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WINTER TERRITORIALITY IN MOUNTAIN LIONS

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Abstract: This paper, covering the first 4 years of a continuing study, reports on preliminary findings concerning territoriality and its function in a mountain lion (*Felis concolor*) population. The research was carried out in the Idaho Primitive Area in central Idaho. Forty-three different lions were captured and marked during four winter and early spring seasons. Thirty-one individuals were recaptured 89 times, making a total of 132 captures during the study. Nine resident adults, captured a total of 59 times, provided the bulk of the data on home range and territoriality. Minimum size of the males' winter home range was constant from year to year, but it varied for females, depending upon their reproductive status. The smallest winter home range for a female, during a single season, was approximately 5 square miles, the largest approximately 20 square miles. Males utilized larger areas. Resident male lions occupied distinct winter territories without overlap, but resident females shared some common areas. Male territories overlapped those of females. Lions exhibited a high degree of tolerant but unsocial behavior. No evidence of territorial defense was noted. Transient lions of both sexes moved freely through occupied territories. A mutual avoidance behavioral mechanism acted to distribute lions in both time and space. Visual and olfactory marks serve to facilitate avoidance between lions.

Limited information is available on home-range size and territoriality of mountain lions. Most data in the literature are based on observations made by hunters or persons engaged in control programs and are of a subjective nature. Young and Goldman (1946:83) listed some distances traveled by individual lions but made no mention of home-range size. Palmer (1954:142) stated that the home range covers "many square miles" and Bruce (1925:4) reported a range of 100 square miles. Other authors cite similar extensive ranges.

Intensive studies of the larger solitary Felidae are few. Recent notable exceptions are the work of Saunders (1963) with lynx (*Lynx canadensis*), and Schaller (1967) with tigers (*Panthera tigris*). Leyhausen and Wolff (1959) and Leyhausen (1965) have studied free-ranging domestic cats extensively, particularly the role of territoriality in populations.

In 1964, a long-term ecological study of the mountain lion was begun in central Idaho. The study was designed to investigate the dynamics of a lion population and to assess the impact of this population on its prey, particularly big-game animals. The second of these objectives will be treated at length in another paper (Hornocker, in press). This paper deals with preliminary findings concerning territoriality and its function in a mountain lion population.

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Table 1. Adult mountain lions captured in the Big Creek Study Area during four field seasons, 1964–1968. Each number refers to a specific lion.

	Males				Females			
	1964–65	1965–66	1966–67	1967–68	1964–65	1965–66	1966–67	1967–68
Residents	3	3	3	3	4	4	4	4
	7	7	–	–	11	11	11	11
	–	18	18	18	12	12	12	12
	–	–	26	26	–	16	–	16
					–	24	–	24
					–	–	29	29
Transients								
	–	20	28	–	1	21	32	–
	5	22						
	8							
	9							
Total Adults Captured & Recaptured	5	5	4	3	4	6	5	6

logical Society. The National Wildlife Federation awarded me a 1-year fellowship in 1965.

A great many individuals contributed directly or indirectly to the undertaking (Hornocker, in press). I am particularly grateful to I. McT. Cowan and D. H. Chitty of the University of British Columbia, and to J. R. Woodworth of the Idaho Fish and Game Department. W. Wiles assisted in all aspects of the field work. I. McT. Cowan and E. Bizeau reviewed the manuscript.

THE STUDY AREA

The research was conducted in an area of approximately 200 square miles in the Big Creek and Middle Fork drainages of the Salmon River within the Idaho Primitive Area. The area of actual useable winter range, arbitrarily that below the 6,000 ft level, is, however, only about 109 square miles. The Primitive Area, 1,910 square miles, lies in central Idaho contiguous to and south of the Salmon River. It is wilderness and is extremely rugged in its entirety; unpopulated expanses of wilderness still exist in many places beyond its boundaries. This area has the greatest elevational relief of any part of Idaho; it is described in detail by Hornocker (in press). Deep snow confines lions and their big-game prey species to the major stream courses, usually below 6,000 ft, for approximately 5 to 6 months in winter and spring. In the Big Creek study area, lions are restricted to the drainage by deep snow and can leave the area only by going downstream to the mouth of Big Creek.

METHODS

Capturing, individually marking, and subsequently recapturing lions was the basic method of obtaining data. Much information was also gained by tracking. Intensive work began each year in late November, and continued until late April or early May. Trained dogs were used to track and capture the lions; each cat was tranquilized with drugs to facilitate handling. Sernylan, a brand of phencyclidine hydrochloride (Parke, Davis and Company, Detroit, Michigan), was injected intramuscularly by means of Cap-Chur syringes fired from a specially designed powder-charge gun. A total of 71

Table 2. The mountain lion population in the Big Creek study area, 1966–67 and 1967–68.

How Determined	Number of Adult Males		Number of Adult Females		Number of Juveniles	
	66–67	67–68	66–67	67–68	66–67	67–68
From Recapture	4	3	5	6	6	6
From Tracks	2	1	1	–	1	2
	6	4	6	6	7	8

Table 3. Number of captures made of nine mountain lions during a 4-year period.

	Individual Lion No.	Number of Times Captured				
		1964–65	1965–66	1966–67	1967–68	Total
Adult Males	3	2	5	3	4	14
	18	–	2	4	1	7
	7	1	1	–	–	2
	26	–	–	1	1	2
Adult Females	4	3	3	2	2	10
	11	–	1	4	3	8
	12	–	1	2	2	5
	16	–	2	–	1	3
	29	–	–	5	3	8
						59

dosages was administered, averaging 1 mg of drug/1.71 lbs of body weight. A total of 541 days was spent in actually searching for and tracking mountain lions during 4 years. Population size was established by recapturing marked individuals throughout the 4-year period. Adult lions captured in successive years, in the same areas, were considered residents; those marked and not recaptured were regarded as transients (Table 1). Information was also obtained by combining recapture information with data obtained from tracks. This was done by relating the time tracks were made to the time of recapture. Data concerning movement and territory size and function were obtained through recaptures and by tracking known individuals. Each set of tracks found was followed and an effort was made to capture each lion tracked. This eliminated any possibility of bias in the recapture data. Boundaries were determined from recapture data and from tracks, and suggest winter territory size. Methods are explained in detail in another paper (Hornocker, in press).

RESULTS

Forty-three individual lions were captured, marked, and released during the 4 years. Thirty-one individuals were recaptured 89 times, making a total of 132 captures during the study. Table 2 shows that 19 and 18 lions were present on the study area in the winters of 1966–67 and 1967–68, respectively. This is slightly below the estimates I made after the first two seasons work in 1964–65 and 1965–66. Ten individuals were captured the first season, and I estimated a total population of 22. Eighteen different lions were handled in 1965–66. I estimated 24 for the total population that year. I believe the more complete data available for the last two seasons more accurately defines the total minimum resident population. In any event, the data suggest that the population has stabilized at about 10 adults which are full-time winter residents. Causes of and evidence for this population stability will be presented in detail by Hornocker (in press).

Nine mature lions which were tracked extensively and captured a total of 59 times provided the bulk of the information on movement and territory size and function (Table 3). Recaptures of other males, while less conclusive with regard to that particular animal's range, support the evidence gained from the adult males which were recaptured more frequently.

Individual winter ranges were determined by plotting outlying points of capture or observation (Dalke 1942:42, Craighead and

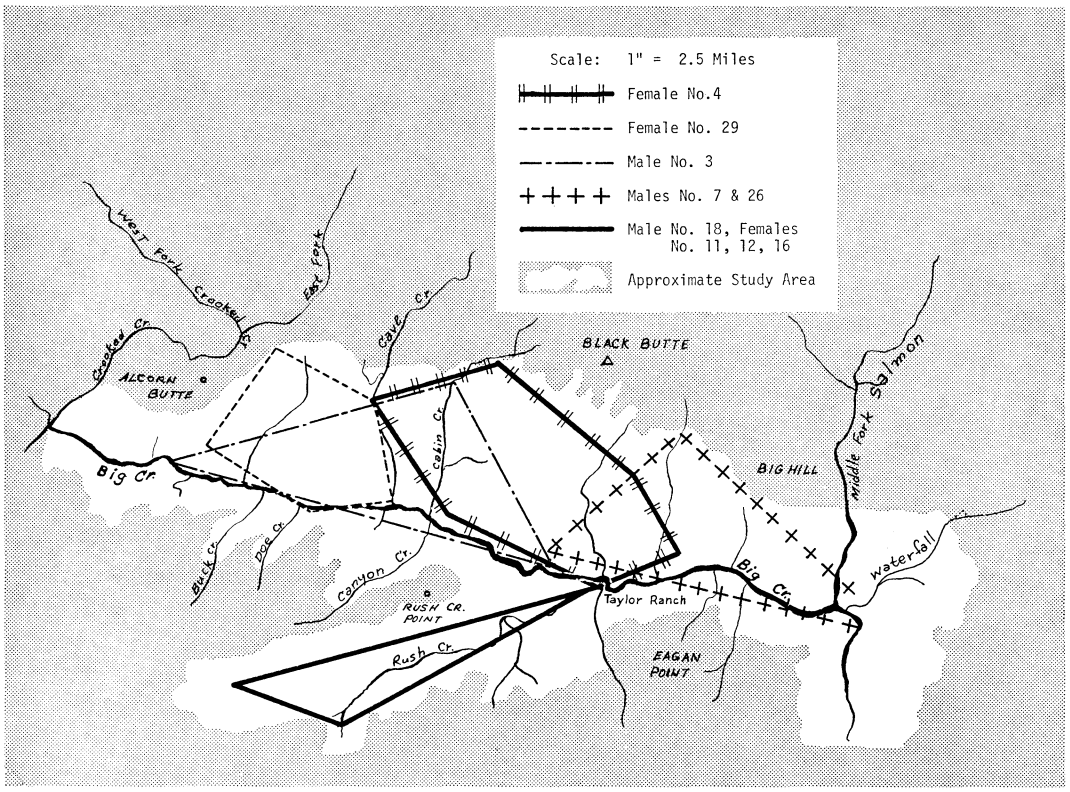

Fig. 1. Minimum winter home range of four male and five female mountain lions.

Craighead 1956:18). "Observation" here applies to those instances when a lion was tracked and subsequently captured.

The winter ranges of four resident adult males and five resident adult females, determined by recaptures during 4 consecutive years, are plotted in Fig. 1.

Males

Fourteen captures during 4 consecutive winters, provided the information used in delimiting the range of male No. 3. The minimum size of this cat's winter range was approximately 25 square miles.

Male No. 18 was captured seven times in a 3-year period. His range was confined to the Rush Creek drainage, a major tributary of Big Creek. The actual area occupied by No. 18 is probably greater than that indicated in Fig. 1.

The winter range of male No. 7 suggested by two captures in consecutive years, was on lower Big Creek and downstream on the Middle Fork; it's extent is not known. No. 7 was not captured in the 1966–67 and 1967–68 seasons and there is a strong possibility he was replaced by No. 26; this male was captured in both those years in this range. All my data indicate that two resident males will not occupy the same range.

Females

Ten captures, made over a 4-year span, established the range of No. 4. No. 11 and No. 12 were captured eight and five times,

respectively, in 3 consecutive years. No. 16 was first captured in 1965–66. We failed to capture her in 1966–67, although tracks suggested she was present. She was captured again in 1967–68. No. 29 was captured eight times in 1966–67 and 1967–68; her distinctive track, noted during the previous 2 years, revealed that she had been in the area since the study began.

The largest area occupied by a female during a single winter was that of No. 4 in 1965–66—approximately 20 square miles. The smallest was No. 29's in 1966–67—about 5 square miles.

All females studied appeared to change the extent of their ranges in different winter seasons. The changes were correlated with the female's reproductive status. In 1964–65, No. 4, accompanied by three approximately 7 to 8 month-old kittens, confined herself to the eastern portion of the range indicated in Fig. 1. In 1965–66, still accompanied by the three kittens (now 18 to 22 months old), she was captured at the furthermost points in Fig. 1. Again with small kittens-of-the-year in 1966–67, she utilized only the western portion of the indicated range.

In 1965–66, female No. 29 had three kittens; alone in 1966–67, she utilized only about one-third of the previous year's range. Similar changes appeared to be made by No. 11, No. 12, and No. 16, over a 3-year period, although data are inconclusive.

My data suggest that a female's reproductive status, and the age and number of her offspring, dictate the extent of her seasonal range in the Idaho Primitive Area. Food is equally available, from the standpoint of numbers, throughout all the lions' ranges. Over-abundant populations of elk (*Cervus canadensis*) and mule deer (*Odocoileus hemionus*) occur in the study area (Hornocker, in press). When alone, a female does not need to utilize a large area, but when accompanied by young kittens, the demands of the family for food, and the flight behavior of the prey animals, dictate that she utilize a larger hunting area. This is limited, however, by the ability of the young to travel great distances.

In the offspring's second year, until the time when the young become self-sufficient, the family requires its greatest amount of food. Thus a larger area is required. Neighboring females make this adjustment without stress—females appear to make the automatic cooperative adjustment, with respect to year-to-year spatial relationships, that Craighead and Craighead (1956:38) found in birds of prey.

Fig. 1 illustrates the overlap of ranges of males and females. The range of male No. 3 overlaps that of two females, No. 4 and No. 29. Females No. 11, 12, and 16 reside in the same range as male No. 18. Female No. 24, captured in 1965–66 and 1967–68 and definitely a resident, occupies the range of males No. 7 and 26. This female has been captured only twice and data are incomplete.

The boundaries plotted in Fig. 1 must not be rigidly interpreted. As stated previously, however, deep snow confines lions to the drainage, usually below 5,500–6,000 ft, and restricts movement other than down-drainage. Transients enter and leave the Big Creek drainage via the mouth of Big Creek. No such movement has been recorded for resident lions. I believe the actual areas utilized by some lions extend beyond that indicated. I do believe, however, that territories *relative to each other* are properly depicted by the capture data. In this respect, the fact that some lions were *not* captured in certain areas is equally as important as capture data on other individuals. Dasmann and Taber (1956:151) used this type of

negative data in determining home ranges of deer.

DISCUSSION

Etkin (1964:21–25) has introduced the "locality" concept of territoriality. He defines territoriality "as any behavior on the part of an animal which tends to confine the movements of the animal to a particular locality." He points out that the locality sense of animals may take a variety of forms, some of which bear resemblance to the classic type (that is, "defense of an area") but differ in that the animal shows no tendency to exclude others of the species from a given area. In Etkin's words (1964: 23–25): "Such a sense of locality, which is characterized by the positive element of attraction to the area without the negative element of driving others off, may be called home range or home-range territory. Unfortunately, the distinction between defended and home-range territory cannot always be maintained in practice, since our knowledge of the natural behavior of animals under the varied natural conditions of their lives is often insufficient to enable us to say to what extent others are excluded from the territory. The unqualified term 'territory' is therefore useful for such cases, and it can readily be qualified as home-range or defended as our knowledge justifies." Etkin's remarks appear apt to this discussion, and I have adopted his usage of the term territory.

The male lions resident in the Big Creek drainage clearly exhibit a spatial distribution of territories. No defense of a territory was noted in the study and transient lions, both males and females, used these territories freely. If a territory were actively defended against an intruder, then the resident would have to approach the intruder to either frighten it or to forcefully drive it from the area. In tracking resident and transient lions literally hundreds of miles, no evidence was found for this occurrence. Nor did any of the lions show evidence of fighting. Female residents, while exhibiting Etkin's definition of territorial behavior, shared the same area. These territories were also overlapped by those of mature males (Fig. 1).

Spatial distribution of territories suggests some type of interaction between individuals, usually of the same sex. Dice (1952: 261–262) states that such a distribution usually results from a defense of territories, although it can occur purely as an effect of the unsocial behavior of the species. Midway in the 1965–66 season, it became apparent that lions were avoiding close contact with one another. Striking examples of this avoidance behavior, which I termed a "mutual avoidance reaction" (Hornocker 1967), were recorded by tracking the animals in snow throughout the remainder of the study. Mature males, both residents and transients, avoided all other lions. The same was true of all females. Social tolerance was exhibited only by males and females during the breeding season, and by females and young during the period of juvenile dependency.

Lack (1954:270) recognized the importance of avoidance behavior, stating ". . . dispersion is primarily due to the avoidance of occupied or crowded ground by potential settlers, not to aggressive behavior of those in occupation." Tinbergen (1968:1413) believes that, in territorial species, "in this system of parceling our living space, avoidance plays as important a part as attack." Numerous examples of avoidance recorded in this study support these views. Avoidance, however, was not limited to "potential settlers"; residents exhibited the same behavior. One striking example, involving males,

is worthy of mention. On January 10, 1967, we captured a young unmarked male in the territory of resident male No. 3. This young male had killed an elk the previous day, had stayed at the kill, and was captured there. Tracks indicated that a large male had passed within 50 yards of the young male and its kill the same day of the capture. The following day we tracked the large male, resident No. 3, and captured him some 3 miles distant. He had made no attempt to challenge the young male transient; apparently he purposely avoided contact once he became aware of the young male's presence.

The same areas were used by different individuals but never at the same time—lions were spaced in time as well as area. Scrape or scratch marks appear important in this spacing. Lions urinate and frequently defecate on top of these marks—a visual as well as olfactory mark is made. All lions, but particularly the males, make these marks in trails, on high ridges, and at lion crossings; some permanent stations occur in each territory. Both males and females invariably visit these sites and ordinarily travel much the same route, whether hunting or seemingly just traveling. On a number of occasions an animal tracked to one of these sites abruptly changed course, sometimes retracing its route for a considerable distance. Invariably it was found that another lion or family of lions was in the area.

Leyhausen and Wolff (1959:670) found that free-roaming domestic cats shared pathways and hunting grounds but emphasized that common use did not mean simultaneous use. The cats "avoid encounters by keeping to a more or less definite timetable." These cats spaced themselves by visual contact but the authors believe that "mammals which live in densely grown habitats . . . [utilize] olfactory markings [which] probably serve to prevent encounters, . . ." These marks function "rather like railway signals," serving to notify newcomers of the presence of another animal. "The individual, before passing by such a mark, regularly covers it with its own, thus 'closing the section.'" (Leyhausen and Wolff (1959:670). Their observations might well have been made on the lions in this study. I arrived at my conclusions concerning territoriality and function of the scrape marks before I had knowledge of their work.

A further function of territoriality—in time as well as in space—appears to be that it affords greater success in securing large prey animals. Mountain lions must employ stealth to place themselves within striking distance. The chances of success in an area already hunted or being hunted by another individual are much less than in an area where prey animals are undisturbed. Crook (1965:199) believes this is a major factor in the territoriality of nesting kingfishers. He states ". . . individual methods of hunting probably ensure greater success per bird than group attacks on easily alarmed fish shoals could allow." Tinbergen (1957:16) also commented that "familiarity with topography allows predators to utilize an area's food resources more efficiently."

The type of nonagressive territorial behavior exhibited by the mountain lions in this study has been reported for a number of other species. Leyhausen (1965) documented it thoroughly for domestic cats. Schaller (1967:239) found resident tigers in India tolerant of transients, but speculated that some males might defend a territory against other males. He felt a self-limiting trend was operating in the population on the local level, "perhaps based on intraspecific intolerance when meeting or sharing a kill and, more subtly, on various

visual and olfactory signals left in the environment."

Territoriality appears to be extremely important in regulating numbers of mountain lions in the Idaho Primitive Area. The actual regulating mechanism or mechanisms acting in this population are not known, though the importance of mortality and dispersal is noted (Hornocker, in press).

The primary function of territoriality in the mountain lion population appears to be a spatial distribution of individuals. This spacing, brought about without apparent conflict, acts to limit population size (see Carrick 1963, Kuhme 1966). Further, this behavioral mechanism makes possible the adjustment of these spatial arrangements with respect to (1) changing environmental conditions, (2) to the presence of other lions, and (3) to the individual female's changing reproductive status. Such a behavioral mechanism appears necessary to the survival of populations of solitary, specialized predatory species. A solitary predator must depend on its physical well-being to survive. Fighting in the defense of a territory has been reported for more gregarious predators, such as wolves (Murie 1944, Cowan 1947, Mech 1966). The mutual-avoidance mechanism appears to have evolved as a much more economical means of spacing solitary individuals. Fighting may occur at times, but I believe it is an extremely rare occurrence.

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