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Sex-obsessed or just sociable? Non-copulatory displays in the hamerkop

Non-copulatory sexual behavior is surprisingly vertebrates. Although sometimes considered unusual or aberrant within a species, in some taxa non-copulatory sexual behavior is widespread, and may even represent the majority of sexual behavior. Such behavior can also happen in many other contexts, including accidental contact, courtship, social bonding, and social structuring (Bagemihl 1999).

Some non-copulatory sexual behavior is relatively easy to classify. For example, male-male mating in damselflies (*Ischnura elegans*) is thought to be maladaptive, likely a case of mistaking males for females (van Gossum *et al.* 2005); similar cases of mistaken identity are also found in vertebrates (eg garter snakes [*Thamnophis sirtalis parietalis*]; Shine *et al.* 2003). In other taxa, like shortfin mollies (*Poecilia mexicana*), non-copulatory sexual behavior may increase the likelihood of successful copulation (Bierbach *et al.* 2012), while, in some species, it may lead to same-sex social pairings or otherwise have an obvious influence on social structure (eg female-female pairs of Laysan albatrosses [*Phoebastria immutabilis*]; Young *et al.* 2008).

The hamerkop (Scopus umbretta) is an unmistakable heron-like bird found in sub-Saharan Africa and in the southeastern Arabian Peninsula. Named for their distinctive "hammerhead", hamerkops are renowned for their massive enclosed nest structures, which may weigh over 90 kg (Wilson and Wilson 1986). Hamerkops build their nests in pairs but may aggregate in large numbers (>250 individuals in 4 km^2) and associate in small social groups of up to 10 individuals (Kaweesa et al. 2012). In December 2012, in Lake Manyara National Park, Tanzania, I observed a trio of hamerkops flying toward a flooded portion of road to drink. One individual picked up a stick from the water and walked to where a second individual stood after drinking (Figure 1); a third hamerkop stood some distance away and eventually flew off. The first individual appeared to present the stick to the second bird before laying the offering on the ground and jumping onto the second hamerkop's shoulders. The bottom individual stood in a flattened horizontal position (Figure 2). Several times, the bottom individual raised its tail to push against the lowered tail of the top individual, but no cloacal contact was attempted. The duo stood like this for several minutes, with the top hamerkop fanning its wings, perhaps to maintain its balance. Afterwards, the top individual jumped down, and the duo walked off the road into the woods, abandoning the stick.



Figure 1. Stick-handling behavior observed in the hamerkop (Scopus umbretta), in Lake Manyara National Park, Tanzania.

Interestingly, stick displays have not been documented in hamerkops, though two distinct forms of stick displays are common in other Ciconiiformes (Kahl 1967). The "Twig Shake" is a courtship display in herons and egrets, in which one bird grasps a small twig with its bill and vigorously shakes it (Hancock and Kushlan 2010). More similar to the behavior that I observed, however, is the "Stick Presentation", which is part of the greeting ceremony between mated pairs in related species during the beginning of the breeding season (Hancock and Kushlan 2010). This ritualized behavior occurs when one individual retrieves a stick suitable for nest building, approaches its partner, and presents it, often with a bow or a call. These behaviors are thought to help develop the pair bond, and may precede both nest building and copulation (Hancock and Kushlan 2010).

The stick handling I observed closely parallels the Stick Presentation ritual described above, and could therefore potentially be a rare social behavior in hamerkops, perhaps serving as a prelude to the non-copulatory mounting that followed. Given that these hamerkops were seen near a nest, however, it is also possible that the hamerkop that picked up and carried the stick may simply have been distracted from bringing this nest-building material to the nest by mounting its companion, as hamerkops generally collect such material individually (Kahl 1967).

In pairs and in groups, hamerkops have been documented performing so-called "ceremonial" behaviors, including non-copulatory mounting between both mates and unmated individuals (Kahl 1967). Non-copulatory 398



Figure 2. Non-copulatory mounting display documented between the hamerkops in Figure 1, shortly after the stick-handling behavior occurred.

mounting in hamerkops occurs in all combinations of sexes, including reverse mounting (female mounting male) and same-sex mounting by both males and females (MacFarlane *et al.* 2007). Hamerkops have even been observed conducting round-robin reciprocal mounting in trios and quartets, and even "stacking", where three or four individuals stand on each other's backs, forming a tower (Bagemihl 1999; MacFarlane *et al.* 2007). These behaviors suggest that non-copulatory mounting in hamerkops likely plays a broader social role than simple courtship, and the widespread nature of this behavior suggests that it is unlikely to simply be an aberrant behavior for this species.

Non-copulatory mounting is common in birds, and is documented in more than 120 species from 37 families (Balcombe 2006). While many cases of non-copulatory mounting are clearly associated with courtship or pair bonding (Nuechterlein and Storer 1989), some avian mounting appears to be related to social interaction outside of the pair bond. Blue-bellied rollers (*Coracias cyanogaster*), for instance, breed and maintain territories in pairs, and use non-copulatory mounting in agonistic situations, potentially as a dominance contest (Moynihan 1990).

Social avian species may use non-copulatory mounting to maintain group dynamics (Cockburn 2004). Harris' hawks (*Parabuteo unicinctus*), for example, exhibit a behavior similar to that of hamerkops, termed "back-standing" or "stacking", where subordinates perch on the backs of dominants, sometimes for extended periods of time (Dawson and Mannan 1991). Similarly, acorn woodpeckers (*Melanerpes formicivorus*) mount each other prior to roosting ("pre-roost mounting"), when emerging from roost holes, and during fights for breeding vacancies; these behaviors do not appear to serve as a prelude to copulation and are not associated with gender (Koenig and Walters 2014).

The observation of an apparent Stick Presentation ritual suggests that the two hamerkops I observed were a mated pair, as this behavior occurs only between mated pairs in similar species. Nevertheless, non-copulatory mounting seems to be a social behavior rather than a sexual one. The inference that it plays primarily a pair-bonding or courtship role does not explain the prevalence of multiindividual mounting (both stacking and reciprocal series of mounts), and non-copulatory mounting between mated pairs of hamerkops has been described when a third individual approaches the nest structure, potentially to indicate non-aggression to the approaching bird (Smith 1977).

Non-copulatory mounting in hamerkops is therefore probably a mechanism for structuring social interactions, and may serve to reinforce non-aggressive relationships.

The potential for other undocumented pair-bonding rituals (eg Stick Presentation), and our lack of information on the purpose of known rituals, suggests that there is still much to learn about this species' social behavior. Although hamerkops are usually described as solitary, cooperative nest building, aggregate nesting, and large, non-breeding social groups have been documented (Steyn 1996). Hamerkops may use ritualized interactions to maintain social bonds with unrelated neighbors, allowing for aggregations when food is plentiful; conversely, hamerkop social groupings may be dynastic in nature, with nepotistic family groups that sometimes behave cooperatively (eg western bluebird [Sialia mexicana]; Dickinson et al. 2016). Further examination of social interactions, particularly using colored leg bands to mark hamerkops, and analysis of the parentage of those individuals, could provide insight into the complex social behavior of this unusual species.

Supporting Information

References may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee. 1318/suppinfo

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