sexual selection theory is which sex is choosy about its mates (Andersson, 1994). Growing studies on sexual selection have documented that females are generally the choosier sex and that males compete for mates, and these differences between sexes arise mostly because females usually invest more in offspring, have lower potential reproductive rates, or are less abundant than males (Trivers, 1972; Emlen and Oring, 1977; Clutton-Brock and Vincent, 1991; Eberhard, 1996; Sih *et al.*, 2014). However, even in species without sex-role reversal, many studies have shown that male mate choice can occur in a wide range of taxa including insects (Bonduriansky, 2001; Byrne and Rice, 2006; Chenoweth *et al.*, 2007; Tigreros *et al.*, 2014), fishes (Kodric-Brown, 1989; Amundsen and Forsgren, 2001; Amundsen and Forsgren, 2003; Agrillo *et al.*, 2008), amphibians (Marco *et al.*, 1998; Liao and Lu, 2009; Yu and Sharma, 2012; Jaworski *et al.*, 2018), reptiles (Olsson, 1993; Weiss, 2002), birds (Jones and Hunter, 1993; Amundsen *et al.*,

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1997; Mank, 2007; Gillingham *et al.*, 2009) and mammas (Szykman *et al.*, 2001; Preston *et al.*, 2005; Charpentier *et al.*, 2010). Male mate choice should occur when the costs of copulation are high or variance in females' fecundity is greater (reviewed in Edward and Chapman, 2011). Although data for increased costs to mate and high variance in female fertility so far are limited, some empirical support exists for this assumption (Kvarnemo and Simmons, 1999; Byrne and Rice, 2006; Nandy *et al.*, 2012; Fitzpatrick *et al.*, 2014).

Male choice is expected to evolve in species in which males are sensitive to cues that are correlated with female fecundity, such as body size or other traits that reliably signal fecundity (Amundsen, 2000; Bonduriansky, 2001; Chenoweth and Blows, 2003; LeBas *et al.*, 2003; Byrne and Rice, 2006). In fact, male mating choosiness can be affected by variations in sex ratio. Some studies have argued that males exhibit mate choice only under high female density and show no mate choice under low female density (Berglund, 1994, 1995). Furthermore, sexual selection theory predicts that male choice should generally be rare if males invest less in parental care because they may be more likely to gain additional mating opportunities (Trivers, 1972; Møller and Birkhead, 1993; Andersson, 1994; Balshine-Earn and Earn, 1998). In addition, variance in male reproductive success is greater than that in females (Petersdorf and Higham, 2016). Thus, males should be favored by natural selection if they maximize their reproductive success by increasing the number of mates, which likely lead to increased genetic representation in future generations (Williams,1975). This pattern has been demonstrated in anurans, as many studies have shown that chorus attendance (nights spent at the breeding site) is correlated with male mating success, whatever the mating system associated with this chorus (review in Wells, 2007). Under such context, male mating success is generally determined by the number but not the quality of mates and thus male preferences for females were not expected.

Compared with female mate choice, few studies have examined mate choice by males and the factors underlying its evolution. In this study, we investigated whether male mate choice is present in the mating pattern of the Asian common toad (*Duttaphrynus melanostictus*) and elucidated the mechanisms by which it occurs.

To do so, field experiments were designed to assess whether males prefer larger gravid females as mates. We hypothesize that, if no male mate choice occurs in the Asian common toad, then, 1) the sex ratio is highly male-biased, 2) males provide no parental care after female egg-laying, and 3) chorus attendance is involved in the mating system.

2. Materials and Methods

2.1. Study site and study species The study site is at Xiachayu, southeast Tibet, China. The climate is subtropical-humid-monsoonal, with an annual precipitation of above 800 mm. Mean annual temperature of this area is 12.0 ℃ and the dominant vegetation type is subtropical evergreen broad-leaved forests (Li, 2014; Hou *et al.*, 2017). In this study, paddy fields close to the Xiachayu town are used by the Asian common toad as spawning sites (28°29′ N, 97°01′ E, 1527 m elevation). The water depth at the sites was among 10–15 cm.

The Asian common toad occurs in southwestern and southern China (including Hainan and Taiwan), Indonesia, India and Sri Lanka (Fei *et al.*, 2012). Female-biased sexual size dimorphism is evident in this toad and clutch size is positively related to female body size (Fan *et al.*, 2013). In addition, several studies have found that the toad is a typical explosive breeder and males engage in mating calls during the breeding period (Gramapurohit and Radder, 2012; Wei *et al.*, 2012).

2.2. Male mate choice experiments Males and spawning females were captured by hand in early May of 2019, and their body size (snout–vent length) was measured using a vernier caliper to the nearest 0.01 mm. A total of 50 adult male toads were treated as the test toads that were randomly divided into five groups. The mean body size of test adult males is 74.89 ± 6.91 (rang: 59.91–85.57) mm. Ten gravid females were chosen as the object toads and were divided into two groups (larger gravid female group: 98.89 ± 5.90 mm, $n = 5$; smaller gravid female group: 70.67 ± 5.41 mm, $n = 5$), with the difference in body size being significant (independent samples t-test: $t = 7.88$, $df = 8$, $P < 0.001$).

The mate choice experiments were performed in a yard (nearly 2 km away from capture sites) from 12–16 May 2019. Both sexes only exhibit active breeding behavior at night, so the experiment was started at approximately 20:00 p.m. each day. All the animals were isolated in separate containers with fresh water for 15 min before being placed into mate choice experiments. The experimental trial performed in a rectangular tank (90 cm length × 40 cm width × 20 cm height) filled with fresh water to a depth of 15 cm, as described previously (Marco *et al.*, 1998; Liao and Lu, 2009). The test males were given a simultaneous choice between larger and smaller gravid females. At the beginning of each group trial (n

= 10), tethered stimulus female was placed randomly at one end of the tank. Then, each test male was covered by a plastic transparent cylinder (12 cm × 15 cm) which was centrally located in the experimental tank. After 5 min, we removed the cylinder of test male and such an observation time is likely enough for test male to judge object females (Liao and Lu, 2009). For the next 10 min, we recorded the time of the test male spent in amplexus with a female. If there was no amplexus after 10 min, the trial was ended and we recorded the test male as making no choice. These instances were excluded from analysis. The tank was flushed with fresh water after each trial so as to minimize olfactory contamination. When the new group trials started, object gravid females were changed by another pair till all experiments were completed. The females were reused in each group experiment because sex ratio is strongly male biased in the study population and we cannot collect enough females to perform these experiments. At last, the toads were released in situ after toe-clipping.

2.3. Breeding data collection During April 28–June 23, 2019, we visited the breeding site daily (18:00–22:30 p.m.) using a 2-V hand light. Timing and length of the breeding season and breeding behavior were determined in the study population. In the early breeding season (May1–15), some single males and both sexes from amplectant pairs were captured and processed as above to examine male mate preference. From May 17 to June 23, the number of amplectant pairs and the single male and female found each day were recorded.

2.4. Statistical analysis All statistical analyses were performed by SPSS 16.0 for Windows (SPSS Inc., Chicago, IL, USA). An independent samples t-test was used to determine whether there were significant differences between two groups of female's body size. Chi-square test was used to test whether males have a preference for larger gravid females. All values are given as the mean ± standard deviation (mean ± SD).

3. Results

3.1. Male mate choice Test males amplexed the larger gravid females in 16 of 50 trials and clasped the smaller gravid female in 14 of 50 trials. Test males did not prefer the larger gravid females to the smaller ones (Chi-square test, χ^2 =0.13, P = 0.715; Figure 1). The time that the test males spend to amplex the larger gravid females was 2.81 ± 2.43 min and that of the smaller ones was 3.93 ± 3.27 min. The time that test males attempt to amplex either gravid female was not significantly different (Student's t test, t =1.07; df =28, P = 0.294).

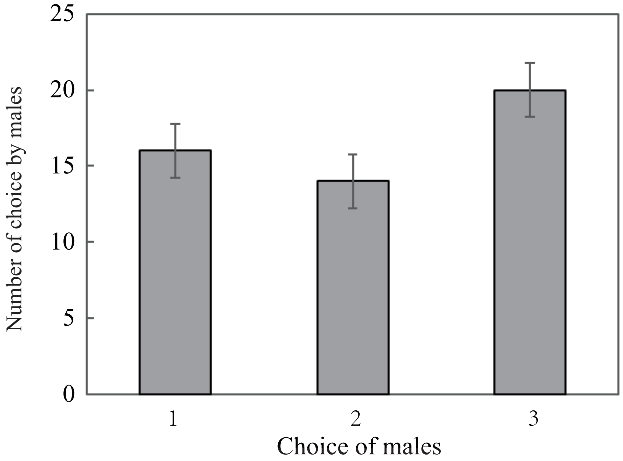

Figure 1 Results of mating preference in the male Asian common toad used for field experiments. 1: males amplexed the larger gravid female; 2: males amplexed the smaller gravid female; 3: males make no choice.

3.2. Breeding characteristics The toads breed in spring and summer (from late April to late June). Males aggregate in paddy fields or permanent ponds at night and vocalize to attract conspecific females. At the beginning of breeding season (near the end of April), some males arrived first and vocalize at night. During this period no females were found at the spawning site. Some days later (ca. one week), we found more single males and females and amplectant pairs were approaching the breeding site. The operational sex ratios were highly skewed towards males in all sampling days as males were usually more than 100 individuals and females were fewer than 5 individuals (Table 1).

In the paddy fields, males usually called at the shallow areas of standing water. They maintained individual distances but did not defend a calling or oviposition site which contain any resources used by females and offspring. The study paddy fields were identified as the common spawning area of the toads. Male chorus tenure lasted more than 50 days in this area. The male chorus competition is intense, but rare involving direct physical wrestling among males. Observations on oviposition behavior indicated that male toads only fertilize eggs but not provide any patterns of parental care to eggs or tadpoles. This is also the case for females as we found there was no parental care from females.

4. Discussion

Our results suggested that in the Asian common toad,

Table 1 Examination of sex ratio in the Asian common toad during the breeding season. S_m = number of single males, S_f = number of single females, S_a = number of amplectant pairs, n_m = total number of males, n_f = total number of females.

Date	S_m	S_f	S_a	n_m	n_f	Sex ratio
17 May	89	9	1	90	10	9:1
18 May	77	2	0	77	2	39:1
19 May	75	1	1	76	2	39:1
20 May	64	0	0	64	0	64:0
22 May	64	0	0	64	0	64:0
23 May	60	1	1	61	2	31:1
24 May	133	1	4	137	5	27:1
25 May	124	2	0	124	2	62:1
26 May	111	0	0	111	0	111:0
27 May	53	1	1	54	2	27:1
28 May	118	1	1	119	2	60:1
29 May	102	2	0	102	2	51:1
30 May	97	0	0	97	0	97:0
1 June	115	2	1	116	3	39:1
3 June	23	0	0	23	0	23:0
4 June	139	0	1	140	1	140:1
5 June	204	2	1	205	3	68:1
6 June	181	4	1	182	5	36:1
7 June	153	1	1	154	2	77:1
8 June	166	0	0	166	0	166:0
9 June	155	2	1	156	3	52:1
10 June	121	1	0	121	1	121:1
11 June	156	3	1	157	4	39:1
12 June	164	4	1	165	5	33:1
13 June	114	1	0	114	1	114:1
14 June	76	1	0	76	1	76:1
15 June	107	1	0	107	1	107:1
16 June	94	0	1	95	1	95:1
17 June	119	1	1	120	2	60:1
18 June	75	1	1	76	2	38:1
19 June	65	3	0	65	3	22:1
20 June	95	3	0	95	3	32:1
21 June	80	1	0	80	1	80:1
22 June	73	3	0	73	3	24:1
23 June	52	1	0	52	1	52:1

males show no mating preferences for larger gravid females, which is consistent with previous results in anurans (Hettyey *et al.*, 2005; Yu and Lu, 2010; Yu and Lu, 2013). The sex ratio was highly male-biased throughout the breeding season and both sexes provided no parental care after egg-laying. In addition, male chorus tenure lasted more than 50 days. Therefore, the mating pattern of this toad species can be defined as prolonged breeding (Wells, 1977). These breeding characters are likely to influence male mating preferences with respect to female size in the toad.

Theory of sexual selection suggests that male' discrimination against smaller gravid females could be adaptive if males obtain more fecundity benefits from mating with larger gravid ones (Andersson, 1994). Numerous studies have found that female' body size is a reliable indicator of fecundity in anuran species (Han and Fu, 2013; Nali *et al.*, 2014; Ma *et al.*, 2015; Monroe *et al.*, 2015), including this toad (Fan *et al.*, 2013). Under such condition, why male mate choice for larger and more fecund females is not present in the mating pattern of the Asian toad? This is most likely caused by the limited breeding opportunities due to strongly male-biased sex ratio. Sex ratio may influence the degree of "choosiness" expressed by each sex and mating choosiness can also be affected by difference in sex ratio (Berglund, 1994, 1995; Jirotkul, 1999; Kvarnemo and Ahnesjo, 1996). If too few females are available for males in the breeding population, then there is a high risk that males may remain unmated during the breeding season. Thus, males cannot afford to be choosy in this system. This is case for the Asian common toad. Our field investigations found that sex ratio of this toad is highly male-biased, for number of males were usually more than 100 and number of females were less than 5 in most of sampling time period. Weir *et al.* (2011) suggest that direct aggression decreases as sex ratio increases beyond 1.99, presumably due to the increased costs of competition as rivals become more numerous. This is just the case in the Asian toad, as contest and scramble competition were not detected in the study population.

In species where males are not responsible for all parental care, males can maximize their reproductive success by mating as many females as possible and male mating choosiness would to be lack in such species (Trivers, 1972; Clutton-Brock and Vincent, 1991). This may be the case for the Asian common toad, which both sexes provide no parental care after egg-laying, and thus male mate choice was absent in this toad. Similar results have also been found in some other anuran species (Yu and Lu, 2010; Yu and Lu, 2013; Hettyey *et al.*, 2005). These male toads do not provide territories, parental care or other resources to females or offspring, however, female toads likely gain other benefits from mate choice (Kirkpatrick and Ryan, 1991). For direct benefits, size-assortative mating has been reported in some chorus frogs (Marquez and Tejedo, 1990; Bastos and Haddad, 1996; Bourne, 1992, 1993), these may be due to the size or weight ratio of pairs in amplexus affects the fertilization rate (Davies and Halliday, 1977; Ryan, 1983; Gibbons and McCarthy, 1986; Robertson, 1990). Although the mating pattern was also observed in this toad species, the ratio of male to female size did not affect fertilization efficiency (Gramapurohit and Radder, 2012; Fan *et al.*, 2013). As for indirect benefits, only high-quality males can bear the costs of the longer chorus attendance and sire higher-quality offspring through the effects of genetic contribution (Friedl and Klump, 2005). In this toad, it is likely that choosy females may gain indirect benefits through obtaining genes resulting in enhanced offspring quality (our unpublished data). This issue needs further investigation.

Many studies suggested that chorus attendance is the major determinant of mating success in chorus frogs and toads (review in Wells, 2007). In order to maximize fitness, males of such species should attempt to mate with as many females as possible by calling and attracting females at the breeding site. Therefore, high mating success of males seems to be due to female preferences for call features which encode information about their body size and physical condition (Bosch and Marquez, 2005; Burke and Murphy, 2007; Richardson *et al.*, 2010; Pettitt *et al.*, 2020), although females may have a trade-off between breeding resource suitability and male quality during mate choice (Cayuela *et al.*, 2017). Furthermore, studies have found that chorus attendance predicts good genes in the Italian treefrog (*Hyla intermedia*) (Botto and Castellano, 2016). Males with good genetic quality engage more mating effort is adaptive because mating effort is likely to result in additional offspring (Apostolou, 2017a, b). For this toad, male chorus tenure lasted more than 50 days may also imply that chorus attendance is correlated with male mating success.

In conclusion, our field experimental results suggest that males of the Asian common toad do not assess larger gravid and smaller gravid females when choosing among them as mates. We speculate that the underlying mechanisms influencing the pattern of male mating preference in the study population may likely to be related to the highly male-biased sex ratio, no parental care provide by the males after egg-laying, and the prolonged breeding season chorus attendance. Future research should focus on how sexual selection on male acoustic signaling and how female preference exert different types of selection pressure on male call traits in this toad species, which will contribute to a better understanding the selective pressures acting on mate choice in chorus anurans.

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