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MOUNTAIN LION SOCIAL ORGANIZATION IN THE IDAHO PRIMITIVE AREA

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MOUNTAIN LION SOCIAL ORGANIZATION IN THE IDAHO PRIMITIVE AREA

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PREFACE

This dissertation was prepared using a manuscript written in a format which would facilitate immediate submission to a national scientific journal for publication. This manuscript was written according to specifications of WILDLIFE MONOGRAPHS.

Approval for presenting the dissertation in this manner was based upon (1) the Graduate Council's policy of accepting a research paper in lieu of a dissertation, and (2) my graduate committee's agreement, dated January 23, 1973.

MOUNTAIN LION SOCIAL ORGANIZATION IN THE IDAHO PRIMITIVE AREA

John C. Seidensticker IV[1]

CONTENTS

CONTENTS (Continued)

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[1] Idaho Cooperative Wildlife Research Unit, University of Idaho, Moscow, ID 83843.

LIST OF TABLES

LIST OF TABLES (continued)

LIST OF TABLES (continued)

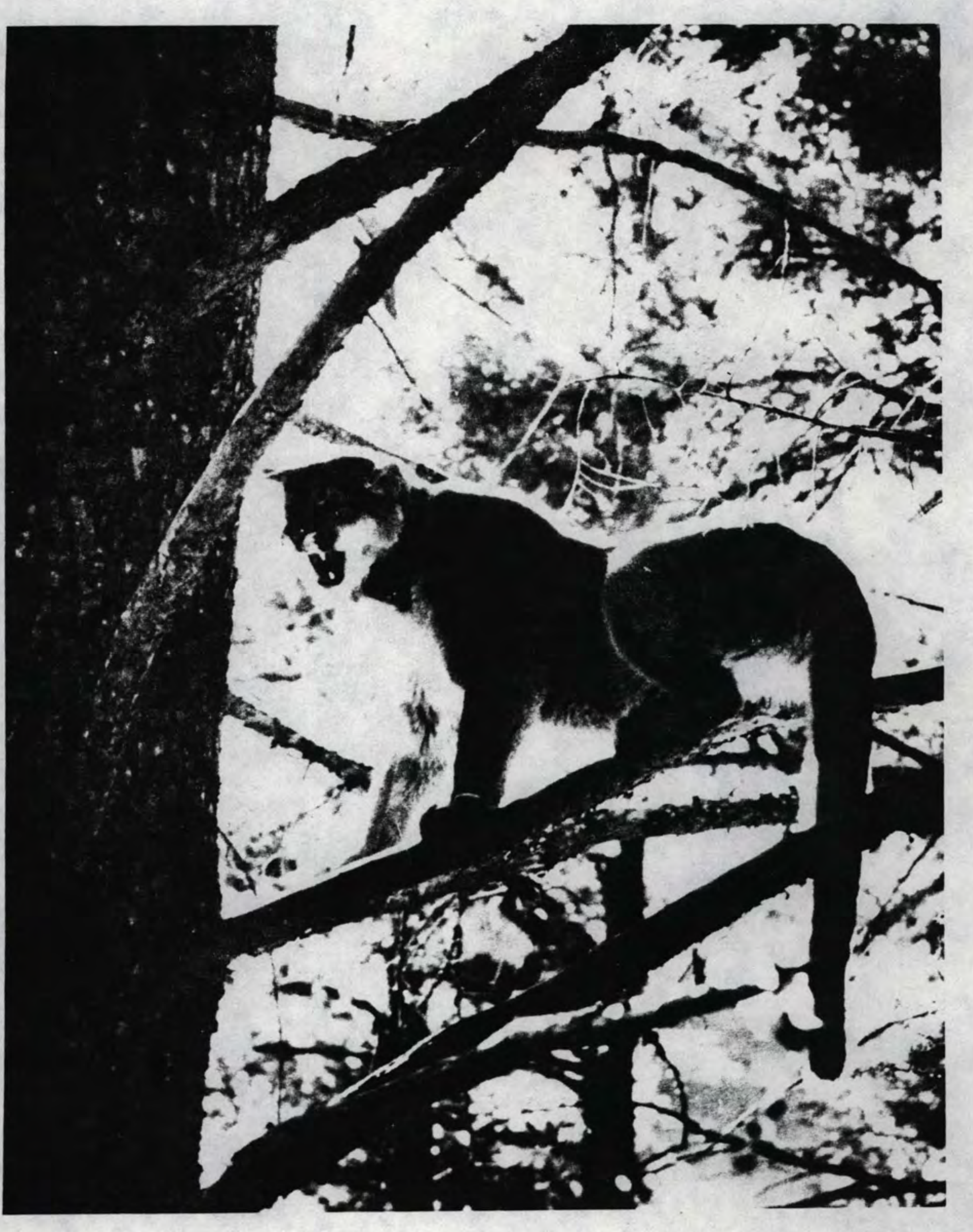
LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF FIGURES (continued)

ABSTRACT

As part of a comprehensive study of mountain lion ecology, the social organization of a lion population in the Idaho Primitive Area was investigated using radiotelemetry. Important to the analysis was that general population dynamics and relationships had been established through recapture methodology over the five previous winters. After independence from the female, mountain lions dispersed, showing no attachment to any particular area. The "transient" females did not reproduce and the "transient" males only rarely bred. When an area adequate in size and resources and free of too many but not independent of other residents was located, the young lion restricted itself more and more to that area. Only with attachment to site did the lion enter the reproductive phase of its life (population component termed "resident"). Home area utilization by resident lions was influenced by the localizing effects of the large ungulate kills and, for females, kitten mobility. The localizing effect of kittens was diminished their second winter; home area utilization by females during these different stages of kitten development differed considerably as a result. In the short run, a lion's home area was in a constant state of flux in terms of location of mule deer and elk (the most important prey resource nine months of the year) in situations where they could be successfully stalked and killed. But over the long run, the conditions in certain areas were such that lions tended to be more successful there in making kills. This demonstrated the advantage of familiarity with the home area, especially for females rearing kittens. Resident lions occupied fairly distinct but usually contiguous winter-spring and summer-fall home areas. No substantial part of any resident lion's winter home area was maintained to the exclusion of all other conspecifics. Resident male home areas overlapped but little. Those of resident females often overlapped completely and were overlapped by resident male areas. Transient lions of both sexes moved about these areas but did not remain. In summer, the pattern was the same. Land-tenure was based on prior right, but the system was not static. Home areas were altered in response to the death or movement of other residents. Young adults established only as vacancies became available. The mountain lion's essentially solitary existence was maintained visually and chemically. A lion's response to close approach of another was dependent upon its population and reproductive status. Over the seven winters from 1965 to 1972 the resident male portion of the lion population remained stable; resident female numbers were constant for three winters but later deaths were never quite compensated. Dispersal of young lions reared on the study area was independent of resident adult density. It was concluded that the lion land tenure system acted to maintain the density of breeding adults below a level set by the food supply in terms of absolute numbers of mule deer and elk. Variation in lion environmental structure resulted in variation in the suitability of home areas and affected the amount of terrain a resident lion utilized. The amount of terrain used by a resident lion as well as the degree of home area overlap between resident females, i.e., density of breeding population, was set by a vegetation-topography/prey numbers-vulnerability complex. The evolution and adaptive values of mountain lion social organization are discussed.



FRONTISPIECE. Female mountain lion No. 46 equipped with radio transmitter treed by hounds. © JCS.

INTRODUCTION

Even though the mountain lion *Felis concolor* L. is secretive and retiring by nature, men encouraged and motivated by a pioneering anti-predator attitude found it easy prey with traps and especially hunting dogs. In the United States particularly, this vulnerability, together with habitat modification and attendant changes in prey populations, has resulted in a great reduction in distribution and numbers until today sizable populations are found only in the remote regions of the western mountains and the Florida Everglades (Cahalane 1964).

In 1964, M. G. Hornocker (1969a, 1970) launched an investigation to gather data on mountain lion population dynamics and to assess the lion's role as a predator in the Idaho Primitive Area. Using primarily a mark-capture-recapture scheme with dogs and snow tracking, he found that in spite of both lion and human predation, populations of mule deer *Odocoileus hemionus* Rafinesque and elk *Cervus canadensis* Erxleben, the major prey species in winter, increased during a 4-year period during which the lion population remained stable. Hornocker (1970:37) postulated that, "Intraspecific relationships, manifested through territoriality, acted to limit numbers of lions and maintain population stability. Dispersal and mortality of young individuals appeared to be important limiting mechanisms."

The recapture and snow tracking methodology, while providing data for the analysis of predation and population dynamics, lacked the precision necessary for a careful analysis of the lion's social organization. A better method of "observing" the highly secretive and mostly solitary lion was clearly needed. To this end we employed a radiotracking system of the type so successfully used for the grizzly *Ursus arctos* L. by Craighead and Craighead (1972).

In this paper I describe the mountain lion social system in the Idaho Primitive Area, its role as a lion density determinant, and discuss its adaptive value. The radiotracking data upon which my analysis is based were primarily gathered from January 1970 to June 1972. In this study with biotelemetry, we used a lion population where the dynamics and general relationships had been established with a recapture scheme through the five previous winters by Hornocker (1969a, 1970) and Wiles.

ACKNOWLEDGMENTS

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Any successful long-term study of a potentially dangerous large carnivore must be a team effort conducted in a spirit of cooperation. I thank Dr. Hornocker, who conceived the study, for giving me the opportunity to conduct the radiotracking studies and for providing unpublished information, helpful advice and suggestions. Wilbur Wiles has assisted in all aspects of the winter work from the inception of the study. He has provided the continuity so important in long-term field investigations. J. Messick radiotracked lions in summer and winter and his contribution, companionship, and enthusiasm are gratefully acknowledged.

Drs. R. Knight, D. Chapman, and D. Johnson gave freely of their time for discussion and manuscript suggestions. My discussions with Drs.

T. Bailey, R. Drewien and R. Hursey were important in developing my thinking regarding some aspects of this paper. A. Dyke and N. Talbott read the manuscript and offered helpful suggestions.

Drs. J. J. Craighead and F. C. Craighead, Jr. provided the opportunity for various periods between 1965 and 1968 for me to hone my skill in the art of radiotracking. A. Johnson of A. R. Johnson Electronics, Moscow, Idaho, was codesigner and manufacturer of the radiotracking equipment I used for lions. His cooperation and prompt service were an enormous help.

For help in the Idaho Primitive Area I thank particularly E. Dodds, Mr. and Mrs. J. Taylor, Mr. and Mrs. R. Gorke, A. Lewis, D. Welch, D. Neider, and Mr. and Mrs. H. Derrick. Veteran pilots B. Dorris, B. Fogg, and P. Remaklus of Johnson Flying Service in McCall provided excellent service.

My wife, Sue, lived and worked with me in the Primitive Area for 18 months and has been a constant source of aid and encouragement.

THE ENVIRONMENT

Located in the Salmon River Mountains of central Idaho, the Idaho Primitive Area encompasses nearly 5,200 roadless square kilometers contiguous to and south of the Salmon River (Fig. 1). This remote region exists in a nearly pristine state with unpopulated expanses of wilderness beyond most of its boundaries.

Strongly influencing physical and biological interactions in the region are the deep, narrow canyons of the Salmon River and its tributaries (Fig. 2). Elevations range from 900 m along the Salmon River and the Middle Fork and South Fork tributaries to mountain peaks of 3,100 m with the major land mass above 1,700 m. The high country that rims many of the canyons is comprised of sharp ridges, glaciated basins and small alpine-like valleys (Fig. 3). The canyons have narrow stream bottoms, steep hillsides, cliffs, and talus slopes. Between 1,400 and 2,300 m in the north central section of the Area is the Chamberlain Basin with gently rolling timbered hills and meadows along broad stream courses that gradually become deep, narrow canyons.

The central Idaho region is almost entirely public domain; the Primitive Area itself covers portions of four national forests. Principal land uses in the Area are restricted now to recreation and some mining. No domestic stock are grazed except for the horses used to support recreation and administration.

We captured lions with hounds in winter in an area of approximately 520 km^2 in the lower Big Creek drainage (Figs. 1 and 4), a major tributary of the Middle Fork of the Salmon River in approximately the center of the Primitive Area. We radiotracked lions from the air over the entire Area and from the ground over most of the northern half.

The big canyons were hot and dry through the summer and early fall. Precipitation varied from an average of 76 cm in upper Big Creek to less than 51 cm along the lower Middle Fork (Rice 1971). There was a rainy period in autumn and in the spring, but much of the precipitation came as snow from late fall through the winter. The lower Middle Fork was essentially snow free for most of the winter but snow accumulation on the higher ridges often exceeded 3 m. From late November through February snow covered most of the big game ranges (area below 1,800 m) in depths from a few cm to a meter depending on slope exposure. The southeast-exposed slopes were often bare after late February. Temperatures reached below -18° C from November through March but remained below this minimum for 2 weeks or more only in December and January. Temperatures above 32° C were common during the day in canyons from late June to August.

In the Primitive Area characteristic vegetation zones reach their best development within fairly definite altitudinal limits but these cannot be rigidly defined. Typically on the exposed sites, the vegetation from the lower zone reaches high into the next, while the vegetation characteristic of the higher zone extends downslope in protected draws. Often the extensions are discontinuous and the resulting interfingering provides great heterogeneity. Of the vegetation zones described by Daubenmire (1952) for Idaho, the ponderosa pine *Pinus ponderosa* Dougl., Douglas fir *Pseudotsuga menziesii* (Mirb.) Frenco, spruce-fir *Picea engelmanni* Parry/*Abies lasiocarpa* Hook., and the sedge grass or alpine-like zone are found in the Area.

The lowest zones, the ponderosa pine and the downward-extending fingers of the Douglas fir, comprise the big game winter range (Figs. 2 and 4). Here there are many bunchgrass-dominated open areas, especially on the well drained southeast-facing slopes. On the exposed slopes and in the little basins higher in the drainages there is an *Artemisia tridentata* Nutt./bunchgrass association. The important winter browse plants, mountain mahogany *Cercocarpus ledifolius* Nutt., bitterbush *Purshia tridentata* Pursh. and lower, spring greesebush *Glossopetalon nevadense* Gray live characteristically in the broken bluff areas and on open, exposed ridges.

Much of the upper Douglas fir and spruce-fir zones are covered with thick stands of seral lodgepole pine *Pinus contorta* Dougl. which dominates after fire. Scattered along stream courses or in bog areas are numerous mountain meadows of various sizes but they form only a small percentage of the total area.

Some mule deer, elk and bighorn sheep *Ovis canadensis* Shaw remain in the lower canyons year long but reach highest density there through the winter when the accumulating snow of late November and early December renders the bulk of the Primitive Area land mass (the area above approximately 1,800 m) uninhabitable. Through December and January, the browse plants of the rough bluff areas, conifers, and dried bunchgrass are eaten (Claar, in prep.). With the opening of the south- and east-facing slopes in mid- to late February, *Poa* spp. begin to green and are increasingly utilized. Through March and April, deer and elk use the greening open slopes and bottoms with increasing intensity, reaching a peak in late April and early May. Then these animals move on, following the spring green-up to the highest elevations (Fig. 3). Flowering, seed-set, and soil moisture depletion occur first on the lower slopes and progress rapidly up the elevational gradient through the hot summer. The ungulates remain at the higher elevations through the summer and fall but descend as snow depths increase in late November.

The extreme topography and attendant climatic and drainage patterns influence not only the observed vegetation patterns but also the length of the growing season and availability of succulent and preferred forage. These in turn affect the movements and seasonal distribution of the ungulates and their symbiont, the lion.

TECHNIQUES AND PROCEDURES

My goal was to follow the day-to-day movements of a number of mountain lions simultaneously through summer and winter as they roamed about a vast mountain wilderness. The logistical methodology for the winter study had been developed by Hornocker and Wiles (Hornocker 1970); I simply modified and expanded the system for summer use.

During the winter we used seven camps established at 10 to 16 km intervals in the Big Creek study area. Each camp was stocked with provisions and equipment by mid-November before the start of the winter field work. Three additional camps, established at the higher elevations, facilitated summer work. Travel on the area was by foot in winter and by foot and horseback in summer although horses served only for stocking and supplying camps. For access to the Primitive Area, we used light aircraft.

From January 1970 to May 1972 a total of 669 days was actually spent searching for, tracking, and radiotracking mountain lions. W. Wiles worked all winter seasons; J. Messick worked from May to September 1971 and from January to April 1972. I was responsible for the radiotracking effort and lived and worked on the area from January 1970 to December 1971 and after that radiotracked from the air. M. Hornocker supervised the overall lion project and frequently visited the area and actively participated in the field work. Normally there were never more than two men working at a time. Together the investigators covered more than 15,300 km on foot between January 1970 and May 1972, while searching for or following the day-to-day movements of lions. Additional kilometers were traveled and time was spent in establishing, stocking, and maintaining the camp system.

Hornocker (1965, 1970) developed and described the methods we used to capture, handle and mark lions. Briefly, three trained hounds were used to capture lions; to escape the dogs lions normally climbed trees. From January 1970 to May 1972, 17 individuals were captured 55 times. Radiotagged lions could be recaptured any time of year; otherwise, we could capture lions only in winter when we had snow for tracking.

All captured lions handled were given intramuscular injections of phencyclidine hydrochloride administered by Cap-Chur syringes fired from a powered-charge gun. Doses were based on estimates of the lion's weight or known individual requirements (Hornocker and Wiles 1972). If drugged lions remained in the tree we lowered them to the ground by rope. If lions jumped from the tree upon being injected, we approached them on the ground. All lions captured for the first time were marked with numbered, colored, aluminum cattle tags and all were tattooed with an identifying number in both ears.

We attached 37 radio transmitters to 15 different mountain lions as described by Seidensticker et al. (1970)(Fig. 5). Of the 15 different lions we radiotracked, we classed nine (3♂♂ and 6♀♀) as residents on the Big Creek study area; four (2♂♂ and 2♀♀) were first captured and radiotracked as large kittens and later as transients as they left the area; two (1♂ and 1♀) were classed as transients. The population history of these lions is outlined in Table 1.

We could only gather the requisite data on population structure and dynamics through the recapture methodology. Since lions are rarely observed in the wild, we utilized the radiotracking system to monitor the day-to-day movements of undisturbed lions. This technique also allowed a rapid analysis of a new individual's population status.

We monitored the movements of radiotagged lions from both the ground and from light aircraft following the general procedure described in Seidensticker et al. (1970). When possible, all radiotagged lions were located from the air during each flight; only selected individuals were radiotracked from the ground. On the ground, a line-of-sight from receiver to transmitter was usually required. When a signal was obtained, we moved closer to the signal source and attempted to locate and accurately plot the location by triangulation. These locations were termed "fixes." If time or topography prevented a close approach, we used the general topography and the single bearing to determine an approximate location which was plotted and recorded as a "bearing-with-distance." General locations in a drainage or on a ridge system were recorded as such but these were not used in the analysis of movements. Each "lion-location-day" represents a lion's position (fix or bearing-with-distance), the first determined if more than one was obtained, on a given day. In the mountain wilderness this was the only practical and often the only possible level of sampling.

We radiotracked mountain lions from light aircraft 97 different times at intervals of 1 to 21 days, for a total of 121.3 h of flying time ($\overline{x}$ = 1.26 h). From the air we located the 15 lions 340 different times.

A digital computer was employed in the analysis of the movement data comprising 1,386 lion-location-days. With each location we recorded elevation, time, and when possible, habitat type, activity, location of big game kills, if present, and any association with other radiotagged lions. Locations were plotted on a map with a 0.162 km^2 (40-acre) grid. Data were reduced to coded form and punched onto cards. Methods of analysis are described with the results. All measurements were in the English system and were later converted to metric. Significant level was $P < 0.05$.

MOUNTAIN LION RESPONSE TO MAN

The way in which lions responded to our presence and activities was analyzed to estimate our influence on their movements and to sharpen our predictive ability with man as an ever increasing and inevitable feature in their environment.

The capture of lions year after year in predictable areas demonstrated that our methodology did not result in any long-term changes in area use. There were short-term shifts which varied with disturbance intensity. In decreasing order of intensity they include: (1) capture with hounds and subsequent immobilization and handling; (2) capture with hounds but not immobilized and handled; (3) close approach by the investigator; and (4) investigator presence in the general area.

In three winters we monitored the response of radiotagged lions from 43 captures with hounds (32 lone individuals, 9 family groups, 1 sibling group and 1 consort pair). The usual response of a lion pursued by trained hounds was to climb a tree but in some instances they sought refuge in caves or bluffs. Lions we monitored which had been treed but not drugged did not move from a capture site until after dark. The distance a lion moved was dependent on whether it was handled or not, and, for a female, the age of her kittens (Table 2). The first movement of a female with small kittens after capture was usually longer than her normal day-to-day movements with kittens the same age. For males, the first movements after capture and handling were shorter than the movements made when the animals were captured but not handled. But these latter movements did not differ from what would be expected under normal conditions. When lions were immobilized and handled, subsequent travel after the first movement was greatly reduced if we had lowered the immobilized cat by rope for an extended distance from a tree or bluff or if the lion remained hanging from the rope while we maneuvered it into a favorable position. Our handling in these situations probably produced a stiff or sore leg. Important here is that the lion initially moved away from the site of unpleasant experience to one of its own choosing where it remained until it recovered.

Lions were captured from mule deer or elk kills 15 times; they returned to these kills on only six occasions (Table 3). If the kill was nearly utilized before capture the lion did not return (N = 6). If the kill was fresh (N = 9), the response depended upon handling or the presence of young kittens. Lion No. 29 did not return to fresh kills when the kittens were young; when the kittens were older and when she was alone, she returned to a new kill (Table 3). Females alone and males returned regardless of whether or not they were immobilized and handled except in the instance of a female which was attacked by our dogs as she was coming out of the effects of the drug.

In our radiotracking we attempted not to interfere with movements and activities of lions. When we began our intensive radiotracking work we knew nothing of lion flight or tolerance distances or the other factors that might affect movements and activities such as habituation, visibility, or response to suddenness of meeting, etc. Most location data were obtained from distances of not under 180 m and frequently much more. This of course reduced our degree of accuracy in pinpointing locations but not in any important way in regard to my study objectives.

Even with the advantage of our radiotracking methodology we could rarely see lions. In most instances it was impossible to tell if the lion was or was not aware of our approach. In some situations it appeared that if the lion was aware of the investigator's presence it froze. If approached, even at a considerable distance (180 m), the cat sneaked away rather rapidly. In some cases the lion froze until the investigator had moved off, then it either remained or moved away rapidly.

When we surprised a lion by silent approach, the lion usually fled. However, when I moved in close to No. 93 in an attempt to determine the exact position of her kill and to see the size and number of her kittens, she slowly advanced toward me until I threw a stick which broke over her shoulder. She ran back into cover, but remained in the vicinity for 5 more days.

Lions did not appear to avoid our sign or our camps except when we were in residence with the hounds. I often found where a lion had utilized trails I had broken in the snow only a few hours earlier. We regularly monitored lion movements from camps where lions at times moved to within a few hundred meters. We occasionally found old tracks made through our camps in our absence. In one instance a female with large kittens killed a cow elk only 30 m from a frequently used camp less than 12 h after I left.

It was clear from monitoring radiotagged lions that they were not responding to our presence or activities in any way that would bias our conclusions. They were predictable in their movements after capture; this was taken into consideration in the data analysis.

SUMMARY OF POPULATION STATISTICS AND DYNAMICS

During eight winters of work in the Big Creek study area, 54 lions, including 16 adult males, 14 adult females, and 24 juveniles (12♂♂ and 12♀♀)(Table 1), were captured and marked. Of 29 lions first captured as adults, only 13 (5♂♂ and 8♀♀) were captured 2 years or more on the study area ("residents" in Table 1). Sixteen adult lions (12♂♂ and 4♀♀) were captured only in a single winter and not recaptured in subsequent years ("transients," Hornocker 1970). Adult female No. 52 (Table 1), first captured during the last winter of study, was considered resident because we were reasonably certain she was present the previous winter. Male No. 28, first captured during the third field season, was recaptured three winters later (January 1970) and during the two subsequent winters; he was considered resident during the last 3 years. Female No. 93, captured only during the seventh winter on the Big Creek study area, was considered resident for reasons that will be explained later. Of the 16 transient lions first captured as adults, 9 males and 2 females were judged to be young animals based on appearance, dentition, and weight. Hornocker (1970) believed that most of the transients captured during the first two field seasons of study were actually self-sufficient offspring of resident females that had not yet dispersed from the area. Three males and one female (Nos. 10, 92, 43 and 21) appeared older. Nos. 92 and 93 were first marked as adults in the Chamberlain drainage, 32 km north of the Big Creek area, during the 1965-66 winter.

The number of adult lions captured varied considerably from winter to winter (Table 4), and was, of course, a function of recruitment, mortality, emigration, immigration and capture success. Hunters killed two resident females (Nos. 4 and 12) during the 1967-68 winter. Male No. 18, last captured early in 1970, probably died before the next winter (Hornocker 1970). Female No. 11 was sacrificed after suffering wounds in an encounter with an elk that would have been fatal. We do not know the fate of male No. 7 or female No. 16; they were older appearing lions who may have died or have been killed. They were not captured and there was no evidence they were present in the study area. Lions marked as kittens were never recaptured in the Big Creek drainage after their first winter of independence.

Tables 1 and 4 are based on capture and recapture data only; in some years additional lions were known to have been present. Recapture data indicated that the adult resident lion population was marked by the third study winter (Hornocker 1970). Hornocker and Wiles (Hornocker 1970) were certain from tracking that female No. 29 was present during the first two winters and that Nos. 24 and 16 were present during the 1966-67 winter; we were reasonably certain that male No. 3 was present during the winter of 1970-71.

The composition of the population on the Big Creek study area during the last seven winters of study is depicted in Fig. 6. Because they were incomplete, data for the first winter are not included. Only capture data are included with the three exceptions discussed above. Transient lions who became self-sufficient during the winter are included. The stability of the resident male portion of the population over seven winters is striking. Resident female numbers were constant for three winters but later deaths were never quite compensated. In the remainder of this paper I have related these observations to the underlying social and ecological factors.

MOVEMENTS AND HOME AREAS

Extent of Movement: Home Area and Dispersal

When one snow tracks unknown mountain lions, their travels seem random and without bounds, an observation emphasized in much of the early lion literature. By recapturing marked lions, Hornocker (1969a) demonstrated that most mature adults (residents) confined their movements to specific areas where they were captured year after year; in addition there was a population component consisting mostly of younger adults which were transients on the study area. This concept of land tenure was confirmed with the radiotracking methodology.

As examples of lion movements, in Figs. 7-11 I show a plot of all lion-location-days for breeding adult Nos. 24 (♀), 28 (♂), 29 (♀), 45 (♀), and 93 (♀) for which our data spanned at least one entire year. Sequential locations are connected to provide insight into movement patterns. These should not be interpreted as actual observed pathways. From these prolonged observations, it was clear that resident adults reused definite areas (sites) although there were seasonal patterns, changes over time, and individual variations.

Occasionally, during the winter and spring, resident lions crossed high, snow-filled passes and transient lions crossed considerable tracts of high country as they moved between big game winter range areas, but normally both classes of lions restricted their movements during this period to the canyon areas below 1,800 m (Table 5). Residents occupied fairly distinct but usually contiguous winter-spring and summer-fall home areas (Figs. 7-11).

Nos. 24 and 29, both accompanied by large kittens, were not found at the higher elevations until after the first week in June. But in the years not accompanied by kittens Nos. 93 and 29 moved to their summer areas by early May. Nos. 28 and 26 (resident males) remained on their winter areas through most of May and in June moved between their higher winter and summer areas. Female residents remained almost exclusively on their summer areas from June through August and males did so from July through August. From September through November, lions used lower elevations more (Table 5). By mid-December, snow accumulation at higher elevations confined the ungulates to winter ranges and the lions had returned to their own winter areas.

The summer areas used by resident lions were larger than winter areas (Table 6) but size varied among years. (Area determinations were based on the irregular polygons formed by connecting the outermost locations.) At times lions moved across their areas between sequential locations. We followed the travels of some lions, including the movements away from the Big Creek drainage in winter, only by air tracking. This was an unbiased procedure as compared with ground observations in that I nearly always located all lions with properly functioning transmitters. Even with the extended intervals between some flights (determined by weather and budgetary considerations), the cumulative area totals are generally comparable.

Contrasting with the rather restricted movements of adult residents were the movements of newly independent kittens and other transients. I radiotracked two litters of kittens which became self-sufficient late in their second winter: 8 March 1971 and 21 March 1972 for female Nos. 93 and 29, respectively. The final family break was made in a portion of the female home area frequented earlier in the winter. The female left the kittens at a kill and did not return. After leaving the female, siblings remained together or came together for short periods before finally going their separate ways.

Within 12 days Nos. 48 and 49 and within 7 days Nos. 47 and 51 had departed the area formerly used together with the female the last few months before independence. All but No. 51 (♀) left the Big Creek drainage immediately. After independence kittens Nos. 48 and 49 roamed widely as did another young transient male, No. 50 (Fig. 12).

Lion No. 50 was first captured and radiotagged in February on upper Big Creek and moved to the Chamberlain drainage (25 km north) by March. In June he moved south across lower Big Creek then north again to the high country between the Chamberlain Basin and the Middle Fork of the Salmon River (Fig. 3), a round trip of about 60 airline km. His transmitter stopped in mid-August. He was killed by a hunter near the mouth of the South Fork of the Salmon River early in 1972, about 40 km from where he was first captured (Fig. 12).

The data on disassociation of females and their young, based on captures with hounds (Hornocker 1970) were far less precise than those obtained through radiotracking but the same general pattern is clear. There was variation in the time of independence and size of kittens at that time.

No lions marked as kittens on the Big Creek study area were recaptured there after their first independent winter (Table 7). Newly independent lions did not restrict their movements; they did not reuse particular areas; there was no attachment to site.

Nos. 45 and 46 (♀♀) were first captured in late November and early December 1970. Their movements over the subsequent two winters document the transition from the transient to the resident phase of a lion's life cycle (Fig. 13). In the first winter No. 45 remained on the Big Creek area until late January and then moved north to the Chamberlain drainage. She was back on Big Creek by 1 June and spent the summer and fall in the headwaters of Chamberlain and Big Creeks. Her transmitter failed shortly after 1 December. We recaptured her and attached a new transmitter in April 1972. She remained on the Big Creek winter range until late May when she moved back to the high country where she had roamed the previous summer and fall (Fig. 10).

No. 46 remained on the Big Creek study area until late May when she moved during a 2-wk period to the West Fork of Chamberlain Creek and back. Her transmitter failed in mid-June but she was reinstrumented in early December of the same year. She remained in the area utilized the previous winter. In summer, she moved to the high country contiguous to her winter area.

During the 1971-72 winter both females (Nos. 45 and 46) restricted their movements to the Big Creek drainage, a sharp contrast to the winter previous (Fig. 13). They both bred successfully for the first time late in their second winter there.

Home Area Utilization

Seasonal and Daily Activity Patterns

Seasonal variation in day-to-day movements of lions was related primarily to prey type (Fig. 14). From September through May in the

Primitive Area, mountain lions killed and fed primarily upon mule deer and elk which, except for fawns and adult female mule deer, are far larger than themselves (Hornocker and Seidensticker, in prep.). Lions dragged kills to protected sites and covered them with whatever was available (snow, leaves, needles). They remained in the vicinity from 1-19 days with only occasional short trips away until the kill was consumed. A kill not closely guarded would have been quickly eaten by a variety of scavengers including the common raven *Corvus corax* L., black-billed magpie *Pica pica* L., golden eagle *Aquila chrysaetos* L., coyote *Canis latrans* Say, and/or occasionally, another lion.

In January, February and March 1971 and 1972, we found lions associated with confirmed kills on 43 percent of the lion-location-days, using the combined data (N = 395) for the most intensively tracked adult lions. We were no more successful in locating lions when they were associated with kills and rather stationary than when they were not and moving about, as tested by comparing the actual time at kill sites and the time between them as determined by intensive snow tracking with radio-tracking data only for two different females (Table 8).

The trend toward increasing movement as the year progressed, shown in Fig. 14, is the effect of fewer kills made during and after late winter (Hornocker and Seidensticker, in prep.). Between kills, lions traveled about, rarely spending over 1 day in the same location. This same movement pattern occurred in summer when small rodents, particularly Columbia ground squirrels (*Spermophilus columbianus* Ord), and an occasional deer and elk were the usual fare.

Body movements produced changes in transmitter signal patterns which were detected as slight variations in beats-per-minute. We used these together with changes in location to determine if lions were moving. From these, I obtained a crude estimate of daily activity. For winter, I lumped location data into day and night categories and calculated the percent classified as active (Table 9). Data on locations were clustered between mid-morning and mid-afternoon, night data near 2200 and 0600. I have few data on the important hours just before and just after sunrise and sunset. Lions were more active during the day in summer (June-August) than at other times of the year (Tables 9 and 10). Movements and/or activity ranged from 14 to 75 percent during the 12 summer days we continually monitored females Nos. 29 and 93 for a number of hours.

Periods when lions were active appeared largely independent of weather. Lions moved while snow was falling and during widely varying conditions of cloud cover and temperature. Light rain mattered little but lions were less active during the long, heavy rains that were frequent in spring and fall.

It was usually not possible to tell from radiotracking if a lion was hunting, just moving about, or traveling. Increased activity during the day in summer is almost certainly related to the availability of the Columbia ground squirrel, whose above-ground activity is wholly diurnal from my observations. In winter, we found mule deer and elk kills that were made in the evening, at night, and during mid-morning. An active prey animal is presumably easier to discover and to stalk. Because of variable patterns in prey activity (Mackie 1970, Craighead et al. 1973), a variable activity schedule may be essential for lions for which vision plays a primary role in hunting.

Distances Moved

The straight-line distances between the first observations on sequential days when I located lions provide an index of the distances lions moved in one day. But variation increased with an increased time interval between sequential locations (Table 11). Adult lions restrict their movements to a specific area which they can and occasionally do cross in a single day. Consequently, I did not combine all sequential location data; as an index of distances progressed, I utilized only straight-line distances between the first locations on consecutive days. Days when lions did not move are not considered here.

Individual lion movements varied considerably (Tables 12 and 13). In both summer and in winter, males moved significantly farther than females. In winter (Table 12) there was no significant difference among sexes nor was there a significant difference for the same individuals between the 1970-71 and 1971-72 winters. During the summer and fall (June-November) in 1971, a female with two kittens approximately 1 yr old (No. 29) moved significantly farther than female No. 93 who, for most of the period, had small kittens (to 5 mo). The male (No. 28) moved significantly farther in summer than during winter. In contrast, a female (No. 93) with older kittens moved farther in winter than in summer when she had a new litter. There was no difference between the winter and summer in the distances moved by No. 29 whose kittens were 6 mo old in December 1970. The maximum straight-line distance moved on consecutive days and between sequential lion-location-days (intervals of 2-10 days) also indicated that males moved farther than females; the longest movements were by transient males (Table 14).

Lions seldom used the frozen waterways and trails as did coyotes wintering in the same areas. Usually lions zig-zag back and forth through thickets, move around large openings, under rock overhangs, up and down little draws and cross and recross creeks. The impression I gained in snow tracking lions was that they were always working back and forth. Through this procedure they are better able to detect a prey animal and launch a successful attack. With the zig-zagging the "net daily distances" are a gross underestimate for the actual distance traveled by a lion.

Movements in Relation to Topography and Habitat

Both winter and summer home areas contained diverse topography and habitats (Figs. 2, 3 and 4). The canyon winter areas were particularly rough and broken: a mosaic of dense Douglas fir timber, open ponderosa pine, sage-grass openings interspersed with bluffs and talus slopes (Figs. 2 and 4). In snow tracking lions we noticed occasionally that they walked around the edge of openings rather than through them but as often as not the tracks next led over an open hillside. Over 95 percent of lion-location-days were associated with timbered and/or rocky broken areas. The summer ranges of Nos. 29 and 93 contained burn areas that were over 1.6 km across at some points. Here the lions often utilized the edge to a considerable degree but only occasionally frequented the open burn areas. Data from radio and snow tracking demonstrated a wide habitat tolerance but cover in a general sense was an important niche component.

While the shape of a lion's range, particularly in winter, is influenced by the elevational relief and attendant snow accumulation, most topographic features, with certain obvious exceptions, do not obstruct lion movements. Even the Middle Fork of the Salmon River, a wide, deep, swift flowing river, was crossed frequently although I believe that in some stretches and during peak snow melt, it might not be crossable, particularly for females with small kittens. Air tracking movement data indicated, however, that resident male No. 26 crossed the river during relatively high flow.

Despite this great mobility we found that lions preferred some passes and corridors for travel which seemed influenced by the general lay of the land. They used these corridors when crossing from one drainage system to another. Different lions used the same general creek crossings, canyons and passes irregularly and infrequently. Occasionally a lion walked in the track of another in snow just as they would sometimes walk in a trail I had broken in deep, difficult snow. No network of snow trails was formed as has been described for wolves *Canis lupus* L. (Mech 1966); nor did lions have the ridged network of pathways which has been described for the house cat *Felis catus* L. (Leyhausen 1965).

Distribution of Home Area Occupancy

Figures 7-11 show that lions were not found in all parts of their home areas equally often. To analyze this occupation density, I partitioned the Big Creek winter range area into 2.6 km^2 (1 mi^2) quadrats and tabulated the number of locations in each (Tester and Siniff 1965, Altmann and Altmann 1970) for the lions for which I had most complete data: Nos. 28 (♂), 29 (♀), 46 (♀), and 93 (♀). A computer program tabulated data where I selected the first horizontal and vertical lines for the grid; the same grid served for data from all lions.

In Tables 15 and 16, I have summarized the distributions of the lion-location-days among the home area quadrats; the quadrats are ordered and listed according to the number of days a lion was located in each with the lowest quadrat being used the most. The total number of quadrats provides an estimate of actual areas used; the number of locations per quadrats expressed as a percent of the total location-days identifies differential range utilization.

For lion Nos. 28, 29 and 93, all older residents, nearly 75 percent of the locations were in 50 percent of the quadrats during the winter-spring period (Table 15). During the first winter No. 46 was resident on the study area, 75 percent of her location-days were in less than 25 percent of the quadrats. In her second winter (1971-72) on the area, the data indicated a trend toward the pattern we found in older adults. Area use was very similar for the adult resident male we radiotracked (No. 28) in both winter-spring periods, but for female No. 29 there was a sharp contrast between the 1970-71 winter-spring period (Dec.-May) when accompanied by 6 to 12-month-old kittens and the 1971-72 winter-spring period. Area use this second winter is strikingly similar to that which we observed for No. 93 during the 1970-71 winter when she was also accompanied by large kittens. Both litters of kittens became independent during March and both females moved to their summer areas before other lions.

For the period June-November, we were able to radiotrack only adult females Nos. 29 and 93 with sufficient frequency to make an analysis of quadrat occupancy (Table 16). No. 93 moved over a larger area than No. 29 but she did this before she had kittens in early summer.

Much of the winter-spring aggregation of lion-location-days

(Table 16) reflects the time lions spent associated with and the localizing effect of the ungulate kills. Radiotracking and intensive snow tracking show that different reproductive classes of lions spent different percentages of their time at kills versus the percentages of time spent moving around between kills (Table 17). Kill association time is only roughly correlated with the species, sex and age (amount of meat) of the kill, and the size and number of lions involved (Hornocker and Seidensticker, in prep.). Although lions nearly always completely utilize their kills, young adult females and females with older kittens spent more time with kills than did adult males and females after the independence of their kittens. Females with older kittens kill more frequently than other classes and this is understandable; young females without kittens appear to extend their time at a kill. Older lions, on the other hand, consume even a large ungulate quickly and there appears to be a limit on the time these lions will linger.

The interval between sequential kills varied from 1 to more than 12 days in winter; sequential kills were rarely made close together (Hornocker and Seidensticker, in prep.). Resident male No. 28 and young females tended to roam more widely before and after kills than did Nos. 29 and 93, the older resident females with kittens (Table 18). There was a strong progressive trend toward the actual site for the 2 days preceding the kill by the older and well established residents Nos. 28 and 29, but not by the other lions. After leaving the kill there was no immediate further attraction to that proximity. To the contrary, it was our impression that lions made a distinct effort to travel to other parts of their home areas (Table 18). Occasionally a lion returned at a later time to a kill site before another kill was made (N = 4), but by that time scavengers had cleaned up the carcass and the lion did not linger.

Movement patterns of females with small kittens were more complex than those of other classes and varied with the individual lion. Between kills during the first winter, the female left the kittens at protected sites in thickets, bluffs, or under large fir trees or at old kills (No. 29 only). Kittens were usually moved each day but occasionally they were left in the same location for 2 days. Moves were usually much less than 1.6 km. From these sites, the female made loops out and back, probably hunting. No. 29 was captured with very small kittens (less than 3 mo old) near a kill late in 1968, and this female brought her 6-mo-old kittens (Nos. 47 and 51, a different litter) to kills late in 1970. No. 93 did not bring her 4- to 5-mo-old kittens to kills in the fall of 1971 and this had been observed earlier in the study for other females. With one kill, the kittens were nearly 0.8 km away from the site and [illegible] moved them to a new location even while she was still returning.

During the kittens' second winter when we radiotagged entire families, family groups most frequently moved about in a cohesive pattern (Table 19). During this second winter until the final break kittens were with one exception always at the female's kill.

The important point here is that kittens were not the localizing factor in the second winter that they were during the first; home area utilization by females during these later stages of kitten development differed considerably as a result (Hornocker 1969a).

Lion Home Areas and Prey Acquisition

Ungulate vulnerability on the Big Creek winter range was not determined by their abundance; various behavioral and ecological factors operated to make some prey classes more vulnerable to lion predation than others (Hornocker 1970). For the lion, the hunting and killing of a large ungulate is a singular activity. Motivated to hunt and to kill, the lion must search and find the prey animal in a situation where it can approach undetected to a distance from which a successful attack can be launched. Although difficult to measure (Hornocker 1970), this distance is probably a function of prey class. The distance seemed shorter for bull elk than for calf elk or fawn mule deer. The avoidance of attack by the ungulate, on the other hand, takes two forms (Kruuk 1964): (1) behavior that modifies the chance of meeting such as habitat-selection, gregariousness, and degree of conspicuousness and (2) overt action that influences the actual outcome of the encounter. A balance must be struck; to waste energy for unnecessary predator avoidance is to reduce energy that could serve other purposes, but death remains always as the alternative.

Both deer and elk varied in their habitat use and grouping tendencies, and the number killed by lions varied with these trends (Hornocker and Seidensticker, in prep.). The mobility of deer and especially elk (Mackie 1970) enables them to adjust rapidly to environmental change and constantly utilize "favorable" portions of their range. ("Favorable" can mean absence of predators as well as availability of preferred forage.) Deer and elk seasonal distribution and habitat use reflected availability of preferred forage and, at times, population pressure (Klein 1965, Mackie 1970, Knight 1970, Claar, in prep.). Important too were disturbances such as pressure during extended hunting seasons which through learning and habituation force ungulates into inaccessible regions that would normally not be used during that season (Knight 1970, Geist 1971, personal observation 1971 in Chamberlain Basin). Hornocker (1970) described how mountain lions keep deer and elk moving on the winter range. When lions remained in the rather localized sites around the kill, deer and elk in the area became aware of the lion's presence and moved from the vicinity. In several instances we observed both deer and elk either running or deer sometimes sneaking away from the vicinity of a lion that we had located through radiotelemetry. Wiles described one instance where an elk in the proximity of a radiotagged lion gave a repeated alarm bark for 10 min before moving on. I never observed deer or elk mobbing (see Eisenberg and Lockhart 1972) a lion. But I have seen mule deer mob coyotes in the Primitive Area and elk mobbing a black bear in Yellowstone Park, and Hornocker (1969b) reported bighorn sheep mobbing a bobcat *Lynx rufus* Schreber. It was apparent that if a mule deer or elk established the lion's position the ungulate moved from the vicinity.

Over the Big Creek winter range kills tended to be aggregated in certain areas. To test this hypothesis, I examined kill distribution through the quadrat occupancy method (Table 20). I restricted this analysis to a 181 km^2 (70 mi^2) area we were continually covering. For the 1970-71 and 1971-72 winters, mule deer and elk kills tended to be aggregated (Table 20) but not independently. It could be argued that a quadrat size of 2.6 km^2 (1 mi^2) is too large to properly show trends, but considering sample size, lions' winter area size, the tendency of lions to drag kills to overhead coverts, and general research conditions, quadrats this size are justified for displaying results quantitatively.

The distribution of kills made by lions over their individual winter areas was examined and compared using the measure of dispersion described by Clark and Evans (1954)(Table 21). In a random distribution R = 1; with maximum aggregation R = 0; with maximum spacing R = 2.15. The kills of both the young newly established females, Nos. 46 and 93, and the older female which was spending her first winter in the Big Creek drainage were randomly distributed and underdispersed, respectively, during the 1970-71 winter. The distribution of kills made over the winter areas over two winters by Nos. 28 (♂) and 29 (♀), both well established residents, demonstrated a strong trend toward aggregation. R values for each winter for No. 29 indicated kills were slightly underdispersed. These analyses demonstrated that (1) there are certain areas where kills are made more frequently than others, (2) these areas are probably the same for both ungulate species, and (3) that over a given year kills made by a resident lion are random or underdispersed over its home area but over the years there are areas where kills are made more frequently.

Taken together the above analysis and description demonstrate that in the short run a lion's home area is in constant flux in terms of seeking of prey (mule deer and elk) in situations where they can successfully be stalked and killed. This is influenced by environmental factors such as weather, ungulate food availability and preferences, and even the movements of lions themselves. But over the long run, the conditions in certain areas are such that lions tend to be more successful there in making kills. Thus, familiarity with the home area is a distinct advantage in the exploitation of the food resource, especially for a female who must kill frequently and with predictable regularity if she is to successfully rear kittens.

DISPERSION PATTERNS AND LION INTERACTIONS

Spatial Patterns: Home Area Overlap

In two winter-spring periods (December-May 1970-71, 1971-72) we radiotracked a total of 9 adult resident lions: older adult resident Nos. 26 (♂), 28 (♂) and 29 (♀) were radiotagged and tracked both winters; from tracks, I was reasonably certain both Nos. 3 (♂) and 52 (♀) were present in 1970-71 but they were not captured and we only followed their movement in 1971-72; No. 24 (♀) was not captured in 1971-72 and because she was an old cat, it was possible that she was dead; No. 93 (♀), an older adult with large kittens, was first captured in the Big Creek drainage in December 1970 and remained until late April; Nos. 45 (♀) and 46 (♀), young adults, establishing as breeding residents, were radiotracked both winters.

In the Idaho Primitive Area, major waterways do not block lion movements and even the major canyons are usually spanned in a lion's travels. As a result, the shape of a resident lion's winter area tends to be linear in the outline of the major drainage systems as influenced by elevational relief and attendant snow accumulation. Changes in range size and the degree of range overlap during the winter are effected through movements up and down the major drainage system or by movement to a different system entirely. We found that no substantial part of any lion's winter-spring home area (December-May) was maintained to the exclusion of all other conspecifics. Home areas of resident males overlapped little but resident female winter home areas sometimes overlapped completely (Fig. 15). Transient lions of both sexes moved through any of these areas (Fig. 12).

In summer the pattern did not differ (Fig. 16). This conclusion is based on observations of the five resident lions Nos. 24 (♀), 28 (♂), 29 (♀), 45 (♀), and 93 (♀) that we tracked long enough to establish their summer areas, supplemented with radio location data obtained over part of the summer period for Nos. 46 (♀) and 26 (♂), the male transients Nos. 48 and 50, and tracks and other sign.

With the death and disappearance of four resident females and one resident male, there was a re-sorting and reshuffling of winter areas. Through the years 1964-68 Hornocker (1969a) did not observe what he considered regions of home area overlap in adult resident males. In the winter of 1968-69, adult male No. 3 was captured once deep in the range of adult male No. 18. No. 92, a male first captured as a large, older adult during the 1965-66 winter in the Chamberlain drainage, was captured in the winter areas of both these males. During the 1969-70 winter males Nos. 26 and 3 were captured in the range of No. 18, a very old appearing male (Hornocker 1970) which was not captured, and we believe he probably died (see above). During 1969-70, we did not capture No. 3 in his former winter area but Nos. 28 and 43, both large adult males, were captured there. Although we radiotagged Nos. 3, 26 and 28, we were only partially successful in monitoring their movements that first winter. Recaptures with hounds and intensive radiotracking during the winters of 1970-71 and 1971-72 demonstrated that No. 28 successfully and to the exclusion of No. 43 established himself in the area formerly utilized by No 3, which transferred to the area formerly utilized by No. 18. No. 26 retained his winter area but with altered boundaries.

Early in December 1970, we tracked No. 28 as he moved through what

At first glance this was somewhat surprising considering the degree of overlap in the ranges of adult resident females (Fig. 15). In the late winter of 1970, we could not find No. 29 in the winter area she had used previously as established by recaptures and snow tracking although she was captured there earlier in the winter. In December 1970 she was captured in her expected area but her tracks indicated she and her small kittens (6 mo) had come from the area formerly utilized by No. 4, a female killed by hunters. During December and January she remained in the area used during previous winters.

At this time No. 93 was moving about the same drainage system although remaining higher for the most part. She was originally captured and marked 25 km north in the Chamberlain drainage early in 1966 and we first became aware of her presence in early December 1970. We captured her and her two large kittens 2 weeks later and attached radio transmitters to all of them. In March, No. 93's kittens became independent. In late April she traveled back to the Chamberlain Basin. She had kittens some time in late June, probably fathered by No. 28 on Big Creek in March. I followed her day-to-day activity from the ground until mid-November. It appeared that she was not going to return to Big Creek for a second winter but this will always remain a mystery for she was killed by a hunter, probably early in the winter, near where she was originally marked. (Her transmitter was recovered by conservation officers of the Idaho Fish and Game Department.)

From the end of January, Nos. 29 and 93 used mutually exclusive portions of the Big Creek winter range. No. 29 remained in the area formerly frequented by the dead female No. 4. No. 93 traveled over a large area including a portion of No. 29's range. This continued until the end of April when No. 29 moved back into the area she had formerly frequented (Fig. 18). By this time, No. 93 had returned to Chamberlain. In 1971-72, No. 29 continued to frequent the area formerly used by No. 4, the dead female. No. 24, in 1969-70 and 1970-71 also appeared to shift her activity more into the lower portion of the area used by No. 4. However, our data on this lion are not as complete as for No. 29.

The movements of Nos. 45 and 46, young females which established home areas in the Big Creek drainage, have already been described. In both winters their home areas were partly or completely overlapped by the home areas of the older resident females. The movements of Nos. 45 and 46 during the 1970-71 winter when No. 93 was present were greatly unsettled and sharply contrasted to their restricted movements during the next winter when she was not present.

The spatial arrangement of adult residents did not differ from that described by Hornocker (1969a) in any important conceptual way. Most significant perhaps was the fact that the spatial arrangement for males was less rigid than the recapture methodology indicated. Resident males would occasionally travel into the frequently used area of an adjacent male, but these movements were of an exploratory nature or in some cases possibly related to females entering estrus. The land covered in these travels could not be considered part of their home areas at that time. Secondly, the range areas were larger for both sexes than the recapture data indicated. Hornocker (1969a) anticipated this and shaped his discussion accordingly. Of particular surprise was the extent of movement up and down the Middle Fork from the mouth of Big Creek by both Nos. 24 (♀) and 26 (♂). These movements resulted in a lower density of resident adults than indicated by Hornocker's (1970) calculations based on the Big Creek study area alone.

Individual Distance

The most frequent "social" behavior pattern in the mountain lion is that of avoiding other lions. Coming increasingly into play with an increasing degree of area overlap, individual distance and the mechanisms by which it is maintained are basic to the social system. To measure this parameter, I designed a computer program that for each adult lion each day calculated the straight-line distance to every other cat whose location was known. I calculated the dispersion of individuals over one region of the Big Creek winter range using the Clark and Evans (1954) technique.

In the winter of 1970-71 lions Nos. 28 (♂), 29 (♀), 46 (♀), and 93 (♀) and for at least 1 mo No. 45 (♀) jointly used a large section of the upper Big Creek big game winter range. In the winter of 1971-72 the same lions with the exception of No. 93 used this same area. No. 26 (♂) was in the lower end of this area occasionally although he never remained long (Fig. 15). Using the distance to the (1) nearest adult lion, (2) nearest other female, and (3) nearest older adult resident, I calculated the degree to which observed distributions departed from random expectations (Table 22). I used data only from air tracking so that the location of every lion was known with precision. Central for this descriptive technique is the area selected; here I used a 163 km^2 (63 mi^2) area that encompassed the winter areas or that portion most frequently utilized for the lions listed. R values ranged from 0.25 to 1.81 where 1 = random, 0 = maximum aggregation and 2.15 = maximum spacing. There were no consistent trends for any particular class or for all individuals. Perhaps most important were the number of R values that indicated a high degree of aggregated and random distributions.

The phenomenon of individual distance, although much discussed, has rarely been carefully measured. Seasonal changes in mean individual distances resulted from both the seasonal variation in area overlap and the larger summer-fall areas (Table 23). Variation between winters was the result of changes in the degree of range overlap particularly for female Nos. 45 and 46. During the 1970-71 winter they roamed widely while in 1971-72 they remained in the Big Creek drainage. The data for resident male No. 26 are biased in that infrequently he moved into the winter area of male No. 28 where we were concentrating our ground tracking effort. During this winter he spent more time in the Big Creek portion of his home area than he did in 1970-71 but not to the extent indicated in Table 23. For the other lions, I believe there is little or no bias involved.

Reproductive status alters mean individual distance over the winter (Table 24). In Table 24 I have included only the Big Creek lions and the data collected in that drainage system. The degree of area overlap did not really vary significantly. As indicated by the association data (below), intraspecific encounters were infrequent and of short duration. Even during winters when females bred, the distance data, where sample sizes were adequate for testing, were significantly skewed positively. The single exception is between Nos. 46 and 29, two females whose ranges nearly completely overlapped during the 1971-72 winter. In this case the coefficient of skewness is nearly 0, that of a normal distribution.

I do not know a lion's detection distance in regard to other lions but it undoubtedly varies and is dependent both on topographic characteristics and lion behavior. I cannot separate out those observations on individual distance in which one individual did not have any idea where the other was. In situations when one lion wanted to find another, whether it was a female looking for kittens after we had treed them in a different part of the drainage or a female and male coming together for mating, contact was accomplished rapidly. Considering the distances usually maintained by residents who used common areas, I was surprised by the degree of aggregation we occasionally observed. Though not in association we found Nos. 28 (♂), 29 (♀), 45 (♀), and 46 (♀) all in the same small drainage or around the same ridge a number of times. Apart from the striking pattern of avoidance I can only generalize that in the mountain lion, individual distance is not rigidly maintained; it is a dynamic phenomenon.

Lion Association Patterns

Adult mountain lions are essentially solitary in their activities; they rarely associate with other lions. The association frequency, defined here as the lion-location-days lions were found very close together or in company with another adult lion, ranged from 5 to 13 percent (Table 25). With the overt encounter as the fundamental unit of any sociological analysis, I examined the number and length of intraspecific encounters. Important here is that I was studying the lion population during a period of adjustment following the deaths of some older residents. Association frequencies under these conditions may have been at a maximum.

We found mountain lions very close to or in company with other lions in the following combinations, listed in descending order of frequency of the number of lion-location-days of observations:

(1)	adult ♂/ adult ♀ alone	21
(2)	adult ♂/ ♀ with large kittens	20
(3)	young adult ♂/ siblings independent of the ♀	4
(4)	adult ♂/ 2 adult ♀♀	2
(5)	young adult ♀/ ♀ with large kittens	2
(6)	young adult ♀/ ♀ with small kittens	1
(7)	adult ♂/ large ♀ kitten	1
(8)	♀ with small kittens/ ♀ with large kittens	1
		52 days

Pertinent observations regarding these 52 lion-location-days are grouped into 17 separate interactions based primarily on the situation (Table 26). Of the 17 interactions, 12 were adult male/female, 3 were adult female/female, 1 was adult male/2 adult females, and 1 was young adult male/independent sibling group (♂ and ♀). With one exception in September, these 17 interactions occurred from December through April on the winter range. This temporal distribution is probably not so much a factor of lion habits as it is of our own research effort and success.

Kills were observed at the site of 10 associations, probably involved at 2 others, and not involved at 5. This differs significantly ($P < 0.05$) from what would be expected in winter based on lion activity at and away from kills (43 percent of time at kills). Schaller (1967: 244) also reported that the tiger *Panthera tigris* L. appeared to socialize more at kills than at any other sites.

In Table 27 I have arranged the associations observed in a matrix to display association frequency of various sex-reproductive classes of adult lions and have ordered these in a cline in Table 28. Males did not associate; females associated but infrequently; females with kittens less than 1 yr old were never found associated with males and only twice with females.

During the 1971-72 winter, we radiotagged all three resident males in the Big Creek drainage. We did not find these males in association in the area shared by all three, along range boundaries, or during the rare forays into adjacent male home areas. One day, two resident males were within 0.4 km of each other in a small drainage but from what we could determine they did not come together. Resident males did not show the signs of frequent fighting as do, for example, large grizzly bears in Yellowstone National Park; the signs of frequent fighting by grizzlies are clearly recorded in the scars about their heads and shoulders.

I did not find females in association with males during their kittens' first winter. One male (No. 18) killed and partly consumed a litter of smaller kittens (Hornocker 1970). Danger to a female's reproductive success is involved at this stage of kitten development. Hornocker and Wiles observed where one female with small kittens abandoned her kill when a male approached and stayed.

During kittens' second winter, males were more frequently found near family groups. At first these approaches were of brief duration. Once a male (No. 26) moved into a large draw and a female (No. 29) with large kittens present moved up the drainage. No. 93 with large kittens moved from her fresh elk kill after adult male No. 28 arrived at the site. Although the situation here was complicated by our presence, the male remained for a number of days.

In the months before and just after the young become independent, the female associates with (tolerates?) adult males and even adult females more frequently and for longer periods (Fig. 19) than at any other time. This I postulate is related to hormonal changes associated with the onset of estrus. Rabb (1959) reported that the longest estrus period in a captive female was 11 days with 8 days the mode and shortest period. The associations where the pair showed cohesive movements over longer periods were probably related to estrus and mating but I can only postulate this; we rarely actually observed the lions and a consort pair as I term this interaction was observed copulating only once (by W. Wiles). A single male was involved in these associations and except in one case, only a single female. All consort pairs followed with biotelemetry involved only resident adults. Earlier in the study a resident female and a young transient male were captured together just after her kittens became independent (Hornocker 1971). Hornocker (1971) felt that this indicated that occasionally adult transient males may breed.

No. 50, a young male, joined No. 93 and her two large kittens 24 days before the kittens became independent. Since No. 50 was previously unmarked and not radiotagged, we first recognized his presence by observing his tracks in snow. After 9 days, we captured the group with hounds and he was instrumented. He remained with the family group for 15 additional days (including 2 more kills) before the female left him and the kittens. She traveled down Big Creek and remained in association with the adult resident male No. 28 for 3 days. No. 50 had removed his transmitter collar just before this last kill. We treed him and the two independent kittens near the kill and reinstrumented him. The day following, the kittens left the kill site with No. 50 on a route that took them from the Big Creek drainage. I located them from the air still together 2 wk later in Chamberlain Creek 25 km to the north over snow-filled passes. Four days later this group had moved down Chamberlain Creek but they were still together. Ten days later the young female (No. 49) was still at the site of the last location (probably indicating a kill had been made), but both males had moved to different parts of the Chamberlain drainage.

This association (between Nos. 93, 48, 49 and 50) differed from the consort pair associations I have described above in: (1) the extended duration of the association; (2) the behavior of the female when she left the kittens and formed a 3-4 day association with No. 28, the adult resident male; (3) the cohesion of the group after capture; the consort pair pursued and captured did not display this subsequent cohesion; and (4) the continued company of the sibling group with No. 50 for nearly 3 additional wk after their independence.

We found no instances where one kitten became independent sooner than the others although this happens with the tiger (Schaller 1967).

Because we radiotracked and snow tracked the female and both kittens for 6 wks before they were joined by No. 50, I see little possibility that No. 50 was in fact a sibling which became independent, left, and then rejoined the family group later.

An alternate explanation of this association is that No. 50, as a young transient, acted like a kitten, was treated as a kitten, and was accepted into the family group as such. He was nearly the same size as the male kitten (59 kg in December). Female domestic cats will accept a strange kitten if it is about the same size and age as their own (Schneirla et al. 1963).

The major point emerging from these observations is that while lions are essentially solitary in their activities and movements, they will join other adults for brief periods, most often adults of the opposite sex (Table 28). The frequency and duration of these associations are related to the female's reproductive status. Females with small kittens appear to avoid encounters with other lions. But as the kittens grow and approach the time of independence and, as I postulate, the female approaches estrus, she becomes more tolerant of males and other females. Peak tolerance is reached during estrus when lions form consort pairs and remain in company, traveling together as long as 16 days.

Mode of Communication in Space

Various olfactory, visual, tactual and auditory mechanisms maintain the patterns of dispersion and interaction that I have described. Only once did we see adult lions confront each other in the wild.

I was not able to observe female-kitten interactions except as tracks in snow. Thus, I know nothing of the postures, gestures, and tactual mechanisms that function in close-range agonistic or cohesive situations.

We know from observing our captives that mountain lions have a variety of close-range vocalizations, but this species does not have in its repertoire what could be classed as a long-range call like that found in *Panthera* or so-called roaring cats (Schaller 1972). Although there are frequent references in both the popular and technical literature to the mountain lion's scream that "shatters the night and rings through the canyons," I did not hear a call that could be classed as such nor have Hornocker or Wiles in 8 years of intensive work with this species both in the wild and in captivity.

Urine, "scrapes," feces and scent from anal or other glands could all serve to advertise a lion's presence and function either to bring lions together or to maintain distance.

In 2 years on both summer and winter areas, J. Messick and I located over 100 sites where mountain lions had scraped soil and/or needles back into a little pile (Figs. 20 and 21) in 1 to 6 places spaced usually less than a meter apart (Hornocker 1969a). At 86 of these sites, we recorded information; 41 sites were tallied while we were snow or radiotracking the lion involved. Scrapes at all but 1 site and possibly 1 other were made by adult resident males. The exceptions were made by adult resident females without kittens. We did not observe scrapes that we could definitely attribute to females with kittens and we snow and radiotracked this class extensively. I was not able to track transient males and female lions extensively in snow but where I did track these classes, I found no scrapes.

The scrapes measured 15 to 46 cm long, 15 to 30 cm wide, and 3 to 5 cm deep. Seventy-one sites were in pine and fir needles, 11 in soil or small pebbles, 2 in snow, and 1 in leaves. Of the sites tallied, only 3 were in the open and not associated with a fir or pine tree (N = 72) or rock face or overhangs (N = 12). Scrapes I measured were 0.3 to 2 m from the tree or bluff. On slopes, the scrapes were always on the downhill side of trees. Only rarely were scrapes found in trails. They were usually off to the side. We found sites near the mouths of canyons, in draws and on ridges; scrape sites appeared to be located where the lay of the land dictated easy passage.

I have followed a male lion through snow kilometer after kilometer before finding a scrape. The next scrape can be kilometers away or it can be within a few hundred meters. The two resident males I tracked most intensively (Nos. 26 and 28) scraped at different rates but both scraped more frequently in the region of home area overlap or along the area edge than toward the center.

Most scrape sites were not reused (Table 29). I determined this by marking scrape sites and recording the number and position of existing scrapes, then rechecking these sites at intervals, especially when a lion was known to be in the vicinity. The number of scrapes per site, i.e., within a small area under a tree or at the base of a bluff, varied from 1 to 6, but the number per site was not necessarily correlated with the reuse of the site. A lion at times made a number of scrapes at one site or upon revisiting a site perhaps just "freshened up" the existing scrape (Table 30).

The reused sites we found were not necessarily on the edges but were dispersed throughout the males' seasonal areas. They were located in situations that appeared to be where topography molded a convenient runway or pass. While I found where a male had revisited his previous scrape site, I did not record an instance of a resident male visiting the known scrape of another but this may occur. I did find resident females visiting these reused stations.

When old male No. 18 (see above) disappeared, the scrape sites in his range were not maintained that winter and gradually any sign at these stations disappeared. Two winters later we found fresh scrapes there and almost certainly they were made by No. 3, the male which had transferred into the area.

I found feces or urine at 17 scrape sites. Placement of the feces was nearly always in or on the pile of needles or soil made near the scrape. We did not find feces placed in the scrape as Bailey (1973a) found for the bobcat. The amount of fecal material varied from a normal scat to an amount I consider analogous to Schaller's (1967) "token" found at some tiger scrapes. Because the presence of urine was difficult to detect, it may perhaps be more prevalent than the data indicated. Both feces and urine were found or detected at sites that were new and not revisited so far as I could detect but they were more prevalent at reused scrape sites (Table 31).

I occasionally found lion scats that were not associated with scrapes of the type I describe above. At the kill, the scats were mostly concentrated in one or a few specific piles and covered with snow or needles. While tracking a female with young kittens and an adult resident female without kittens I found scats covered by a pile of needles along their trail. In one kitten bedding area away from the kill, I found a small scat covered this way and I suspect these were made by the kittens. Bailey (1973a) reported that female bobcats and kittens bury scats during the early periods of the kittens' development. Occasionally, I found lion scats that were not associated or covered with scrapes. Once an adult resident male was responsible but the rest were not found while tracking known lions. Hornocker (personal communication) reported females with kittens left uncovered feces in a few cases.

I found sites where both males and females urinated that were not associated with the scrape site. At these sites, it appeared that the lion simply stopped, urinated and went on its way. I found in tracking two different male kittens where they did not stop but urinated on the move. Neither Hornocker or I through observation of sign in the wild or of our captive cats saw where the lion had paused and urinated deliberately on vegetation or rocks as has been described for the bobcat (Bailey 1973a), tiger (Schaller 1967), African lion *P. leo* L. (Schaller 1972), snow leopard *P. uncia* Schreber (Schaller 1971), leopard *P. pardus* L. (Eisenberg and Lockhart 1972, Schaller 1972), and cheetah *Acinonyx jubatus* Schreber (Eaton 1970, Schaller 1972). We think that mountain lions do not "urine mark."

Holly—
Young ♂
cougar
killed @
Ramey—
There was
urine spray
adjacent
carcass,
in Forbs
24" high.

We do not know how mountain lions use their anal glands with respect to scent marking but it is likely that these glands are important in communicating information regarding an individual's residential status, and perhaps reproductive condition. It is possible that scent from these glands is deposited in conjunction with and/or independently of the scrape sites.

I gathered needles from an older-appearing scrape and from under an adjacent tree and put these in a well used path in the pen of a 4-year-old captive male. I could detect no unusual odor in either group of needles. The male ignored the control needles and at first did not respond to those from the scrape. Then, as he was standing almost over these needles, he put his head down and lifted it in a grimace similar to that described for other cats (Fig. 22). He sniffed these needles for a few minutes, then ignored them. Thus, the needles from the scrape did elicit a response while the control did not. Apparently some residual scent was left in the needles but its source (urine, anal gland secretion or whatever) was unknown. (In regard to scent marked needles, we noted that the hounds could pick up scent in them long after the odor had disappeared from substrates.)

It was nearly impossible to determine from tracks how a lion responded to scrapes in the wild because most were placed back under a tree or some other site protected away from snow. I did not observe any of what could be considered abrupt changes in direction after visiting a scrape as Hornocker (1969a) reported but I did find where lions veered at an angle up or down to go directly to a scrape site. On one walk with the captive 4-year-old male M. Hornocker and I observed him grimace then roll and rub his back in the needles under a fir tree. We were reasonably certain that there were old lion scrapes there. A young captive female released from her pen occasionally grimaced upon sniffing a variety of objects: a twig, a rock or a pile of needles. I tested her response to bobcat urine in needles and she did not grimace. She grimaced in response to mine.

While following females with kittens I have seen scratches on trees. These were all fresh and I have no evidence that would indicate these trees were revisited. I observed the young captive female rake her claws along the lower trunk or exposed root of a tree. Rather than serving any communication function, I believe this acts simply to sharpen the claws. The leopard (Eisenberg and Lockhart 1972) and jaguar *P. onca* L. (Darwin as cited in Schaller 1967) reportedly use scratching trees as part of their communication repertoire.

The antithetical difference in scraping between resident males and females is striking. Males scrape more frequently near the edge of their home areas and the stimulus situation here may increase aggressive motivation. Perhaps the scrapes made by males are symbolic or ritualized redirected aggressive acts as suggested by Ralls (1971) and others. In contrast to the scrapes and conspicuous placement of feces and urine by males, females rarely scraped and frequently covered their feces. The result is an "interruption" in these visual signals. For lions using common areas, individual distance is probably maintained through numerous channels such as visual contact, the presence of tracks augmented with urine, feces, and/or scent from the anal or possibly other glands either independently or in conjunction with scrapes. Judging from the sex differences, distribution and reuse patterns, I suggest that scrapes themselves do not function primarily in maintaining individual distance. Rather, they appear important in demarcating home areas particularly for adult males indicating to the passer-by that "an adult male is in residence." Secondly, they act as visual signals to olfactory information. Bailey (1973a, b) arrived at similar conclusions for bobcats but there the situation is reversed. Resident female bobcats made scrape stations similar to those made by male lions. Unlike the female lion, female bobcats maintain mutually exclusive areas as far as other resident females are concerned while the home areas of resident male bobcats overlap strongly.

LAND TENURE AS A POPULATION DENSITY DETERMINANT

To assess the role of social behavior as a factor in population limitation, one must measure its impact on rates of natality and mortality. The requisite conditions which show that behavior through socially induced mortality or induced depression of recruitment limits the breeding population have been set forth by Watson and Moss (1970: 170) in a succint tabular model:

> (1) "A substantial part of the population does not breed, either because animals die; or because they attempt to breed but they and/or their young all die; or because they are all inhibited from breeding even though they survive, and may breed in later years.
>
> (2) "Such non-breeders are physiologically capable of breeding if the more dominant or territorial (i.e., breeding) animals are removed.
>
> (3) "The breeding animals are not completely using up some resource such as food, space, or nest sites. If they are, the resource itself is limiting.
>
> (4) "The mortality or depressed recruitment due to the limiting factor(s) changes, in an opposite sense to, and at the same rate as, other causes of mortality or depressed recruitment."

I have summarized the observations on the lion population statistics for the Big Creek study area over seven winters (Fig. 6). To briefly review, during the winter of 1969-70 there was a reshuffling of range areas by resident males. No. 28 established himself as a resident in the area formerly utilized by No. 3; No. 3 moved to the area left empty by the demise of No. 18; and No. 26 retained his former area. Another older male, No. 43, was captured that winter in the area formerly used by No. 3 but he was not present in subsequent years.

Above I pointed out that transient males could probably breed, citing as evidence the capture of a young transient male with a resident female shortly after her kittens became independent. But, as determined by radiotracking, the majority of the breeding is clearly accomplished by the resident males. From these observations it is clear that the presence of an adult resident male is the primary factor limiting the density of resident males under the environmental regime present during this study.

The resident female portion of the lion population only partially recovered from the deaths of three resident females during the fourth winter of the study and the probable death of one other after that. This is in strong contrast to the situation we observed for males. Through the early years of the study (Fig. 6) transient females were captured but none was captured in the fifth or sixth winters. I interpret this simply as the absence of transient females. This is understandable when the following are considered: (1) The sex ratio of kittens is parity while the sex ratio of adult residents is 2♀♀:1♂. (2) Females, especially those with small kittens, are easier to find and kill than are males for hunters on trips of short duration. A female must continually return to her kittens, and in so doing, she leaves many tracks in a localized area. If her tracks are found she will inevitably be in the vicinity and the hounds will quickly find her. A male, on the other hand, is not restricted to a localized area and, unless he makes a kill, will move farther. (3) Adult females are subject to more stress and hazards than are males. The female must hunt and kill large potentially dangerous prey more frequently than males and at regular predictable intervals if she is to succeed in rearing her kittens, increasing the likelihood of accidental death (Gashwiler and Robinette 1957). (4) Resident females demonstrated a greater tenacity to their home areas than did males, and they rarely wandered from these.

Even though we did not observe a 1:1 replacement of the resident females that were killed or died, the evidence clearly supports the hypothesis that the presence of resident, breeding females is what limits the female breeding population. Important here were our observations on two young females (Nos. 45 and 46) which established home areas and their response to the number of resident females present (Nos. 29 and especially 93).

Zoo records (Rabb 1959) indicate that female mountain lions first come into heat and can produce kittens at 2.5 yr of age. Age at independence varies, but both litters we radiotracked became independent late in their second winter making them just under 2 yr of age at a minimum. If both young females (Nos. 45 and 46) were captured for the first time at the beginning of their third winter, then they did not breed successfully until late in their fourth winter of life at the earliest. Hornocker (1971) postulated that reproduction is suppressed in young females until they are socially mature. This is dependent on site attachment--the possession of a permanent home area. The suitability of an area in which a young female may settle depends in part on the presence and number of older resident adult females. Delayed social maturation which is dependent on site attachment can result in suppressed reproduction. This does not mean that the range areas of adult resident females must remain static; our observations indicate they were not. An established female may alter or eventually change her home area but this occurs only with the movement or death of adjacent resident females.

Observations on population turnover indicated that males and females were independent in their response to the death of a resident lion: the disappearance of four resident females did not leave an opening for another resident male. I postulate the reverse is also true: the death of a resident male does not leave an opening for another resident female.

I have discussed thus far only the land tenure system as it affects breeding density. This is not synonymous with population regulation or limitation although most literature is in total confusion on this point, resulting primarily from various definitions of population. To simply point out that the presence of a resident lion prevents a lion of the same sex from settling and breeding is not sufficient to invoke population regulation. If a young female or male did not settle in Big Creek, it may have settled elsewhere and have become a successful breeder. Even if dispersing lions settled in marginal habitats, the total population of breeding adults will increase. Brown (1969b) and Fretwell (1972) provide excellent graphic presentations on this point. Frequently the transient lions are identified as surplus. This is unfortunate, in my view, for under the present environmental regime with its decimating factors, the transient represents a delayed addition to the resident population rather than a by-product of population regulation.

Watson and Moss (1970) have noted that one still cannot invoke social behavior as a factor limiting the population even if conditions 1 and 2 of the tabular model are satisfied. One must demonstrate that the breeding animals are not completely using up some resource such as food.

Hornocker (1970) found that the adult resident lion population in the Idaho Primitive Area remained stable in spite of an increase in the density of the principal prey species, mule deer and elk, over the first four winters of this investigation. He further concluded that the lion population and human hunting pressure together were not limiting the prey populations although this predation did dampen oscillations in prey numbers. We have subsequently observed some fluctuations in prey numbers but these were not correlated with the number of lions on the area and their feeding rate and Hornocker's conclusions in this regard stand (Hornocker and Seidensticker, in prep.). The resident lion breeding population appears to be then below the level set by the food supply in terms of absolute numbers of deer and elk. The important question here is not how lion density is maintained but rather, how is the density level established?

The emerging picture from our intensive long-term observations is that lion land tenure is dynamic and flexible. The effect of prior residence is clear, but lions do not inherit home areas intact. Rather, there is a re-sorting of space among older lions first. Why do well established breeding adults shift to new areas? What determines range size? What determines the degree of area overlap, particularly among females?

Variation in home area size demonstrates that the amount of terrain a resident lion occupies (Table 6) is not a simple function of body weight and metabolism (McNab 1963) or some psychological limit (Wynne-Edwards 1962). The land over which a lion roams is variable in terms of cover, topography, ungulate numbers and carrying capacity and prey vulnerability. The size of the lion winter areas is not directly correlated with prey density (Fig. 23). Habitat characteristics set carrying capacity and ultimately determine the number of prey species present (Hornocker 1970, Hornocker and Seidensticker, in prep., Claar, in prep.). The topographic rugosity of lower Big Creek and the lower Middle Fork which forms the winter range area of both resident Nos. 26 (♂) and No. 24 (♀), for example, supports a lower ungulate density than the comparatively gentle winter range areas where in 1971 Nos. 28 (♂), 29 (♀), and 93 (♀) or in 1967 Nos. 3 (♂), 29 (♀) and 4 (♀) resided. Intermediate in terms of deer and elk density is the Rush Creek drainage, but it is here lion densities were greatest--Nos. 18 (♂), 11 (♀), 12 (♀), and 16 (♀) lived here--at least during the first five winters of study before the females there were killed. For a stalking predator like the lion to succeed in killing a large and potentially dangerous ungulate, it must approach undetected to within a critical distance as Hornocker (1970) pointed out. This is dependent upon the distribution and number of suitable environmental situations. The variation in environmental structure results in differences in the suitability of home areas. This is supported by the prey acquisition analysis, where we found kills were more frequently made in some areas than in others, and by the shifts of winter home areas by well established residents. Thus, the amount of terrain a resident lion uses and the degree of area overlap for females are a function of a vegetation-topography/prey numbers-vulnerability complex. Taken together this is habitat in its widest sense (Fretwell 1972) for the lion. The limits are probably established through energy considerations which act both as an ultimate and a proximate determinant. Lion breeding density thus is maintained through the lion's land tenure system which is an adaptation for efficient food resource utilization (see discussion below).

We have few data regarding compensation for mortality, but some points can be made. We found that dispersal of young, newly self-sufficient lions reared on the study area was independent of resident adult density. That is, young lions dispersed even with open areas available. We did not then have compensation for adult mortality in terms of our study area although it was nearly 520 km^2 in size. Neither did we observe an increase in the number of kittens reared by the two remaining resident adult lions following the deaths of the four resident females. This indicated to me that females were producing as many kittens as possible in terms of availability and vulnerability of the principal food resource. Jonkel and Cowan (1971) made similar observations for the black bear in the spruce-fir zone in Montana.

SYNTHESIS AND SPECULATION

Mountain Lion Social Organization: A Summary

The frequency of interactions between lions (Tables 27 and 28) was dependent upon the lion's population status and reproductive class (social role, Crook 1970), i.e., the same lion in a different social role would respond differently to the same set of stimuli. The female and her offspring formed the only enduring social unit. Breeding (consort) pairs and recently independent siblings formed cohesive units, but these were of brief duration.

A mountain lion's essentially solitary existence is both with and without an external reference in space depending on the lion's social role, and it is probably maintained through a variety of means. As a technique for regulating social interactions, minimum individual distance is controlled either by permitting or limiting the approach of another lion by withdrawing or driving it away and/or through appeasement, threat or simple advertisement which can be visual, chemical or vocal (Kummer 1971). Overt fighting between lions is very rare or lacking. The long distance call, a seemingly good advertisement strategy, is also lacking although vocalizations are important at close range. Area use analysis and such strong localizing factors as small kittens and the ungulate kills showed that no timetable is involved in avoiding encounters. Based on the "nearest neighbor" analysis, much of the time resident lions were located at random in relation to each other in their common areas.

It was difficult to establish the direction of avoidance. After adult lion associations, both would go their own ways although it appeared that with consort pairs, the male moved away from the area first. In an encounter with a resident male out of his home area, a female turned and went deeper into her area and away from his. He did not follow. At kills, females with kittens were at times supplanted by resident males. A young resident female was not supplanted at her kill after an encounter there with a resident female with small kittens. The next winter this female joined the same family and her big kittens at a kill. More significant was that the majority of the time a lion did not approach the kill of another when traveling through the same drainage. Based on association patterns (Table 27), or lack thereof, as is the usual case, females with small kittens are the most sensitive to another lion's presence. Less sensitive were females with large kittens, females without kittens and finally males. There was total avoidance (termed mutual avoidance by Hornocker 1969a) between males and females with small kittens, females without kittens and adult males (Table 28).

As reported by Hornocker (1969a) and confirmed through radio-tracking, no substantial part of any resident lion's home area is maintained to the exclusion of all other conspecifics. Resident male home areas overlapped little. But resident female areas often overlapped completely and were overlapped by resident male areas. Transient lions of both sexes moved through these areas but did not linger.

These resident lions are the breeding population. The mating system can be classed as promiscuous in the sense that each lion's reproductive life might involve a number of different sex partners and the pair bond, if it can be called that, is of short duration. This, however, is misleading. We observed that during one estrus period, a female was associated with a single resident male. This same male can and perhaps does sire a number of her litters. The resident male breeds with a number of different females whose home areas overlap his own. In this sense then, the mating system is polygynous.

Land tenure is based on prior rights. Home areas are altered in response to the death or movements of other residents and young adults establish home areas only as vacancies become available. While home areas are well covered, no boundaries are patrolled. In a long-lived species such as the lion, they do not have to be patrolled, especially when the species' memory is excellent as it is in cats (Warren 1960) and when time must be invested in more important matters. Home areas are maintained through a lion's presence which can be indicated through various chemical and visual signs.

Attempting to emphasize the restricted and predictable pattern of land tenure of adult residents, Hornocker (1969a) chose to term these areas *territories*. *Territoriality* was defined ". . .as any behavior on the part of an animal which tended to confine its movements to a particular locality" (Etkin 1964:21-22). A more traditional approach has been to define territory as a "defended area" (Noble 1939). Tinbergen (1957) emphasized that territory was the outcome of two distinct tendencies each of which could occur without the other: site-attachment and intraspecific hostility. With exactly what constitutes defense of an area or intraspecific hostility in question, Wilson (1971:195) redefined territory ". . .as an area occupied more or less exclusively by animals or groups of animals by means of repulsion through overt defense or advertisement."

In a further attempt to broaden the concept, Fretwell (1972:92) defined territorial behavior as ". . . any site-dependent display behavior that results in conspicuousness and in avoidance by other similarly behaving individuals."

I have not used the labels territory or territoriality in presenting the movement or lion interaction data because of the semantic conflicts and muddled concepts brought to mind. I felt that a more descriptive and neutral term was best. I chose to term the area over which resident lions roam *home areas*. In the lion's land tenure scheme transient lions are nomads and do not have home areas; these are restricted to the reproductive phase of their life cycle. Adult residents can and do alter and shift their home areas and occasionally wander from them. I do not include occasional wanderings or the area between summer and winter areas if disjunct as part of home areas (Geist 1971).

With increasingly refined data, concepts must be adjusted and rearticulated. Hornocker has rightly and repeatedly emphasized that the lion's land tenure system could be termed whatever one wanted as long as the label is defined with adequate data. I feel too much emphasis has been placed on the rather ambiguous and ill-defined concepts of territory and territoriality. At this stage of conceptual development of mammalian social systems, pigeonholing and ill-defined conceptual frameworks must be avoided. Rather, emphasis should be placed on collecting data on the form and frequency of interactions between individuals and how these interactions are related to the use of space.

Social organization or *system* as I have used these terms is the manner in which conspecifics are positioned in space and time relative to each other and to other features of the environment (Morrison and Menzel 1972). Traditionally, terms such as solitary, asocial and dispersed have been used to characterize social systems of the type we found operating for the mountain lion. There is ample room for objection with these terms as there is for such societal labels as hierarchy (absolute or relative), territoriality, home range, etc. Masked are the social roles involved (Bernstein and Sharpe 1966) or the nature of the land tenure and mating system and the indirect communication channels (Leyhausen 1965, Schaller 1967, Eisenberg et al. 1972). Obscured too are intraspecific variations due to differences in food, interspecific competition or other environmental factors in different parts of a species range or at different seasons (Kruuk 1972, Eisenberg et al. 1972). As proposed by Eisenberg et al. (1972), the descriptive although cumbersome dispersed noncohesive family group would seem to be appropriate here but if one must label, solitary is easier so long as the underlying social structure is understood.

Ecology and the Evolution of Mountain Lion Social Organization

As a lion grows older, it passes through a series of relatively discrete behavioral stages: kitten, transient adult, resident adult. Through most of the kitten stage the lion is totally dependent upon its mother and restricted in its movements to her home area. Following independence the young lion roams about displaying no attachment to any particular site. Dispersing females do not breed, at least successfully, and dispersing males breed only rarely. When an area adequate in size and resources and free of too many other residents is located, the young lions restrict themselves more and more to that area. With attachment to the site, the lion enters the reproductive phase of its life and settles into its adult sex role.

The long expected life-span of adult lions and resulting slow rate of population turnover make vacancies where a young lion might settle and successfully rear young widely scattered. Vacancies can be found only through a nonrestricted pattern of movement such as we observed in newly independent lions. Such a movement pattern would be adaptive in locating vacant or new suitable areas that are formed through the frequent but unpredictable wildfires. The large cervids readily colonize, through their own dispersal patterns, burned areas utilizing the seral vegetation such as shrubs, grasses and herbs that grow after a mature forest burns. Small fires keep an area in a dynamic state by altering habitat characteristics and ungulate carrying capacity. These smaller fires are important perhaps in altering habitat desirability and influence shifts in the home areas of adult lions. More important to young lions are the holocausts that burn over hundreds and perhaps even thousands of square kilometers like those that occurred in northern Idaho earlier this century. Here excellent cervid habitat was created where it was previously nonexistent or marginal at best.

This explains the dispersal of young males from the Big Creek study area where the drainage was filled with long-lived, well-established adult males. But why did newly independent females leave when there were openings near their natal areas, openings which in fact were later occupied by young females which moved in from other areas?

Considering the low adult turnover rate and that most breeding is probably accomplished by the resident male, for a female or a male to remain near its natal area inbreeding would very likely result. In domestic chickens, Craig and Baruth (1965) found that dominance rank was directly related to heterosis. Further, it has been demonstrated that at least for caribou, hybridization resulted in increased viability of offspring and fewer barren females (reference cited by Geist 1971). If this holds true for a species such as the lion, then, through reproductive advantage, the dispersal patterns would have been firmly fixed.

Considering their dispersal pattern one would predict mountain lions to be an effective colonizing species. In a vast mountain mass like that of central Idaho, it appears that this has indeed been the case. Over the last 30 years, the lion population in the Big Creek drainage has been greatly reduced or eliminated a number of times (W. Wiles, personal communication), yet the lion population always re-established. The speed at which this occurs, as is apparent from the observations presented here, is dependent on the number of young lions produced in adjacent areas.

With the strong anti-predator feelings that prevailed during the first part of this century, both wolves and mountain lions were eliminated from all but the remotest regions of the West. That lions have never re-established, for example, in some of the isolated mountain masses in parts of Montana can be explained in part by the continued methodical destruction of predators by both private individuals and bureaucratic agencies. But why, even in totally protected areas such as Yellowstone

National Park, have lions apparently never re-established in any numbers (G. Cole and D. Huston, personal communication) after the original population was destroyed? We do not know precisely what a young lion uses for clues in determining what is a suitable area and what is not. Certainly the vegetation-terrain/prey abundance-vulnerability complex is important. So too is a population source of transient lions. Considering the lion's land tenure and mating system I postulate that other lions, particularly members of the opposite sex, are needed to initiate attachment to site. Important here is the fundamental difference between the efficient colonization of newly created habitat or empty contiguous areas such as occur in large mountain masses and the situation in disjunct, isolated areas. This difference explains why, even though lions occasionally roam through areas such as Yellowstone, breeding populations do not or have been so contrastingly slow in re-establishing.

In the mountain lion, males have no nutritional responsibility for their young. On the one hand, this is not surprising considering mammalian physiological characteristics. On the other hand, while monogamy is rare in mammals, it is best known in the terrestrial carnivores (Eisenberg 1966). In a species like the wolf which preys upon large dangerous animals, often in open country, cooperation probably aids in food acquisition and results in individual selection for cohesive social units (Eisenberg 1966, Mech 1970, Schaller 1972, Kruuk 1972). Further, in some canids, natural selection has favored the behavioral mechanisms of food-providing for the female by the male. This is especially important in a species with altricial young which restrict the parents' mobility. The mountain lion, too, kills large potentially dangerous prey but unlike the wolf, a pursuit predator, the lion is a stalking predator whose success depends almost solely on the element of surprise. In the broken land where lions find sufficient cover to stalk and launch successful attacks, the prey are usually scattered and time-consuming to find. Under these conditions a solitary social structure is apparently the most effective life style.

Site attachment is not a requisite for survival but rather a phenomenon that comes into play during the reproductive phase of the lion's life cycle. For a successfully reproducing female, the best strategy for exploiting the food resource at the constant predictable rate necessary for rearing kittens is to gain familiarity with and attachment to the best available site. A failure to find food at predictable intervals is much more severe for the female in terms of reproductive fitness than it is for males. Darwinian selection favors those individuals which reproduce successfully and contribute the most genes to future generations. Males can increase their number of offspring by mating with more than one female; females can do this only by successfully rearing their own (Orians 1969). As a result, the advantage of familiarity with the land in terms of hunting success, while a factor, does not have the overriding importance for males that it does for females. This explains, at least in part, why in other solitary species such as bobcats (Bailey 1973b) and weasels *Mustela nivalis* L. (Lockie 1966) if there is a food shortage males abandon home areas before females. It also accounts for the rather slow response by resident female mountain lions to the areas left open through the death of other resident females in adjacent areas as compared with males.

If the male's reproductive success could be improved by increasing the number of females with which he successfully breeds, then one would expect rather keen competition for the opportunity. But this strategy is constrained by other considerations. In the mountain lion, the reproductive cycle is not synchronized by a specific breeding season as it is in so many temperate species. A female can breed approximately every other year but if she loses a litter of kittens she will apparently come into estrus shortly and breed again (Hornocker 1970, Robinette et al. 1961, Rabb 1959). Thus, the opportunity to breed with the rather widely dispersed females is rather limited and fairly unpredictable. Also important in maximizing the male's reproductive success is familiarity with particular females (Zajanc 1971) and their habits. This apparently has been best achieved by restricting his movements to a particular area. The better quality the area, perhaps the more females will be in residence. But there are still other and possibly more important factors.

The energy costs paid by ingesting food can be conveniently divided into three categories: (1) basic maintenance; (2) extra work, social interaction, excitement, illness, and climatic stress; and (3) reproduction and growth. As Geist (1971) pointed out, the first two take precedent over the third. Unless a lion continually obtains enough energy over and above that required for maintenance and work, it will become a reproductive failure. A solitary predator's survival, particularly one which lives by killing dangerous animals much larger than itself, depends upon its physical well-being. As Hornocker (1969a) has emphasized, lions cannot afford the luxury of a potentially damaging agonistic encounter. Selective forces, especially for reproducing females, probably favor behavior which reduces excitement and work involved in social interactions. In addition, females should avoid meeting other lions, particularly males, to reduce the danger to small kittens. This puts a premium on sociality with little or no overt aggression. These considerations explain to a large degree the adaptive nature of the adult lion interaction patterns we observed. We did not observe any sign of adult males overtly interacting with other males. At stake here is the risk of injury in an agonistic encounter. All the factors acted together on females to increase avoidance and reduce social interaction. As would be expected, resident females spent less time associated with other lions than did adult males. All factors are brought to bear most intensively on females with kittens; females with small kittens were most sensitive to our recapture methodology and to other lions to the extent that a male could supplant them at their kills. Movements restricted to a specific area by an adult male to the exclusion of other adult resident males act to reduce interference indirectly benefiting his own offspring. Taken together this explains the small degree of overlap between male ranges and particularly why male ranges overlap those of females. But why do female ranges overlap?

The land inhabited by lions is variable in terms of availability of prey, adequate cover, water, etc. I have already postulated that the density of resident lions is a function of the vegetation-terrain/prey numbers-vulnerability complex with limits set by proximate and ultimate energy considerations. But given an even distribution of resources (prey distribution, prey abundance, and suitable conditions where kills can be made), would not the same food be available if two females used the same sized area but rather than total overlap, partitioned the region into exclusive areas of the same size? This is the land tenure situation in the bobcat (Bailey 1973b). The life of a resident female lion is in a constant state of flux as she is either rearing kittens or pregnant. A female with small kittens is quite restricted in her movements because of their limited mobility and constant need for attention. She lacks the mobility of other lions, even females with large kittens. As I have described above and as Hornocker (1970) emphasized, deer and elk, the most important prey species for most of the year, move out when they become aware of a lion's presence. These large ungulates are highly mobile and the move can be kilometers. The highly mobile nature of the prey resource, as compared with the prey resources of bobcats, for example, coupled with the problems of aggressive neglect (Ripley 1961) make it seem unlikely that a female could maintain an exclusive area of sufficient size to provide food for herself and her kittens throughout their development. Even if she could maintain an adequate size area, the highly mobile prey resource would be constantly shifting in response to her presence, a distinct disadvantage considering the restricted nature of her movements. Rather, to a point, the presence of other lions in an area would increase her chances of hunting success in that they counter the movements of the large ungulates which must move in respect to the activity of several lions, not just one as would be the case with an exclusive area.

My approach in this paper has been to offer a view of the function of mountain lion social organization in relation to its ecology, its causes rather than effects (Fisler 1969). The alternative view is well entrenched in the literature: the social system has evolved because of its limiting effect on population size which prevents overpopulation and the resulting destruction of prey populations (Wynne-Edwards 1962). Watson and Moss (1970) consider this ". . . beyond our present capacity to test by practical observation and experiment in the field." Other serious reviewers have expressed similar views (Brown 1969a and references cited therein). In this discussion, I have emphasized the role of the large ungulates, mule deer and elk, as a factor shaping and maintaining the lion social system because they are the most important food source through 9 months of the year in the Idaho Primitive Area. But considering the observed flexibility and dynamic nature, it would be wrong to assume the system could not differ given a smaller sized prey resource, different environmental structure and/or the presence of another big cat--the jaguar. That this is indeed the case with many species has been well established (Eisenberg et al. 1972, Kruuk 1972). But how mountain lion social organization adjusts to a different environmental regime must await further study.

All of this demonstrates not so much what we know about this one sensitive wildlife species but more about what we do not. Sensitive, threatened, and endangered species stand as both a challenge and as an index of our culture's land ethic and its ultimate chance for survival. The challenges facing agencies charged with preserving and managing such species are indeed complex. Simplistic conventional wisdom will not suffice.

SUMMARY

As part of a comprehensive study of mountain lion ecology, the social organization of a lion population in the Idaho Primitive Area was investigated using radiotelemetry. Important to the analysis was that general population dynamics and relationships had been established through recapture methodology over the five previous winters.

The response by mountain lions to investigators was dependent upon disturbance intensity and the reproductive status of the lion. It was clear from monitoring the movements of radiotagged lions that they did not respond to investigator activities in any way that would bias conclusions.

After independence from the female, mountain lions dispersed, showing no attachment to any particular area. The "transient" females did not reproduce and the "transient" males only rarely bred. When an area adequate in size and resources and free of too many but not independent of other residents was located, the young lion restricted itself more and more to that area. Only after establishment of a home area did the lion enter the reproductive phase of its life (population component termed "resident").

The home area utilization by resident lions was influenced by the localizing effects of the large ungulate kills and, for females, kitten mobility. The localizing effect of kittens was diminished their second winter; home area utilization by females during these different stages of kitten development differed considerably as a result.

In the short run, a lion's home area was in a constant state of flux in terms of location of mule deer and elk (the most important prey resource 9 months of the year) in situations where they could be successfully stalked and killed. But over the long run, the conditions in certain areas were such that lions tended to be more successful there in making kills. This demonstrated the advantage of familiarity with the home area, especially for females rearing kittens.

Resident lions occupied fairly distinct but usually contiguous winter-spring and summer-fall home areas. No substantial part of any resident lion's winter home area was maintained to the exclusion of all other conspecifics. Resident male home areas overlapped but little. Those of resident females often overlapped completely and were overlapped by resident male areas. Transient lions of both sexes moved about these areas. In summer, the pattern was the same.

Land-tenure was based on prior right, but the system was not static. Home areas were altered in response to the death or movement of other residents. Young adults established only as vacancies became available.

The mountain lion's essentially solitary existence was maintained visually and chemically. A lion's response to the close approach of another was dependent upon its population and reproductive status. Females with small kittens were most sensitive to another's presence. Females with large kittens, females without kittens and males were less disturbed by the presence of another lion. Avoidance between adult males, males and females with small kittens, and females without kittens was total.

Over the seven winters (1965-1972) the resident male portion of the lion population remained stable; resident female numbers were constant for three winters but later deaths were never quite compensated. Dispersal of young lions reared on the study area was independent of resident adult density.

It was concluded that the lion land tenure maintains the density of breeding adults below a level set by food supply in terms of absolute numbers of mule deer and elk. Variation in lion environmental structure resulted in variations in the suitability of areas and affected the amount of terrain a resident lion utilized. The amount of terrain used by a resident lion as well as the degree of home area overlap between resident females, i.e., density of breeding population, was set by a vegetation-topography/prey numbers-vulnerability complex.

The form of mountain lion sociality has been molded by a wide variety of factors. In the analysis of its adaptive value, I have considered how reproductive requirements, mobility, mode of prey acquisition, food supply (type, availability, and vulnerabilty), habitat characteristics and other predators and scavengers through the energy budget and reproductive success affected social interactions and communications, dispersal, land tenure and home area utilization.

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Table 1. Adult mountain lions captured on the Big Creek study area during 8 winter seasons. (Each number refers to a specific lion.)

Population	♂♂								♀♀							
Status	64-65	65-66	66-67	67-68	68-69	69-70	70-71	71-72	64-65	65-66	66-67	67-68	68-69	69-70	70-71	71-72
Residents	*3*	*3*	*3*	*3*	*3*	*3*	-	*3*	-	-	*29*	*29*	*29*	*29*	*29*	*29*
	7	7	-	-	-	-	-	-	-	*24*	-	*24*	*24*	*24*	*24*	-
	-	-	*26*	*26*	*26*	*26*	*26*	*26*	-	16	-	16	16	-	-	-
	-	18	18	18	18	-	-	-	4	4	4	4	-	-	-	-
						28	*28*	*28*	11	11	11	11	-	-	-	-
									12	12	12	12	-	-	-	-
															45	*45*
															46	*46*
															93	*52*
Transients	5	20	*28*	-	92	40	*50*	-	1	21	32	-	-	-	*44*	-
	8	22				41										
	9					43										
	10															
Transients marked as kittens	-	19[1]	-	27	33	-	*48*[1]	*47*[1]	-	6[1]	14	-	35	-	*49*[1]	*51*[1]
					34						15					
Total	5	5	4	4	6	6	3	3	4	6	7	6	4	2	6	4

[1] Indicated spent part of the winter season with mother, not included in total.

Italicized numbers indicate population status and history of radiotagged individuals.

Table 2. Movement of mountain lions from the capture site when no ungulate kills were involved.

	Handled		Not Handled	
Lion No.	Distance Moved (km)	Days to Next Location	Distance Moved (km)	Days to Next Location
♂♂ alone				
03	0.6	2		
	1.0	7		
26	2.9	1	3.7	1
	0.3	1		
28	1.3	1	5.8	2
	2.7	4		
♀♀ alone				
24	1.3	2		
45	0.3	1		
46	2.1	1		
	0.3	1		
93	1.6	1		
♀♀ with kittens				
29(S)[1]	2.4	1	2.3	1
	6.8	4	6.0	7
29(L)	1.5	1	0.3	1
			0.6	1
93(L)	0.3	1	3.7	1

Table 2 (continued).

	Handled		Not Handled	
Lion No.	Distance Moved (km)	Days to Next Location	Distance Moved (km)	Days to Next Location
Consort pair				
52 (♀)	1.3	2		
03 (♂)			1.8	2
Sibling group				
48, 49 & 50	23.8	7		

[1] Size S = small kittens (0-12 months); L = large kittens (12-24 months)

Table 3. Mountain lion response when captured near ungulate kills.

Lion No.	New or Older Kill	Handled or not	Response
♂♂ alone			
03	0	Yes	Left
26	0	No	Left
26	0	Yes	Left
28	N	No	Returned
28	N	Yes	Returned
♀♀ alone			
45	N	No	Returned
46	N	Yes	Returned
29	N	Yes	Returned
93	N	Yes	Left
♀♀ with kittens			
29(S)[1]	N	No	Left
29(S)	N	No	Left
29(L)	0	No	Left
29(L)	N	No	Returned
Sibling group			
48, 49 & 50	0	Yes	Left
Consort pair			
52 & 03	0	Yes (♀)	Both Left

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[1] Size S = small kittens (0-12 months); L = large kittens (12-24 months)

Table 4. The mountain lion population as determined by captures and recaptures on the Big Creek study area.

Winter	Adult Males	Adult Females	Juveniles	Total
1964-65	5	4	1	10
1965-66	5	6	7	18
1966-67	4	7	4	15
1967-68	4	6	6	16
1968-69	6	4	3	13
1969-70	6	2	1	9
1970-71	3	6	4	13
1971-72	3	4	2	9

All young lions with the female for only part of the winter are classed as juveniles.

Table 5. Elevational distribution (in percent) of mountain lion locations combining data from January 1970 to June 1972.

Elevation ft (m)	Jan. - May	June	July, Aug.	Sept. - Nov.
3000-3900 (900-1200)	2	0	0	1
4000-4900 (1200-1500)	27	2	1	1
5000-5900 (1500-1800)	62	39	15	20
6000-6900 (1800-2100)	8	38	48	62
7000-7900 (2100-2400)	1	18	19	15
8000-8900 (2400-2700)	0	2	14	1
9000- + (2700- +)	0	1	1	0

Table 6. Seasonal and yearly total home areas (km^2).

	Winter-Spring		Summer - Fall	Yearly
Lion No.	1970-71	1971-72	1970 or 1971	Total Area
03 (♂)	--	41	--	NA[1]
26 (♂)	220	NA	NA	NA
28 (♂)	145	96	293	453
24 (♀)	142	--	163	306
29 (♀)	62	93	106	173
45 (♀)	132	99	207	373[2]
46 (♀)	243 (78)[2]	52	NA	NA
52 (♀)	--	31	--	NA
93 (♀)	106	--	114	220

[1] NA = Radiotagged but data not adequate for home area determination.

[2] Includes Big Creek area only, see text.

Table 7. Captures after independence of lions marked as kittens on the Big Creek study area.

				Capture Dates		
Lion No.	Sex	Mother's No.	Weight (kg)	Last Capture with Mother	Alone on Study Area	Remarks
6	♀	4	33	1/12/66		
					4/ 3/66	
19	♂	4	36	1/30/66		
					2/21/66	
14	♀	29	19	3/26/66		
			34		12/20/66	Captured off SA[1] - 19 km 8/11/67
					12/31/66	
15	♀	29	18	2/26/66		
			37		2/ 2/67	Killed off SA - 48 km between
					2/13-20/67	2/13 and 2/20/67
27	♂	12	15	12/25/66		
			43		1/28/68	

Table 7 (continued).

Lion No.	Sex	Mother's No.	Weight (kg)	Last Capture with Mother	Capture Dates Alone on Study Area	Remarks
33	♂	29	25	3/26/68		
			52		3/15/69	
34	♂	29	25	3/26/68		
			40		11/23/68	Killed off SA - 64 km
			48		1/31/69	1/31/70
35	♀	16	32	4/ 1/68		
					1/30/69	
48	♂	93	59	3/ 8/71		
					3/9-10/71	Radiotracking (See Fig. 12)
						Also captured and probably killed
						88 km off SA 12/16/71

Table 7 (continued).

Lion No.	Sex	Mother's No.	Weight (kg)	Last Capture with Mother	Capture Dates Alone on Study Area	Remarks
49	♀	93	50	3/ 8/71		
					3/9-10/71	Radiotracking (see Fig. 12)
47	♂	29	50	3/17/72		
					3/18-29/72	Radiotracking
51	♀	29	32	3/17/72		
					3/18-5/6/72	Radiotracking

[1] SA = Big Creek Study Area.

Table 8. A test for bias in locating radiotagged mountain lions.

	No. 29 (♀)	No. 93 (♀)
Days associated with kill:		
Observed	47	20
Expected	46	17
Days between kills:		
Observed	43	20
Expected	44	23
	$\chi^2 =$ 0.05[1]	$\chi^2 =$ 0.92[1]

[1] Not Significant ($P > 0.05$)

Table 9. Mountain lion activity periods in winter.

Daylight:	
Total locations	1,189
Percent active	14
Dusk to sunrise:	
Total locations	72
Percent active	40

Table 10. Summer (June - August) diurnal activity of three adult female mountain lions.

Lion Number	29	93	24
Number of lion location days	47	21	19
Percent active	55	43	47

Table 11. Straight-line distances (km) between sequential lion-location-days, December 1970 - November 1971.

Day Interval Between Sequential Locations	No. 28 (♂)			No. 29 (♀)			No. 93 (♀)		
	N	$\overline{x}$	SD	N	$\overline{x}$	SD	N	$\overline{x}$	SD
1	50	3.2	2.7	46	2.3	1.4	68	1.8	1.1
2	13	4.5	1.9	13	3.4	2.3	14	2.6	2.4
3	11	7.6	5.0	12	3.7	2.6	10	3.5	3.4
4	6	8.4	6.8	9	2.7	3.1	5	3.9	2.3
5	5	11.6	7.6	8	4.5	3.7	5	3.9	2.7
6	6	9.0	9.3	3	5.8	--	4	2.3	--
7	2	4.8	--	1	10.0	--	2	3.9	--
8	1	6.9	--	0	--	--	2	2.7	--
9	2	7.4	--	1	1.8	--	1	1.6	--
10	2	4.0	--	1	1.3	--	1	7.6	--
10+	0	--	--	3	5.3	--	3	12.2	--

Table 12. Straight-line distances (km) between sequential locations on consecutive days of radiotagged mountain lions in two winters.

	1970-71			1971-72		
Lion No.	N	$\overline{x}$	SD	N	$\overline{x}$	SD
26 (♂)	--	--	--	8	2.6	1.3
28 (♂)	45	2.9	2.4	41	2.6	1.9
29 (♀)	21	2.1	1.3	68	1.9	1.3
46 (♀)	21	2.3	1.1	23	1.8	1.6
93 (♀)	33	2.1	1.3	--	--	--

$\overline{x}$ differences between winters are not significant at 0.05 level for 28, 29 and 46.

$\overline{x}$ differences between sexes are significant for each winter; $\overline{x}$ differences among females are not significant for each winter.

Table 13. Straight-line distances (km) between sequential locations on consecutive days for radiotagged mountain lions, summer 1971.

Lion Nos.	N	$\bar{x}$	SD
29 ♀ with large kittens	23	2.1	1.4
93 ♀ with small kittens	35	1.6	1.0
28 adult resident male	5	5.5	4.3

All means $P < 0.05$

Table 14. Maximum straight-line distance (km) between sequential locations on consecutive days and sequential locations to 10 days apart by radiotagged mountain lions.

		Winter		Summer	
		Interval in Days		Interval in Days	
Lion No.	Status[1]	1	2-10 (No.)	1	2-10 (No.)
♂♂					
03	R	10.9	12.6 (9)	--	--
26	R	8.2	20.4 (4)	12.9	22.7 (6)
28	R	5.5	10.6 (7)	--	20.4 (3)
48	T	--	23.8 (7)	--	34.1 (4)
50	T	--	23.8 (7)	6.1	24.1 (4)
♀♀					
24	R	3.7	13.2 (10)	--	16.9 (6)
29	R	4.8	7.7 (5)	5.3	11.3 (5)
45	R	3.7	12.1 (4)	--	22.2 (7)
46	R	7.6	12.6 (2)	--	27.4 (3)
93	R	5.5	11.3 (5)	4.3	7.2 (4)

[1] R = resident; T = transient

Table 15. Quadrat occupancy data for selected adult resident mountain lions from December - May.

No. Locations per 2.6 km^2 (1 mi^2)	28 (♂)				93 (♀)		29 (♀)				46 (♀)			
	1970-71		1971-72		1970-71		1970-71		1971-72		1970-71		1971-72	
Quadrat	No.[1]	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time
1	14	15	14	16	15	18	7	10	13	11	13	16	6	10
2	3	6	9	21	4	12	4	12	3	6	2	6	5	15
3	3	9	1	3	8	32	5	20	5	10	--	--	1	5
4	4	16	--	--	--	--	1	6	2	8	1	6	2	12
5	3	15	3	18	1	7	2	14	5	20	1	7	--	--
6	1	6	2	14	--	--	--	--	1	5	1	8	1	9
7	--	--	--	--	2	18	1	10	1	6	1	10	--	--
8	--	--	--	--	--	--	1	11	1	7	2	22	--	--
9	--	--	--	--	--	--	--	--	1	7	--	--	--	--
10	2	20	1	11	1	13	--	--	--	--	--	--	--	--
11	--	--	--	--			--	--	1	9	--	--	1	17

Table 15 (continued).

No. Locations per 2.6 km^2 (1 mi^2)	28 (♂)				93 (♀)		29 (♀)				46 (♀)			
	1970-71		1971-72		1970-71		1970-71		1971-72		1970-71		1971-72	
Quadrat	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time
12	1	12	--	--			1	17	--	--	--	--	--	--
13			--	--					--	--	--	--	--	--
14			--	--					--	--	--	--	--	--
15			1	17					1	12	--	--	--	--
16											1	23	--	--
17													--	--
18													--	--
19													--	--
20													--	--
21													1	32
Total Quadrats Occupied	31		31		31		22		34		22		17	

Table 15 (continued).

No. Locations per 2.6 km^2 (1 mi^2) Quadrat	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time	No.	% Time
No. Quadrats with 75% Lion-Location-Days	13		14		14		10		14		5		6	

---

[1] No. of lion-location-days

Table 16. Quadrat occupancy data for 2 resident adult female mountain lions, June-November, 1971.

No. Locations per 2.6 km^2 ($1 mi^2$)	No. 29		No. 93	
Quadrat	No.	% of Time	No.	% of Time
1	14	28	15	17
2	7	28	7	21
3	3	18	1	4
4	2	16	2	10
5	1	10	1	6
6			--	--
7			1	9
8			1	10
.			.	.
18			1	23
Total Quadrats Occupied	27		29	
Quadrats with 75% Lion-location-days	14		11	

Table 17. Amount of time mountain lions spent associated with big game kills as determined by intensive snow and radiotracking.

Lion Sex-Age Class	No. of Days	No. of Kills	Percent Time Associated With Kills	Percent Time Between Kills
Adult ♂	70	3	46	54
Adult ♀ alone	24	2	41	59
Young adult ♀♀	84	3	58	42
Adult ♀♀ with 2 large kittens	76	8	59	41

Table 18. Linear distance (km) of mountain lions from the kill site before kill was made and after lions left.

	Linear Distance from Kill Site							
Days Before	28 (♂)		29 (♀)		93 (♀)		45 & 46 (♀♀)	
Making & After	(N=8)		(N=13)		(N=8)		(N=7)	
Leaving Kill	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
10	2.4	1.3	3.5	2.3	6.4	3.5	6.4	4.5
9	5.5	2.7	3.2	2.4	2.9	1.9	8.0	7.1
8	5.6	4.0	3.4	1.6	3.5	2.4	13.4	--
7	7.6	3.4	3.2	1.9	3.2	2.1	8.4	3.7
6	6.4	2.6	3.4	1.9	2.4	1.8	6.8	5.8
5	7.4	1.1	3.9	1.9	2.9	1.8	3.4	1.8
4	6.0	2.4	3.2	1.9	3.1	1.8	2.9	--
3	5.3	3.2	3.2	1.9	2.9	1.4	3.7	--
2	3.5	1.8	3.2	1.8	3.1	1.9	2.9	--
1	2.1	0.6	2.7	1.8	1.4	1.3	0.6	0.3
0	0		0		0		0	
1	1.4	0.6	2.3	1.3	2.6	0.6	4.1	2.7
2	3.2	1.8	3.1	1.1	3.4	1.0	2.4	1.3
3	4.2	2.7	3.5	1.8	3.4	0.8	3.7	2.9
4	3.4	2.7	2.9	1.4	4.0	3.1	3.1	1.0
5	5.3	3.4	4.0	2.7	5.0	5.3	--	--
6	6.0	2.6	4.3	2.4	5.0	5.0	3.7	--
7	7.1	3.1	4.7	2.3	4.0	1.8	3.1	1.4

Table 18 (continued).

Days Before Making & After Leaving Kill	Linear Distance from Kill Site 28 (♂) (N=8) $\overline{x}$	 SD	 29 (♀) (N=13) $\overline{x}$	 SD	 93 (♀) (N=8) $\overline{x}$	 SD	 45 & 46 (♀♀) (N=7) $\overline{x}$	 SD
8	7.1	2.6	4.5	2.1	4.2	1.3	3.2	--
9	5.6	1.9	5.1	2.3	4.2	1.6	5.1	2.9
10	2.9	2.6	5.0	2.4	6.4	4.5	2.9	1.1

N = Total kills for each lion. Our data were not complete for every day. $\overline{x}$ and SD's are based on available data.

Table 19. Association of radiotagged kittens (Nos. 47, 48, 49 and 51) and their mothers (Nos. 29 and 93) in the winter months before independence.

km Located from	No. of Locations			
Adult ♀	Dec.	Jan.	Feb.	Mar.
0 - 0.39	19	68	64	30
0.40 - 0.79	6	2	3	11
0.80 - 1.19	1	1	5	2
1.20 - 1.60	3	2	1	0
1.61 +	4	13	0	3

Table 20. Distribution of mule deer and elk kills made by mountain lions, Big Creek drainage, winters 1970-71, 1971-72.

No. of Kills Per 2.6 km^2 (mi^2) Quadrat	Mule Deer	Elk
1	15	10
2	4	9
3	2	1
4	0	1

Total quadrats searched = 70

Total quadrats with kills = 33

Quadrats with both species = 9

Quadrats with only elk = 21

Quadrats with only mule deer = 21 $\chi^2 = 0.9$

$P > 0.05$

Table 21. Spacing of mule deer and elk kills made by mountain lions on their winter range areas.

Lion No.	Time Period	No. Kills	Average Distance Between Kills (km)	R[1]
28 (♂)	Winters 1970-71, 1971-72	8	1.8	0.78
29 (♀)	Winters 1970-71, 1971-72	21	1.0	0.83
46 (♀)	Winters 1970-71, 1971-72	10	1.9	1.00
93 (♀)	Winter 1970-71	10	3.5	2.15

[1] R = Measure of spacing (Clark and Evans 1954); in a random distribution R = 1; with maximum aggregation R = 0; with maximum spacing R = 2.15.

Table 22. Spatial relationship of selected mountain lions.

Flight Date	Dispersion Values (R)[1] All Adult Resident Lions	Female Only	Older Adults Only
1/27/71	1.10	1.05	0.37
2/ 8/71	0.83	0.99	1.29
2/13/71	1.31	1.24	1.16
2/20/71	0.76	0.45	1.72
3/16/71	1.25	1.29	1.41
3/19/71	0.77	0.70	0.97
4/ 1/71	0.87	1.03	0.70
4/ 4/71	0.45	0.27	0.83
4/13/71	1.67	1.28	1.81
4/19/71	1.56	1.32	1.64
4/26/71	0.32	--	--
4/29/71	0.91	--	--
1/30/72	0.25	--	--
2/ 4/72	0.53	--	--
2/21/72	0.61	--	--

Table 22 (continued).

	Dispersion Values (R)[1]		
Flight Date	All Adult Resident Lions	Female Only	Older Adults Only
4/14/72	0.88	--	--
4/23/72	0.73	--	--

[1] R = 1 in random distribution; R = 0 under conditions of maximum association and R = 2.15 under conditions of maximum spacing (Clark and Evans 1954).

Table 23. Linear distance (km) between adult resident mountain lions, 1970-1972.

Lion Nos.		24 (♀)			26 (♂)			28 (♂)			29 (♀)			45 (♀)			46 (♀)			93 (♀)			52 (♀)		
		N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD
3 (♂)	W[1]	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	S	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	W	--	--	--	4	21.4	17.1‡[2]	4	16.6	10.0‡	7	12.2	8.4‡	--	--	--	3	18.3	9.7	--	--	--	6	9.7	15.3†
24 (♀)	W				7	7.2	5.1†	8	20.8	5.0‡	8	17.4	4.7	5	45.2	3.1	8	25.3	3.7	8	28.8	7.2	--	--	--
	S	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	W	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
26 (♂)	W							11	25.1	6.4‡	11	17.9	4.8‡	7	31.1	10.0	10	23.0	6.1	9	33.3	8.5	--	--	--
	S							4	27.7	9.5	3	25.9	2.9	2	36.4	3.2	3	46.0	22.0	3	56.8	7.2	--	--	--
	W							9	10.9	7.2‡	23	8.0	6.1‡	--	--	--	6	12.7	6.6‡	--	--	--	3	11.6	6.6‡
28 (♂)	W										50	5.1	3.4†	22	11.4	11.7†	49	4.5	2.9†	47	6.4	6.4†	--	--	--
	S										25	13.4	15.4‡	6	17.5	9.5‡	7	11.6	11.4†	21	27.8	6.1	--	--	--
	W										65	4.0	2.7†	14	3.5	1.9†	50	3.5	3.4†	--	--	--	11	9.3	2.9‡
29 (♀)	W													22	11.7	11.9†	37	6.0	3.7†	34	9.5	8.5†	--	--	--
	S													7	25.1	11.4	11	13.4	11.4	25	36.4	4.2	--	--	--
	W													9	3.7	1.8†	50	4.7	2.6‡	--	--	--	16	7.2	2.6‡
45 (♀)	W																16	13.8	11.7†	17	14.2	11.6‡	--	--	--
	S																1	20.6	-- ‡	14	21.7	5.0	--	--	--
	W																9	4.7	4.0†	--	--	--	--	--	--
46 (♀)	W																			40	7.4	7.4‡	--	--	--
																				5	20.4	14.0	--	--	--
																				--	--	--	11	9.5	1.9‡

[1] Season: W = 12/1/70-5/31/72; S = 6/1/71-11/30/71; W = 12/1/71-5/3/72.

[2] ‡ = Contiguous or slight overlap of seasonal range; † = Strong overlap in seasonal range.

Table 24. Frequency distribution of linear distances (km) between adult mountain lions with strongly overlapping areas during winter.

Lion Nos.	28(1)-	28(1)-	28(1)-	28(1)-	28(1)-	28(1)-	28(1)-	29(2)-	29(2)-	29(2)-	29(3)-	29(3)-	93(3)-	93(3)-	45(4)-	45(4)-
(Status)[1]	29(2)	29(3)	93(3)	45(4)	45(4)	46(4)	46(4)	93(3)	45(4)	46(4)	45(4)	46(4)	45(4)	46(4)	46(4)	46(4)
Year[2]	7	8	7	7	8	7	8	7	7	7	8	8	7	7	7	8
km	N=50	N=66	N=44	N=13	N=14	N=43	N=50	N=31	N=14	N=37	N= 9	N=48	N= 7	N=37	N= 8	N= 9
0	0	7	3	1	1	1	12	1	1	0	0	3	0	1	0	0
0.2 - 1.4	5	6	3	1	2	5	8	4	2	3	4	4	0	9	4	3
1.6 - 3.1	9	11	10	7	2	16	7	4	6	3	2	7	1	3	2	2
3.2 - 4.7	13	16	11	1	5	7	9	2	2	11	1	13	2	5	1	0
4.8 - 6.3	10	17	4	3	4	4	4	7	3	9	0	11	4	7	0	1
6.4 - 7.9	4	6	8	0	0	11	4	2	0	3	0	7	0	3	0	1
8.0 +	9	3	5	0	0	4	6	11	0	8	2	3	0	9	1	2
$\overline{x}$	5.5	4.8	5.1	3.1	3.9	4.5	3.5	8.2	2.4	5.9	3.7	4.7	5.3	5.8	2.9	4.7
SD	3.4	3.2	4.5	1.8	1.8	2.7	3.4	6.9	1.8	3.5	1.8	2.6	1.3	5.6	2.9	4.0
B	1.43‡	1.10‡	1.93‡	--	--	0.83‡	0.88‡	1.41‡	--	1.00‡	--	-0.01	--	2.06‡	--	--

[1] Status: adult♂ = 1; adult♀ with small kittens = 2; adult♀ with large kittens = 3; young adult♀ without kittens = 4.

[2] Year: 7 = winter 1970-71; 8 = winter 1971-72

B = the moment coefficient of skewness and is zero for normal distributions. ‡ indicates statistics significant at the 0.05 level.

Table 25. Association records of adult mountain lions as determined by radiotracking.

Lion No.	Total Days Located	Days Located Found in Association with Other Radiotagged Lions	
		N	%
26 (♂)	63	3	5
28 (♂)	231	30	13
29 (♀)	252	14	6
45 (♀)	74	5	7
46 (♀)	150	16	11
93 (♀)	154	20 (16)[1]	13

[1] Found associated with No. 50 on 16 consecutive lion-location-days (see text).

Table 26. Summary of mountain lion interactions as determined by radiotracking.

No.	Year and Month	Designation of Lions Involved[1]	Probable or Actual Duration (Days)	No. of Location Days	Kill Involved	Movement as a Cohesive Group or Pair	Investigator Interference	General Remarks
1	Jan. 71	28♂/45♀	< 1	1	No	No	No	
2	May 71	28♂/46♀	< 1	1	No	No	No	
3	Sept. 71	28♂/29♀ 2L[1]	< 1	1	Probably	No	No	Kill not located but every sign indicated one present.
4	Feb. 71	28♂/93♀ 2L	< 1	1	Yes	No	Yes	Kill by 93 (♀). 93 and kittens ran from kill when approached by investigator with hounds but returned. 28 (♂) came to kill and 93 and kittens left. 28 remained at least 2 days.
5	Jan. 72	26♂/29♀ 2L	< 1	1	No	No	No	Two days before the interaction, 26 (♂) moved into canyon with 29 and kittens. They left and he remained. They were located together briefly after dark; 26 left the drainage that night; 29 and kittens left next morning.
6	Dec. 70	29♀ S/45♀	< 1	1	Yes	No	Yes	29 and kittens moved into small canyon where 45 had a kill. The lions were within 90 m of each other but kittens were not at kill; from tracks 29 was. We captured all 4. 29 and kittens left canyon that night; 45 remained and finished her kill.
7	Jan. 70	29♀ S/93♀ L	< 1	1	Yes	No	No	29 was with kittens at a kill; 93 and kittens moved down canyon and were stopped within 90 m, but interactions unknown. That night 93 moved on down canyon and made kill. 29 left drainage next day.
8	Jan. 72	28♂/29♀ 2L	3	2	Yes	?	Yes	Family group separate but 28♂ was very close to 51 (L♀). 28 was not with family group next day when we ran them. The day following family group and 28 were at fresh kill made by 29 (♀).

Table 26 (continued).

No.	Year and Month	Designation of Lions Involved[1]	Probable or Actual Duration (Days)	No. of Location Days	Kill Involved	Movement as a Cohesive Group or Pair	Investigator Interference	General Remarks
9	Jan. 72	3♂/52♀	2+	1	Yes	Yes	Yes	Wiles observed male copulating with female near a kill. Hounds disturbed cats; he ran lions because female unmarked. Both lions treed. Marked female - 52. Female was near site treed and male was 1.8 km distant 2 days later. Tracks indicated they were in vicinity of kill for number of days before located.
10	Jan. 72	26♂, 29♀ 2L	2	2	Yes	?	No	26♂ and 29♀ were located a little higher in canyon than kittens and kill. The next day the ♂ kitten was with the kill, 29 and the ♀ kitten were in the next canyon 0.8 km distant and the male 26 was with them. On the 3rd day they had separated.
11	Jan. 72	46♀, 29♀ 2L	2	2	Yes	No	No	All were found at a kill site. 46 left after 2 days but the family group remained.
12	Mar. 71	28♂, 93♀	3	3	No	Yes	No	93♀ left her kittens and 50♂ at a kill and came down Big Creek to 28's (♂) location. They remained together for 3 days. He left 1 day sooner than she from this site.
13	Feb. 72	28♂, 29♀ 2L	3	3	Yes	Yes	No	Day 1: The kittens were at a kill. 29♀ and 28♂ were together 5 km away. Day 2: All were at the kill. Day 3: 29 and 28 were 3 km away and kittens were at kill.
14	Apr. 72	28♂/45♀	5	3	No	Yes	No	28♂ and 45♀ were radiotracked as they moved down a creek bottom together. 2 days later they were 0.8 km apart in a small canyon moving. The next day they had moved 6.4 km and were 0.4 km apart moving through a canyon.

Table 26 (continued).

No.	Year and Month	Designation of Lions Involved[1]	Probable or Actual Duration (Days)	No. of Location Days	Kill Involved	Movement as a Cohesive Group or Pair	Investigator Interference	General Remarks
15	Mar.-Apr. 72	46♀/28♂, 29♀	16	13	Possibly	Yes	No	28♂ and 46♀ were found together in nearly same location on 10 radio-location-days spanning a 14-day period. 29♀ joined them on the 12th and 14th days. 28 and 46 had moved from this location on day 15 and were found moving together the 16th but separated after that.
16	Feb.-Mar. 71	93♀ 2L/50♂	24	14	Yes - 4	Yes	Yes	50, a young transient ♂, joined the family group at a kill and moved with them over the next 24-day period.
17	Mar. 71	50♂/sibling group (Nos. 48♂ and 49♀)	11+	4	Yes	Yes	Yes	They left the Big Creek drainage after 93♀ left there for the last time, moving together for 24 air-line km. We reinstrumented 50.

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[1] L = large kitten (over 12 mo); S = small kitten (under 12 mo)

Table 27. Sociality of adult mountain lions.

	Total Days Found Associated With:				
Class	♂	♀ alone	♀ and L kittens	♀ and S kittens	Total
♂	0	23	20	0	43
♀ alone	23	0	2	1	26
♀ and L kittens	20	2	NO[1]	1	23
♀ and S kittens	0	1	1	NO	2

[1] No opportunity to observe this association.

Table 28. Association (total days) of the various mountain lion sex-reproductive classes.

Sex-reproductive Class	Total Lion-Location Days Associated With: ♂	♀
♂	0	43
♀ with S kittens	0	2
♀ with L kittens	20	3
♀ alone	23	0

Table 29. Reuse of scrape sites.

	No. of Sites Reused	No. of Sites Not Reused	Total
While tracking adult males	3 (10%)	27 (90%)	30
All others	8 (14%)	48 (86%)	56

Table 30. Number of scrapes per site.

	No./Site		
	1	> 2	Total
No. of Sites	70	16	86
No. of Sites Reused	3	8	11

Table 31. Feces or urine at scrape sites.

	Reused	Not Reused	Total
Total Sites	11	75	86
Sites with Feces or Urine	7	10	17

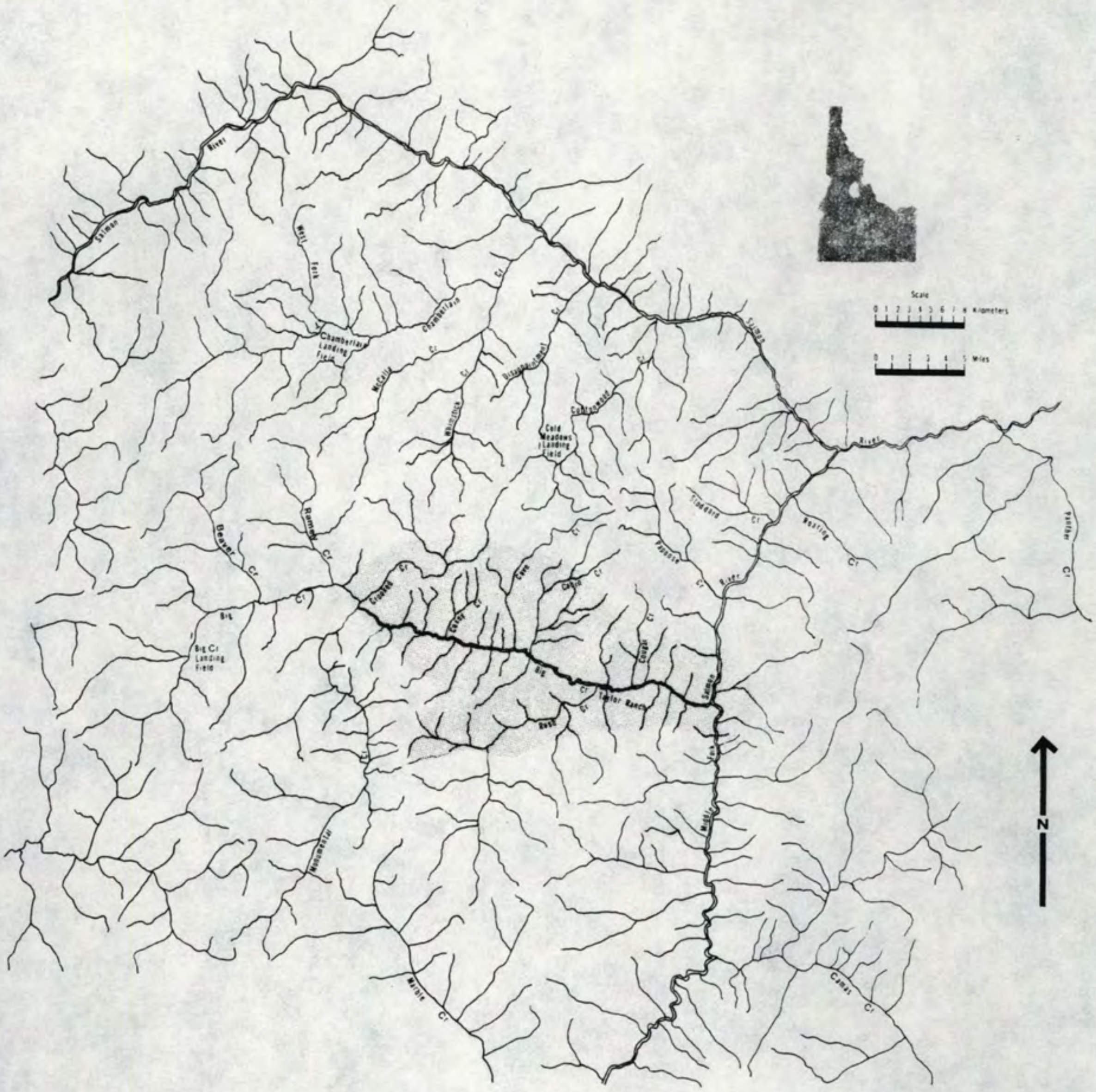

Fig. 1. The study area with place names. The geographic location is shown by the inset. The winter study area in the Big Creek drainage is shown by crosshatch. (1 mi = 1.6 km)

Fig. 2. The Middle Fork of the Salmon River. © JCS.

Fig. 3. The high country that rims the canyons of the Salmon River and its tributaries.

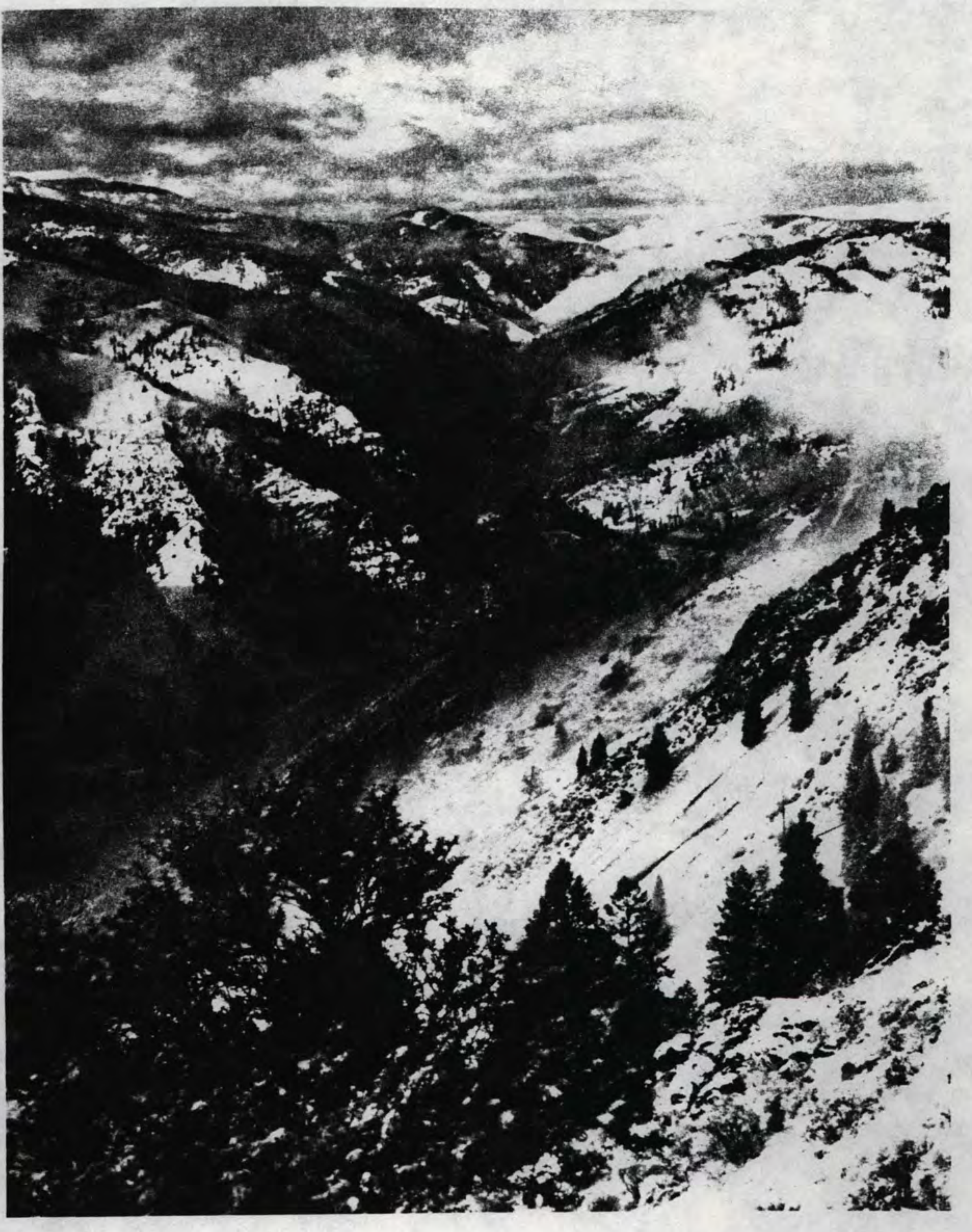

Fig. 4. The main study area in winter, the lower Big Creek drainage. © JCS.

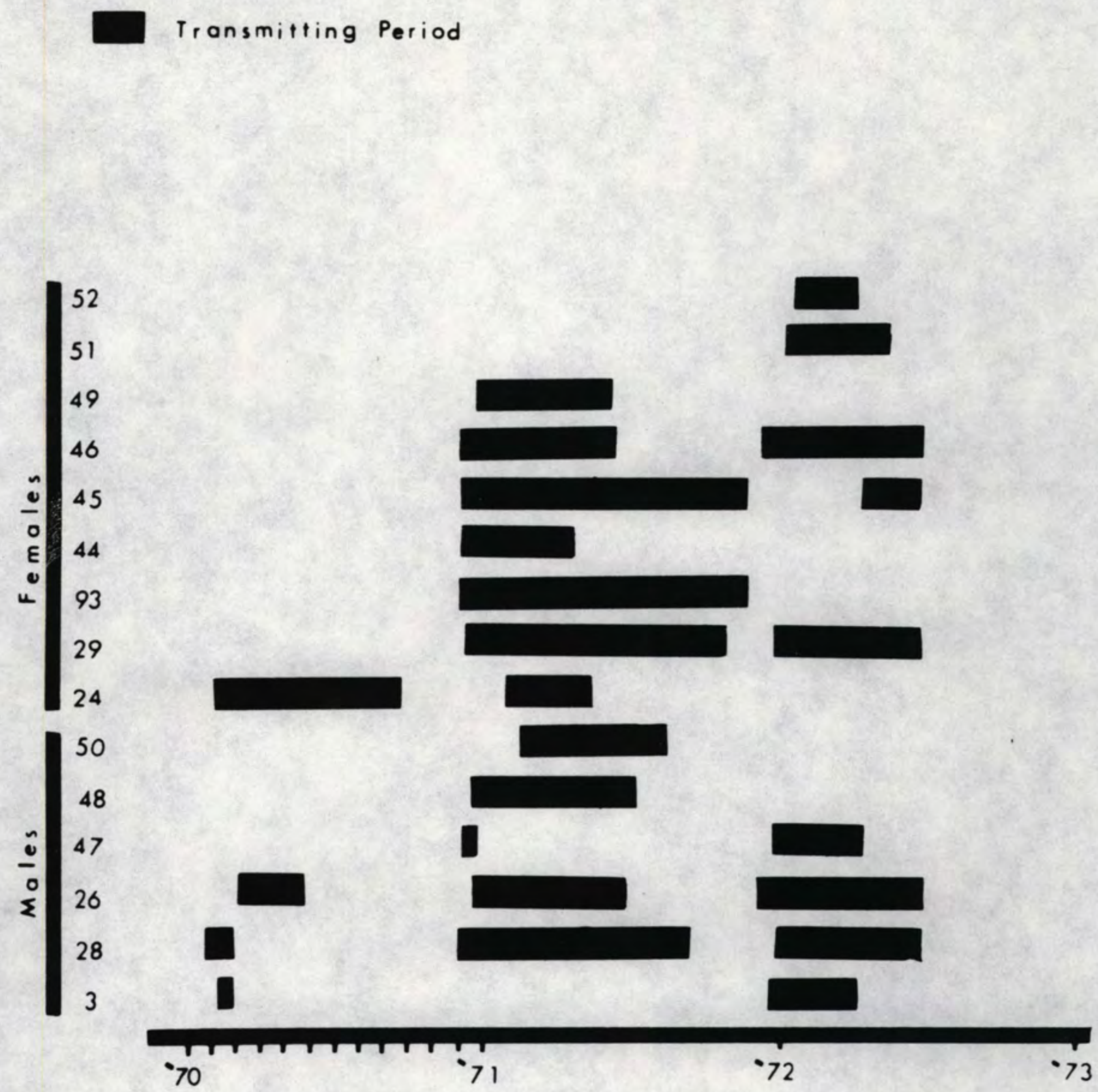

Fig. 5. Distribution of radiotracking periods for individual mountain lions.

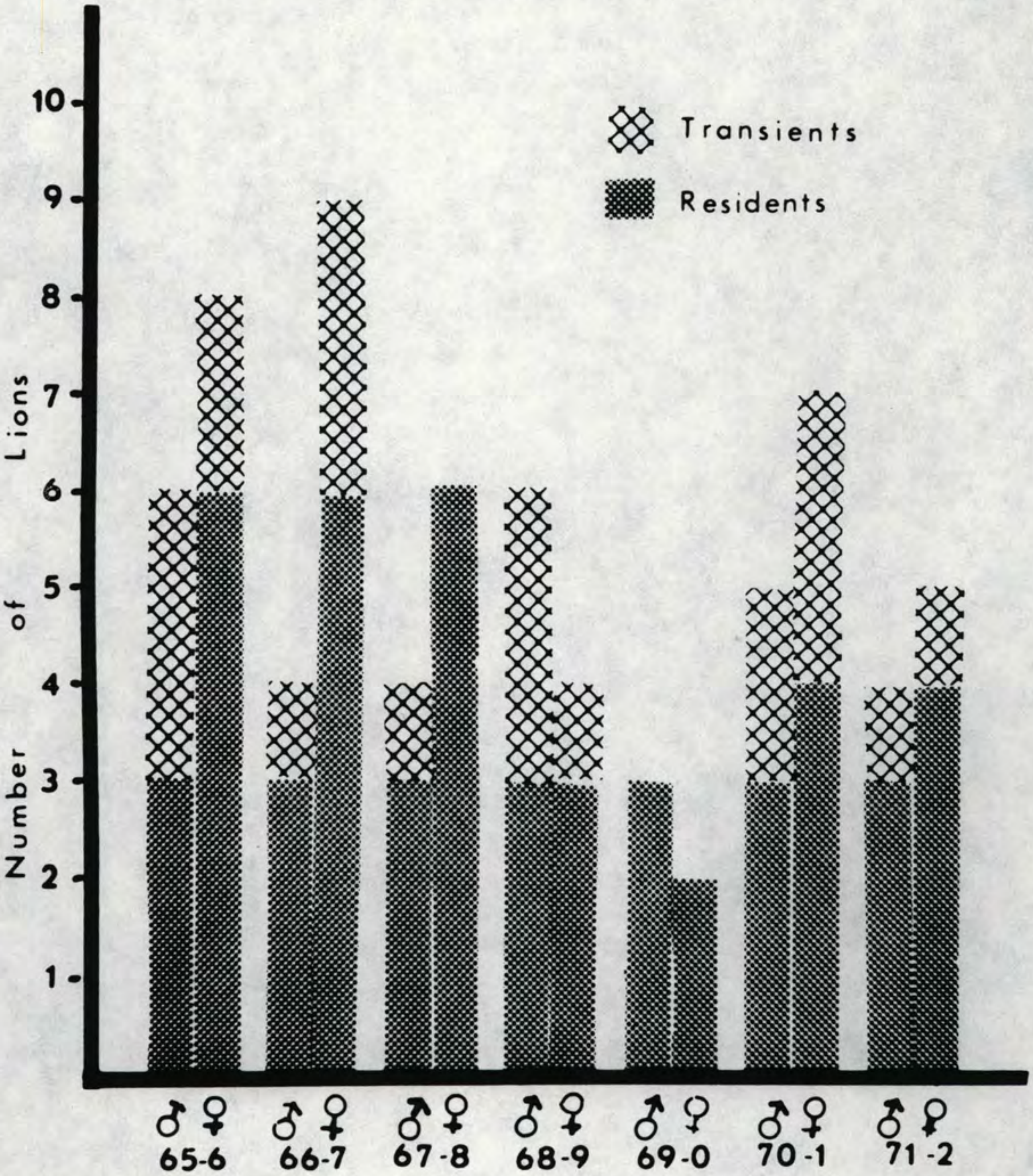

Fig. 6. Lion population composition during the winters 1965-66 through 1971-72.

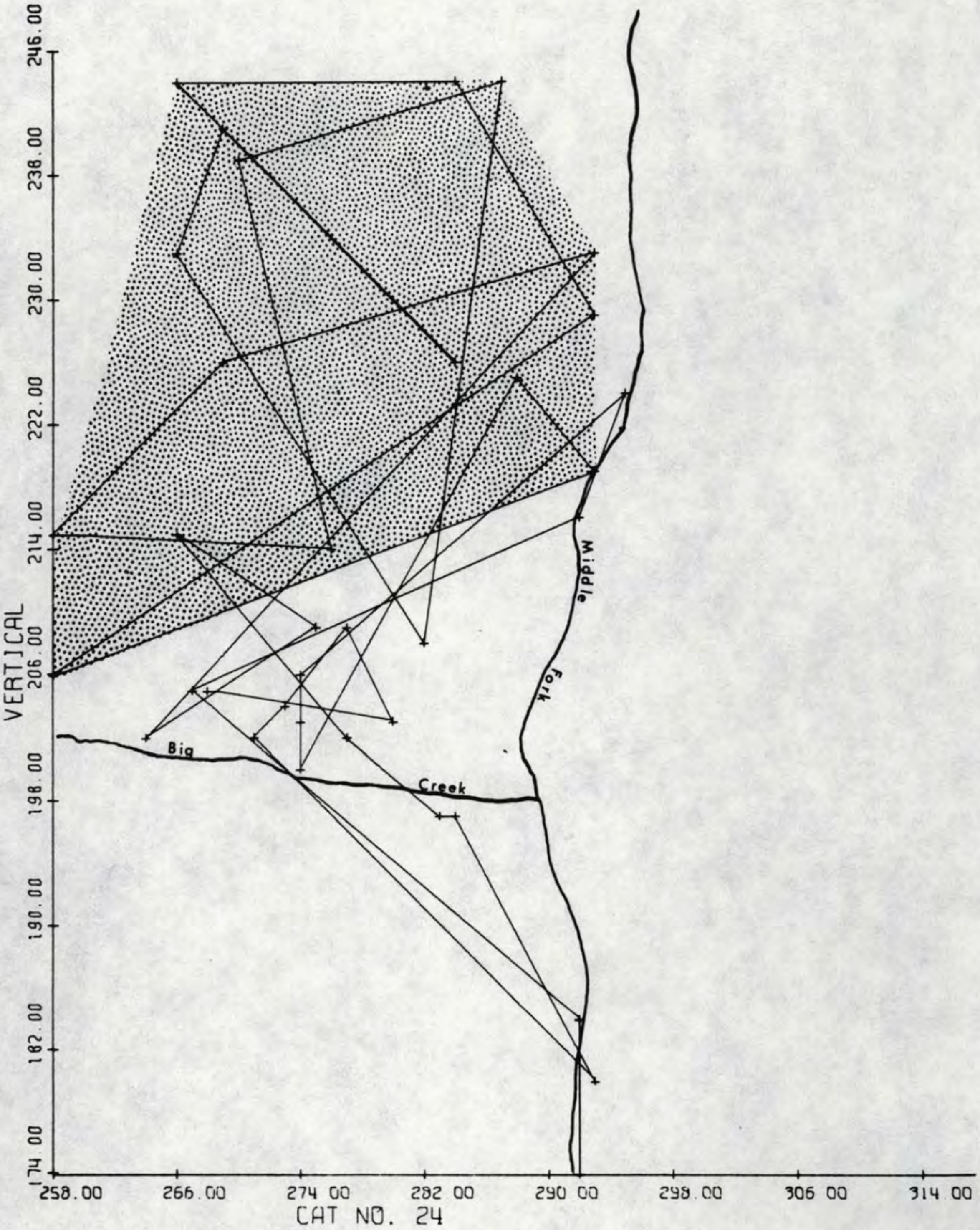

Fig. 7. Plot of location data for resident female No. 24, Feb. 1970 - May 1971. Each grid unit = 0.4 km (0.25 mi); crosshatch area approximates summer area.

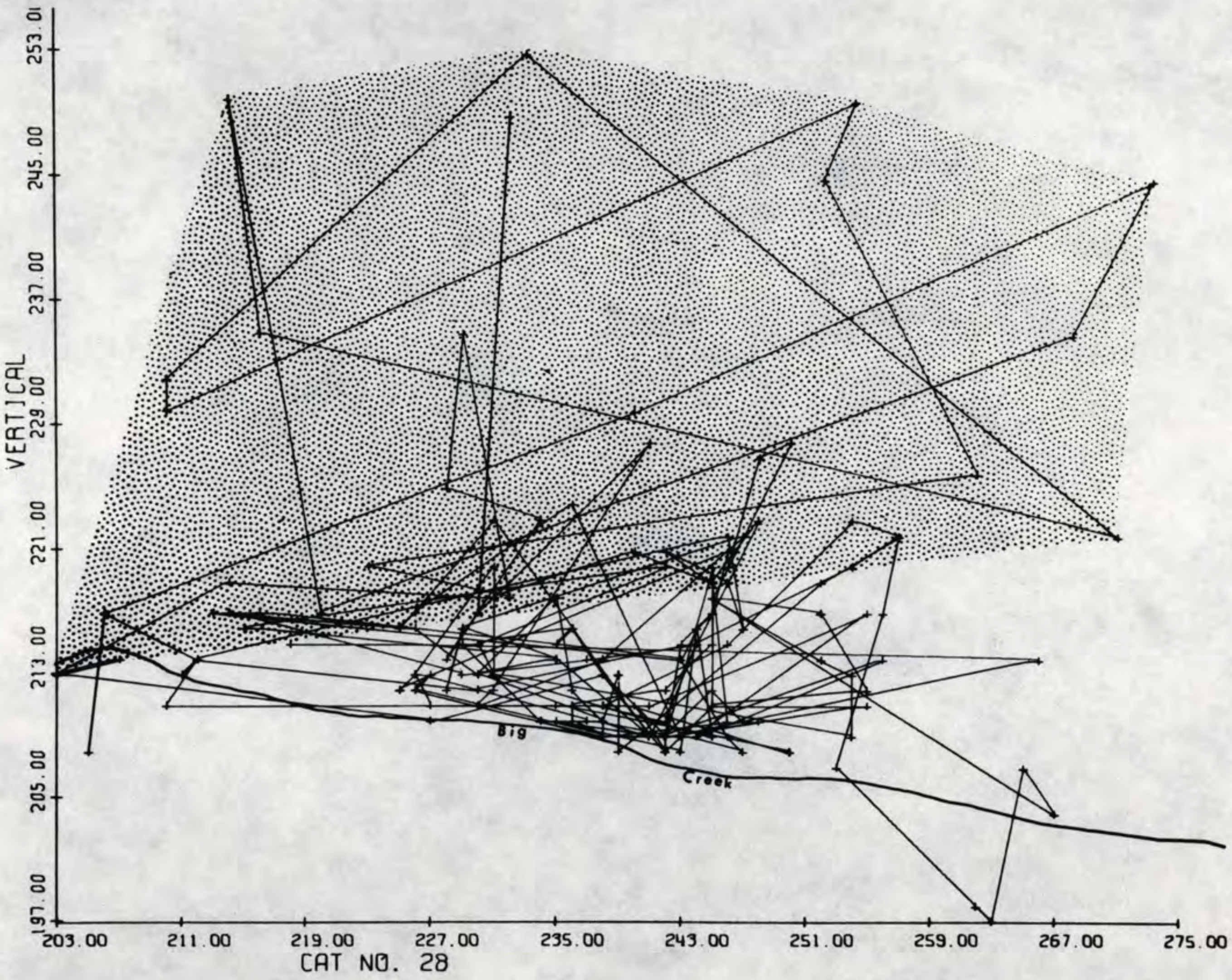

Fig. 8. Plot of location data for resident male No. 28, Jan. 1970 - June 1972. Each grid unit = 0.4 km (0.25 mi); crosshatch area approximates summer area.

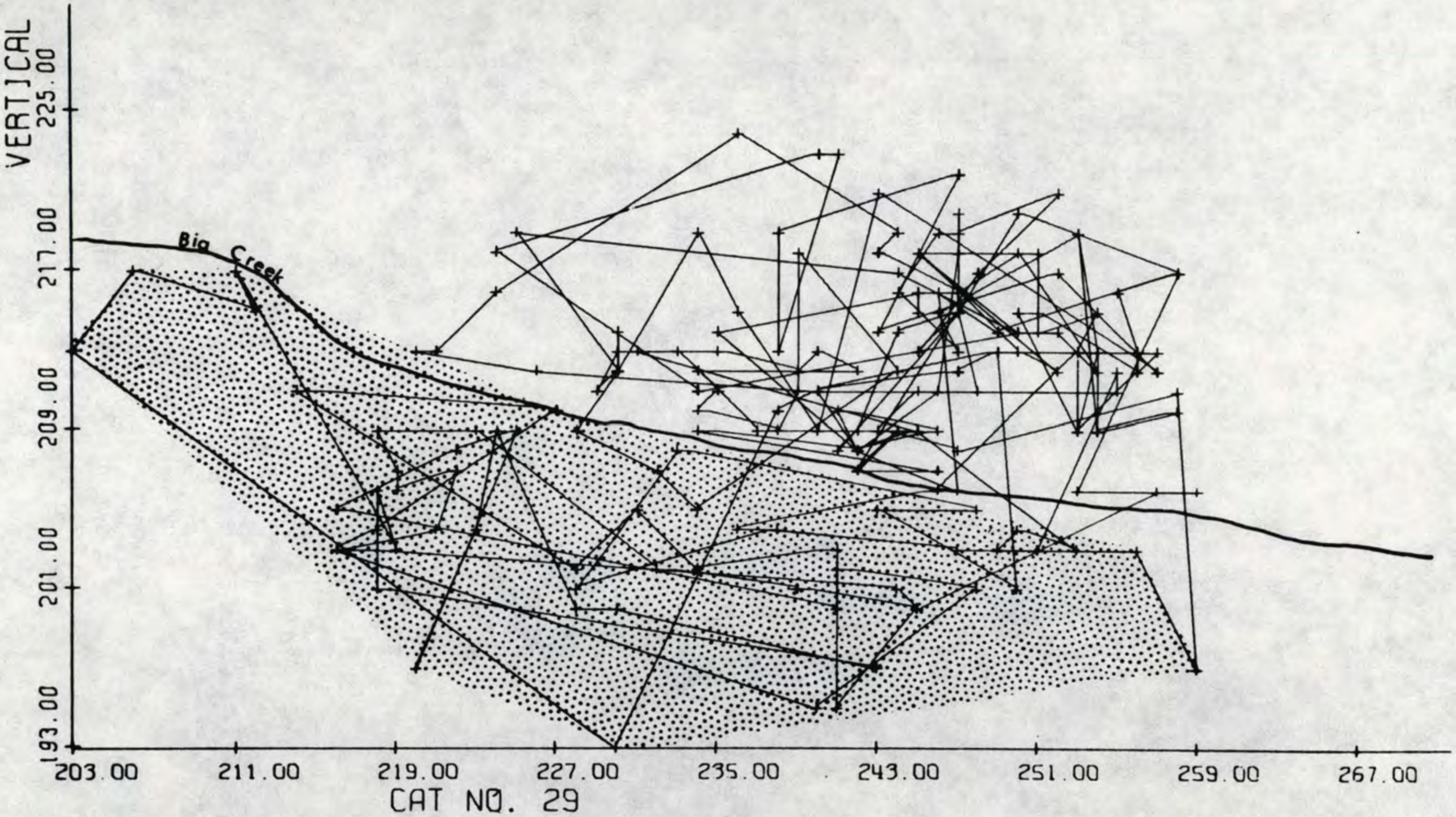

Fig. 9. Plot of location data for resident female No. 29, Dec. 1970 - June 1972. Each grid unit = 0.4 km (0.25 mi); crosshatch area approximates summer area.

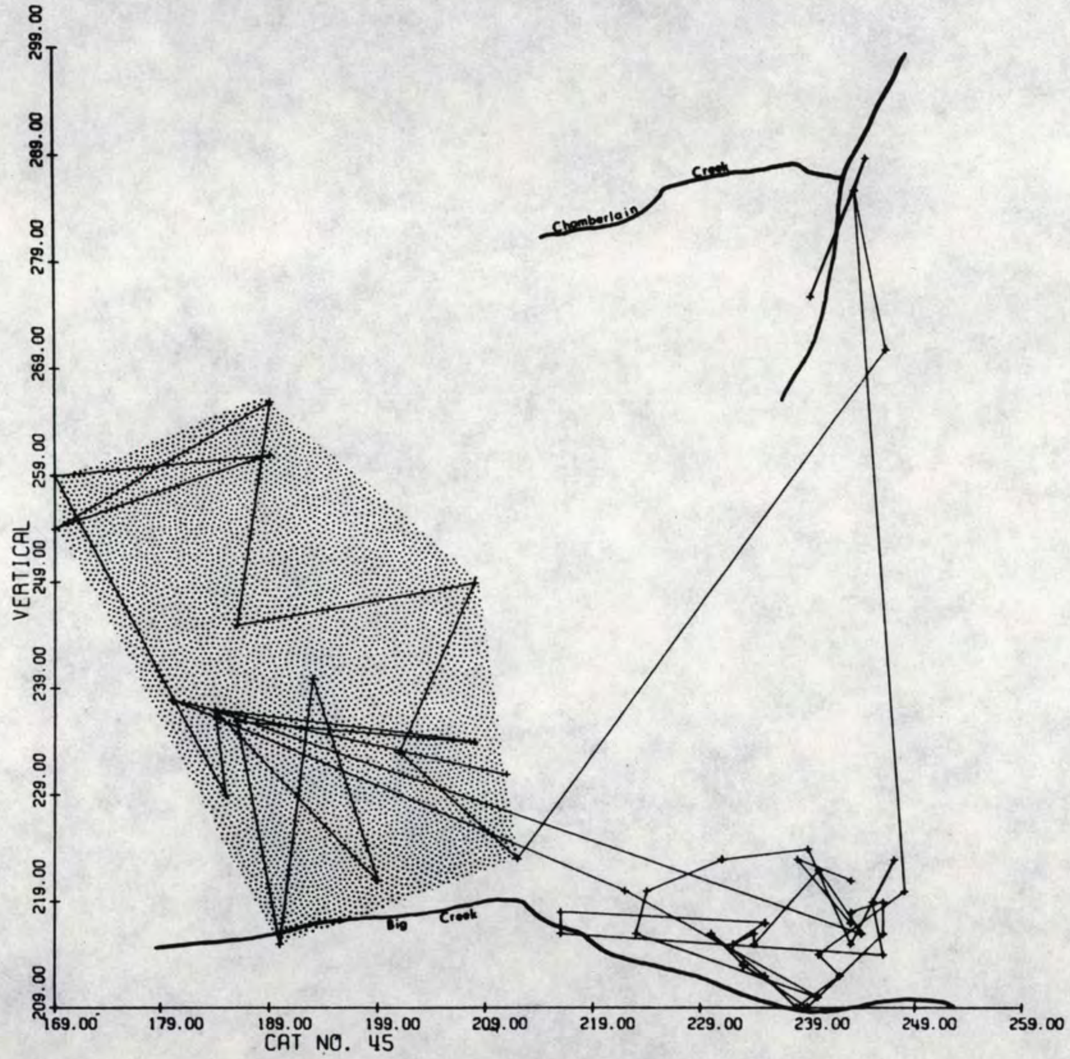

Fig. 10. Plot of location data for young adult resident female No. 45, Nov. 1970 - June 1972. Each grid unit = 0.4 km (0.25 mi); crosshatch area approximates summer area.

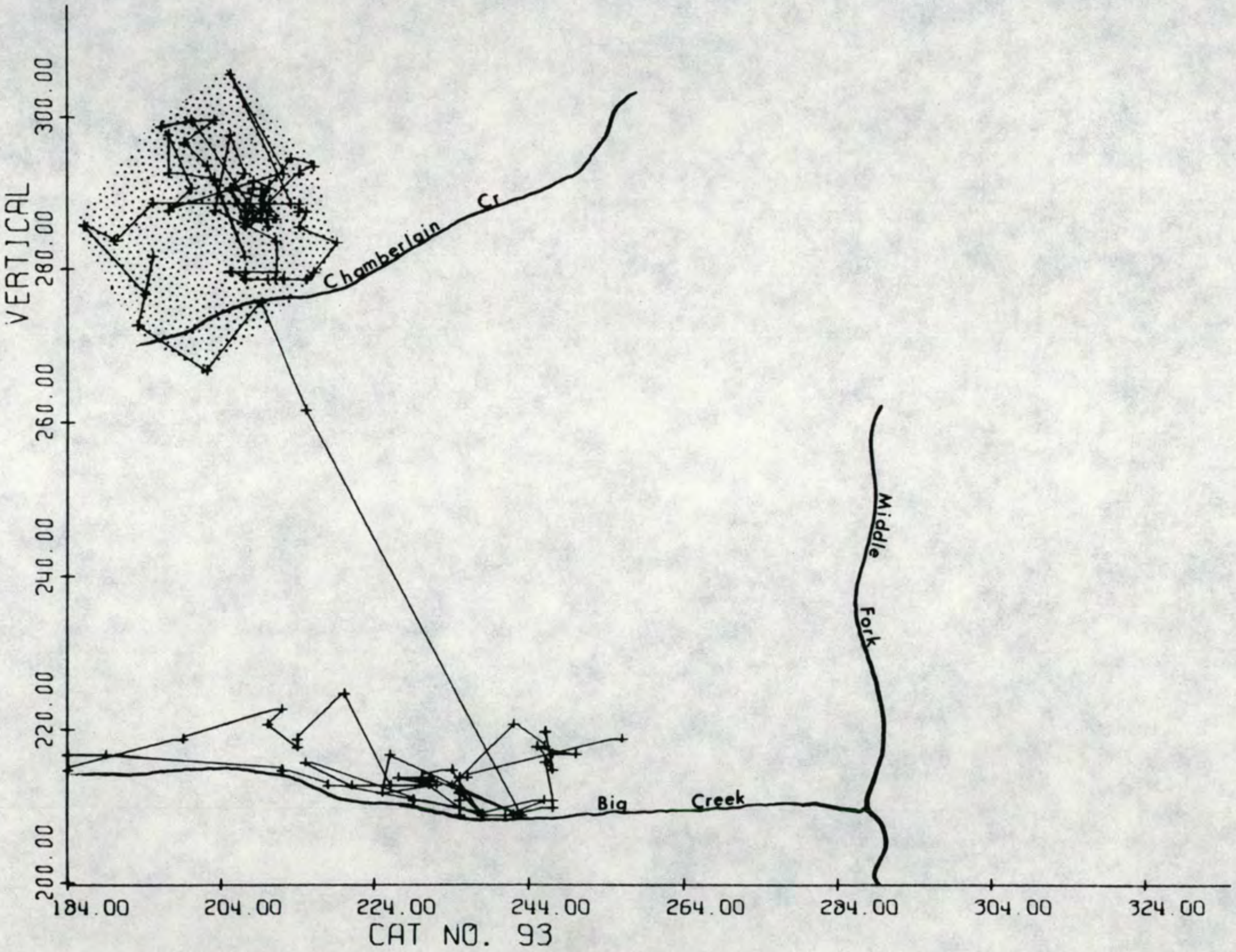

Fig. 11. Plot of location data for resident female No. 93, Dec. 1970 - Nov. 1971. Each grid unit = 0.4 km (0.25 mi); crosshatch area approximates summer range area.

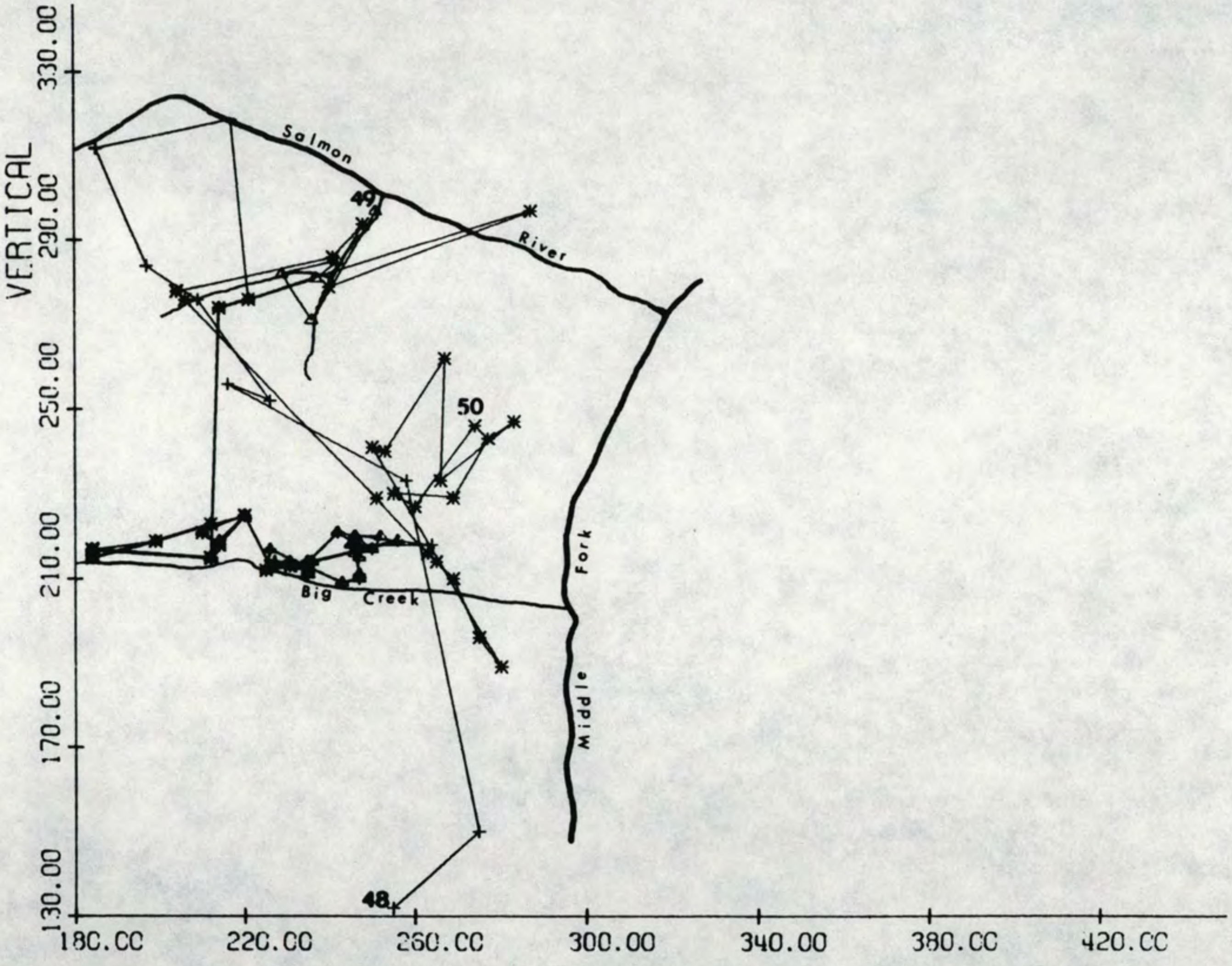

Fig. 12. Movement of lion Nos. 48 and 49 during their second winter with their mother and after independence and of No. 50, a young transient male. One grid unit = 0.4 km (0.25 mi).

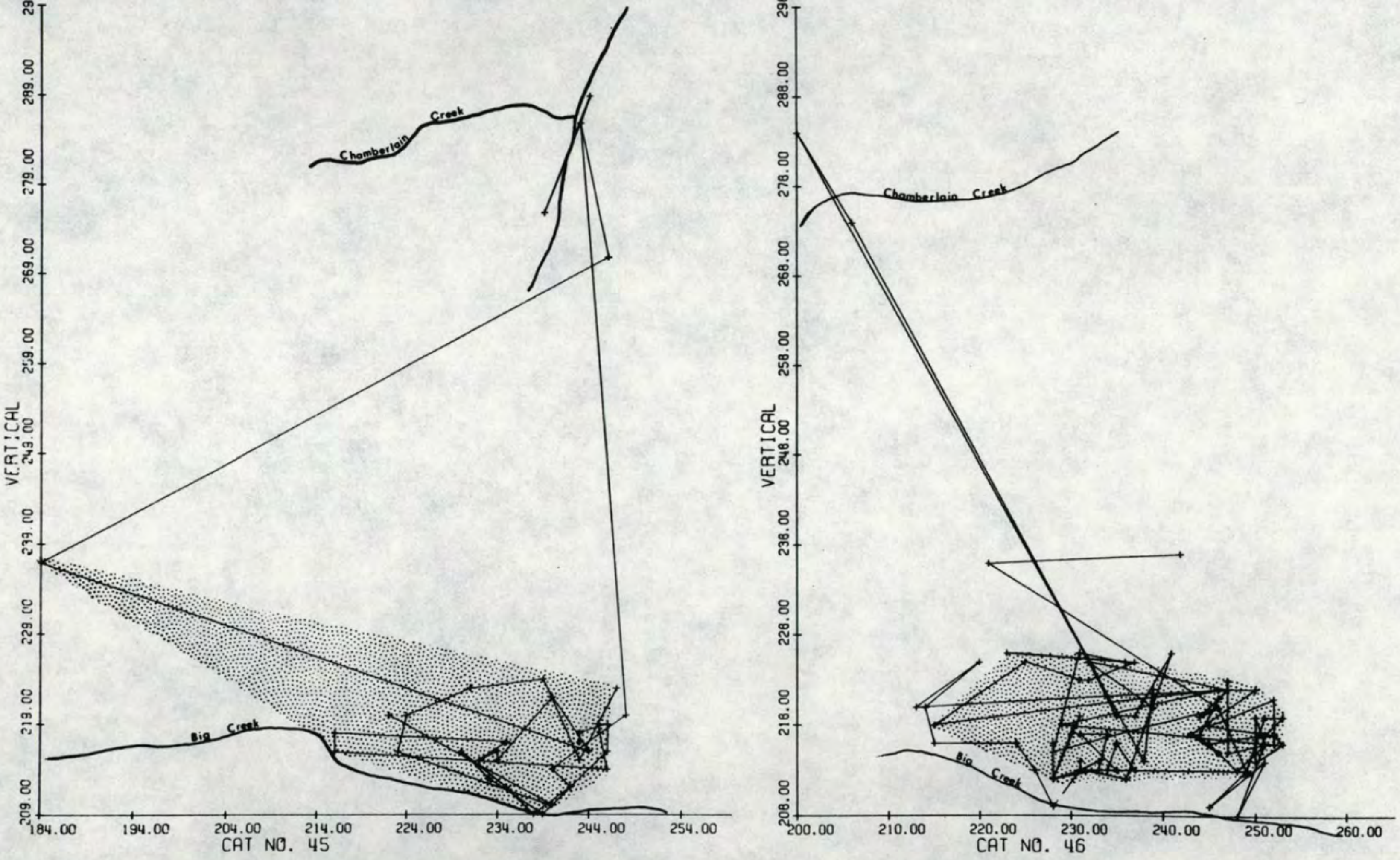

Fig. 13. Plot of location data for female Nos. 45 and 46 during their first (1970-71) and second (1971-72) winters after capture on the Big Creek study area. (A = winter 1970-71; B = winter 1971-72). Crosshatch area approximates 1971-72 winter area. One grid unit = 0.4 km (0.25 mi).

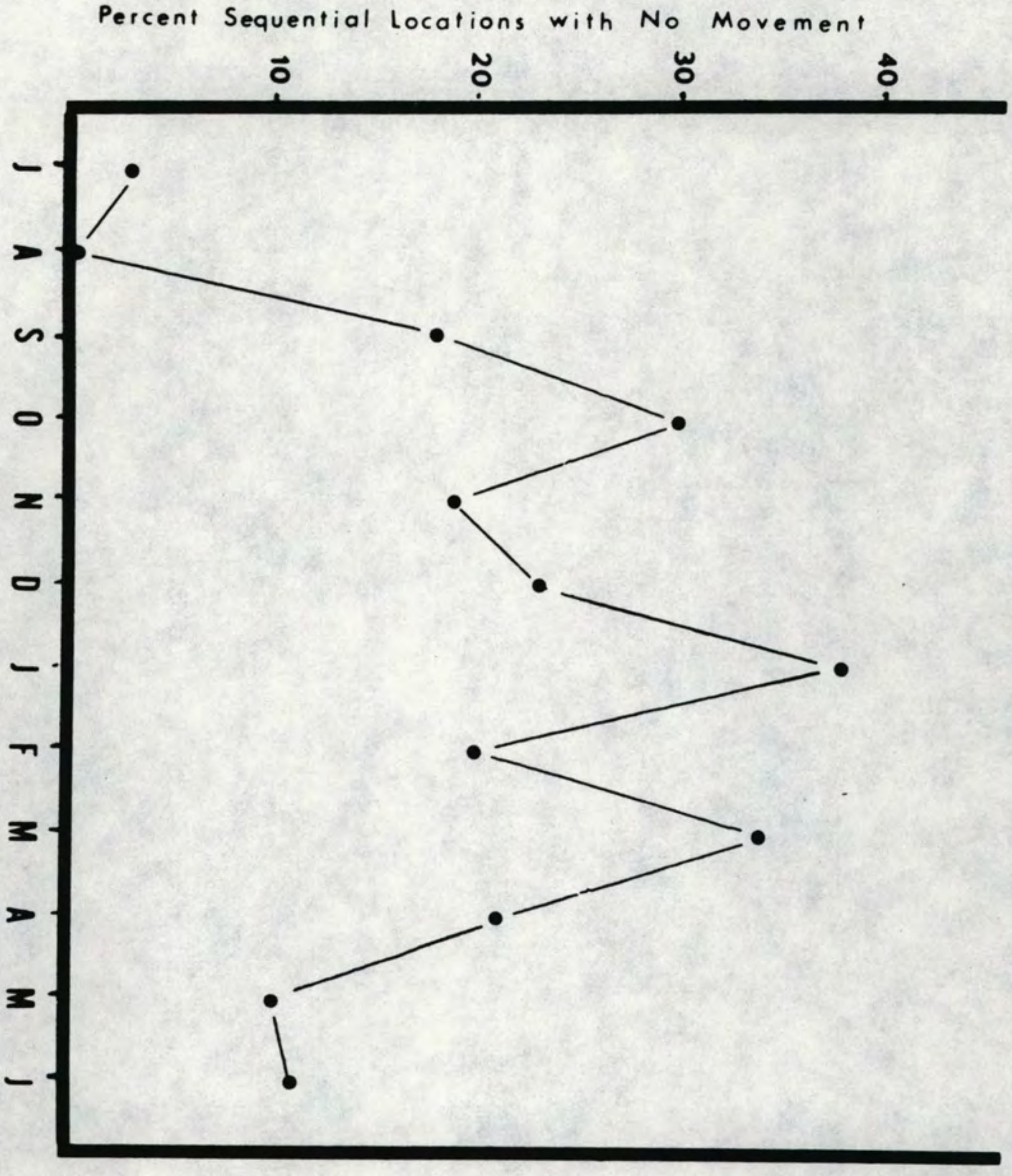

Fig. 14. Mountain lion day-to-day activity based on the percent sequential lion-location-days with no change in location.

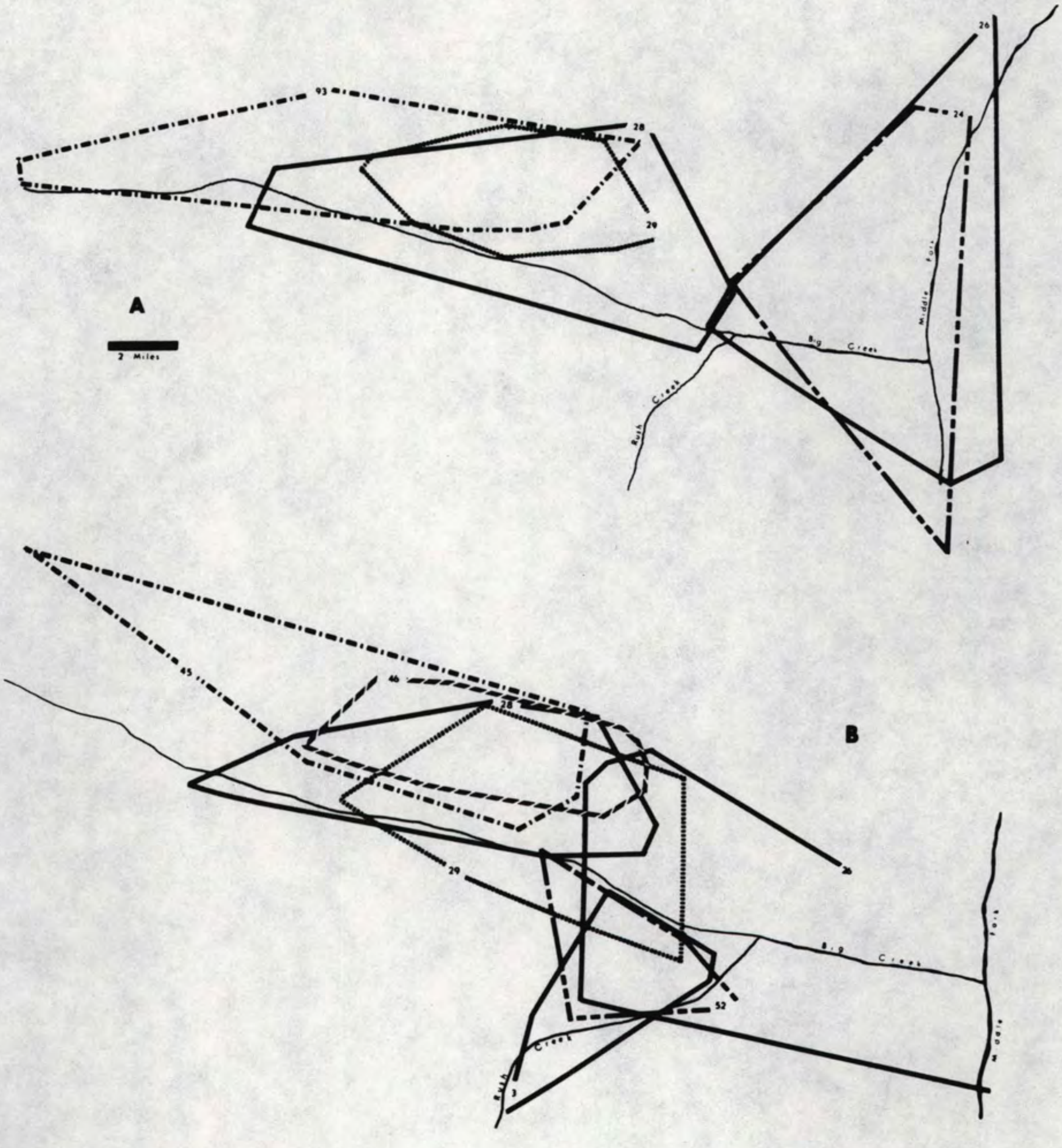

Fig. 15. Winter home areas of breeding resident radiotagged mountain lions. A = 1970-71; B = 1971-72. (1 mi = 1.6 km).

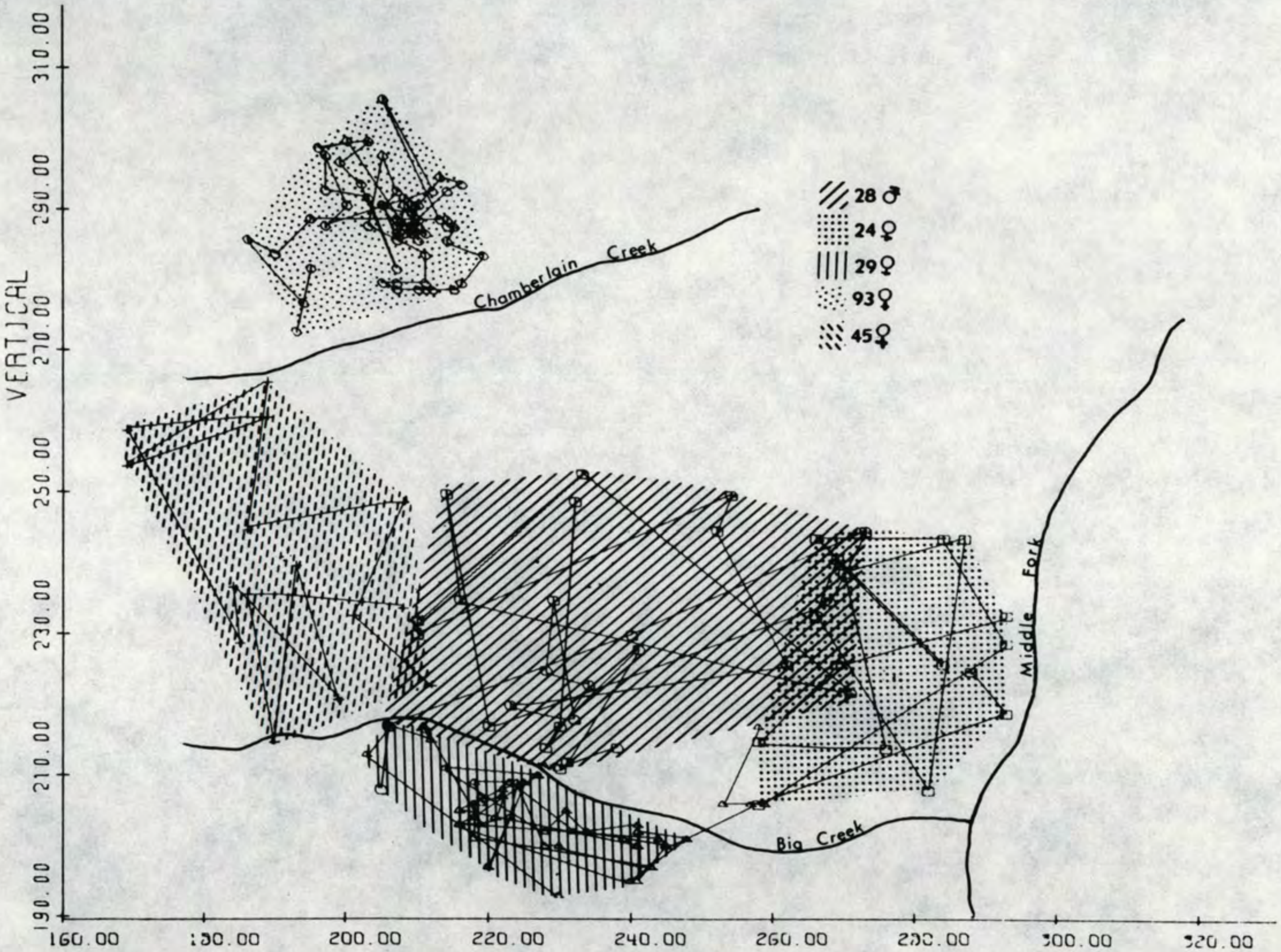

Fig. 16. Movements of resident mountain lions in summer and fall. All area determinations were made in 1971 with the exception of the 1970 data for female No. 24. One grid unit = 0.4 km (0.25 mi).

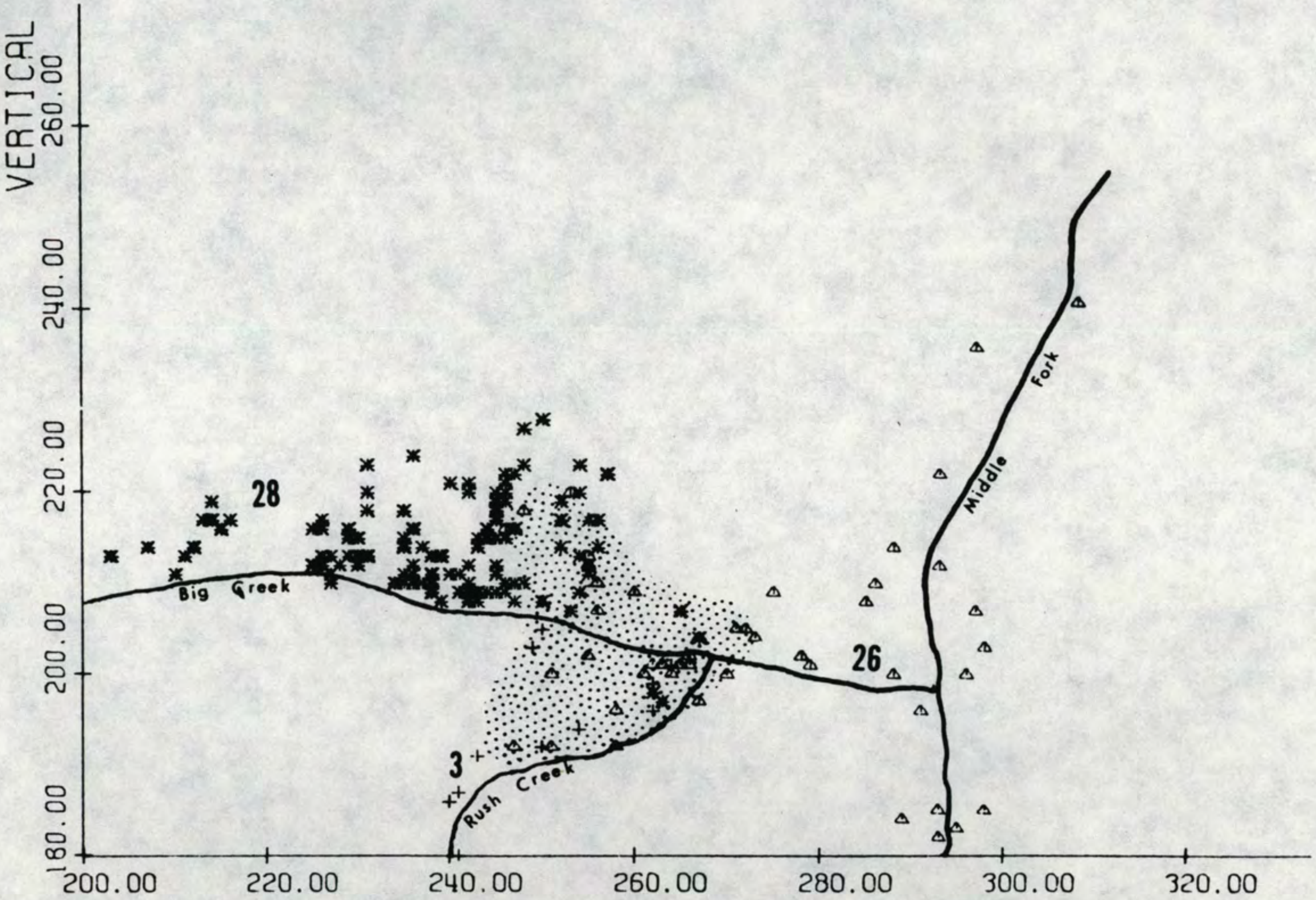

Fig. 17. The locations of three resident males (Nos. 3, 28, and 26) over three winters: 1969-70, 1970-71, 1971-72. Crosshatch region approximates region of winter area adjustment, see text. One grid unit = 0.4 km (0.25 mi).

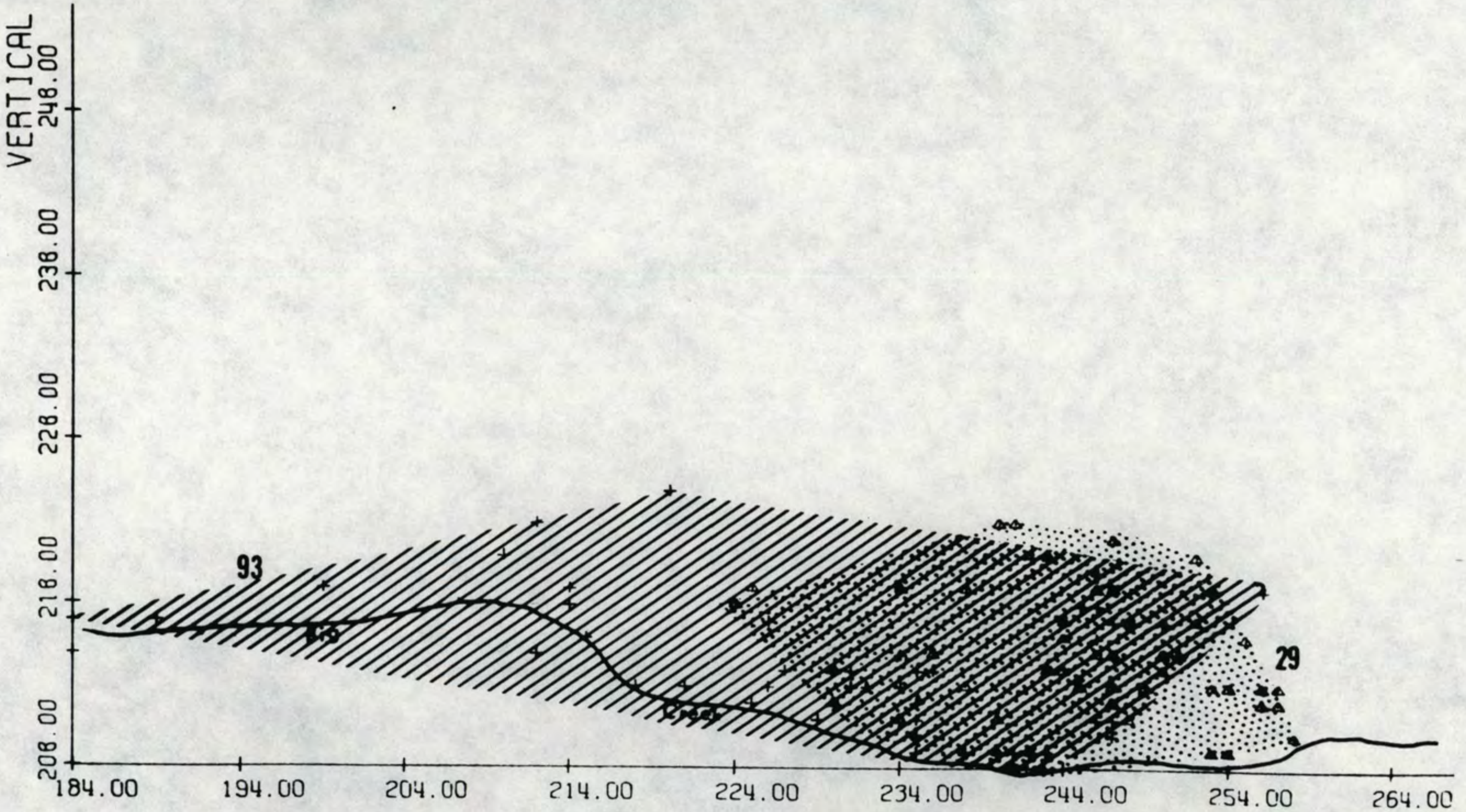

Fig. 18. The movements of female Nos. 29 and 93 during the 1970-71 winter. One grid unit = 0.4 km (0.25 mi).

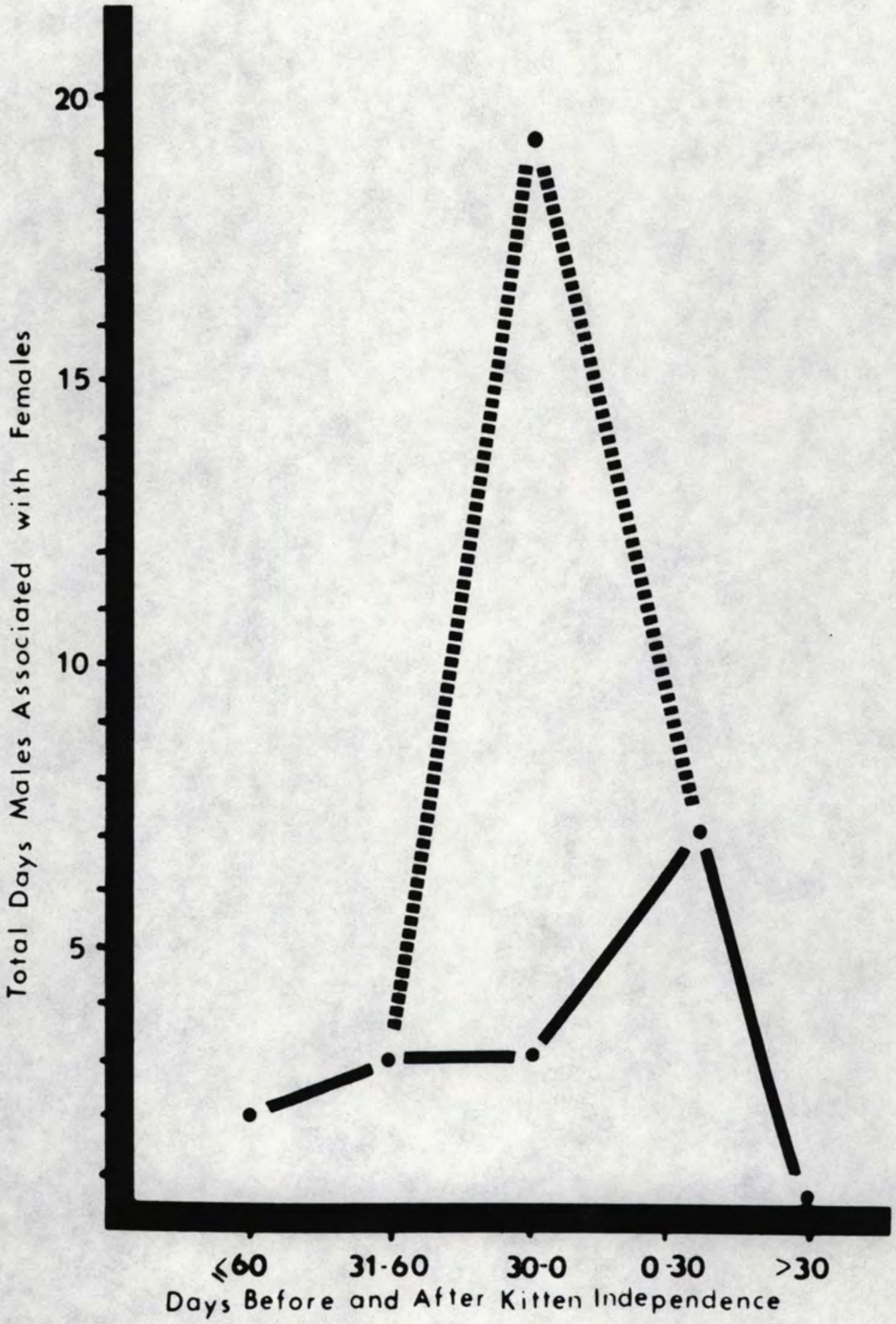

Fig. 19. Days females were found in association with adult males before and after the independence of their kittens. Solid line includes the data for Nos. 50 and 93; the broken line does not (see text).

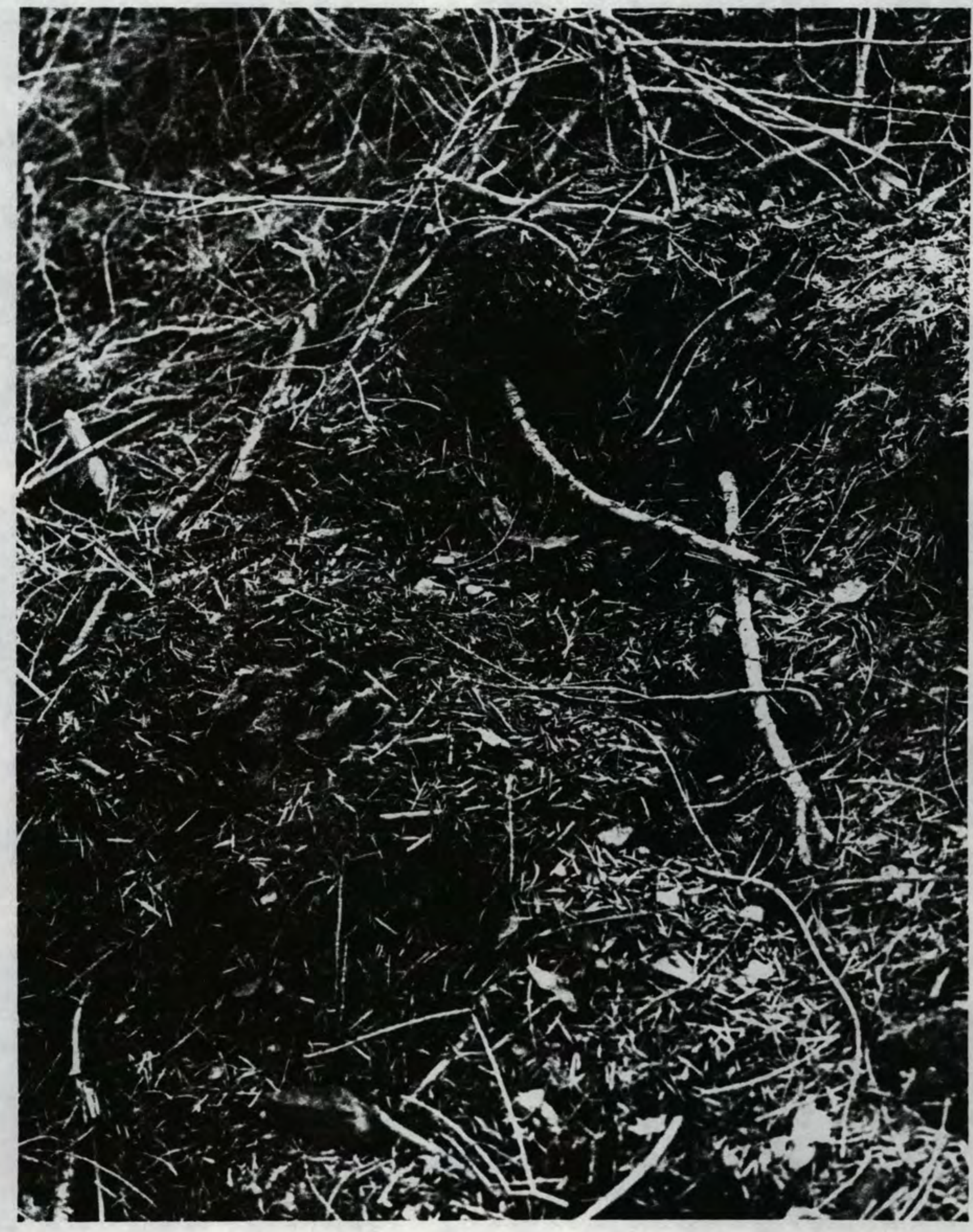

Fig. 20. Mountain lion scrape.

Fig. 21. Mountain lion scrapes at the base of a big Douglas fir.

Fig. 22. Grimace face of a young female after sniffing scent.

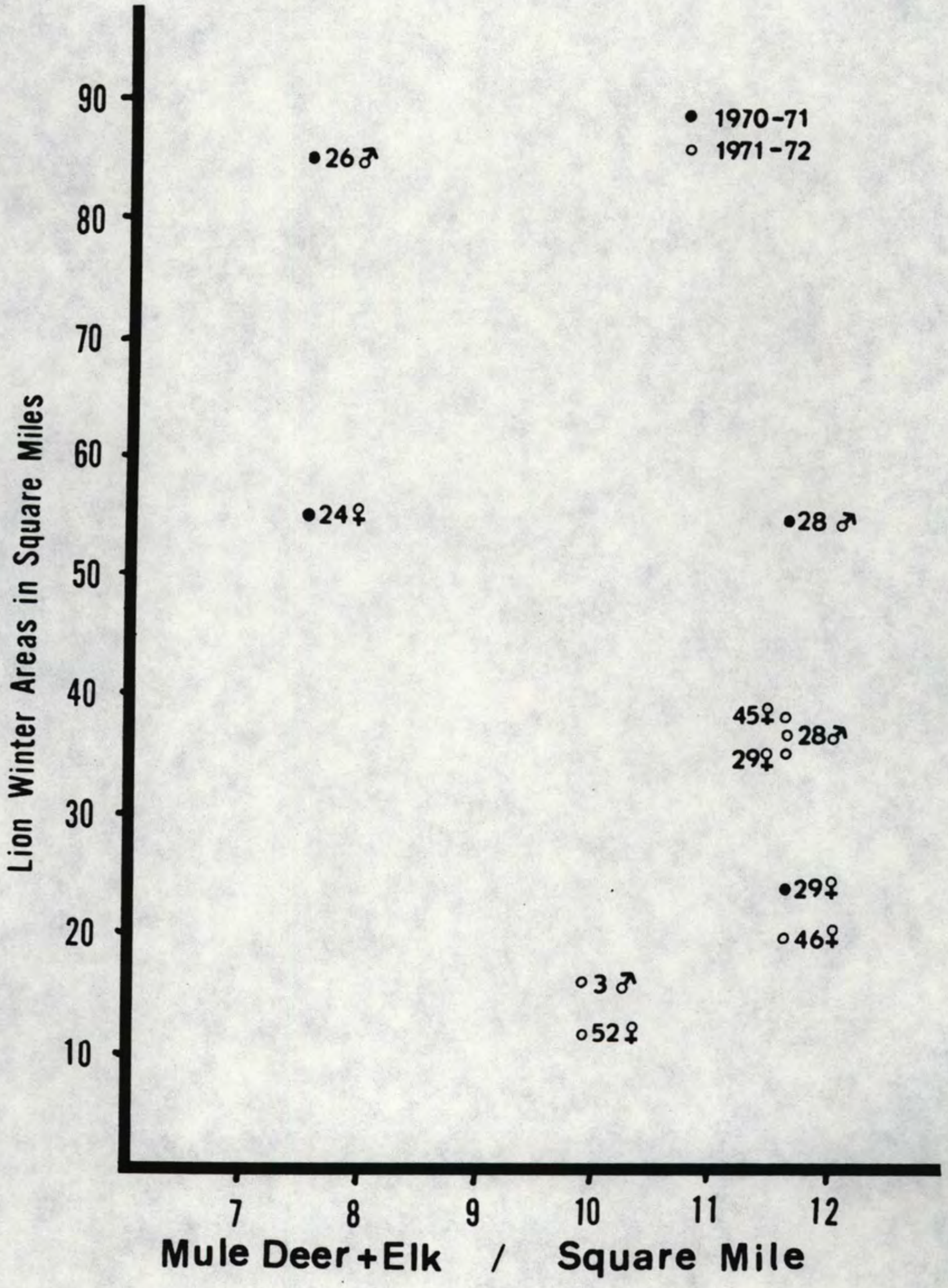

Fig. 23. Mule deer and elk density and lion winter area sizes, winters 1970-71, 1971-72. The ungulate census was based on counts from helicopters made during periods of maximum concentration in open areas during the spring of 1971. ($2.6\ km^2 = 1\ mi^2$).