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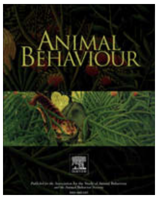

The mechanisms of sexual selection in a lek-breeding anuran, *Hyla intermedia*

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In lek mating systems, sexual selection is thought to operate through two main mechanisms: endurance rivalry and female choice. We investigated the role of these mechanisms in explaining variation in male mating success in a typical lekking anuran, the Italian treefrog, *Hyla intermedia*. The results suggested that both chorus attendance and calling quality may affect male mating success, and that selection on these traits may indirectly result in selection for males with higher-than-average body condition. Both generalized linear models (GLM) and cubic-spline regressions (CSR) showed a monotonic relationship between mating success and chorus attendance, suggesting open-ended directional selection on male chorus tenure. GLMs on call acoustic properties showed a significant association of mating success with several highly intercorrelated call temporal properties (i.e. call rate, pulse rate and call duration), but not with call spectral properties. In both cases, however, CSRs provided evidence that the relationships of the call properties with mating success are unimodal, with peaks close to (spectral properties) or above (temporal properties) the population means. As often observed in anurans, chorus attendance explained much more variation in mating success than did calling quality. However, contrary to what is often assumed, we argue that the important role of endurance rivalry does not reduce, but rather emphasizes, the role of female choice in sexual selection.

In lek mating systems, males typically defend small display areas and fight against intruders of the same sex, and females can choose their mates by moving relatively freely both within and between several male aggregations (Höglund & Alatalo 1995). Sexual selection on males in these mating systems is thought to operate through two distinct mechanisms: endurance rivalry and female choice. Endurance rivalry is an interaction-independent mechanism of sexual selection (sensu Murphy 1998) in that it promotes differential mating success by favouring males that, independent of their competitive ability with regard to direct male–male interactions, remain reproductively active during a large part of the breeding season (Andersson 1994; Andersson & Iwasa 1996). Unlike endurance rivalry, female choice depends on the male–female interaction, since it arises by the propensity of females to mate with certain phenotypes (Jennions & Petrie 1997). Female choice was first proposed by Darwin (1871) to explain the evolution of extravagant male secondary sexual traits and, ever since, it has been the most controversial part of his theory of sexual selection (Andersson 1994). Initially, there was controversy about whether female choice actually exists (Cronin 1991). Then, with the accumulation of field and experimental evidence supporting Darwin's hypothesis, the controversy moved on to the proximate mechanisms and ultimate causes of female preferences (Andersson 1994). More recently, the controversy has revolved around the role of female preferences in selection: whether they actually influence female mating decisions and how important female choice is, with respect to endurance rivalry, in determining differential male mating success (Friedl & Klump 2005).

Many anurans with a prolonged breeding season (Wells 1977) show lek-like mating patterns: males aggregate in choruses and provide only sperm to females, which directly approach and initiate mating with one of the many calling males within the chorus (Ryan 1985; Sullivan et al. 1995). Owing to the ease of carrying out field and laboratory investigations on frog and toad mating behaviour, these species have often been used as models in studies of sexual selection. The large amount of data that have been accumulating in the last three decades (reviewed in Halliday & Tejedo 1995; Sullivan et al. 1995; Ryan 2001; Gerhardt & Huber 2002) provides us with a puzzling empirical contradiction: studies in laboratory conditions have consistently shown that females possess often strong and highly accurate preferences for certain call properties (reviewed in Gerhardt & Huber 2002), whereas studies in natural conditions have provided little evidence that such preferences are actually expressed (Sullivan 1987; Arak 1988; Lopez & Narins 1991; Passmore et al. 1992; Cherry 1993; Friedl 2006). Furthermore, since in almost all studies where the appropriate data have been collected, a positive association between mating success and chorus attendance has been observed (reviewed in Halliday & Tejedo 1995; Friedl & Klump 2005), some authors have concluded that, in

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anurans with a prolonged breeding season and a lek-like mating pattern, female choice plays (if any) only a secondary role and that the most important mechanism of sexual selection is endurance rivalry (Friedl & Klump 2005).

Is this conclusion justified? Have female preferences actually been unimportant in the evolutionary history of male displays? In a recent review, Sullivan & Kwiatkowski (2007) proposed two main reasons that would lead researchers to underestimate the role of female choice in the field. The first reason is empirical: most field studies have small sample sizes and too low a statistical power to reject the null hypothesis of no association between mating success and display characteristics. The second reason is theoretical: female preferences may be multivariate, in that several properties of male display may simultaneously affect female choice and their interaction may make it difficult to detect their net effects. There is, however, a third theoretical reason that may explain why selection through female choice is so difficult to detect in lekking anurans: female choice and endurance rivalry are not independent mechanisms of sexual selection because the latter depends on the former.

To understand the causal association between the two mechanisms of sexual selection in lek mating systems, the male mating strategy should be better viewed as a problem of optimal allocation of reproductive effort among several nights of calling competition (Lucas et al. 1996). Under conditions of strong female choice, a male should only join the nightly competition if he has enough energy to advertise close to the average level of the chorus; otherwise the probability of being chosen by a female would be so low that the male would do better to stay ‘at home’. Since advertising is a highly energetically demanding activity (Taigen & Wells 1985), males of poor quality would maximize their probability of being chosen over the entire breeding season by allocating proportionally more energy per single night than males of high quality, whose proportionally lower nightly investment would allow them to spend more nights calling at the breeding site. Under conditions of strong female choice, we should thus expect small between-male variation in nightly advertising and large between-male variation in chorus attendance. In contrast, when female choice is weak, because males that advertise much below the average still have appreciable probabilities of being chosen by females, the optimal allocation strategy of both low-quality and high-quality males would be the one that maximizes the number of nights at the breeding site to the detriment of the amount of energy allocated per single night. Under these conditions, we should expect variation in chorus attendance to be smaller than variation in nightly advertising. Unless female choice is highly costly, this solution may not be evolutionarily stable because large between-male variation in nightly advertising would increase female choosiness and would lead males to adjust their advertising strategy accordingly. However, independent of the costs and benefits of female choice and of their effects on the optimal male advertising strategy, this argument should make clear that female choice influences male behaviour both in the short term (nightly competition) and in the long term (chorus attendance) and, thus, that interpreting endurance rivalry and female choice as two alternative and independent mechanisms of sexual selection may be misleading.

We investigated the association between reproductive behaviour and mating success in males of a typical lek-breeding anuran, the Italian treefrog, *Hyla intermedia* (Nascetti et al. 1995), in which the pattern of female preferences has been described by means of both univariate and multivariate playback experiments in laboratory conditions (Rosso 2003; Rosso et al. 2006; Castellano & Rosso 2006, 2007). We addressed three questions: (1) does chorus attendance influence male mating success; (2) are female preferences expressed in natural conditions and do they result in selection on male acoustic characteristics; and (3) is there any evidence that selection through female choice on male mating behaviour could result in correlational selection on male body size and condition (thus eventually providing indirect benefits to choosing females)?

METHODS

Study Site

Our research was conducted near Cameri (Novara, Italy, 45°21′N, 8°66′E; 178 m above sea level) inside ‘Parco della Valle del Ticino Piemontese’ (PVTP). We consused a population of Italian treefrogs during two breeding seasons (2006 and 2007).

The study site was one of three neighbouring paddy fields that the PVTP authority have been using as reproductive sites in a long-term amphibian conservation project since 2001. The two closest breeding sites of Italian treefrogs were 150 m and 350 m from the study site. A system of irrigation channels conveys water to the three paddy fields from the nearby Ticino river, thus permitting direct water-level control. In both years of study, the paddy fields were flooded at the end of April and their water level was kept approximately constant (with a maximum depth of about 60 cm) for the entire breeding season until autumn, when the paddies were drained. In addition to Italian treefrogs, the paddy fields were visited by several other anuran species: spadefoot toads, *Pelobates fuscus insubricus*, green toads, *Bufo viridis*, edible frogs, *Rana* kl. *esculenta*, and pool frogs, *R. lessonae*.

Surveys in previous years (S. Castellano, unpublished data) showed that the amphibian distribution was not homogeneous among paddy fields and that treefrog breeding activity was mostly concentrated in the southernmost area. For this reason, we limited our study to this site and surveyed the other two occasionally (see below) to estimate movements between fields. The study site covers an area of 0.13 ha with a perimeter of about 170 m; it borders a paddy field to the north, cultivated fields to the south and east, and a small woodland to the west. Since most treefrogs were found to repair to the woodland during the day, along the western side, we built a discontinuous drift fence to slow down (but not to prevent) the treefrogs’ nightly migration to the breeding site. The fence was made from seven polythene sheets, 6 m long and 1 m high, spaced at 3 m intervals. Sheets were buried 5 cm below the soil surface to prevent animals burrowing under them.

Sampling and Marking Techniques

In both years, the treefrog breeding season started as soon as the site was flooded (29 April in 2006 and 28 April in 2007) and lasted for about a month (until 29 May in 2006 and 27 May in 2007). On every night during this period, we carried out two types of censuses: (1) by walking up and down along the drift fence, we caught treefrogs during their nightly migration to the breeding site; (2) by moving along the shoreline, we caught treefrogs in reproductive activity. Observations were usually made between 2100 and 0100 hours, a time period coinciding with the sustained chorus activity. Unlike shoreline censuses, in which capture probability depended on how an individual made himself conspicuous to the surveyors, the drift fence censuses were unbiased with respect to the reproductive behaviour of individuals.

When we captured a male (either at the drift fence or in the water), we recorded his position and behaviour and we checked if he was already marked. The position was determined according to a reference system of numbered sticks positioned along the breeding-site shoreline at 1.5 m intervals. The behaviour was assigned on the basis of the following four categories: paired, calling (with an inflated vocal sac), silent (with deflated vocal sac), satellite (with deflated vocal sac and close to, usually less than 30 cm away from, a calling male). If the male was marked, we