WEIGHTS, GROWTH, AND SURVIVAL OF TIMBER WOLF PUPS IN MINNESOTA

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ABSTRACT.—Weights, growth rates, canine tooth lengths, and survival data were obtained from 73 wild wolf (*Canis lupus*) pups that were 8 to 28 weeks old when live-trapped in three areas of northern Minnesota from 1969 to 1972. Relative weights of wild pups are expressed as percentages of a standard weight curve based on data from captive pups of similar age. These relative weights varied greatly within litters, between litters, and between years; extremes of 31 to 144 percent of the standard were observed. Growth rates ranging from 0.05 to 0.23 kilograms per day were observed, and similar variations in general development and in replacement and growth of canine teeth were noted. Survival data based on radio-tracking and tag returns indicated that pups with relative weights less than 65 percent of standard have a poor chance of survival, whereas pups of at least 80 percent of standard weight have a high survivability. Pups born in 1972 were especially underweight, probably a result of declining white-tailed deer (*Odocoileus virginianus*) densities in the interior of the Superior National Forest study area.

The importance of studying the survival of wolf pups as a means of better understanding the population ecology of wolves has been recognized by several authors (Jordan *et al.*, 1967; Rausch, 1969; Pimlott *et al.*, 1969). However, the literature contains few data on pup biology. Forest-dwelling wolves are difficult to observe during the snow-free months, and pups are particularly elusive until they travel with the pack in early autumn. Data gathered from hunter-killed wolves (Stenlund, 1955; Rausch, 1967) are usually collected during winter after the pups are nearly grown and much natural mortality has already occurred (Pimlott *et al.*, 1969). As a result, available data on development and survival of young wolves have been restricted largely to occasional records of individual wild pup weights (Stenlund, 1955; Kuyt, 1962; Rausch, 1967; Pimlott *et al.*, 1969) supplemented with growth studies of captive wolves (Pulliainen, 1965; Kuyt, 1972).

During our separate ecological studies of wolves in Minnesota (Mech and Frenzel, 1971; Van Ballenberghe, 1972; Mech, 1972, 1973), we each conducted intensive live-trapping programs to determine population structure and obtain animals for radiotelemetry studies. The wolves captured included many pups because much of the trapping took place during late summer and early autumn. This paper documents some growth characteristics of wild wolf pups, points out extreme variations that appear typical, and discusses the implications of survival data gathered from many of the pups through subsequent recaptures and telemetry observations. The subspecies of wolf involved in these studies is believed to be the eastern timber wolf (*Canis lupus lycaon*), but Mech and Frenzel (1971:60–62) have proposed

that there may still be genes present in the Minnesota population attributable to the great plains wolf (*Canis lupus nubilus*).

Study Area

Most of the wolves taken in this study were from the Superior National Forest of northeastern Minnesota, an area described by Stenlund (1955) and Mech and Frenzel (1971). Within the Forest, Van Ballenberghe generally concentrated his efforts in the eastern quarter and Mech in the adjacent central quarter (Mech, 1973). Seasonal differences in prey populations exist in both regions. The eastern quarter includes along its eastern edge one of the highest winter concentrations of white-tailed deer (*Odocoileus virginianus*) in Minnesota (Van Ballenberghe *et al.*, 1975). The western region also includes a deer concentration area and scattered pockets of wintering deer in its western portion. However, the contiguous interior zones of both regions contain a large area nearly devoid of deer from December through March, and packs that live and breed there have recently begun winter migrations to the deer-concentration areas to the east and west. During our study the area devoid of deer in winter has increased each year; the first winter that wolf packs in the interior zone migrated was 1971–72. In both regions deer densities appear to have declined yearly throughout the study.

Wolf pups were also captured in two other regions of Minnesota. In the Hill City area, some 145 kilometers (90 miles) southwest of the Superior National Forest study area, study animals were trapped by Robert Chesness of the Minnesota Department of Natural Resources incidental to a coyote (*Canis latrans*) study and radioed in collaboration with Mech. This area is in the peripheral range of the wolf where wolf densities are relatively low; deer density in the area occupied by the wolves is unknown. The other region where wolf pups were captured is the Red Lake area, 193 kilometers (120 miles) northwest of the Forest study area. This region lies within the primary wolf range, but intensive exploitation of wolves occurs there and the deer density is several times that of the Forest study area. Data from the Red Lake area were contributed by Steven Fritts, University of Minnesota, who is conducting wolf studies in cooperation with Mech.

Methods

Wolves were captured with Newhouse No. 4 and No. 14 steel traps set near baits and scent posts or in wolf trails (Kolenosky and Johnston, 1967; Mech, 1974). Trapping was conducted from July through November 1969 to 1972, with concentrated effort occurring during September and October. Wolves were captured both indiscriminately and through deliberate efforts to sample specific packs by trapping near rendezvous sites (Joslin, 1967).

Some captured animals were handled without drugs and others were anesthetized with phencyclidine hydrochloride and promazine hydrochloride, following procedures outlined by Seal *et al.* (1970). Pups were ear-tagged and weighed; those large enough were fitted with radio transmitter collars similar to those described by Mech and Frenzel (1971) and Mech (1974). The teeth of each pup were examined, and observations of canine tooth eruption and replacement recorded. Lengths of permanent upper canine teeth from gumline to tip were measured down the labial midline with dial calipers. Pups were distinguished on the basis of the presence of deciduous canines (Mech, 1970:140) or of permanent canines less than 21 millimeters long. Blood samples of up to 30 cubic centimeters were drawn from some of the captured pups to assess their nutritional status and detect signs of disease or other physiological abnormalities (Seal *et al.*, 1975).

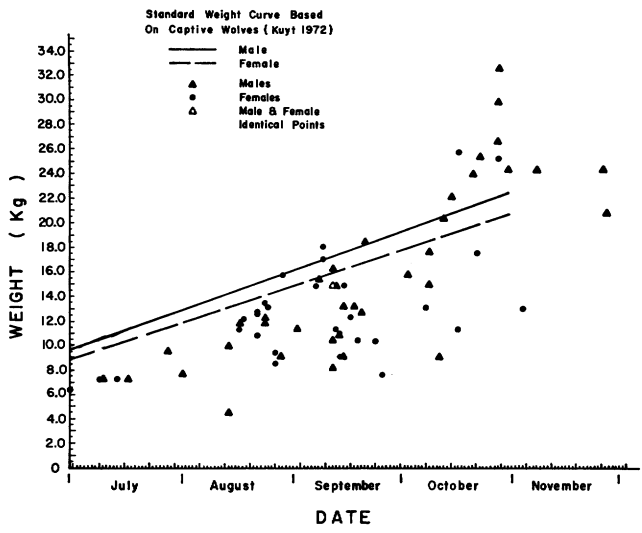

FIG. 1.—Weights of 72 wolf pups live-trapped in northern Minnesota in 1969 to 1972.

To compare weights of wild pups captured on different dates we constructed a standard weight table for each sex from the data of Kuyt (1972:28). The standards were based on weights of two male and two female captive wolves fed an optimum diet from birth to 16 weeks of age. The rate of growth of the captives during the last three weeks of observation was used to extrapolate standards eight additional weeks to allow determination of relative weights for Minnesota pups caught in late October. A 24 April birth date was arbitrarily assumed for Minnesota pups when their relative weights were calculated from the standard tables. Relative weight for a given pup is its percent of standard weight for its assumed age at the date of capture.

Wolves were released near their capture sites, and most showed little evidence of injury as the result of trapping or handling methods. We observed no radio-tagged pups that were rejected by their pack associates following capture.

Survival data for tagged pups accrued primarily from aerial radiotelemetry studies of them and their packs, as described by Mech and Frenzel (1971:8–9). Many pups were subsequently recaptured by our trapping efforts; others were killed on the study areas by various human activities including sport hunting and trapping, and some apparently died natural deaths.

We assume here that the wolf packs studied are basically family groups and that only one female in each pack produced a litter in any given year. During extensive studies of these packs for several years, no evidence was found to contradict this assumption.

RESULTS

The trapping efforts of four field seasons, 1969 to 1972, resulted in the capture of 73 wolf pups including 37 in the central Superior National Forest, 25 in the eastern part of the Forest, eight in the Hill City area, and three in the Red Lake area. Yearly totals ranged from 13 in 1969 to 26 in 1970. Most pups were captured from late August to mid-October when Minnesota pups are approximately 14 to 22 weeks old.

TABLE 1.—*Background data on the capture, growth, and survival of 73 wolf pups live-trapped in northern Minnesota, 1969–1972.*

Wolf number	Sex	Date of capture	Study area	Pack affiliation	Weight		Relative weight** (percent)	Upper canine		Fate
					Kilograms	Pounds		Type	Length (mm)	
109	F	23 August 1969	Central SNF*	Stony Lookout	11.8	26	83	D***	—	Recaptured 21 October 1970
113	F	27 August 1969	Central SNF	Sawbill	9.5	21	65	D	—	Unknown
119	F	14 September 1969	Eastern SNF	Manitou River	9.1	20	57	D	—	Unknown
121	M	14 September 1969	Eastern SNF	Manitou River	10.9	24	61	D	—	Killed by humans, 26 October 1969
127	F	19 September 1969	Central SNF	Jack Pine	10.5	23	63	D	—	Killed by humans, 15 January 1970
137	F	26 September 1969	Eastern SNF	Houghtaling Creek	7.7	17	45	P	6.9	Unknown
166	F	1 July 1969	Central SNF	Sawbill	6.4	14	69	D	—	Unknown
167	M	28 July 1969	Central SNF	Jack Pine	9.5	21	75	D	—	Survived at least through 23 August 1973
169	M	1 August 1969	Central SNF	Jack Pine	7.7	17	59	D	—	Unknown
170	F	9 July 1969	Central SNF	Jack Pine	7.3	16	72	D	—	Unknown
173	M	17 July 1969	Central SNF	Jack Pine	7.3	16	63	D	—	Unknown
348	F	14 July 1970	Central SNF	Jack Pine	7.3	16	69	D	—	Unknown
378	M	24 August 1970	Central SNF	Jack Pine	11.8	26	76	D	—	Recaptured 10 October 1970
391	F	13 September 1970	Central SNF	Jack Pine	11.4	25	71	P	5.0	Killed by humans, approximately 15 November 1970

* Superior National Forest.
** See Text.
*** D-deciduous; P-permanent.

TABLE 1.—*Continued.*

Wolf number	Sex	Date of capture	Study area	Pack affiliation	Weight		Relative weight** (percent)	Upper canine		Fate
					Kilograms	Pounds		Type	Length (mm)	
393	M	13 September 1970	Central SNF	Jack Pine	15.0	33	85	P	4.5	Survived at least through 19 August 1974
407	M	21 September 1970	Central SNF	Jack Pine	18.6	41	100	P	5.0	Killed by humans, 4 December 1970
516	M	10 July 1971	Central SNF	Jack Pine	7.3	16	69	D	—	Unknown
641	M	17 August 1970	Eastern SNF	Temperance River	11.8	26	79	D	—	Recaptured 8 May 1971
648	F	22 August 1970	Eastern SNF	Temperance River	10.9	24	77	D	—	Unknown
650	F	22 August 1970	Eastern SNF	Temperance River	12.8	28	90	D	—	Killed by humans, 31 October 1970
651	M	31 October 1971	Eastern SNF	Temperance River	—	—	—	P	19.0	Killed by humans, 31 October 1971
656	M	2 September 1970	Eastern SNF	Cross River	11.4	25	69	D	—	Unknown
664	M	8 September 1970	Eastern SNF	Timber Lake	15.5	34	90	D	—	Killed by humans, 4 January 1971
670	M	12 September 1970	Eastern SNF	Houghtaling Creek	16.4	36	93	D	—	Unknown
672	F	12 September 1970	Eastern SNF	Houghtaling Creek	15.0	33	94	P	5.0	Unknown
682	M	15 September 1970	Eastern SNF	Manitou River	9.1	20	51	D	—	Unknown
684	M	15 September 1970	Eastern SNF	Houghtaling Creek	13.2	29	73	P	5.0	Recaptured 15 October 1970
686	M	20 September 1970	Eastern SNF	Ward Lake	12.7	28	69	P	7.0	Killed by humans, 8 February 1972
692	M	13 October 1970	Central SNF	Sawbill	20.5	45	97	P	18.7	Unknown
819	M	14 August 1971	Eastern SNF	Temperance River	4.5	10	31	D	—	Unknown

* Superior National Forest.
** See Text.
*** D-deciduous; P-permanent.

TABLE 1.—*Continued.*

Wolf number	Sex	Date of capture	Study area	Pack affiliation	Weight		Relative weight** (percent)	Upper canine		Fate
					Kilograms	Pounds		Type	Length (mm)	
821	M	14 August 1971	Eastern SNF	Temperance River	10.0	22	69	D	—	Survived at least through mid-January 1972
823	F	17 August 1971	Eastern SNF	Ward Lake	11.4	25	83	D	—	Survived until at least mid-February 1972
825	F	22 August 1971	Eastern SNF	Ward Lake	10.9	24	77	P	3.0	Unknown
827	F	22 August 1971	Eastern SNF	Ward Lake	12.7	28	90	D	—	Survived until at least mid-February 1972
833	M	12 September 1971	Eastern SNF	Dyer's Lake	10.5	23	59	P	—	Killed by humans, 21 December 1971
835	F	15 September 1971	Eastern SNF	Onion River	15.0	33	93	—	—	Unknown
837	M	28 October 1971	Eastern SNF	South Brule	30.0	66	132	P	19.6	Unknown
843	M	31 October 1971	Eastern SNF	Devil's Track	24.5	54	106	P	16.8	Unknown
1073	M	26 November 1969	Central SNF	Jack Pine	24.5	54	—	P	19.0	Killed by humans, 3 January 1970
1075	M	27 November 1969	Central SNF	Jack Pine	20.9	46	—	P	14.0	Survived at least through 29 March 1971
2217	F	17 October 1970	Central SNF	Jack Pine	11.4	25	60	P	16.0	Killed by humans, 3 November 1970
2219	M	21 October 1970	Central SNF	Quadga Lake	24.1	53	110	P	—	Survived at least through 2 March 1971

* Superior National Forest.
** See Text.
*** D-deciduous; P-permanent.

TABLE 1.—*Continued.*

Wolf number	Sex	Date of capture	Study area	Pack affiliation	Weight		Relative weight** (percent)	Upper canine		Fate
					Kilograms	Pounds		Type	Length (mm)	
2221	F	22 October 1970	Central SNF	Harris Lake	17.7	39	91	P	16.0	Died about 10 July 1971
2223	M	23 October 1970	Central SNF	Quadga Lake	25.5	56	115	P	16.0	Survived at least through 11 January 1971
2225	M	28 October 1970	Central SNF	Jack Pine	26.8	59	118	P	20.5	Killed by humans, 14 February 1973
2226	M	28 October 1972	Central SNF	Glenmore Lake	32.7	72	144	P	15.0	Survived at least through 14 November 1972
2232	F	28 October 1972	Central SNF	Glenmore Lake	25.5	56	127	P	18.0	Survived at least through 25 January 1973
2247	M	8 November 1972	Central SNF	Harris Lake	24.5	54	—	P	18.0	Survived at least through 1 May 1973
2268	F	29 August 1971	Hill City	Hill City	15.9	35	108	P	9.5	Killed by humans, 16 January 1972
2405	M	9 October 1971	Central SNF	Harris Lake	15.0	33	73	P	8.0	Survived at least through 29 November 1971

* Superior National Forest.
** See Text.
*** D-deciduous; P-permanent.

TABLE 1.—*Continued.*

Wolf number	Sex	Date of capture	Study area	Pack affiliation	Weight		Relative weight** (percent)	Upper canine		Fate
					Kilograms	Pounds		Type	Length (mm)	
2411	M	15 October 1971	Central SNF	Pagami Lake	22.3	49	104	P	4.5	Killed by humans, 22 October 1972
2417	F	17 October 1971	Central SNF	Glenmore Lake	25.9	57	136	P	19.0	Killed by humans, 27 January 1973
2423	F	4 November 1971	Central SNF	Sawbill	13.2	29	63	P	—	Died about 1 December 1971
2443	M	12 September 1972	Central SNF	Jack Pine	15.0	33	85	P	10.5	Survived at least through 19 August 1974
2445	F	17 September 1972	Central SNF	Jack Pine	12.3	27	75	P	12.5	Survived at least through 29 April 1974
2447	F	24 September 1972	Central SNF	Jack Pine	10.5	23	62	P	10.5	Unknown
2453	F	18 August 1972	Red Lake	Clear Lake	12.3	27	89	P	10.5	Killed by humans, 3 February 1973
2455	F	24 August 1972	Red Lake	Clear Lake	13.6	30	95	P	12.0	Survived at least through 1 August 1974
2457	M	24 August 1972	Red Lake	Clear Lake	12.3	27	78	P	12.0	Killed by humans, 19 November 1972
2459	M	12 September 1972	Central SNF	Jack Pine	8.2	18	46	D	—	Survived at least through 10 November 1972

* Superior National Forest.
** See Text.
*** D-deciduous; P-permanent.

TABLE 1.—*Continued.*

Wolf number	Sex	Date of capture	Study area	Pack affiliation	Weight		Relative weight** (percent)	Upper canine		Fate
					Kilograms	Pounds		Type	Length (mm)	
2464	M	3 October 1972	Central SNF	Pagami Lake	15.9	35	80	P	13.5	Died about 28 November 1972
2468	F	8 October 1972	Central SNF	Quadga Lake	13.2	29	72	P	7.0	Died about 28 October 1972
2474	M	12 October 1972	Central SNF	Quadga Lake	9.1	20	43	P	12.5	Died about 21 October 1972
2489	M	9 October 1972	Central SNF	Harris Lake	17.7	39	86	P	20.0	Survived at least through 5 April 1974
C-2	F	9 September 1970	Hill City	Hill City	18.2	40	116	P	—	Unknown
C-4	F	9 September 1970	Hill City	Hill City	17.3	38	111	P	—	Unknown
C-62	F	25 August 1971	Hill City	Hill City	13.2	29	93	—	—	Unknown
C-79	F	7 September 1971	Hill City	Hill City	15.0	33	97	D	—	Killed by humans, 21 November 1971
C-170	F	27 August 1972	Hill City	Hill City	8.6	19	59	D	—	Died before 15 September 1972
C-174	M	28 August 1972	Hill City	Hill City	9.1	20	57	P	6.0	Died before 9 September 1972
C-179	F	14 September 1972	Hill City	Hill City	10.9	24	68	D	—	Unknown
M-1	M	15 September 1970	Eastern SNF	Grand Marais	15.0	33	84	—	—	Killed by humans, 15 September 1970
M-2	M	18 September 1970	Eastern SNF	Ward Lake	13.2	29	72	—	—	Killed by humans, 18 September 1970

* Superior National Forest.
** See Text.
*** D-deciduous; P-permanent.

FIG. 2.—Two male wolf pup littermates (Nos. 819 and 821, Table 1) on 14 August 1971 showing extreme differences in size (weight ratio = 2.2:1) and pelage development.

Weights

Weights of pups ranged from 4.5 to 32.7 kilograms (10 to 72 pounds) (Fig. 1). Weights of wild pups compared with standard weights of captive pups, calculated as described above, indicated extreme variation among wild pups. Observed weights ranged from 31 to 144 percent of the standards (Table 1). Most pups captured after mid-August exceeded 7.7 kilograms (17 pounds), but pups as light as 9.1 kilograms (20 pounds) were captured as late as 12 October. In contrast, weights of 18.2 to 27.3 kilograms (40 to 60 pounds) were achieved by most pups captured after mid-October, and one pup taken on 28 October weighed 32.7 kilograms (72 pounds).

The mean weight of male pups captured during specific periods was generally greater than that of females, but some females exceeded the standard curve for males (Fig. 1). From 15 August to 15 September females heavier than their male counterparts were frequently captured.

Much variation in weight occurred among pups known to belong to the same litter. The ratio of weights for two males of the Temperance River Pack (Males 819 and 821) captured at the same rendezvous site on the same day was 2.2 to 1. Similar ratios were recorded for members of the Jack Pine Pack in 1970 and 1972 (Table 1). In 1972 when all surviving pups from the Jack Pine Pack were captured at about the same time, their weights were 8.2 and 15.0 kilograms (18 and 33 pounds) for two males, and 10.5 and 12.3 kilograms (23 and 27 pounds) for two females.

Pups of lower relative weight than their littermates sometimes also displayed retarded development of adult pelage. They retained a reddish, wooly-textured coat lacking guard hairs (Fig. 2) for longer periods than their heavier siblings.

TABLE 2.—*Yearly proportions of Minnesota wolf pups of low relative weight.*

	1969	1970	1971	1972
Pups captured	11	26	15	16
Proportion of pups less than 80 percent of standard weight	.91	.46	.33	.56

Year-to-year variations in pup weights, irrespective of pack affiliation, were illustrated by the proportion of each yearly sample of pups that was less than 80 percent of standard weight (Table 2). In 1969, 10 of 11 pups weighed less than 80 percent of the standard; only 5 of 15 pups were similarly underweight in 1971. Relative weights of pups in the Hill City Pack were consistently higher in 1971 than in 1972. Similar variation between years was seen in litters of the Jack Pine Pack in 1969, 1970, and 1972.

Growth Rates

Extreme variation was also apparent in growth rates of pups. Weight gains were determined for 10 tagged pups recaptured at intervals of 26 to 99 days. Individual mean growth rates varied from 0.05 to 0.23 kilograms (0.10 to 0.51 pounds) per day and appeared unrelated to relative weights at initial capture (Table 3). The captive male and female pups raised by Kuyt (1972) gained an average of 0.11 and 0.09 kilograms (0.24 and 0.19 pounds) per day, respectively, between their twelfth and sixteenth weeks, and displayed relatively uniform growth.

Variability in weight continued as pups grew to yearling age (Table 4). Male pup 641 weighed only 20.0 kilograms (44 pounds) as a yearling whereas other yearling males (2489 and 686) exceeded 27.3 kilograms (60 pounds).

TABLE 3.—*Growth rates of wild timber wolf pups. Rates were computed from weight changes observed during successive captures.*

Wolf number	Sex	Initial capture date	Percent standard weight	Recapture date	Interval between captures (days)	Growth rate (kg/day)
650	F	22 August 1970	90	31 October 1970	70	0.09
684	M	15 September 1970	73	15 October 1970	30	0.05
378	M	24 August 1970	76	20 September 1970	27	0.09
407	M	21 September 1970	100	17 October 1970	26	0.12
2225	M	21 September 1970	107	28 October 1970	37	0.23
391	F	13 September 1970	71	17 October 1970	35	0.15
2217	F	26 August 1970	75	14 October 1970	49	0.07
1075	M	19 August 1969	82	27 November 1969	99	0.09
2457	M	24 August 1972	78	19 November 1972	87	0.17
C-79	F	7 September 1971	97	21 November 1971	75	0.06

TABLE 4.—*Yearling and adult weights attained by certain timber wolves captured as pups in northern Minnesota.*

Wolf number	Sex	Initial capture date	Initial weight		Relative weight (percent)	Recapture date	Months between captures	Recapture weight	
			Kilograms	Pounds				Kilograms	Pounds
2489	M	9 October 1972	17.7	39	86	4 May 1973	7	28.6	63
2225	M	28 October 1970	26.8	59	118	14 February 1973	28	37.7	83
686	M	20 September 1970	12.7	28	69	12 May 1971	8	28.2	62
167	M	28 July 1969	9.5	21	75	20 September 1970	14	29.1	64
641	M	17 August 1970	11.8	26	79	8 May 1971	9	20.0	44
393	M	13 September 1970	15.0	33	85	22 May 1972	20	34.5	76
2417	F	17 October 1971	25.9	57	136	27 January 1973	15	37.3	82
2411	M	15 October 1971	22.3	49	104	22 October 1972	12	23.6	52
2221	F	22 October 1970	17.7	39	91	29 June 1971	8	25.9	57
1075	M	19 August 1969	12.3	27	82	23 September 1970	13	26.8	59

Relatively heavy pups tended to be heavy yearlings or adults, as Kuyt (1962) also found. A notable exception was Male 2411, which dispersed from his pack at the age of about 10 months and subsequently gained little weight.

Dentition

Development of dentition, like weight parameters, varied considerably among the wild wolf pups we captured. Most pups caught prior to mid-September retained deciduous upper canine teeth, but permanent canine eruption was noted as early as 18 August (Female 2453, Table 1). Newly erupted canines were evident in some pups as late as mid-October when other individuals had canines approaching adult size (Fig. 3). Canine tooth length and body weight were poorly correlated ($r = .62$); some individuals ranging in weight from 11.4 to 32.7 kilograms (25 to 72 pounds) possessed canines of approximately equal length, and individuals weighing about 18.2 kilograms (40 pounds) had canines from 5 to 20 millimeters long (Fig. 4). Data on canine development of captive pups are poorly represented in the literature. Mech (1970:140) cited one captive pup with 10 millimeter upper canines at 21 weeks of age.

Survival

Telemetry data and recapture information relative to survival were obtained for 48 (66 percent) of the tagged pups. Few physical injuries due to handling were observed, and all pups seemed viable upon release.

The mean relative weight of 26 pups that survived from 3 months to 4 years postcapture was 93 percent of standard weight. Of these 26 pups, only seven had relative weights below 80 percent; these ranged from 63 (Female 127) to 79 percent (Male 641). The mean relative weight of six pups that

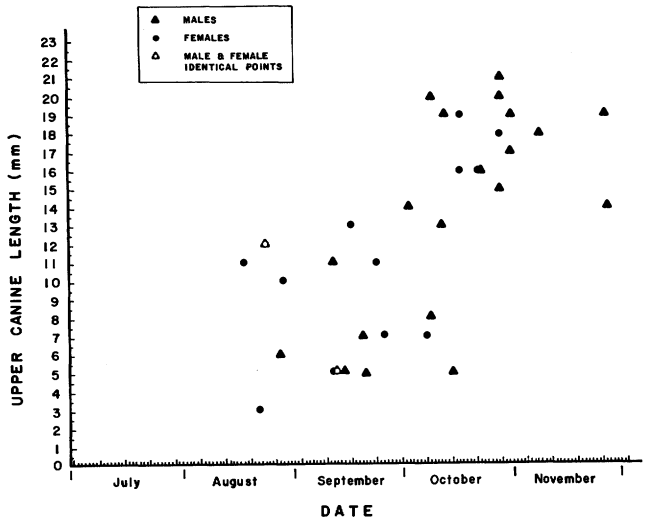

FIG. 3.—Lengths of permanent upper canines of 36 wolf pups.

died of nonhuman mortality 2 weeks to 2 months postcapture was 63 percent (range = 43–80). Many of the pups with low relative weights that were not radio-tagged were never recaptured on the study areas despite intensive research trapping efforts and moderate sport hunting and trapping pressure. We assume that many of these pups succumbed undetected.

An indication of the approximate period when such mortality may have occurred may be obtained from the distribution of the pooled yearly proportions of pups that weighed more than 80 percent of standard during 3-week

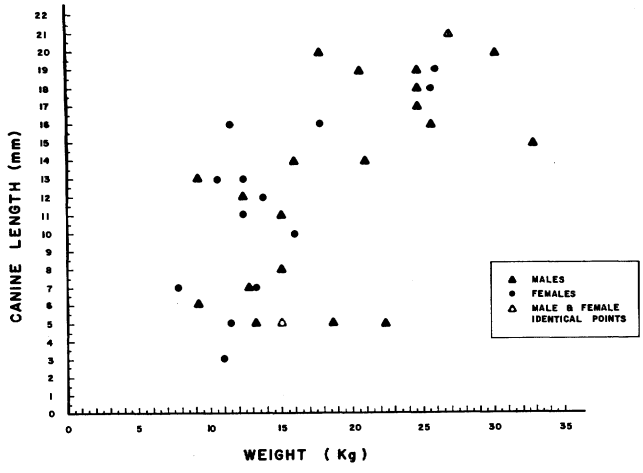

FIG. 4.—Upper canine length versus body weight of wolf pups.

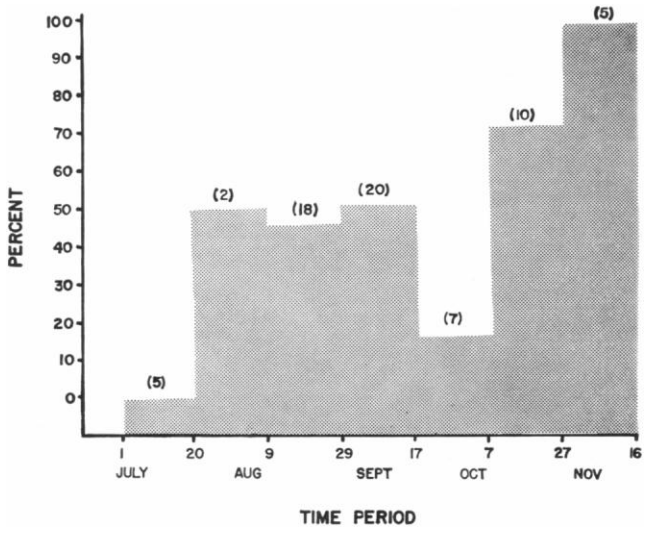

FIG. 5.—Percent of wolf pups over 80 percent standard weight for various 20-day periods. Numbers in parentheses are the number of pups live-trapped during the indicated intervals, 1969 to 1972.

periods, July through mid-November (Fig. 4). It appears that September may be a critical month in this respect, for the percent of pups with relative weights greater than 80 percent of standard dropped to less than 15 percent from 17 September to 7 October (Fig. 5). It then increased to more than 70 percent from 7 to 27 October and reached 100 percent after 27 October. We interpret this to mean that by early October most of the underweight pups had already died, leaving only individuals in relatively good condition. Similarly, Stenlund (1955) noted wild Minnesota pups as light as 12.7 kilograms (28 pounds) in September and October but reported none lighter than 18.2 kilograms (40 pounds) after 1 November.

The precise cause of death for many of the pups recovered was not determined due to advanced decomposition of their carcasses. Some, however, were obviously emaciated, and blood samples taken earlier had indicated that they were in poor nutritional condition (Seal *et al.*, 1975).

DISCUSSION

These data on weight, growth, development, and survival of wild wolf pups show considerable variation. Wide differences are apparent among members of a litter, members of different litters born in a given year, and individuals born in different years to a particular pack. In most cases it is not known that pups born to a given pack were necessarily produced by the same female each year, but in many cases they probably were. Pups of the same sex and the same litter sometimes displayed marked differences in

relative weight. Growth rates among certain individuals varied five-fold. Variations in the mean relative weight of pups born in different years suggested factors operating over a wide area that acted to suppress pup weights during some years. Data presented on survival show that many pups of low relative weight are not recruited into the population as yearlings.

Although some pups as underweight as 63 percent of standard survived for at least 3 months postcapture and other animals as heavy as 80 percent of standard succumbed, these were extreme exceptions. Our data indicate that pups less than approximately 65 percent of standard weight have a low chance of survival, those at least 80 percent of standard have high survivability, and those between 65 and 80 percent of standard depend critically on improved nutrition for survivial to yearling status.

Several possible sources of the observed differences in growth parameters are evident. These include: (1) broad distribution of parturition dates; (2) inherent genetic or behavioral variations in growth potential; and (3) differences in nutritional status.

Birth dates for most of the pups examined were unknown, but the available evidence suggests that most litters were born during a short period each year. Rausch (1967) reported that most adult female wolves in Alaska conceived during a 2-week period. Some 2-year-old Alaskan wolves bred somewhat later (Rausch, 1967:256), but about 65 percent of 20 2-year-old females had conceived during the peak of adult breeding. The spring age structure of wolves from one portion of northeastern Minnesota suggested that about 33 percent of the breeding females were 2 years old (Van Ballenberghe, 1972).

Observations of wolf breeding behavior in Minnesota and on nearby Isle Royale, Michigan, suggest that pups in those latitudes are born in late April. Mech (1966), Mech and Frenzel (1971:22), and our data include six observed copulatory ties from 1959 to 1972; all occurred between 18 February and 27 February. Thus, we conclude that most Minnesota wolves are born during a 2- to 3-week period in late April. Individual litters may be born earlier or later, but widely divergent birth dates probably do not explain much of the weight variation evident in pups captured in early autumn. Differences in birth date obviously do not account for the range of weights observed among pups of the same litter.

Individuals having wide differences in inherent growth potential have been documented for several canids. Smith (1939), Layne and McKeon (1956), and Storm (1966) showed that full-term red fox (*Vulpes fulva*) pups varied markedly in weight. Latimer (1950) determined the relationship of the heaviest and lightest fetus in each of 35 domestic dog (*Canis familiaris*) litters and found an average ratio of 1.31 (1.08–2.61), but found no predictable relationship between these ratios and litter size or average weight of the entire litter. There is evidence for certain domestic mammals that birth weight is proportional to ultimate weight achieved (Weaver and Bogart,

1943). Kuyt (1962) observed that the lightest member of three wild wolf littermates he tagged in July remained lightest when the pups were recaptured in February.

Differences in individual growth potential of wolves may not become apparent until the pups are several weeks old. Such differences may be due to behavioral as well as genetic factors. Mech (1970) and Fox (1972) observed social status determination among 4-week-old captive pups raised without adults, which showed that potential for status differentiation exists at an early age. During food shortages, dominant pups may receive more food and attain greater weights than subordinate pups. Kuyt (1972) raised two male pups to 14.1 and 15.5 kilograms (31 and 34 pounds) at 16 weeks despite equal weights from birth to 4 weeks.

We believe that both behavioral and growth potential differences among wild pups account for a portion of the variation observed among relative weights of individuals captured during the same year. Other factors must account for significant year-to-year differences.

The quality and quantity of prey eaten and the frequency of its consumption probably influence the growth of wild wolf pups more than any other single factor. Campbell (1951) experimentally produced two-fold differences in weights of domestic dog pups fed diets of 12 percent versus 20 percent protein. Kuyt (1972:26) found that quantities of bison (*Bison bison*) averaging less than 1.4 kilograms (3 pounds) per day per individual were insufficient to maintain 2-month-old captive wolves, but that 1.6 kilograms (3.5 pounds) of food per pup per day allowed normal growth. We believe that these figures closely approximate the requirements of pups in the wild, for wild pups probably are no more active in their restricted rendezvous sites than are captive pups.

Our data on growth rates of wolves indicate that wild pups grow at highly variable rates; they must be well adapted to periods of food scarcity and abundance. We observed individuals that gained up to 1.6 kilograms (3.6 pounds) per week (Table 3), a growth rate 2.8 times that of captive wolves of comparable age (Pulliainen, 1965). Maintenance of weight over long periods instead of growth, as well as actual weight loss following sudden gains, probably both occur in wild pups and may account for those pups with long permanent canines but low relative weight (Fig. 4). These uneven growth rates probably also explain why some wild pups exceeded standard weights derived from pups raised on a regular feeding schedule.

The relative weight and condition of Minnesota wolf pups vary greatly from year to year (Table 2 and Seal *et al.*, 1975). Other studies (Rausch, 1967; Jordan *et al.*, 1967) have indicated similar variation elsewhere. Much of the variation may be caused by annual differences in the available food supply.

The primary prey of wolves in northeastern Minnesota is the white-tailed deer. Van Ballenberghe *et al.* (1975) found that wolves exploited fawns

heavily from mid-June to mid-July. During this period 81 percent of the food items in wolf scats consisted of deer and 48 percent of these items were fawns. Toward late summer the diversity of the diet increased, wild fruits became important, and deer were less frequently taken. Years of low fawn production could result in malnourished pups since fawns apparently are a major source of food for pups at a critical time in their development. It is noteworthy that we observed many pups of low relative weight in 1969 following a winter of extreme severity and surplus killing of deer by wolves (Mech and Frenzel, 1971:51–59).

Mech (1973) hypothesized that decreases recorded in average pack size for several wolf packs on the Superior National Forest during 1972 were linked to a recent, continuing deer decline in northeastern Minnesota. Such decreases in pack size apparently stemmed, at least in part, from the inability of some packs to rear sufficient numbers of young in the presence of declining prey. Thus one might expect to find that the 1972 relative pup weights were significantly lower than in previous years. Table 2 suggests that this is true except for 1969 when all captured pups had low relative weights.

However, to more accurately assess the relationship between wolf pup weights and declining deer and wolf populations, three refinements in the analysis must be made. First, comparable distributions of capture dates must occur between years in order to properly compare yearly differences in relative weights. Since grossly underweight pups may die during late summer (Fig. 5) a trapping program conducted after late September could result in biased relative weights. Our relative weight data of 1971 and 1972 are comparable: four pups of 15 captured in 1971 and five of 16 captured in 1972 were caught after 7 October. Thus the increased proportion of pups of low relative weight in 1972 (Table 2) probably accurately reflects a lower nutritional status of pups during that year.

Second, the 1969 and 1972 data were basically from pups captured in the central Superior National Forest, whereas the wolves captured in 1970 and 1971 included other packs from eastern portions of the Forest. The area devoid of wintering deer is in the interior of the Superior National Forest where the wolf decline has begun (Mech, 1973). When pup data from only the interior packs (Jack Pine, Harris Lake, Quadga Lake, and Kawishiwi River) are considered, the mean relative weight of captured pups decreased from approximately 89 percent in 1970 and 1971 to 72 percent in 1972 (Table 5).

Third, comparing only relative weights of pups from different packs could give a false view of relative pup production unless total number of pups produced is also considered. Some packs may produce several surviving young, most of which may be underweight, while other packs produce only a few pups of normal weight. When this is considered, the severity of 1972 becomes most apparent. For example, the Jack Pine Pack raised seven pups in 1969, averaging 75 percent of standard, seven in 1970 averaging 81 percent, and an

TABLE 5.—*Mean relative weights of pups from four neighboring packs in the interior of the Superior National Forest. Because of the lack of independence of data from pups within a single litter, the varying number of pups sampled from different litters, and from single packs for different years, it was deemed that a standard statistical test of significance for these differences would be misleading.*

Year	Number of pups	Mean percent of standard weight
1970	10	90
1971	3	89
1972	9	72

unknown number in 1971 (only one was caught, weighing 69 percent of standard). However, in 1972 it apparently produced only four pups, and they averaged 67 percent of standard.

Not only were fewer pups and pups of low relative weight generally produced in 1972 by interior packs, but also the blood parameters of the 1972 pups from interior packs were significantly abnormal compared to previous years. From the accompanying paper featuring a study of various blood parameters in 32 of the same pups discussed in the present paper (Seal *et al.*, 1975), the following represents the comparative distribution of deviant blood parameters by year: 1970, one pup of 14 had one deviant parameter; 1971, two pups of seven had a total of four deviant parameters; and 1972, 10 pups of 11 showed a total of 29 deviant blood characteristics.

It should be apparent from our data that considerable variation in wolf pup development exists in Minnesota wolves within packs, between packs, and among years, and that relative pup weights are useful indices of the general condition of wolf populations, especially when supplemented with data on litter size and blood characteristics.

The extreme variation apparent in Minnesota wolf pups also indicates that caution is necessary in trying to classify wolves into age categories on the basis of size through ground or aerial observations during winter (Mech, 1966; Jordan *et al.*, 1967; Wolfe and Allen, 1973). Such attempts could be highly misleading because during years of good pup production some pups would be adult-size by winter, as indicated by our 32.7 kilogram (72 pound) pup (Male 2226) taken in October, thus leading to the impression that no pups were produced. In years of poor pup production, underweight pups might readily be apparent as smaller members of packs, leading to the incorrect conclusion that the production and condition of pups was good that year.

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