Variety is the Spice of Life: Female Lizards Choose to Associate with Colour-Polymorphic Male Dyads

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Abstract

We test the idea that male colour polymorphism in a lizard (red vs. yellow headed) may be maintained by a female preference for associating (and presumably mating) with both male morphs rather than only one. In female choice experiments on single males of different colours, females did not preferentially associate with either morph. However, when females were allowed to choose between pairs of males of the same vs. different colours, they preferred to associate with male pairs that were polymorphic. We suggest that this may be the result of selection arising from polyandrous mating benefits and show experimentally that polyandry results in increased hatching success. Most theoretical models of the evolution of mate choice assume that mate choice is costly. We test this assumption by releasing females into polymorphic vs. monomorphic groups in the wild, under the hypothesis that females move more between males in polymorphic groups and therefore suffer higher risks of mortality from predation. In accordance with this prediction, females released into polymorphic male groups were less likely to be recaptured than females released into monomorphic groups, with evidence to suggest that this is because of increased mortality and not increased dispersal. We propose that this cost could be (partly) balanced by polyandrous fitness benefits.

Introduction

Sexual selection is one of the strongest evolutionary forces known and may result in evolutionary responses in the wild on a par with those in controlled breeding experiments in captivity (Endler 1992). It may act before or after copulation (Andersson 1994; Birkhead & Møller 1998), and with or without sexual conflict and antagonistic selection acting on both males and females (Arnqvist & Rowe 2005). Despite this field attracting a great deal of attention, its multitude of facets, such as the origin of mate preferences and multiple sexual signals within the same species, are still poorly understood. This applies in particular to causal links between sexually selected signals and other secondary sex traits, the proximate benefits they may result in, and the fitness benefit these may accrue (Lailvaux & Irschick 2006). For a more complete introduction to this field, we refer readers to the excellent reviews that have been published in this area in recent years (e.g. Andersson 1994; Arnqvist & Rowe 2005).

In the majority of studies of sexual selection, males of the same species employ the same reproductive tactic and male reproductive success is usually dictated via variation in one or several secondary sex traits that are the same for all males (Andersson 1994). However, in some species males occur in different morphs, which presents an intricate evolutionary problem since, should these morphs differ in fitness, the less successful ones are expected to disappear from the population over evolutionary time. Some alternative solutions to this enigma prevail: morphs may be conditional, for

example, change with size, resulting in the same fitness for the morphs only at the switch point from one morph to another (the literature contains hundreds of examples; Gross 1996, e.g. salmon and sun fish, Gross 1985, 1991). Alternatively, coexisting, genetically determined morphs may have the same fitness and frequencies or one morph may have lower fitness but occur in a higher frequency in the population (mixed strategy set, relatively few examples exist; Gross 1996; but see Schuster & Wade 2003). Evolutionary analysis of their stable strategies (ESS) usually relies on game theory solutions (Nash 1951; Maynard-Smith 1982).

The role mate choice has in driving such evolutionary divergence and the maintenance of multiple morphs within the same species and population is to the best of our knowledge only studied in one single case in the wild (Sinervo & Lively 1996), although laboratory studies suggest that in guppies *Poecilia reticulata*, male polymorphism is maintained by female mate preferences (Brooks 2002; Lindholm et al. 2004). Selection for within-sex polymorphism may, however, be driven by male–male interactions, which can lead to the evolution of alternative reproductive phenotypes such as dewlap colours in male tree lizards *Urosaurus ornatus*. This trait reliably signals differences in fighting ability (Thompson & Moore 1991, 1992; Hews et al. 1994, 1997), as does neck colour in the ruff *Philomachus pugnax* (Lank & Smith 1987).

In summary, colour polymorphism may be selected for or maintained by a variety of selective forces. If males of different morphs contribute differently to a female's fitness, then females could, hypothetically, evolve towards (1) becoming 'male morph specialists', i.e. mating with only one morph (assortative mating) or (2) be under selection to spatially organize themselves in order to maximize mating opportunities with males of all morphs to increase any cumulative fitness benefits.

We used the Australian painted dragon *Ctenophorus pictus* as a model to study mate choice in a polyandrous lizard. In this species, males occur primarily in two different morphs with red or yellow head colouration (Fig. 1), neither of which show obvious background colour matching and both are distributed throughout our study site (Cogger 2000; Healey et al. 2007). Red males dominate yellow males in competition for resources and females (Healey et al. 2007), whilst yellow males sire three times more offspring in staged sperm competition trials than red males (Olsson et al. in press). Whether these morph-specific attributes facilitate different reproductive tactics in the wild is as yet unproven, but if this is the case, then it would have important consequences for female fitness and therefore subsequent female reproductive tactics.

In the current work, we study the following in four separate experiments: (1) female mate preference for single males of different head colours, (2) female preferences for polymorphic vs. monomorphic male dyads and (3) polyandry effects on offspring viability. Finally, as most theoretical models of mate choice evolution contain a cost parameter (reviewed in Andersson 1994), it seems appropriate to test this assumption in our natural population with a focus on the proposed mate choice trait – male polymorphism. Under the assumption that individual recognition of different males is facilitated as males are rendered distinct by their colour polymorphism, females in areas where sympatric males are polymorphic should be motivated to elevate their activity levels because of the increased spatial demands of travelling between neighbouring male territories to facilitate multiple mating with different males. They would subsequently be at risk of suffering concomitant elevated predation costs. We therefore use data from a field experiment (4) in which females were released into polymorphic or

Fig. 1: Two male morphs of the Australian painted dragon *Ctenophorus pictus*.

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monomorphic male groups in the wild to assess associated female survival costs.

Materials and Methods

The painted dragon lizard *C. pictus* is a small (snout-vent length 65–95 mm, mass 8–16 g) diurnal lizard of typically sandy habitats and low vegetation with a range covering central and western New South Wales to Western Australia (Cogger 2000). Males are highly territorial and polymorphic with yellow or red head and face colouration (Healey et al. 2007). Morph colouration has no spectral UV reflectance component and morph colour is perceived as discrete morphs as opposed to continuous variation in colour (Healey et al. 2007). Females are considerably less conspicuous and cryptically coloured. This study was approved by and conducted in compliance with Wollongong University animal ethics protocols AE 04/03, AE 04 and AE 05. A scientific license was also issued under the National Parks and Wildlife Act 1974 by the National Parks and Wildlife Service, New South Wales, Australia.

Female Preference Trials on Single Males in an Enclosure in the Wild

During the mating season (October), females and males were captured by noose at Yathong Nature Reserve, New South Wales 145°35′E; 32°35′S. Just prior to each trial, females were exposed to a male not participating in the trial in order to test her receptivity, which can be confirmed by the lack of 'tail waving' and lifting of the cloacae from the ground when approached by the male. Tail waving is a species-specific rejection behaviour that only takes place in the temporal window when females are not receptive to males (Houston 1978; M. Olsson, M. Healey & T. Uller, pers. obs.). All males and females used in these trials were receptive and kept in separate cages (750 mm × 500 mm × 400 mm) until the onset of the experiments, fed crickets and meal worms and were sprayed with a fine mist of water.

Thirty-six naturally red or yellow size-matched males (a maximum of 3 mm difference in snout-vent length) were kept under the same conditions until the onset of the experiments. A red and yellow male were then introduced into a 2 m × 1 m cage where one-third was divided into two different compartments, separated by a plywood screen. The male compartments were screened off from the female by a Perspex (clear 'plastic glass') board with a hinged gate, which allowed a female to enter a male's cage but not vice versa (see Olsson 2002 for details). The female was released at the far end of the cage under an inverted Perspex box with the males in full view and left to acclimatize for 5 min before the box was gently removed. The male mean snout-vent length was 65.4 mm (±3.96, SD) and mean mass was 11.09 g (±1.84, SD). When a female entered or attempted to enter a male's compartment more than five times without attempting to enter the rival male's compartment, the male she was positioned in front of was considered her preferred partner.

Female Preference Trials on Male Dyads in the Laboratory

Male and female offspring from a wild population from Yathong Nature Reserve were reared at the University of Wollongong in separate cages (170 mm × 116 mm × 103 mm) and fed crickets and meal worms dusted with calcium and multivitamins. They were sprayed twice daily with a fine mist of water. All lizards were held separately from hatching and thus had no interaction with other lizards prior to our experiment.

Once male colouration was evident (at around 60 d), a single female was allowed to choose either of two male dyads, a polymorphic one vs. a monomorphic one (red–red and yellow–yellow were used in equal frequencies). The dyads composed of size-matched males (mean difference in mean male mass between monomorphic and polymorphic cages = 0.38 g ± 0.23 SE, $t = 1.68$, $p = 0.100$, $df = 58$), housed in Perspex tanks, hereafter known as tanks 'A' and 'B' (1720 mm × 500 mm × 230 mm), with sand substrate and a brick perch site. A third tank 'C', placed between the two male tanks, housed the female. The Perspex facilitated a clear view of all tank occupants. At the end of tank 'C' one exit led to tank 'A', another to tank 'B'. A sliding Perspex door kept this exit area closed off from the female until a trial commenced.

To standardize the expression of male colouration, males were randomly assigned red or yellow and painted using water-based tattoo paint (Spuck Balding, NY, USA), mixed to match (to the human eye) the natural red and yellow of the males and covering any natural colouration. Two males were placed in tank 'A' or tank 'B' and allowed to settle for 15 min. Simultaneously, a female was placed in tank 'C' and allowed to settle for the same period. The door was then raised remotely, denoting the beginning of the trial, which then ran for 30 min or until the female had left through one of the exits, thereby

making her 'choice'. At the end of each trial, the female was removed and not re-used. Male dyads were then swapped, i.e. the occupants of tank 'A' were placed in tank 'B' and vice versa, to remove any tank bias with respect to female choice.

Monomorphic and polymorphic tanks did not differ with regards to male activity (i.e. duration and bouts of display behaviour by males towards both females and other males). Tank A and tank B were scored for highest level of activity and tested against equal distribution in morph categories ($\chi^2 = 0.0009$, $p = 0.98$, $df = 1$), therefore, we pooled all data for statistical analysis. Four females were tested each day, and, the tanks were thoroughly cleaned with alcohol and the sand replaced. Seventy-six females were tested in total, using 77 males. Each male was used four times. The rationale for this was that males were only used to create a mate choice scenario, hence no aspect of male behaviour was a component of our analysis (female is the statistical unit). Furthermore, as the same males were used in four consecutive trials, any change of male behaviour over time was paralleled in all four males in a given trial. Each female was used once.

Female Mating Experiments in the Laboratory: Offspring Viability

We analysed the effect on hatching success (percentage of hatched young) of monandrous vs. polyandrous copulations. Females were tested for receptivity by introducing a sexually active male into the female cage prior to the mating trials and rejection/receptivity behaviours were assessed in the same manner described for the female preference trials on single males in an enclosure in the wild. Females were mated with one randomly chosen male (monandrous mating) or two males in succession (polyandrous mating). As this experiment was conducted before the polymorphic preference had been identified, colour was not considered. When females were mated with different males, females that were used more than once were included in the data set under the assumption that offspring viability (using (log) hatching success as a proxy) is based on genetic complementarity of parents. Infertile eggs are easily identified in this species (they lack turgor) and we subtracted those from the clutch size to estimate the hatching success of fertilized eggs only. There was no difference in fertility between monoandrous and polyandrous females (mean values for monandrously and polyandrously mated females, 0.08 ± 0.06, SE, $n = 24$ and 0.17 ± 0.12, SE, $n = 15$; t-test, $t = 0.71$, $p = 0.48$, respectively). Sons and daughters were identified by hemipenis eversion at hatching (Uller et al. 2006).

Release Experiment in the Wild

In order to assess the costs of the polymorphic vs. monomorphic environment, we measured female survival following release. Because painted dragons are annuals (less than 10% are recaptured after a second hibernation; M. Olsson & M. Healey, pers. obs.), we equated 'survival' with recapture during the breeding season. In early spring, from the period 2 Sept. to 20 Nov., the release sites were surveyed twice a day (weather permitting lizard activity) and lizards captured by noose. Dispersal distance was measured as it provides a potential confounder of estimates of female mortality if females from one group simply dispersed further than those from the other group. The dispersal of recaptured lizards from the release experiment was estimated as the distance travelled per day from the release site of the lizard to the recapture site using GPS (Global Positioning System) readings. In order to assess emigration from the study area, we surveyed approx. 3 km on either side of the study area without being able to confirm emigration.

One hundred and twenty-three males and 123 females were released at Yathong Nature Reserve on three separate occasions, 24 Mar., 14 Apr. and 12 May 2005, i.e. in the late Australian autumn just prior to hibernation. Males were released into groups of three of the following experimental categories; all red ($n = 13$ groups), all yellow ($n = 9$ groups), red–yellow–red ($n = 9$ groups) or yellow–red–yellow ($n = 10$ groups) and released along one transect through our study site with a size-matched female. The position of each group along the transect was haphazard. A distance of 60 m separated each male/female pair. Between male triads, 240 m was left clear on either side. Females released into the two male triad categories are hereafter referred to as 'polymorph females' vs. 'monomorph females'. To standardize lizard phenotype, all males were painted with their natural head colour if known. Those that bore no indication of colouration were randomly assigned colour and painted accordingly.

Results

Female Preference Trials on Single Males

In the 18 trials, females chose the naturally coloured red-headed male in eight cases and the naturally

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coloured yellow-headed male in 10 cases (Binomial test, p = 0.82).

Female Preference Trials on Male Dyads

Fifteen females of 76 did not make an apparent choice within the trial period and were excluded from the analysis. Females preferred to associate with polymorphic male dyads in 64% of trials, with a corresponding 36% preferences for monomorphic male dyads ($\chi^2 = 4.74$, p = 0.029, df = 1, chi-squared test on raw frequencies 22 vs. 39 monomorphic vs. polymorphic choices against a 50:50 expected distribution).

Female Mating Experiments in the Laboratory: Offspring Viability

Hatching success was positively correlated with sex ratio (r = 0.36, p = 0.02, n = 39) and clutch size (r = 0.42, p = 0.01) and we therefore controlled for these effects by including these variables as covariates in an ANOVA with mating system (polyandrous vs. monandrous matings) as factor, and hatching success as response variable. The model was significant ($F_{3,\ 35} = 5.7$, p = 0.003, $R^2 = 0.33$), with both covariates significant ($F_{\text{sex ratio}} = 6.8$, p = 0.01, df = 1; $F_{\text{clutch size}} = 4.5$, p = 0.040, df = 1) and with a borderline significant effect of mating system (i.e. polyandrous vs. monandrous F = 4.0, p = 0.050, df = 1). Hatching success was 72% (±0.07 SE, n = 24) in monandrous females and 84% (±0.05 SE, n = 15) in polyandrous females.

Release Experiment into the Wild

In spring, the younger males from our release experiment were replaced by larger males (hatched from earlier clutches the previous year) and the male release groups therefore dissolved. However, as we monitored the study population every day when weather permitted lizard activity, from when lizards emerged from hibernation and therefore before the usurping of the young males by the older ones had occurred, our female re-sighting and recapture patterns still reflect effects of release category (monomorphic vs. polymorphic male groups) on female spatial patterns and recapture rate. Recapture rate from the two monomorphic categories showed no significant differences (Fisher's exact test, FI = 2.03, p = 0.091, three of 24 all yellow females were recaptured vs. 10 of 29 all red).

We recaptured four females from 19 polymorphic male groups and 13 females from 22 monomorphic groups. This reduced recapture rate from females in polymorphic groups is statistically significant (Fisher's exact test, FI = 5.98, p = 0.013). Furthermore, females showed the same level of dispersal per day regardless of which category they were released into (0.261 m ± 0.08 and 0.265 ± 0.07, for monomorph vs. polymorph females, t = 0.03, p = 0.98, df = 14, respectively). Thus, recapture rates are likely to represent differences in survival and not emigration from the study area.

Discussion

Although the study of sexual selection in lizards has a long tradition with classic work being carried out on this taxon (e.g. Noble & Bradley 1933; Trivers 1976), few studies have focused explicitly on mate choice. Early work on sand lizards *Lacerta agilis*, failed to identify mate choice on the sexually dichromatic green male colour, with more recent work making similar observations on performance traits in *Anolis* (Lailvaux & Irschick 2006), and with reviews across taxa reaching similar conclusions (Tokarz 1995; Olsson et al. 2005; Olsson & Madsen 1998). In a few cases, however, female choice on male phenotype has been confirmed (reviewed in Olsson & Madsen 1998). One such case is our own observations of female preference for MHC (Major Histocompatibility Complex) dissimilarity in sand lizards (Olsson et al. 2003). However, although we confirmed female preference for more genetically dissimilar males, and non-random pairing in the wild of males and females (lower MHC relatedness than expected by chance), we still cautioned the reader that females are sedentary, never reject males within their receptive time window, and larger males have lower relatedness with their partners than do smaller males. Thus, the direct target of sexual selection in this case may be males, which show preferences for dissimilar females and not vice versa (Olsson et al. 2003). In a recent study, Hamilton & Sullivan (2005) rightly caution against staging mate choice experiments on single male traits, as female mate preferences may be based on multiple traits. We agree that such multiple-trait approaches to mate choice are very worthwhile although they are not free of their own logical and statistical problems. First, traits that are strongly sexually dimorphic and can be demonstrated to be used for combat or communication in males but not females could be more parsimoniously explained by intra-sexual selection than mate choice. Second, including multiple correlated traits increases the risk for multicollinearity

effects (that typically inflate the chances of identifying significant multiple, correlated predictors when univariate methods fail to do so; Allison 1991, pp. 48–51), this leads to a concomitant risk of incorrectly identifying mate choice when there is none. In the current study, we tried to avoid this problem by size-matching males and then assess female mate preferences for head colour but could not confirm such an effect.

Our experiments in the laboratory did show female preferences for polymorphic male dyads rather than monomorphic ones and with a polyandry effect on offspring viability. Thus, females may benefit from encountering and copulating with several males in succession. How relevant are these results for inferring evolutionary scenarios in the wild? At our study site, male painted dragons defend unidirectional territories along man-made fire trails (surrounding vegetation is too dense to provide suitable habitat and the open roads are avoided, probably because of predation). Thus, females face a spatial environment where multiple males can be viewed and compared. Territorial males spend most of the day defending and patrolling their territories and guarding females against frequent interlopers (Healey et al. 2007). As females are site-tenacious on male territories, they encounter sympatric males of the same and different morphs in the wild (although morph preferences in this setting have not yet been tested). Female tendencies to preferentially organize themselves with males of different rather than the same morphs could be selected for in a number of ways. For example, females associated with polymorphic males may experience lower levels of male aggression if this becomes reduced in a polymorphic environment with increased capacity for individual recognition, compared with a monomorphic one, as seen in cichlid fish (Seehausen & Schluter 2004). However, our release experiment suggests a more complex selection scenario; females in polymorphic male groups had a lower recapture rate. One explanation for this result may be increased dispersal, which runs counter to our hypothesis of polymorphic male preference and which we refute with our daily dispersal data (no difference between female release categories into groups of males of the same vs. different morphs). A more plausible explanation is that females released into polymorphic groups suffered higher mortality, associated with elevated mating activities of females in polymorphic situations, increased time away from the relative safety of the burrow and greater risk of predation (Le Galliard et al. 2005; Svensson et al. 2005). This may point to the existence of a fitness advantage balancing this mortality cost. For example, in the sand lizard *L. agilis*, females that mate with multiple males have more viable offspring (Olsson et al. 1994), and promiscuous female common lizards *Lacerta vivipara* have higher fertility (Uller & Olsson 2005). Similar correlations between polyandrous females and offspring viability have been found across a wide range of taxa including arachnids, insects and birds (Birkhead & Møller 1998). In our study, polyandrous females gained increased hatching success compared with monandrous ones. However, considering that this effect only constitutes a 12% hatching success advantage over monandrous females, polyandry benefits *per se* seem insufficient to balance these mortality costs.

In summary, females do not discriminate between single males of different head colour but preferentially associate with polymorphic as opposed to monomorphic male dyads. The efficacy of individual recognition in this species is currently untested, but by mating with males that differ phenotypically, a female could increase the likelihood that the males with whom she is multiply mating are in fact different males. We propose that if females have already evolved polyandry for reasons of enhanced offspring viability (or other potentially overlooked fitness benefits), selection for multiple mating with males of different phenotype may contribute to the evolution and maintenance of male polymorphism.

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