

Note

An observation of incest avoidance in Gray Wolf (*Canis lupus*)

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Abstract

Free-ranging Gray Wolf (*Canis lupus*) tends to avoid inbreeding, but there is no information about how they manage this avoidance. Our observation of a female wolf in Yellowstone National Park actively rebuffing her father's sexual advances but then copulating with a distantly related male is the first and only report of one means by which wolf pack members avoid inbreeding.

Key words: Behaviour; *Canis lupus*; Gray Wolf; inbreeding avoidance; incest; reproduction; Yellowstone National Park

Free-ranging Gray Wolf (*Canis lupus*) tends to avoid inbreeding (Smith *et al.* 1997), although when the chances of such avoidance are low, such as in captivity (Packard *et al.* 1985) or on Isle Royale (Wayne *et al.* 1991), they will inbreed. Some work shows that avoidance occurs primarily within packs, but not necessarily outside the pack (Geffen *et al.* 2011). Generally, wolves avoid inbreeding by (1) not copulating with related pack members, (2) male-biased dispersal and copulating with non-relatives, and (3) female-biased subordinate breeding (vonHoldt *et al.* 2008). However, no information has been available about the specific mechanism or mechanisms that might facilitate the avoidance of inbreeding. Here we describe an instance of copulation avoidance between closely related members of the same pack even though both animals successfully copulated with unrelated pack members.

Several members of the Junction Butte Pack in Yellowstone National Park (YNP), Wyoming, USA, were radio-collared (Smith *et al.* 2015). R.M. located and observed these wolves and their packmates daily as often as possible for four years from the ground using binoculars and a 60× spotting scope during daylight (McIntyre 2019, 2020, 2021). A combination of radio frequency and/or natural body markings made each wolf individually identifiable. At the time of this observation, the pack consisted of 11 members,

including five radio-collared adults (dominant female 970F, dominant male 911M, subordinate male 890M, and subordinate females 907F and 969F), as well as two other adults and four offspring from the previous year (Table 1). The genetic relatedness (vonHoldt *et al.* 2020) of the five collared wolves was as follows: (1) unrelated: 890M/907F, 970F/911M, and 890M/969F, (2) offspring/parent: 907F/911M and 969F/911M, (3) full sibling: 907F/969F, and (4) cousins or more distant: 890M/911M, 890M/970F, 907F/970F, and 969F/970F; Table 2).

Wolf 911M helped raise his daughter 907F to the end of the year, then dispersed but returned to the pack about a year later. Wolf 907F's mother, who was not collared, was observed copulating only with 911M the year 907F was born but could have copulated with others when not observed. Although we did not observe 890M provisioning 907F as a pup, he regularly attended the den and provisioned the pack, so there is every reason to believe that he did.

On 16 February 2016 between 0743 and 1646, R.M. made the following observations. Wolves 907F and 890M were seen in a copulatory tie at 0801 for several minutes but for an unknown total period. When canids copulate, they remain hooked together for varying periods in a "copulatory tie". Throughout the day, 907F and 969F repeatedly averted their tails to wolf 890M (unrelated or very distantly related to

TABLE 1. Status of adult radio-collared members of the Yellowstone National Park Junction Butte Pack of Gray Wolf (*Canis lupus*) in February 2016.*

Wolf no.†	Age, years	Rank	Relationships
890M	4 or 5	Subordinate	Immigrant
907F	3	Subordinate	Daughter of 911M and a non-collared female
911M	at least 5	Dominant	Immigrant father of 907F and 969F
969F	3	Subordinate	Daughter of 911M and a non-collared female
970F	at least 4	Dominant	Immigrant

*The pack also included two non-collared adults and four offspring from 2015.

†F = female, M = male.

TABLE 2. Pairwise relatedness matrix estimated from 598 single nucleotide polymorphism genotypes for five focal Gray Wolf (*Canis lupus*) in Yellowstone National Park.

	907F	911M	969F	970F
890M	0.001	0.114	0.033	0.025
907F		0.493	0.445	0.099
911M			0.482	0.000
969F				0.173

Source: vonHoldt *et al.* (2020).

Note: F = female, M = male.

those females), but never averted them to their father, 911M. Female tail aversion signals estrus and allows copulation (Concannon *et al.* 1977). Wolf 911M repeatedly tried to copulate with 907F, but 907F blocked each of his attempts, often by rolling over on her back. Male wolves cannot force copulation with female wolves; i.e., both wolves must be willing for a copulatory tie to be successful.

Once 911M bedded and appeared to give up trying to copulate with 907F, 907F went to 890M and, at 1605, they copulated and tied for 15 min. While they were tied, 911M still tried to mount 907F and even did some thrusting.

During these observations, dominant wolf 970F, considered the mate of 911M, several times averted her tail to 911M, but he ignored her. He was previously seen copulating with her on 8 and 10 February.

All three of these females denned in April, with 907F and 969F denning together and producing a total of at least nine pups. Both male wolves 911M and 890M attended the den and helped provision the pups. Wolf 970F denned away from the pack at a remote location and died of unknown cause(s) soon after the time when she should have borne pups; it was unknown whether she had produced any pups.

Most wolf packs include a pair of unrelated parents and their immature offspring; thus, within such groups, incest is not even possible. However, Yellowstone's Junction Butte pack included both related and unrelated mature individuals. This observation of

both females 907F and 969F averting their tails and copulating with less-related wolf 890M but not their father, 911M, and 907F's rebuffing sexual advances by her father, is the first and only report of one of the possible ways in which wolf pack members avoid inbreeding. It also suggests the hypothesis that incest avoidance tends to be furthered by female wolves rather than males, as in non-human primates (Pusey 1990).

Author Contributions

Writing – Original Draft: L.D.M. and R.M.; Writing – Review & Editing: L.D.M. and R.M.; Conceptualization: L.D.M.; Investigation: R.M.; Methodology: R.M.; Formal Analysis: L.D.M. and R.M.

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