Animal Behaviour 116 (2016) 131–137

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Female active sampling of male paint on bowers predicts female uncertainty in mate choice

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ARTICLE INFO

Article history:
Received 5 October 2015
Initial acceptance 19 November 2015
Final acceptance 11 February 2016

MS. number: A15-00848R

Keywords:
active sampling
mate assessment
mate choice
mate sampling
mate search
multiple mating
Ptilonorhynchus violaceus
satin bowerbird
sexual selection
uncertainty

It can be difficult to assess the degree to which a female attends to an individual element of a multi-component male courtship display. Quantifying behaviours where females actively sample a male display element (such as smelling or tasting a chemical signal) can provide detailed information about differences between females in their sampling behaviour and reliance on that element in making mate choice decisions. Bower 'paint' is a unique male sexual display trait found in satin bowerbirds, *Ptilonorhynchus violaceus*. Male bowerbirds masticate dried hoop pine (*Araucaria cunninghamii*) needles and apply this paste to the inside walls of their bowers. Female bowerbirds move among bowers of different males until they choose a mate. Recent mate searching experience and other factors appear to affect this process. Females visiting bowers taste the paint when they nip at the painted wall. Why females sample paint is unknown, but there is now strong evidence that female sampling of paint is important in mate selection. We tested the hypothesis that tasting is related to female uncertainty in mate choice. We found that a greater tendency of females to taste paint on bowers was associated with three measures of female mate choice uncertainty: (1) more frequent female visits to bowers, (2) mating with multiple males and (3) switching frequently among visited males. We suggest that high rates of tasting are predictive of female uncertainty in mate choice, perhaps due to some females initially having limited information about the quality of potential mates.

Mate searching and assessment are often complicated processes in species where males have multi-element sexual displays. Courted females are exposed to different display elements either simultaneously, sequentially, or both, as they receive displays while progressing through the mate selection process. In many species, females passively observe or listen to display elements as they are courted. It is difficult to know to what degree individual females attend to all or a subset of the elements of a male's display and how they are used to make mating decisions. Several studies indicate that females may be selective in their use of information from particular display elements. For example, Hebets and Uetz (1999) found that females of different spider species respond differentially to the individual components of male multimodal displays. Coleman, Patricelli, and Borgia (2004) showed that older females use different male display elements than younger females. Yorzinski, Patricelli, Babcock, Pearson, and Platt (2013) showed that, during courtship, female peafowl direct most of their attention at or below the male's head rather than focusing on the intricate and elaborated feathers of the train.

Measuring female behaviours corresponding to 'active' sampling of a male display element could provide detailed information on the degree to which females attend to, or even 'resample', a particular element and to what extent different females vary in the attention given to that element. Active female sampling behaviours can be quantified, which is a challenge to do for passive behaviours such as observing (but see Yorzinski et al., 2013) or listening. Quantifying active female sampling of individual male display traits during female mate assessment could provide insight into both the female's 'mental state' and her need to use a particular display trait in her mate choice. For example, the level of active sampling could indicate a female's level of interest in a potential mate while also helping her resolve whether to mate with him. Therefore, quantifying female active sampling of display traits could be exceedingly valuable in assessing the function of

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http://dx.doi.org/10.1016/j.anbehav.2016.03.017
0003-3472/

different male display elements, how females assess these elements and how differences among females account for observed differences in mating behaviours. Female active sampling behaviour may indicate individual variation in the pattern of decision making and reveal differences in how individual females use particular male display elements.

Active sampling of male traits seems commonly related to chemical traits such as olfactory or gustatory cues. In mammals, sniffing by females of male faeces, urine or glandular fluids can affect mate choice and fetal development (Singer, Beauchamp, & Yamazaki, 1997). Female *Drosophila* touch males to sample cuticular pheromones (Howard, Jackson, Banse, & Blows, 2003) as do female crickets (Thomas & Simmons, 2009), female beetles (Peterson, et al., 2007) and females in other insects. Chemical signals are now recognized as important in avian communication (Hagelin & Jones, 2007; Whittaker, Gerlach, Soini, Novotny, & Ketterson, 2013). Chemosensory signals are part of the complex, multimodal displays of crested auklets, *Aethia cristatella* (Hagelin, 2007; Hagelin, Jones, & Rasmussen, 2003). Bird odour is predictive of reproductive success in a common passerine, dark-eyed juncos, *Junco hyemalis* (Whittaker et al., 2013). In addition, chemosensory signals are suspected in the 'exploded lek' system of the endangered kakapo, *Strigops habroptilus* (Gsell, 2012; Hagelin, 2004). However, chemical display traits have not been identified in other lekking birds apart from 'paint' applied to bowers by male satin bowerbirds, *Ptilonorhynchus violaceus*, and tasted by mate searching females (Bravery, Nicholls, & Goldizen, 2006; Hicks, Larned, & Borgia, 2013; Robson, Goldizen, & Green, 2005).

In addition to active sampling of male display traits, female signals to males in response to male displays may also reveal females' mental states. Signals differ from active display trait sampling because they function to influence the behaviour of the displaying male. For example, female cowbirds produce wing strokes in response to males singing attractive songs. This stimulates males to sing more of these effective songs, triggering female copulatory postures (Gros-Louis, White, King, & West, 2003; King, West, & White, 2003; West & King, 1988). Female wolf spiders have receptive postures that have been used to demonstrate preferences for particular components of male displays (Hebets & Uetz, 1999). Females also often signal readiness to mate (e.g. Demary, Michaelidis, & Lewis, 2006; Patricelli, Uy, & Borgia, 2004; Patricelli, Uy, Walsh, & Borgia, 2002; Santangelo, 2005).

Satin bowerbird males have displays involving multiple elements that include the bower, bower decorations and coordinated visual and vocal displays, which are assessed by females in multiple visits to bowers (Borgia, 1985; Patricelli et al., 2002; Robson et al., 2005; Uy, Patricelli, & Borgia, 2000). Studies of satin bowerbirds have demonstrated the value of quantifying variable female behaviours during courtship that reveal a female's mental state. Males court females at their bowers with energetic dancing and vocal displays (Coleman, Patricelli, Coyle, Siani, & Borgia, 2007; Loffredo & Borgia, 1986). A female visiting a bower typically starts in a standing position and then after several visits, lowers into a crouch, indicating her comfort with the male and his display, and finally lifts her tail to signal her readiness to copulate (Patricelli et al., 2002). Female age affects display preferences, with older females preferring intense male courtship displays and young females attending more to blue decorations (Coleman et al., 2004). Young females appear to be threatened by intense courtships, which often cause them to startle out of a crouch position and sometimes leave the bower (Coleman et al., 2004; Patricelli et al., 2004). These studies of crouching signals have allowed us to consider how female behaviour in the bower can indicate a female's reaction to male displays and her readiness to mate. Even with this information, however, it can be difficult to determine to what degree and when in the mate selection process a female is focusing on a particular aspect of male display because crouching is likely influenced by multiple elements of the male display and also occurs relatively late in the mate searching process (Patricelli et al., 2004).

The paint applied to bowers by male satin bowerbirds is a trait used by females in mate assessment (Hicks et al., 2013). Throughout the mating season, male satin bowerbirds chew dried hoop pine (*Araucaria cunninghamii*) needles and apply the resulting brown paste on the inside of their bower walls, focusing on the area midway up the walls at beak level. Bravery et al. (2006) found that males painted for 24% of the total amount of time they spent at their bowers, roughly equal to the time spent on bower building. In addition, Robson et al. (2005) found that male painting rate is correlated with mating success. During visits to bowers, females nip at the bower walls and swallow, appearing to taste the paint (Bravery et al., 2006; Hicks et al., 2013; Robson et al., 2005). Such tasting occurs at 39% of all courtship visits (Bravery et al., 2006; Robson et al., 2005), suggesting that paint may be a chemical signal used in mate assessment. More specifically, Reynolds et al. (2009) speculated a role for paint in kinship recognition. Hicks et al. (2013) showed that females' revisits to bowers are reduced by paint removal.

Studying female bowerbird sampling of paint offers a potentially important and novel window into female assessment of males. While crouching by a female acts as a signal indicating the female's comfort and her readiness to mate (Patricelli et al., 2004, 2002), tasting could provide information about how a specific display element, paint, may affect female decision making during mate searching. In addition, tasting behaviour can occur at any point in the mate searching process, including early during mate searching, or even when the male is absent from his bower. By studying this behaviour, we can examine how tasting relates to mate assessment. We can measure (1) whether and when females taste during mate searching, (2) whether individual female differences relate to differences in tasting behaviour and (3) whether individual differences in tasting behaviour provide insight into a female's mental state during her search.

Female mate searching can be difficult to quantify. However, in the Wallaby Creek bowerbird population (New South Wales, Australia), we have been able to uniquely band most females and follow them through the mate searching process using video cameras positioned at bowers that automatically turn on when birds arrive. In the first detailed examination of female satin bowerbird mate searching, Uy, Patricelli, and Borgia (2001a, 2001b) showed that most females visit a sample of the males in the population, which they narrow down across subsequent visits. Females vary in the initial number of males they visit, total number of visits and the speed at which they conclude their mate search (Uy et al., 2001a). After multiple visits to males, most females (84%) choose a single male for a mate (Reynolds et al., 2009). Although this suggests that females become more certain about their mate choice as they progress towards mating, the pattern of this narrowing process varies among females. A subset of singly mating females, referred to as 'faithful' females, mate with the same male as the previous year, with less searching than other females that switch mates between years (Uy et al., 2000, 2001a). This suggests that females who switch mates, referred to as 'unfaithful' females (Uy et al., 2000), are less certain of who their mate will be than faithful females, at least in early stages of mate selection.

Here we relate female differences in tasting behaviour to differences among females in their mate searching and mating behaviour. During a preliminary study of female tasting behaviour, we examined this behaviour across various visit types at bowers: visits without courtships, courtships, and courtships ending in copulation. We found significant differences in tasting behaviour