Sexually selected females in the monogamous Western Australian seahorse

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Studies of sexual selection in monogamous species have hitherto focused on sexual selection among males. Here, we provide empirical documentation that sexual selection can also act strongly on females in a natural population with a monogamous mating system. In our field-based genetic study of the monogamous Western Australian seahorse, *Hippocampus subelongatus*, sexual selection differentials and gradients show that females are under stronger sexual selection than males: mated females are larger than unmated ones, whereas mated and unmated males do not differ in size. In addition, the opportunity for sexual selection (variance in mating success divided by its mean squared) for females is almost three times that for males. These results, which seem to be generated by a combination of a male preference for larger females and a female-biased adult sex ratio, indicate that substantial sexual selection on females is a potentially important but under-appreciated evolutionary phenomenon in monogamous species.

Keywords: female-biased adult sex ratio; genetic monogamy; opportunity for sexual selection; sexual selection differential and gradient; sex role reversal; Syngnathidae

1. INTRODUCTION

The application of molecular methods to the study of parentage in natural populations has transformed our understanding of natural mating systems. With this revolution has come the insight that most socially monogamous species are actually genetically polygamous (Avice 1994). However, one under-appreciated reality is that true monogamy does exist among a surprisingly wide range of species, such as birds (Marks *et al.* 1999; Henderson *et al.* 2000; Haggerty *et al.* 2001), mammals (Ribble 1991; Brotherton *et al.* 1997), lizards (Gardner *et al.* 2002) and fish (DeWoody *et al.* 2000; Taylor *et al.* 2003), including the subject of this study, the Western Australian seahorse, *Hippocampus subelongatus* (Jones *et al.* 1998; Kvarnemo *et al.* 2000). Given the widespread occurrence of genetic polygamy, sexual selection in truly monogamous species has been a somewhat neglected topic.

In monogamous species, sexual selection can be generated by variation in mate quality, mate competition and assortative pairing (Parker 1983; Johnstone *et al.* 1996). In addition, under biased adult sex ratios, low-quality individuals of the sex in excess may be subject to sexual selection, because they may fail to find mates altogether (Price 1984; Andersson 1994). Early theory on sexual selection in monogamous species was motivated by observations of epigamic traits in males of monogamous birds (Darwin 1871). This historical bias has resulted in a

pre-supposition that sexual selection acts on males rather than on females in monogamous species (Kirkpatrick *et al.* 1990; Dearborn & Ryan 2002). A recent comparative paper on the family Syngnathidae (pipefishes and seahorses), in which all the species exhibit male pregnancy, strengthens this bias by suggesting that polygamy is associated with sexual selection on females, whereas monogamy is associated with sexual selection on males (Wilson *et al.* 2003). However, both generally and specifically such conclusions are premature: generally, because from a theoretical standpoint sexual selection should be able to act on either sex of a monogamous species, and specifically, because the relative intensity of sexual selection on the sexes has never been quantified in a natural population of any monogamous syngnathid fish.

Previous genetic studies of a population of the Western Australian seahorse demonstrate that males receive eggs from only one female for each brood (Jones *et al.* 1998), maintain long-term monogamous pair bonds over successive brood cycles (although split pair bonds also occur; Kvarnemo *et al.* 2000), and form pairs size assortatively (Jones *et al.* 2003). Presumably size-assortative mating translates into assortative mating according to quality, as fecundity in seahorses correlates positively with body size in both the sexes (Vincent & Giles 2003). Here, we focus on sexual selection in a natural seahorse population. In particular, we combine parentage data with demographic data to investigate how size-based mating patterns and the adult sex ratio influence sexual selection in this species.

2. MATERIAL AND METHODS

The present study of a natural population of the Western Australian seahorse, *H. subelongatus* (previously named *Hippocampus angustus*), is based on genetic data on pair formation (Jones *et al.* 2003) and observational data on

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movement patterns. The study site is ca 45 km south of Perth, Western Australia. The seahorses occurred within an area of approximately 100×65 m, in close proximity to 25 pylons of a jetty (2–5 m deep), and ca 82 stumps (remains of pylons of a demolished jetty) nearby, at ca 8–10 m depth. As the bottom substrate is fairly loose mud, there are very few sites, other than the pylons and stumps, with habitat suitable for seahorses, within at least 100 m in any direction. The field study lasted 47 days, from the end of January to late March 1999, during which the water temperature was 23–25°C. The fish were monitored by SCUBA diving 2–5 days per week, for a total of 22 days. We collected all adults once and brought them to the jetty briefly. We fastened a unique tag loosely around the neck of each seahorse and took a small fin clip for later genetic analysis. Measurements of head length (top of coronet to tip of snout) were taken to the nearest 0.1 mm using calipers. We also measured head–vent length using calipers and tail length using a ruler. As head length can be measured reliably and is correlated with body size, we use head length for the analyses presented in this study. However, the results are similar if we use total length (head–vent length + tail length) instead of head length, which can be explained by extremely high correlations between head length and total length in both the sexes (females: $r=0.90$, $p<0.001$; males: $r=0.90$, $p<0.001$). A small sample of embryos (mean $n=17.6$) was taken from the broods of pregnant males, using a capillary tube and bulb, to deduce maternity of these broods. We returned each individual to its original location immediately after tagging and sampling. At each dive, we recorded the position and reproductive status of all tagged adults, and males pregnant with a second brood were re-sampled. From the previous work, we know that mobility and behaviour are not affected adversely by the tags and that males are not harmed by brood sampling (Kvarnemo *et al.* 2000). Details on tagging, fin clipping and brood sampling are reported elsewhere (Kvarnemo *et al.* 2000).

For the microsatellite assessment, we used three previously characterized seahorse loci, *Han03*, *Han06* (Jones *et al.* 1998) and *Han16* (Jones *et al.* 2003). The DNA extraction protocol, PCR conditions and sequencing details are described elsewhere (Jones *et al.* 1998, 2003). All females, pregnant males and embryos sampled from each brood were assayed for all the three microsatellite loci. Female mating status was determined by comparing the maternal genotype for each clutch, deduced by subtracting the known paternal allele from each embryo's genotype, to the genotypes of the sampled adult females. The microsatellite loci are highly polymorphic and we were able to match mothers to clutches with very high probability (Jones *et al.* 2003), because each female in the population exhibited a unique three-locus genotype.

Adult sex ratio was calculated as number of males/(males + females), thus ranging from 0 to 1, with 0.5 being unbiased. For the analyses of adult sex ratio data, we used binomial test to test for deviations from 0.5 and χ^2 -test for comparing the adult sex ratio in different size classes. Comparisons of re-sightings, body size and patterns of mobility were analysed using ANOVA or ANCOVA. To estimate sexual selection on body size (head length), we calculated the selection differentials and the standardized selection differentials for males and females (Lande & Arnold 1983). The former is simply the average head length of all adult individuals of one sex minus the average head length of all mated individuals of the same sex, as shown in figure 2. The standardized selection differential is based on

Table 1. Adult sex ratio of the Western Australian seahorse in the study area. (Adult sex ratio was calculated as number of males/(males + females). The deviation from an expected unbiased sex ratio of 0.5 was tested using a binomial test.)

year	males	females	adult sex ratio	<i>p</i> -value
1997	23	40	0.37	0.04
1999	43	60	0.42	0.11
2000	14	36	0.28	0.003
Total	80	136	0.37	0.001

ln-transformed data standardized to have a mean of 0 and a variance of 1. For a single trait, the standardized selection differential is equal to the standardized selection gradient, so statistical significance can be tested using a simple linear regression (Lande & Arnold 1983). For each sex, the opportunity for sexual selection (I_s) was calculated as the variance in mating success divided by its mean squared (Arnold & Wade 1984; Shuster & Wade 2003).

3. RESULTS

The adult sex ratio in our study population was female biased. In the year in which we conducted the majority of the research reported here (i.e. 1999), we tagged 43 male and 60 female adult seahorses, resulting in a proportion of males of 0.42. This observation, together with data from two additional years (table 1), suggests that the adult sex ratio in this population is consistently female biased. As the adult sex ratio estimates are based on surveys or collections of fish in the field, one possible explanation for an apparent female bias could be that females are easier to find. However, such an explanation is very unlikely, because the tagged males and females from 1999 were re-sighted the same number of times (mean $\pm$ s.e., males: 5.2 ± 0.6 times, females: 4.5 ± 0.5 times; one-way ANOVA: $F_{1,101}=0.88$, $p=0.35$).

The females tended to be slightly, but non-significantly, larger in body size than the males (mean $\pm$ s.e., head length, males: 33.84 ± 0.59 mm, females: 35.33 ± 0.60 mm; one-way ANOVA: $F_{1,101}=2.97$, $p=0.09$), but their size ranges were similar (males: range = 17.7 mm, min–max = 27.3–45.0 mm, females: range = 18.4 mm, min–max = 28.0–46.4 mm) and the variances did not differ between the sexes (males: $s^2=15.1$, females: $s^2=21.2$; $F_{\max}=1.4$, $p>0.05$). As in most other fish, seahorses continue to grow throughout life (Curtis & Vincent 2006; C. Woods 2006, unpublished data), so size provides a rough guide to relative age. Dividing the size range of each sex evenly into three size classes in order to test if the adult sex ratio becomes more female biased with age, however, we found no such pattern ($\chi^2=3.27$, $p=0.19$; table 2).

Based on our molecular analysis of parentage for the 1999 sample, 25 males were shown to have mated with 23 known (tagged and sampled) and 4 unknown females. Out of the 25 males, 12 were screened for two successive broods and 13 for single broods. Out of the 12 males, 9 (75%) re-mated monogamously with their old partner, whereas 3 mated with new partners. An additional 11 males were documented to be pregnant but were either not sampled or sampled too early to provide analysable DNA. We also sampled 36 females whose genotypes did not match any of the broods. These females are treated as

Table 2. Adult sex ratio in three size classes of seahorses studied in 1999. (For each sex separately, the head-length range was divided evenly into the three size classes. Owing to indeterminate growth, relative size provides a rough guide to relative age in seahorses. Adult sex ratio was calculated as number of males/(males + females).)

size (age)	males	females	adult sex ratio
small (young)	19	32	0.37
intermediate	20	18	0.53
large (old)	4	10	0.29
total	43	60

Figure 1. Home range size of mated and unmated males and females of the Western Australian seahorse was estimated from the number of different sites (pylons and stumps) at which each individual was seen. Since this number depends heavily on the total number of times an individual was seen, the latter was entered as a covariate.

unmated, although they could have mothered some of the broods of the 11 males we failed to sample successfully. We also lacked a genetic sample from one female, which therefore was excluded from all further analyses. Hence, our data cover 36 mated males, 23 mated females, 7 unmated males that were never seen pregnant, and 36 presumably unmated females.

From our data on re-sightings and on mating status, we found that males that were seen pregnant maintained relatively small home ranges, whereas both mated and unmated females and unmated males moved over significantly larger areas (figure 1). Movement rates were quantified as the number of different sites (pylons and stumps) at which each individual was seen, with number of re-sightings as covariate, and sex and mating status as factor (ANCOVA, factor: $F_{3,94} = 1.25$, $p = 0.30$, covariate: $F_{1,94} = 131.7$, $p < 0.001$, interaction: $F_{3,94} = 7.24$, $p < 0.001$). The significant interaction thus stemmed from the tendency for mated males to appear at fewer distinct sites than did unmated males, mated females and unmated females.

Mated females were significantly larger in size, as estimated from their head length, than unmated ones (one-way ANOVA: $F_{1,57} = 4.46$, $p = 0.039$). However, mated and unmated males did not differ in size (one-way ANOVA: $F_{1,41} = 0.007$, $p = 0.93$). Consistent with this observation, there was a positive selection differential for female head length of +1.54 mm, whereas for males the selection differential was -0.02 mm (figure 2). Similarly,

Figure 2. Sexual selection differentials in the Western Australian seahorse. The figure shows head length (mm) of unmated and mated male and female seahorses. For each sex, z_1 (solid vertical line) is the mean head length of all mated and unmated individuals and z_2 (dotted vertical line) is the mean head length of mated ones. The difference between z_1 and z_2 gives the selection differential s . For females, s is clearly positive ($36.95 - 35.41 = 1.54$), whereas for males s is slightly negative ($33.82 - 33.84 = -0.02$).

the standardized selection differential (which is the same as the standardized selection gradient) for females was 0.342 s.d., which is significantly larger than 0 (linear regression of relative fitness on standardized head length, $p = 0.038$), whereas for males it was -0.013 ($p = 0.87$).

Our results also show that the opportunity for sexual selection (I_s) is considerably higher for females than for males. Assuming that only females documented to have mated actually did so (23 mated and 36 unmated females), I_s is 1.59 for females and 0.271 for males. However, a more conservative assumption for female mating status might be that each pregnant male for which we do not have genetic data received eggs from one of the 'unmated' females (resulting in 34 mated and 25 unmated females; for the calculation it does not matter which ones they were). This assumption generates an I_s for females of 0.748, which is still a substantial value for the opportunity for sexual selection, almost three times as large as that for males.

4. DISCUSSION

In this study, we show that sexual selection can be substantial, not only in polygamous species, but also in monogamous ones. In fact, our value 0.342 for the standardized selection differential puts seahorses in the top 25% of documented values of sexual selection intensities on a list of 200 species with a variety of mating systems for which such data have been compiled (Kingsolver et al. 2001). Even more importantly, we show for the first time that sexual selection can act strongly on females in a monogamous species. However, we did not find any corresponding sexual selection on males. Our result therefore challenges the established opinion that sexual selection acts on males rather than on females in species that mate monogamously (Darwin 1871; Kirkpatrick et al. 1990; Dearborn & Ryan 2002).

Arguably, our observation of intense sexual selection on size in females of the Western Australian seahorse is generated by a combination of size-assortative pairing and female-biased adult sex ratios. In the early literature on

sex-role reversal, some authors predicted that seahorses would be sex-role reversed, with stronger sexual selection on females than on males (Wittenberger 1981; Trivers 1985). However, more recently, other scientists (Clutton-Brock & Vincent 1991; Vincent *et al.* 1992; Vincent 1994) have challenged this assumption, arguing on the basis of behavioural studies that seahorses have conventional sex roles, which generates the prediction that males should be the sex under stronger sexual selection. Although the interpretation of these studies with respect to sexual selection in nature has been questioned before (Jones *et al.* 2001), ours is the first study to quantitatively determine which of the sexes is under stronger sexual selection in a field population of seahorses. Our results show that females, but not males, are under sexual selection in our focal population of the Western Australian seahorse.

We do not know the mechanism of the observed sexual selection on females, i.e. whether it is generated by intra-sexual competition among females for males or by inter-sexual mate choice as a consequence of male preference for large females. The answer to this question will call for future, detailed behavioural studies. However, it is possible that both selective processes play a part, as has been found in two species of sex-role reversed pipefishes (Berglund & Rosenqvist 2003). Similarly, we do not yet know whether it is female size *per se* that is selected, or any character that correlates with body size, such as age (longevity) or fecundity. However, one expectation may be that female size should be of greater direct importance in intra-sexual competition, whereas traits like fecundity could be of greater importance in male choice, as such a trait may convey a direct benefit to a choosy male.

Seven of the males remained unmated over the study period. Yet, all of the unmated males were at least 3 mm larger in head length than the smallest males that were seen pregnant (figure 2). Hence, we are confident that they were all sexually mature. There was no numerical shortage of unmated females, with 5.1 unmated females to every unmated male, and individual females of all sizes were found among the unmated ones (figure 2). Furthermore, although mated males moved relatively little, both females and unmated males moved considerably within the study site (figure 1). Thus, it seems that these males should have been able to find unpaired mates within two months. Still, the combination of relatively low mobility and a high level of mutual choosiness may account for these unmated males. Since our study only covered part of one reproductive season, it is also possible that some of the 'unmated' males had been breeding prior to our study and had only temporarily interrupted their reproductive efforts.

We found the adult sex ratio in our study population to be female biased. An apparent female-biased adult sex ratio would be generated if females were more easy to detect than males. However, our re-sighting data do not support such an explanation for the observed female bias, as tagged individuals of both sexes were re-sighted equally often. Furthermore, since the pregnant males were most sedentary, we might instead have biased our re-sightings towards them, as we gradually became familiar with where to expect to find certain males. Such conditions did not apply to females. Hence, we believe our observed female-biased adult sex ratio reflects the true adult sex ratio correctly.

This female bias in the adult sex ratio is consistent over multiple years, even though the deviation from an equal sex ratio is sometimes not statistically significant (table 1). Nevertheless, in a predominantly monogamous population even a slight bias is likely to have pronounced effects on the reproductive success of excess individuals, because they will be unable to find mates. As predicted, females, and in particular small females, were the ones that suffered most from the biased sex ratio. Since the inclusion of mated females in the unmated group may have masked greater phenotypic differences between the groups, our study is likely to provide a conservative estimate of the strength of sexual selection in this population.

While the female excess can explain the documented (intra or inter) sexual selection in this sex, this selection does not explain why there are fewer males in the first place. Trivers (1972) remarked that 'where the sex ratio can be shown to be unbalanced in monogamous birds there are usually fewer females, but in polygynous or promiscuous birds there are fewer males' and continued 'This result is particularly interesting since in all other groups in which males tend to be less numerous monogamy is rare or nonexistent'. Our present result with fewer males than females in a monogamous species is thus in clear contrast to these observations. Nevertheless, frequency-dependent selection should maintain a sex ratio at birth near equality, assuming male and female offspring are equally costly to produce. Thus, any temporarily female-biased adult sex ratio should quickly return to unity. Yet, the fact that our data show a consistent female bias over several years suggests that we must seek other explanations to our observed adult sex ratios.

Consistent with Trivers (1972), one possible explanation for the female excess could be that the heavy paternal investment increases male mortality relative to that of females. If this were the case, then the adult sex ratio would be expected to be unbiased among young adults, but turn female biased among old ones. Using body size as an estimate of age, however, we found no evidence in favour of this hypothesis (table 2). Furthermore, adult sex ratios vary greatly among syngnathids. Female biases have been found in most cases, but male biases also occur (Matsumoto & Yanagisawa 2001; Bell *et al.* 2003 and references therein), making the explanation above even less likely since all syngnathids show elaborate paternal care. Hence, it is not yet known why the adult sex ratio is female biased in the Western Australian seahorse. Understanding adult sex ratio biases in monogamous species is a question that calls for further consideration, especially as the patterns of sexual selection are strongly influenced by the sex ratio.

In conclusion, although polygamous species generally are under stronger sexual selection than monogamous ones, our results show that sexual selection can be substantial also in monogamous species. Of greater importance, however, we provide the first empirical documentation that sexual selection can act strongly on females in a monogamous species, contradicting the historical assumption that sexual selection acts on males rather than on females in species with a monogamous mating system (Darwin 1871; Kirkpatrick *et al.* 1990; Dearborn & Ryan 2002). Given the growing number of taxa for which monogamy has been genetically documented, sexual selection on females in monogamous species is a neglected topic worthy of considerably more empirical attention.

We thank Anna Karlsson for field assistance, DeEtte Walker and John Avise for their help with microsatellite analyses, Sami Merilaita and anonymous referees for comments, Department of Zoology at the University of Western Australia for SCUBA equipment, and funding to G.I.M., Swedish Research Council and Magn. Bergvall Foundation for funding to C.K. and the National Science Foundation for funding to A.G.J. This research adheres to the ASAB Guidelines for the use of animals in research and was approved by the Department of Fisheries in Western Australia and the Animal Ethics Committee at the University of Western Australia.

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