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Social organization of the red squirrel (Tamiasciurus hudsonicus) in lodgepole pine (Pinus contorta) and Douglas-fir (Pseudotsuga menziesii) habitats

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SOCIAL ORGANIZATION OF THE RED SQUIRREL (*TAMIASCIURUS HUDSONICUS*) IN LODGEPOLE PINE (*PINUS CONTORTA*) AND DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII*) HABITATS

By

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Social Organization of the Red Squirrel (Tamiasciurus hudsonicus) in Lodgepole Pine (Pinus contorta) and Douglas-fir (Pseudotsuga menziesii) Habitats (57 pp.)

Director: Lee H. Metzgar H.M.

Territory size and rates of territorial and agonistic behavior in the Red squirrel (Tamiasciurus hudsonicus) were contrasted in lodgepole pine (Pinus contorta) and Douglas-fir (Pseudotsuga menziesii) habitats. These habitats provide greatly contrasting food supplies.

Squirrels occupying 2, 4.25 ha study areas within each habitat were live-trapped and marked during the summers of 1977 and 1978. Conifer seed production in study areas was estimated for both years. In the fall 1978 an index of territory size was calculated for 13 squirrels and rates of territorial and agonistic behavior were measured weekly in each study area.

Conifer seed production and squirrel numbers were relatively constant in the lodgepole habitat, while the population in Douglas-fir increased substantially with increasing seed production from 1977 to 1978. Squirrels defended territories of equal size in the two habitats probably because the sections of lodgepole forest with territories and the Douglas-fir habitat provided about equal energy. Juveniles occupied larger territories than adults while adult males and females defended areas of equal size. Calling rates decreased as winter approached, corresponding with decreasing activity in response to lower temperatures and completion of cone caching. Squirrels gave rolled R calls at similar rates in the two populations. Squirrels in Douglas-fir gave squeak calls at more than twice the rate of lodgepole squirrels and used chee calls less frequently. Squirrels in the more dense population in Douglas-fir may give more squeak calls because they function in aggression. In addition, squirrels in Douglas-fir may give fewer chee calls, which function in alarm behavior, because more dense populations may experience lowered predation exposure per individual.

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INTRODUCTION

The social organization of a population is shaped partially by its environment. If social behavior has evolved through selective pressure, differences in social organization are generally adaptive. Many behavioral components demonstrate great phenotypic plasticity. Adjustments to specific habitats either genetically or phenotypically would help demonstrate how environments produce different types of social organization. The demography of a population also influences social behavior. How the environment affects social organization can be inferred only in the context of a population's demography (Armitage 1977).

Some interspecific differences in social organization appear to be correlated with habitat. In the African weaver birds (Ploceinae), interspecific differences are found in population dispersion, territorial behavior and mating systems. Forest species tend to be insectivorous, solitary, monogamous and demonstrate mobile territorial behavior. In more arid habitats species tend to be granivorous, gregarious-colonial and polygamous (Crook 1964). In colonial species, territorial behavior tends to be stationary. Solitary behavior appears adaptive for the forest insectivore whose food is cryptic, easily disturbed and widely dispersed. Similarly, monogamy may be advantageous where food supplies are constant but relatively sparse requiring involvement of both sexes in parental care. Gregariousness and polygamy seem adaptive in open environments with local patches of super-abundant food. In this case, the male does not participate in parental care and can increase his success via polygamy (Crook 1964).

The social organization of African antelope varies considerably. Jarman (1974) hypothesized that social structure is related to body size and ecology. Smaller species are more efficient as selective foragers and require items of greater energetic content. These items tend to be scarce and dispersed in comparison with the grass used by larger species. The smaller species tend towards small, dispersed social groups. Larger species occur in herds as a result of grass utilization, producing higher biomass levels and the need for group defense in open habitats (Jarman 1974).

Intraspecific differences in behavior may demonstrate environmental influences more clearly because differences are less likely to be produced by phylogenetic history. The relationship between ecology and social organization will be better understood through the study of differences within species. Relatively little work has been done on intraspecific variability in social organization. In several primate species, social organization appears to vary between populations in different habitats (Crook 1970). The size and permanence of Lion (Panthera leo) social groups varies with food productivity. In habitats of marginal productivity, such as the Kalahari, lions live in small prides or are solitary (Eloff 1973). Columbian ground squirrel (Spermophilus columbianus) social behavior differs between populations (Steiner 1974; Betts 1976). However, adequate demographic and ecological data are lacking in order to interpret these differences (Betts 1976). Similarly, populations of the yellow-bellied marmot (Marmota *flaviventris*) demonstrate diverse social behavior (Barash 1973, 1974; Armitage 1977). Barash (1974) proposed that these differences constitute adaptations to local habitats. These differences, however, could also be produced by differences in population density, age-sex structure, the population's history and characteristics of individual members (Armitage 1977).

The ecology and social organization of the red squirrel (*Tamiasciurus hudsonicus*) has been studied fairly extensively. The social structure of this species is basically territorial. A territory is defined as any defended area (Noble 1939). Red squirrels have almost always been found to be territorial with the defended areas inhabited by only one individual of either sex (Gordon 1936; Clarke 1939; Hatt 1943; Cowan and Robinson 1954; Kilham 1954; and C. Smith 1968). Evolution of territorial systems occur when a resource is in short supply (Brown 1964), and in this species food most probably is this resource. Food is periodically scarce, appears to be limiting, and is easily defendable in a centrally located cache (C. Smith 1968; Kemp and Keith 1970). Furthermore, territory size seems to be inversely proportional to food abundance (C. Smith 1968). Other possible resources include females, space and nesting sites. Since territories are exclusive regardless of sex, they do not function to monopolize mates. Neither nest sites nor space are likely to be in short supply (C. Smith 1968).

In some regions, transient winter territories defended mainly by subadults have been found in suboptimal deciduous habitat. In the spring, the subadults disperse to compete with prime territory owners in mature conifer stands (Kemp and Keith 1970). C. Smith (1968) observed females either abandoning their territories to the young or transporting them to a nest at the edge of their territory. There is also some evidence that juvenile dispersal is more limited when food is abundant (Kemp and Keith 1970). C. Smith (1968) hypothesized that the mode of territorial acquisition by transients is related to seasonal variation in food distribution. Throughout much of the year when food is dispersed, squirrels attempt to take over peripheral areas of other territories. In the early spring, food is concentrated at cache sites and immigrants tend to take over an entire territory.

Territorial defense is suspended only by females in heat and when animals concentrate at pollen food sources. Chasing and various vocalizations are used in territorial defense. The "rolled R" call (Embry 1970) or "Chir-r-r" (Klugh 1927) possibly functions as a territorial advertisement (Embry *loc. cit.*). A "squeak" call (Embry *loc. cit.*) probably indicates a high level of aggressiveness to conspecifics (Embry *loc. cit.*; C. Smith 1968). A subdued growl is often used in aggressive situations when individuals are in close proximity (Embry *loc. cit.*). The most frequently given call is the "Chee" or "bark", which has usually been interpreted as an alarm call (C. Smith 1968). Embry (*loc. cit.*) pointed out its importance in breeding behavior while Searing (1977) considered it an aggressive call of less intensity than the "rolled R."

Red squirrels occupy diverse habitats with greatly differing food availability. Many differences in social organization could exist between populations in different habitats. Examining social organization in lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) should expose considerable differences in this species, if they exist. Lodgepole pine and Douglas-fir forests have greatly contrasting food supplies. Lodgepole cones are relatively poor fare, yielding energy at only one-fourth the rate of Douglas-fir cones (C. Smith 1968). Both species tend to be prolific seeders in Montana with lodgepole being somewhat more consistent. Lodgepole pine produces good or fair crops approximately 77% of the time while Douglas-fir does 59% of the time (Boe 1954). The serotinous cone (held on the tree) characteristic is widespread among lodgepole stands in the Rocky Mountain region (U.S.D.A. Handbook 271, 1965). In the absence of fire, seeds may accumulate on the trees for up to 40 years (Lotan and Jensen 1970) providing a relatively stable food base which is dispersed and available year-round (C. Smith 1970). Douglas-fir seeds are available dispersed on the trees only from August to November.

Several differences in social organization may occur between these two populations. Territory size varies intraspecifically in many species and in Tamiasciurus may correlate with food supply (C. Smith 1968). Population stability and fluctuation of territory boundaries could vary with the consistency of the food source. Juvenile dispersal and consequently age ratios may be influenced by food abundance (Kemp and Keith 1970). Territorial and agonistic behavior could respond to food distribution and abundance. Variation in rates of territorial and agonistic behavior is unstudied in the red squirrel. My objective was to contrast: 1) territory size, and 2) rates of territorial and agonistic behavior in populations occupying lodgepole pine and Douglas-fir forests.

STUDY AREAS

Squirrel populations were studied in the upper Miller Creek drainage of the Sapphire Mountains, 22.5 km southeast of Missoula, Montana, (Figure 1). Two study areas were established in each habitat. The lodgepole pine areas were in the Lolo National Forest. The Douglas-fir areas were on the Waldbillig ranch.

Lodgepole I

This area is on level ground at an elevation of 1318 m (Figure 1). Lodgepole dominates the area. Douglas-fir, western larch (*Larix occidentalis*), ponderosa pine (*Pinus ponderosa*), subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) are also present. The shrub layer is sparse in most of the area. Common understory plants are arnica (*Arnica cordifolia*), lupine (*Lupinus* spp.), beargrass (*Xerophyllum tenax*), twinflower (*Linnaea borealis*), glacier lily (*Erythronium grandiflorum*), Oregon grape (*Mahonia repens*) and bearberry (*Arctostaphylos uva-ursi*). Mountain maple (*Acer glabrum*) is common on the eastern edge of the area. In May 1978 half the area was thinned, removing approximately 20% of the lodgepole on the affected site.

Lodgepole II

This area is .6 km south of lodgepole I (Figure 1) at an elevation of 1384 m. Most of the area lies on a gentle north-facing slope. A shallow ravine slices through the lower part of the transect. The lodgepole dominated forest also contains Douglas-fir, western larch,

Figure 1. Map of upper Miller Creek area showing locations of study areas.

L1 - Lodgepole I

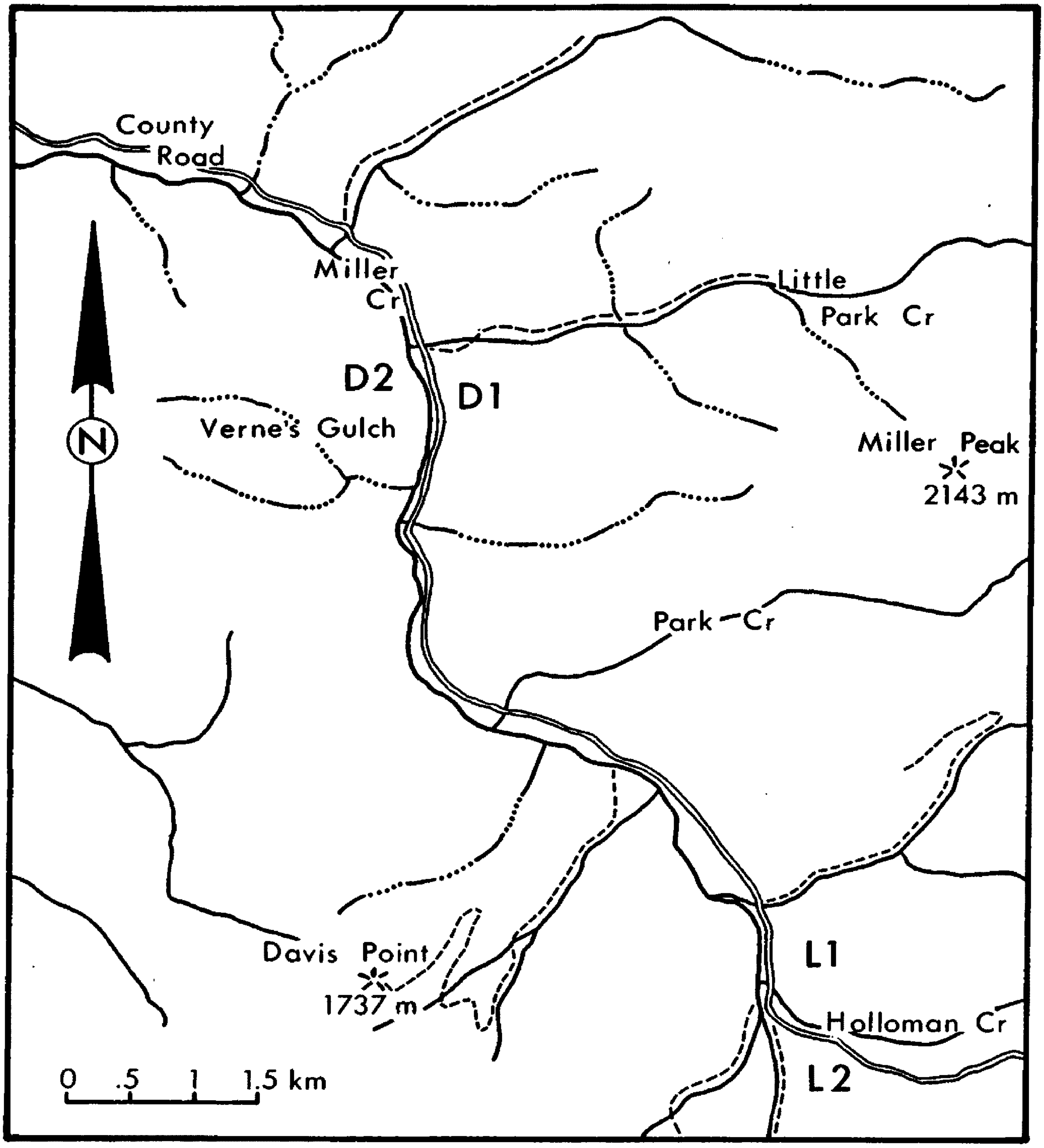
L2 - Lodgepole II

D1 - Douglas-fir I

D2 - Douglas-fir II

═══ Improved road

- - - Unimproved road


County Road
Miller Cr
Little Park Cr
D2
D1
Verne's Gulch
N
Miller Peak
2143 m
Park Cr
Davis Point
1737 m
L1
Holloman Cr
L2
0 .5 1 1.5 km

subalpine fir and Engelmann spruce. The shrub layer is dense and dominated by mountain maple and willow (*Salix* spp.). Common understory species are arnica, lupine, beargrass, prince's pine (*Chimaphila umbellata*), thimbleberry (*Rubus parviflorus*), big whortleberry (*Vaccinium membranaceum*), twinflower, Oregon grape, wild rose (*Rosa* spp.), strawberry (*Fragaria bracteata*), trillium (*Trillium ovatum*) and glacier lily.

Douglas-fir I

The Douglas-fir areas are located on the opposing east- and west-facing slopes of a canyon at an elevation of 1214 m (Figure 1). The areas have slopes of 30% and are separated by a narrow stream bottom vegetated primarily with thinleaf alder (*Alnus tenuifolia*), redosier dogwood (*Cornus stolonifera*), Douglas hawthorne (*Crataegus douglasii*) and Engelmann spruce. Douglas-fir I is nearly a pure stand of Douglas-fir. Ponderosa pine and western larch are present toward the upper edge and spruce toward the lower edge. Over much of the area the shrub layer is dominated by ninebark (*Physocarpus malvaceus*). Other common understory species are mountain maple, snowberry (*Symphoricarpos albus*), serviceberry (*Amelanchier alnifolia*), wild rose, Oregon grape, bearberry, twinflower, arnica, spiraea (*Spiraea betulifolia*), strawberry, false solomonseal (*Smilacina racemosa*), pinegrass (*Calamagrostis rubescens*) and elk sedge (*Carex geyeri*).

Douglas-fir II

The vegetation is very similar to that described for the Douglas-fir I area. However, a few lodgepole pines are found here. In the more xeric conditions along the upper edge, bitterbrush (*Purshia tridentata*) and balsamfoot (*Balsamorhiza sagittata*) are present.

MATERIALS AND METHODS

Food Production

Conifer seed was the only food source measured and probably provided most of the food for these squirrel populations. In coniferous forests, red squirrels consume conifer seeds primarily although fungi, buds, angiosperm seeds, cambium, pollen and bark are sometimes utilized (Brink and Dean 1966; M. Smith 1968; Finely 1969; Rusch and Reeder 1978). In the late summer, fall and early winter of 1978, virtually every squirrel observed feeding was consuming conifer seeds. In the summer of 1978 I attempted to estimate mushroom density, but abandoned the effort as density seemed very low and the estimate consumed too much time.

Conifer seed production was measured in three ways. First, three seed-traps (45 x 9 cm high x 91 cm long) were placed in each study area in 1977 and 1978. In addition, the visual cone crop rating system of Gregory (1959) was used in the Douglas-fir areas. This technique assigns abundance classes to trees based on cone counts of branches that represent the crown. I assigned abundance classes to 111 and 95 Douglas-firs in 1977 and 1978 respectively. Finally, the serotinous cone seed crop was estimated using the equation of Lotan and Jensen (1970). This method uses mean d.b.h. (Diameter breast-high), mean age and number of serotinous cone type trees per acre to estimate the number of serotinous cones per acre. I examined 30 lodgepole pines to determine mean d.b.h. and aged these trees using an increment borer.

This method provides only a rough estimate but avoids the need to fell plot trees and is considered representative for mature stands in the northern Rocky Mountain region (Lotan and Jensen 1970). The number of seeds per cone was estimated by examining 40 serotinous lodgepole cones. Seed extracted from these cones or from seed traps were opened to determine viability.

Live-trapping

A transect (274.3 m), with stakes marking stations every 18.3 m, was placed in each area. An effort was made to mark all squirrels in an area (approximately 4.25 ha) surrounding each transect. From early July to early September 1977 and from early June to late September 1978, squirrels were live-trapped. Limited trapping continued through mid-November 1978. Traps (13 x 13 cm high x 40 cm long) were placed on cone caches and runways at dawn and checked every three hours. Sunflower seeds were used as bait. Traps were covered with cedar shakes or forest litter to provide shelter.

Squirrels were handled using a weighing bag and handling cone developed by Halvorsen (1972). A hole was punched into each ear through which colored-plastic tubing was tied for field identification (Halvorsen, pers. comm.). Squirrels were toe-clipped for permanent identification. Animals were aged by weight and pelage (Halvorsen, pers. comm.). Ear-tag color combination, toe-clip number, weight, age, sex, breeding condition and location were recorded upon initial capture.

Population Size

Population size was estimated directly by counting all marked and unmarked residents of an area. A resident was defined as a squirrel that occupied and defended a territory and included juveniles still living on a maternal territory. Any territory within or overlapping a 4.25 ha area surrounding each transect was counted. Directly counting residents seemed to be the most appropriate method. Because each red squirrel conspicuously defends a large, relatively permanent site, I could consistently locate even unmarked animals. In addition, territorial and cone caching behaviors readily allowed me to distinguish between resident and vagrant squirrels. Because traps were not placed in marked squirrels' territories and trapping periods extended over several weeks to a month in each area, the methods did not fulfill the conditions of random sampling, discrete time intervals between sampling and relatively short sampling periods necessary for mark recapture methods (Southwood 1966). I could have used observations as recapture data, but because I attempted to locate marked squirrels primarily, marked and unmarked individuals were not sampled equally.

Squirrel populations were monitored continuously by direct observation and tracking. To accomplish this, one area was surveyed intensively each week from 11 October 1977, to 4 February 1978. Beginning at dawn and continuing for approximately 2 hours, I slowly traversed a transect and recorded any marked or unmarked squirrels seen. During the period 11 February to 29 May 1978, one transect was surveyed intensively and the other three traversed quickly on approximately every fifth day. From early June to early December 1978 each area was surveyed several times a week unless it was being trapped.

Territory Size

Locations of marked animals were plotted on maps throughout the study. Squirrels were easily identified using an 8 x 36 binocular and ear-tag color combinations. Locations were determined using a compass and by pacing from a point on the transect.

From 29 September to 8 December 1978, an intensive effort was made to estimate territory size. Most measures of home range or territory size vary with the number of location records, territory shape and the distribution of records within the territory (Jennrich and Turner 1969; Metzgar 1972). I used an index of territory size that is independent of sample size and makes no assumptions regarding territory shape or the distribution of records within the territory. This index, $S\infty$, was adapted for transects from Metzgar and Sheldon (1974). Only location records collected under certain conditions contributed to $S\infty$ calculations. In order to maintain independence of observations, I attempted to obtain location records once a week. Squirrels were always located between dawn and 1200 hours. I minimized observer influence on location records by using only the location where an individual was first observed.

The Mann-Whitney U-Test was used to contrast the distributions of $S\infty$ from the two habitats.

Territorial and Agonistic Behavior

Rates of calling and of chasing were measured throughout the study. Beginning at dawn and continuing for about 3 hours, I slowly traversed the sampled transect and counted the number of occurrences of 4 types of calls and of chasing. Calls that originated from very far away (e.g. a distant ridge) were not included. Because it is difficult to estimate the distance from which a sound originates, I preferred to use only calls from some restricted distance from me. I initially attempted counting only calls from relatively close (55 m), but abandoned this method because it included very few calls. Consequently, counting all calls within hearing seemed to be the most appropriate method and the number of calls sampled was divided by hours of observation and population size to estimate the hourly calling rate per individual.

This method roughly estimates calling rates per individual. However, it is reasonable to assume that I could hear similar distances in the two habitats and that population density close to a transect differed little from the density in the immediate surroundings. Accordingly, this method should provide reasonable estimates of relative calling rates between habitats. Call rates obtained in this way are termed population method call rates.

Beginning in late September 1978 and continuing for 11 weeks through early December, behavior rates were measured once weekly in each area. However, no rates were measured during the third week of November and rates were measured only in lodgepole area II and Douglas-fir area II on the week of 25 September. Thus, I measured behavior rates 9 times in lodgepole I and Douglas-fir I and 10 times in lodgepole II and Douglas-fir II.

Behavior rates were also measured by observing individual squirrels and these rates are termed individual method behavior rates. One adult was selected in each area and observed once a week at about the same time (usually after 1200 hours). In addition to measuring behavior rates, the general activity and food the squirrel consumed was recorded. I found that waiting quietly near the large, centrally located cache allowed me to effectively observe a squirrel. I did not begin counting calls until the individual was clearly identified and then observations continued for about 2 hours. No call was counted unless either the individual I was observing was seen calling or I was sure it had called while momentarily out of view. Of 486 total calls, 182 (38%) occurred while the squirrel was out of view and the proportions of calls unseen were very similar in the 2 habitats (lodgepole, 39%; Douglas-fir, 36%).

The 2 methods for obtaining call rates (population and individual methods) yielded nearly identical results. Data presented are from the population method unless otherwise noted.

The rates of the rolled R, squeak and chee calls were analyzed, but the number of observations of the growl and of chasing were too few to allow analyses. A strong seasonal trend was observed in the analyzed calls and results from the 4 study sites were matched weekly. The weekly results from the two areas within each habitat were combined and the Wilcoxon Matched-pairs Signed-ranks Test was used to test for differences between calling rates from the two habitats. Because I found the same seasonal trends in calling rates for both habitats, weekly calling rates from the 2 habitats were combined and the relationship between the average calling rates and advancing season were tested by Spearman rank correlation.

One-tailed statistical comparisons were utilized and $\alpha = 0.05$.

RESULTS

Food Production

Douglas-fir productivity varied greatly while lodgepole provided food more consistently. The rating system yielded Douglas-fir cone counts of few (0-10 on tree) on most trees in 1977 and of common (10-20 cones per limb) or abundant (20 or more cones per limb) on about half the trees in 1978. Douglas-fir habitat seed production increased dramatically from an average of 36,620 sound Douglas-fir seeds (S.E = 12,207) per hectare in 1977 to 2,276,557 seeds (S.E = 489,933) per hectare in 1978. These results estimate production very roughly as they are based on only 6 seed-traps in 1977 and 4 in 1978 (2 were discarded because squirrels had consumed cones on the screens). Seed-trap results typically display such high variability (Shearer 1980).

The data required to estimate serotinous-cone numbers were obtained in 1979. Because the variables in the prediction equation (d.b.h., tree age and serotinous-cone type tree density) vary little over a few years, 1979 calculated values were used for both 1977 and 1978. Substituting the appropriate mean age and estimated d.b.h. values for 1978 and 1977 produced differences in energy production of less than 2%. Because serotinous cones produced most of the lodgepole habitat's seed energy, that habitat consistently contained abundant food. There were an estimated 85,334 serotinous cones per hectare in lodgepole area I and

33,585 per hectare in lodgepole area II. Cones averaged 20.5 sound seeds (S.E = 2.21) in area I and 15.8 sound seeds (S.E = 1.67) in area II.

Energy per hectare was calculated using values from C. Smith (1970) for lodgepole pine, Douglas-fir and Engelmann spruce seed. Western larch seed weights were taken from the U.S.D.A. Handbook 450 (1974) and caloric value was estimated as 7.0 kcal per gram, close to values for other conifers (C. Smith 1970). Even if larch seed energy values differ substantially from this estimate, they contributed little to total available energy, and I found no evidence of squirrels consuming larch cones. In the Douglas-fir forest, the energy available from conifer seeds increased tremendously from 1977 to 1978 while lodgepole habitat energy levels increased much less (Table 1). In 1978, energy levels were probably considerably higher in the Douglas-fir than in the lodgepole habitat.

Weights of Squirrels

The populations were trapped at somewhat different times in the summer. Thus female weights, which varied greatly due to pregnancy and lactation, are not contrasted. Adult male weights from the 2 populations (Table 2) were not significantly different (2-tailed t-test; $t = .516$, 15 df; $P > .10$). In both habitats adult males averaged 9 grams more in 1978 than in 1977 (Table 2). This difference was not significant (2-tailed t-test; $t = 1.331$, 10 df; $P > 10$; $t = 1.433$, 3 df; $P > .10$).

Table 1. Mean conifer seed energy (Kcal per hectare) in each habitat. Standard errors are shown in parentheses and data from the 2 study sites within each habitat are averaged.

	Habitat	Kcal per hectare		
		Dispersed seeds	Calculated serotinous seeds	Total seed energy
1977	Lodgepole	2,373 (1,058)	18,240	20,613
	Douglas-fir	2,308 (698)		2,308 (698)
1978	Lodgepole	7,222 (3,909)	18,240	25,462
	Douglas-fir	131,653 (28,398)		131,653 (28,398)

Table 2. Mean weights of adult male squirrels (g). Mean weights are shown for each year and for both years combined.

	Lodgepole		Douglas-fir	
	N	Mean Weight	N	Mean Weight
1977	8	235.5	3	232.0
1978	4	244.5	2	241.0
1977-1978	12	238.5	5	235.6

Food Habits and Use of Space

Lodgepole habitat squirrels switched from a lodgepole cone diet in 1977 to exclusively Douglas-fir cones in 1978. In the late summer and fall of 1977 lodgepole area squirrels consumed primarily lodgepole cones and caches examined that winter contained predominantly lodgepole cones. Beginning in August 1978, virtually every lodgepole area squirrel observed feeding was consuming Douglas-fir cones and caches were of Douglas-fir cones exclusively. Squirrels inhabited most of the lodgepole area in 1977 but avoided tracts of pure lodgepole in 1978 and concentrated around isolated Douglas-firs in the lodgepole habitat. In June and July 1978 many residents with territories of pure lodgepole disappeared leaving roughly 60% of the habitat unoccupied. Population size in lodgepole pine varied little as squirrels also immigrated into the area to claim territories around clumps of Douglas-fir. In the fall of 1978 squirrels occupied approximately 50% of the lodgepole habitat and 9 of 12 territories centered around isolated Douglas-firs.

Douglas-fir forest squirrels cached spruce, Douglas-fir and ponderosa pine cones in 1977 but cached only Douglas-fir cones in 1978. Sections of Douglas-fir habitat were deserted in 1977 but squirrels occupied virtually the entire area in 1978. In the fall of 1977 and the winter of 1977-78, I found little evidence of squirrel activity over much of the Douglas-fir habitat. In the summer and fall of 1978 I found no unoccupied space.

Population Size

Population size and dynamics were similar for study areas within each habitat (Table 3). Total population size in lodgepole pine was relatively stable while the Douglas-fir population increased from 5

Table 3. Resident red squirrel numbers in study areas. Entries represent the total numbers of marked and unmarked residents known to be present.

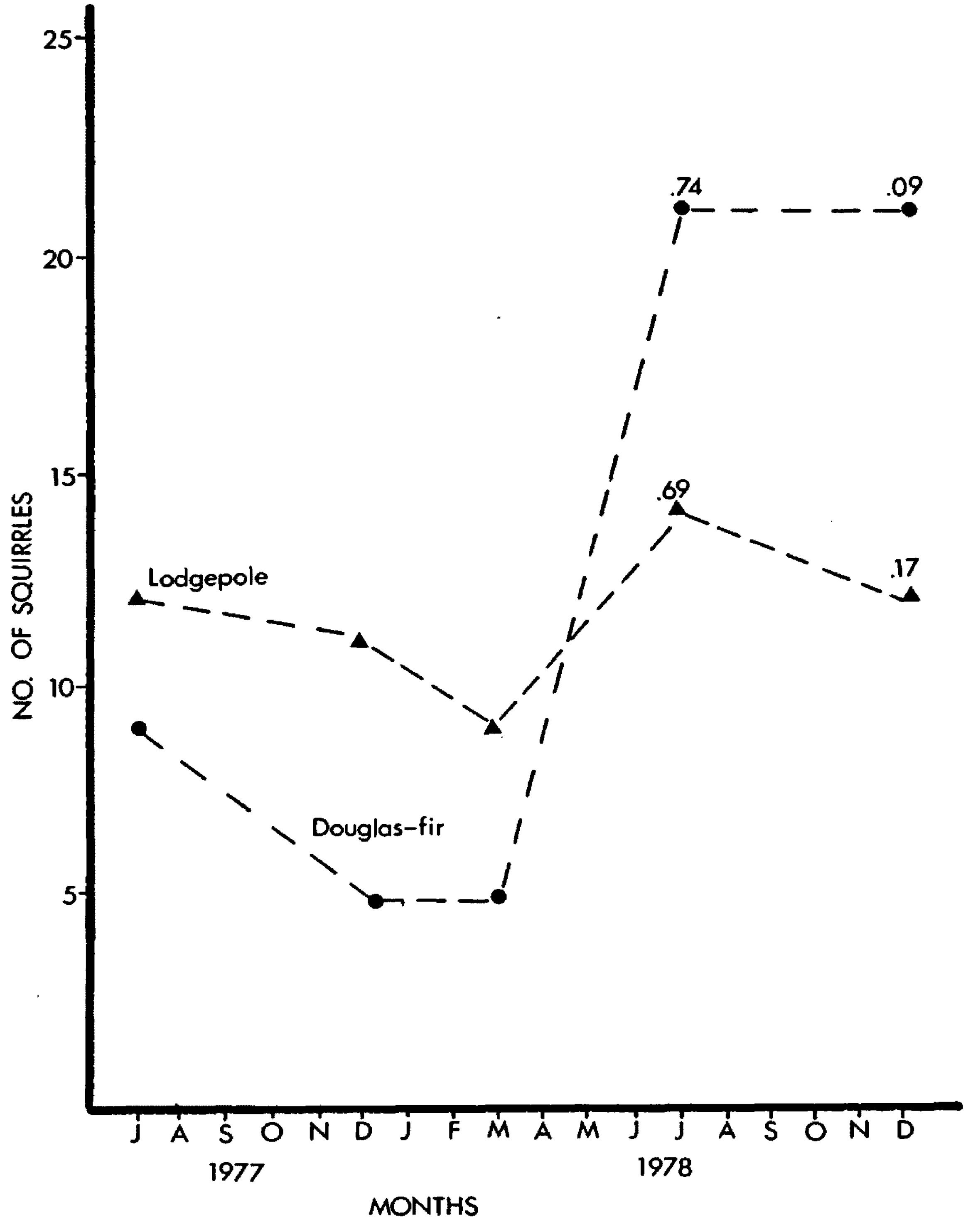
	Squirrel numbers				
	1977		1978		
Study areas	July	December	March	July	December
Lodgepole I	6	7	5	8	6
Lodgepole II	6	4	4	6	6
Total	12	11	9	14	12
Douglas-fir I	4	2	2	13	10
Douglas-fir II	5	3	3	8	11
Total	9	5	5	21	21

residents in early winter 1977 to 21 in July 1978 (Figure 2). Both populations declined between July and December 1977, probably due to juvenile dispersal. They increased in spring and early summer 1978 as a result of immigration and recruitment. As in 1977, the lodgepole population declined slightly between July and December 1978, while the Douglas-fir population size remained constant.

The history of association between animals may be important in determining rates of social behavior (Armitage 1977). The history of association was expressed as the proportion of residents that are new. A resident was new if it had not inhabited the study area during the previous population estimate. Because unmarked residents constituted about half of the population (54% in July and 48% in December) and an unmarked vagrant could conceivably replace an unmarked resident without being detected, these proportions are rough estimates. However, I believe that most unmarked residents were effectively and consistently recognized. C. Smith (1968) also found that he could consistently recognize unmarked squirrels using territorial boundaries and individual peculiarities. The proportion of new residents was similar in the two populations in 1978 (Figure 2).

Rates of social behavior may also be associated with the age-sex structure of a population (Armitage 1977). In the fall of 1978 (28 September to 8 December) age and sex ratios of captured residents differed little between habitats. In the lodgepole and Douglas-fir habitats adults constituted 44% (N = 9) and 46% (N = 11) of the captured residents respectively. Males made up 67% (N = 9) of the lodgepole and 70% (N = 10) of the Douglas-fir marked residents. Males also predominated among adults (63%; N = 8) and juveniles (73%; N = 11).

Figure 2. Changes in red squirrel numbers in each habitat, 1977-1978. Each point represents the sum of the squirrel numbers from the 2 study areas within each habitat. The numbers above the lines in 1978 represent the proportions of the populations that are new (not present during previous population estimate) residents.



NO. OF SQUIRRLES
25
20
15
10
5
Lodgepole
Douglas-fir
.74
.09
.69
.17
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
1977
1978
MONTHS

Rusch and Reeder (1978) found a predominance of males after early summer due to high adult female mortality in late summer and fall; however, they found juvenile sex ratios did not differ significantly from 1:1.

Territory Size

All observations of marked animals between 28 September and 8 December 1978, were plotted on study area maps (Figures 3-6). I located an average of 70% of the marked squirrels each week (Table 4).

The maximum distance between locations that would occur if a squirrel was observed an infinite number of times ($S\infty$) was estimated for 13 squirrels (Table 5). This represents 39% of the total population. For these squirrels, 98 of 121 plotted observations (81%) were collected as described earlier and were appropriate to use in calculating $S\infty$ values. The other 23 records were not used because they were collected as I followed a squirrel immediately after recording its initial location and its movements could have been influenced by me. $S\infty$ values were not calculated for 4 marked squirrels because they disappeared (#31, #35, #38, #33) and for 2 captured late in the season (#43, #44). $S\infty$ could not be calculated for squirrel #42 because its records did not conform to the assumptions of the analysis.

Squirrels defended territories of about equal size in the lodgepole and Douglas-fir habitats. The median $S\infty$ value for all residents was nearly the same in lodgepole pine (67 m) as in Douglas-fir (60 m) and this difference was not significant (Table 6). When only adults are contrasted, territory size is again virtually identical in the 2 habitats (Table 6) and the difference is not significant. C. Smith (1968) and Rusch and Reeder (1978) also contrasted red squirrel

Figure 3. Location records for marked residents of Douglas-fir area I, Fall 1978. Each point represents the observed location of a marked squirrel.

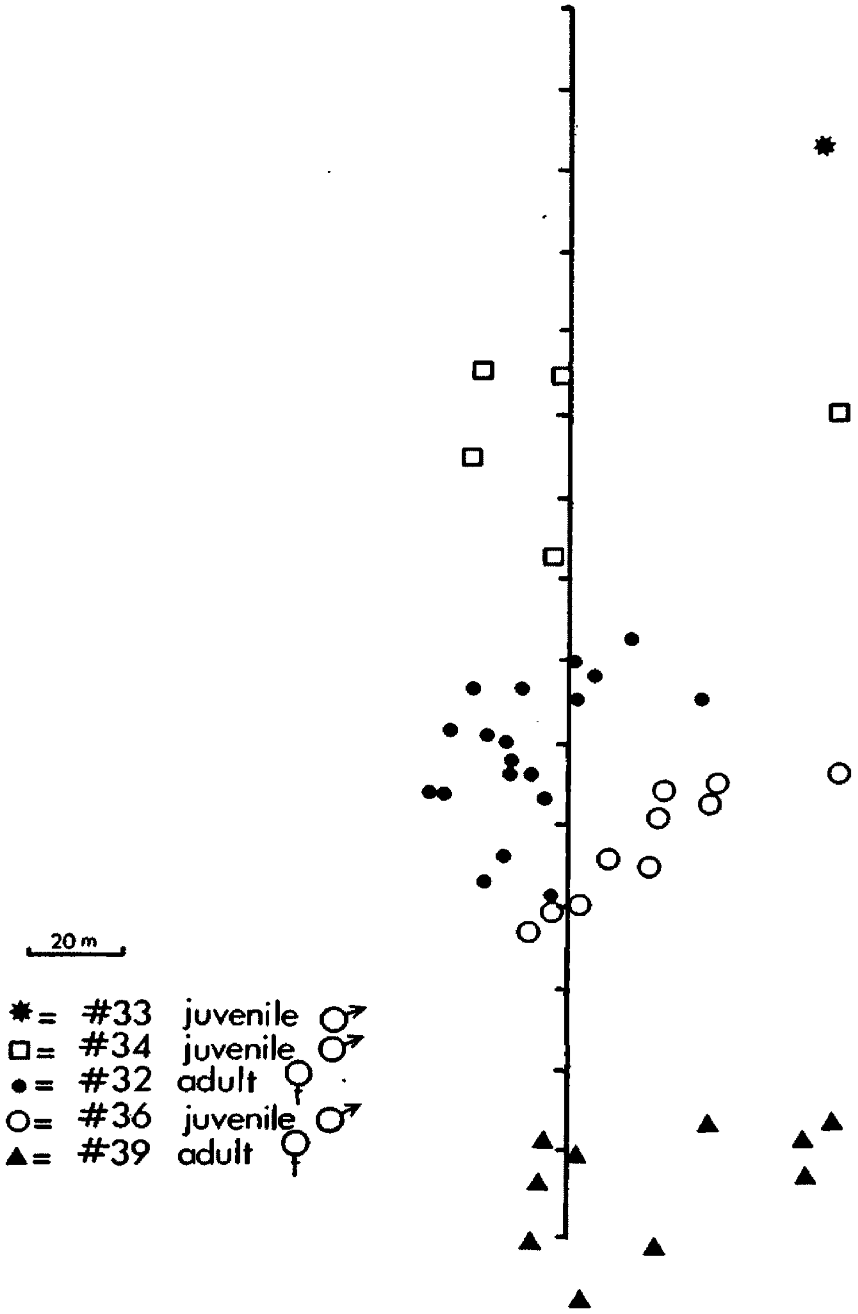

20 m
✱= #33 juvenile ♂
□= #34 juvenile ♂
●= #32 adult ♀
○= #36 juvenile ♂
▲= #39 adult ♀

Figure 4. Location records for marked residents of Douglas-fir area II, Fall 1978. Each point represents the observed location of a marked squirrel.

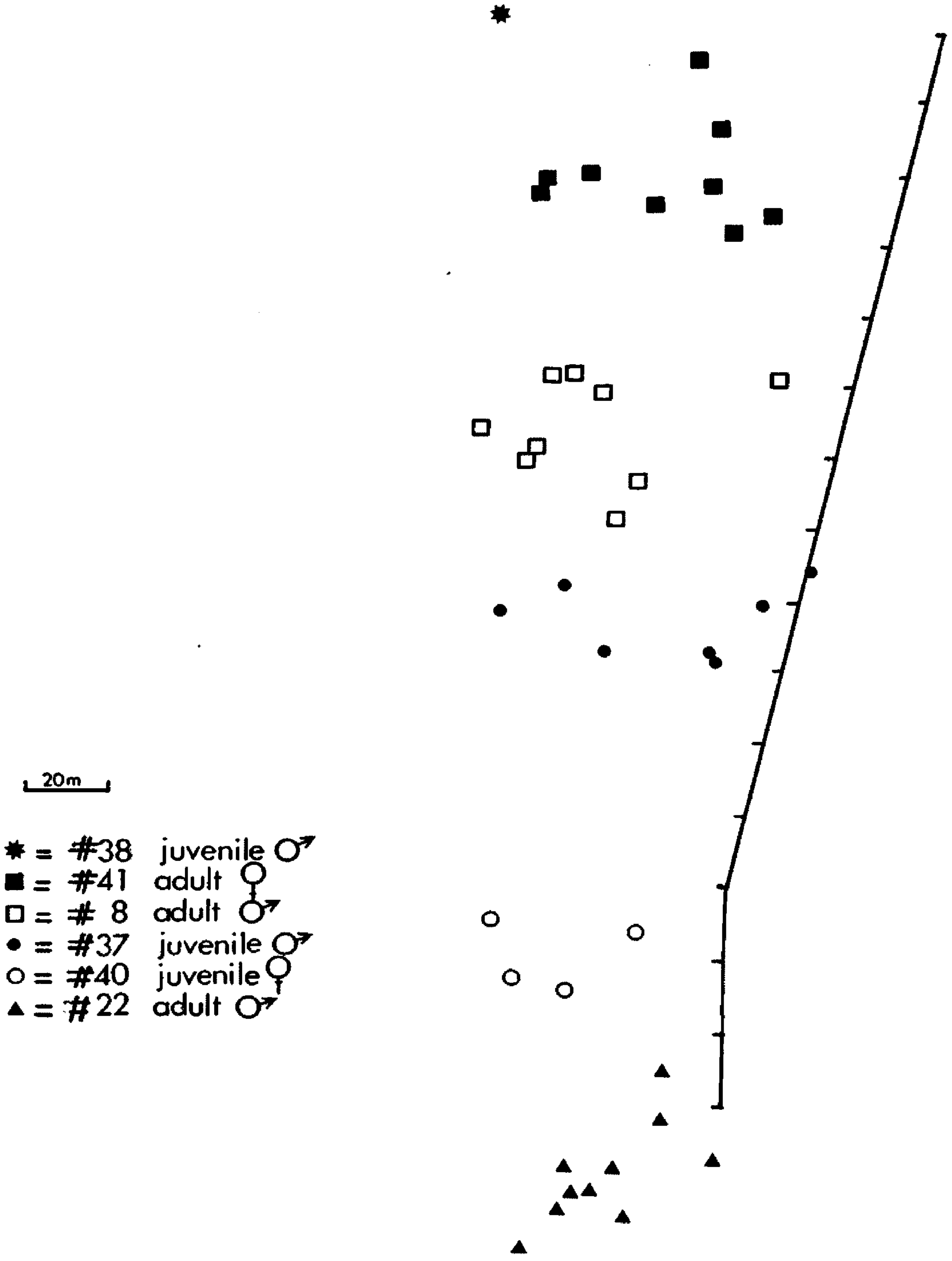

20m
✸ = #38 juvenile ♂
■ = #41 adult ♀
□ = # 8 adult ♂
● = #37 juvenile ♂
○ = #40 juvenile ♀
▲ = #22 adult ♂

Figure 5. Location records for marked residents of lodgepole pine area I, Fall 1978. Each point represents the observed location of a marked squirrel.

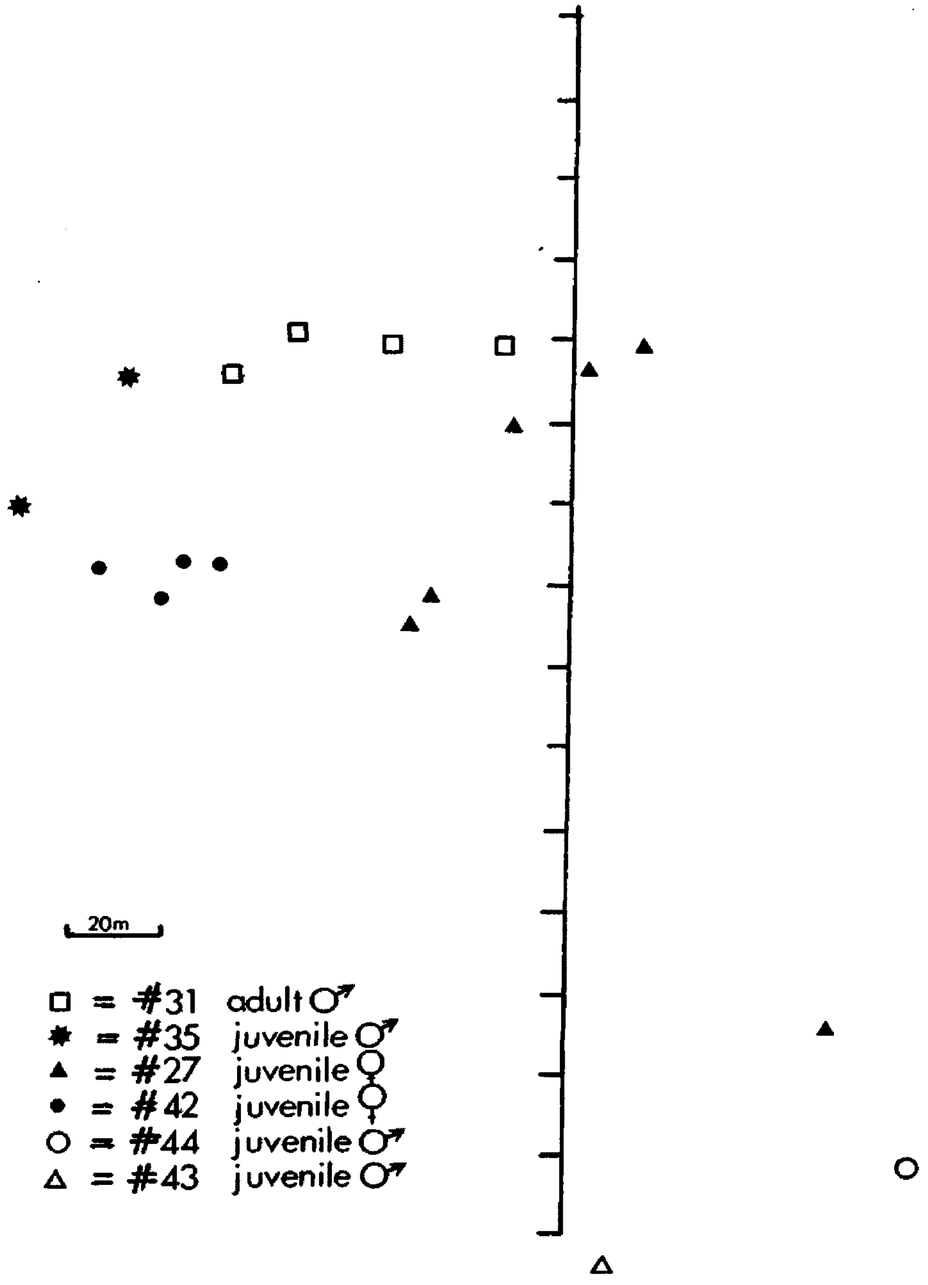

20m
□ = #31 adult ♂
✸ = #35 juvenile ♂
▲ = #27 juvenile ♀
● = #42 juvenile ♀
○ = #44 juvenile ♂
△ = #43 juvenile ♂

Figure 6. Location records for marked residents of lodgepole pine area II, Fall 1978. Each point represents the observed location of a marked squirrel.

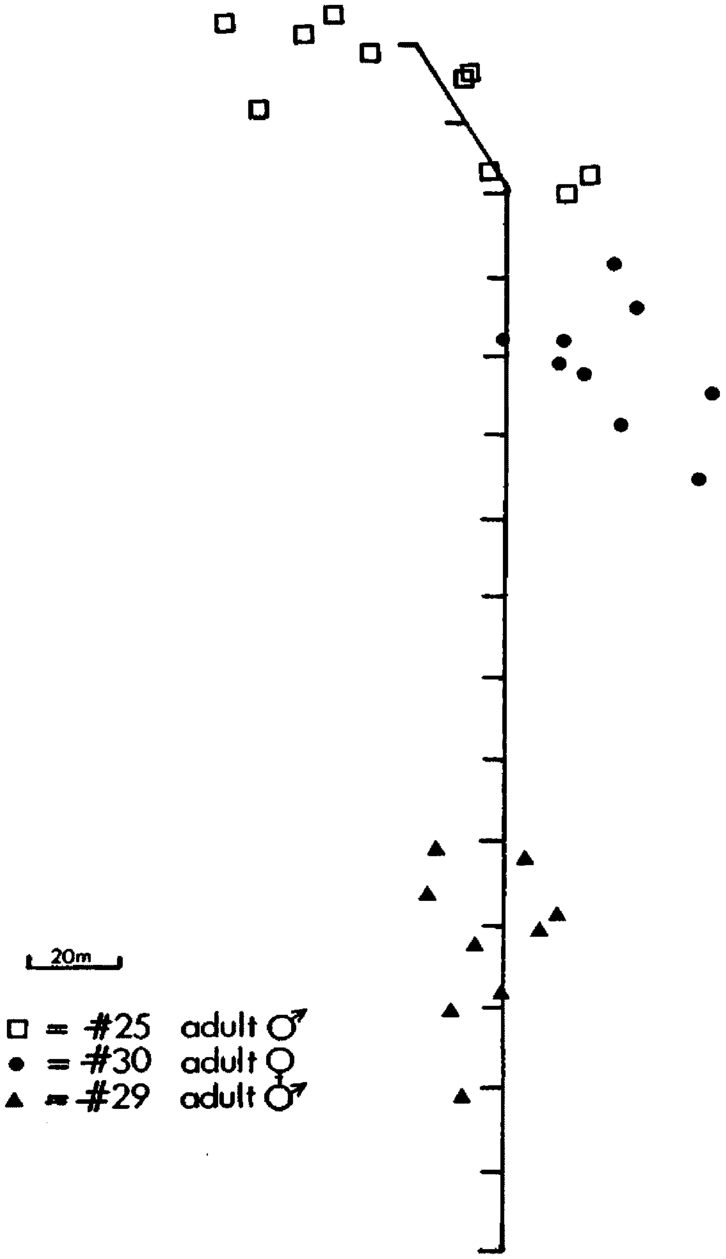

20m
□ = #25 adult ♂
● = #30 adult ♀
▲ = #29 adult ♂

Table 4. Seasonal changes in red squirrel numbers and locatability. Estimated population sizes are shown for each week of the study. The number of marked squirrels that were located each week are contrasted with the number of squirrels that had been marked. Each number represents the sum of all 4 study areas.

	Total sizes of populations	Number marked in populations	Number of marked located	Percent of marked located
25 September	35	15	9	60
2 October	35	15	12	80
9 October	34	14	12	86
16 October	34	13	12	92
23 October	34	14	11	79
30 October	35	16	15	94
6 November	34	15	12	80
13 November	33	14	6	43
27 November	33	14	8	57
4 December	33	14	4	29

Table 5. Territory sizes (S^{∞}in m) and number of location records for individual squirrels from each habitat. Calculated S^{∞} values are shown for each squirrel in addition to the number of location records upon which each S^{∞} value is based.

	Number of individual	Age and sex	S^{∞}	Number of records
Lodgepole pine	27	Juvenile female	161	3
	30	Adult female	51	8
	25	Adult male	70	6
	29	Adult male	63	7
Douglas-fir	39	Adult female	63	7
	36	Juvenile male	72	6
	32	Adult female	60	9
	34	Juvenile male	131	4
	37	Juvenile male	76	5
	8	Adult male	58	8
	41	Adult female	54	8
	22	Adult male	51	7
	40	Juvenile female	37	3

Table 6. Comparisons of territory size (median S_{∞} in m) between populations in each habitat. Median S_{∞} values are shown for the 2 study areas within each habitat and for both areas combined. The habitat medians for both all residents and adults only are contrasted between habitats.

	Median S_{∞} in m						
	Lodgepole pine			Douglas-fir			
	I	II	Population median	I	II	Population median	Significance of difference between habitats
All residents	161 (n = 1)	63 (n = 3)	67	68 (n = 4)	54 (n = 5)	60	P = .252
Adults	-	63 (n = 3)	63	62 (n = 2)	54 (n = 3)	58	P = .286

territory sizes between relatively unproductive pine (lodgepole or the similar jack pine Pinus banksiana) and more productive habitats. For comparison with these studies, I calculated an area estimate by assuming squirrels defended a circular territory with a diameter of S_∞. While Rusch and Reeder (1978) and C. Smith (1968) found that territory size can double in less productive pine habitats, in this study, calculated area estimates in Douglas-fir were only one-fifth smaller than in lodgepole pine (Table 7).

Adults occupied substantially smaller territories than did juveniles. The adult median S_∞ was 17 meters less than the juvenile (Table 8) and this difference was significant ($P = .047$). Area calculations show that adults defended territories 39% smaller in size (.68 acre) than did juveniles (1.12 acre). Adult males and females defended areas essentially equal in size (Table 8).

Territorial and Agonistic Behavior

Behavior rates from each study area were compared weekly (Tables 9-12). Squirrel activity and calling decreased as winter approached. Squirrel movements decreased and locating them required more time after unusually severe weather arrived in early November. I encountered far fewer marked squirrels per hour after 9 November (.42) than before (1.42) and rates of observation declined with advancing season ($P < .05$; Figure 7). Rolled R, squeak and chee calling rates were also negatively correlated with advancing season (All $P < .05$; Figures 8-10). However, individual method chee calling rates failed to diminish as winter approached ($P > .05$; Figure 11).

Squirrels gave rolled R calls at periodic intervals as well as during agonistic encounters. Individually observed squirrels gave

Table 7. Comparisons of red squirrel territory sizes (acres) between habitats of pine and other conifers. Territory size area estimates from populations in pine are contrasted with those from other coniferous habitats and percent differences are shown for each study. Area estimates for the present study were calculated by assuming a circular territory with a diameter of $S\infty$.

References	Territory Size (Acres)		Percent difference
	Pine	Other conifers	
Present study	0.87	0.70	19.5
Rusch and Reeder (1978)	1.63	0.59	63.8
C. Smith (1968)	1.88	1.01	46.3

Table 8. Comparisons of territory sizes (Median S_{∞} in m) between age and sex classes. Median S_{∞} values were computed for data combined from the 2 habitats and the number of individuals per group are shown in parentheses.

	Median S_{∞}(m)
Adults	59 (n = 8)
Juveniles	76 (n = 5)
Adult males	60 (n = 4)
Adult females	58 (n = 4)

Table 9. Rolled R calling rates (calls/hr/individual) from the 4 study areas compared weekly. Estimated calling rates from all study areas are shown for each week during Fall, 1978.

Week	Lodgepole I	Lodgepole II	Douglas-fir I	Douglas-fir II
25 September		6.3		12.0
2 October	6.9	8.7	9.9	7.5
9 October	12.7	9.0	13.6	8.4
16 October	13.5	6.4	10.5	7.8
23 October	9.2	5.3	11.7	5.3
30 October	9.7	6.2	13.5	7.9
6 November	4.4	4.6	7.1	5.9
13 November	6.1	2.8	6.5	3.0
27 November	9.2	3.7	0.55	1.3
4 December	2.2	.67	3.1	1.4
Mean	8.2	5.4	8.5	6.1

Table 10. Squeak calling rates (calls/hr/individual) from the 4 study areas compared weekly. Estimated calling rates from all study areas are shown for each week during Fall, 1978.

Week	Lodgepole I	Lodgepole II	Douglas-fir I	Douglas-fir II
25 September		0.46		2.1
2 October	0.62	0.43	1.9	1.4
9 October	4.7	0.07	3.9	2.4
16 October	2.0	0.30	1.3	0.69
23 October	1.2	0.67	1.9	0.32
30 October	0.72	0.72	2.0	1.7
6 November	0.16	0.50	0.58	0.39
13 November	0.29	0.31	1.1	0.13
27 November	0.66	0.16	0.13	0.18
4 December	0.05	0.0	0.49	0.08
Mean	1.2	0.36	1.5	0.94

Table 11. Chee calling rates (calls/hr/individual) from the 4 study areas compared weekly. Estimated calling rates from all study areas are shown for each week during Fall, 1978.

Week	Lodgepole I	Lodgepole II	Douglas-fir I	Douglas-fir II
25 September		1.8		1.7
2 October	2.5	2.2	1.4	1.3
9 October	2.3	1.7	1.2	1.2
16 October	1.9	1.3	1.4	0.75
23 October	1.8	1.5	0.63	1.1
30 October	1.4	1.4	0.64	0.85
6 November	0.59	0.95	0.65	1.1
13 November	0.89	0.51	0.51	0.49
27 November	1.2	0.82	0.48	0.46
4 December	0.55	0.06	1.0	0.39
Mean	1.5	1.2	0.88	0.93

Table 12. Rates of growl calling and of chasing (behaviors/hr/individual) from the 4 study areas compared weekly. Estimated behavior rates from all study areas are shown for each week during Fall, 1978. The 2 rates are shown as rate of growling/rate of chasing.

Week	Lodgepole I	Lodgepole II	Douglas-fir I	Douglas-fir II
25 September		0.0/0.0		0.0 / .04
2 October	0.28/0.0	0.0/0.0	0.0 /0.0	0.0 / .04
9 October	0.07/ .07	0.0/0.0	.09/ .04	0.0 /0.0
16 October	0.07/0.0	0.0/0.0	0.0 /0.0	0.0 /0.0
23 October	0.14/ .05	0.0/0.0	0.0 / .08	0.0 /0.0
30 October	0.0 /0.0	0.0/0.0	0.0 /0.0	0.0 /0.0
6 November	0.0 /0.0	0.0/0.0	0.0 /0.0	0.0 /0.0
13 November	0.0 /0.0	0.0/0.0	.06/0.0	0.0 /0.0
27 November	0.0 /0.0	0.0/0.0	.03/0.0	0.02/0.0
4 December	0.0 /0.0	0.0/0.0	0.0 / .04	0.0 /0.0
Mean	.06/ .01	0.0/0.0	.02/ .02	.002/.01

Figure 7. The decline in rates of observation (marked squirrels/hr) as the season advances. Each point represents the number of marked squirrels located per hour for each weekly period. Data from the 4 study areas are summed to obtain total weekly squirrel numbers and hours of observation.

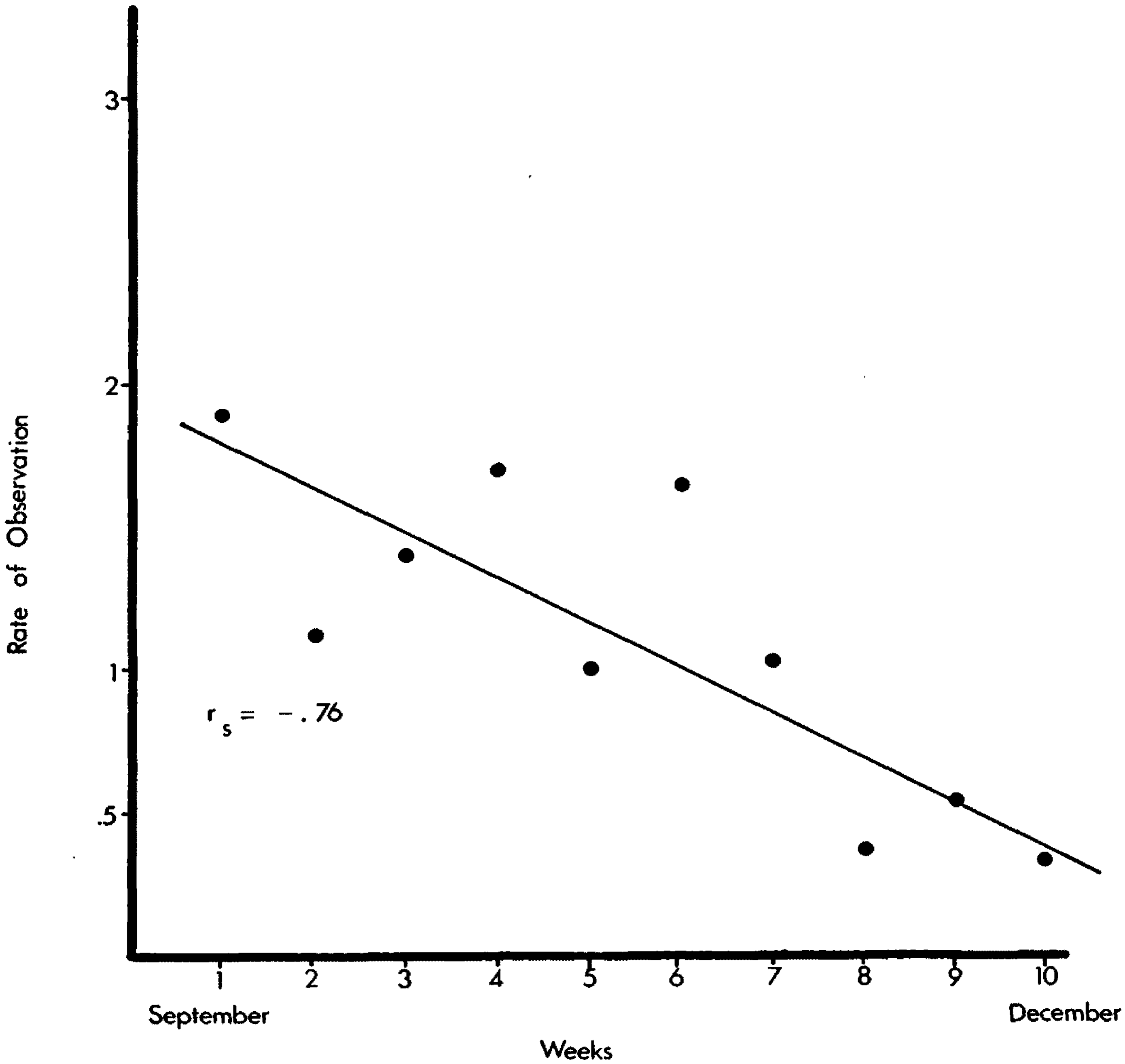

3
2
1
.5
Rate of Observation
$r_s = -.76$
1
2
3
4
5
6
7
8
9
10
September
December
Weeks

Figure 8. The decline in mean rolled R calling rates (calls/hr/individual) as the season advances. Each point represents the average of the weekly calling rates from the 2 habitats.

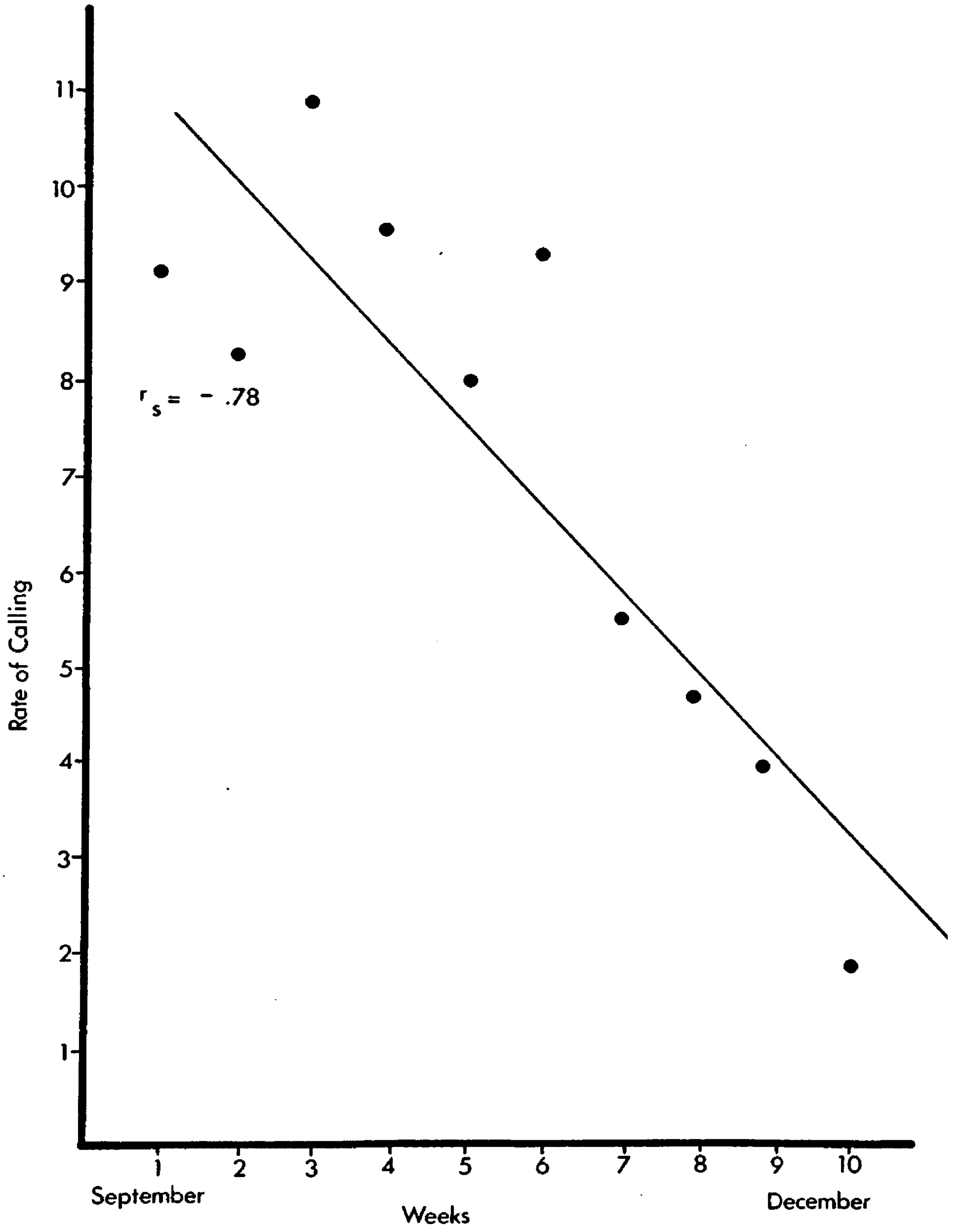

Rate of Calling
11
10
9
8
7
6
5
4
3
2
1
$r_s = -.78$
1
2
3
4
5
6
7
8
9
10
September
Weeks
December

Figure 9. The decline in mean squeak calling rates (calls/hr/individual) as the season advances. Each point represents the average of the weekly calling rates from the 2 habitats.

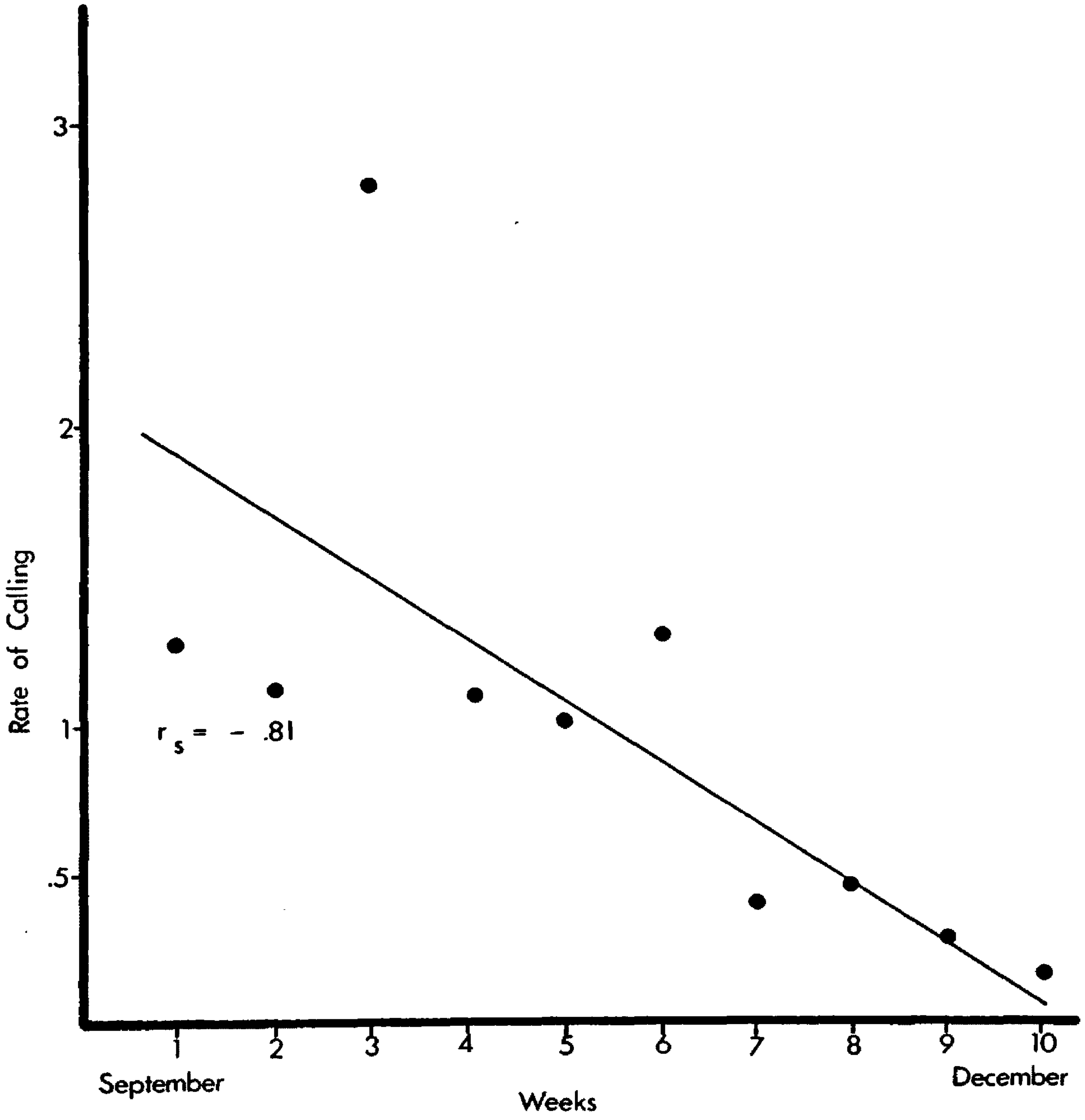

3
2
1
.5
Rate of Calling
$r_s = -.81$
1
2
3
4
5
6
7
8
9
10
September
December
Weeks

Figure 10. The decline in mean chee calling rates (calls/hr/individual) as the season advances. Each point represents the average of the weekly calling rates from the 2 habitats.

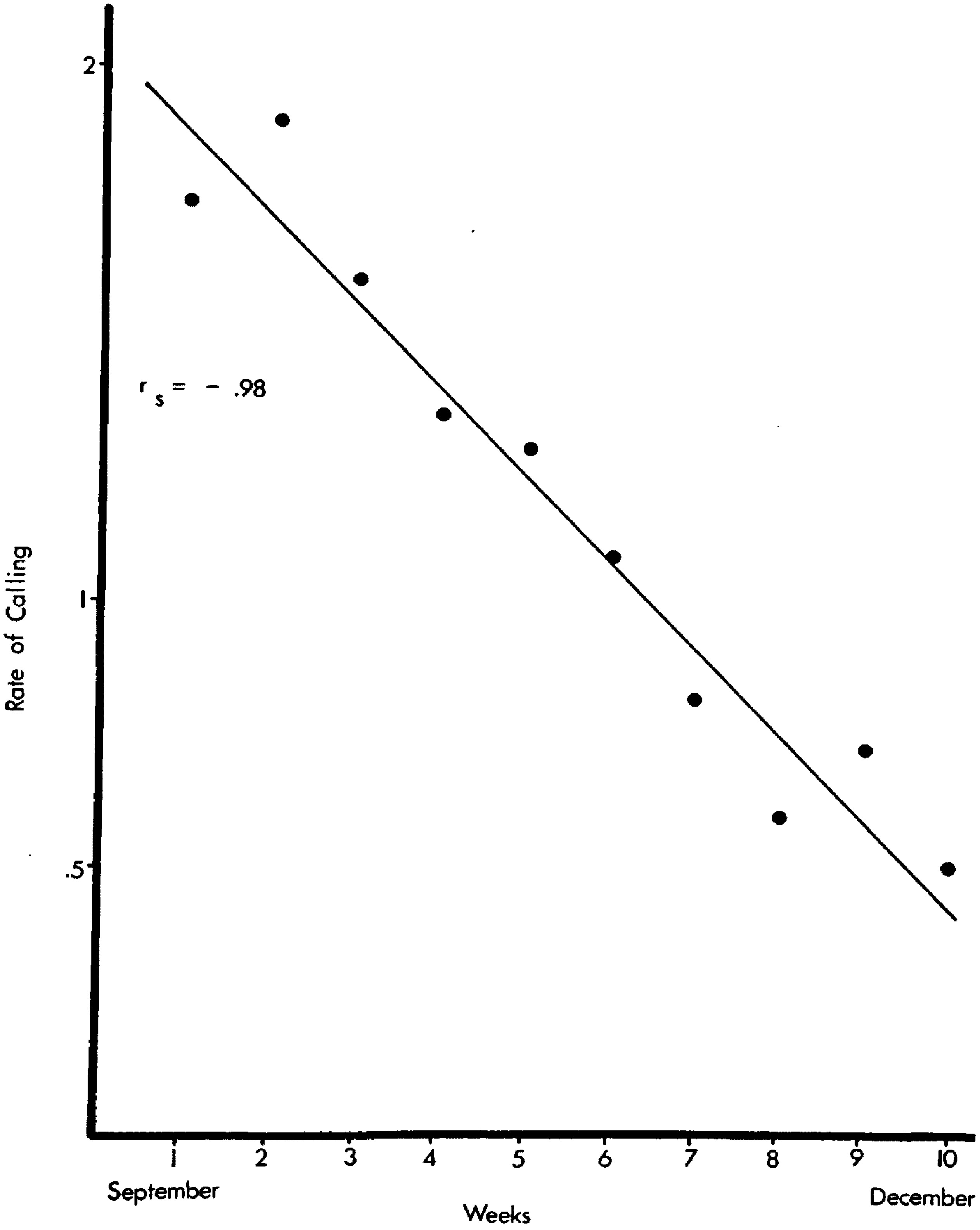
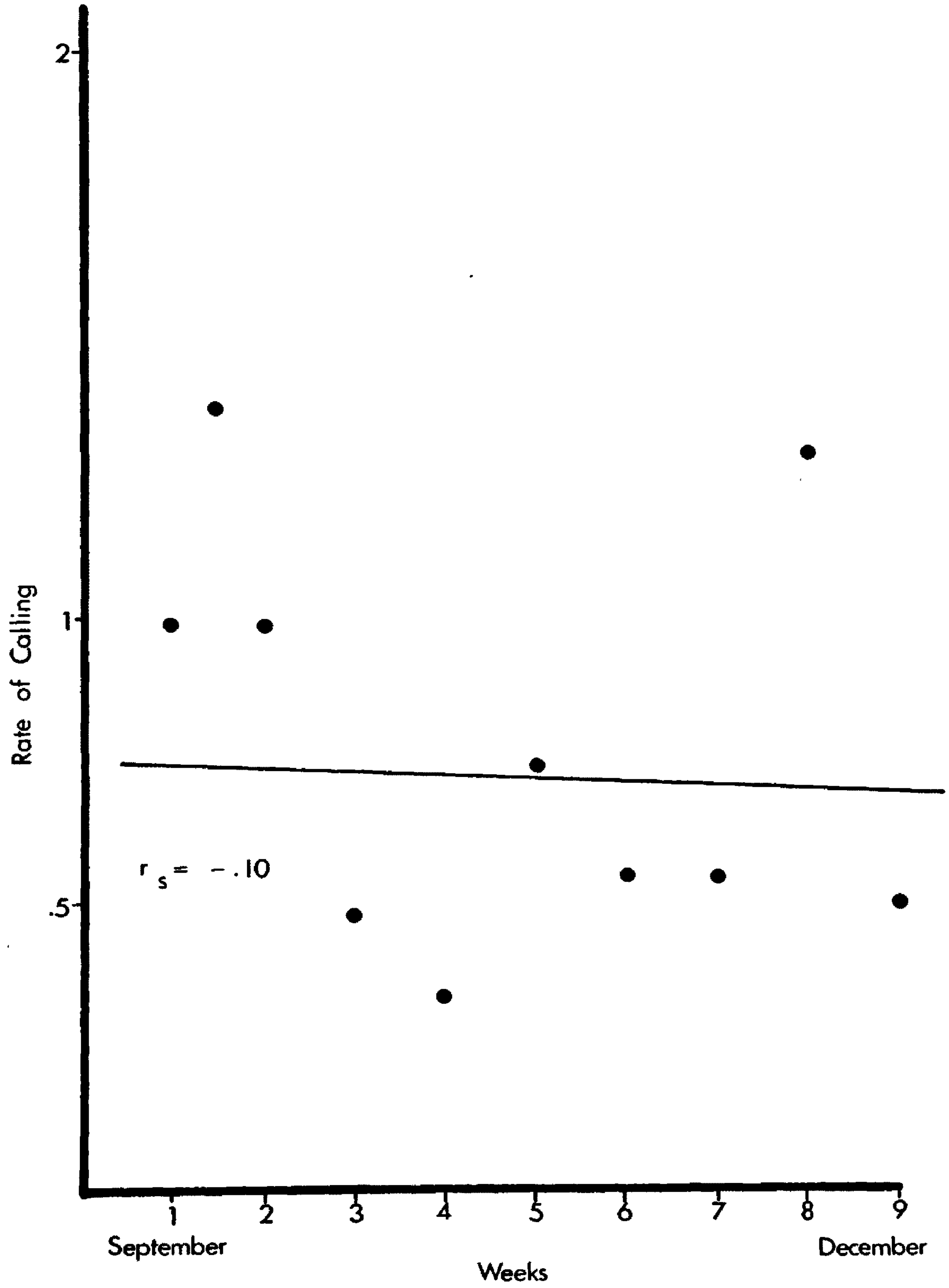

2
1
.5
Rate of Calling
$r_s = -.98$
1
2
3
4
5
6
7
8
9
10
September
Weeks
December

Figure 11. Mean chee calling rates (calls/hr/individual) from individual method versus advancing season. Each point represents the average of the weekly calling rates from the two habitats.


2
1
.5
Rate of Calling
$r_s = -.10$
1
2
3
4
5
6
7
8
9
September
December
Weeks

most of their rolled R calls in the absence of any apparent agonistic behavior. Typically, a squirrel would move through its territory and occasionally pause and call or call after completing an activity (e.g. storing a cone, transporting nest material). Territory defenders gave rolled R calls in 9 of 10 closely observed agonistic interactions in the fall of 1978. Typically, the defender used the call as another squirrel approached its territory or while it faced in the direction of a fleeing intruder at the conclusion of a chase. Squirrels gave rolled R calls at similar rates in the 2 habitats (Table 13) and the difference was not significant.

Squirrels used squeak calls about 10% as frequently as rolled R calls (Table 13) and only in agonistic situations. A squirrel gave squeaks as it actively repelled an intruder and in association with rolled R calls as another squirrel approached its territory. Squirrels in Douglas-fir habitat issued squeak calls at nearly 2.5 times the rate of those in lodgepole (Table 13).

Squirrels most frequently gave chee calls in apparent response to other species. I elicited 26 of 45 chees recorded by the individual method and I could not determine what prompted the remaining calls. Red squirrels also give chees during breeding behavior (Embry 1970) but were not breeding when I made these observations. The trend in chee calling was the reverse of the other calls as Douglas-fir squirrels called at 60% the rate of lodgepole squirrels (Table 13). The individual method calling rates failed to show this difference between habitats. However, the fact that I approached these squirrels closely and frequently elicited chee calls may have obscured any difference between the populations.

Table 13. Comparisons of calling rates (Median calls/hr/individual) between populations in lodgepole and Douglas-fir habitats. Median rates of rolled R, squeak and chee calling are contrasted between the 2 populations. Each entry represents the median of the weekly calling rates in each habitat. Habitat weekly calling rates were computed by combining the weekly rates from the 2 study areas within a habitat.

	Median calls/hr/individual		
Call	Lodgepole pine	Douglas-fir	Significance of difference
Rolled-R	6.3	7.5	P = 0.068
Squeak	.46	1.1	P = 0.019
Chee	1.4	.85	P = 0.015

DISCUSSION

Squirrel population density appears to relate to food availability. The lodgepole areas provided food more consistently than the Douglas-fir habitat in which productivity varied immensely. Lodgepole area squirrel numbers were relatively constant, while the Douglas-fir population increased substantially as a good cone crop followed the virtual failure of 1977. *Tamiasciurus* populations can respond rapidly to oscillations in food supply by redistributing themselves (C. Smith 1968; M. Smith 1968; Rusch and Reeder 1978) and possibly by varying reproductive effort (Kemp and Keith 1970).

Squirrels favor Douglas-fir cones and use pure lodgepole forests primarily during Douglas-fir cone crop failures and as juveniles when they are excluded from more optimum habitats. Lodgepole habitat squirrels switched from lodgepole to Douglas-fir cones in 1978, although lodgepole cones were readily available, and deserted homogenous lodgepole stands they had occupied in 1977. These observations agree closely with other accounts of red squirrel populations in these habitats (Finley 1969; C. Smith 1970).

Territory Size

Squirrels defended territories of equal size in the two habitats. Juveniles maintained larger territories than adults while adult males and females occupied areas of equal size. Lodgepole habitat squirrels may have defended atypically small areas in 1978 because sections of lodgepole forest provided as much energy as the Douglas-fir habitat. Territory size in lodgepole pine was half that found by other workers in lodgepole pine and the similar jack pine (*Pinus banksiana*) and approximated those in more productive habitats (Table 14). Territory size in *Tamiasciurus* relates inversely to food abundance (Kemp and Keith 1970; Layne 1954; Rusch and Reeder 1978; C. Smith 1968; M. Smith 1968) and the principal food is conifer seed (Brink and Dean 1966; Finley 1969; Rusch and Reeder 1978; M. Smith 1968). In 1978, Douglas-fir areas appeared to contain more conifer seed energy than did lodgepole areas. However, the variance of these energy estimates was enormous. Additionally, since lodgepole habitat territories clustered around scattered Douglas-firs, randomly placed seed traps may have underestimated Douglas-fir seed production on territories. Furthermore, while squirrels weigh less (Rusch and Reeder 1978) and overwinter more poorly (C. Smith 1968) in less productive habitats, squirrels in this study weighed the same and overwintered equally well (1978-1979) in the 2 habitats suggesting they provided about equal energy.

Juveniles may have required larger territories because they forage less efficiently (C. Smith 1968; Weigl and Hanson 1980). In this study, they occupied stands of smaller, less mature conifers perhaps necessitating broader movement. C. Smith (1968) found juveniles defended smaller areas than did adults. However, he measured territories in late September and juvenile territories may not expand fully until later (*pers. obs.*; Zirul 1970). Furthermore, relatively high regional population densities may have limited the area available to young squirrels in Smith's areas.

Table 14. Comparisons of red squirrel territory sizes (acres) between habitats of pine and other conifers. Area estimates for the present study were calculated by assuming a circular territory with a diameter of $S\infty$.

Habitat	Location	Reference	Acres per territory
Pine	Montana	present study	0.87
	Alberta	Rusch and Reeder (1978)	1.63
	B.C.	C. C. Smith (1968)	1.88
Other conifers	Montana	present study	0.70
	Alberta	Rusch and Reeder (1978)	0.59
	B.C.	C. C. Smith (1968)	1.01

Territorial and Agonistic Behavior

Squirrels called less frequently as the season progressed from early fall to winter. This corresponded with decreasing activity in response to decreasing temperature and completion of cone caching. Squirrel movements decreased to practically zero during severe early December weather. Taiga red squirrels greatly reduce activity as winter approaches (Zirul 1970). At low ambient temperatures, red squirrels spend more time in their nests (Ackerman and Weigl 1970; Pauls 1978) where body temperature is lowered slightly, reducing daily energy expenditure (Pauls 1979).

Squirrels in general gave fewer chee calls as winter approached, while individually followed squirrels did not, probably because this call functions in alarm behavior (C. Smith 1978) and squirrels were responding to me. Squirrels seemed to chee call in response to predators and when I approached closely as C. Smith (1978) also reported. My observations disagree with Searing's (1977) suggestion that the chee is a low intensity aggressive call given more frequently in the winter when squirrels interact less frequently. Squirrels in this study showed a strong tendency to give fewer chee calls as winter approached.

Squirrels gave rolled R calls at similar rates in the 2 populations. Douglas-fir squirrels gave squeak calls at more than twice the rate of lodgepole squirrels and used chee calls less frequently. My result for rolled R calling is consistent with the hypothesis that squirrels broadcast this call as a territorial advertisement (Embry 1970; C. Smith 1978). Because squirrels advertise in the absence of conspecifics (Embry 1970; _per_. _obs_.), calling rates may respond relatively weakly to differences in population characteristics.

Douglas-fir squirrels gave more squeaks than lodgepole squirrels, probably because squeaks function in aggression and Douglas-fir squirrel populations were more dense and contained more juveniles. Squirrels give squeaks only when conspecifics approach or invade their territories (Embry 1970; C. Smith 1978) which should occur more frequently in denser populations. Juveniles elicited aggression as they dispersed through residents' territories and I believe that Douglas-fir squirrel populations contained proportionally more juveniles. Population density and age ratios affect agonistic behavior in marmot populations (Armitage 1977).

The presence of immigrants can also influence agonistic behavior (Armitage 1977). However, my populations contained similar proportions of new residents. Differences in food distribution could directly produce differences in aggression levels. However, in 1978, food was distributed similarly on territories in the 2 habitats, as all squirrels consumed Douglas-fir cones exclusively and lodgepole squirrels defended territories around clumps of Douglas-fir. Habitat structure itself could affect social behavior. Jenkins (1961) observed that partridges (Perdix perdix) interacted less in dense vegetation. Because squirrels interacted more in the visually denser habitat, the difference in aggression levels was probably not related to visibility.

Why Douglas-fir habitat squirrels gave fewer chee calls is difficult to explain. If chee calls harass predators and warn conspecifics (C. Smith 1978), then individuals in dense populations may call less because they experience fewer predators. Larger groups of animals should detect predators more effectively (Lack 1968; Hoogland 1979). Hoogland (1979) found that individual prairie dogs (Cynomys) were less alert in dense populations and at the center of a group. Although a solitary, forest species undoubtedly depends much less on group alertness, the dense population in Douglas-fir may have lowered predation exposure per individual.

The lodgepole pine and Douglas-fir study areas did not provide as dramatic a contrast in food supply as I had expected. In 1978, territories in the 2 habitats produced and distributed food similarly. However, in the habitats as a whole, food was distributed very differently. This marked change in distribution may have created differences in social behavior. The lodgepole areas were more heterogeneous as they contained patches of mixed forest. Because squirrels in the lodgepole habitat shunned sections of pure lodgepole, population density was half that in the Douglas-fir habitat although squirrels defended similar sized territories. An individual squirrel in the Douglas-fir habitat should have had to actively repel intruders more often than a squirrel in lodgepole pine whose territory abutted vacant areas on several sides. Thus, the squirrel population in Douglas-fir experienced higher agonistic levels. Spatial organization may also have affected alarm behavior. An individual squirrel in Douglas-fir may have experienced fewer predators than a squirrel in lodgepole pine because its numerous neighbors more effectively detected and discouraged potential predators.

An alternate interpretation of these results exists. If squirrels in the Douglas-fir habitat enjoyed increased security against predators, they might have devoted more time to aggressive behavior. However, because red squirrels invest little time in either territorial or antipredator behavior (C. Smith 1968), these activities probably do not compete for time.

Territory size often relates inversely to food availability (Pitelka et al. 1955; C. Smith 1968; Moss 1969; Cody and Cody 1972; Gill and Wolf 1975; Gass et al. 1976; Myers et al. 1979; Gass 1979). The proximate causal mechanism which produces this correlation is difficult to identify. Animals could adjust territory size directly to food density or food density could indirectly determine territory size by affecting intrusion pressure (Myers et al. 1979; Ewald et al. 1980). The latter hypothesis probably explains the relationship between territory size and food density in several bird species (Krebs 1971; Meyers et al. 1979). My results and those of C. Smith (1968) suggest that red squirrels may adjust territories to a size determined by food density and respond little to intrusion pressure. Red squirrel territory size relates inversely to food abundance (Layne 1954; Kemp and Keith 1970; C. Smith 1968; Rusch and Reeder 1978). In my study, squirrels in the two habitats defended territories of equal size although squirrels in Douglas-fir lived in populations twice as dense and interacted aggressively more often than did squirrels in lodgepole pine. C. Smith found that squirrels defended territories of different sizes in populations subjected to similar pressure from vagrant squirrels. Of course, my conclusion must remain very tentative as these studies measured intrusion pressure only very generally.

Red squirrel territoriality should produce strong selection for defense of territories adjusted rigidly in size to food density. Red squirrel territoriality probably functions to defend a food supply critical for overwinter survival (M. Smith 1968; C. Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978) and squirrels without territories or that defend suboptimal territories suffer high mortality (C. Smith

1968; Kemp and Keith 1970; Rusch and Reeder 1978). Furthermore, if red squirrels adjust territory size to ensure food availability in lean years, as proposed by Rusch and Reeder (1978), then territories should strongly resist intrusion pressure.

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