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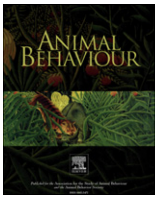

Experiments on colour ornaments and mate choice in king penguins

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Research on animal ornaments used in mate choice has largely focused on males, particularly for bird species with sexually dimorphic coloured patches of feathers and integument. Relatively less information is available for coloured ornaments of sexually monomorphic species and the use of these ornaments during mate choice. The king penguin, *Aptenodytes patagonicus,* is a monogamous marine bird in which both sexes show very similar coloured ornaments (UV and yellow–orange colours on the beak, yellow–orange auricular feathers, and yellow to rusty-brown breast feathers). These ornaments have previously been implicated in mate choice. We used manipulative experiments to test the role of coloured feather patches in the choice of partners that occurs during pair formation. Experimental reduction of auricular patch size delayed pairing, and alteration of auricular and breast patch colour from yellow to white caused an even stronger delay (white treatments gave adults the appearance of immature birds). Surprisingly, we found that time to pairing did not differ between treatments for females, but males showed significant delays in pairing in general and especially when treated. Thus, females seemed to be more selective in mate choice than males, a phenomenon that might be explained by a male-biased sex ratio in the colony. Nevertheless, our results indicate that choice of mate may be much stronger in one of the sexes in what appears to be a sexually monomorphic species, for which we expected sexual selection to favour mutually strong male and female mate choice.

Most of the activities in the daily lives of birds rely on vision (Bennet et al. 1996). Thus, it is natural to focus on colour patterns when studying the social life of birds. Many birds present extravagant patterns of colours that are thought to be involved in the process of mate choice, an important component of the process of sexual selection (Darwin 1871; Andersson 1994). Colour patterns may convey important information to potential mates. For example, colour ornaments can signal individual condition (e.g. Hill 2000; McGraw et al. 2002) or immune system strength (e.g. Møller et al. 1998). It is reasonable to suppose that both vision and colour, including ultra violet (UV) and other colours, may be used in the process of mate choice (Hunt et al. 2001). Colour patterns of passerine birds have received a lot of attention (e.g. Banks 2001; Örnborg et al. 2002; Faivre et al. 2003), but there are fewer studies on the serially or strictly monogamous and almost monomorphic marine birds (Jones & Hunter 1993; Cuthill et al. 2000; Kraaijeveld et al. 2007).

In passerine birds, males are often brightly coloured, suggesting strong sexual selection for colour ornaments. These generally small birds usually breed annually or even more often, with clutches of several eggs at a time (e.g. Bennett & Owens 2002). In marine birds, reproductive patterns are typically slow. Clutches are usually small, produced at best annually, and most of the time clutches are not replaced if lost early in the breeding cycle (Burley 1977; Johnstone et al. 1996; Jouventin et al. 1999; Amundsen 2000; Schreiber & Burger 2001; Shirihai 2002). Under such circumstances, investment by both sexes may be necessary for the success of the clutch. Both parents make similar parental contributions by protecting eggs and chicks, and by returning from foraging trips to feed the chicks. This suggests that the choice of a mate should be extremely important for both members of a pair. A poor choice might well mean reproductive failure. Thus, for marine birds, mate choice may be made mutually, perhaps resulting in the sexual monomorphism that occurs in colour ornaments (Kokko & Johnstone 2002). If aspects of coloured ornaments display information on individual quality, we might expect to find the same underlying physiological mechanisms and the same aspects of quality reflected in both sexes. Darwin (1871) believed that elaborate ornamental traits expressed in both sexes might be favoured by mutual selection driven by both male and female competition for mates. So, one might expect to see

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mutual mate choice in seabirds. To test this hypothesis, we investigated whether the size and colour of ornaments are involved in mate choice.

We used manipulative experiments to examine whether visual signals are involved in mate choice for the king penguin, *Aptenodytes patagonicus*. This species is an ideal model for the study of mate choice, partly because preliminary indications are that colour ornaments are important (Jouventin 1982; Jouventin et al. 2005; Nolan et al. 2006; Dobson et al. 2008). King penguins are socially monogamous and sexually monomorphic (Jouventin 1982). Both males and females contribute to parental care and a single parent cannot raise an egg and subsequent chick alone. Both sexes have coloured ornaments: an auricular patch of dull yellow or orange feathers, yellow to rusty-brown breast feathers, and a beak spot on the lower mandible that reflects yellow to orange and UV colours (Jouventin 1982; Jouventin et al. 2005, 2008; Nolan et al. 2006; Dobson et al. 2008). These studies found that colour ornaments are important in mate choice, particularly the size of the auricular feather patch and UV reflectance from the beak (also see Jouventin et al. 2009).

Incubation and rearing of king penguin eggs and chicks is shared by a pair. It takes about 14 months for them to produce and incubate an egg, and raise and fledge the single chick (for penguins, fledging is the time when chicks enter the sea). The pair then moult, forage at sea, and begin the breeding cycle again (Weimerskirch et al. 1992). Cooperation and coordination between mates is essential for successful reproduction (Jouventin & Lagarde 1995). Most successful birds produce one egg per year, but fledge only one chick every 2 years. Thus, choice of a high-quality mate should be an important part of the reproductive process. A poor choice of partner that results in reproductive failure and leads to a new breeding attempt would inevitably be costly in time and energy. In addition, mate choice is made repeatedly throughout life, since king penguins mate with new partners in about 80% of all pairings (Olsson 1998). The lack of fidelity towards former mates itself might lead to the evolution of mutual ornamentation if both sexes select the highest-quality mate possible (Kraaijeveld 2003).

In two pioneering experiments on king penguins, Stonehouse (1960) and Jouventin (1982) approached the question of ornaments and their influence on pairing efficiency by manipulating auricular plumage. They found that the extreme removal of yellow feathers by cutting or masking made it difficult or impossible for manipulated individuals to acquire a mate. These preliminary findings were confirmed by experimental reduction of auricular patch size of males (Jouventin et al. 2008), showing that males with masked auricular feathers were slower to find a mate than controls. Other experiments also showed the possible importance of colours in sexual selection, such as associations of UV brightness of the beak spot and body condition of males (Dobson et al. 2008), brightness of yellow breast feathers and immunocompetence in males (Nolan et al. 2006), yellow–orange colour of auricular and beak patches and the age of birds of both sexes (Nicolaus et al. 2007), or the size of auricular patches and strength of territory defence by both sexes (Viera et al. 2008).

This background of study suggests the importance of colour and size of ornaments on mate choice of king penguins. From the theory of sexual selection, we hypothesized that individuals of both sexes with more highly coloured or larger ornaments should be favoured as mates during the pairing process. To test this, we examined the relationship of ornament colour or size and the time that displaying males and females took to find a mate and form a pair bond. We manipulated the size and colour of feathers patches of both males and females. We expected that alteration of the ornaments (reduction of size or suppression of colour) could delay pairing. The experimental manipulations tested whether the quality of auricular and breast patches were important to pair formation. Latency to pairing for manipulated individuals was compared to a control sample.

METHODS

Study Area and Data Collection

We studied king penguins in the Southern Indian Ocean, at Cape Ratmanoff, on the Courbet Peninsula of Kerguelen Island (49°14′S, 70°34′E), in a colony that contained more than 80 000 breeding pairs. In November and December 2006, we captured unpaired individuals on courtship grounds along the edges of the nesting colony, after observing these individuals perform courtship calls for several minutes. Individuals were sampled in pairs, but they were not yet bonded to each other. To ensure that these individuals had not yet formed a pair bond, we walked between the potential pair to see whether they used calls to reunite. In king penguins, a male and female maintain close physical proximity to each other during the courtship process, and also during the time before egg laying (Jouventin 1982). Paired birds perform fewer courtship calls, but still occasionally display to reinforce the pair bond (Jouventin 1982; Wachtmeister 2001). To bond, two birds learn each other's vocal signatures (Jouventin 1972; Derenne et al. 1979; Jouventin & Roux 1979; Robisson et al. 1989; Aubin & Jouventin 1998; Jouventin et al. 1999; Lengagne et al. 1999), and can easily reunite if separated. We did not sample birds that reunited, leaving a sample of individuals that were displaying but had not yet become bonded to a mate. Subsequent pairing, however, was recorded when our sampled birds were seen in attendance with a partner inside the egg-laying areas of the colony. This necessary reproductive step occurs after individuals learn each other's calls and have spent a few days together at the periphery of the colony.

For a sample of 84 birds, each was weighed to the nearest 0.10 kg with an electronic balance and the length of the left flipper (wing) was measured in mm. Callipers were used to measure the beak and width of the auricular patch. Each individual was banded with a temporary numbered plastic flipper band to allow individual identification during observations using binoculars. We took photographs of the auricular patch using a Canon digital camera (EOS 350D), with a 30 cm standard ruler set in a metal framing device attached to the camera. All the birds were photographed in the same position and at the same focal distance to ensure comparable data. To quantify the size of the auricular patch, we used the public domain NIH Image J program (U.S. National Institutes of Health, Washington, D.C.; http://rsb.info.nih.gov/ij/).

In the field, birds were sexed by voice (Derenne et al. 1979). However, we took 1 ml of blood and later confirmed the sex of individuals using the molecular method of Griffiths et al. (1998). We modified the size or colour of breast and auricular patches to test influences on pairing latency for males and females. Latency to pair was calculated from the day of manipulation to the day they were observed paired with a partner. The colony was searched daily to follow marked individuals and evaluate their status as courting or paired, although we also recorded banded birds whenever they were observed. Courting birds often displayed to several potential partners before pairing, whereas paired birds displayed only together and ceased calling unless they were separated in the colony. They also moved around the colony together and eventually usually found a site for egg laying within the nesting regions of the colony.

Patch Size Reduction and Colour Changes

For each of our treatment groups, some sampled birds could not be followed to pairing or identified as definitely not pairing. Thus,