ECOLOGICAL STUDIES OF WOLVES ON ISLE ROYALE

ANNUAL REPORT

1982-83

ECOLOGICAL STUDIES OF WOLVES ON ISLE ROYALE*

Annual Report - 1982-83

(Covering the twenty-fifth year of research)

by

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Cover page drawing by Fred Montague, RFD #5, Monticello, Indiana 47960

SUMMARY

During the past year the Isle Royale moose population continued to recover from the low level reached in the late 1970's; the rapid decline of the wolf population in 1980-82 was reversed, and wolf numbers now approximate the average level of the 1960's. These fluctuations are consistent with our hypothesis of long-term cyclicity in this island predator-prey system (Fig. 1).

In 1982 pups were born to all 4 breeding females present in the population. Thirteen pups survived in 3 packs in winter 1983, bringing wolf numbers to 23. Territorial skirmishes continued, as the old "Gang of 4" (now West Pack II) claimed 2/3 of the island. The Harvey Lake Pack (HLP) was chased from its own kills by both adjacent packs. In one observed encounter the HLP alpha female was caught and attacked by the West Pack II, but she was then allowed to escape. Wolf kill rates were relatively low and carcass utilization high, reflecting low vulnerability of moose in winter. Also, the small size of some pups this winter may reflect a low food supply in summer. We believe that the present food supply will not be adequate to support continued survival and expansion of all 3 wolf packs.

The moose calf cohort in 1982 was large, although proportionately lower than the record cohort of 1981. The current population is estimated at 900 moose, including about 400 calves and yearlings. Recent cohorts have not been readily killed by wolves, even as calves in winter. Wolves are now preying primarily on moose born during the late 1960's. These moose, born during the last period of high moose density in 1965-70, exhibit a much higher incidence of arthritis than moose born during periods of lower density.

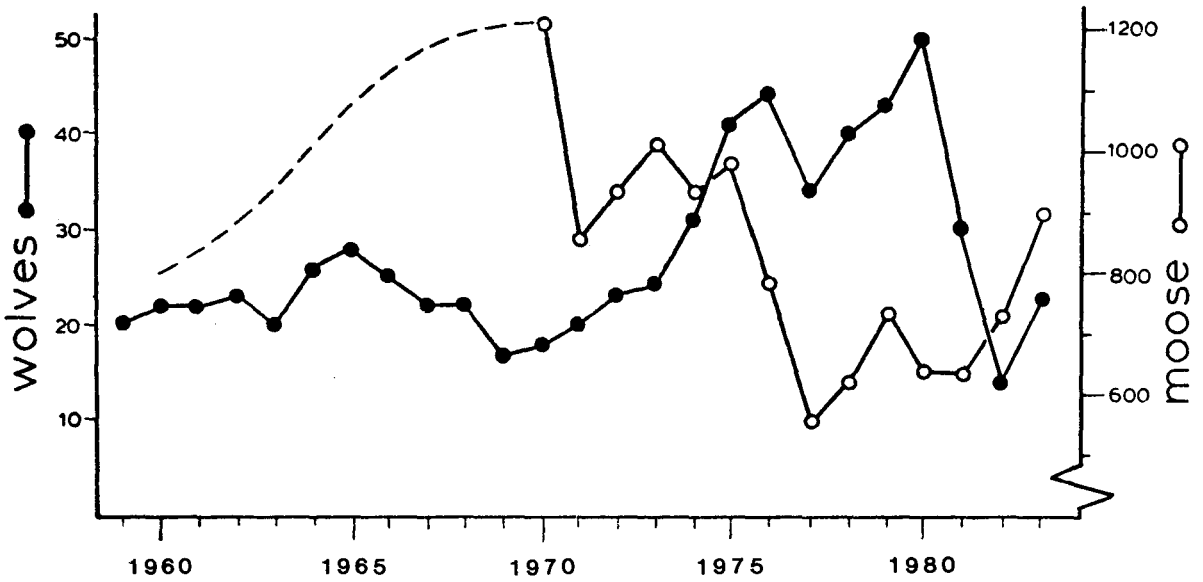


Figure 1. Isle Royale wolf and moose population levels, 1959-83.

PERSONNEL, SCHEDULES, AND PUBLICATIONS

Field work was conducted during June-August 1982 and mid-winter 1983, and an aerial survey was made in October 1982. Field personnel during summer field work in 1982 were scheduled as follows:

May 25 - July 31: Rolf and Carolyn Peterson et al.
May 25 - August 15: Kenneth L. Risenhoover
May 25 - August 28: Timothy G. Laske
June 17 - August 28: Patrick R. Charmley

Ph.D. student Ken Risenhoover initiated a study of foraging and anti-predator strategies in moose. He conducted the aerial survey of moose during October 21-23, with pilot Donald E. Glaser (Grand Rapids, Minn.)

The 1983 winter study extended from 18 January to 10 March. Pilot Donald E. Glaser, field assistant Douglas W. Smith, and Peterson were present during the entire period. Flying time totaled 107 hours. National Park Service personnel assisting during this period were Craig C. Axtell (18 January - 1 February) and Carol L. Maass (1-16 February). Supply flights were flown by the Ely Aviation Unit, Superior National Forest, U.S. Forest Service.

The following articles were published during the past year (reprints available upon request):

Peterson, R. O., J. M. Dietz, and D. L. Allen. 1982. Depletion of bone marrow fat in moose and a correction for dehydration. J. Wildl. Management 46:547-551.

Peterson, R. O., J. M. Scheidler, and P. W. Stephens. 1982. Selected skeletal morphology and pathology of moose from the Kenai Peninsula, Alaska and Isle Royale, Michigan. Canadian J. Zoology 60:2812-2817.

Peterson, R. O. and J. D. Woolington. 1982. The apparent extirpation and reappearance of wolves on the Kenai Peninsula, Alaska. Pages 334-344 in F. H. Harrington and P. C. Paquet (eds.). Wolves of the world. Noyes Publ., Park Ridge, N.J.

THE WOLF POPULATION, 1982-83

Following a 72% reduction in 1980-82, the wolf population now appears to have stabilized (Fig. 2). By 1983 wolf numbers had increased from 14 to 23 as only 4 adults died and 13 pups survived to mid-winter.

During the wolf population crash of 1980-82, at least 53 wolves died on Isle Royale. At no time during this period did an ice bridge to the mainland exist, so wolves could not have dispersed from the island. Intraspecific aggression evidently played an important role in the recent wolf decline. Carcasses of 2 adult wolves were recovered in summer 1982. Both had washed ashore on the south side of the island. One had numerous tooth puncture marks on its head. It is likely that both wolves were killed on open ice by other wolves. Five carcasses of adult wolves have now been recovered since 1980. Three were probably killed by other wolves, while 2 apparently died of old age/malnutrition. Both of the latter 2 wolves exhibited freshly-broken ribs, probably inflicted by moose.

Of the 4 wolf groups present in 1982, 3 were distinguished in 1983. The following pack names apply:

1982 winter	1983 winter
"Gang of 4"	West Pack II
Harvey Lake duo	Harvey Lake Pack
Daisy Farm duo	East Pack II
SW duo	not present

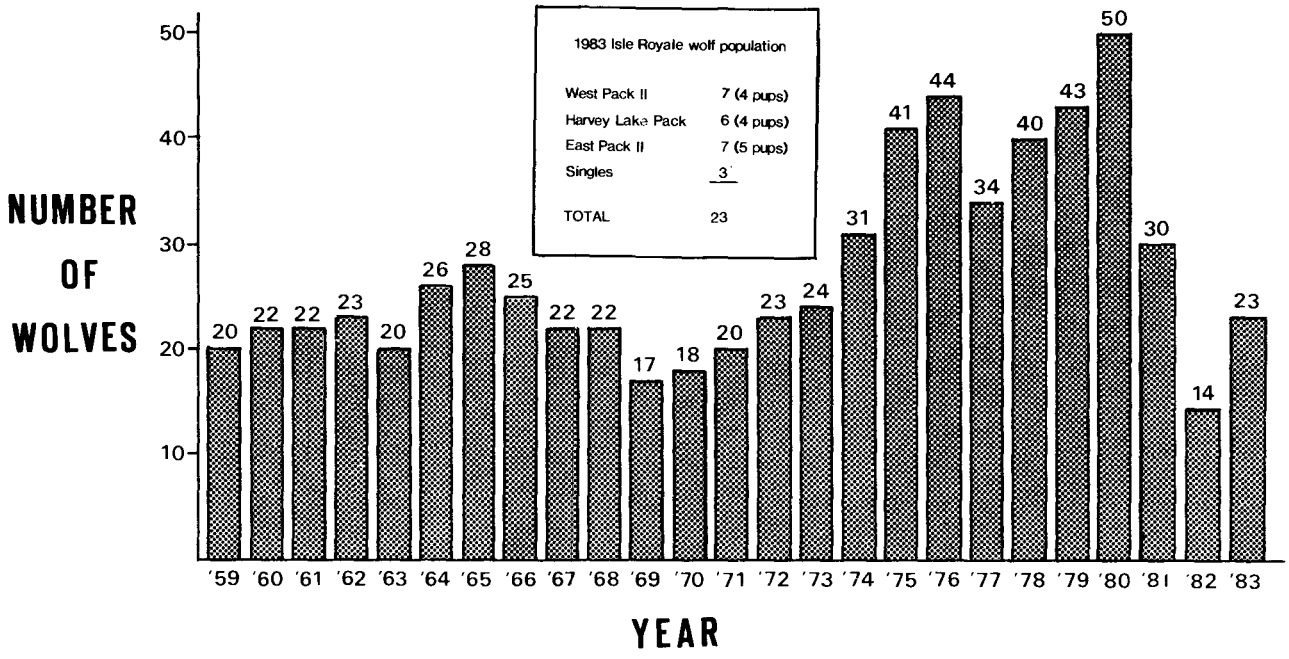


Figure 2. Isle Royale wolf population fluctuations, 1959-83.

Summer, 1982

Wolf pups were born to all 4 breeding females in 1982. Three of the litters were located in areas traditionally occupied by the West, East, and Harvey Lake packs, respectively. The fourth litter consisted of only 1 pup, very likely born to the SW duo. During the previous winter this pair was sedentary in the interior of the SW end of the island, virtually surrounded by the "Gang of 4", traveling the shoreline. The SW duo did not occupy an identifiable territory. Although the pup and at least 1 adult were alive in August 1982, the SW duo was not identified in winter 1983.

From howling we estimated that at least 9 additional pups were present in summer 1982 in the 3 territory-holding packs. Winter observations revealed that actually 13 pups survived from these 3 litters. In winter some of these pups were readily identified by their small size, suggesting suboptimal body growth rates in summer 1982. Analysis of summer wolf scats (Fig. 3) showed continued reliance on moose calves and beaver in summer. Wolf utilization of beaver continues to be significant, and incidence of beaver in wolf scats shows no correlation with beaver numbers (see page 18).

Wolf pups were about as numerous in summer 1981 as in 1982, yet only 0-2 of the 1981 pups survived to winter, and the population subsequently dropped to an all-time low. High mortality in the 1981 pups is still unexplained; disease, starvation, and intraspecific killing encompass virtually all likely causes of such high pup losses. For numerous reasons, starvation and killing by other wolves are unlikely explanations. Disease, perhaps parvovirus, remains a possibility, but exposure to this disease cannot be verified without handling some of the remaining wolves. A small number of foxes are being checked for evidence of exposure.

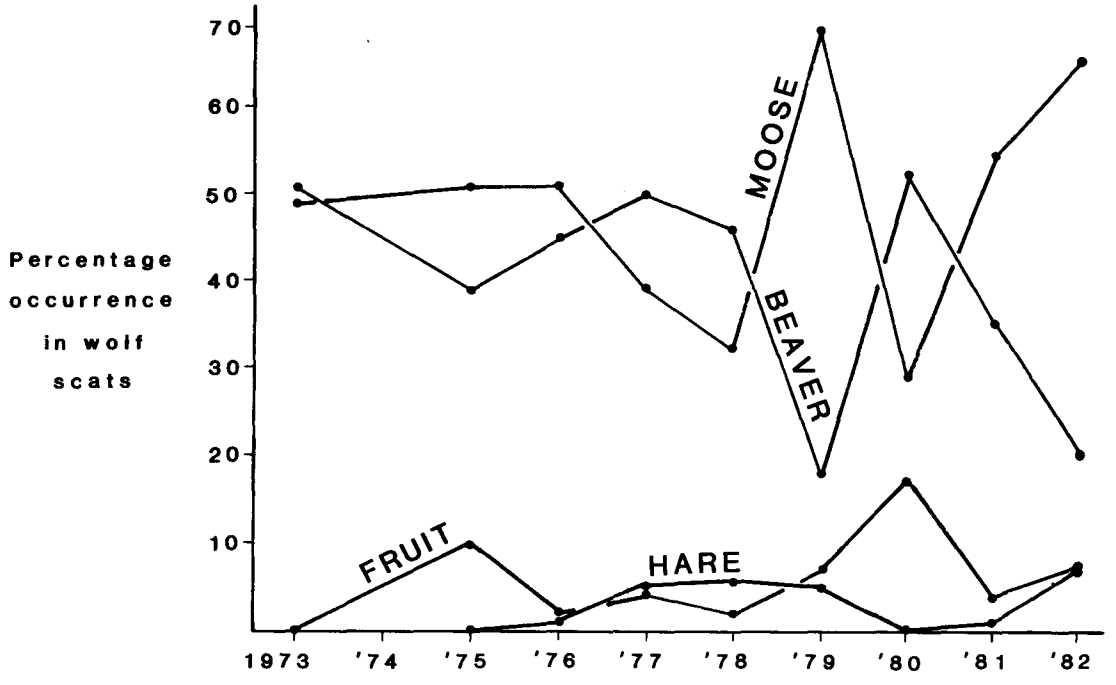


Figure 3. Summer diet of Isle Royale wolves, as indicated by percentage occurrence among food items in wolf scats.

Winter, 1983

Three packs totaling 20 wolves plus 3 additional animals comprised the 1983 population. The East Pack II and Harvey Lake Pack both consisted of a breeding pair plus 5 and 4 pups, respectively, while the West Pack II contained 3 adults and 4 pups (Fig. 4).

While spatial organization of packs stabilized somewhat in 1983, there remained considerable overlap among the 3 packs (Fig. 5). The West Pack II, which in 1982 traveled the entire island, has now settled in the SW 2/3 of the island. Harvey Lake Pack and East Pack II divided the remaining 1/3 of the island.

Courtship behavior in the alpha pair of both East Pack II and Harvey Lake Pack was observed on 14 February. On 23-24 February courtship behavior was observed in the West Pack II alpha pair and blood noted in urine from the alpha female. Copulation was observed in this pair on 1 March (Fig. 6).

On 1 March we observed the West Pack II follow tracks to a kill where the HLP was feeding. The HLP ran off without hesitation as soon as West Pack II emerged at the kill site. The West Pack II, led by the alpha pair, continued to chase the HLP. During the chase the West Pack II overtook but did not attack a HLP pup. Finally, the HLP alpha female was caught after a mile-long run. For about 2 minutes the 6 wolves in West Pack II crowded around and attacked the HLP alpha female, who snapped defensively and writhed on her sides and back. Then, suddenly, the pack ceased the attack and the HLP female quickly and with very submissive posture left the area. Subsequent ground-tracking revealed only a few drops of blood at the scene of the attack, and the tracks of the HLP alpha female soon joined those of other pack members. West Pack II remained in the area the next day, our last day of field work, and the HLP could not be located. We believe the most plausible explanation for the West Pack II ceasing their attack on the HLP female is that she was a relative.

The average predation rate for all 3 packs in 1983 was 1 kill/pack/ 9.1 days, considerably below the long-term average (Table 1). Daily food consumption ranged from 4.5 kg/wolf in the West Pack II to 3.8 kg/wolf in the East Pack II. The 3-pack average of 4.1 kg/day/wolf indicates moderate kill rates. Wolf travel rates were lower than average in 1983, perhaps because shoreline ice was generally absent.

The 1983 skirmishes, together with the history of the Isle Royale wolf population, suggest that the current food base is not sufficient to support 3 large wolf packs. The Harvey Lake Pack appears to be the least secure group. This pack has existed since 1980 but has not yet successfully raised any young to the age of 18 months. Previously this pack inhabited the middle of the island where few moose were found, but this year the HLP moved east and was able to exploit moose concentrations formerly outside its range. Although food availability for the HLP was similar to the other packs, the HLP traveled about 50% farther between kills than West and East packs.

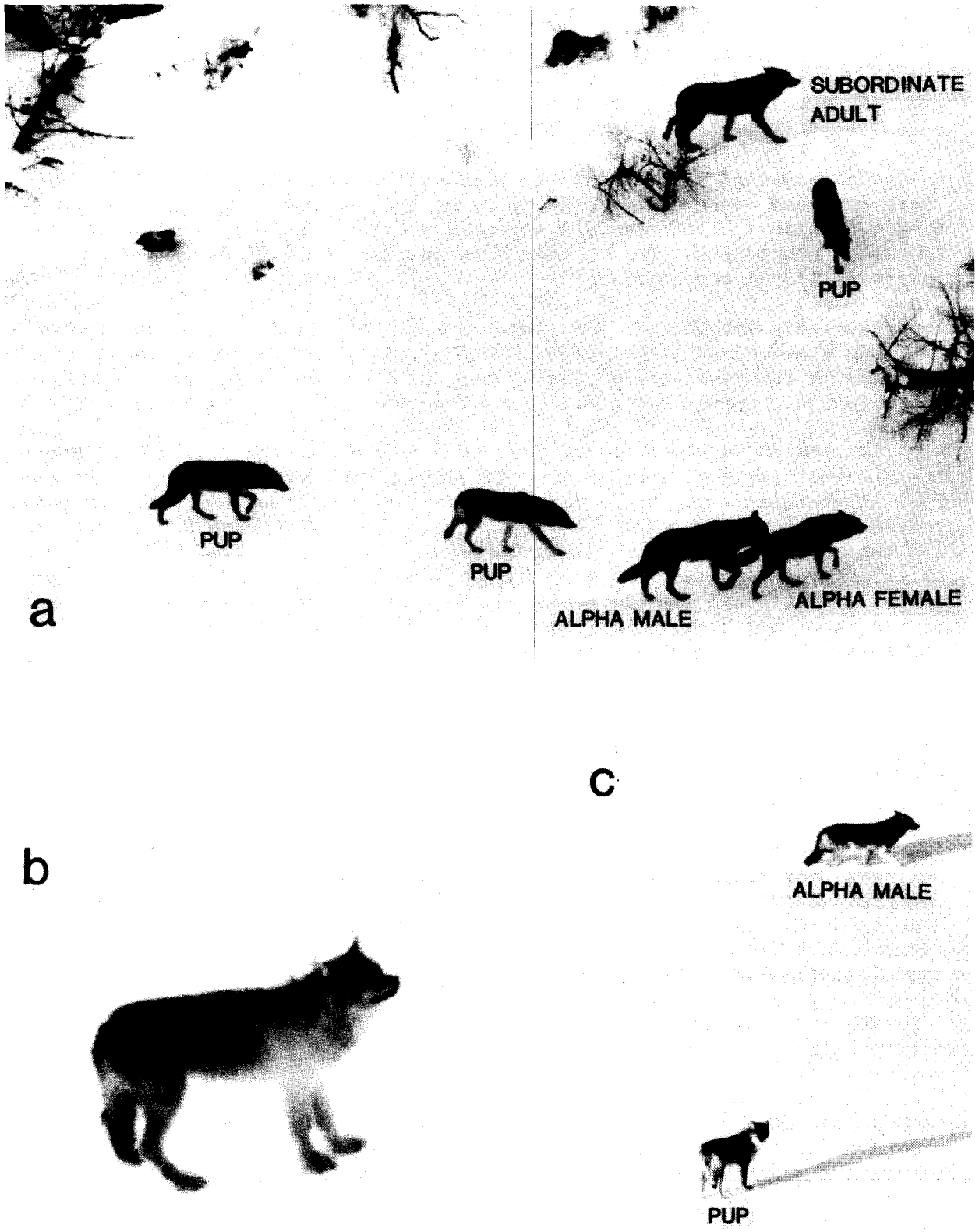


Figure 4. Isle Royale wolves, 1983. a) West Pack II, b) West Pack II pup, c) Harvey Lake Pack wolves.

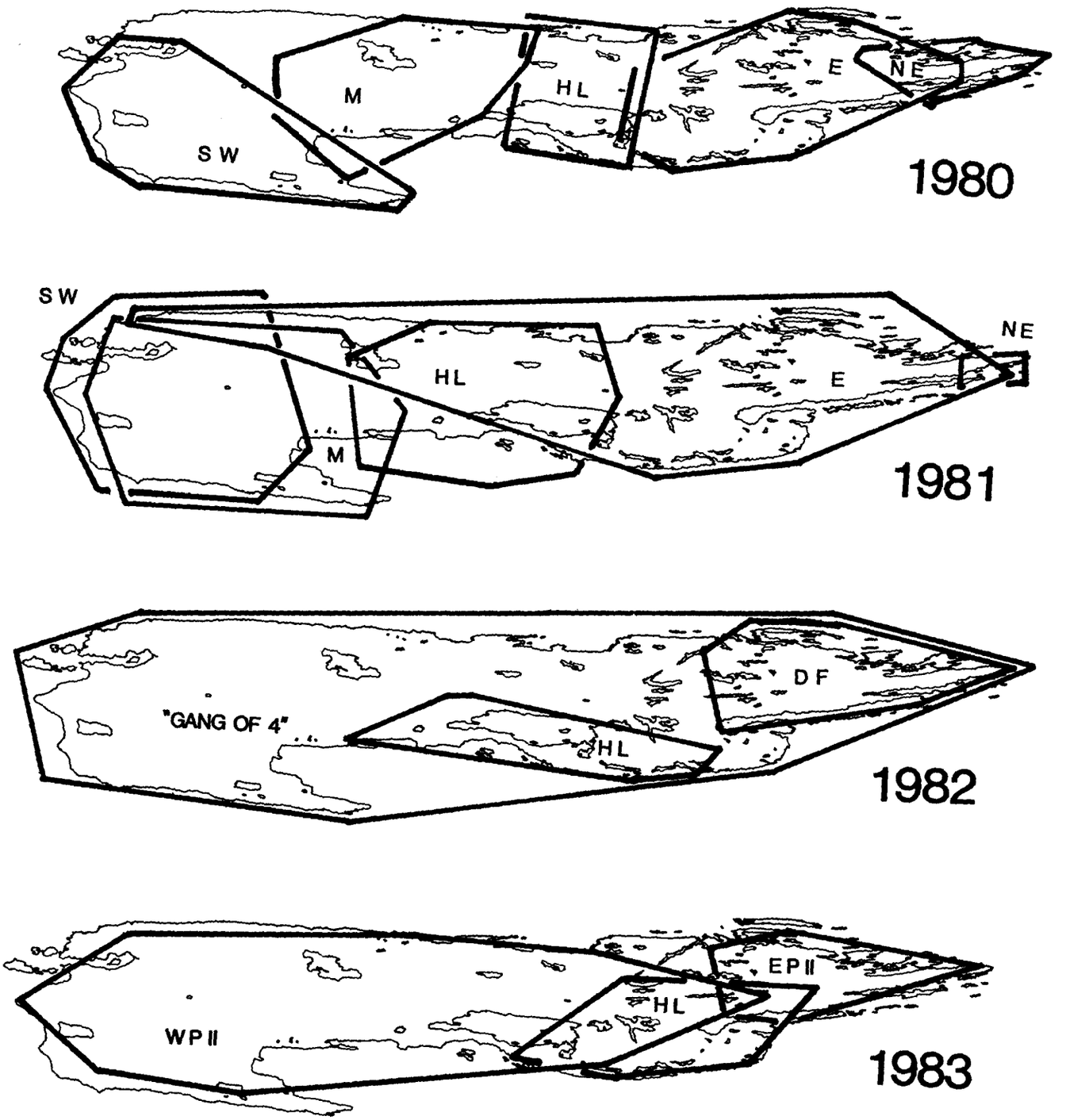


Figure 5. Wolf pack movements at Isle Royale, 1980-83.

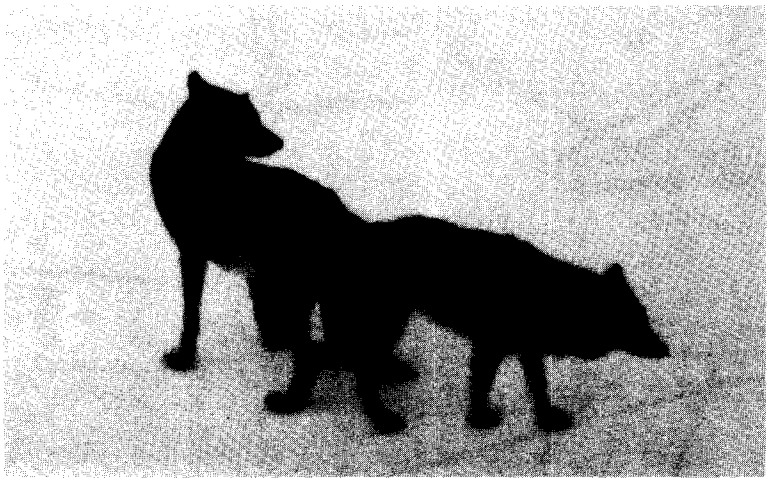


Figure 6. Copulation in alpha pair, West Pack II, 1 March 1983.

Table 1. Travel and kill rates for Isle Royale wolf packs.

	West Pack II 1983	Harvey Lake Pack 1983	East Pack II 1983	All packs, 1971-82 average (sample size)
Pack size	7	6	7	9.0 (29 packs, 12 yrs)
Travel rate (km/day)	7.7	6.6	4.2	10.7 (8,768 km/819 pack-days)
Kill interval (days)	7.8	10.4	10.5	5.0 (1,258 pack-days/251 kills)
Travel between kills (km)	45.1	65.5	41.4	39.4 (7,918 km/201 kills)

The stability of the Isle Royale wolf population in the 1960's was impressive, prompting an important question: Why didn't wolves increase along with the moose in the 1960's? The current 3-pack population will surely provide a test of the hypothesis that wolf numbers in the 1960's were limited by the social dominance of 1 large pack, preventing a wolf increase in spite of a sustained increase in moose density. The alternate hypothesis is that wolf numbers were limited by food supply: low moose vulnerability during the moose increase of the 1960's limited expansion of the wolf population, regardless of its organization. The latter hypothesis will be disproved if wolves continue to recover significantly beyond present numbers.

It is common practice for wildlife managers and researchers to estimate prey loss to wolves by multiplying wolf density by an assumed "per wolf" predation rate. Actual kill rates by wolves are rarely measured, so data from Isle Royale provide a valuable opportunity to assess factors that determine the number of moose killed by wolves. The correlation between measured kill rates and wolf density on Isle Royale is significant only at $\underline{P} < 0.20$, and the correlation coefficient is very low ($r^2 = 0.21$). That is, one cannot predict or accurately estimate the number of moose killed by wolves simply from knowledge of the number of wolves present. For a given wolf density (e.g., 1 wolf/25 km^2), the 95% confidence interval for the estimated kill rate is 58% of the estimate itself. We propose that moose vulnerability, not wolf density, largely determines the magnitude of loss to wolves. The gradual decline in wolf kill rates on Isle Royale in the late 1970's is best explained as a result of progressive removal of vulnerable moose from the population. In fact, wolf kill rate is better correlated with time ($\underline{P} < 0.005$, $r^2 = 0.87$) than wolf density (Fig. 7b), in accordance with our hypothesis.

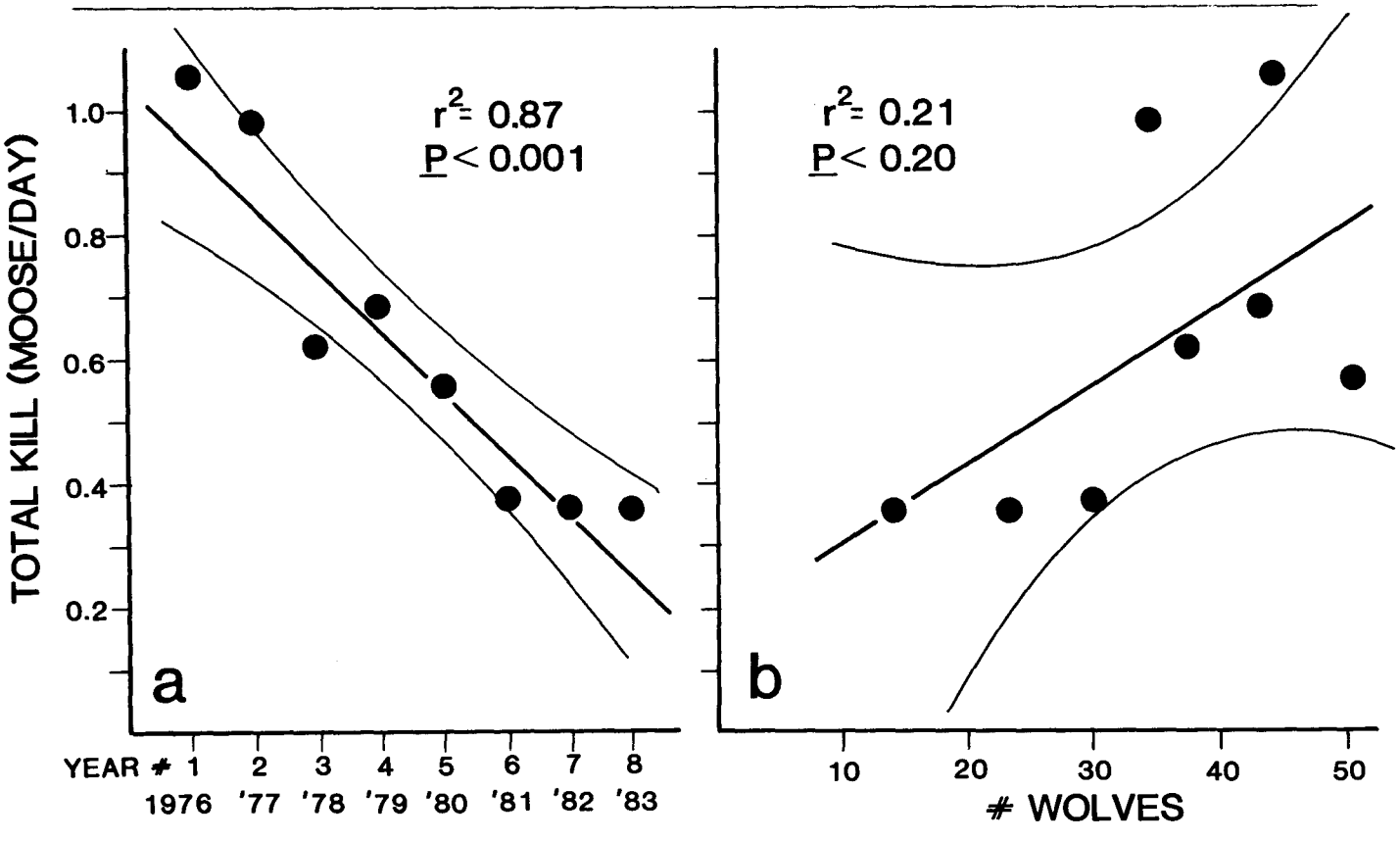


Figure 7. Correlations between (a) wolf kill and time, 1976-83 and (b) wolf kill and wolf density. Regression lines and 95% confidence intervals are shown.

THE MOOSE POPULATION, 1982-83

Accurate data on moose population fluctuations are required for a refined understanding of wolf-moose interaction. We currently use several independent methods of estimating moose density: a summer ground index, a winter aerial index, and a stratified sampling in winter of 12-15% of the island using intensive circling over small plots. Estimated absolute recruitment and mortality, combined with data on population composition, provide an additional check on recent annual estimates.

1983 census

A stratification survey prior to this year's winter census revealed that moose were not highly concentrated as usual in coniferous habitats along shorelines. Instead, moose were more widely distributed over both ends of the island, with the 1936 and 1948 burns in the middle of the island little-used. After 1 February, an obvious shift to conifer cover occurred as the frequency of moose observations from the survey aircraft dropped by 50%. Fortunately, all plots were counted before 1 February, when observability of moose was uniformly high. Random plots on the main island covered 13% of the land area, and a complete count was made of all small islets, where moose density is usually 3-4 times higher than on the main island.

The 1983 census estimate and 95% confidence interval was 900 $\pm$ 195 moose. Over a quarter of the island supported virtually no moose (Fig. 8), while 85% of the moose were estimated to occur on 44% of the land area (the 2 high-density strata plus small islands). The 1982 estimate was 729 $\pm$ 209 moose. Although confidence intervals overlap, estimated recruitment and mortality suggest a net increase of about 150 moose since 1982.

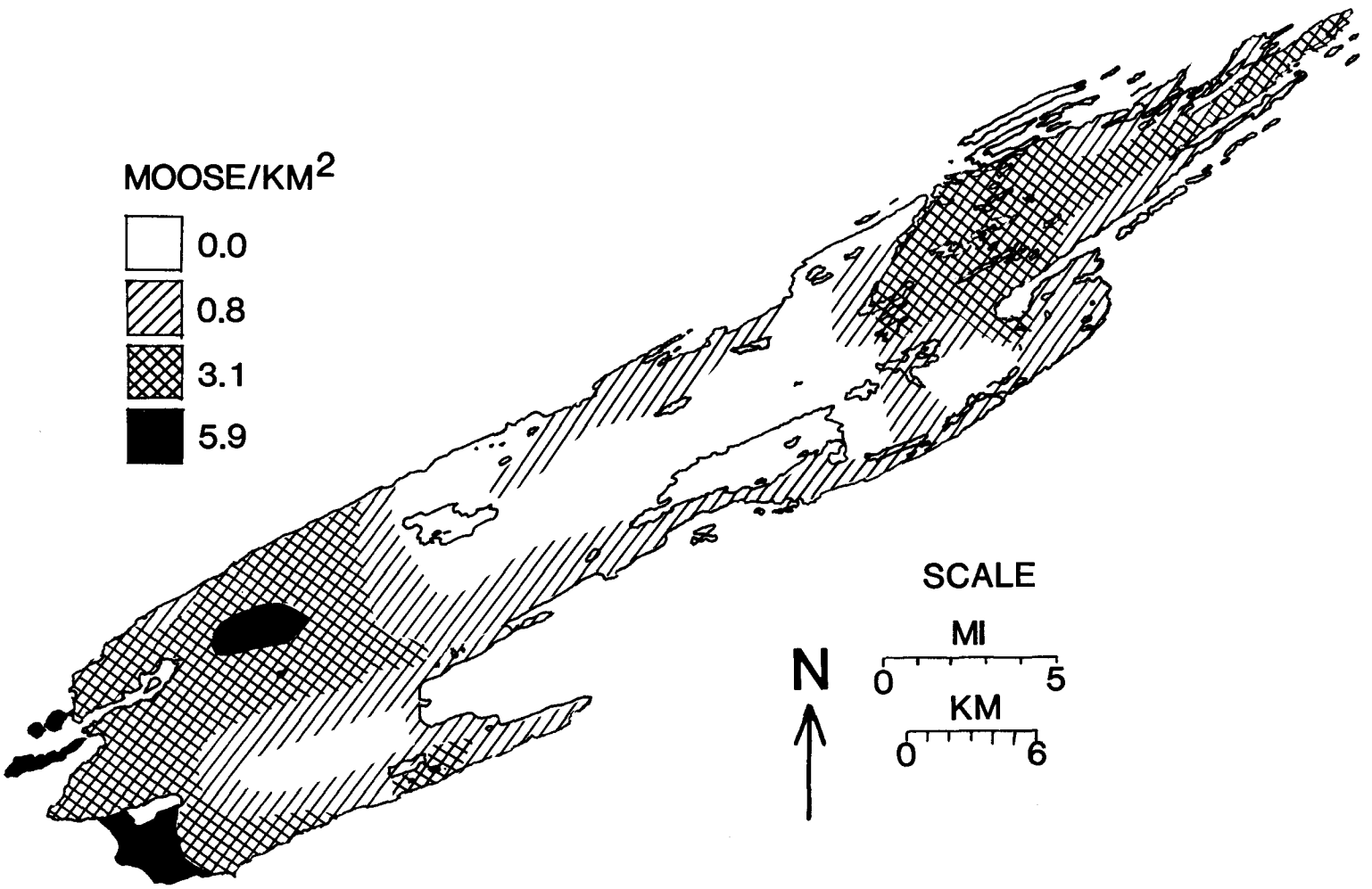


Figure 8. Midwinter moose distribution on Isle Royale, January 1983.

Survival of 1981 and 1982 calves

Aerial surveys in October (after leaf-fall) and in midwinter have confirmed high calf survival during the last 2 years. During 1972-80 calf abundance in October averaged 23 calves/100 cows (range: 10-37). In 1981 we found 61 calves/100 cows and in 1982, 37 calves/100 cows (44 when corrected for unproductive yearlings). The proportion of calves on census plots in January was 27% in 1982 and 24% in 1983. Twin calves were virtually non-existent in winter before 1982, but 6 sets were noted in 1982 and 5 in winter 1983. All current indicators point to high recruitment, on the order of 200 calves during each of the past 2 years.

The 1981 cohort has continued to survive at a high rate as yearlings. During the October survey in 1982 we tallied as many yearlings as calves (yearlings were judged on antler criteria, with an even sex ratio assumed.) Subsequent observations in winter suggested that we may have underestimated yearling bull abundance using our previous antler criteria.

High yearling moose abundance was further indicated by an unusually high occurrence of small-antlered bulls in winter 1983. During the previous 10 years only 7 antlered animals were recorded in winter. In 1983 alone we observed 39 antlered bulls-- none were spike bulls, most had forked antlers, and a few had up to 4 tines on each antler (Fig. 9). We assume that these antlered animals were yearlings, representing the abundant 1981 cohort. Superior antler growth probably reflects rapid body growth in these moose. Metatarsal length at 9 months of age, largely determined by *in utero* growth rate, averaged 340 mm in the 1981 cohort ($N = 4$), compared to a mean value (and standard deviation) of 325 $\pm$ 12 mm for moose born in the early- to mid-1970's. Although antlers were being dropped during observations in the last half of January, antlered bulls comprised 10.6% of 508 moose observed; with an even sex ratio assumed, a minimum of 21% yearlings was present in January 1983. Thus 45% of the estimated 900 moose present in 1983 were born in 1981 or 1982.

Figure 9. Yearling bull moose born in 1981. Superior antler development and large body size characterize the 1981 cohort.

Moose mortality, 1983

Remains of 24 moose were located during the 1983 winter study (Fig. 10). Except for one malnutrition death, all were killed by wolves. Island-wide loss to wolves during the 1983 study period was 0.36 moose/day, identical to the 1982 loss rate. Projected over 6 months from 1 November through 30 April, this would produce a relatively low loss of 65 animals.

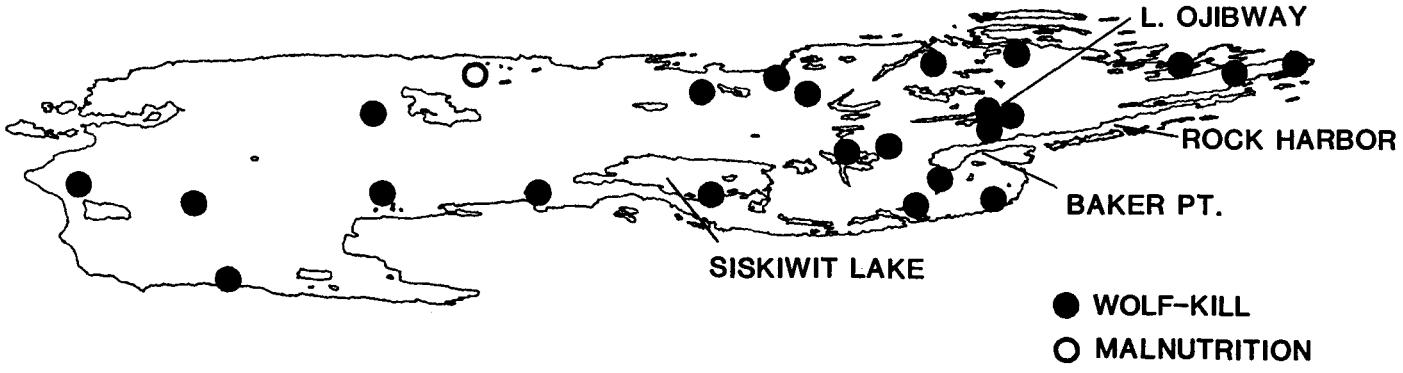


Figure 10. Distribution of all moose carcasses located during 1983 winter study, together with place names mentioned in text.

The age distribution of moose dying in recent years on Isle Royale is skewed heavily toward old moose (Fig. 11), animals born during the 1960's. Degenerative joint disease (osteoarthritis) has become an increasingly important debilitating factor for aged Isle Royale moose. Among moose dying during 1958-74, the incidence of arthritis among males and females greater than 7 years old was 39% and 11%, respectively. Since 1975, however, arthritis has been found in 71% and 55% of the males and females, respectively (Fig. 12). A possible explanation for this remarkable increase is that moose born during a period of high moose density in the late 1960's were more likely to develop arthritis later in life because of adverse developmental effects early in life.

Nineteen wolf-killed moose were examined thus far from 1983 (Fig. 13). Three were calves and the rest were old adults. Thirteen of the 16 wolf-killed adults exhibited either arthritis or periodontitis.

One observation in 1983 indicated the strong cow-calf bond that exists among moose. The East Pack II, consisting of an alpha pair and 5 pups, fatally wounded a calf moose but were unable to drive the calf's mother from the carcass. After spending a day in the vicinity, the wolves left and did not return for more than a week. The cow moose continued to defend the carcass of its calf from foxes and ravens for 48-60 hours. By the time the wolves returned to consume the calf, foxes had eaten and cached about half of the carcass.

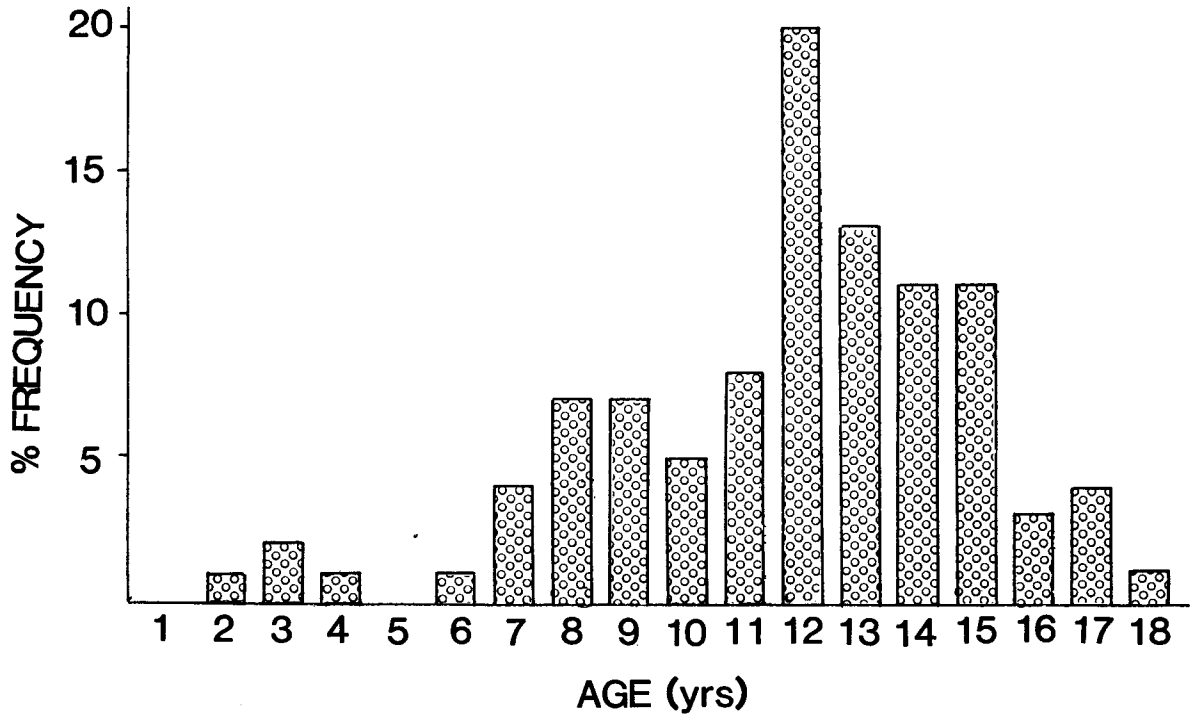


Figure 11. Age distribution of moose (> 1 yr old) dying on Isle Royale, 1979-82.

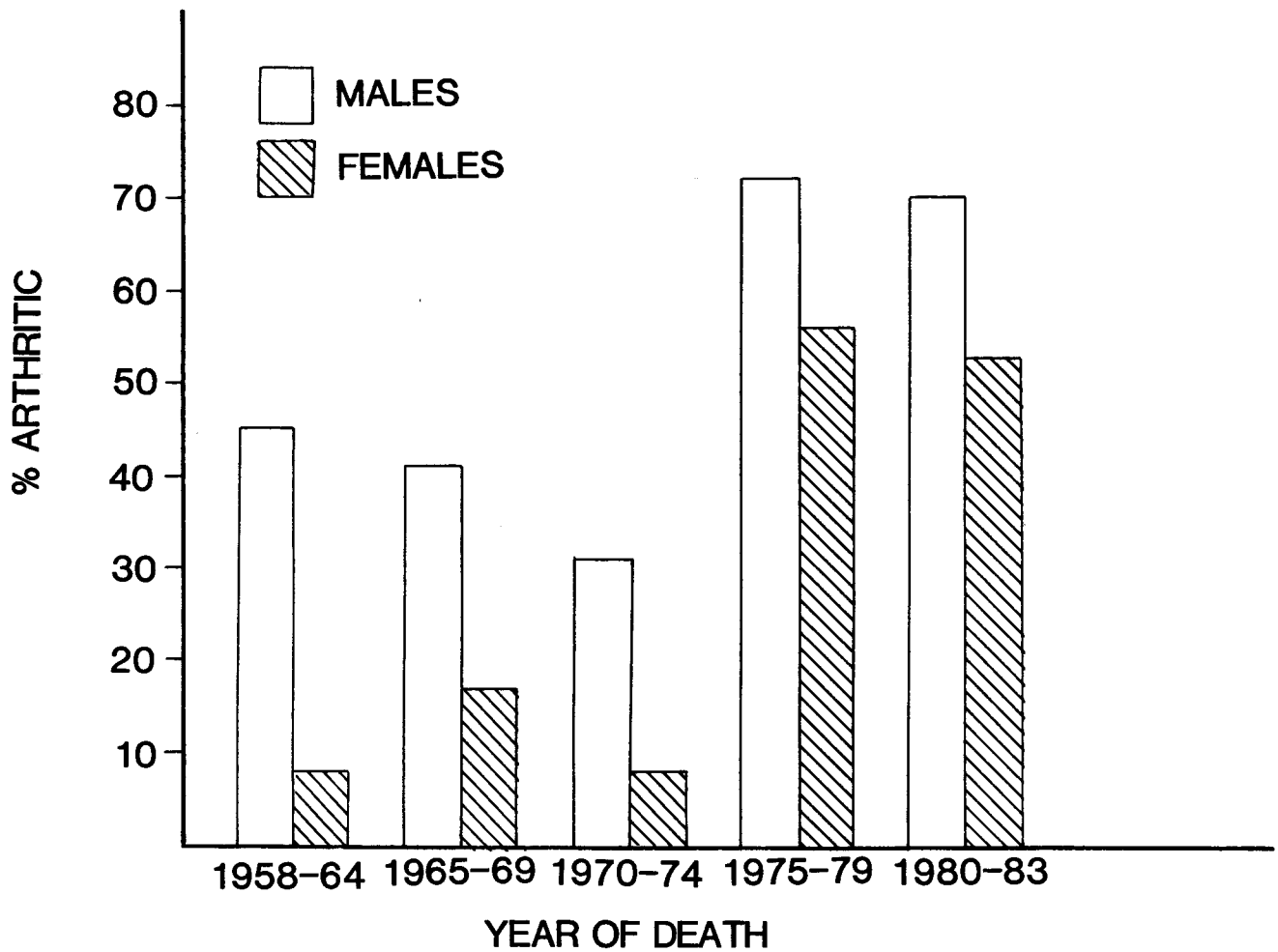


Figure 12. Incidence of arthritis among Isle Royale moose (> 7 yrs old).

A consideration of reproductive strategies in ungulates (e.g. Geist, V. 1982. Behavior. Pages 219-277 in J. W. Thomas and D. E. Toweill (eds.), Elk of North America. Stackpole Books, Harrisburg, Penn.), suggests different strategies by which males and females maximize reproductive success. Geist's hypothesis predicts that females should behave so as to maximize survival of offspring, even at the expense of feeding on poor quality forage. Males, on the other hand, should segregate from females, especially cows with calves, and seek high quality forage that will allow maximum body and antler growth.

The above predictions are borne out by a preliminary analysis of the spatial distribution of dead moose at Isle Royale. Moose calves were found primarily along the shoreline, probably near their birth site, where water provides the best means of escaping wolves during summer. Cow moose (almost all without calves) were more randomly distributed in the island's interior, and bulls appeared primarily in the interior, especially where cows were not found (Fig. 14). This suggests that cow moose will predominate among adults killed near the shoreline of the island (where most mid-winter wolf kills are found), a previously-unexplained phenomenon that was noted almost 10 years ago.

Figure 13. Typical utilization of wolf-killed moose, 1983.

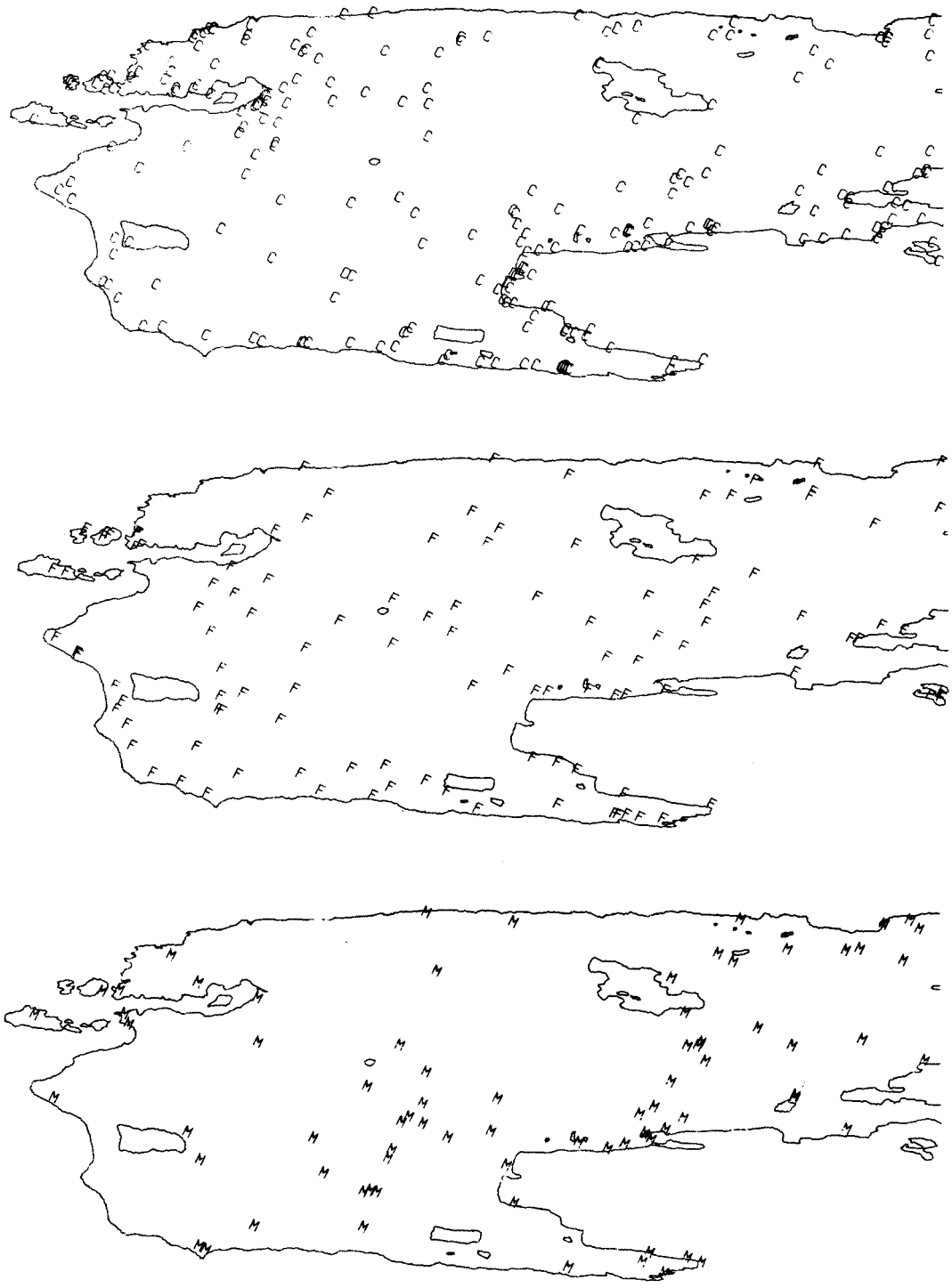


Figure 14. Spatial distribution of dead moose at Isle Royale. C = calves, < 1 yr old; F = females > 1 yr old, almost all unaccompanied by calves; M = males > 1 yr old.

WINTER WEATHER AND SNOW/ICE CONDITIONS

Warm and cloudy weather characterized the 1983 winter study period. Average minimum temperature was the highest since 1963, when record-keeping began. After mid-February temperatures hovered near freezing and for 5 days beginning 3 March temperatures remained above freezing and rapid snowmelt began. A supply flight scheduled for 28 February was unable to reach the island for 11 days and our departure was delayed 6 days. In seven weeks there were only 8 completely sunny days.

Precipitation during the winter study was 3.2", including 1.2" of rain during 3-7 March. Prior to the rain, maximum snow depths during the study remained at 50-60 cm. Strong freeze-thaw surface crusts persisted during the last 2 weeks of February. In the absence of this crust wolves were hampered considerably by soft snow during several observed encounters with moose.

There was almost no shoreline ice in 1983 and no ice bridge formed to the mainland. There were no ice bridges to most islets surrounding the main island and none were visited by wolves.

OTHER WILDLIFE SPECIES

In spite of the exceptionally warm winter weather, we did not observe a high level of beaver activity-- none were recorded among wolf-kills. In winter 1983 beaver activity was noted at 6 sites and otter activity at 5 sites.

Fox observations were relatively low (Fig. 15), probably because there was no shoreline ice and fresh wolf-kills were infrequent. Both foxes and ravens utilized abundant mountain ash fruit in January.

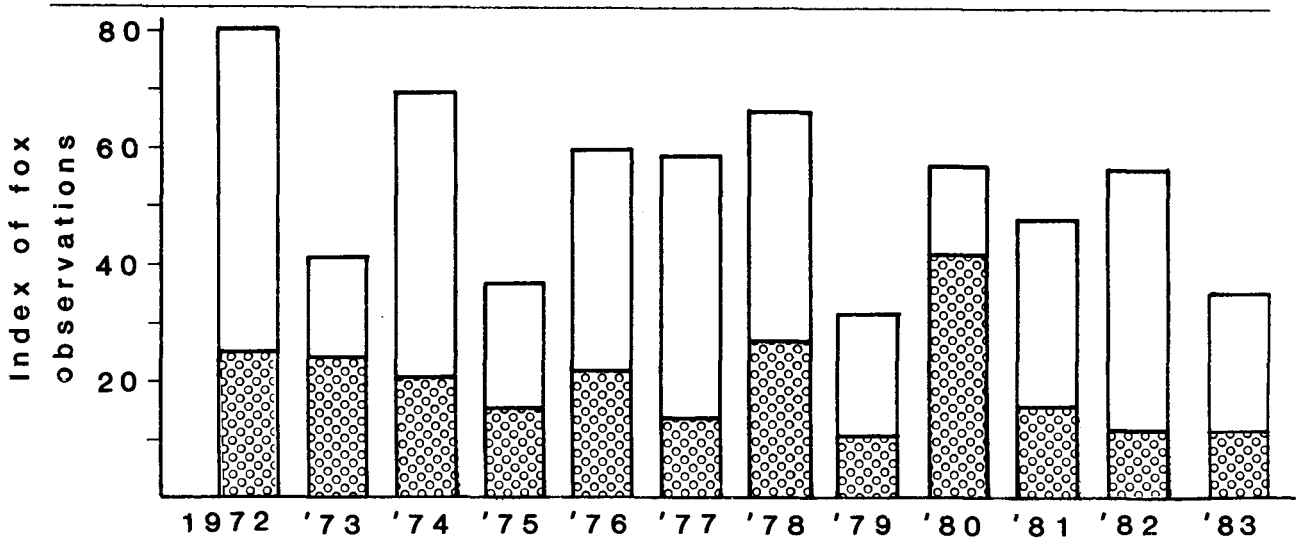


Figure 15. Midwinter fox index, 1972-83. The lower bar is the number of foxes seen > 1 km from a moose carcass/100 hrs flying time, while the upper bar is the sum of the maximum number of foxes seen on each moose carcass.

Beaver studies, 1982 (special supplement by P. C. Shelton)

Recent fluctuations in beaver numbers at Isle Royale suggest an important influence of wolf predation in beaver population dynamics. The recent history of beaver roughly parallels that of moose. Beaver increased during the 1950's and '60's after a reduction that may have been caused by a tularemia epizootic. A total count in 1974 revealed 286 colonies with food piles (Table 2). By this time the incidence of beaver in the summer wolf diet had increased and the wolf population was expanding rapidly. Subsequent counts in 1978 and 1980 revealed a steady decline to 45% and finally 29% of the 1974 level, respectively. The decline was most significant for stream-dwelling beaver, and we have hypothesized that the increase in wolf predation caused the decline. Total counts of beaver colonies are now conducted biennially. The 1982 aerial count was of special interest since it was the first since the wolf population crash.

During the periods 25 May - 3 June and 12-18 October, 1982, Philip C. Shelton surveyed beaver activity and populations. Charles R. Davis assisted in the spring trip, which consisted of reconnaissance by small boat, canoe, and on foot of 27 active sites located from the northeast end of the island to the wouthwest end of Siskiwit Lake. The October trip included live-trapping 5 beavers, ground visits to 9 active sites, and most importantly, the aerial survey of the entire island, counting colonies with fresh food piles or other signs of current activity. Fred Stroble of Shawano Flying Service piloted the float-equipped Super-Cub for the aerial count, which was done during 13 hours flying time, 14-16 October. Since 1962 all aerial surveys of Isle Royale beaver have been done by Shelton, with no changes in pilot since 1974.

Table 2. Aerial counts of beaver colonies, Isle Royale National Park.

	Colonies with Food Piles					Sites with Fresh Cutting or Fresh Mud on House or Dam	Total Sites with any Sign of Activity
		Number (%) by Habitat*					
Year	Total Number	Stream	Lake	Harbor	1936 burn		
1962	125	84(67)	26(21)	15(12)	43(34)	-	-
1974	286	251(88)	24(08)	11(04)	102(36)	30	316
1978	129	99(77)	19(15)	11(08)	48(37)	27	156
1980	83	58(70)	17(20)	08(10)	18(22)	39	122
1982	125	93(74)	24(19)	08(06)	31(25)	28	153

*Stream, lake, and harbor proportions add to 100.

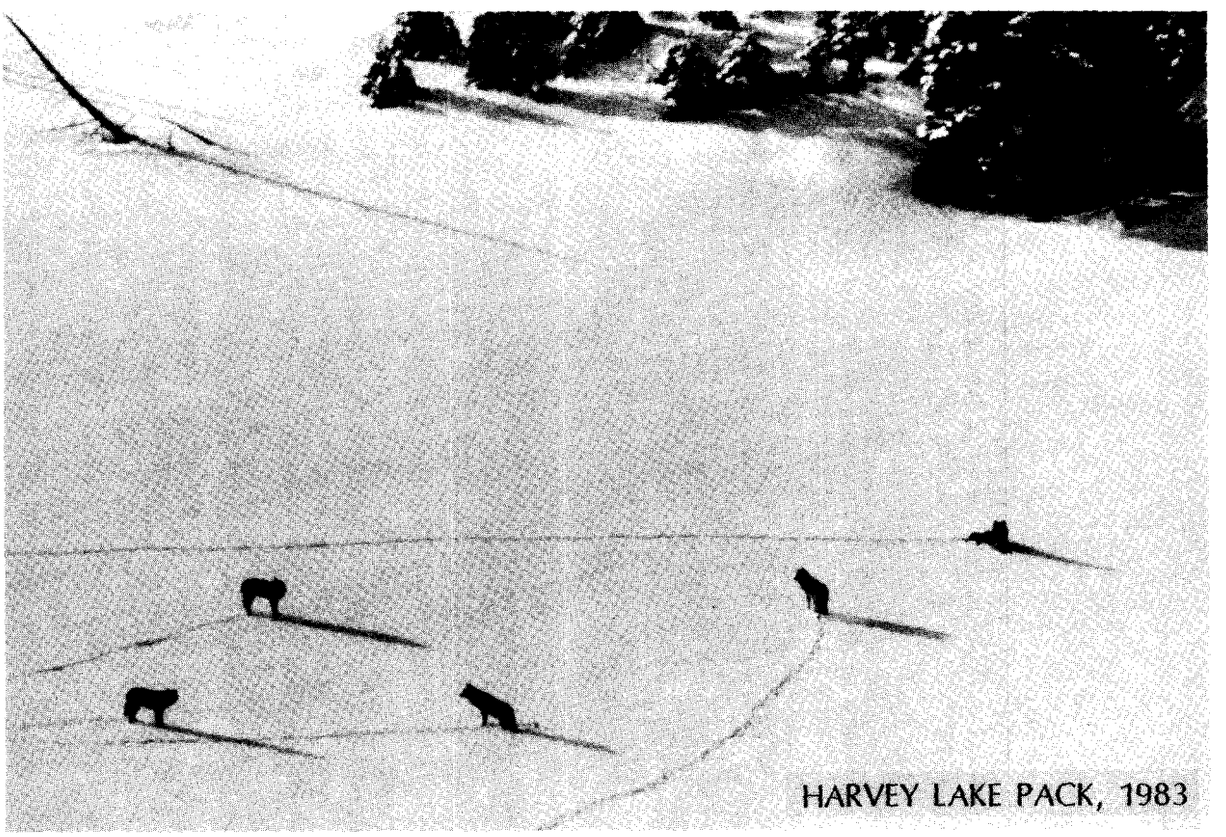
The 1982 results indicated a recovery of beaver colony numbers to approximately the same level as 1978 and 1962. Favorable weather conditions and sufficient leaf fall for good visibility allowed a satisfactory aerial count. Examination of the data by habitat reveals that the number of harbor colonies remained the same as in 1980 (8 sites). Intensive continuous use for 3 to 5 decades has resulted in extreme depletion of food resources in some of these sites, and at two long-established colonies in Rock Harbor (Dollar Bay and Mott Island) human activities may have discouraged beaver reoccupation. Lake colonies increased in the same proportion as the total, and stream colonies increased slightly in percent of the total. The slight increase in percentage of colonies in the 1936 (22 to 25%) suggests that food depletion at these sites may be more complete than in the older forest types.

The number of sites with signs of activity other than a food pile dropped back to the 1978 level from the high number of 1980, when it was suspected that such sites represented colonies broken up by intensive wolf predation. The subsequent decline in wolves may have allowed scattered beavers to find mates and establish larger colonies.

Live-trapping was more successful in 1982 than in 1980. Five beavers were captured in 14 trap-nights at two colonies, Lake Ojibway and Baker Point. Only two beavers were caught in 26 trap-nights in 1980. Four of the beavers caught in 1982 were kits, three at Baker Point and one at Lake Ojibway, and an adult female was handled at Lake Ojibway. All were in good health and of normal weight. Two of the Baker Point kits had parasitic beetles on their rumps (6 and 1); no beetles were found in combing the rumps of the other three animals. There is no reason to infer any change in parasite load from these observations.

During the May-June trip 21 sites which were active in 1980 were visited; 18 of these were still active. During this period 9 sites were found active that were not known to have been active in 1980. The ratio of active sites in 1980 to 1982 from these figures (1:1.3) is close to the ratio shown from the aerial counts (1:1.5).

No extensive data were obtained on beaver-food relationships, but aspen (preferred food) was being used at 14 of 27 active sites in May and June and at 5 of 9 active sites visited in October. In most of these cases only one or a few trees were cut. Availability of aspen, both old growth and also younger trees in the 1936 burn, continues to decline. Birch was used at 18 of 27 sites in May and June and at 5 of 9 sites visited in October. Although observations were not quantified, cutting was also noted at several sites observed during the aerial survey in October.



HARVEY LAKE PACK, 1983