The Canadian Field-Naturalist

Sixty years of White-tailed Deer (*Odocoileus virginianus*) yarding in a Gray Wolf (*Canis lupus*)–deer system

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Mech, L.D., and S.M. Barber-Meyer. 2019. Sixty years of White-tailed Deer (*Odocoileus virginianus*) yarding in a Gray Wolf (*Canis lupus*)–deer system. Canadian Field-Naturalist 133(4): 343–351. https://doi.org/10.22621/cfn.v133i4.2136

Abstract

This article synthesizes information from over a six-decade period of studies of White-tailed Deer (*Odocoileus virginianus*) use of a winter yard and subject to Gray Wolf (*Canis lupus*) predation in northeastern Minnesota. It also adds spring migration data from 35 adult female deer and fawns studied there during 1998, 1999, 2001, 2014, and 2017. Twenty-nine of these deer migrated in spring a mean distance of 29 km (SE = 4), a maximum distance of 78 km, and at a mean bearing of 83° (SE = 12; range 21–348). These findings are similar to those from 49 deer (both sexes) from the same yard studied during 1974–1984, that migrated a mean distance of 25 km (SE = 1.8) and a mean bearing of 77° ± 4 SE. Between the two periods, the wolf population fluctuated considerably, the winter range of deer in the area where these deer spent summer greatly diminished, and both derechos and fires disturbed the habitat. This study attests to the selective advantage of the migratory tradition of deer in this yard.

Key words: *Canis lupus*; deer yard; migration; *Odocoileus virginianus*; predation; predator-prey relations; White-tailed Deer; wolf; yarding

Introduction

White-tailed Deer (*Odocoileus virginianus*) migrate between summer and winter ranges in many northern areas (summarized by Nelson 1998). Two main drivers of these migrations have been proposed: (1) the need for optimal protection from adverse winter weather (Townsend and Smith 1933; Severinghaus and Cheatum 1956; Ozoga 1968) and (2) grouping to minimize predation risk (Nelson and Mech 1981, 1991; Messier and Barrette 1985).

Most studies of migratory deer populations have been short term, describing migration distances, timing, and triggers for seasonal movements. One exception is an investigation of deer movements in southeastern Quebec that also depicted the extent of two deer yards over three decades (Lesage *et al.* 2000). Studies of deer migratory behaviour in areas where Gray Wolves (*Canis lupus*) are the primary predator of deer have been conducted for as long as 10 years (Forbes and Theberge 1995; Theberge and Theberge 2004), 15 years (Fieberg *et al*. 2008), and 28 years (Hoskinson and Mech 1976; Nelson and Mech 1981, 1987; Nelson 1995, 1998; Nelson *et al.* 2004). However, we know of no migratory White-tailed Deer herd subject to wolf predation that has been investigated for more than three decades.

As part of a long-term study of wolf ecology and population trend in northeastern Minnesota (Mech 2009), we have also researched White-tailed Deer there since 1964 (Mech and Frenzel 1971; Hoskinson and Mech 1976; Nelson and Mech 1981, 1987; Nelson 1998; Nelson *et al*. 2004). During that time, the amount of winter range of the deer herd we studied diminished greatly (Mech and Karns 1977). Forty-five years later, some 3000 km^2 that deer previously used for decades during winter remained devoid of wintering deer (Nelson and Mech 2006), and most, and probably all, of it still remains devoid of wintering deer (Mech *et al*. 2018). In addition, various habitat disturbances and other important changes detailed below have occurred in the wolf study area.

The wolf study area (Figure 1) lies in northeastern Minnesota, USA at about 47.60°N to 48.7333°N and 90.8167°W to 91.8333°W excluding the northwest quarter of that region and includes much of the Garden Lake deer yard (GLY) along its western edge

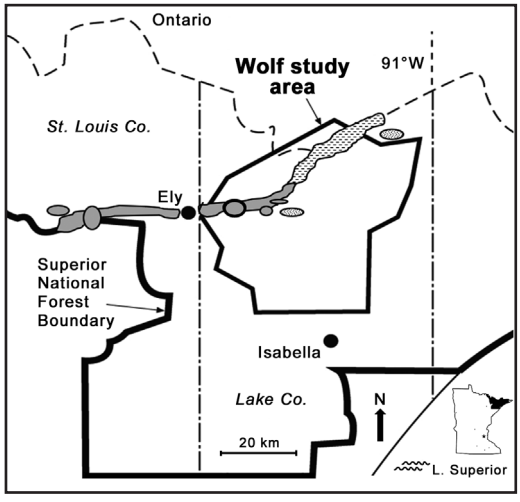

Figure 1. The wolf study area with the Garden Lake Yard (GLY). Irregular grey and stippled areas represent the GLY as described by Mech and Karns (1977). Grey and stippled ovals represent areas listed as deer yards by Arnold *et al*. (1961). Stippled areas (both irregular and oval) are where deer have not overwintered since the early 1970s (Mech and Karns 1977; Nelson and Mech 2006; Mech *et al*. 2018). The darker bold oval just east of Ely is the GLY proper, where White-tailed Deer (*Odocolieus virginianus*) from previous studies mentioned in the Introduction and the present study were radio-collared. Inset map shows location of Superior National Forest (black) in Minnesota.

near Ely, Minnesota, USA. The GLY is named for the area around Garden Lake and the adjacent area near the Winton Hydroelectric Power Plant where wintering deer concentrate the most under the most severe conditions and where deer were fed artificially in the early 1970s and probably for some time before that. Deer have continued to concentrate in the GLY during winter and to migrate to summer ranges in and through the wolf study area for over 60 years. We studied the migratory behaviour of deer in this yard from 1974 through 1984 (Hoskinson and Mech 1976; Nelson and Mech 1981, 1987, 1991; Nelson 1998) and again during 1998 through 2017. We document here the continued winter concentration of deer in that yard and their annual migrations despite those changes and despite a wolf population that depends on them for most of their diet (Barber-Meyer and Mech 2016). We also compare 1998–2017 demography and migratory status of the deer in that yard with results from 1974–1984 (Nelson and Mech 1981, 1987). The objective of this study is to demonstrate the extreme degree to which a migratory tradition in a given deer yard under natural conditions of wolf predation can persist, a record duration to our knowledge, and to compare the migratory behaviour over the period of this study.

Study Area

The extent of the GLY over the years has been described variously, no doubt because (1) deer populations fluctuate greatly over the decades, and (2) deer use of winter range, and thus their migration movements, vary considerably by season, temperature, and snow conditions (Nelson 1995). As these conditions change, deer may move toward or away from winter yards, sometimes wintering for long periods only partly along their route to areas where they would concentrate more during the most extreme conditions (Nelson and Mech 1981). The Pohenegmook and Lac Temiscouata deer yards in southeastern Quebec, Canada provide a good example of such changes (see Figure 3 in Lesage *et al*. 2000).

In 1953, the GLY was thought to encompass 128 ha, not including other yards west and east-northeast of the GLY (Erickson *et al*. 1961). Mech and Karns (1977) considered the GLY more inclusively, stretching from about 35 km west-southwest of Ely to Ely, about 25 km east of Ely, and then northeast about 12 km, totalling about 72 km long, and centring on the Garden Lake area (Figure 1). In the mid-1970s the GLY was thought to extend about 16 km east-northeast (Hoskinson and Mech 1976) and later as holding ≤800 deer (Nelson and Mech 1987). East of Garden Lake, deer currently continue to winter along the area that Hoskinson and Mech (1976) described at times as far as some 18 km east of Garden Lake.

Whether deer wintering elsewhere in the more expansive GLY other than those from the capture area (Nelson and Mech 1981, 1987, this study) migrate in the same direction to summer ranges as those deer radio tracked is unknown.

The GLY lies along the western edge of our long-term wolf study area (Mech 2009) which covers about 2060 km^2 including the migration routes along which the wintering GLY deer travel to their summer ranges (Figure 1). The wolf study area is situated well within the Minnesota wolf range (Fuller *et al.* 1992), and wolves have never been extirpated from the wolf study area. The area is replete with lakes and waterways, and American Beaver (*Castor canadensis*) and Moose *(Alces americanus*) are also available to wolves there (Mech and Karns 1977; Barber-Meyer and Mech 2016; Mech *et al*. 2018). Black Bear (*Ursus americanus*) is the only other major predator of deer in the region (Kunkel and Mech 1994), although Coyote (*Canis latrans*), Fisher (*Martes pennant*), Bobcat (*Lynx rufus*), and Canada Lynx (*Lynx canadensis*) inhabit the area and could prey on fawns. General habitat, topography, and weather in the study area were described by Nelson and Mech (1981, 2006) and Heinselman (1996).

In July 1999, a derecho windstorm leveled about 1600 km^2 of the forest through which some of the GLY deer migrate (National Oceanic and Atmospheric Administration 1999; Nelson and Mech 2006). Another derecho struck in 2016 that also affected the migration routes of these deer (Minnesota Department of Natural Resources 2016).

In 2000 and 2007, fires burned 431 km^2, just northeast beyond where radio-collared GLY deer migrate to but which could include summer ranges of other GLY deer (Fites *et al.* 2007). In 2011, the Pagami Creek fire burned 376 km^2 in which some GLY deer summered, or through which they migrated (Nelson and Mech 1987). Other habitat changes during the study included forest maturation, and alterations and variation in logging practices from clear cutting to total protection.

Weather conditions also changed considerably throughout the study. Snow depth, density, and persistence, especially during the past decade, differed from earlier in the study, including winter 2010–2011 when snow depth was extremely low and winter 2013–2014 when snow was very deep and fluffy.

White-tailed Deer have inhabited the region for many decades. Johnson (1922) considered deer common from 1912 to 1915. In 1938, Olson (1938: 330) published a map showing deer present in every township in the wolf study area. From 1948 to 1952, Stenlund (1955) documented wolf-killed deer in winter on most of the major lakes there. Erickson *et al.* (1961) stated that deer were abundant in the Northern Forest Zone, which included our wolf study area, for more than 40 years, and those authors listed 16 winter yarding areas they checked in or near our wolf study area between 1949 and 1958. Estimated deer densities in the Northern Forest Zone (although not necessarily in our wolf study area) ranged from 5.9 to more than 7.8/km^2 in the late 1930s (Erickson *et al.* 1961).

By the mid-1970s, almost no deer spent winter in the northeastern third of the wolf study area, and wolves there lived primarily on Moose and probably beavers (Mech and Karns 1977). Deer that had wintered there had succumbed to a combination of deteriorating habitat (maturing forests), a long series of severe winters, and heavy wolf predation (Mech and Karns 1977). Deer have not been observed overwintering there since, despite regular winter flights (Nelson and Mech 2006; Mech *et al.* 2018). Deer numbers along the southern and western edges of this area dropped to about 0.8 deer/km^2 (Floyd *et al.* 1979) and in 2011 pre-fawn densities averaged <2/km^2 (Lenarz and Grund 2011). To the east of the wolf study area, deer migrated during autumn to winter yards along the shore of Lake Superior (Nelson and Mech 1981) and reached yarding densities during 1968–1976 of 39 to 55/km^2 (Mech and Karns 1977). Deer from those yards moved at least 22 km northwest inland (Morse and Zorichak 1941; Nelson and Mech 1981).

Deer that wintered in yards along the west side of the wolf study area, primarily in and around Garden Lake, 8.8 km east-northeast of Ely, migrated in spring southeastward to northeastward for up to 54 km at a mean bearing of 77° (Nelson and Mech 1987).

Moose have also occupied the region for many decades. Johnson (1922) found Moose very common in 1912–1915 but scarce in 1920. Olson (1938) estimated a Moose density of 1/6.4 km^2 based on his observations during 1920–1936 and his discussions with various wardens, trappers and other woodsmen, but Stenlund (1955: 22) considered their numbers "not high" during 1948–1952. An historical estimate of Moose density from 1915 to 1970 over the entire northeastern Minnesota Moose range, which included our wolf study area, was 1/3.8 km^2 to 1/21.9 km^2 (Peek *et al.* 1976). From 1984 to 2016 in this Moose range, densities based on annual aerial counts were 1/1.7 km^2 to 1/5.5 km^2 (calculated from Moose-count data; Mech *et al.* 2018). Moose numbers in the overall northeastern Minnesota Moose range peaked in 1989, 1996, and 2006, declined to less than half their 2006 level by about 2012, and then leveled off for several years (DelGiudice 2017; Mech *et al.* 2018).

Wolves have inhabited the region throughout recorded history (Olson 1938; Stenlund 1955; Mech and Frenzel 1971). Wolf numbers in the wolf study area varied from 23–32 in winter 2016–2017 (L.D.M. and S.M.B.-M. unpubl. data) to 97 in 2008–2009, a density ranging from 11–16/1000 km^2 to 47/1000 km^2 during 1968–2017 (Mech 1973, 1986, 2009; Mech *et al.* 2018). During and after the major deer decline in the 1970s, wolf numbers there also declined considerably and did not reach former levels until about 2000 after recovering from a prolonged infection by canine parvovirus (Mech *et al.* 2008). A few years after Moose numbers began declining in 2006 and deer numbers declined due to severe winters, the wolf population began dropping to its lowest level during the study, 23–32 animals (Barber-Meyer and Mech 2016; Mech *et al.* 2018).

The primary migration routes and many of the summer ranges of the GLY deer we studied usually fell within the territories of two wolf packs, known as the Wood Lake and Ensign Lake Packs in earlier publications (Mech 1973, 1986). Over the decades, the actual locations of these pack territories varied considerably, and other packs that used parts of the GLY, the deer migration routes, or the summer ranges of the GLY deer formed and disintegrated as well. At times, as many as four radioed packs, totalling up to 29 members during winter used the GLY (L.D.M.,

S.M.B.-M., and M.E. Nelson unpubl. data). In addition, wolf packs sometimes inhabited the GLY year around. One such pack that inhabited 39 km^2 including Garden Lake itself hosted the highest wolf density ever recorded anywhere, 182 wolves/1000 km^2 during winter, from 1 April 1998 through 30 March 1999 (Mech and Tracy 2004).

Based on 39 years during which the Wood Lake Pack was radio-collared and 24 years in which the Ensign Lake Pack was radio-collared between 1973 and 2017, their winter pack sizes averaged 5.3 ± 0.41 SE and 5.6 ± 0.55 SE and ranged up to 11 and 12 members, respectively (L.D.M., S,.M.B.-M., and M.E. Nelson unpubl. data). The numbers of wolves in these packs did not follow the trajectory of the overall wolf numbers in the wolf study area, but rather remained relatively constant from winter 1973–1974 through about 2006, although they declined after that (Mech 1973, 1986, 2009; L.D.M.,S.M.B.-M., and M.E. Nelson unpubl. data). In any given year, the packs that used the area including the GLY deer summer ranges and migration routes usually migrated to the Garden Lake area itself during autumn and back to the deer summer ranges in spring (Mech and Boitani 2003; L.D.M. and S.M.B.-M. unpubl. data) except when resident packs resided year around there.

Methods

Using Clover traps from 1998 to 2017, we live trapped, anesthetized, ear tagged, and radio collared deer within 1.4 km of the GLY (Mech and Barber-Meyer 2020). Three others were captured near Snowbank Lake, some 23 km east northeast of Garden Lake but still in the more expansive definition of the GLY discussed above. In the current study we excluded the three Snowbank Lake deer (included in a study by Nelson *et al*. [2004]) because that area was not included in the Nelson and Mech (1987) area with which we compare our data. Our GLY captures were basically in the same area where deer (both sexes) from this yard were studied earlier (Hoskinson and Mech 1976; Nelson and Mech 1981, 1987). We extracted an incisor from adults for aging by Matson's Laboratory (Missoula, Montana, USA). We located the deer by aerial radio tracking or by global positioning system (GPS) collar locations during June, July, and August until at least two consecutive locations were in the same general area to determine their summer ranges (because generally once on summer range they remain in a relatively small area [Nelson and Mech 1999]) and again each winter when they returned to the winter yard (Nelson *et al*. 2004). We examined the approximate spring migration routes of deer collared with prototype Advanced Telemetry Systems (Isanti, Minnesota, USA) drop-off GPS radio collars (details in Merrill *et al*. 1998), including some studied by Nelson *et al*. (2004).

We plotted individual deer summer locations and a summary location representing the centre of the winter deer capture locations on Google Earth Pro 7.1.7.2606 and measured the migration distances and directions via the Google Earth Tool function after converting UTMs of these locations to latitudes and longitudes via "Convert Geographic Units online" (http://www.rcn.montana.edu/resources/converter.aspx). Although fawns captured during the same year and at the same location as an adult female and migrating to the same summer range as the adult (or not migrating but remaining at the same summer range as the adult) might have been fawns of the adult, we still included the fawns as independent data. We used Statistix 9.0 (2008) to compare migratory status (including fawns) between our 1998–2001 and our 2014/2017 results using Fisher's Exact Test, respectively, and also to those from a previous study in the same area (Nelson and Mech 1981, 1987). We compared age structures (excluding fawns) between 1998–2017 and those from the previous study (Nelson and Mech 1981, 1987) via the Mann-Whitney *U*-test in R version 3.5.1 (R Core Team 2018). We considered all differences significant at alpha = 0.05.

Results

We live-trapped and radio-collared 27 adult does and eight fawns during winters 1998–2001, 2014, and 2017 in or near the GLY and aerially radio-tracked them to their summer ranges (Table 1), including eight whose spring migrations were studied in detail by Nelson *et al*. (2004). Apart from fawns, their mean age was 6.3 (SE = 0.8) years (Figure 2). All of the 19 deer we radio-collared in 1998–2001, including fawns, migrated to summer ranges, but six (including two fawns) of the 16 that we followed in 2014 and 2017 remained during summer within 3 km of their winter capture point, a significant difference between these two periods (Fisher's Exact = proportion

Table 1. Female White-tailed Deer (*Odocoileus virginianus*) or fawns of either sex radio-collared (first capture only) in Garden Lake Yard, Ely, Minnesota, USA, 1998–2017 and radio-tracked to their summer ranges. Six deer did not migrate.

Year	*n* (# fawns)	Age (year)*	
		Mean	Range
1998	8 (2)	5.6	3–11
1999	5 (0)	7.2	1–13
2001	6 (1)	3.7	1–13
2014	4 (1)	6.3	5–8
2017	12 (4)	7.1	2–13
1998–2017	35(8)	6.3	1–13

*27 adults and yearlings; excludes two adults of unknown age.

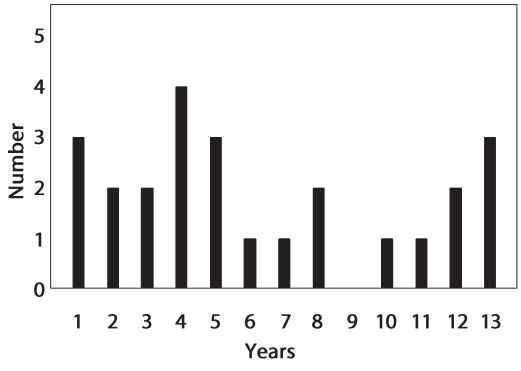

FIGURE 2. Age structure of adult and yearling female White-tailed Deer (*Odocolieus virginianus*) live-trapped (first capture only), in or near the Garden Lake Yard, Minnesota, 1998–2017, radio-collared, and followed to summer range.

difference 0.375, $P = 0.005$). The mean age of the four adult non-migrating deer was 7.3 and that of the 21 non-fawn migrators was 6.1. The age structures of the groups did not differ (W = 33, $P = 0.53$).

The 35 adults and fawns migrated in spring a mean distance of 29 km (SE = 4), a maximum distance of 78 km, and at a mean bearing of 83° (SE = 12; range = 21–348) excluding the six non-migrators (Table 2; Figure 3). Although the deer during different years of the study varied in the distances and directions to which they migrated, most of the annual mean migration distances were 21–36 km, and most of the annual mean migration bearings were 58–90° (Table 2). The 114° mean bearing for five deer in 1999 was heavily influenced by one deer whose migration bearing was 348°. Excluding that deer, the mean bearing was 55° (SE = 14). Notably, two other deer captured in the same general location as deer that migrated east-northeastward migrated in markedly different directions southwest, and south. Excluding all three deviant deer, and the non-migrators, the mean summer migration bearing was 65° (SE = 4; $n = 26$), the basic direction that the GLY extended. The mean migration distance of this sample was 29 km (SE = 4; 4–78 km).

Discussion

The sample of 35 does and fawns we studied from 1998 through 2017 generally was similar to that of the does and fawns studied from 1974–1984 in the same area (Nelson and Mech 1981, 1987). We compared these two periods (19 and 10 years long) because those were the periods for which we had comparable data. There was no significant difference in the radio-collared doe:fawn ratios (37:19 versus 39:28) between the early and later capture samples (Fisher's Exact = proportion difference 0.079, $P = 0.46$). The mean age of adult does of the earlier sample was 5.0 years and that of the later sample was 6.3 years. The age structures of the groups did not differ (W = 359, $P = 0.24$). The 1998–2017 sample of does and fawns that we followed through spring migration migrated similarly in mean distance (25 km ± 1.8 SE) to those from 1974–1984, but not maximum (78 km this study versus 54 km, measured from Nelson and Mech [1987: Figure 2.2]). They were also similar in the general directions they migrated (77° ± 4 SE; Nelson and Mech 1987). Of the 49 GLY deer (18 males: 31 females) whose spring migrations were studied from 1974 to 1984, 42 migrated (Nelson and Mech 1987), and with our 1998–2017 sample of 35 does and fawns, all except six migrated, a non-significant difference between proportions of migrators during the two periods (Fisher's Exact = proportion difference 0.029, $P = 0.77$).

The demography and migration we studied in the sample of deer wintering in the GLY differed little

TABLE 2. Migration distance and direction of White-tailed Deer (*Odocoileus virginianus*) that were radio-collared during 1998 through 2017 and followed to their summer ranges. Fawns possibly of collared does were included separately.

Year	No. of deer	No. migrating	Summer migration				Remarks
			Distance (km)		Direction (°)		
			$\bar{x}$ ± SE	Maximum	$\bar{x}$ ± SE	Range	
1998	8	8	36 ± 6	62	64 ± 8	26–97	
1999	5	5	31 ± 4	45	114 ± 60	21–348	
2001	6	6	26 ± 10	58	78 ± 17	39–153	
2014	4	1	2 ± 2	8			Includes three non-migrators
2014	4	1	8	8	58	—	Excludes three non-migrators
2017	12	9	21 ± 7	78			Includes three non-migrators
2017	12	9	28 ± 7	78	90 ± 18	36–226	Excludes three non-migrators
1998–2001	19	19	31 ± 4	62	81 ± 16	21–348	
2014–2017	16	10	16 ± 5	78			Includes six non-migrators
2014–2017	16	10	26 ± 7	78	87 ± 16	36–226	Excludes six non-migrators
1998–2017	35	29	24 ± 3	78			Includes six non-migrators
1998–2017	35	29	29 ± 4	78	83 ± 12	21–348	Excludes six non-migrators

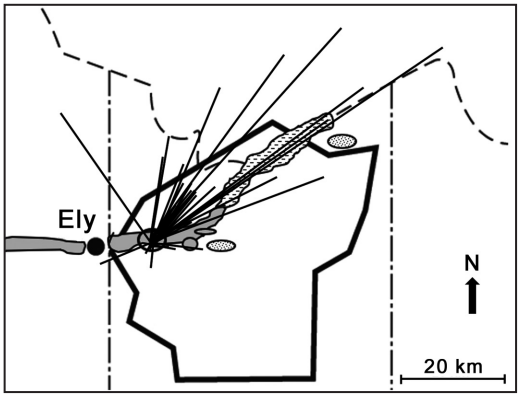

Figure 3. Distances and directions of spring migrations of 29 adult female and fawn White-tailed Deer (*Odocolieus virginianus*) radio-collared in the Garden Lake Yard during five winters between 1998 and 2017 (Table 1). Six of the original sample of 35 did not migrate.

from those studied there during 1974–1984. During the interim, several important environmental changes took place, as discussed in the Introduction.

Throughout this period and despite the changing deer, Moose, and wolf populations, as well as the widespread habitat upsets (e.g., derechos, forest fires, snowpack differences, changes in forestry practices), the majority of GLY deer continued to migrate each winter to the GLY the way they have for decades. Furthermore, we cannot extrapolate our findings to other migrating ungulate-wolf systems and would expect each deer yarding situation to be different because each local yarding ecology will be different.

Nelson (1995, 1998) and Nelson *et al*. (2004) provided details of the earlier migrations. The wolves that inhabited the major portions of the GLY deer summer and winter ranges maintained their numbers through about 2006. After Moose began to decline in 2006, the number of these wolves decreased, but packs continued to migrate each year for which we had data, presumably in response to the deer migration (L.D.M. and S.M.B.-M. unpubl. data), similar to wolf packs in Algonquin Park, Ontario, Canada (Forbes and Theberge 1995; Theberge and Theberge 2004).

During summer, the major age class of deer that local wolves kill are fawns (Nelson and Mech 1986; Barber-Meyer and Mech 2016), although the availability of beavers and Moose might buffer that predation (Mech and Karns 1977; Barber-Meyer and Mech 2016). Evidence from other parts of the wolf study area suggests that individual fawns are visited by wolves on average in summer about 5.5 times/100 days (Demma and Mech 2009) to daily (Mech *et al*. 2015), although the rate of fawn predation is unknown. Regardless, even though fawns comprise a high percentage of the diet of wolves in summer (Barber-Meyer and Mech 2016), enough fawns have survived in the summer ranges of the GLY deer each year to sustain the migrating deer population over the decades.

GLY migrating deer spend 31–356 hours during migration and adhere closely to a straight line during the trip (Nelson *et al*. 2004). While migrating, deer are much more vulnerable to wolf predation than at any other time as adults (Nelson and Mech 1991), so the persistence of GLY deer either abandoning summer range or favouring winter range or both during winter must have some strong adaptive value. Reducing vulnerability to wolf predation during winter when deer are in poor nutritional condition (DelGiudice *et al*. 1992) and hindered by snow conditions (Mech *et al*. 1971) was the explanation Nelson and Mech (1981) gave for deer in this area migrating to areas of high deer density, i.e., the GLY, listing several advantages to yarding. This benefit was one of the points Nelson and Mech (1981) proposed as an anti-predator effect of yarding. We further note that Poszig and Theberge (2000) did find that non-yarding deer in their study were "highly vulnerable" when migrating wolves returned to their territory.

Kolenosky (1972) had already shown that wolves tended to kill deer along the edges, rather than the centre of the deer yards he studied, and further support for the antipredator explanation for deer migration and yarding has since been found in other studies. In northwestern Minnesota, wolves also tended to kill deer along the edges of yarding areas rather than in the densest areas (Fritts and Mech 1981) as did Coyotes in Quebec (Messier and Barrette 1985).

On the other hand, Poszig and Theberge (2000) found evidence in Ontario that tended to dispute the hypothesized antipredator advantages of deer yarding. The only benefit of yarding they proposed would be an enhanced trail network through the snow that might give deer in high densities more of an advantage in escaping wolves.

Henderson *et al*. (2018) emphasized the role of density-dependent competition for home ranges in winter that forced deer to space out during summer to obtain adequate nutrition. The spacing out of migrating deer to their summer ranges, where their fawns are born, provides far more habitat per deer to obtain nourishment, with summer being the season of annual replenishment (Silver *et al*. 1969; Moen 1978; DelGiudice *et al*. 1992). However, it also brings several other survival benefits related to wolf predation: (1) familiar escape terrain and habitat; (2) an area with a proven history of survival characteristics; and (3) separation from other fawns that would attract

predators. Fawns are most vulnerable during late spring and early summer (Kunkel and Mech 1994; Carstensen *et al*. 2009), so widely spaced fawns reduce the chance that any individual fawn would be detected by predators, thus increasing survivability (although reducing potential benefits of group vigilance and defense).

None of these benefits of return to summer range or migration to winter range (Nelson and Mech 1981) conflict with the Henderson *et al*. (2018) findings, for in complex ecosystems both foraging and predation risk are factors between which animals must find trade-offs that enhance their survival (Lima and Dill 1990). Within the context of these trade-offs, our study demonstrates that, in an area where wolf predation is the major natural mortality for adult deer, long deer migrations between winter and summer ranges and yarding in winter produces strong enough survival value for the behaviour to have persisted for over six decades and many generations.

Author Contributions

Writing – Original Draft: L.D.M.; Writing – Review & Editing: L.D.M. and S.B.-M.; Conceptualization: L.D.M.; Investigation: S.B.-M.; Methodology: L.D.M.; Formal Analysis: L.D.M. and S.B.-M.; Funding Acquisition: L.D.M.

Acknowledgements

This study was supported by the United States Geological Survey (USGS) with the cooperation of the Superior National Forest. We thank numerous volunteer wildlife technicians for assisting with the deer captures; several United States Forest Service pilots for safe flying; and Dr. M.E. Nelson (USGS retired) for collecting the 1998–2001 data and for critiquing an early draft of the manuscript. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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Received 10 September 2018
Accepted 23 January 2020