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PERSPECTIVE

Unexplained patterns of grey wolf *Canis lupus* natal dispersal

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ABSTRACT

Natal dispersal (movement from the site of birth to the site of reproduction) is a pervasive but highly varied characteristic of life forms. Thus, understanding it in any species informs many aspects of biology, but studying it in most species is difficult. In the grey wolf *Canis lupus*, natal dispersal has been well studied. Maturing members of both sexes generally leave their natal packs, pair with opposite-sex dispersers from other packs, near or far, select a territory, and produce their own offspring. However, three movement patterns of some natal-dispersing wolves remain unexplained: 1) long-distance dispersal when potential mates seem nearby, 2) round-trip travels from their natal packs for varying periods and distances, also called extraterritorial movements, and often not resulting in pairing, and 3) coincidental dispersal by individual wolves from a given area in the same basic directions and over the same long distances. This perspective article documents and discusses these unexplained dispersal patterns, suggests possible explanations, and calls for additional research to understand them more clearly.

INTRODUCTION

Dispersal is a pervasive characteristic of life forms, so understanding it informs many aspects of biology (Taylor & Taylor 1977). Alongside the vast array and variation in life forms, dispersal patterns also vary considerably (Clobert et al. 2013). Nevertheless, a thorough understanding of dispersal in any organism holds potential for shedding light on dispersal in others. Because of a combination of factors favourable to the study of dispersal in grey wolves *Canis lupus* (here referred to as 'wolves'), much new information has been learned about wolf dispersal in the last few decades.

Wolves were listed in 1967 as an endangered species in the contiguous 48 United States under the U.S. Endangered Species Preservation Act of 1966, protected by the U.S. Endangered Species Act of 1973, and have been increasing in the USA since then, as well as in Europe, so they have been well studied (Mech & Boitani 2003, Musiani et al. 2010, Spotte 2012). In addition, the concurrent advent of radio-tracking (Cochran & Lord 1963) and aerial radio-tracking of wolves (Kolenosky & Johnston 1967, Mech 1970) greatly fostered the study of wolf movements, including dispersal (Mech & Frenzel 1971, Mech 1987, Gese & Mech 1991, Boyd et al. 1995, Boyd & Pletscher 1999, Sparkman et al. 2011, Jimenez et al. 2017). Global positioning system (GPS) tracking improved dispersal research even more by detailing actual movement routes (Merrill et al. 1998), but it took several years for the use of this technique to study wolf dispersal to become common.

Wolves of both sexes disperse both near and far from their natal packs (summarised by Mech & Boitani 2003). Dispersing wolves leave the security and resources of their natal territory; seek a new territory, resources, and an unrelated mate (Smith et al. 1997); then breed, and start their own packs (Rothman & Mech 1979, Fritts & Mech 1981). Thus, dispersal functions to help wolves find the necessary combination of a wolf-pack-free area, food resources, and a suitable mate (Fritts et al. 2003), although dispersal is not the only approach for wolves to reproduce (Mech & Boitani 2003). Dispersing wolves must find potential mates through following scent marks (Rothman & Mech 1979), wolf tracks, and through howling (Harrington & Mech 1979). Because wolf populations were exterminated in so many parts of their original range and are now recovering there (Chapron et al. 2014, Mech 2017), many wolf dispersal studies involve animals dispersing to the frontiers of their current population and facilitating range expansion (Mech et al. 2019). Whether wolves are dispersing within a saturated or expanding population will also influence their dispersal movement patterns, although the details of those differences have not been studied. Those dispersing within a saturated population would find no vacant areas to colonise, whereas those in an expanding population would usually find such areas along the frontier of the population.

While dispersing, wolves often travel far from their natal territories and return (Fritts & Mech 1981, Messier 1985, Merrill & Mech 2000). Some dispersed wolves settle and reproduce close to their natal territories (Mech 1987), while others disperse over straight-line distances of more than 1000 km (Wabakken et al. 2007). Distant wolf dispersers have reproduced as far as 590 km from their natal packs, for example, Oregon Wolf OR7 (https://en.wikipedia.org/wiki/OR7 accessed 30 July 2019). Still others make round trips of more than 4000 km without pairing (Merrill & Mech 2000). Besides natal dispersal, adult wolves that have paired and lost their mate sometimes travel long distances (Burch 2012). Information about most such extensive extraterritorial trips lacks details, but recent detailed data based on new technology beg questions about the precise function of these excursions and allow inferences to be drawn that can lead to a better understanding of extraterritorial travel, not only in wolves but possibly also in other species.

The current perspective article deals with natal dispersal. Shields (1987:4) defined natal dispersal as "the movement of a propagule between birth place or natal group and first breeding site or group", but the current article uses the term to describe movement of individual wolves that leave their natal pack; they might or might not have been known to breed elsewhere. This article reviews basic information about wolf natal dispersal and focuses on some unusual and difficult-to-explain wolf dispersal patterns. The objective is to point out these unusual dispersal patterns so that researchers can attempt to determine their selective advantages. This will help to inform our knowledge of wolf dispersal and possibly the dispersal of other organisms. The article will describe known wolf dispersal patterns, define three important unexplained patterns of dispersal, and then discuss each separately.

EXPLAINED AND UNEXPLAINED NATAL DISPERSAL PATTERNS

During natal dispersal, wolves use a variety of movement patterns: 1) predispersal travel (Fritts & Mech 1981, Messier 1985, Gese & Mech 1991, Mech et al. 1998, Boyd & Pletscher 1999, Mancinelli & Cuicci 2018, but see Blanco & Cortés 2007); 2) disperse from the natal pack, but remain in pack territory (Fritts & Mech 1981, Mech 1987, Blanco & Cortés 2007); 3) disperse, pair, break up, and reintegrate with the natal pack (Mech & Seal 1987); 4) disperse and establish a new pack adjacent to the natal pack (Fritts & Mech 1981, Mech 1987, Boyd & Pletscher 1999); 5) disperse and float among the local population, searching for an opportunity to mate and produce offspring (Mech & Frenzel 1971, Peterson et al. 1984, Messier 1985); 6) disperse unidirectionally (i.e. generally in the same direction) for long distances (Mech & Frenzel 1971, Mech 1987, Merrill & Mech 2000, Wabakken et al. 2007, Davis 2012); 7) disperse, pair and split up serially (Mech & Boitani 2003); 8) disperse unidirectionally for long distances and return to the natal population (Fritts & Mech 1981, Stephenson & James 1982, Merrill & Mech 2000); and 9) disperse and join other packs (Fritts & Mech 1981, Peterson et al. 1984, Messier 1985, Mech 1987, Boyd & Pletscher 1999, Merrill & Mech 2000). Most of these natal dispersal movement patterns result in pairing and producing new packs, so they are easily explained (Mech & Boitani 2003). In some cases, wolves from the same pack, even littermates, have different dispersal patterns (Mech 1987, Ream et al. 1991).

On the other hand, there have been several unexplained cases in which wolves from the same packs have dispersed in the same general directions over the same long distances, even though they were not together. Early analyses of wolf dispersal from the Perch Lake wolf pack in north-eastern Minnesota, USA, showed three members of this pack all dispersing north-eastward over distances of more than 180 km (Mech 1987), and additional cases from the same pack and another pack displayed the same trend (Table 1). Wolves in Finland showed similar dispersal patterns (Kojola et al. 2006), as did three male wolves from a single territory in Sweden. The latter dispersed over straight-line distances of 145-255 km over an arc of only 12° (measured from Milleret et al. 2019; Fig. 2B).

Some such wolves even end up in the same pack or territory. Two male and female sets of wolves from a Montana pack behaved similarly (Boyd & Pletscher 1999). One of these sets dispersed nine months apart, but the wolves were found three years later, 150 km away, in the same pack. The other set dispersed a week apart and were found together 170 km away three months later in the same pack. Mech (1995) reported a similar coincidence in Minnesota (Table 1 and below). Gable et al. (2019) reported on two male wolves caught 9.8 km apart, two months apart in north central Minnesota; they dispersed separately, moving north over >330 km, and a few months later were together.

Additional analyses of dispersing wolves from the Sawbill wolf pack in north-eastern Minnesota (Mech 1995, L. David Mech, unpublished data) and from the

Table1. Perch Lake and Sawbill pack grey wolves *Canis lupus* that dispersed in similar directions, over similar distances in north-eastern Minnesota, USA (Mech 1987, 1995, Mech, unpublished data)

				Date			
Wolf	Sex	Age (years)[1]	Pack	Left study area	Recovered new area	Direction	Distance (km)
61	M	3-5	Perch	20 November 1987	12 March 1989	59°	309[2]
5331	M	1	Perch	22 October 1982	August 1983	56°	288[2]
6073	F	1	Perch	24 February 1981	December 1982	62°	289[2]
6441	M	1	Perch	3 May 1983	27 December 1983	67°	189[3]
6761	F	1	Perch	29 March 1986	31 March 1989	68°	182[3]
183	M	4	Sawbill	21 March 1990	24 October 1990	330°	270[4]
5781	M	1-2	Sawbill	14 December 1978	29 December 1981	334°	265[4]
873	F	1	Sawbill	23 December 2002	15 January 2004	59°	129[5]
441	F	1	Sawbill	3 September 1992	15 October 1993	62°	132[5]

[1]Age at dispersal (underlined = known; other ages are estimated).
[2]Each of these three was recovered 27 km from the others.
[3]8 km apart.
[4]11 km apart.
[5]8 km apart.

Perch Lake pack (Mech 1987, L. David Mech, unpublished data) yielded more interesting coincidences. Five members of the Perch Lake pack from 1982 to 1989, including three from the Mech (1987) study, all dispersed 182-309 km at directions from 56° to 68° (Table 1). Two of them ended up 8 km apart, and the other three of them 27 km apart from each other (Fig. 1). The proportion of these five (of 18 possible) dispersers heading in directions only 12° apart was significantly different from random dispersal directions (Yate's corrected chi-square = 4.11; $P = 0.04$; Pearson's chi-square = 6.15; $P = 0.01$).

Mech (1995) studied two individuals from the Sawbill pack's territory that dispersed some 270 km away at

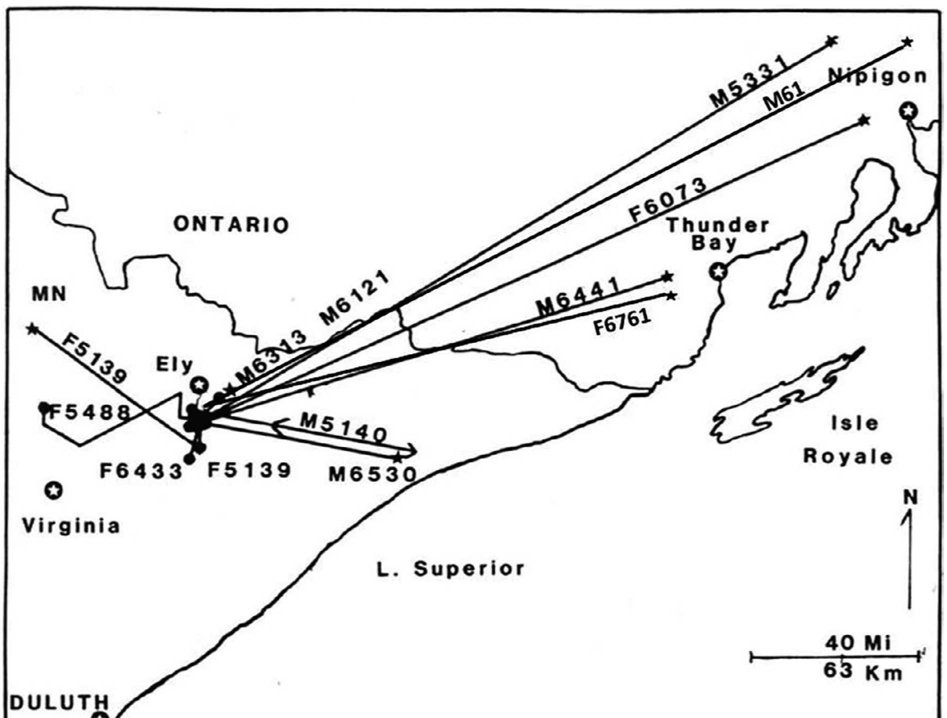

Fig. 1. Distances and directions of Perch Lake grey wolf *Canis lupus* pack dispersers from their natal pack in Minnesota, USA (Table 1; modified from Mech 1987).

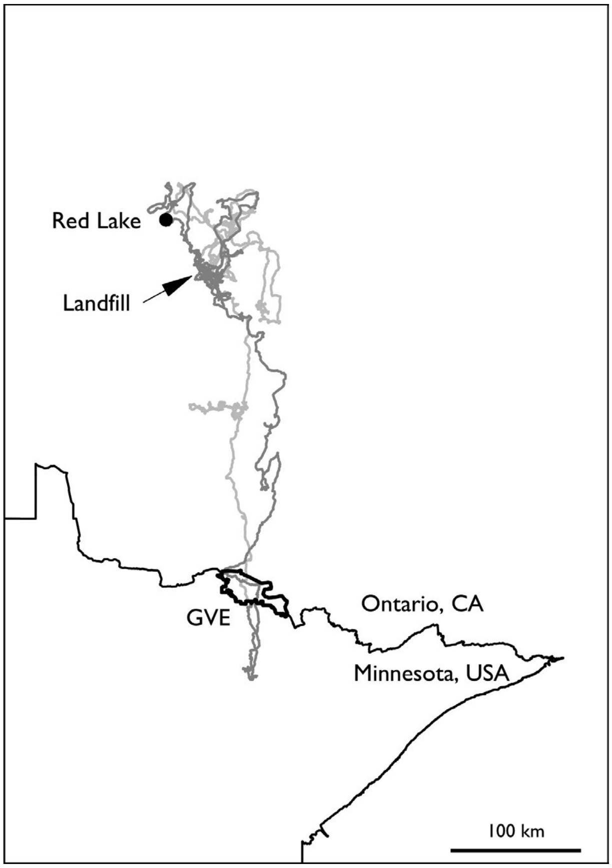

Fig. 2. The dispersal movements of two dispersing grey wolves *Canis lupus*, V057 (light grey line) and V059 (dark grey line), from the Greater Voyageurs Ecosystem (GVE, bold black polygon), Minnesota, USA, into Ontario, Canada. Both wolves were fitted with GPS collars that took locations every 20 minutes. Both wolves dispersed in spring 2018 and eventually localised around a landfill (waste disposal) site southeast of Red Lake, Ontario (figure adapted from Gable et al. 2019).

330°–334° several years apart, but were recovered 11 km from each other (Table 1). Two other members of this pack dispersed >180 km in a 3° arc (59-62°) and were found 8 km apart (Table 1). In each case, the dispersal direction of each member of the pair was significantly different from random (Yate's corrected chi-square = 13.76, 8.76; P = 0.0002, 0.003, respectively). This tendency of some wolves from the same pack to disperse to the same area, as well as the propensity of some wolves to disperse many kilometres unidirectionally away from their natal packs, rather than floating more haphazardly around the local population, remains unexplained.

Conceivably, some unidirectional dispersers first float far and wide before ending up far from their packs and thus give the impression that they dispersed unidirectionally. The wolves in Table 1, for example, had seven months to three years to get from their natal pack to their endpoints, and their locations in the interim were unknown.

On the other hand, as radio-tracking technology improved with the development of satellite and GPS tracking (Merrill et al. 1998), it became clear that some wolves do disperse unidirectionally soon after leaving their packs (Merrill & Mech 2000, Wabakken et al. 2007, Davis 2012). This includes two wolves from the same general area, although from different packs, that dispersed 330 and 387 km straight-line distances unidirectionally 19 days apart, in the same basic direction but with different routes and ended up together some 381 km away (Gable et al. 2019; Fig. 2). One of these animals had been born into the pack in which it was caught. The history of the other is unknown, so, although it was caught near the centre of a pack's territory, it could have been from some other pack or area, for soon after collaring, it left the territory (Gable et al. 2019).

The inclination of some wolves to return to their natal packs or populations after dispersing far from them is a third unexplained dispersal pattern. Records of wolves making round trips from their packs or natal populations range from merely moving 6 km from and back to the natal pack territory (Fritts & Mech 1981) to moving as far as 460 km from and back to the natal population (Merrill & Mech 2000). Time temporarily away from the natal pack or population varied from a few days (Fritts & Mech 1981) to 17 months (Mech 1987).

To summarise, three common wolf natal-dispersal patterns have yet to be explained: 1) long-distance, unidirectional dispersal; 2) round-trip travels or extraterritorial movements: return of dispersers to the natal pack or population after dispersal; and 3) coincidental long-distance dispersal: in the same basic direction, and at times the same distance, as other wolves from the same pack or populations. Regarding the second pattern, three questions arise: 1) what motivates this pattern; 2) why is the movement unidirectional; and 3) why do some wolves return home?

LONG-DISTANCE DISPERSAL

With long-distance, unidirectional dispersal, the dispersal paths are generally straight lines as though the goal is to get quickly to a new area. A key question is what the advantage of that would be over random nomadism in the population surrounding the natal pack. In the known cases of unidirectional dispersal, wolves and prey were present for long distances around the natal packs, and in at least some cases in which some wolves moved far, other wolves that remained closer did find mates and territories (Mech 1987, Gese & Mech 1991). Travelling far will guarantee that the environmental conditions will be different from those at the starting point, but for distant, unidirectional dispersal to be a selective advantage, the distant conditions would have to be universally different enough in a biologically meaningful way. The only such conditions apparent to this author are decreased genetic relatedness to local wolves (Mech 1987, Boyd et al. 1995, Geffen et al. 2011) and decreased competition from dispersing littermates. Furthermore, in unsaturated populations, moving too far from the core population would reduce the chances of finding a mate (Jimenez et al. 2017).

Genetic relatedness of wolf packs decreases with distance (Lehman et al. 1992, Meier et al. 1995, Cullingham et al. 2016), and, generally, mated wolves are not closely related (Smith et al. 1997, VonHoldt et al. 2008). In one study, longevity of wolf pairs was inversely related to the inbreeding coefficient of the male member (Milleret et al. 2017). Thus, distantly dispersing wolves might be seeking unrelated mates. Consistent with that hypothesis is evidence that distantly dispersed wolves did mate far from their natal packs (Mech 1987, Mech 1995, and Oregon Wolf OR7). However, two pieces of evidence from other dispersers are inconsistent with that. First, some wolves pair in areas close to their natal packs (Fritts & Mech 1981, Mech 1987, Lehman et al. 1992, VonHoldt et al. 2008). Second, the several cases mentioned above in which wolves from the same packs travel to the same distant areas mean that not all distantly dispersing wolves are distantly related (Table 1, Fig. 1). Nevertheless, the proportion of closely related wolves becomes smaller, the farther away a wolf travels (Forbes & Boyd 1997, Carmichael et al. 2001, Geffen et al. 2011). Some wolves mate with others in the area near their natal packs, perhaps because those individuals happened to find unrelated mates that had dispersed from distant packs, whereas unidirectionally dispersing packmates might not have found them after a certain period, so they dispersed far away. Unidirectional dispersal also suggests that wolves might possess an ability to detect relevant information, such as prey density or habitat, for very long distances (Frame et al. 2004), or that they may be influenced by landscape features (Boyd et al. 1995) or by some unknown factor.

ROUND-TRIP DISPERSAL

Trying to explain dispersals in which the disperser returns to the natal pack or population is complicated by the amount of variation in this type of movement, and by the way in which various authors have described and labelled this behaviour. Fritts and Mech (1981) called it dispersal, with one wolf returning over a two-month period after travelling to an area a straight-line distance of 138 km away. Stephenson and James (1982) considered extraterritorial movements to be round trips, but Peterson et al. (1984) used 'dispersal' and 'extraterritorial movements' interchangeably, and found that 15 of 20 such movements during January to May were round trips. Boyd et al. (1995) defined two types of extraterritorial movement: 1) dispersers were wolves that remained permanently at least 40 km from their natal territory; and 2) long-distance travellers were those that moved more than 40 km away and associated with more than one pack. Few, if any, of the wolves studied by Boyd et al. (1995) made round trips. Messier (1985) considered any movement of a wolf to more than 5 km away from its pack territory an 'extraterritorial movement', but of 56 such instances, 45 involved returning to the pack. Messier also called such round trips 'predispersal trips'. Mech (1987) described some such trips in detail but considered them as dispersals, but Gese and Mech (1991) called them 'predispersal forays' and found them to be common, as did most other researchers (Van Ballenberghe 1983, Ballard et al. 1987, Fuller 1989, Boyd & Pletscher 1999, Merrill & Mech 2000). Fuller (1989) called them 'temporary excursions'.

All of the previous studies and their terminology were based on information from standard very high frequency (VHF) collars that only allowed relatively infrequent location data. Since GPS collars have been used, much more detail about these trips has been learned. Examining 'extraterritorial forays' as defined by Bekoff (1977) for several GPS-collared wolves in Italy, Mancinelli and Cuicci (2018) considered them to be predispersal movements if they were round trips and preceded dispersal. Those movements took longer and involved longer distances than other extraterritorial forays.

The longest such round-trip wolf travel seems to be that of known-age, 2-year-old female 7804 that left her natal territory in Minnesota on 26 March 1999, travelled a minimum of 4251 km to a point 494 km away and returned to her natal area on 21 September 1999 (Merrill & Mech 2000). There is some indication that female wolves may make more round-trip movements than males. That was the case in Quebec, Canada (Messier 1985), but samples in other studies were too small to decide, or the sex was not given.

Some dispersers return to their natal pack or territory after pair-bonding but failing to reproduce (two females; Mech 1987). Others return having not paired (Fritts & Mech 1981, Mech 1987, Merrill & Mech 2000).

Regarding the motivation for beginning these round trips, Fritts and Mech (1981) and Mech (1987) assumed it was to seek mates and new territories. Van Ballenberghe (1983) implied that he believed the same. Peterson et al. (1984) considered round trips exploratory. Messier (1985), however, showed that relative prey scarcity tended to promote round trip extraterritorial movements, although those movements also occurred in his high-prey area. The other factors associated with such movements were the predominance of yearlings, females, and a winter dispersal peak around the breeding season (Messier 1985). The common finding from all these studies is that it is primarily maturing wolves that make round-trip extraterritorial forays, just like with all other patterns of natal dispersal. Thus, the basic motivation for these round trips could well be the same as for other dispersal patterns: maturing wolves are seeking mates and territories (Mech & Boitani 2003).

Round trips differ from other patterns of dispersal, in that no mates are found during the trip. Given that some round trips are as short as a few days or weeks (Messier 1985, Mech 1987, Fuller 1989, Mancinelli & Cuicci 2018), such trips might seem to be exploratory. However, some dispersing wolves paired within a few days or weeks (Fritts & Mech 1981, Mech 1987), so mate-seeking cannot be ruled out as a motivation for even short round trips, as Van Ballenberghe (1983) and Messier (1985) also believed. On the other hand, it seems unusual that a wolf (7804 above) that travelled for six months along the frontier of the Minnesota and Wisconsin wolf range, or one that travelled through saturated wolf range for two months (Merrill & Mech 2000), could not find mates. The wolf population in those areas was increasing and expanding in the directions both wolves travelled in, so those areas should have contained many other dispersing wolves, i.e. potential mates. Although such a move might be in search of food rather than a mate, similar to such moves that breeding wolves sometimes make (Frame et al. 2004), food abounded in the areas through which wolf 7804 travelled, and this wolf was not yet a breeder (Merrill & Mech 2000). This leaves open the question why long-distance, unidirectional dispersers travel so far, and further documents that these movements are not well understood.

The next question is why, after being away from their natal packs for so long (over six months), some wolves return. In some cases, they leave again after a few days (Merrill & Mech 2000), but in others, they remain for months (Mech 1987). Perhaps returning wolves obtain more food while with their packs (Messier 1985). However, wolf 7804 (Merrill & Mech 2000), after returning to her natal area for two days, left again. Also, wolf 5399 in the same study began his round trip just as white-tailed deer fawning began, generally an easier time for single wolves to hunt anywhere (Kunkel & Mech 1994, Demma et al. 2007, Demma & Mech 2009). Returning to a natal territory almost guarantees that there will be competitors for food. Thus, this explanation appears questionable.

A better explanation is that survival is better in natal packs. Wolves that manage to remain in their natal packs the longest generally survive the longest (Peterson et al. 1984, Messier 1985, Fuller 1989, Pletscher et al. 1997). They might also have the best chance of breeding success, although not necessarily so, for Boyd and Pletscher (1999) found no difference in survival rate of dispersers and bidders. Competition to remain in a natal pack must be high, and dispersers must be those that lost in the competition. Furthermore, because of the uncertain nature of a hunting lifestyle and fluctuating food supply (Mech et al. 2015), pack social dynamics must change frequently. Thus, some wolves that were expelled at a time of less food but returned later might find less competition within their natal pack than when they left, either because hunting and food supply improved or because other pack members left. The returning wolves might then reintegrate and try to remain longer in order to increase their chance of survival or breeding success.

COINCIDENTAL DISPERSAL

The hardest pattern of wolf dispersal to explain is when some members of the same pack, presumably siblings or littermates, disperse unidirectionally in the same basic direction and sometimes over about the same distance. That pattern suggests a possible genetic involvement in dispersal (Mech 1995, Chen et al. 1999, Mech & Boitani 2003, Matthews & Butler 2011). In several areas, including the general area where the Perch Lake pack (Table 1) lived and the Rocky Mountains, USA (Jimenez et al. 2017, but see Boyd et al. 1995), dispersers generally headed in random directions (Gese & Mech 1991). Those studies included large samples. Conceivably, a large population would include packs with innate tendencies to disperse in various directions, such that members of the whole population would disperse in random directions, whereas members of individual packs would each tend to disperse primarily in a single direction. If that is the case, however, it must be that the tendency to disperse in a single general direction is not total, for the Perch Lake pack did include members that dispersed in several directions (Mech 1987).

Another possible explanation is that packs from which multiple members disperse in almost the same exact direction are located where landscape features attract them in that direction, as Boyd et al. (1995) concluded, although why a landscape feature would attract wolves to travel in a certain direction is unknown. Wolves do prefer roads, trails, and frozen waterways on which to travel (Mech 1970). However, on a larger scale, they travel on almost any kind of terrain, and little stops them. A wolf in Italy traversed across four fenced four-lane highways, several railways, and even greater impediments (Ciucci et al. 2009). Wolves in the northern Rocky Mountains generally dispersed in a northerly direction parallel with the continental divide, but at least two crossed the divide (Boyd et al. 1995).

The five Perch Lake pack dispersers that all headed in a 12° arc north-eastward direction did parallel a general north-eastward lay of the land (Fig. 1). Several large lakes, for example, are oriented that way, paralleling the shore of Lake Superior some 70 km from the straight lines between dispersal starting and ending points (Mech 1987). Still, at the scale of a wolf travelling, it seems very unlikely that the topography, geography, or land physiognomy or habitat would be such as to focus travel in one direction. Furthermore, other Perch Lake pack members dispersed in several other directions (Fig. 1). Also, north-eastern land orientation would not explain the northerly direction in which two of the Sawbill pack members dispersed.

Because all the above cases of coincidental dispersals except those of Gable et al. (2019) involved only known dispersal points and recovery points, actual travel routes were unknown. Conceivably, actual routes could have been quite circuitous, and knowing those routes might provide insight into reasons for the apparently coincidental routes, for example. This is where new data from GPS tracking (Merrill et al. 1998) will be most valuable. The actual routes of two wolves with GPS data indicate that both wolves dispersed northwards using fairly direct routes paralleling and overlapping each other, even though they dispersed about a month apart and one wolf made a 60-km loop south before its northward trek (Fig. 2; Gable et al. 2019).

The coincidental settling or recovery of dispersed members of the same packs, not only in the same basic direction but also about the same long distance from their natal packs, is intriguing, but at least the same distances might be more easily explained. In most of the cases described above, recovery of the dispersed wolves was by Canadian hunters or trappers, most of whom are probably clumped more around more accessible areas, thus biasing dispersal recovery (Mech et al. 1998). For example, the general regions where the five Perch Lake pack members (Table 1) were recovered were within 35 km of Canadian cities. Thus, wolves that travel near that area are more vulnerable to being killed by hunters. Also, wolf densities there would be lower than those of the surrounding area, creating a population sink effect that could cause immigrating wolves to settle there. These facts, however, do not explain why so many dispersers head in the general direction of this area when starting so far away.

FUTURE RESEARCH

Several features of the natal dispersal of some wolves are not explained by individuals' attempts to find mates and suitable areas in which to settle. "Dispersal is a process of central importance for the ecological and evolutionary dynamics of populations and communities, because of its diverse consequences for gene flow and demography" (Saastamoinen et al. 2018: 574). Details about dispersal are difficult to obtain for many species. However, because of the factors outlined earlier, especially the recent use of GPS collar tracking (Merrill & Mech 2000, Wabakken et al. 2007, Ciucci et al. 2009, Kojola et al. 2009, Gable et al. 2019), the possibility of obtaining much more information about wolf dispersal has the potential to add critically to the knowledge we have of dispersal in general. In that respect, the questions and speculations discussed in the current paper suggest questions and hypotheses that future studies can explore and test.

Two recent studies set an excellent example of the types of hypotheses that can be tested using the latest technology. One involved investigation of natal habitat-biased dispersal, examining the possible influence of prey density, brown bear *Ursus arctos* density, human density, human accessibility, land-cover variables, and wolf density on the probability of territory establishment by dispersing wolves (Sanz-Perez et al. 2018). Wolves dispersing <40 km tended to settle in areas similar to their natal areas, whereas those settling farther away did not. The other study tested whether exposure to humans in natal habitat influenced territory selection by dispersing wolves (Milleret et al. 2019). Wolf pairs whose female was born in areas of high anthropogenic influence showed a weak tendency to settle away from humans. These studies bear repeating in various other regions within the wolf's geographic range. Other influencing variables could be tested, and the role of the above and other variables in influencing other aspects of dispersal could be examined, for example actual dispersal routes, whether round trips are made, and dispersal distance, direction, and duration. In this way, sooner or later, at least some of the unexplained wolf dispersal patterns will be understood.

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