

Breeding displacement in gray wolves (*Canis lupus*): Three males usurp breeding position and pup rearing from a neighboring pack in Yellowstone National Park

Gray wolves usurp breeding position

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Abstract

Gray Wolves (*Canis lupus*) are territorial, group living carnivores that live in packs typically consisting of a dominant breeding pair and their offspring. Breeding tenures are relatively short and competitive, with vacancies usually occurring following a breeder's death, and are often filled by unrelated immigrants or by relatives of the previous breeder. The frequency and conditions of active breeder displacements are poorly understood. Position changes in the dominance hierarchy are common yet rarely documented in detail. We describe a turnover in male breeding position in a wolf pack by males from a neighboring pack in mid-summer 2016 in Yellowstone National Park. Over the course of two months, three males from the Mollie's pack displaced the breeding male of the neighboring Wapiti Lake pack, joined the pack's two adult females, and subsequently raised the previous male's four approximately three-month old pups. In the four years following the displacement (2017 to 2020), at least one of the intruding males has successfully bred with the dominant female and most years with a subordinate female (who was one of the pups at the time of displacement). The pack reared pups to adulthood each year. Male breeding displacements are likely influenced by male-male competition and female mate choice. These changes are the result of individuals competing to improve breeding position and may lead to increased pack stability and greater reproductive success. We report in detail on the behavior of a closely observed breeding displacement and we discuss the adaptive benefits of the change.

Key words: Wolf, *Canis lupus*, Yellowstone National Park, breeding, alpha, usurp, dominant, mate-choice, male-male competition, displace

Introduction

The opportunity to breed is an important driver in the behavior of most animal species, including large mammals [1]. However, many species of mammals are relatively short-lived, resulting in a more constrained timeframe to breed [2]. Access to breeding opportunities, therefore, are often met with conflict and reproductive competition [3]. As a result, breeding positions in social mammals often have high turnover rates [4]. Reproductive competition is observed in a broad range of taxa (e.g., social carnivores, primates, ungulates, and pinnipeds), with reproductive skew resulting from individuals vying for dominance to maximize reproductive success [5]. Changes in mammalian breeding status can occur with one male usurping another, as intrasexual competition tends to be more severe among males than females. In cases where male breeding status changes, females may stay with the male that they prefer, with mate selection likely coming from physical, genetic, behavioral, and situational cues. Mate preference is thought to select for individuals most likely to bring the greatest direct and indirect fitness benefits [5]. While breeding competition and sociality can have negative consequences, it can also be highly advantageous. For example, group living can be essential to the survival of the group members, with benefits ranging from hunting to territorial disputes to cooperative breeding [6-9].

Wolves are social animals that can exhibit complex and dynamic dominance hierarchies, ranging from simple linear structures to sex/age graded structures [10]. In unexploited populations, they also demonstrate sex-specific breeding strategies, with females more likely to obtain breeding positions through natal philopatry (breeding in the pack they were born into, either through positional inheritance from a same-sex relative or by becoming a subordinate breeder), while males typically become breeders through dispersal (filling a breeder vacancy, usurping a dominant breeder) and temporary female affiliations [11]. Such dispersal strategies,

with males more likely to disperse and females remain in their natal pack, can lead to matrilineal pack structures [12]. As a result, most wolf packs consist of a male and female adult who are unrelated to each other, their offspring from one or more years, and sometimes other adults that are related to either the dominant male or female [13]. The highest-ranking individuals usually breed, and obtaining a breeding position, especially in packs where multiple breeders occur, can lead to aggressive competition [10, 14-15]. In captivity, old dominant males have been killed by their male offspring [14, 16], but such aggression is relatively rare in the wild [15, 17].

Most studies that report intense competition for breeding dominance in wolves are from observations in captivity. Competition for dominant breeding positions in the wild appears to be minimal, as most pack structures involve close-kin family groups, with parents naturally maintaining dominance over their offspring [10, 15]. In Quebec, an intruding male assumed the breeding position at the time of the death of the former breeding male [18]. In Denali National Park, intraspecific conflict between two packs led to two members of the attacking pack using the other pack's den with two unknown wolves, which may be an example of displacement [19]. In Yellowstone National Park (YNP), we have been able to observe breeder turnovers in the wild more frequently, helping us better understand how this behavior occurs in wild wolf packs.

Since the reintroduction of wolves to YNP in 1995, such rare events as the forced change from an original breeding male by a new male have been observed more often due to the visibility of several wolf packs [20]. In some cases, dominant males were killed by a neighboring pack and subsequently one or more of the attackers filled in the breeding vacancy. In other cases, breeding males were displaced from their hierarchical position but remained with the pack as a subordinate. Most of these cases involved related males. In the third category, breeding males were displaced from their hierarchical position but chose to disperse instead of staying as a

subordinate. Here we observe one such event in detail. We discuss the importance of this event to long-term pack success. We also discuss female mate choice as the main factor leading to successful displacements of a male breeding position while acknowledging that male-male competition can influence that choice.

The two packs described here are the Mollie's pack and the Wapiti Lake pack. The Mollie's pack lineage was originally reintroduced into YNP in 1995 and has continued to live in the park's interior to the time of publication [11]. The Wapiti Lake pack formed in the park's interior in 2014, although the dominant female was born in this area and had been a resident since 2010. The two packs shared some overlap in their territories (Fig 1). Since the formation of the Wapiti Lake pack in 2014, the proximity of their territory to the territory of the Mollie's pack resulted in occasional aggressive territorial encounters.

Fig 1. Wolf Pack Territory Map before and after Displacement. 95% minimum convex polygons of the home ranges of the Wapiti Lake pack and the Mollie's pack prior (2014-2016) to the displacement of the Wapiti Lake breeding male 755M (left) and post (2016 to present) displacement (right) in Yellowstone National Park. Proximity of the two packs' territories likely led to displacement of breeding male 755M, as described in this writing.

Wapiti Lake dominant breeding male 755M was displaced over the course of the 2016 summer by three adult males from the Mollie's pack. This result was likely a result of male-male competition and female mate choice [21-22]. Several factors influenced competition and mate choice in this instance, including male age, the number of males, male size, relatedness, and presence of dependent pups. The result of the displacement was seemingly adaptive for the

female breeders and male intruders, and likely positively impacted future reproduction and pack success. For the displaced older male 755M, the fitness outcome may have been negative, although the displacement led to an observation of him breeding within another pack and possibly producing pups. Before he became a founding member of the Wapiti Lake pack, he left another pack he formed in northern YNP after his mate was harvested, meaning he produced offspring in three packs during his life. As an old adult, any chance to breed may be an unexpected addition in reproductive output. The aim of this writing was to report on a unique observation of dominant male displacement in gray wolves and discuss resulting implications, which was achieved.

Methods

Observations occurred within YNP, with the majority occurring in Hayden Valley (44.6886°N, 110.4655°W) between 7 July 2016 and 12 August 2016. The valley is mostly open with some coniferous forest cover and several bodies of water, including the Yellowstone River. Openness allows for easy observation within Hayden Valley. Furthermore, the study area is transected by the park road, which provides access for visitors and researchers and serves as the main platform for observing wolves. Elevations within YNP range from 1500-2400 meters, with Hayden Valley at approximately 2300 meters in elevation [23]. Vegetation in the study area consists of lower elevation montane ecoregion Douglas firs (*Pseudotsuga menziesii*), Wyoming big sagebrush (*Artemisia tridentata*), and grasslands dominated by *Festuca* sp. to more closely canopied lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*).

The study area also contains abundant wildlife, including ungulates such as American bison (*Bison bison*) and American elk (*Cervus canadensis*), and large carnivores, such as grizzly bears (*Ursus arctos*) and American black bears (*Ursus americanus*). The primary prey of wolves

in the study area is elk [24]. An abundance of elk and other prey, including bison, enables a high wolf density in YNP (averaging 56 wolves/ 1000 km² with fluctuations between 20 and 98 wolves/ 1000 km² [9]). Over the past decade, wolf densities have remained relatively constant, hovering around 40 wolves/ 1000 km² [25].

The Yellowstone Wolf Project monitors wolves using radio collars deployed in winter with the objective of maintaining enough collars to track packs. Wolves were captured from the air using helicopters. The Wolf Project consistently monitors wolves through aerial and ground radiolocation and observation. All capture and handling protocols were conducted in accordance with the NPS (IACUC permit IMR_YELL_Smith_wolves_2012) Institutional Animal Care and Use Committees. Telazol is used to anesthetize wolves. At the time of capture, newly collared wolves are assigned unique identifiers (an ordered-numeric followed by a sex identifier, e.g., 755M), which are used below to delineate specific collared wolves from uncollared wolves. Telemetry was used to locate wolves and spotting scopes and binoculars were used for observation. Observation notes were recorded on a voice recorder and then transcribed to data forms and a journal. Several individuals were involved in the observation process and collaborated to summarize the behavior they witnessed. Most of the adult wolves involved were recognized by experienced observers. In this case we were able to easily distinguish each of the six adult individuals and one pup involved in this encounter. The three gray pups all looked similar and were not individually recognizable. (Fig 2).

Fig 2. Notable wolves involved in the displacement. Notable wolves involved in the displacement of Wapiti Lake breeding male 755M by males from the Mollie's pack in the

summer of 2016. Note the age differences between the males from the Mollie's pack and 755M. Adult wolves were easily identifiable.

Results

The two packs involved in the encounter described here were the Wapiti Lake pack and the Mollie's pack. These packs occupy adjacent territories in central YNP, and territorial forays by the Mollie's pack into the Wapiti Lake pack's territory were common (Fig 1). At the time of the displacement, the Wapiti Lake pack consisted of seven wolves, including dominant breeding male 755M, a white dominant breeding female, a gray female yearling, three gray pups, and one black pup (Fig 2). The Mollie's pack consisted of sixteen adult wolves and four pups. The entire Mollie's pack was not involved in this encounter and significant members of this pack included three-year old male 1014M, two-year old male 1015M, and a black male two-year old (Fig 2). The first known encounter leading up to breeder displacement in the Wapiti Lake pack was observed on 7 July 2016. The final observation took place on 12 August 2016 because 755M was not observed near the pack again. There was considerable variation in the size and age between the male wolves involved in this encounter. At the time of capture, the radio-collared Mollie's males weighed 56 kg and 58 kg at 2 and 3 years old respectively, and eight-year-old 755M weighed 40 kg (Table 1). In male wolves, body mass tends to decrease with age, indicating 755M was likely even smaller than his capture weight, which was two years prior to the capture of the Mollie's males [26]. By leveraging a genetically derived population pedigree [27]), we estimated little difference in the males' relatedness to the unsampled dominant female, determined by their relation to her close relatives (Table 2). There was a large difference in relatedness to the gray female yearling. We discuss later how these factors could have contributed to this encounter's outcome.

Table 1. Weight of notable male wolves.

Male Wolf ID	Pack	Weight (kg)	Capture Date	Age at Capture
755M	Wapiti Lake	40	17 January 2014	8
1014M	Mollie's	56	26 January 2016	3
1015M	Mollie's	58	26 January 2016	2

Weight of notable radio collared male wolves involved in the displacement of Wapiti Lake breeding male 755M. Note the size differences in the two males from the Mollie's pack and Wapiti Lake male 755M. In addition to being outnumbered, 755M was much smaller than the three invading males. Male wolves tend to lose mass as they age [26], indicating 755M was likely smaller at the date of displacement than his capture date.

Table 2. Coefficients of relatedness for genetically sampled wolves.

	Wapiti Dominant Male <i>712M</i> (Father)	Female <i>1093F</i> (Mother)	1091F
755M	0.0163	0.1684	0.4702
1014M	0.1086	0	0.0479
1015M	0.1393	0.0218	0.0808
1155M	0.1086	0	0.0326

Coefficients of relatedness for genetically sampled wolves involved in the displacement of Wapiti Lake dominant male 755M in Yellowstone National Park. The uncollared black male from the Mollie's pack was later captured and assigned the number 1155M. The gray female yearling was also later captured and assigned the number 1091F. The Yellowstone Wolf Project has not genetically sampled the Wapiti Lake dominant breeding female, so her parents' (712M and 1093F) coefficients of relatedness are included here. The closest related wolves are father-

daughter pair 755M and 1091F (0.4702). See vonHoldt et al. 2020 for genotyping methods used to estimate relatedness [27].

Daily observation summaries

7 July 2016: In the morning, seven wolves from the Mollie's pack, including 1014M, who was a black three-year old male, were observed near the Wapiti Lake pack's rendezvous site (i.e., pup rearing homesite [26]) in Hayden Valley.

9 July 2016: At 2050, six wolves from the Mollie's pack, including 1014M, were observed near the Wapiti Lake pack's rendezvous site after the Wapiti Lake pack moved into the trees.

10 July 2016: At 0543, three black wolves from the Mollie's pack, including 1014M and 1015M, chased the Wapiti Lake breeding male 755M and the breeding female. From this day on we recognized the three black wolves involved, who were brothers. The other four Mollie's wolves returned to their own territory and did not participate further in this encounter. The Wapiti Lake pair split up and the intruding males chased the female. The breeding pair from the Wapiti Lake pack regrouped with the Wapiti Lake female yearling and the three males from the Mollie's pack moved out of sight. By 1300, GPS points showed 1014M south of the Wapiti Lake pack's rendezvous site. At 1600, the Wapiti Lake breeding female and two pups were seen back in the pack's rendezvous site.

11 July 2016: Around 1200, 1014M and another black wolf were seen in the rendezvous site with the Wapiti Lake pack's breeding female and female yearling. This was the first day the Wapiti females were seen interacting with the Mollie's males in a friendly way. The wolves sniffed each other, and the females jumped on the males and put their heads on their backs. This is typical wolf courting behavior. This behavior was also observed in the evening. The Wapiti

218 Lake breeding male, 755M, was seen at 2230 a few kilometers away from the rendezvous site.

219 No Wapiti Lake pups were seen.

220 **12 July 2016:** In the morning, 755M's radio signals indicated he was in the rendezvous site. At

221 1645, 1015M, a black male, and the two Wapiti Lake females were seen together in the

222 rendezvous site.

223 **13 July 2016:** At 1150, two males from the Mollie's pack and two females from the Wapiti Lake

224 pack were seen in Cascade Meadows (44.7336°N, 110.5093°W), a regular hunting area for the

225 Wapiti Lake pack. At 1256, 755M was seen attempting to cross the road near the rendezvous

226 site. He successfully crossed at 1530. He was then seen near the rendezvous site with the four

227 pups from the Wapiti Lake pack. GPS points indicated 1014M was in the traditional territory of

228 the Mollie's pack in the evening.

229 **14 July 2016:** In the morning, 755M was seen in the rendezvous site. At 1430, the two males

230 from the Mollie's pack and two females from the Wapiti Lake pack were seen in the rendezvous

231 site. They were seen in the same area in the evening. Blood on the breeding female's face

232 indicated the wolves had made a kill. This might be an indication that the females had made their

233 choice regarding which males to stay with as the focus was back to regular wolf life (e.g.,

234 hunting) instead of on the intruding males.

235 **15 July 2016:** At 0810, 755M and the Wapiti Lake yearling female were seen south of the

236 rendezvous site. At 1100, the two Mollie's males were seen chasing 755M. The chase was slow

237 paced. The Wapiti Lake females followed the males from the Mollie's pack. The four pursuing

238 wolves disappeared behind a hill and were not seen again. After looking back, 755M went out of

239 sight. At 2015, the breeding female and two Mollie's males were seen to the south of the

240 rendezvous site.

16 July 2016: Around 0900, the two Wapiti females were seen near the rendezvous site with three Mollie's males including 1014M, 1015M, and the uncollared black two-year old. The Wapiti Lake yearling was seen putting her head over the backs of 1014M and 1015M. The breeding female did this to 1014M. He then put his head over the back of the female. She playfully lunged and nipped at him. Raised leg urinations were seen from all three males, indicating dominance, and both females marked with them, indicating pair-bonding [29-30]. The wolves began to travel south. They encountered an elk herd at 1439. The chase ended out of sight but was successful. The breeding female was seen alone carrying an elk leg to the north of the rendezvous site early in the evening. She was likely feeding the pups. At 2143, the breeding female and the three Mollie's males were seen near the carcass.

17 July 2016: No wolves were seen in the morning. Weak radio signals indicated 1014M was near the rendezvous site. In the afternoon, the two Wapiti Lake females and three Mollie's males were seen near the rendezvous site. They likely killed an elk calf. The female yearling played with the males.

18 July 2016: Around 0800, the two Wapiti Lake females and three males from the Mollie's pack were in the carcass area from the previous night. The wolves remained in the area until dark. This is the last day 1014M's radio collar functioned.

19 July 2016: At dawn, two males from the Mollie's pack were seen near the rendezvous site. Former breeding male 755M was located from the air southeast of the rendezvous site. He crossed the road moving towards the rendezvous site at 2030.

20 July 2016: At 0930, the two Wapiti Lake females and three males from the Mollie's pack were seen near the rendezvous site. At 1930, the five wolves were then seen with the four Wapiti

263 Lake pups, sired by 755M, near the rendezvous site. This was the first direct observation of the
 264 Mollie's males with the Wapiti Lake pups.

265 **21 July 2016:** At 0656, the five adult wolves (two Wapiti Lake females and three Mollie's
 266 males) were seen with the four pups. During the morning all the adults were seen greeting the
 267 pups. At 0847, 755M was seen briefly 300 meters east of the other wolves. At 1630, the wolves
 268 were seen again. One of the Mollie's males played with a pup.

269 **22 July 2016:** At 0736, the five adults and four pups were seen near the rendezvous site. When
 270 1014M moved toward the pups, they rushed to greet him. The female yearling played with two
 271 of the Mollie's males. All three males played with the pups. At 1757, 755M was seen near the
 272 other wolves. Although he got close, neither 755M nor the main pack seemed to be aware of
 273 each other. Later in the evening, the three Mollie's males saw and chased 755M at a trot.

274 **23 July 2016:** After 0700, all five adults and four pups were seen near the rendezvous site. At
 275 1150, 755M was seen east of the other wolves. One of the collared Mollie's males slowly chased
 276 him out of sight. In the evening, 755M was seen in the rendezvous site alone. The other five
 277 adults were seen to the south chasing elk.

278 **24 July 2016:** At 0801, there were brief views of the gray female yearling and some pups in the
 279 rendezvous site. The pups came out and played while the yearling went out of sight. At 1015,
 280 755M appeared and bedded near the playing pups before he approached them. They greeted him.
 281 By 1215, 755M left and crossed the road to the west. At 1405, the five adults returned to the
 282 rendezvous site from the south. The three Mollie's males smelled the area and scent marked.
 283 There were brief sightings of the five adults in the evening.

284 **25 July 2016:** At 0837, there were brief sightings of a gray pup and the gray female yearling.
 285 Radio signals from 755M indicated he was in the area, but he was not seen. In the evening the
 286 five adults and four pups were seen in the rendezvous site.

287 **26 July 2016:** At 0752, two of the pups were seen. Around 0900, the five adults and two other
 288 pups were seen near the rendezvous site. Shortly after this, 755M appeared in the area and
 289 walked by the breeding female. They did not seem aware of each other as neither looked in the
 290 direction of the other. He moved out of sight at 0930. Later, the three Mollie's males followed
 291 his scent into the trees. The Mollie's males reappeared in a gap in the trees with two of the pups
 292 and the yearling female. They greeted each other at 0944. The breeding female followed their
 293 scent. At 0946, 755M appeared again moving the opposite direction. He passed all the other
 294 wolves without being noticed. At 0955, he had a tucked tail, flat ears, and was glancing around
 295 in all directions. He moved out of sight. The other wolves appeared on the same trail moving
 296 quickly in his direction. They moved out of sight in the same area where 755M disappeared.

297 They came back into view and moved back to the rendezvous site. The uncollared Mollie's male
 298 smelled the area where 755M was with a raised tail at 1056. At 1100, 755M was seen crossing
 299 the road away from the rendezvous site. In the evening, the pups and five adults were seen in the
 300 rendezvous site.

301 **27 July 2016:** Around 0842, the five adults were seen west of the road from the rendezvous site.
 302 They went out of sight moving west. There were some brief sightings of the pups in the
 303 rendezvous site. At 1615, 755M was seen in the rendezvous site with the breeding female and at
 304 least three of the pups. The yearling and the three Mollie's males were not seen.

305 **28 July 2016:** At 0852, three pups and the yearling female were seen in the rendezvous site. An
 306 aerial wolf tracking flight found 755M about three miles north of the rendezvous site. At 1315,

the breeding female crossed the road from the west and went to the rendezvous site. She fed and played with all four pups. At 1400, the yearling female and the three Mollie's males unsuccessfully attempted to cross the road from the west. At 2037, the breeding female, yearling female, pups, and 755M were seen in the rendezvous site. The three Mollie's males were not seen.

29 July 2016: By 0700, the three Mollie's males, breeding female, female yearling, and the four pups were seen in the rendezvous site. A gray pup greeted 1014M. The wolves moved out of sight. Around 1905, the adults chased a bison calf. The pups were seen in the rendezvous site. At 1945, 755M emerged from the trees and the pups greeted him. He was visibly nervous, exhibiting a tucked tail and flattened ears, but remained with the pups until dark.

30 July 2016: At 0600, all nine pack members (Wapiti female adults, four Wapiti pups, and three Mollie's males) were seen after the adults came into the rendezvous site. The uncollared Mollie's male played with the pups and the female yearling. At 1314, 755M was seen briefly in Cascade Meadows, several kilometers west of the rendezvous site. The nine wolves were seen again in the evening in the rendezvous site.

31 July 2016: Before 0800, the nine wolves were seen in the rendezvous area. At 0924, 1014M and 1015M began running towards something. Former breeding male 755M came out of a gully but quickly retreated as the two Mollie's males ran toward him. The two Mollie's males went out of sight behind him. All the wolves eventually went out of sight in that area. Around 1908, 755M appeared, but was chased by the three males as the female went to the pups. The uncollared male was less interested, but 1014M and 1015M continued the chase. Abruptly, 755M stopped and stood his ground. Although contact could have been made, none was observed. The males backed off and all the wolves bedded approximately 50 meters away from 755M.

1 August 2016: At 0803, the nine wolves were seen in the rendezvous site. In the evening they were seen again. Signals from 755M indicated he was the area, but he was not seen.

2 August 2016: At 0751, the five adults were seen in the rendezvous site. The pups eventually appeared. Former breeding male 755M appeared and two of the Mollie's males began to trot toward him. He bedded and howled. The Mollie's males also bedded. At 0803, 755M got up and moved away, looking back often. The Mollie's males got up and followed him before bedding again. He continued uphill. He bedded at 0813. He got up and moved out of sight at 0832. He came back out at 0910 and looked at the other wolves. He bedded and continued to watch them. He eventually got up and moved out of sight after rolling in an area where the other wolves scent marked. At 1900, 755M was seen coming out of the trees and he then bedded in the rendezvous site. The other adults appeared, and he quickly moved off. Two of the pups ran toward him. One of the Mollie's males chased him off slowly. The pups and the adults turned and disappeared into the trees. He followed them at a distance.

3 August 2016: By 0752, the nine wolves were seen in the rendezvous site. The adults moved to a nearby bison carcass. At 0927, 755M appeared to the north of the other wolves. He went out of sight. At 1800, 755M was seen in the rendezvous site with the yearling female and the pups. The other four adults arrived from the east and 755M got up and approached them. One black slowly chased 755M. The chase quickly ended, with all the wolves bedding. The three Mollie's males and 755M bedded about 75 meters apart by 2020.

4 August 2016: At 0814, the four pups were observed playing. The yearling female and 755M were bedded nearby watching them. The wolves moved out of sight by 1125. At 1940, the pups came out of the trees. The yearling and 755M reappeared as well. Suddenly, 755M raised his tail and ran towards the pups in an aggressive manner. The pups ran into the trees, but quickly

returned and licked 755M's muzzle seeking food. The pups then moved to the yearling female and licked her muzzle. The two adults bedded down, and the pups played. They moved out of sight by 2022. At 2145, the breeding female crossed the road and returned to the rendezvous site. The three males from the Mollie's pack were unable to cross due to traffic.

5 August 2016: Early in the morning, the five adults and the four pups were seen in the rendezvous area. At 0910, 755M was seen near the road. He had fresh puncture marks in his thigh and his fur had blood on it. He was limping, but the wound was not severe. He moved out of sight at 1025. The other nine wolves were seen in the rendezvous site in the evening.

6 August 2016: Only the pups were visible in the rendezvous site in the morning and the evening. Radio signals from 755M indicated he was in the area, but he was not seen.

7 August 2016: All nine of the wolves were seen in the rendezvous site in the morning and the evening. Radio signals from 755M indicated he was north of the rendezvous site.

8 August 2016: All nine of the wolves were seen in the rendezvous site in the morning and all but the yearling female were seen in the evening. Radio signals from 755M indicated that he was further north than the previous day.

9 August 2016: The nine wolves were seen in the rendezvous area in the morning and the evening. Signals from 755M were the farthest north they had been, near Dunraven Pass (44.8054°N, 110.4484° W).

10 August 2016: In the morning, the adults were seen around a bison carcass and the pups were in the rendezvous site. All the adults and three pups were seen in the rendezvous site in the evening. Radio signals from 755M still indicated he was around Dunraven Pass.

11 August 2016: In the morning and evening all nine wolves were seen in the rendezvous site. Radio signals indicated that 755M was back in the area.

12 August 2016: At 0708, the four pups were seen in the rendezvous site. A flight located 755M moving toward the rendezvous site. After he checked the area, the pups saw him and ran to him. They greeted him, seeking food. At 1015, the pups and 755M greeted each other again. They moved out of sight. At 1059, the other adults approached the rendezvous site. The pups came out to greet them. At 1150, 755M swam across Alum Creek and crossed the road away from the other wolves. Only the four pups were seen in the rendezvous site in the evening. Former breeding male 755M was not seen with the Wapiti Lake pack again.

Wolf 755M was not seen with the Wapiti Lake pack again. He was observed twice in Hayden Valley after displacement on 26 August 2016 and 4 September 2016 but was not observed interacting with other wolves. By the winter of 2016-2017, 755M joined the Beartooth pack (approximately 60 kilometers NW of Hayden Valley), was observed breeding within the pack, and may have fathered a litter of pups before he went missing in spring 2017. The three males from the Mollie's pack remained with the Wapiti Lake pack females and pups. 1015M became the dominant breeding male and bred with the dominant female and the yearling female in 2017 and the dominant female and another yearling female in 2018. The pack produced twelve pups in two litters in 2017 and seven pups in two litters in 2018, totaling at least nineteen pups, before 1015M dispersed and joined a different pack (along with the uncollared male).

Subordinate male 1014M then became the dominant breeder in Wapiti Lake and bred with the dominant female and another adult female in 2019 and 2020. The pack produced nine pups in two litters in 2019, eight pups in two litters in 2020, and at least ten pups from two litters in 2021. This displacement then resulted in at least forty-six pups produced at the time of this publication.

Discussion

Breeder displacement events are rarely observed, and most observations of displacement either result in mortality or expulsion of the breeding individual within a short period of time. This case is unique for multiple reasons. First, the length of the displacement was exceptionally long, just over a month. Second, the displacement was relatively amicable. There were no physical attacks observed, and chases were not high intensity. The only indication of the possibility of a violent encounter were puncture marks observed in 755M's thigh. At points, 755M even bedded as close as 75 meters to the intruding males. However, because wolves are not always in observers' viewsheds or may be active at night, there were likely several interactions that were not recorded. Third, the presence of young pups has rarely been documented in displacement events. This displacement is an example of a rarely observed transition of breeder status in a wolf pack.

For a social species, changes in rank and/or breeding status are rarely observed. We were able to follow the daily events of one such event. On average, about 33% of wolves in YNP are in a breeding position at any given time, and when there is a breeding vacancy the position is usually filled quickly. This encounter describes a different strategy of wolves forcing a breeding vacancy in a pack and pack females changing their male-allegiance. The Wapiti Lake instance is unique in its duration, which occurred over a longer period than most other cases of dominant males being displaced. This possibly occurred due to the proximity between the Wapiti Lake and Mollie's pack territories, giving the intruding males easy access to the Wapiti Lake pack's territory. This case is also unique because it occurred during summer, when inter-pack aggression is typically low [17, 25]. This specific displacement was likely heavily influenced by timing and presence of pups. The pack was stationary at a rendezvous site and this dynamic likely extended the transition to the new males.

During the summer of 2016, the seven member Wapiti Lake pack consisted of three adults and four pups and the Mollie's pack consisted of sixteen adults and four pups. The presence of pups in this displacement event also provides important context as it may have influenced the outcome. At the time of the first encounter the four Wapiti Lake pups were around 11 weeks old and weighed approximately 12 to 16 kg depending on sex [26, 31]. At this age, the pups were recently weaned off milk but still had deciduous teeth. At this age they relied on the adult wolves to regurgitate or bring meat to them, and their mobility was limited to within and around the rendezvous site. This breeding displacement, which resulted in the exchange of an old male for three large prime-aged males, may have had important implications for these pups during a critical period in their growth and development.

All three males were brothers and had likely worked out their dominance positions in relation to each other. They may have worked together to join the Wapiti Lake pack and hierarchy was not obvious until the next breeding season. At times, dominance between the three brothers was unclear. The four pups from the Wapiti Lake pack were fed by 755M and the breeding female during the initial stages of the displacement but were quickly accepted by the intruding males, although we never recorded the males regurgitating or bringing food to the pups.

The intruding males from the Mollie's pack chased 755M several times in July and August. The chases were of low intensity and aggression (e.g., running at only a trot or lope), possibly because the invading males knew that 755M did not pose a threat, as he was much smaller and older than the Mollie's males (Table 1). This relatively passive response might be expected if the wolves were related, however, they were not significantly close relatives (Table 2). Old wolves are also known to be important in territorial conflict, likely due to their

knowledge in avoiding dangerous situations [9]. Breeding male 755M may have survived these encounters due to his age and experience. In total, there were six chases observed. In two cases, 755M remained near the other wolves after the chase. In one case he bedded near them. However, there were also five times 755M entered the rendezvous site and greeted his pups and former mate. This behavior occurred most frequently when the males from the Mollie's pack were absent.

Unlike the behavior of newly dominant African Lions (*Panthera leo*), the newly dominant males did not kill the Wapiti Lake pups because infanticide is highly unusual in wolves [17, 32]. Due to wolves only breeding once a year, female wolves do not have spontaneous estrus following lost offspring as is observed in wild felids [11, 33]. The pups may be allowed to live because pack size is important to various measures of pack success [7-8, 25, 34]. In addition, allowing the pups to live might have been a strategy to allow future breeding partners to live (although one of the gray pups was a male). In fact, one of the gray pups bred with at least one of the intruding males in 2018, 2019, 2020, and 2021.

There were two cases in which 755M stayed near the other wolves after being chased. He was also observed standing his ground and approaching the other males during these encounters. This may have been an attempt to rejoin the pack as a subordinate member.

In another instance, 755M visited the rendezvous site and chased the Wapiti Lake pups aggressively before he realized they were his own pups. Wolves have been observed momentarily not recognizing their packmates in territorial conflict, and this may have occurred in this instance. This behavior could indicate that 755M was waiting until one of the other males was alone before attempting to regain his position through aggression. Although it is uncertain why 755M remained in the area so long, there is some indication that he was looking to either

regain his breeding position, rejoin the pack again in a subordinate role, or continue providing for his offspring.

Typically, displaced males are either violently displaced through mortality or violently displaced through expulsion from the pack. In rare instances, males have been allowed to remain with the pack following displacement. In YNP, these cases frequently involve related wolves. In the Wapiti Lake case, 755M was not related to the intruding males from the Mollie's pack, and this may have been why they did not allow him to remain with the pack.

Female choice is another important aspect of successful displacement since the behavior of the females from Wapiti Lake made it clear they preferred the Mollie's males over 755M by day four, when they displayed playful behavior toward them. The relationship between male-male competition and female mate choice is poorly understood, and the interaction between the two is a continued subject of debate [21]. Female choice is also understudied in mammalian species [22]. However, female mate choice is likely evolutionarily adaptive, as seen in this case. The Wapiti Lake pack went from having one male adult to having three male adults. In addition to the number of males, their size and age may have been a factor. The two radio collared Mollie's males were larger (at capture) than 755M (Table 1). They were also younger and at the prime age for hunting large prey (two and three years old), whereas 755M was past prime hunting age at eight years old [35]. This change likely provided greater breeding success and protection of resources and pack members. The number of wolves in a pack, the number of old individuals in a pack, and the number of large males in a pack are the leading factors in the determination of which pack is successful in intraspecific conflict [9]. Therefore, the three Mollie's males had the advantage over 755M in two of the three categories, including pack size and overall body weight. However, 755M was older than the three males. This factor is

important because intraspecific conflict is the leading cause of death for wolves in YNP [12]. Wolf pup production is also maximized when a pack reaches eight wolves [8] and the exchange of three males for one got the pack closer to that size. Large males are also important in subduing large prey, such as elk and bison [35], and litter survival is positively correlated with increasing number of prime age (2–6-year-old) males [11]. By choosing three large, prime-age males, the breeding female may have ensured that her pack would have the advantage in territorial conflict, pup-raising, and hunting large prey, thereby furthering survival.

Additionally, the females' acceptance of the intruding males was likely influenced by male-male competition wherein the three Mollie's male essentially drove out 755M and stayed in the Wapiti Lake pack's territory. It is possible the females had to accept the new males if they wanted to remain in their multigenerational territory, protecting and raising the non-mobile pups. At a different time of year, without stationary offspring, they may have made a different choice. However, all behavior by the females indicated that by day four they were enthusiastically treating the Mollie's males like pack mates and future breeding partners (e.g., playing, play-bowing, jumping on each other with wagging tails, etc.).

Choosing the three Mollie's males also may have resulted in greater reproductive success. Female wolves incur greater cost related to reproduction than males, likely causing females to select mates more carefully [11]. The three males were unrelated to both the breeding female and the female yearling, giving both females the opportunity to breed and produce pups. Wolves generally avoid breeding with close relatives [13]. 755M was the father of the gray female yearling, and therefore the only female 755M could breed with was the dominant female, which is the typical breeding situation in an average wolf pack. However, in the new pack

structure the yearling female could breed with any of the three new male pack mates and did not have to disperse or find a temporary mate during the breeding season.

The Wapiti Lake pups from 2016 were accepted into the pack in the long-term, and as of 2021 at least one of the gray females remains with the pack as the beta female. She has since been observed breeding and has produced pups. The other three pups lived with the pack until at least 20 months old and then their fate was unknown. In 2017, both adult females in the Wapiti Lake pack produced litters that were sired by at least one of the three males from the Mollie's pack. Between the two females, twelve pups were born and survived to the end of year. The Wapiti Lake became the largest pack in YNP, with twenty-one individuals. Several pups produced in 2017 joined or formed packs of their own once they reached dispersal age, thereby passing on the genes of the Wapiti breeding females and at least one of the Mollie's males. As of 2021, five packs in the Greater Yellowstone Ecosystem have breeding members that were born into the Wapiti Lake pack after displacement (Fig 3). Four pups, two sired by 1015M and another two likely sired by one of the three intruding Mollie's males, went on to become dominant breeding individuals in four different Greater Yellowstone Ecosystem packs. Conversely, of the eight pups produced by 755M during his two-year tenure as the dominant male of the Wapiti Lake pack, only five survived to their first winter, and none were known to have formed new packs.

Fig 3. Resulting Wolf Pack Map. Gray wolf packs in the Greater Yellowstone Ecosystem with breeding individuals descended from the Wapiti Lake pack after the displacement of dominant male 755M in the summer of 2016. As of 2021, at least four packs in the ecosystem had dominant breeding individuals producing offspring that were descended from the Wapiti Lake

dominant female. Pups produced post displacement are listed in parenthesis below pack names. Former dominant male 755M sired eight pups during his tenure, of which five survived to the end of the year. None were known to form new packs.

As of 2021, the Wapiti Lake pack has produced at least 46 pups since the 2016 displacement, all of which were likely sired by one of the three Mollie's males. Up to the end of 2020 the pack produced 36 pups, 35 of which survived to the end of the calendar year in which they were born, for a survival rate of over 97%. In 2017, all twelve pups produced survived, in 2018, six of the seven pups produced survived, in 2019, all nine pups produced survived, and in 2020, all eight pups produced survived. In 2021, the pack produced at least 10 pups, but survival is not assessed until the end of the calendar year and therefore was not available at the time of this writing. Comparatively, the typical mid-winter survival rate of wolf pups in YNP is around 70% [12]. It's worth noting that pup survival rates are likely an overestimation, given that initial counts take place following pup emergence from dens, which typically occurs 10-14 days after birth, a period where pup deaths could go undocumented. Nonetheless, this reproductive success would likely not have been observed had 755M remained the breeding male. If 755M remained with the pack, only the breeding female would be likely to breed and produce pups.

At eight years old, 755M was well past his prime. In the unlikely event 755M had been the dominant male breeder the following four years instead he may have produced an average litter of 4-5 pups each year [8] for approximately 18 pups. With a smaller pack to feed and protect them, survival would likely have been average at best. The intruding males could breed and produce pups with the breeding female, yearling female, and the three female pups. The intruding males were also in the prime of life at two and three years old. However, it is important

to note the value of age and older wolves can sometimes have outsized positive impacts on their pack due to their experience and accumulated knowledge, especially in inter-pack fights [9], so 755M would have been valuable to the pack in some ways as well.

The causes and consequences of reproductive competition and mate choice in wolves are not well understood but are an important aspect to wolf fitness. Breeding tenures are often short, and given that wolves have short lives, selection for traits that aid in attaining breeding positions is predicted to be strong [11]. The detailed observation of breeder displacement, subsequent offspring rearing, and new breeding pair formations described here advances our understanding of wolves. As additional cases are found and older cases are further studied, more conclusions may be made about competition for breeding position in wolf packs. Further research into the nuances of breeding displacements, such as the ramifications of these events on pack stability, mate choice, and reproductive success, may help fill an important knowledge gap in our understanding of social dynamics in territorial, social carnivores.

Acknowledgements

We wish to thank Mark Hebblewhite and Matt Metz for reviewing early versions of the manuscript and for data management. We thank Elizabeth Carroll for data collection. We appreciate the cooperation of Ron Blanchard, Laurie Lyman, Doug McLaughlin, and Kathie Lynch who were willing to share their observations of the interactions between the Wapiti Lake pack and the Mollie's pack. Thanks to Rebekah SunderRaj for manuscript review and editing.

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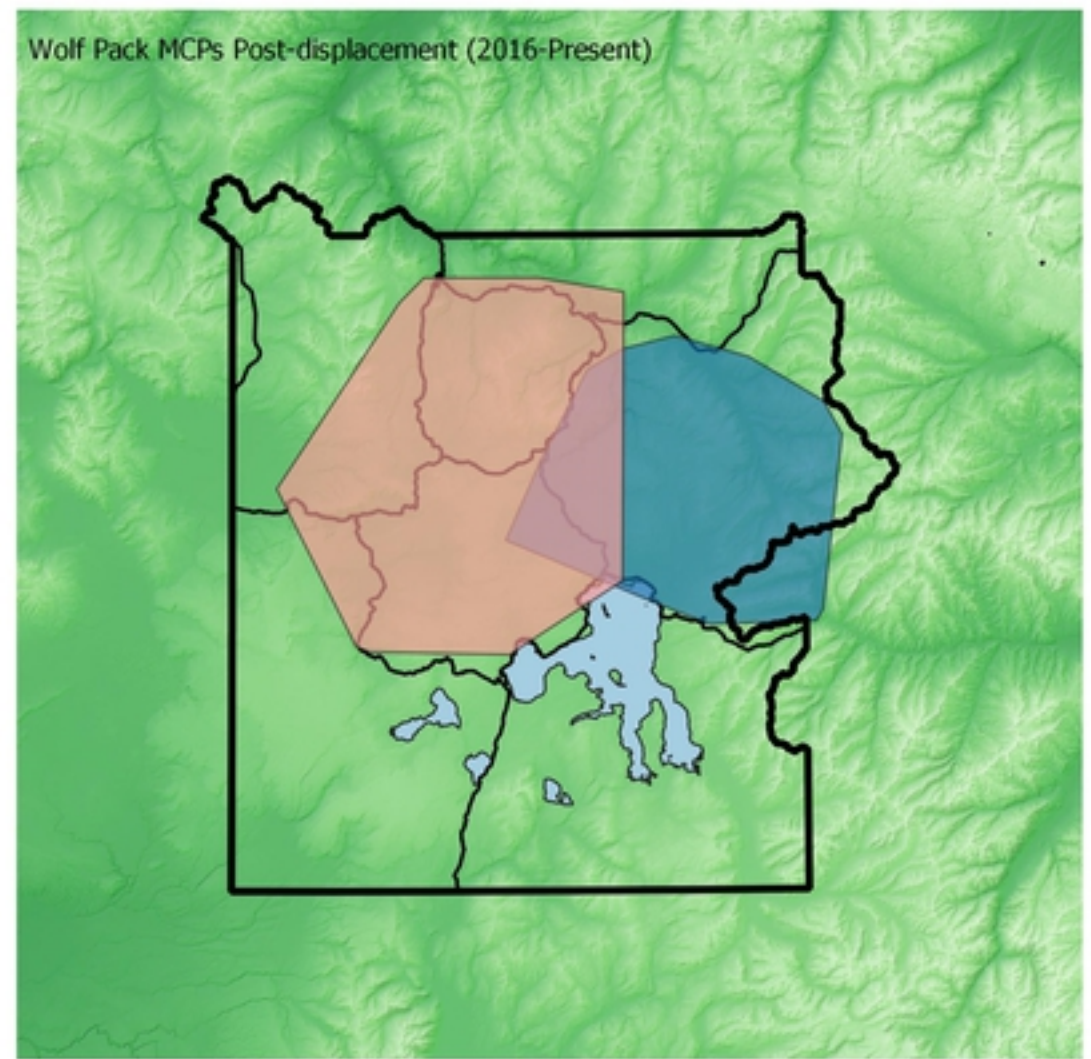
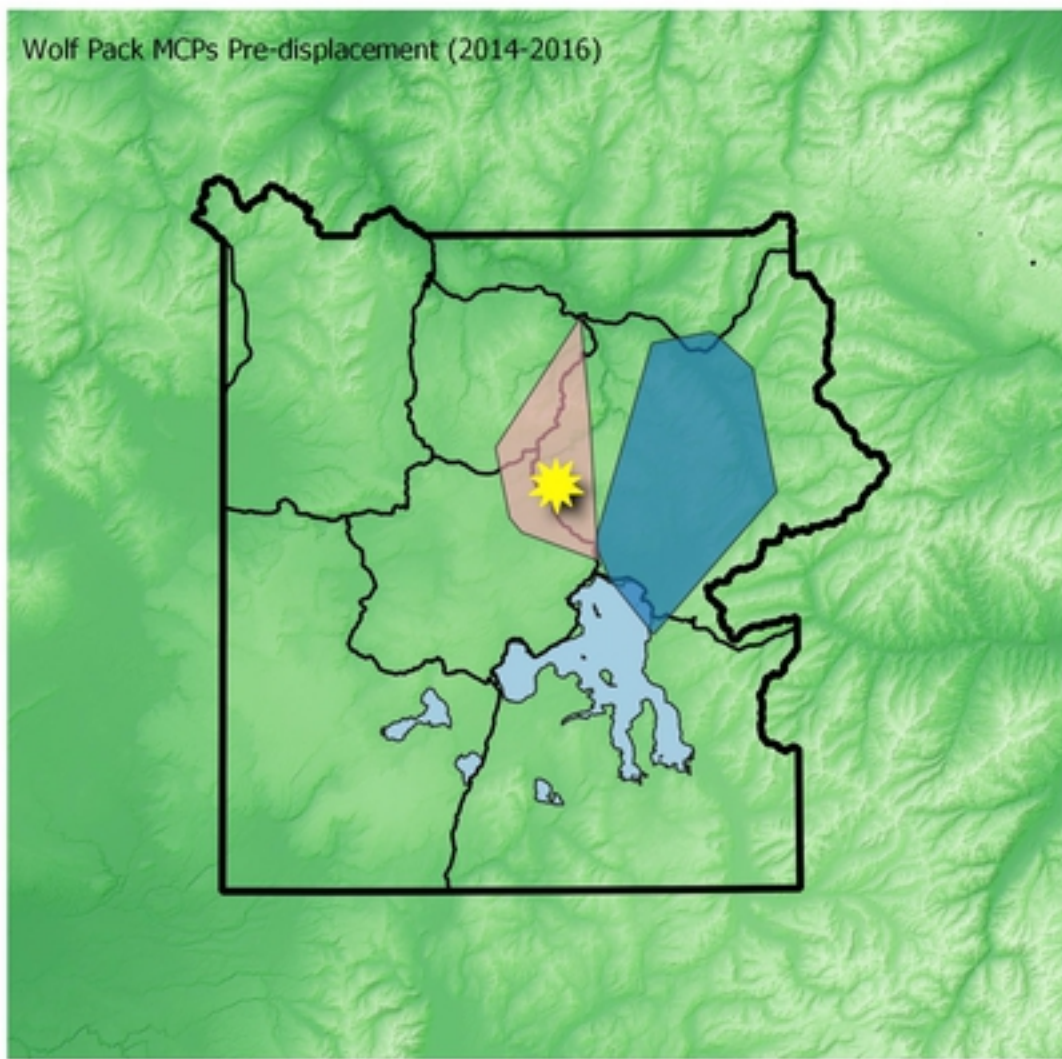
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0 10 20 km

Figure 1








	Wolf ID	Pack	Gender	Age	Color
	1014M	Mollie's	Male	3	Black (White Box on Collar)
	1015M	Mollie's	Male	2	Black (Black Collar)
	Mollie's Male	Mollie's	Male	2	Black
	755M	Wapiti Lake	Male	8	Silver/ Blue
	Wapiti Lake Dominant Female	Wapiti Lake	Female	5	Light gray, turning white
	Wapiti Lake Yearling	Wapiti Lake	Female	1	Gray
	Wapiti Lake Pups (4 pups)	Wapiti Lake	3 Female, 1 Male	<1	3 Gray, 1 Black

Figure 2

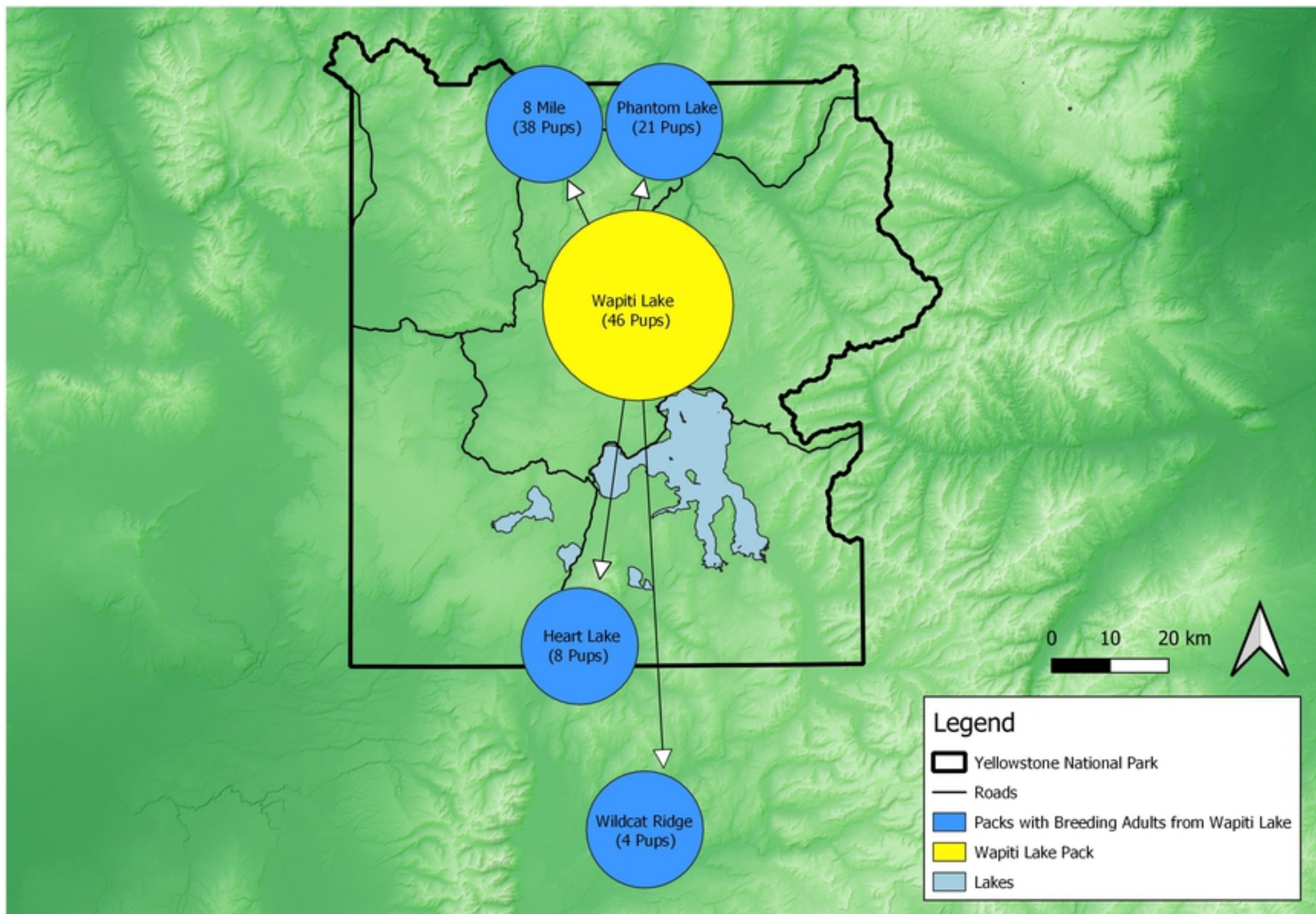


Figure 3