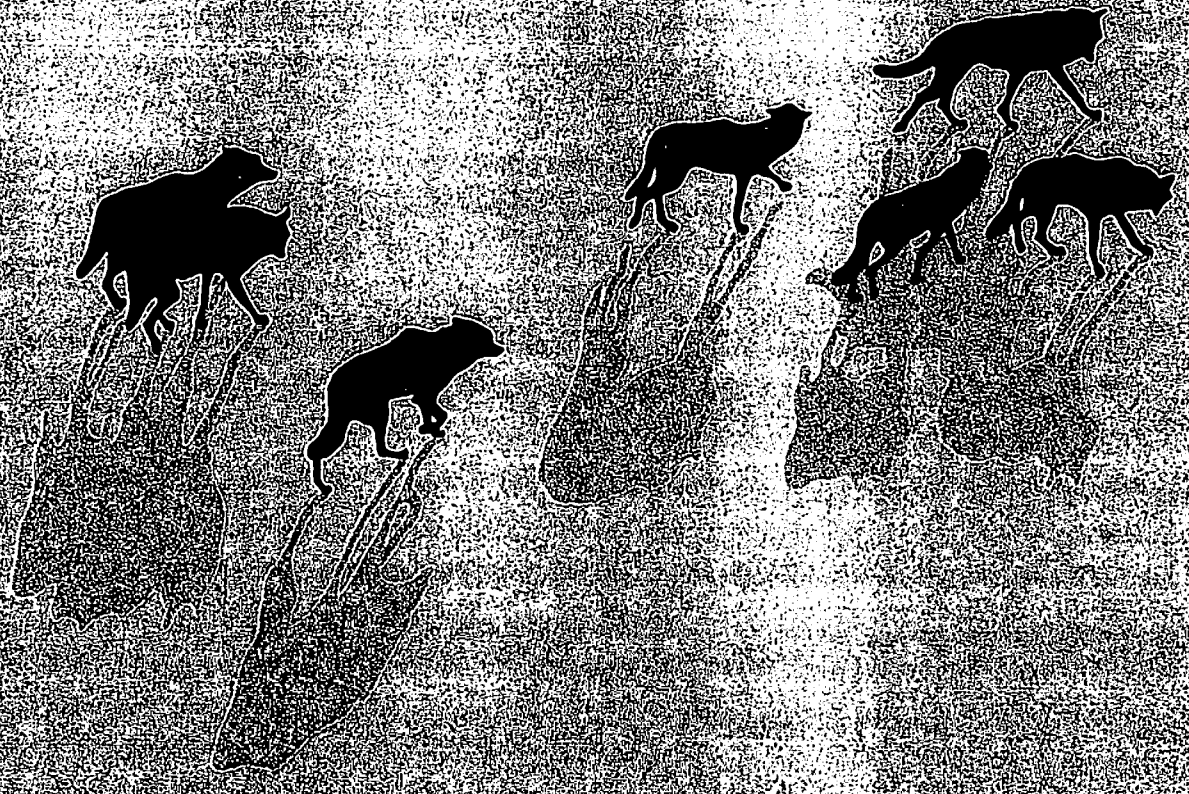
ECOLOGICAL STUDIES OF WOLVES ON ISLE ROYALE

ANNUAL REPORT

1981-82



ECOLOGICAL STUDIES OF WOLVES ON ISLE ROYALE*

Annual Report - 1981-82

(Covering the twenty-fourth year of research)

by

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

SUMMARY

Abrupt changes were observed during the 24th annual study of Isle Royale wolves and moose. The wolves declined further from their recent historic peak and reached the lowest level documented for the species since its arrival on Isle Royale in the late 1940's. Moose calf abundance was the highest ever documented at Isle Royale and about three times higher than the average of recent years.

Two years ago, the record-high wolf population of 50 included five territorial packs, with territory boundaries generally honored. Food stress was obvious, however, and pack size was steadily declining. A year later, with 30 wolves present, the food situation seemed no better and packs often trespassed into neighboring territories. In 1982 only 14 wolves remained, and the dominant pack of 4 wolves claimed almost the entire island. Three other breeding pairs and 4 single wolves were found, but these were actively tracked and likely chased by the dominant "Gang of Four." We surmise that direct killing of wolves by other wolves contributed to the rapid wolf decline, although we found no dead wolves in 1982. We witnessed a complete turnaround in wolf food availability by 1982, and all groups of wolves had ample food.

Changes in the moose population, probably prompted by the wolf decline, were no less dramatic. Swelled by almost 200 calves, the moose population increased to over 700 in 1982. A substantial rebounding of moose is certain if subsequent cohorts of calves match that born in 1981.

If wolves exhibit a moderate rebuilding of numbers within a couple years, as we expect, this predator-prey system should soon approximate that described 25 years ago. Accumulating evidence suggests that we are witnessing a predator-prey cycle with an extended period of fluctuation.

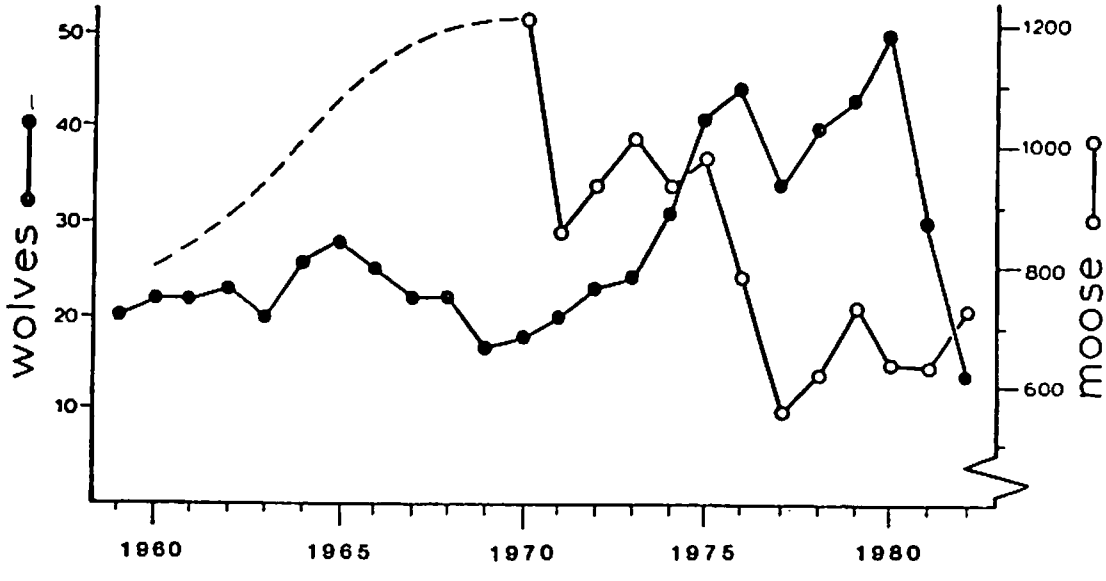


Figure 1. Isle Royale wolf and moose population levels, 1959-1982.

PERSONNEL AND SCHEDULES

During 1981-82 a master's degree was completed by Philip W. Stephens, whose thesis was entitled "Population trends of Isle Royale moose, 1970-81." His analysis served as the basis for the representation of moose population fluctuations shown in Figure 1. Richard E. Page began work on a Ph.D. program in July 1981, and plans to focus on modeling wolf and moose populations in order to clarify essential features of this predator-prey interaction and better understand mechanisms of population regulation.

Summer field personnel concentrated on examinations of moose carcasses and searched for summer wolf activity, especially evidence of wolf pup production and survival. Hiking mileage of all summer personnel totaled 877 km, including 356 km off-trail. Peterson directed summer field work in 1981, with personnel scheduled as follows:

May 27 - August 29, 1981: Rolf and Carolyn Peterson et al.
May 27 - August 26, 1981: Douglas W. Smith
May 27 - July 1, 1981: Michael K. Phillips
July 3 - July 25, 1981: Noel K. Hanson
July 31 - August 29, 1981: Richard E. Page

During October 19-22, Rick Page conducted a composition survey of moose, piloted by Donald E. Glaser (Grand Rapids, MN).

The 1982 winter study of wolves and moose extended from January 20 to March 9. Peterson and Page were present the entire period, with the research aircraft again piloted by Don Glaser. Participating National Park Service personnel were: Craig C. Axtell, Jan. 20 - Feb. 9; Charles L. Dale and Bruce E. Weber, Feb. 9 - 23; Larry T. Wiese and J. Robert Stottlemyer, Feb. 23 - Mar. 9. Supply flights were again flown by the Ely Aviation Unit, Superior National Forest, USFS.

THE WOLF POPULATION, 1981-82

In the last 2 years the wolf population declined from 50 to only 14, a 72% drop. An ice bridge to the mainland was not present during the winters of 1979-80 or 1980-81, and in 1981-82 continuous ice to the mainland did not form until after we had arrived and obtained a preliminary wolf count. Thus the decline reflected not only poor recruitment but exceptionally high mortality. During the past year alone we estimate that, including pups born in 1981, about 25 wolves perished on the island. In the last 2 years, we have recovered only 3 carcasses of dead wolves, all adults. One was killed by other wolves and two others (very old wolves) died of malnutrition. A partial skeleton of an adult wolf that died of unknown causes in 1981 was also recovered.

During the first year of decline, when wolves dropped from 50 to 30, much of the reduction occurred in the "peripheral" portion of the population, which consisted of single wolves or recently-formed pairs. The peak population of 50 included 11 non-territory-holders, but only 3 remained among the 30 wolves present a year later. Meanwhile, the number of wolves in established packs dropped from 39 to about 27.

During the past year, however, pack members were lost at a phenomenal rate, and all packs but one were eliminated or reduced to just 2 members. Wolf pack size has been declining rapidly in the last 3 years, from 10.3 wolves/pack in 1979 to 2.5 wolves/pack in 1982.

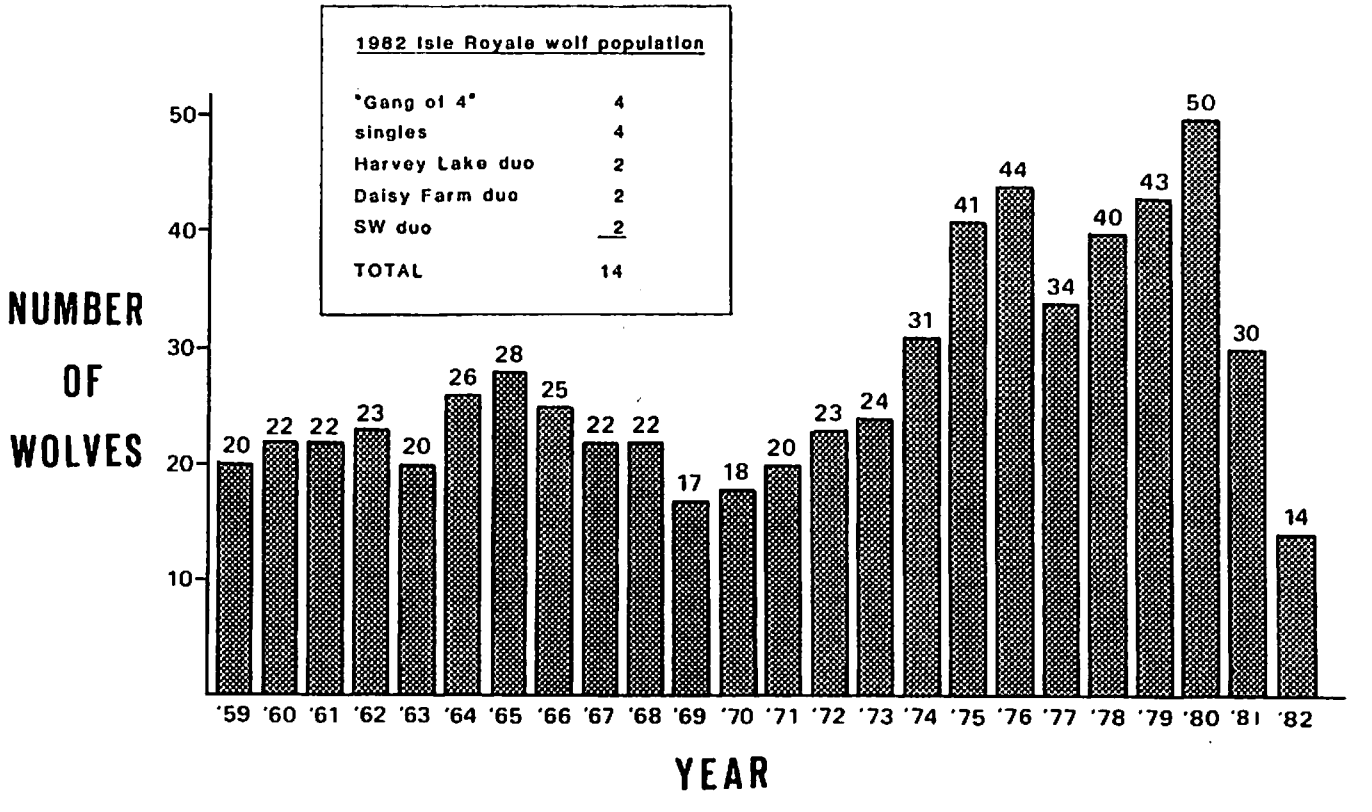


Figure 2. Isle Royale wolf population fluctuations, 1959-82.

Summer, 1981

We located 3 litters of wolf pups in 1981, mostly in traditional homesites previously occupied by the East Pack, Harvey Lake Pack, and Southwest Pack, respectively. All litters were small and each was estimated to consist of 3 pups, implying an island total of about 9 pups. All 3 litters of pups were monitored at least until mid-August. Subsequent observations in winter indicated that only 0-2 pups survived, but no details are known on causes of pup mortality. Notably, the wolves at the East Pack site never responded to our howls, although some spontaneous howls were heard.

Wolf scat analyses indicated continuing reliance on moose in summer, with beaver an important secondary source of food (Figure 3). Over 90% of the moose occurrence was calf hair.

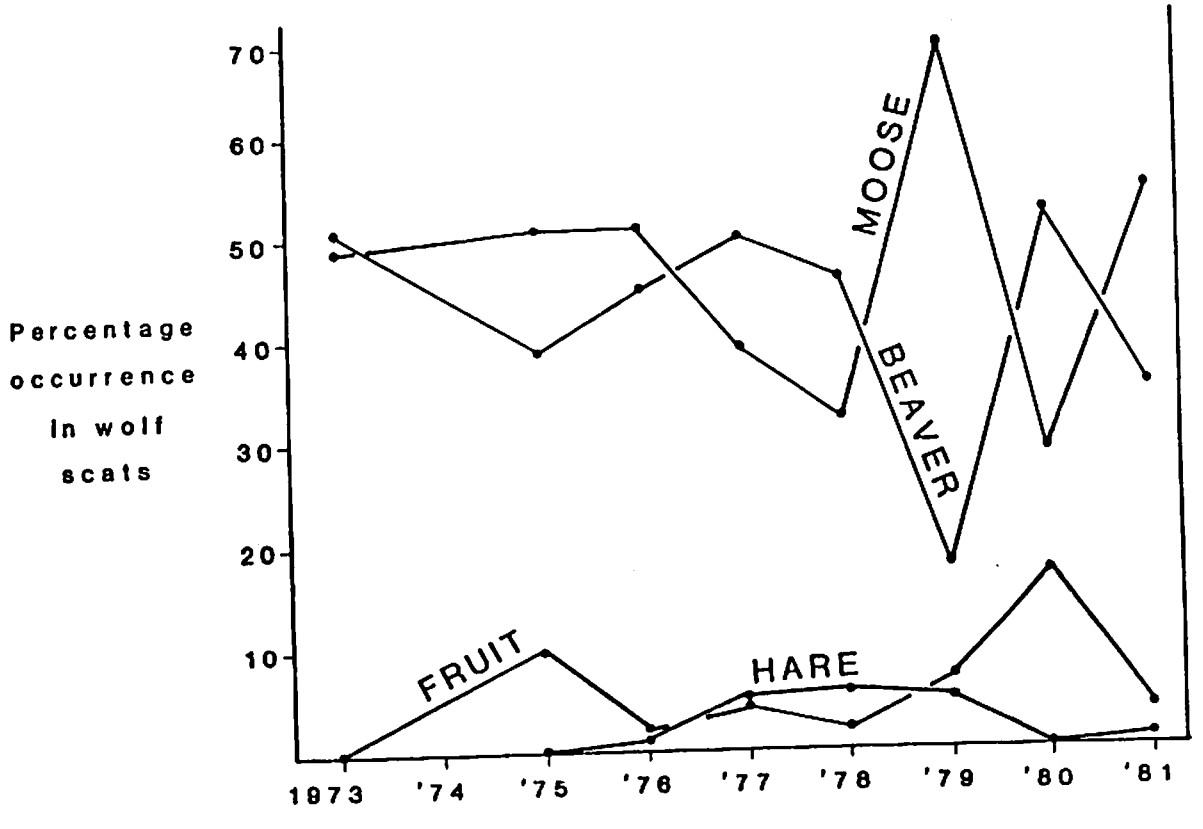


Figure 3. Summer diet of Isle Royale wolves, as indicated by percentage occurrence among food items in wolf scats.

Winter, 1982

In 1982 the social organization of the wolf population, pack sizes, feeding ecology, and spatial organization all were characterized by a complete break with the past. We found only one pack larger than 2 animals, and that contained only 4 wolves. In addition to the dominant pack (temporarily called the "Gang of Four"), we found 3 discrete pairs that remained together for the entire study period, plus 4 single wolves (see Figure 5).

The Gang of Four ranged over the entire island in a pattern of rapid movements that was broken for only short periods when the pack made a kill. Most of their activities were centered in the middle and SW portions of the island; for this reason we speculate that this pack was a remnant of the old Southwest or Middle packs (see Figure 4).

The SW Duo (no relationship to the old Southwest Pack implied) remained localized in the interior of the island at the extreme SW end. For over 3 weeks they remained stationary near the carcass of a bull moose they killed, and also consumed a cow moose that died of malnutrition nearby. Otherwise, this pair traveled little and rarely ventured out to the island's shoreline, where the Gang of Four regularly traveled.

The Harvey Lake Duo spent most of the study period in the middle of the island on the south side (centered at Malone Bay - see Figure 11 for locations mentioned in text). This was the only group that we could trace with reasonable certainty to a previous pack (the old Harvey Lake Pack). This pack, first identified in 1980, included 2 pups in the first winter and 1 pup in the second, but in 1982 only an alpha pair was present.

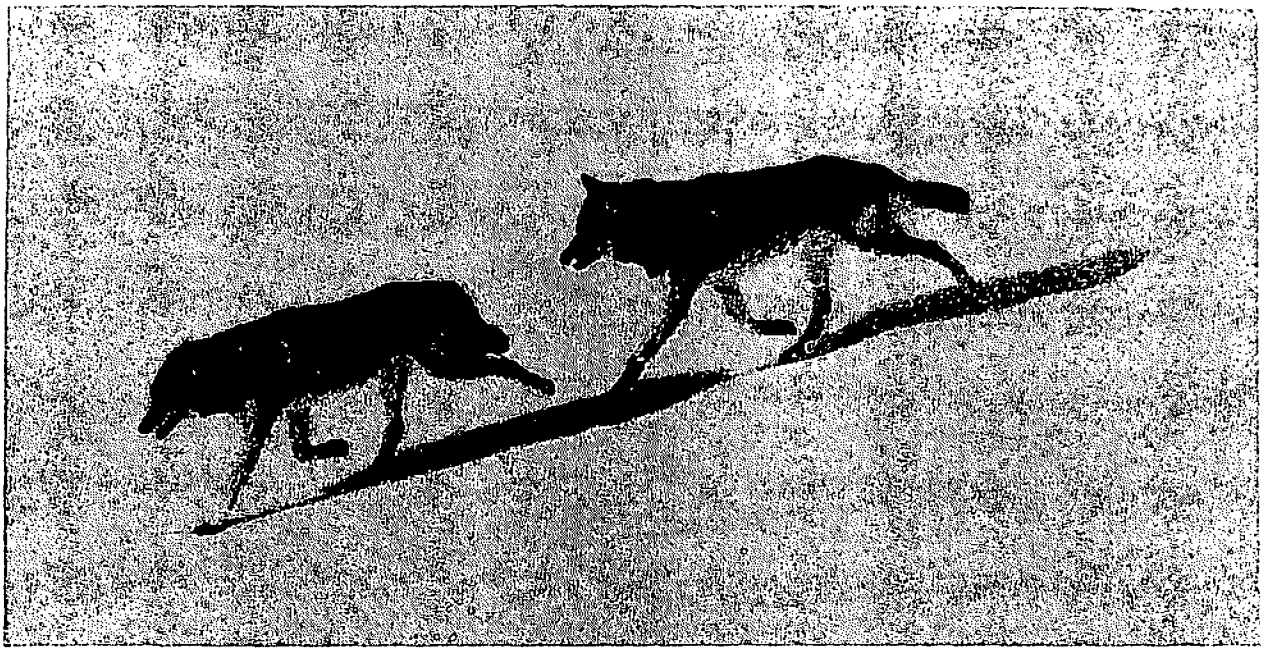


Figure 4. Alpha female (first) and alpha male of the Gang of Four. This pack established a territory that appeared to cover most of the island, and in 1982 they traveled at an exceptionally rapid gait (above), scent-marked frequently, and traveled widely over the island.

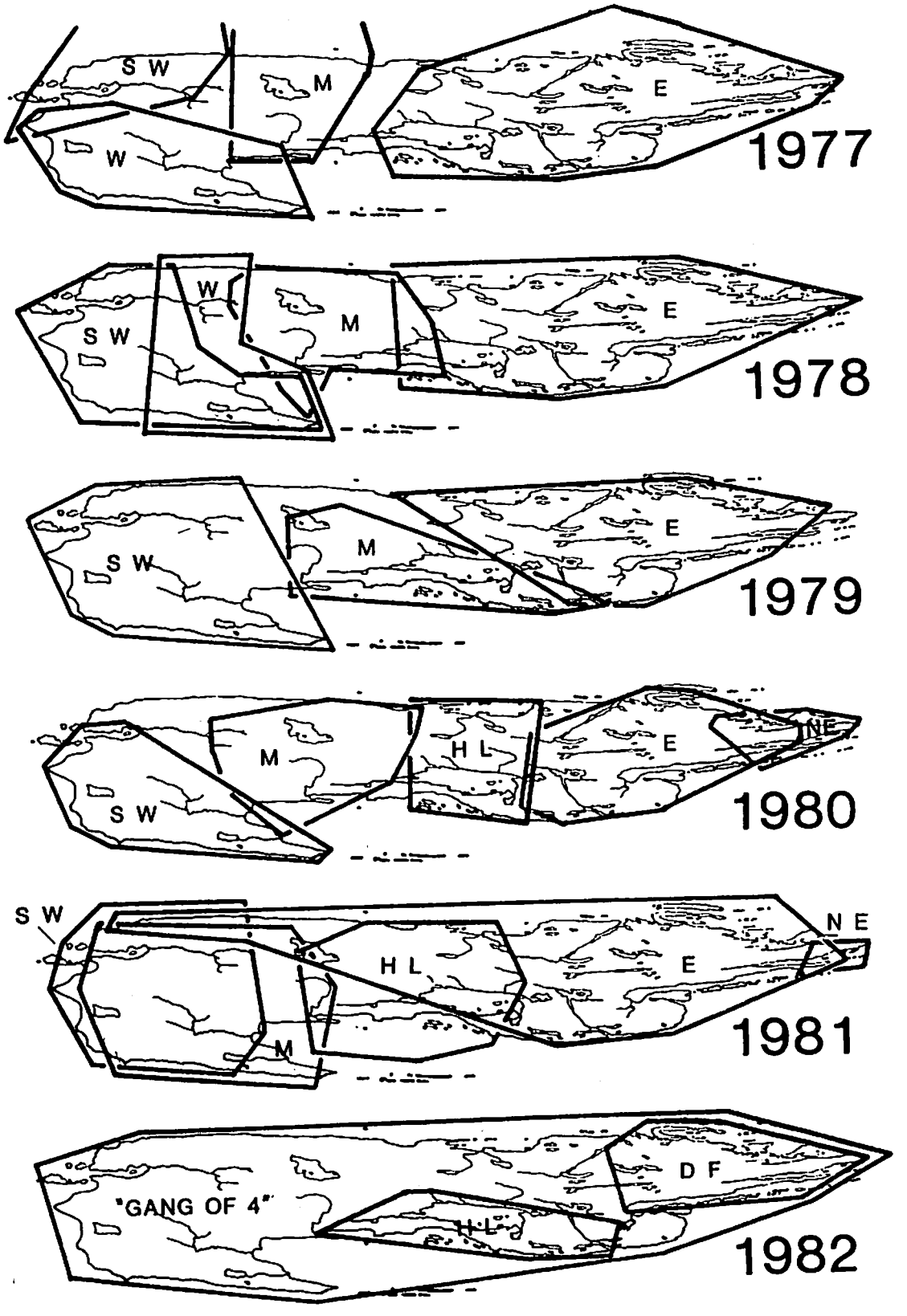


Figure 5. Wolf pack territories at Isle Royale, 1977-82. Note the decline from five packs in 1980 to one(?) in 1982, with extensive overlap in 1981. SW = Southwest Pack, M = Middle Pack, W = West Pack, E = East Pack, HL = Harvey Lake Pack or Duo, DF = Daisy Farm Duo.

The male appeared to be the same wolf as in 1980 and 1981, but a different female was present this year. On Feb. 18 this pair was chased off one of their kills and pursued for over 5 km by the Gang of Four; thereafter they abandoned their old territory and moved to the north side of the island, where they fed briefly on a moose calf on Amygdaloid Island that had probably been wounded by another wolf pair, the Daisy Farm Duo. The Harvey Lake Duo apparently split-up temporarily after being chased from this kill by the Daisy Farm Duo, but later the two were re-united and they were located last feeding on a fresh kill of their own near Moskey Basin.

The Daisy Farm Duo ranged over the northeastern third of the island. On Feb. 25 we observed the Gang of Four as they tracked this pair; this time the four wolves frequently watched their back-trail as they followed the Duo's tracks, often rushing off the trail in apparent response to airplane noise or unknown stimuli. The Gang of Four was several hours behind the Daisy Farm Duo, and after tracking them for about 2 km, the 4 wolves ran very excitedly off the trail and ceased following the pair. It was our impression that the four wolves were nervous and uncertain, and it is noteworthy that during the remainder of the study they did not again venture into the space utilized by the Daisy Farm Duo. Unfortunately, we had no clue as to the origin of this pair. Their territory was formerly occupied by the East Pack, which had been led by the same alpha female ever since its beginning in 1971. The East Pack had consistently declined in number since reaching a peak of 18 wolves in 1975, and in 1980, for the first time, we found no evidence of pup production in this pack. By 1982 the East Pack alpha female (at least 11 years old) was dead, and only the Daisy Farm Duo remained in the East Pack territory.

Evidently four breeding females were included in the 14 wolves left in 1982. We observed frequent courtship behavior in the Gang of Four (alpha pair), Harvey Lake Duo and Daisy Farm Duo. We did not observe actual coupling, but characteristic tracks indicating a copulatory tie were found on Feb. 3 (Harvey Lake Duo), Feb. 21 (Daisy Farm Duo), and Feb. 23 (Gang of Four). On Jan. 31 the Harvey Lake female exhibited vulval bleeding and was under close "surveillance" (genital sniffing) by the male. Likewise on Feb. 17, just prior to the appearance of "mating tracks", blood was seen in the urine of the female in the Daisy Farm Duo. The Southwest Duo was generally inactive during observations, but we did observe considerable nose-to-nose greeting behavior and friendly body contact, which we interpreted as courtship behavior.

The Gang of Four was unusually mobile, traveling at an exceptionally rapid gait (Figure 4) and covering an average of 19.0 km/day. They paid close attention to other wolf tracks and were frequently observed actively tracking other wolves. In addition to chasing the Harvey Lake Duo, we observed the pack chase a single wolf from a dead moose, then give up pursuit after about 1 km (see Table 1 for travel comparisons).

Throughout their travels, the alpha pair in the Gang of Four scent-marked at a high frequency. During 4.2 hours of observation when the pack was traveling, the alpha male and female marked at the average rate of once every 4.4 minutes.

All in all, the activities of the dominant pack were quite atypical-- the extensive travel pattern, high rate of travel and scent-marking, and their high level of interest in following non-pack members. Our interpretation is that this pack was highly motivated to patrol their new territory and actively expel all other wolves. We speculate that direct killing of wolves by other wolves was an important factor in the decline of all packs during the past year.

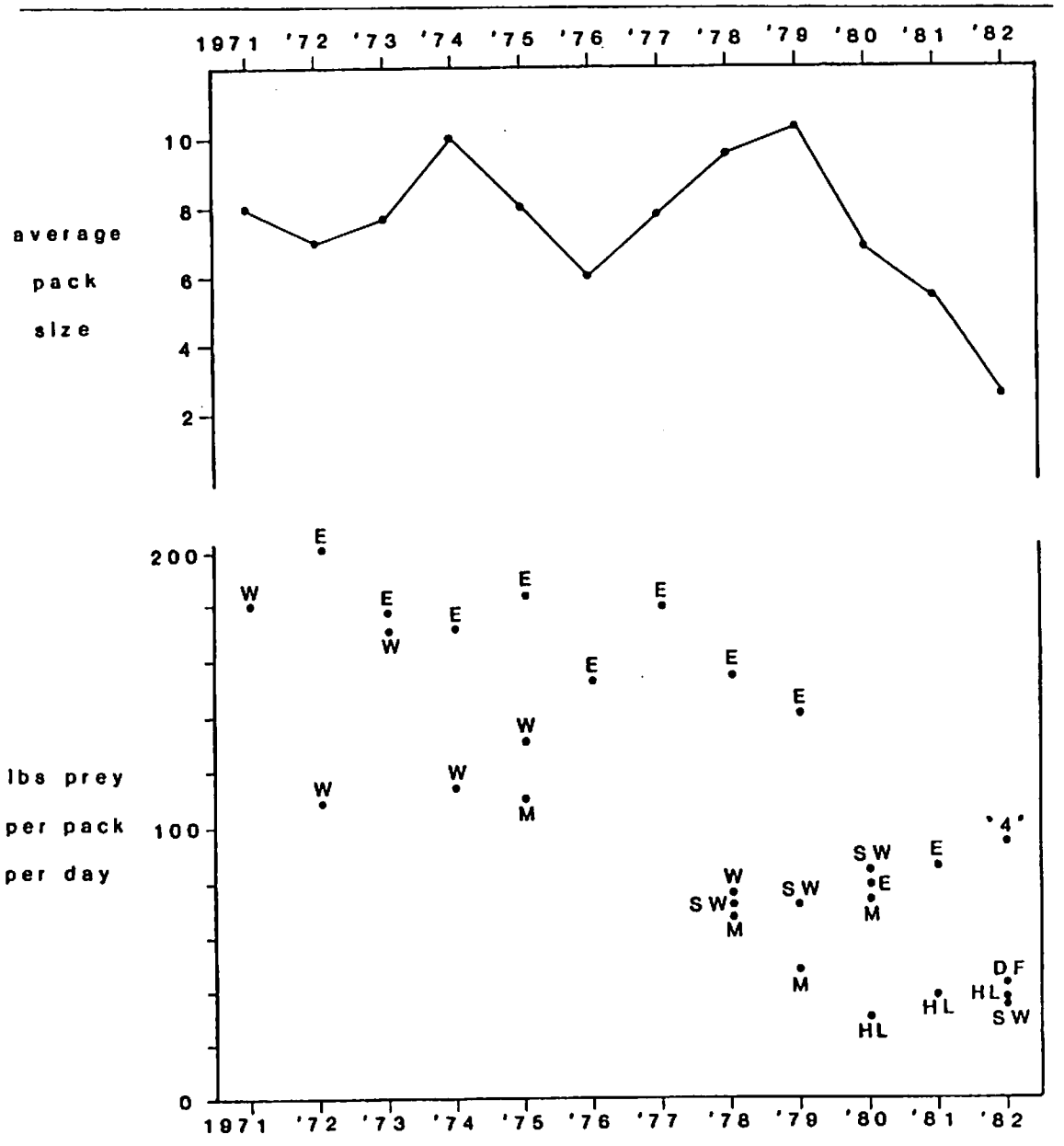


Figure 6. Trends in average pack size and food availability for each pack. Because of the steep decline in pack size, food availability for each individual in the Gang of Four ("4") in 1982 was higher than any previous measurement. Pack designations provided in Fig. 5 caption.

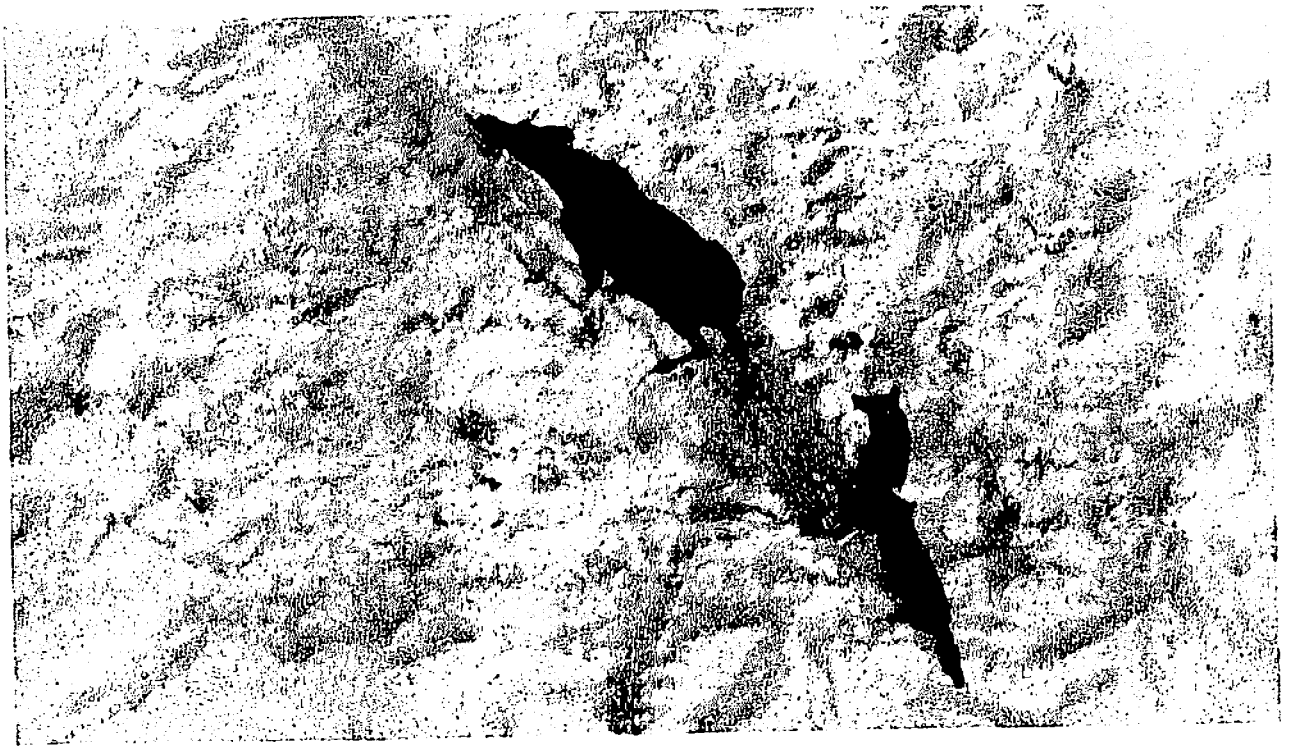
In obvious contrast to recent years, wolves in 1982 had an abundant source of food in winter. This was a direct result of the substantial drop in wolf density and, for the Gang of Four, a tremendous enlargement of their territory. The Gang of Four killed moose at an average interval of 5.5 days and, since the pack was so small, an average of about 11 kg of food was available per day for each pack member.

The duos lagged only slightly behind the Gang of Four in food supply While the duos stayed by their kills for days or even weeks until they were reasonably well cleaned-up, the Gang of Four seemed more intent on traveling than hunting and feeding-- it was not uncommon for them to kill a moose at night, feed briefly, and travel several more kilometers before morning. They invariably returned to their kills, but utilization was low after the carcasses froze and more recent kills were available elsewhere. One kill of a yearling moose by the Harvey Lake Duo was observed (Figure 7).

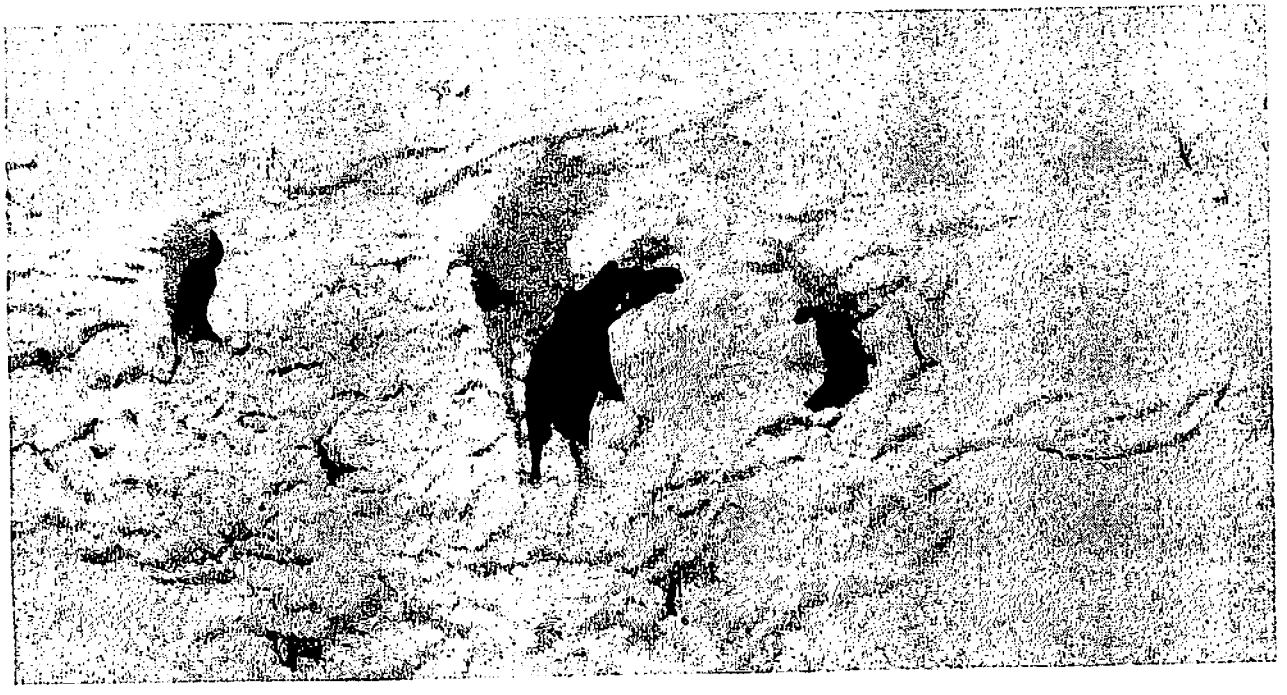
Table 1. Composite Isle Royale wolf pack, summarized from data on 29 wolf packs studied during 1971-1982*.

	All packs, 1971-82	Sample size
Average pack size	9.0 wolves	29 packs in 12 years
Average travel in winter	10.7 km/day	8,768 km in 819 pack-days
Average kill rates (moose)	1 kill/5.0 days	251 kills in 1,258 pack-days
Average amount of travel between kills	39.4 km	201 kills in 7,918 km
Average proportion of calves among wolf-killed moose	31%	251 kills

*These data were compiled in January, February, and March, and can be considered reliable only for the winter period (November - April).



(a)



(b)

Figure 7. The Harvey Lake Duo brings down a yearling moose. Through bites to the rear legs (c), the moose was finally immobilized. About 30 minutes after the initial attack, the moose was pulled down as it walked downslope toward a spruce tree; the male then rested (d) while the female began to feed.

(c)

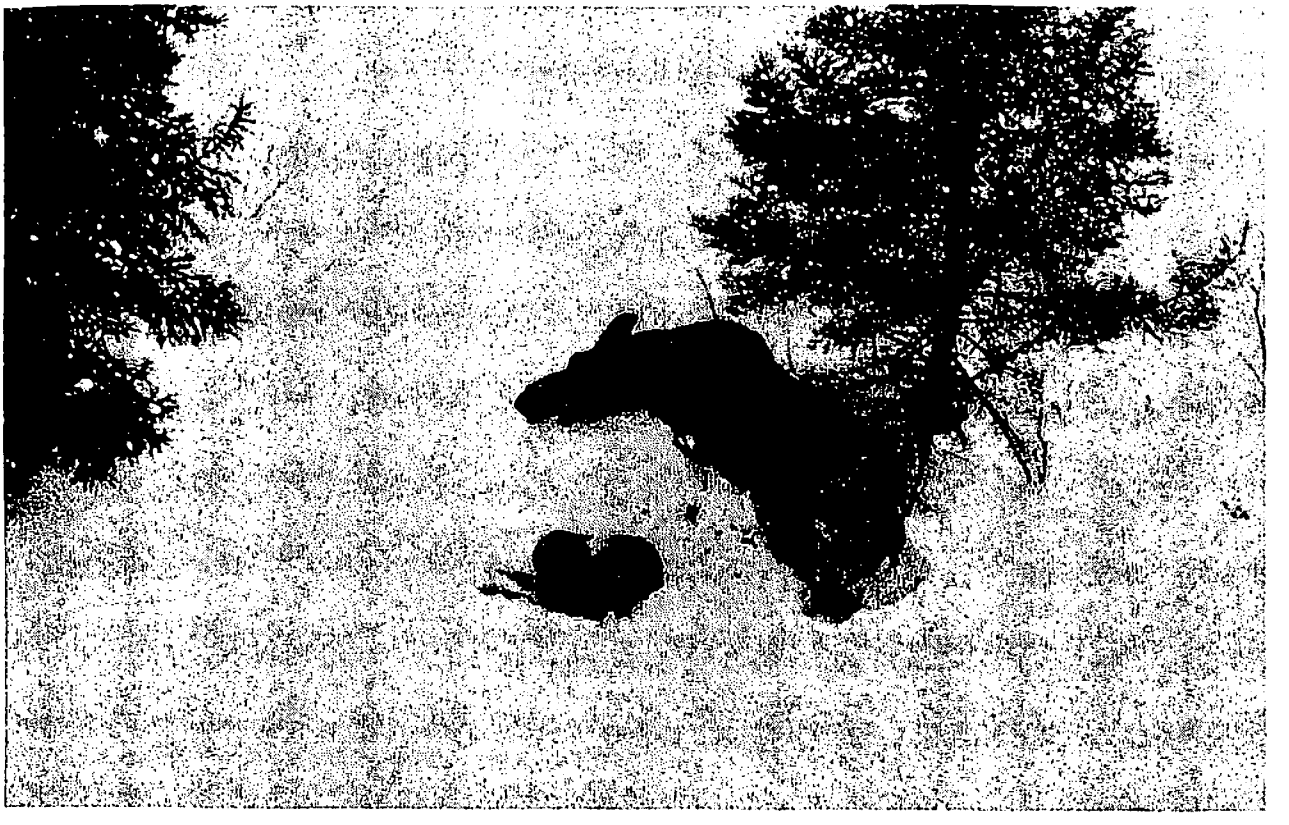


Figure 7. (continued) (d)

THE MOOSE POPULATION, 1981-82

Our current technique for estimating the size of the moose population each year, developed by Phil Stephens, involves integrating winter and summer indices of abundance with results of a winter census. The census is based on a sample of intensively-flown quadrats covering 10-15% of the island. Preliminary regression equations were developed which relate the indices and the census (the only total population estimate obtained directly), producing additional estimates based on summer and winter indices. Our "best estimate" is defined as the mean of the census and the 2 indices. In the absence of a census, the 2 indices alone can be used. This method provided annual estimates of the moose population since 1970 (Figure 1). The regression equations are now based on only 5 data points, but we expect to improve the regression equations with subsequent comparisons between census and indices; this may ultimately lead to slight changes in our "reconstructed" history of the moose population over the past decade.

1982 census

As in 1981, we intensively-counted all moose on small islets surrounding the main island, and added this figure to the total estimated from 65 plots on the main island, distributed among 4 strata of moose density (Figure 8). The resulting 1982 estimate (and 95% confidence interval) was 729 (±30%) moose, compared to the census estimate of 481 (±27%) in 1981. Of course, these figures are subject to interpretation because of large confidence intervals. Our best estimate (censuses and indices combined) for the 1981 population was previously 650 moose, considerably higher than the census alone suggested. However, the difference between the census estimates in 1981 and 1982 is consistent with the almost 200 calves (27%) estimated in winter, 1982. For the present we will adopt the census results, which indicate about 500 moose in 1981 and about 700 in 1982. "Best estimates" for the last 2 years will later be developed using revised regression equations.

Survival of 1981 calves

All data point to unusually high survival in the 1981 calf cohort. During the summer of 1981, twin calves were commonly reported near most major campgrounds. Observations of research personnel, mostly in backcountry areas, indicated about 50 calves per 100 cows (compared to an average of 33 calves per 100 cows over the previous 11 years). The first reliable data was obtained in an October aerial survey, aided considerably by fresh snow. Classification of 198 moose indicated 61 calves/100 cows, compared to an average of 23 calves/100 cows over the previous 9 years (Figure 9). Counts in winter confirmed exceptionally high survival of 1981 calves-- 27% of the moose counted on census quadrats were calves. Assuming an even sex ratio, this would imply 54 calves/100 cows in winter, indicating little loss between the fall and winter counts. Since the beginning of these studies in 1958, the highest previous proportion of calves observed in winter was about 18%, recorded several times in the 1960's.

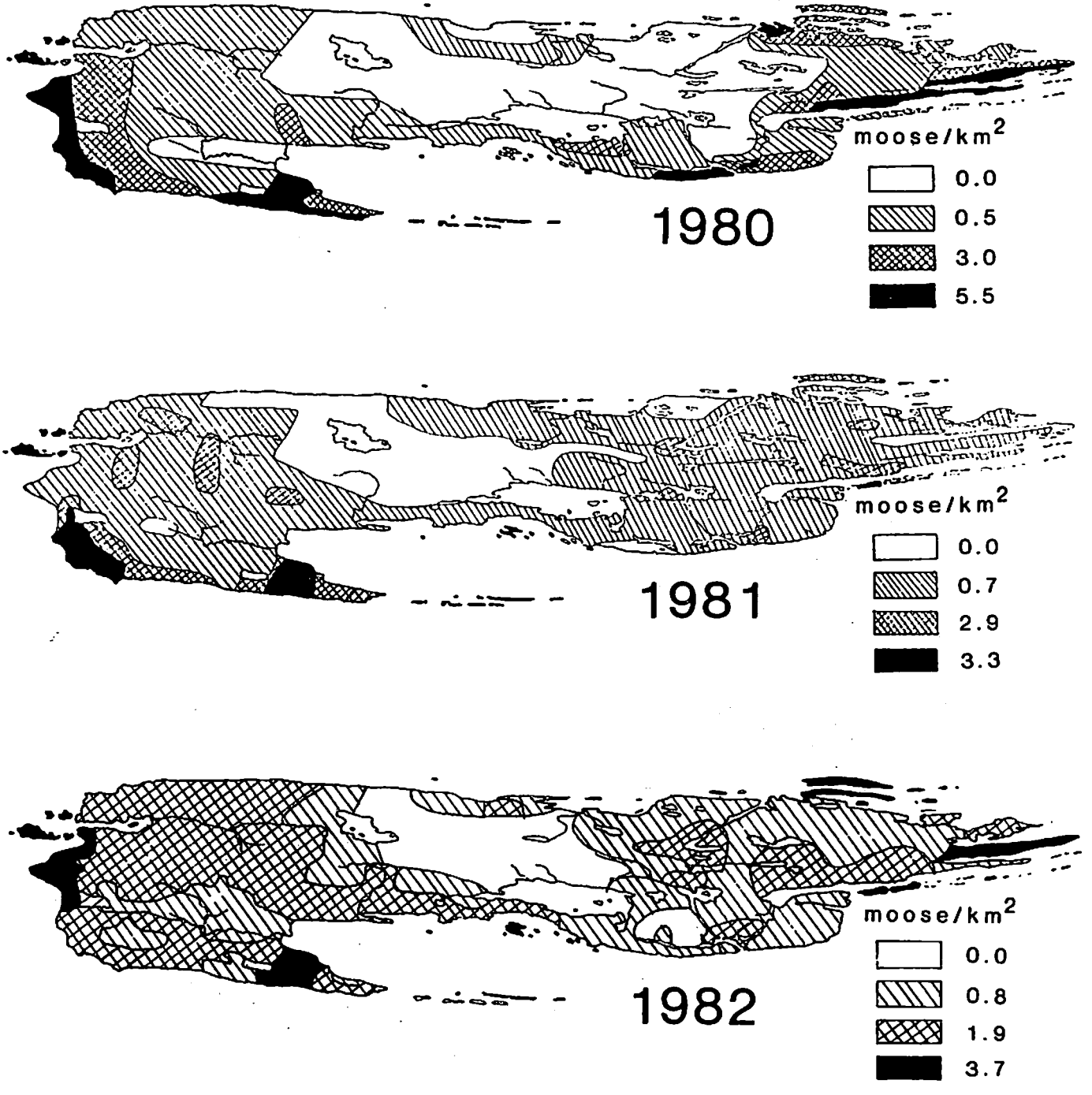


Figure 8. Midwinter distribution of moose on Isle Royale, 1980-82, illustrating the 4 strata of relative moose density determined during annual censuses.

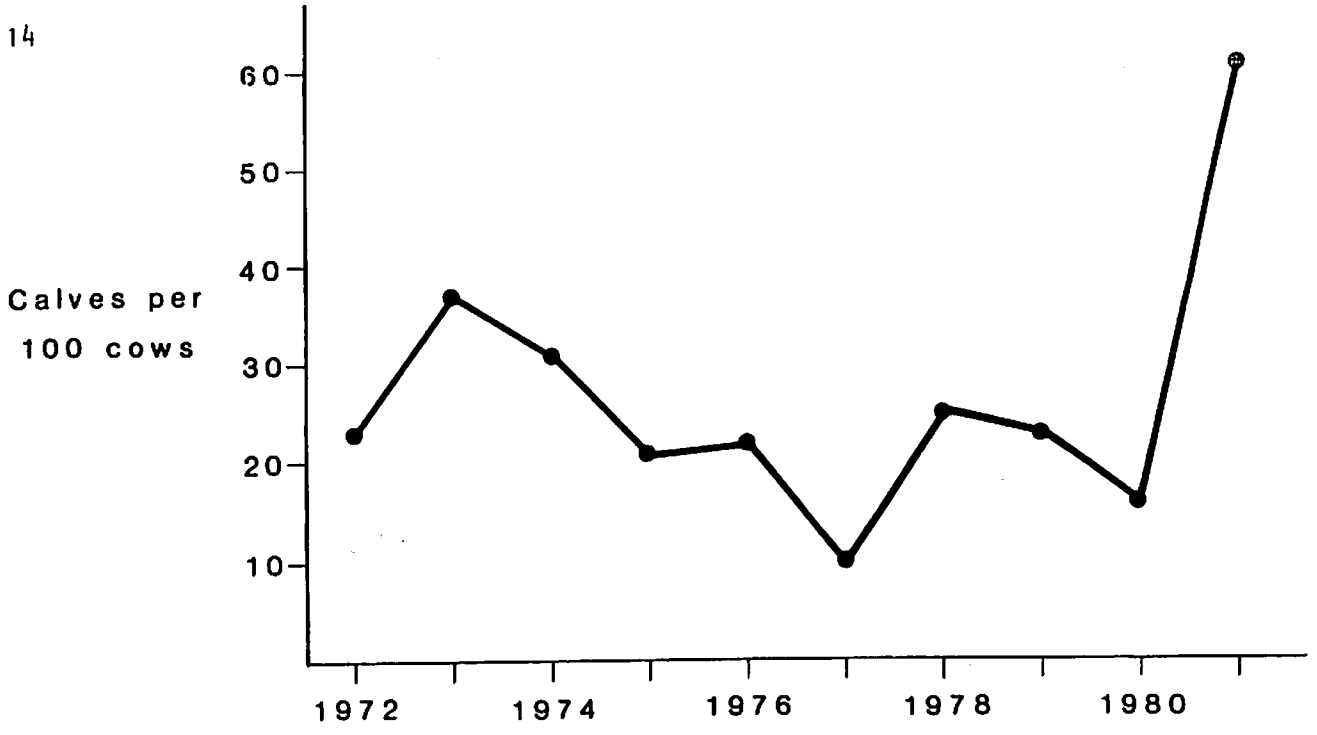


Figure 9. Moose calf survival, as indicated by annual aerial surveys conducted after leaf-fall in October.

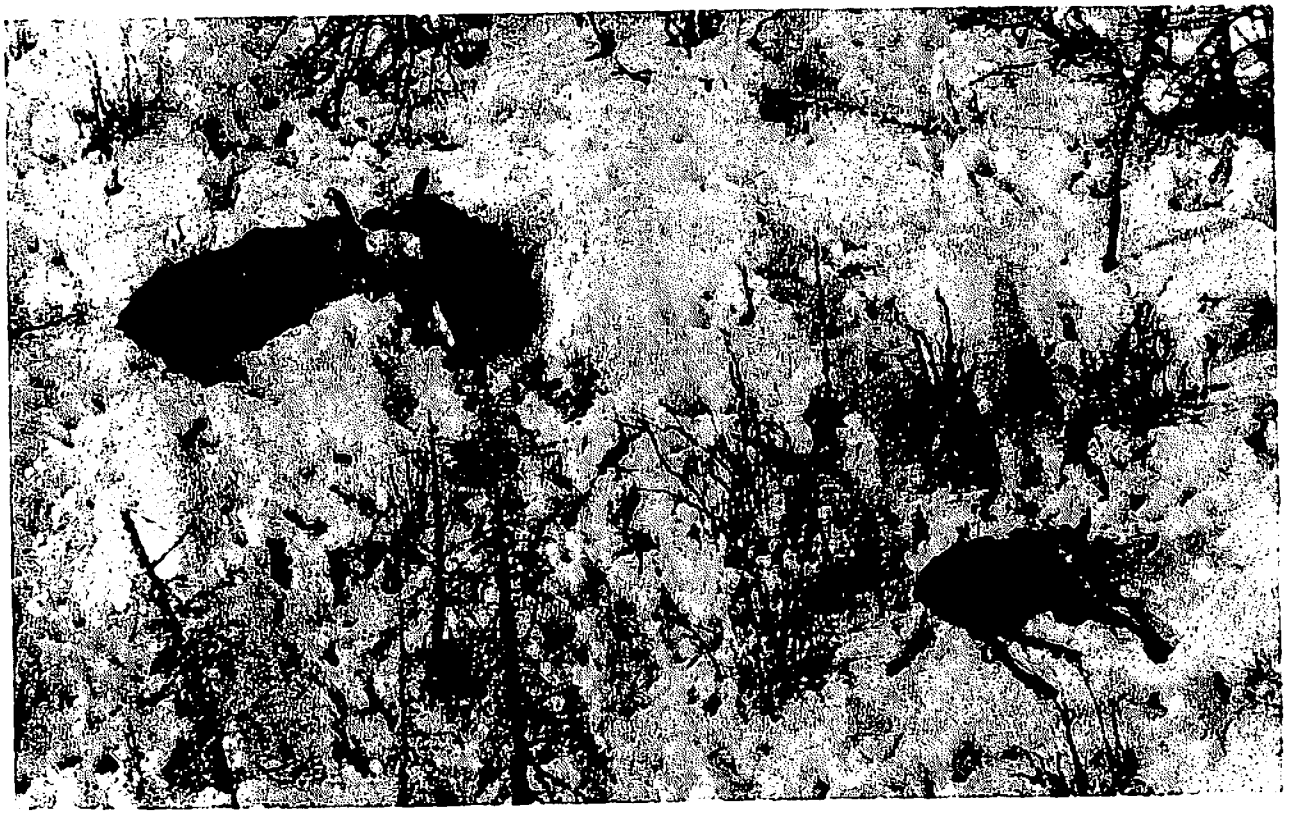


Figure 10. Moose cow and twins resting on small offshore island. While rarely observed in previous years, six sets of twins were recorded in winter, 1982.

Six sets of twin calves were observed during the 1982 winter study, all near shorelines or on small islands. Of the 3,800 moose recorded during observations since 1972, twin calves had been seen in winter only twice previously.

We attribute most of the increased calf survival to decreased wolf predation pressure. Winter severity, of course, has a bearing on calf survival. While the winters of 1979-80 and 1980-81 were slightly below average in severity (indicated by total snowfall - see Figure 15), they were not unusually so. The winters of 1972-73 and 1976-77 were much less severe, yet calf survival improved moderately only in 1973.

Moose mortality, 1982

Of the 27 dead moose located during the 1982 winter study, 19 were killed by wolves. Seven of the remaining eight moose have been examined; five died of malnutrition, one fell from a cliff and suffered a broken back, and one died after getting a leg caught between two birch trees. The distribution of dead moose in 1982 is shown in Figure 11.

Bone marrow fat values were determined for most moose examined thus far in 1982. Fat values fell into 2 classes (Figure 12), those above 50% and those below 20-25%. Much of the "fat" in the lower value group was actually cellular debris occurring within the marrow cavity, and almost all fat had been utilized.

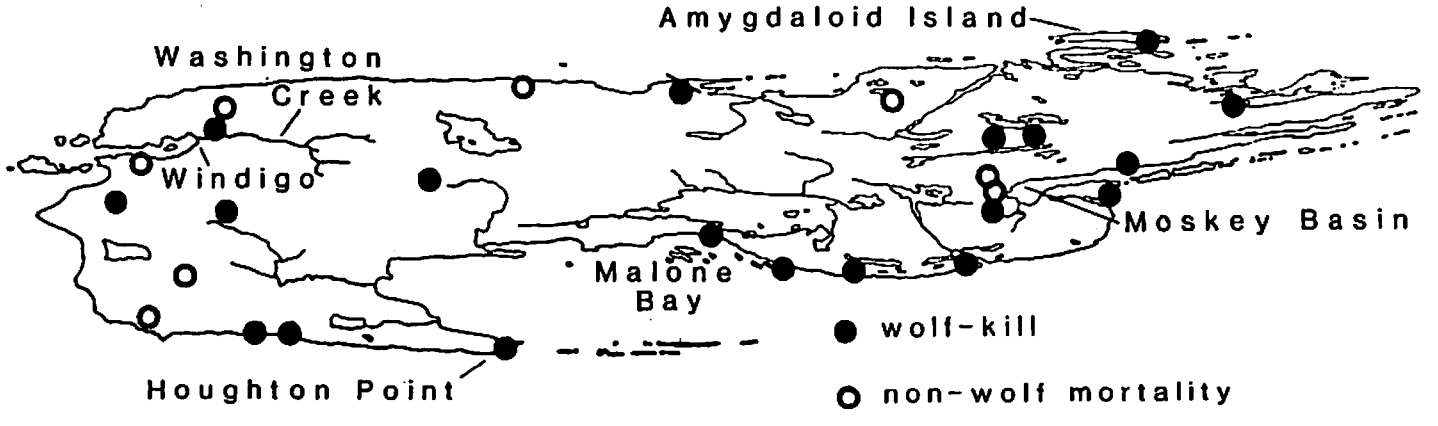


Figure 11. Distribution of all moose carcasses located during 1982 winter study, together with place names mentioned in text.

We expected that wolves would exploit the abundance of calves this winter, so we were surprised to find that only 38% (6 of 16) of the wolf-killed moose examined thus far were calves, comparable to the 30-35% calves usually found in the past. Bone marrow fat levels in 4 of 6 wolf-killed calves were quite high, suggesting that the 1981 cohort was generally in good condition. We will be making a concerted effort to collect data on metatarsus length and braincase volume for calves to check for any response in calf body size and development; wolf utilization of carcasses has been so high in recent years that calf bones have not been available for collection.

The bulk of the wolf-kills examined thus far in 1982 have been old adults. After age determinations (now in progress) have been made, we will be able to evaluate whether an unusual abundance of very old moose (born in the late 1960's) may have buffered predation on moose calves. Previously we noted an inverse correlation between the proportion of calves and the proportion of old adults in the wolf-killed sample, but since calves seemed to be preferred prey we assumed that this group would buffer predation on old adults, not vice versa.

Historic fluctuations in the moose population

Moose on Isle Royale have increased and declined three times since colonizing the island in the early 1900's. The last sustained increase occurred in the 1960's, over a decade after wolves had become established and 25 years after any habitat renewal by fire. A possible cause for this anomalous increase was suggested by long-term weather data collected at the Thunder Bay airport, about 40 km N of Isle Royale (Figure 15). The early 1950's was a period of high snowfall and followed an apparent dieoff of moose at Isle Royale in the late 1940's. There followed, beginning in the late 1950's, a series of several winters with record-low snowfall. Possibly this series of mild winters played an important role in the subsequent increase of moose.

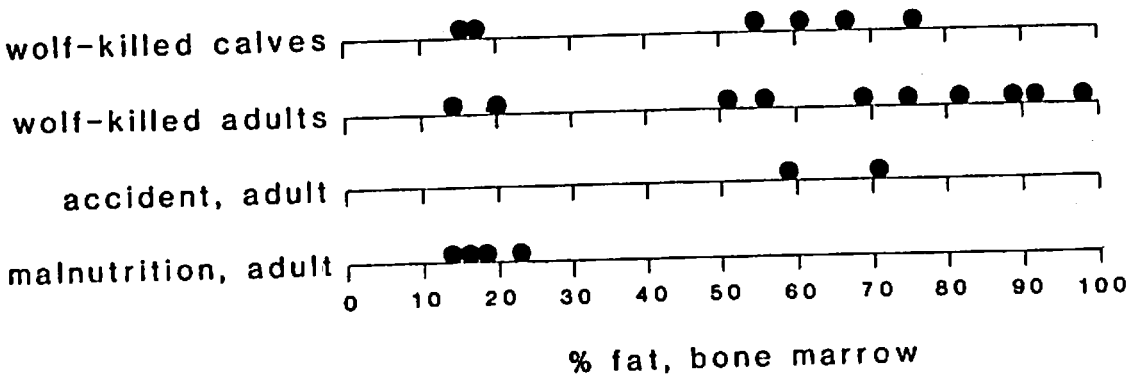


Figure 12. Femur marrrow fat levels for dead moose examined in 1982, separated according to age and cause of death.

OTHER SPECIES

In winter, 1982, otter activity was noted at 6 sites and was especially prevalent in the Washington Creek drainage. Beaver activity was observed after the middle of February at 7 sites. A beaver was killed and eaten by wolves at Houghton Point in February.

Fox observations over the past 11 years (Figure 13) show no obvious trends, and from this we infer a relatively stable fox population, probably resulting from a low-density, non-cycling snowshoe hare population (due to the impact of moose browsing on hare food and cover). We propose that the difference in body size between wolves and foxes allows them to co-exist-- i.e. foxes are able to effectively escape from wolves. Such was not the case for Isle Royale coyotes, which disappeared within a few years after establishment of wolves.

The status of the beaver population is of great interest, in view of the 75% decline between 1974 and 1980. Currently, a total count of occupied lodges is conducted every 2 years by Philip C. Shelton, who plans to conduct the 1982 survey in October.

A gyrfalcon (recorded only once previously at Isle Royale) stopped briefly on the ice (tundra habitat?) near Windigo in February, then took off and flew over the ice-covered channel toward the Canadian mainland.

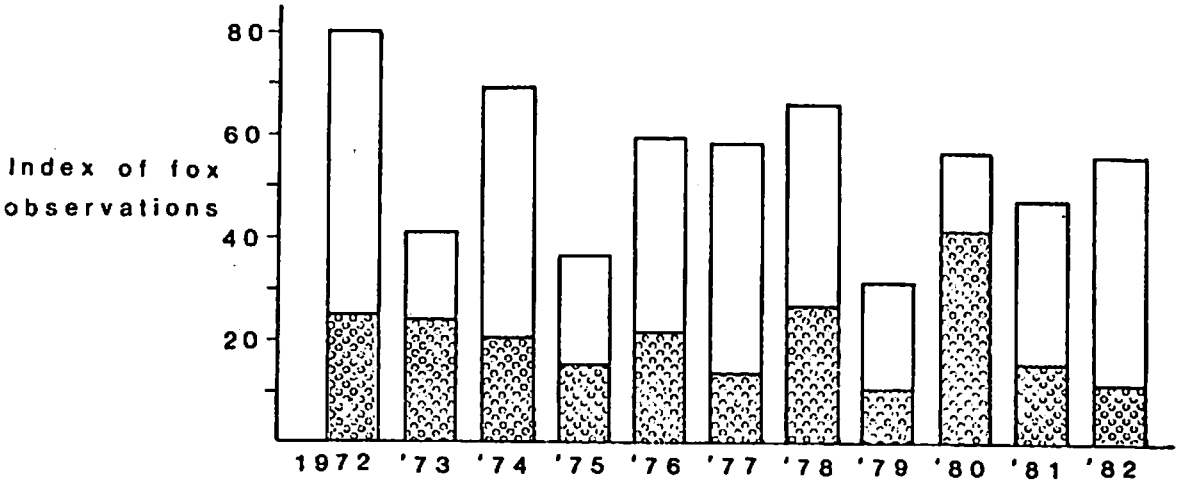


Figure 13. Midwinter fox observations, 1972-82. The lower portion of each bar (small circles) corresponds to the number of foxes seen more than 1 km from a moose carcass/100 hours flying time, while the upper portion of each bar (clear) is the sum of the maximum number of foxes seen on each moose carcass.

WINTER WEATHER AND SNOW CONDITIONS

The 1981-82 winter was slightly colder than average, with temperatures at our winter base camp at Windigo averaging +21.7 deg.F (daily maximum) and -1.7 deg.F (daily minimum). Temperature extremes (at the weather station) were +41 deg.F on Feb. 20 and 22 and -25 deg.F on Feb. 4 (Figure 14).

Snow depth ranged between 40 and 60 cm when we arrived in January, and density was very low with no crusts in the snow profile. On Jan. 21-23 a 50-cm snowfall occurred and snow depths as high as 100 cm were briefly recorded before the snowpack settled back to the 50-70 cm range, slightly above average. Freeze-thaw during a warm spell on Feb. 16-22 created a surface crust that supported about 1,400 g/cm^2 near the base camp. After the crust formed, moose shifted increasingly toward conifer cover. Wolves could usually walk on top of the crust but often broke through when running. With continuous ice around the shoreline of Isle Royale, wolves made relatively little use of the island's interior.

In terms of snowfall, the last three winters have been relatively mild. Figure 15 shows annual snowfall totals for Thunder Bay, Ontario. Snowfall there shows a general correlation with the integrated snow depth measurements previously used for a winter severity index (from Grand Marais, MN), and Thunder Bay is the closest station with long-term weather records on a year-round basis. An automatic precipitation gauge recorded continuous snowfall data for the first time at Isle Royale in 1981-82; hopefully such data will be available in subsequent years.

A bridge of continuous ice between Isle Royale and the mainland formed after Feb. 3, but appeared to have some open channels when we left on March 9. The ice cover was continuously rearranged by wind action in February, resulting in especially rough ice along the north side of Isle Royale. Wolf travel over the ice would have been difficult, and we had no indications of wolf movement across the ice.

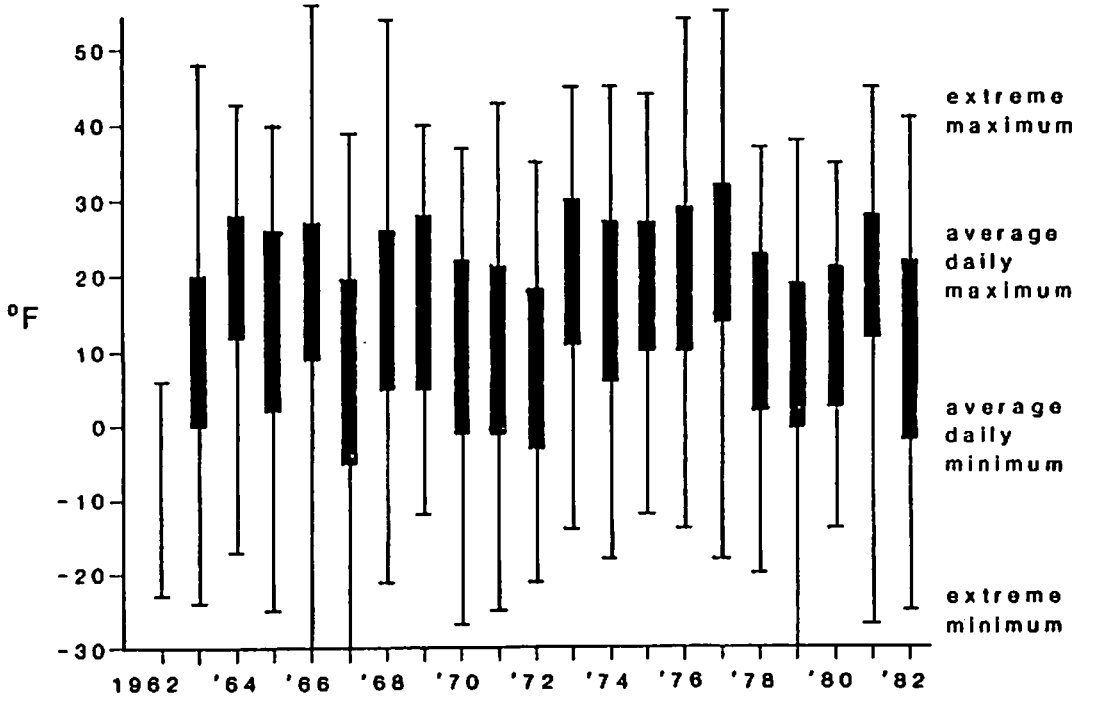


Figure 14. Temperatures in midwinter at Windigo weather station.

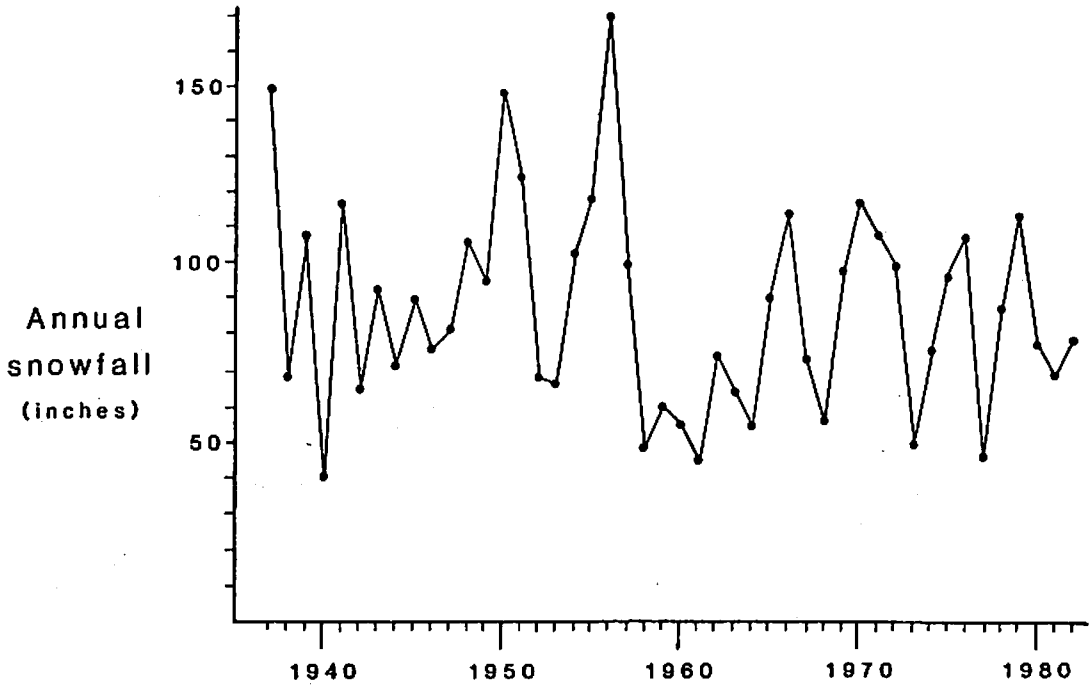


Figure 15. Annual snowfall at Thunder Bay, Ontario, about 40 km N of Isle Royale. "1980" corresponds to snowfall during the winter of 1979-80, etc.

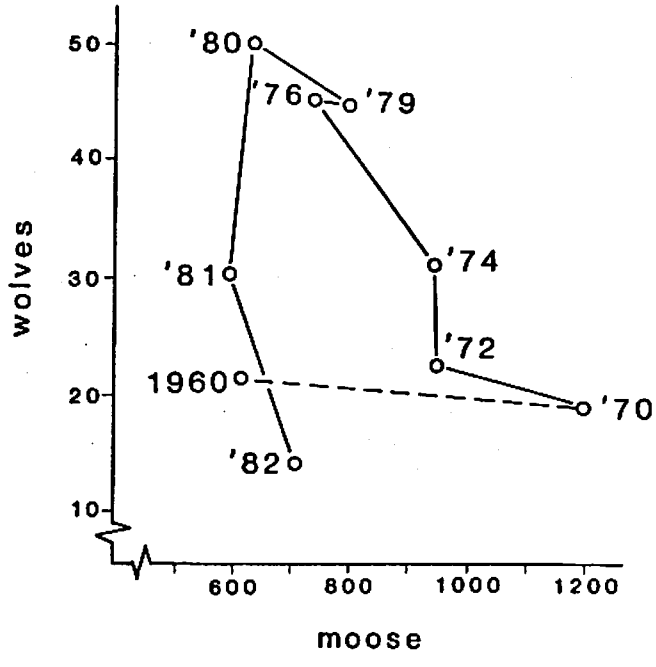


Figure 16. Phase plane of wolf-moose interaction at Isle Royale, suggesting long-term cyclicity.

OUTLOOK FOR WOLVES AND MOOSE/RESEARCH DIRECTION

The rapid "reorganization" of the wolf population, the resurgence of the moose population, and turnaround in wolf food supply all point to an imminent reversal of the wolf decline. However, the critical immediate factor that will determine next year's population is how many litters of pups will be produced and survive in 1982. Of course, much depends on the size of the territory finally claimed by the Gang of Four, since it is doubtful that this pack will tolerate another breeding pair in their territory. Of the three pairs present this winter, the Daisy Farm Duo seemed most secure; the other two duos are probably at some risk at least until the Gang of Four settles down during the summer pup-rearing period. While our 1983 expectations are uncertain, we believe that within a couple years one or two packs will begin to rebuild within consolidated territories, implying a moderate increase in the wolf population.

If subsequent cohorts of moose calves survive as well as the 1981 cohort, the moose population will rebound rapidly from the relatively low plateau occupied since about 1977. If this occurs, of course, some of our previous ideas about the roles played by food, weather, and predation in the dynamics of Isle Royale moose will be modified. We anticipate more adequate answers to the following questions:

(1) What role does food supply/weather play in determining moose calf survival and rate of increase, and how does it interact with wolf predation?

(2) How are predation losses and effects of food supply/weather related to moose population density?

(3) Is a predator-prey cycle a dominant feature of wolf-moose interaction, with the plane of interaction only set by moose food supply in a general way (loose feedback)?

We are especially interested in the apparent pattern of cyclicity that may be emerging (Figure 16) in moose and wolf population fluctuations, as it appears that this predator-prey system is returning to approximately the same state as in the late 1950's, when this project began. We expect that the next few years will provide data that is of critical importance to one of our principal long-term objectives-- understanding the principal factors that regulate interacting populations of large mammalian predators and prey.