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Male-male sexual behavior in Japanese quail: Being "on top" reduces mating and fertilization with females

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ABSTRACT

Male Japanese quail (*Coturnix japonica*) engage in vigorous same-sex sexual interactions that have been interpreted as aggressive behavior reflecting dominance relationships. The consequences of this behavior for reproductive success, and whether it is a form of competition over mating and fertilization, are unclear. Three experiments were conducted to determine the effect of seeing or interacting with another male on a male's subsequent mating and fertilization success with females. A vigorous interaction with another male in which the subject performed more cloacal contact movements (movements to try to make contact with the other bird's cloacal opening) reduced subsequent mating and fertilization success with a female to a similar extent as a prior mating with a different female. Receiving one or more cloacal contacts from another male was less detrimental for subsequent success. The mere presence of another (stimulus) male delayed mating initiation in those male subjects that approached the stimulus first instead of the female. These results do not support the idea that the male "on top" in male–male sexual interactions is the dominant bird who goes on to achieve greater reproductive success. Instead, the results are consistent with male–male sexual behavior as an occasionally costly by-product of strong mating motivation.

1. Introduction

Same-sex sexual behavior has been observed in many species and in both wild and domestic animals (Bailey and Zuk, 2009). Numerous hypotheses have been proposed to explain such behavior (Vasey and Sommer, 2006; Poiani, 2010). Some of these concern possible adaptive functions to help explain how the behavior is maintained over evolutionary time even though it has similar costs as heterosexual behavior (for example, sexually transmitted diseases or increased predation risk) but without the obvious direct fitness benefits of mating with the other sex. Sexual behavior between males has often been hypothesized to be a form of competitive dominance establishment that, like some other forms of male–male competition over mating, would be expected to have benefits in the form of greater reproductive success for the dominant individual. On the other hand, it is also possible that male–male sexual behavior is non-adaptive or an epiphenomenon of a high level of mating activity.

Male–male sexual behavior occurs in a number of birds (MacFarlane et al., 2010) but because many of the reports are from wild populations there are few experiments testing causal hypotheses about the consequences of the behavior for reproductive success. In the experiments reported here, the subjects are Japanese quail. Domestic male quail housed individually typically initiate mating immediately when placed with a female, and even those that are slower to mate usually initiate mating within the first 5 min if they mate at all (Schein et al., 1972). Mating consists of grabbing the feathers of the female's head or neck, mounting (placing both feet on her back) and reaching back with the wings spread to try to achieve cloacal contact (termed a "cloacal contact movement") (Fig. 1A and supplemental video 1). Because males of this species mate reliably and rapidly, Japanese quail are the most important avian model for analysis of the neural and hormonal mechanisms of copulatory behavior (Adkins-Regan, 1996; Ball and Balthazart, 2004).

Males are very sexually active with both sexes, however. When tested with another male, a vigorous interaction occurs in which each bird tries to mount the other and achieve cloacal contact, occasionally succeeding (Adkins, 1974) (Fig. 1B and supplemental video 2). Beginning with Kuo (1960), these male–male interactions have nearly always been interpreted as fighting or aggressive conflict (e.g., Tsutsui and Ishii, 1981; Ramenofsky, 1984; Hirschenhauser et al., 2008). The male that is more often "on top," i.e., the one that performs more mounts or cloacal contact movements, has

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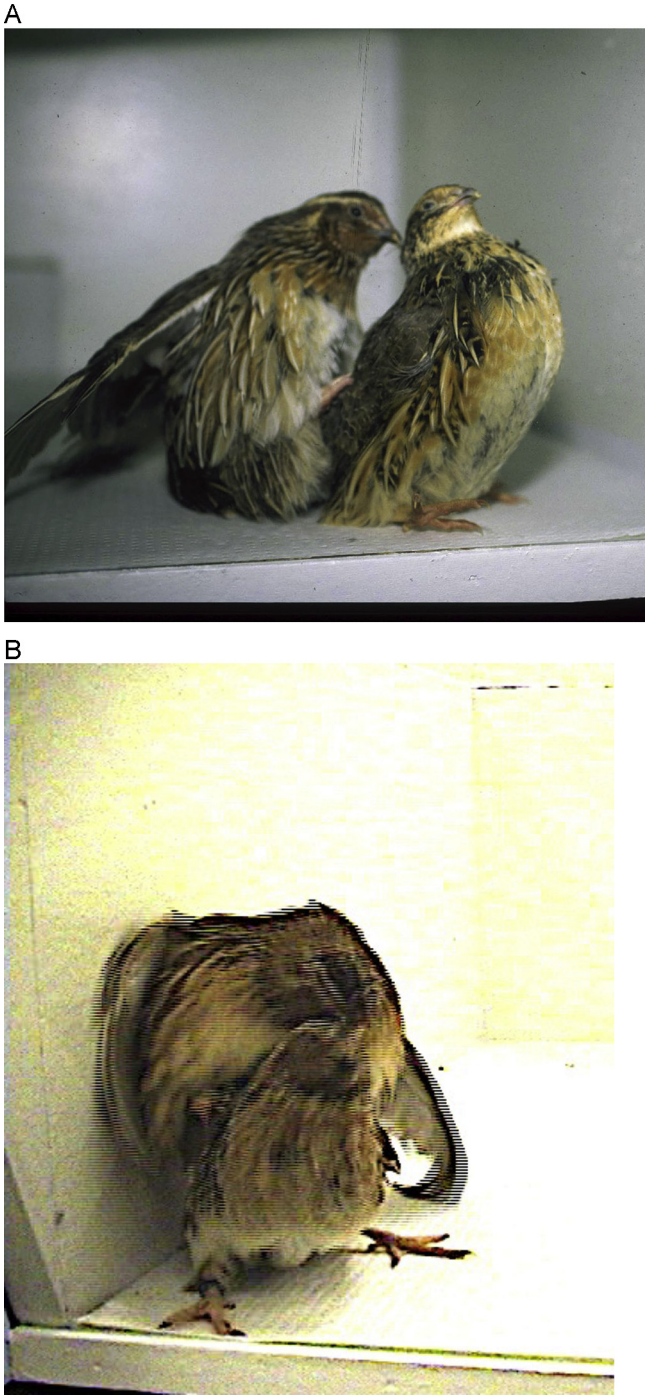

Fig. 1. Japanese quail sexual behavior. (A) A cloacal contact movement by a male (on the left) in a mating interaction with a female. See also supplemental video 1. (B) A cloacal contact movement by the male "on top" in an interaction with another male. Image captured from video. See also supplemental video 2, from which the image was captured.

been repeatedly described as dominant (e.g., Riters and Balthazart, 1998). Mating attempts with unreceptive females have a similarly vigorous and aggressive quality, and forced copulations are common (Adkins-Regan, 1995; Ophir and Galef, 2003).

Although the sexual and aggressive behavior of wild Japanese quail has not been reported, the closely related European quail (*Coturnix coturnix*) has had a reputation for centuries as a highly "salacious" bird famous for its "lust" (Ray, 1678, p. 170). This suggests that the vigorous sexual tendencies are species-typical characteristics of both members of the genus and not an artifact of the recent domestication of the Japanese quail. Reports from the field of *C. coturnix* as well as observations of genetically near-wild *C. japonica* in outdoor enclosures suggest flexible mating systems combining short-term pair relationships, mate switching and extra-pair matings (Nichols 1991; Rodriguez-Teijeiro et al., 2003; Sardà-Palomera et al., 2011). Males do not incubate the eggs or care for the chicks, which is consistent with the results of a comparative analysis of birds showing an association between more frequent male–male sexual behavior and absence of paternal care (MacFarlane et al., 2010).

The consequences for reproductive success of the male–male sexual interactions of Japanese quail are unclear. Females have been shown to prefer the males described as the subordinates in the interactions (Ophir and Galef, 2003) but which male succeeds in fertilizing more eggs is not known and forced copulation can override female preference (Adkins-Regan, 1995). Here three questions are addressed.

First, what is the influence of the presence of another male, but without allowing a direct interaction, on a male's mating and fertilization success with a female (Experiment 1)? If the other male, a stimulus male, is perceived as a reproductive competitor but one that is unable to access the female (a subordinate status), the mating male (the subject) might be expected to show the enhanced mating and fertilization of a dominant individual. If, on the other hand, the stimulus male is a sexual opportunity or sexual stimulus, the effect on the subject could be negative (the subject has a conflict over which bird to mate with first), especially if the subject approaches the stimulus first instead of the female, or positive (the other male adds additional sexual stimulation and enhances the subject's sexual motivation), especially if the subject approaches the female first. See Table 1 for a summary of the hypotheses and predictions for this and the following two experiments.

Second, how is a male's mating and fertilization success affected by a prior sexual interaction with another male? If those interactions are dominance encounters, and the dominant individual is the male "on top," the dominant would be predicted to be successful at mating with and fertilizing females (Experiment 2). Alternatively, the male "on top" might be exhausted or sexually depleted (satiated) and less successful in a subsequent encounter with a female.

Third, what is the effect of receiving cloacal contact (CC) from another male on the CC recipient's mating and fertilization success (Experiment 3)? If those males are subordinates, a detrimental effect would be predicted for their success in a subsequent encounter with a female, both for behavioral reasons (the stress of defeat) and because of the role of male foam in sperm competition. Male Japanese quail produce a large amount of meringue-like foam from a special gland. The foam is passed to the cloaca along with the sperm during insemination. Foam enhances a male's fertilization success in a competitive mating situation with another male (Finseth et al., 2013). Because male–male interactions also occasionally result in insemination, it is possible that the inseminator's foam might reduce the fertilization success of the recipient when the latter then mates with a female. If so, that would suggest that copulating with another male could be a competitive reproductive tactic, a hypothesis supported in a study of Razorbills (*Alca torda*) that found that mounting other males was positively correlated with success at extra-pair copulations with females (Wagner, 1996). Alternatively, quail same-sex sexual behavior could be a tactic by the animal being mounted to divert the mounter from mating with females or to make the mounter waste his ejaculate (including foam, in the case of quail), a different sperm competition tactic (Jamieson and Craig, 1987; Birkhead and Møller, 1992). In this hypothesis the male "on the bottom" is not affected negatively with respect to success with females, and instead the male "on top"