AN ABSTRACT OF THE THESIS OF

Amy L. Hacker for the degree of Master of Science in Wildlife Science presented August 12, 1991.

Title: Population Attributes and Habitat Selection of Recolonizing Mountain Beaver.

Redacted for Privacy

Abstract approved: ______________________

Bruce E. Coblentz, Ph.D.

I investigated the population attributes and habitat selection of mountain beaver (*Aplodontia rufa*) recolonizing clearcuts in the Coast Range mountains of Polk and Lincoln counties, Oregon between June 1989 and August 1990. The population characteristics of colonizing mountain beaver were evaluated in 12 stands of 3 types: 1-year-old clearcuts assumed to be inhabited entirely by immigrants, 4- to 5-year-old clearcuts inhabited by immigrants and their descendants, and 40- to 60-year-old forest stands assumed to support stable mountain beaver populations. Mountain beaver rapidly recolonized vacant habitat created by previous trapping efforts; after only 1 year, densities in clearcuts were statistically indistinguishable from forest sites ($P = 0.7$). Populations in 1-year-old clearcuts had more juveniles ($P = 0.03$) and had a female bias ($P = 0.02$) when compared with the predominantly adult male populations in the other two stand types. Individuals from clearcuts were heavier than those from forest sites ($P < 0.05$). Approximately half of the juvenile females in clearcuts reproduced; no juvenile females were found to be reproductively active in forest stands. Among juvenile females that conceived, those in 1-year-old clearcuts had larger litter sizes than those in 4- to 5-year-old clearcuts ($P < 0.05$).

The 8 clearcuts were used to identify habitat features selected by recolonizing mountain beaver. Clearcuts were colonized irrespective of distances < 400 m from edge (R^2 = 0.01). Six habitat variables were selected by stepwise logistic regression to model colonized versus non-colonized habitat. Mountain beaver selected areas with high amounts of small (<25-cm) and large (>25-cm) woody debris, forage plants, and uprooted stumps; they were likely to colonize areas that had highly penetrable (soft) soils and areas near drainages. The logistic function that included these 6 variables had a correct classification rate of 85% based on a jackknife procedure. Forest managers may find these habitat features useful in predicting mountain beaver recolonization and damage.

Population Attributes and Habitat Selection of Recolonizing Mountain Beaver (*Aplodontia rufa*)

by

Amy L. Hacker

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Department Head of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

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This thesis is lovingly dedicated to Ky A. Hacker.
May you always feel the wind, hear the birds, and marvel at bugs (wherever you find them).

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

POPULATION ATTRIBUTES AND HABITAT SELECTION OF RECOLONIZING MOUNTAIN BEAVER (*Aplodontia rufa*)

INTRODUCTION

Mountain beaver, *Aplodontia rufa*, are among the most primitive living rodents. They are herbivorous (Voth 1968), semi-fossorial, and are active above ground primarily at night (Ingles 1959). They inhabit extensive burrow systems and habitually use surface trails. Although they do not share nest sites (Martin 1971, Voth 1968) their home ranges overlap (Lovejoy 1972, Martin 1971) and densities seem to be a function of suitable habitat (Feldhamer and Rochelle 1982). The family Aplodontidae is monotypic; there are seven subspecies recognized (Godin 1964).

Mountain beaver occur exclusively in western North America. Their distribution extends from southern British Columbia south to central California and east to the Sierra Nevada and Cascade mountain ranges. They are found in moist areas at elevations < 2,200 m (Feldhamer and Rochelle 1982). Rainfall and edaphic conditions that promote succulent vegetation and high burrow humidity (Voth 1968) probably define current distributions. In the Oregon Coast Range, mountain beaver inhabit a variety of plant communities and seral stand conditions (Maser et al. 1981).

Mountain beaver are economically important because they damage Douglas-fir (*Pseudotsuga menziesii*) seedlings and saplings in western Washington, Oregon, and northern California (Campbell and Evans 1988, Borrecco and Anderson 1980, Hooven 1977). They cause tree mortality, deformity, or growth losses that can result in under-stocked plantations (Crouch 1968, Staebler et al. 1954, Scheffer 1929). Typically, they clip seedlings near the base and use them as forage or in nest building (Borrecco and Anderson 1980, Hooven 1977). Timber production is currently reduced by mountain beaver on approximately 140,000 ha of forest land in the Pacific Northwest. Damage, estimated in the millions of dollars per year, is expected to increase if more land is converted to early seral stages (Evans 1987).

Control programs are conducted in early seral stands with potential or actual mountain beaver damage. These programs normally consist of kill-trapping all mountain beaver in the clearcut or young stand. Because this method is costly and only partially effective in mitigating damage, there is a need for research into the species' behavioral ecology to improve the long-term success of damage control (Campbell and Evans 1988, Smurthwaite 1986, Feldhamer and Rochelle 1982). Removing all mountain beaver from plantations with high population densities creates vacant habitat which may provide "dispersal sinks" (see

Lidicker 1975). I conducted this study to determine how long habitat remains vacant after trapping, the population attributes and relative success of animals that disperse into vacated habitat, and the habitat features that are selected by colonists. Specifically, the objectives of this study were to determine:

1. the distribution and relative abundance of mountain beaver recolonizing clearcuts 1 and 4-5 years after removal trapping,
2. if density, sex ratio, age composition, body mass or productivity differed among untrapped forest stands, clearcuts 1 year after removal trapping, and clearcuts 4-5 years after removal trapping, and,
3. habitat variables that predict where mountain beaver will recolonize clearcuts after removal trapping.

STUDY AREAS

The study was conducted in Polk and Lincoln counties, Oregon, on managed forest lands on the western slope of the Coast Range mountains. The landscape varied from gently rolling to precipitous, with elevations ranging from 90 to 360 m. Soils were moderately deep and well-drained (Knezevich 1979). The climate was cool and moist with mean minimum January temperature of 0° C and mean maximum July temperature of 27° C. Mean annual precipitation ranged from 203 to 224 cm (NOAA 1985). The dominant commercial tree species was Douglas-fir, which occurred over a range of seral stages throughout the area.

Twelve study sites were established (Appendix A): 8 were clearcuts that had been replanted with Douglas-fir seedlings and 4 were second-growth stands. Clearcuts were selected to maximize similarities among them, especially with regard to site preparation. Site preparation included broadcast burning of slash followed by complete removal trapping of mountain beaver just prior to tree planting. Foresters removed mountain beaver with Conibear #110 traps placed in active runways and checked every 2 to 5 days until mountain beaver captures were insignificant (2 to 3 weeks). Mountain beaver were also removed from a 100-m border surrounding the clearcuts. Herbicide was applied to all sites at least once after reforestation (Appendix B). The 8 clearcuts consisted of 2 age classes of 4 sites each. One group had been reforested in the winter of 1988-89 (1-year-old clearcuts) and the others were reforested either in the winter of 1984-85 or in the winter of 1985-86 (4- to 5-year-old clearcuts). The clearcuts were 9.6 to 55.2 ha.

In addition to the 8 clearcut stands, I selected 4 forested reference stands. Mountain beaver had never been trapped from these areas. Forest stands were mixed-species second-growth predominated by 40- to 60-year-old Douglas-fir. Hardwood species included vine maple (*Acer circinatum*), red alder (*Alnus rubra*), and California hazel (*Corylus cornuta californica*). Generally, the shrub layers were sparsely developed, and the understories were dominated by western sword fern (*Polystichum munitum*) and salal (*Gaultheria shallon*). In addition to minimizing differences among these stands with respect to vegetation, slope, and aspect, I only used forested stands with > 4 mountain beaver burrows/ ha.

CHAPTER 1

POPULATION ATTRIBUTES OF RECOLONIZING MOUNTAIN BEAVER

METHODS

Portions of each of the 12 study areas were selected as sites from which to kill-trap all resident mountain beaver for intensive population analysis. I adjusted the size of these trapping areas such that each included approximately 35 trap stations. Trap stations were either the center of an active, well-defined burrow system < 10 m in radius, or every 10 m within extensive tunnel networks. Fresh piles of vegetation and dug earth were present at the entrances of active burrow systems. Trapping areas ranged in size from 1.3 to 6.0 ha (Table 1.1). Within the 8 clearcuts, the trapping areas bordered the forest next to the clearcut, extending 100 m into the clearcut and varying from 133 to 600 m along the edge. Trapping areas in forest stands were also rectangular with the short sides being 100 m.

I sampled mountain beaver from 2 March to 3 April 1990 with Conibear #110 traps. My goal was to completely remove mountain beaver from the trapping areas. Two traps were placed in active burrows or surface trails within 3 m of each trapping station. I checked the traps 1, 2, 4, 6, and 8 days after placement. All sprung traps were reset in place. Three stands, 1 of each type, were trapped concurrently to equalize the effects of different trapping periods on population parameters. Replicates were trapped consecutively. To ensure that effective removal of mountain beaver populations had occurred, burrows were examined for evidence of mountain beaver use 1 week after cessation of trapping. I found such evidence in only 1 case. Because it was on the border of the trapping area, I judged this animal to be an immigrant, and considered the trapping effort complete.

Trapped mountain beaver were tagged for identification and then frozen. They were later thawed and examined for sex, age, mass, length, and reproductive status. The number of fetuses or placental scars were counted in pregnant and lactating females.

DENSITIES

I adjusted naive densities by adding a 10-m boundary strip to the trapping area to correct for the "edge effect" (Wilson and Anderson 1985) and approximate the area actually inhabited by the trapped population. Ten meters was approximately 1/2 the diameter of an average burrow system (pers. obs.). Although a home range exceeds burrow diameter (Martin 1971), animals were trapped only within burrow systems. These "effective trapping areas" were then used to calculate mountain beaver densities. Chi-square procedures were used to determine if a difference in capture likelihood as a function of trapping day existed between males and females. Expected capture frequencies under the null hypothesis were homogeneity between males and females on each trapping day.

Prior to trapping, I walked 10 50- x 1-m belt transects within each trapping area and counted the number of existing mountain beaver tunnels within them. Population densities were regressed as a function of transect burrow counts to determine if animal density could be predicted by the sum of the mountain beaver tunnels counted along these transects.

AGES

I estimated mountain beaver ages by the degree of closure of the distal epiphyseal femoral suture (Pfeiffer 1958). Femurs were removed, defleshed, and air-dried prior to examination. Because all mountain beaver are born during April or May each year, the femoral epiphyseal sutures represent yearly age classes. Three age classes were established as defined by Pfeiffer (1958): juveniles < 1-year-old, yearlings 1- to 2-years-old, and adults > 2-years-old. Pfeiffer (1956) indicated that it might be possible to age male mountain beaver on the basis of baculum length; therefore, this measure supplemented observations of the femoral sutures. Scheffer (1929) and

Voth (1968) aged mountain beaver on the basis of body mass, but Lovejoy and Black (1979) found considerable overlap in body mass among age classes.

I used Kruskal-Wallis tests (Siegel 1956: 184-193) to compare the proportion of animals classified into each age category among stand types for each sex separately and for both sexes combined.

SEX RATIOS

The percent capture of females was compared among stand types using Kruskal-Wallis tests (Siegel 1956: 184-193). This comparison was made for each age class separately and for all age classes combined. Additionally, for each stand type, observed sex ratios were compared with the model of equal proportions of males and females captured (z- tests).

ANIMAL SIZE

Animal size was evaluated by measuring the mass and length of each individual. I recorded animal mass to the nearest 0.1 g and body length (distance from the tip of the snout to the end of the terminal vertebral bone) to the nearest 0.1 cm.

Population categories (age, sex, and stand type) that were significant predictors of mountain beaver mass were determined using 3-way ANOVA (Sokal and Rohlf 1981: 374-

387). Analysis of covariance (Sokal and Rohlf 1981: 509-530) with animal age as the covariate was used to determine whether mass, length, and mass:length of mountain beaver varied among the stand types after accounting for variation due to differences in age composition.

REPRODUCTION

Mountain beaver reproduction is highly seasonal. In Oregon, the testes descend in late December or early January and males remain in reproductive condition through late March (Feldhamer and Rochelle 1982). Females are monestrus and mate in mid-to-late February (Lovejoy and Black 1974, Lovejoy 1972); parturition occurs in late March through early April (Feldhamer and Rochelle 1982). I trapped mountain beaver in March because that is when they were in reproductive condition.

Reproductive status was determined for males and females. I excised the uterus of each female and counted developing embryos or pigmented sites of implantation. Female reproductive condition was recorded as pregnant, lactating, or nulliparous. Uteri of females that have bred are clearly distinguishable from those that have never bred (Pfeiffer 1958, pers. obs.). In no case was an animal found to have previously bred and not show signs of current pregnancy or lactation. Litter sizes were determined when possible and numbers of viable and resorbing embryos were recorded separately.

I assessed the reproductive condition of male animals based on teste size (enlarged versus not enlarged). The distribution of testicular mass was bimodal and the lower peak was comprised of only juvenile males (Fig 1.1). The higher peak was made up of males of all ages. Testicular mass therefore seemed to be a reasonable criterion for reproductive maturity; however, I did not attempt to measure actual spermatogenesis. Reproductively immature males had teste weights ranging from 0.03 to 0.22 g. Reproductively mature males had teste weights ranging from 0.28 to 1.61 g. I used likelihood-ratio tests (G^2) to test the null hypothesis that the probability of an animal being reproductive was the same for all stand types (Agresti 1990: 48-49). Expected frequencies were homogeneous among stand types. Separate tests were conducted for each age class and sex. ANOVA was used to compare litter sizes of reproductive females among stand types and animal age classes.

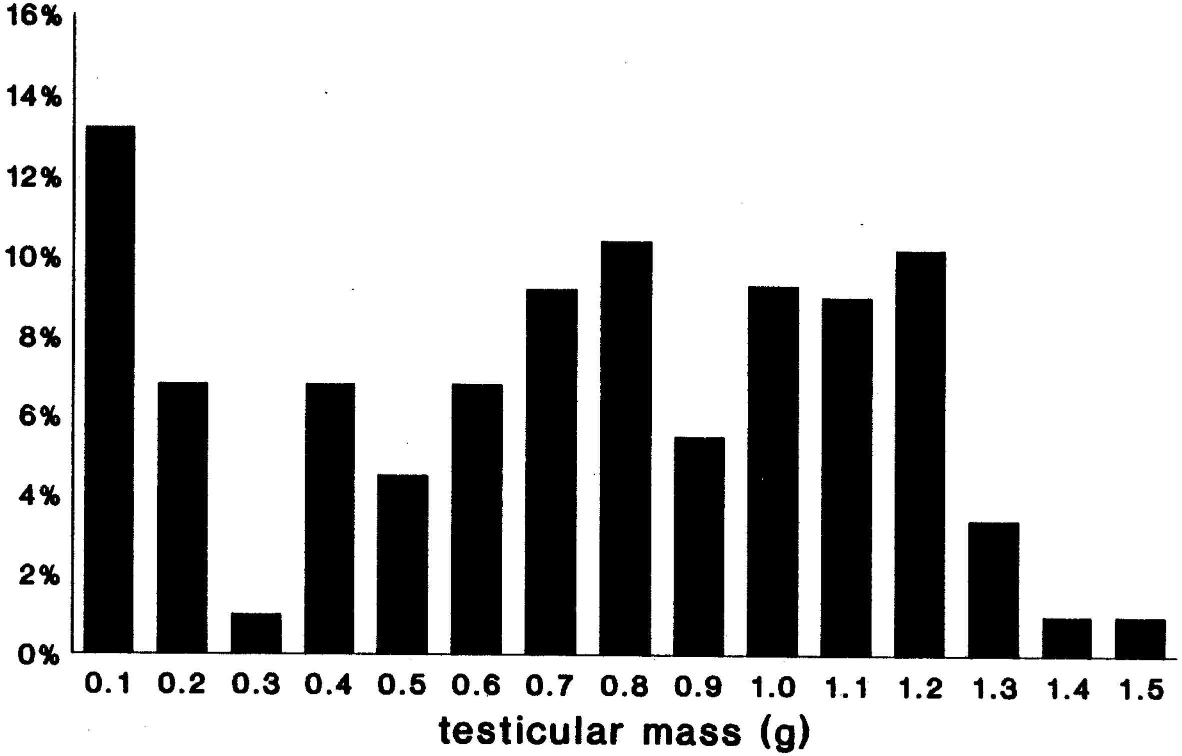

Fig 1.1 Bimodal distribution of mountain beaver testicular mass (N = 139).

RESULTS

SAMPLE SIZES AND DENSITIES

An average of 21.8 (SD = 5.5) animals were trapped in each trapping area, totalling 262 mountain beaver from 36.3 ha. (Table 1.1). The numbers of individuals captured were similar among stand types: 86 from 1-year-old clearcuts, 89 from 4- to 5-year-old clearcuts, and 87 from forest stands. Number of mountain beaver captured declined in a curvilinear fashion, with 75% of all captures occurring within the first 2 trapping days (Fig 1.2). There was no evidence of heterogeneity of capture frequency as a function of sex (X^2 = 1.98, P > 0.7).

Estimated densities ranged from 2.3 to 18.2 animals/ha ($\bar{X}$ = 7.1, SE = 1.2). The highest density occurred in a 4- to 5-year-old clearcut. The lowest density occurred twice; in a forest stand and in a 4- to 5-year-old clearcut. Densities did not differ among stand types (F = 0.38; P = 0.7). Because the trapping area locations were based partially on the presence of mountain beaver sign, this statistical inference is valid only for portions of stands that support mountain beaver populations.

Estimated population densities were significantly predicted by tunnel counts (R^2 = 0.59; P = 0.0003). The regression equation for predicting density based on the sum

Table 1.1 Number of mountain beaver captured and estimated densities (number/ha) in 3 stand types in the Coast Range mountains, Oregon, 1990.

stand type	stand	number trapped	trapping area (ha)	density/ha	predicted density/ha[a]
1-yr-old	3	23	2.5	7.2	10.6
	6	18	2.5	5.6	6.4
	9	30	4.0	6.0	4.5
	12	15	2.5	4.7	4.5
				$\bar{X}$ = 5.9	
				SE = 0.6	
4- to 5-yr-old	1	21	2.0	8.1	16.7
	4	19	2.5	5.9	6.4
	7	32	1.3	18.2	14.8
	10	17	6.0	2.3	2.2
				$\bar{X}$ = 8.1	
				SE = 4.0	
forest	2	17	6.0	2.3	4.1
	5	26	2.0	10.0	8.7
	8	26	2.0	10.0	9.4
	11	18	3.0	4.7	8.1
				$\bar{X}$ = 6.8	
				SE = 2.2	

[a] predicted density/ha = 0.33 + 0.38 x burrow count

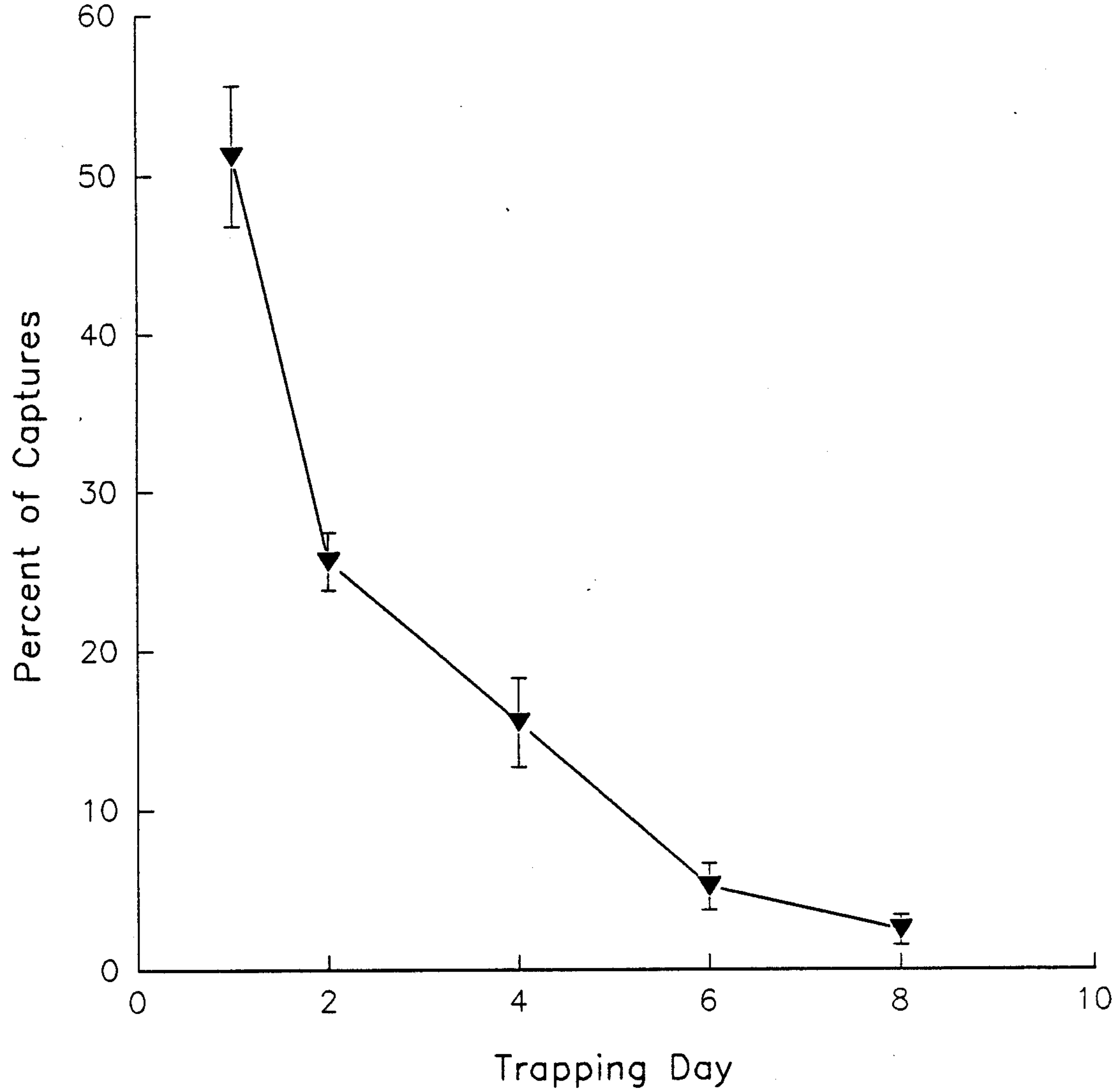

Fig 1.2 Percent of total mountain beaver captures (SE) by trapping day, Coast Range mountains, Oregon, 1990 (N = 262).

of the mountain beaver tunnels counted along 10 50-m transects was:

density = 0.33 + (0.38 x burrow count) animals/ha

I used this equation to calculate predicted mountain beaver densities in each of the trapping areas (Table 1.1).

Ninety-seven individuals (29.5% of all captures) of 9 additional species were trapped (Appendix C). Non-target captures did not decrease appreciably over the course of trapping (Appendix D).

AGES

Age distribution of captured mountain beaver was 86 (33%) juveniles, 93 (35%) yearlings, and 83 (32%) adults. The proportions of juvenile and adult mountain beaver differed among the stand types (Kruskal-Wallis $X^2 = 7.0$, df = 2, $P = 0.03$ (juv.); $X^2 = 8.0$, df = 2, $P = 0.02$ (adult)); the proportion of yearling mountain beaver did not differ among stand types ($X^2 = 1.0$, df = 2, $P = 0.6$). One-year-old clearcuts had fewer adults and more juveniles, and forest stands had more adults and fewer juveniles than expected under the null hypothesis of stand type homogeneity (Fig 1.3).

Examining the sexes separately, 27.7% of the males were classified as juveniles, 34.0% as yearlings, and 38.2% as adults. These percentages did not differ among stand types for any of the age classes (Kruskal-Wallis $X^2 < 2.9$,

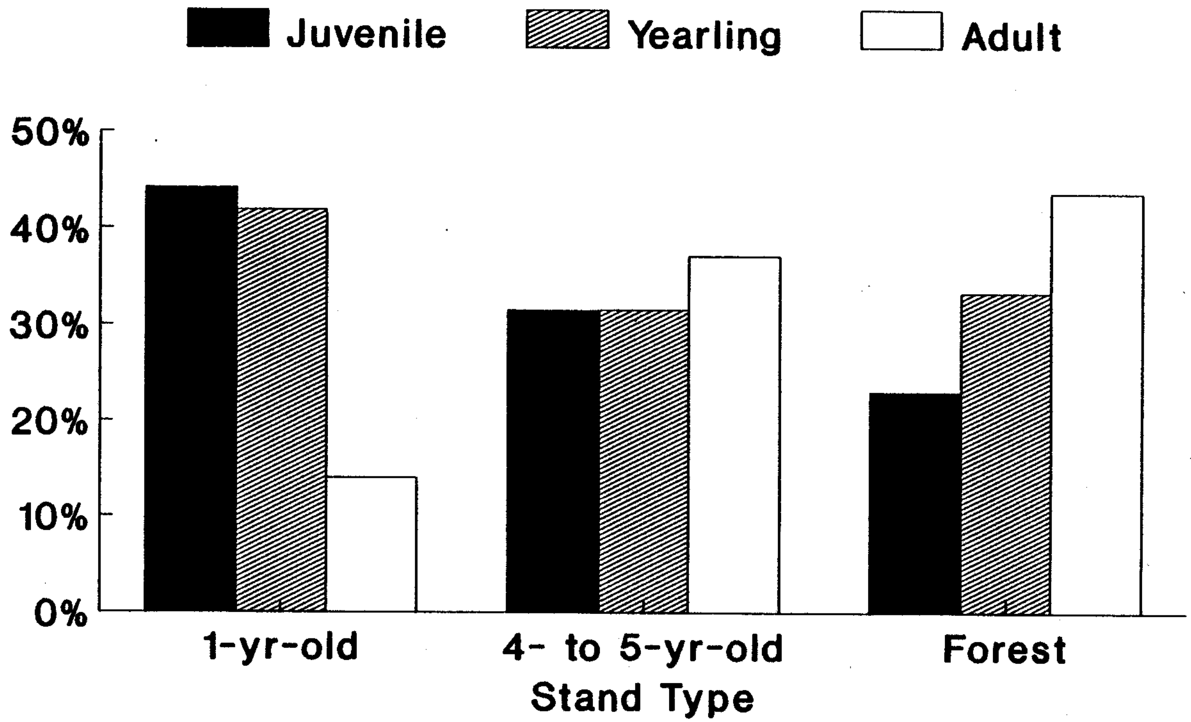

Fig 1.3 Age composition of mountain beaver populations in 3 stand types, Coast Range mountains, Oregon, 1990 (N = 262).

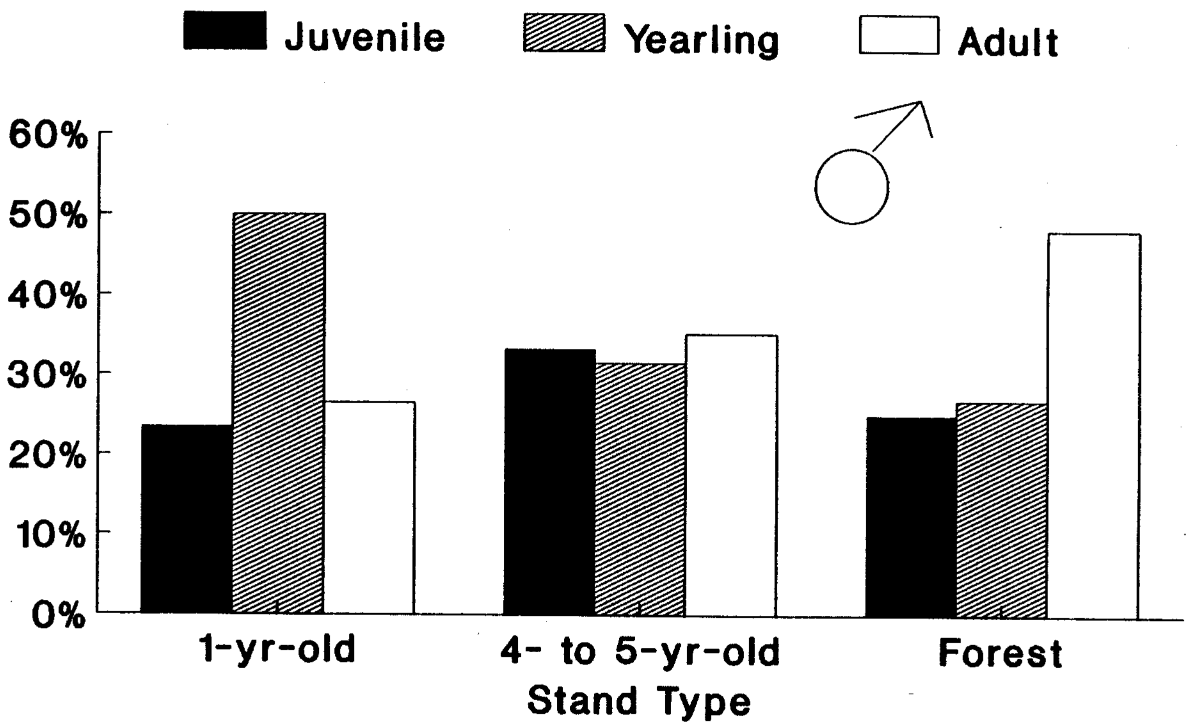

Fig 1.4 Age composition of male mountain beaver in 3 stand types, Coast Range mountains, Oregon, 1990 (N = 142).

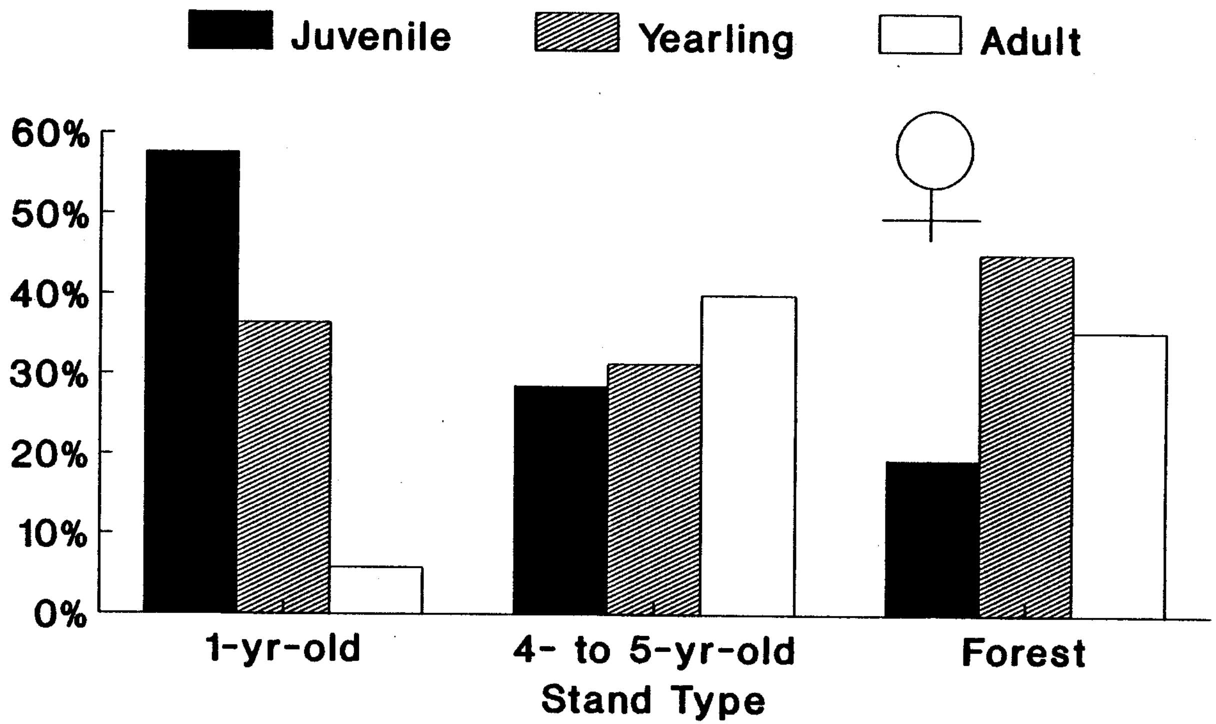

Fig 1.5 Age composition of female mountain beaver in 3 stand types, Coast Range Mountains, Oregon, 1990 (N = 120).

df = 2, $P > 0.2$, 3 cases, Fig 1.4). The proportions of juvenile and adult females differed among the stand types (Kruskal-Wallis $X^2 = 8.6$, df = 2, $P = 0.01$ (juv.); $X^2 = 6.7$, df = 2, $P = 0.04$ (adult), Fig 1.5); the proportion of yearling females did not differ among stand types ($X^2 = 1.3$, df = 2, $P = 0.5$). The differences were largely attributable to 1-year-old clearcuts, which had a preponderance (57.7%) of juvenile and a paucity (5.8%) of adult females.

SEX RATIOS

The proportion of mountain beaver that were female differed among stand types (Kruskal-Wallis $X^2 = 7.5$, df = 2, $P = 0.02$). One-year-old clearcuts had a higher proportion (60.5%) of females than males ($z = 1.94$, $P = 0.06$). Conversely, both 4- to 5-year-old clearcuts and forest stands had higher proportions of males (60.7% and 64.4%, respectively) than expected by chance under the null model of equal sex ratios ($z > 2.1$, $P < 0.05$, both cases, Table 1.2). For juveniles, the proportion that were female differed among stand types (Kruskal-Wallis $X^2 = 7.9$, df = 2, $P = 0.02$). In 1-year-old clearcuts, 79% of the juveniles were female; in 4- to 5-year-old clearcuts, 34% were female; and in forest stands 30% were female. Differences in percent females among stand types were not significant

Table 1.2 Sex ratios of mountain beaver in 3 stand types in the Coast Range mountains, Oregon, 1990.

	Stand Type					
	1-yr-old		4- to 5-yr-old		Forest	
Animal Age Class	N	♀:♂	N	♀:♂	N	♀:♂
Juvenile[a]	38	3.75[b]	29	0.53	20	0.43
Yearling	36	1.10	27	0.69	29	0.93
Adult	12	0.33	33	0.74	38	0.41[b]
Total[a]	86	1.53	89	0.65[b]	87	0.55[b]

[a] proportion female differed among stand types ($P < 0.05$)

[b] Sex ratio different than 1:1 ($P < 0.05$)

for the other two age classes (Kruskal-Wallis $X^2 < 2.7$, $P > 0.3$, both cases).

ANIMAL SIZES

Juvenile, yearling, and adult mountain beaver weighed 674.5 (SE = 7.2), 817.8 (8.3), 885.4 (9.9) g, respectively, and mass increased significantly with age ($F = 161.3$, $P < 0.0001$). There was an additional effect of stand type on body mass ($F = 8.2$, $P < 0.001$); animal mass was lower in the forest stands. Mean mass (±SE, weighted by age class) did not differ between 1-year-old and 4- to 5-year-old clearcuts (809.7 ± 8.5 and 803.3 ± 8.2 g, respectively, $P = 0.6$). Mass of mountain beaver trapped from forest stands (764.8 ± 8.4 g) was lower than mass in either of the other stand types ($P < 0.001$, both cases). There was no difference in body mass between the sexes ($F = 2.17$, $P = 0.14$).

There was a significant interaction between animal age and stand type ($F = 2.7$, $P = 0.03$). Mass of mountain beaver increased more rapidly as a function of age in 4- to 5-year-old clearcuts than in either of the other 2 stand types (Fig 1.6).

Analyses of the other size parameters (length, mass:length) yielded similar results.

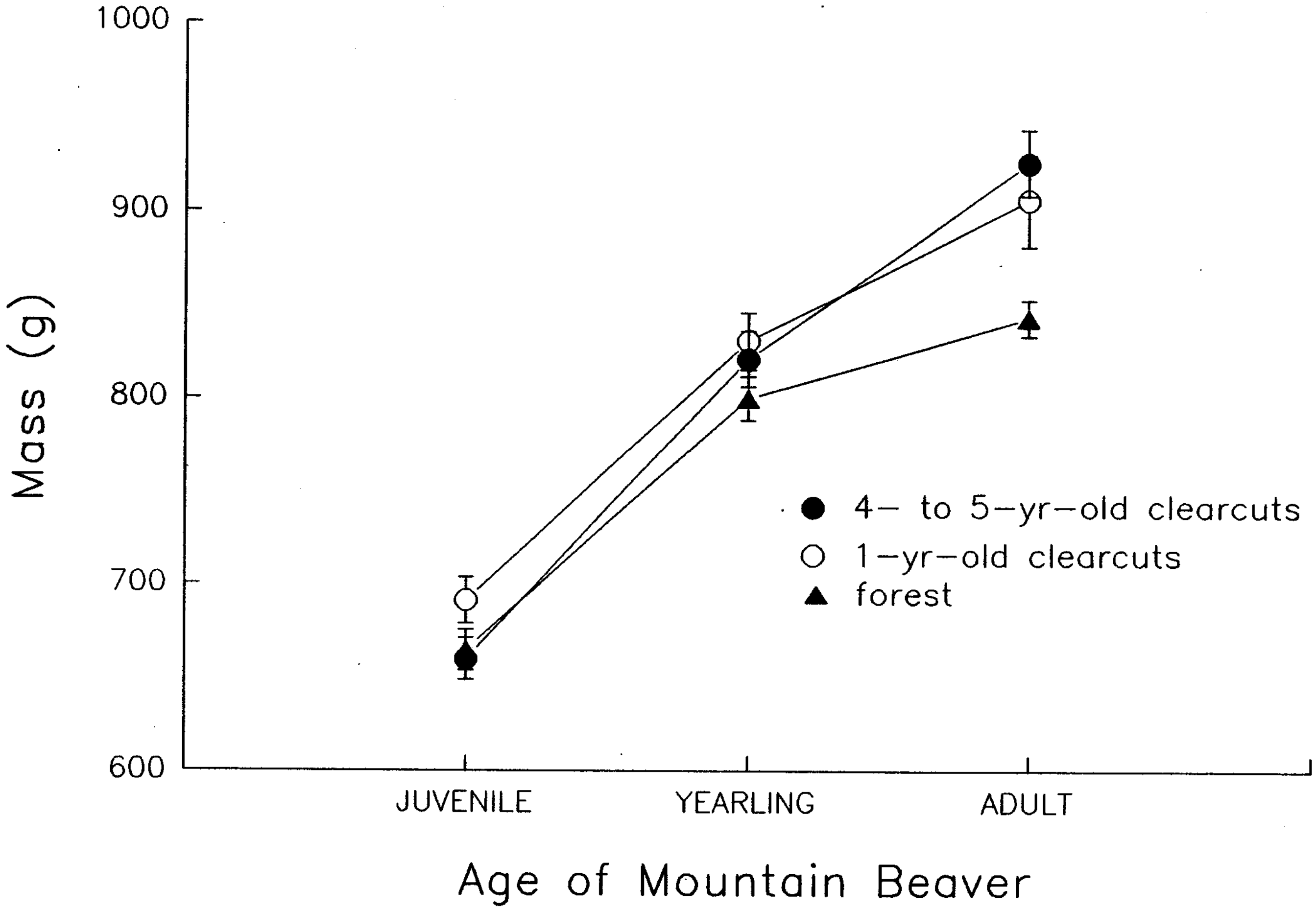

Fig 1.6 Mean mountain beaver mass (SE) in three stand types, Coast Range mountains, Oregon, 1990.

REPRODUCTION

The proportion of females that reproduced varied with animal age. Nineteen of 45 (42%) juvenile females, 40 of 44 (91%) yearling females, and all 28 (100%) adult females were reproductive (pregnant or lactating). The proportion of reproductively active yearling females did not differ among stand types ($G^2 = 3.1$, $P = 0.2$). The proportion of reproducing juvenile females differed among stand types ($G^2 = 7.3$, $P = 0.03$). No juvenile females bred in forest stands, but 50% bred in 1-year-old clearcuts, and 44% bred in 4- to 5-year-old clearcuts.

The proportion of males in reproductive condition also varied among age classes. Eleven of 40 (27.5%) juvenile males were reproductively mature while all 49 (100%) yearling and 55 (100%) adult males were in reproductive condition. Juvenile male reproductive maturity differed among stand types ($G^2 = 7.2$, $P = 0.03$). Most juvenile males in forest stands and 4- to 5-year-old clearcuts (71.4% and 88.9%, respectively) failed to show signs of reproductive maturity, while most (62.5%) juvenile males in 1-year-old clearcuts were in reproductive condition.

Among females that bred, mean litter size increased with age ($F = 7.08$, $P < 0.01$, Table 1.3). Differences were significant only between juvenile and adult females ($P < 0.05$). Litter sizes did not differ among stand types for all ages combined ($F = 2.3$, $P > 0.1$) or within yearling and adult age classes ($P > 0.15$, both cases). There were no reproductively active juvenile females in forest stands, so I compared litter sizes of juvenile females between the other 2 stand types. Litter sizes were greater in 1-year-old clearcuts (2.6 ± 0.3 SE) than 4- to 5-year-old clearcuts (1.2 ± 0.3 SE; $P < 0.01$).

Table 1.3: Mountain beaver litter sizes by animal age and stand type, Coast Range mountains, Oregon, 1990.

	Stand Type											
	1-year-old			4- to 5-year-old			Forest			All stands		
Animal age	X	SE	N	X	SE	N	X	SE	N	X	SE	N
Juvenile	2.57	0.25	14	1.25	0.25	4	N/A*			2.28	0.24	18
Yearling	3.07	0.29	14	2.70	0.34	10	2.62	0.27	13	2.81	0.17	37
Adult	3.33	0.67	3	3.54	0.29	13	2.73	0.27	11	3.18	0.20	27
All	2.90	0.18	31	2.89	0.24	27	2.67	0.19	24	2.82	0.12	82

* No juvenile females reproduced in forest stands.

DISCUSSION

I used existing forest management practices to create a semi-experimental system in which to assess population attributes of mountain beaver that colonize "dispersal sinks". Dispersal is often risky and chances of survival may be low (Jones 1989); evolution of this behavior requires a successful disperser to accrue more benefit from dispersing than from not dispersing (Dobson 1982). The nature of these benefits may involve an escape from inbreeding depression (Greenwood 1980), or immediate somatic or reproductive advantages derived from avoidance of intraspecific competition or gained from better habitat (Waser 1985, Moore and Ali 1984).

Animals trapped from 1-year-old clearcuts were immigrants and I assumed that the composition of these populations reflected the population composition of successfully dispersing mountain beaver in general. This may be a faulty assumption in cases where resident populations are not completely removed (Verts and Carraway 1986), or where dispersal of unmanipulated populations into unoccupied habitat is an anomalous occurrence (Dobson 1981). Forest management in western Oregon has created large areas of potential mountain beaver dispersal sinks similar to those of the present study, therefore these results are probably analogous to many of the dispersal patterns that occur within this harvesting regime. Because enhanced fitness may not be immediately manifested, I also sampled mountain beaver populations 4-5 years after creation of the initial vacant habitat. This allowed comparison of the success of the original colonists and their offspring with that of reference forest stands that supported stable mountain beaver populations.

Mountain beaver rapidly colonized vacant habitat created by previous trapping efforts. Within 1 year of removal trapping, mountain beaver densities were statistically indistinguishable from stands that were never trapped. Densities varied widely among stands, but not as a function of stand type. If mountain beaver densities reflected habitat suitability, habitat selection was based on stand characteristics other than clearcut age (see Chapter 2). Mountain beaver tolerated very high densities (18.2 animals/ha on 1 site) implying that habitat suitability rather than social factors limited observed densities.

Animals that inhabit early seral habitats typically have short lives, high reproductive rates, and the capability to disperse widely. Although mountain beaver primarily select successional habitat, they are long-lived (Lovejoy and Black 1979) and have low yearly productivity (Maser et al. 1981). Despite these life history attributes, they are able to rapidly colonize vacant habitat. In Oregon, when mountain beaver are found in closed-canopy forests, their home ranges typically include canopy openings or "gaps" (Neal and Borrecco 1981). Effective colonization of these small openings has probably been more important, evolutionarily, than colonization of larger openings resulting from extremely rare catastrophic events such as fire. Gap formation may have been unpredictable compared to the life expectancy and probable dispersal distance of mountain beaver (Spies et al. 1990). Production of surviving offspring would not be expected to exceed production of vacant, accessible, suitable habit. Because habitat suitable for dispersing young was, historically, patchily distributed in space and time, the probability of propagules finding and colonizing such areas had high inter-annual variability. Given this scenario, it is not surprising that mountain beaver evolved to maximize their lifetime reproductive success with long lives and conservative annual reproduction.

Mountain beaver colonization rates varied by sex and age. Sex ratios in 4- to 5-year-old clearcuts and forest stands were consistent with previously reported values that indicate mountain beaver typically have male biased sex ratios (Lovejoy and Black 1979, Voth 1968, Hubbard 1922). Immigrants (individuals trapped from 1-year-old clearcuts) were predominantly young females. Sex-related differences in colonization were a statistical rather than a categorical phenomenon. Both sexes were represented in the population of immigrants, but females colonized clearcuts at greater rates than did males.

There has been some discussion as to whether sex ratio biases observed in trapping studies reflect true population parameters (Buskirk and Lindstedt 1989, Hurley 1987). In trapping studies unequal sex ratios may be a product of unequal capture probabilities (Buskirk and Lindstedt 1989, Rusch and Reeder 1978). If females had lower capture probabilities I would expect their capture frequency to have declined less rapidly assuming all animals were eventually captured. No difference between male and female trap vulnerability was detected and sex ratios varied between a preponderance of males to an excess of females. The observed ratios, therefore, seemed to accurately reflect the true sex ratios.

The pattern of female-biased colonization found in mountain beaver is somewhat anomalous among mammals. Males are the primary dispersers in most mammalian species (Greenwood 1980, Dobson 1982). A few instances of female biased dispersal are known in mammals (e.g. Jones 1988, Howard 1986, Pusey 1980) but causal explanations of this phenomenon are limited.

Female colonists were younger than females trapped from the other stand types. Colonizing females were predominantly juveniles (57.7%) and almost all (94.4%) were

< 2 years old. Juveniles accounted for less than 34% of the females in each of the other stand types. The ages of male colonists were not significantly different from non-colonists; males that successfully dispersed seemed to do so irrespective of age. The age composition of mountain beaver in 4- to 5-year-old clearcuts represented a transition between the initially young colonizing population and the older, stable, untrapped population (Fig. 1.2).

Natural selection may favor juvenile dispersal for many reasons. Immatures of 1 sex are typically the primary dispersers (Greenwood 1983, 1980). When habitat is saturated, it seems logical that juveniles, who are frequently subordinate, might be forced to vacate their natal home ranges. Philopatric young may compete directly with their parents for food, dens, or reproductive opportunities (Waser and Jones 1983). Because young animals are frequently inferior competitors, they may maximize their own success by dispersing to areas in which competition is less intense (Murray 1967).

Colonizing mountain beaver obtained somatic and reproductive advantages over their non-dispersing conspecifics. Individuals that colonized 1-year-old clearcuts and those that inhabited 4- to 5-year-old-clearcuts were heavier than those from untrapped populations. Sub-adult mountain beaver in 4- to 5-year-old clearcuts seemed to have had greater growth rates than those in forest stands. I found no sex-related differences in mass or presumed growth rates in any of the stand types, although other researchers have found such differences (Lovejoy and Black 1974); the somatic benefits obtained by colonists were not different between males and females.

In addition to increased size, juvenile colonists derived reproductive benefits from dispersal. Prior to this study, juvenile females were thought to be non-reproductive (Feldhamer and Rochelle 1982, Lovejoy and Black 1979, Pfeiffer 1958). Similarly, I found no reproductive juvenile females in untrapped stands. In 1-year-old and 4- to 5-year-old clearcuts, however, 50.0% and 44.4%, respectively, of juvenile females became pregnant. Among juvenile females that conceived, those in 1-year-old clearcuts had larger litter sizes than those in 4- to 5-year-old clearcuts. A significant reproductive advantage was accrued to juvenile females that successfully immigrated into under-occupied habitat and those recruited into more productive successional habitat.

Yearling males had a higher probability of reaching sexual maturity in 1-year-old clearcuts than in either of the other 2 stand types. Onset of reproductive maturity may be tied to the chances of actually reproducing or may simply be a product of somatic condition. Because of female-biased sex ratios, males in 1-year-old clearcuts had greater average per capita reproduction relative to males in stands with male-biased sex ratios. This may translate into increased reproductive chances for younger males if social subordination ordinarily limits their ability to successfully compete for mating opportunities. Male gonadal condition may not be indicative of fitness benefits, however, because juvenile males are unlikely to breed in polygamous species when adult males are present. Nevertheless, mountain beaver seem to be physiologically capable of breeding as juveniles.

Which sex disperses more frequently has been hypothesized to be a function of the species' mating system (Greenwood 1980) or to result from sex-specific differences in competition for habitat resources or breeding opportunities (Moore and Ali 1984). Data on the social structure and mating system of mountain beaver are insufficient to attempt an explanation of apparent female-biased dispersal based on these parameters. The reproductive and somatic benefits of successful dispersal to juvenile females are demonstrably high while increased proportions of reproductively mature juvenile males are of dubious significance. Colonization of vacant suitable habitat may be female-biased simply because the benefit-to-cost ratio of dispersal is higher for females than for males.

The advantages mountain beaver derived from dispersal into newly created successional habitat were measurable and probably not unique to managed forest ecosystems. Both male and female colonizers obtained somatic benefits from their movement, and females also benefitted reproductively. These benefits provide an adequate causal explanation of dispersal in this species and may also explain the observed sex ratio bias among dispersers. Reproductive and somatic advantages realized by dispersers may result from inhabiting higher quality habitat or from reduction of intra-specific competition.

MANAGEMENT IMPLICATIONS

On the western slope of Oregon's Coast Range mountains, mountain beaver populations rapidly recolonize clearcuts from which they have been removed. This is consistent with forest managers' reports of persistent mountain beaver damage to Douglas-fir in spite of extensive trapping efforts. Additionally, the reproductive potential of the colonizing populations is high. Immigrants to the clearcuts are predominantly females with high rates of potential life-time fecundity. Many breed during their first year of life; essentially all are likely to breed the following year.

Mountain beaver are found predominantly in early successional habitat. Current forest management practices create large areas of such habitat each year. Given vast quantities of suitable habitat and a rapidly dispersing organism, it seems unlikely that mountain beaver damage will be effectively controlled through physically removing the animals. Habitat manipulations (Chapter 2) that either discourage colonization or that provide alternate food sources will probably provide the most efficient long-term damage control.

CHAPTER 2

HABITAT SELECTION OF RECOLONIZING MOUNTAIN BEAVER

METHODS

To assess the distribution of mountain beaver in each clearcut, active burrows were counted along transects to determine if, following removal trapping, recolonization began around the edges and progressed inward at some measurable rate.

Mountain beaver population densities were predicted by tunnel counts along 50-m transects (Chapter 1, p. 13); I therefore used this technique to assess mountain beaver distribution throughout each clearcut. Eight 50 x 1-m belt transects parallel to the edge of each clearcut were surveyed in December 1989 at the following distances from the edge: 10, 25, 50, 75, and 100 m. To accommodate differences in clearcut size and shape, additional sets of 8 transects were walked every 50 m until the center of the clearcut was reached. Each concentric ring of 8 transects was approximately equally spaced around the clearcut, beginning with a randomly selected point. Active mountain beaver burrows and tunnels within each transect were counted. I pooled all transect burrow counts and regressed them as a function of distance from clearcut edge.

The 2 clearcut stand types were used to identify habitat variables selected by colonizing mountain beaver. Within each clearcut, I collected habitat information on plots that were colonized and plots that were not colonized by mountain beaver. Habitat sampling plots were selected by establishing a 50 x 50-m grid system on each clearcut and systematically selecting grid intersections (beginning with a randomly selected intersection) as the center of each potential non-colonized plot. I visually inspected 0.05-ha (12.7-m radius) circular plots (CPs) centered on the selected grid intersection for the presence of mountain beaver sign including burrows, tunnels, or clipped vegetation. Habitat plots were sampled as non-colonized when there was no evidence of mountain beaver activity in the entire plot. Selected grid intersections with evidence of use by mountain beaver within the CP were not included in these analyses. Colonized habitat sampling plots were centered on the burrow system closest to each grid intersection, with the additional restriction that the two CPs be non-overlapping. When there were no mountain beaver burrows within 100-m of a grid intersection, only a non-colonized plot was sampled. Colonized plots were centered on the presumed nest site or area of highest use. A minimum of 10 colonized plots were sampled on each clearcut.

I used 0.05-ha (12.7-m radius) circular plots to sample physical, vegetational, and dead wood habitat characteristics of colonized and non-colonized plots. Dead wood habitat components (number of uprooted stumps, number of small stumps, number of large stumps, and coarse woody debris volume) were recorded by decay class (class 1: > 95% bark cover, class 2: < 50% bark cover, class 3 < 5% bark cover).

I visually estimated percent cover of under-story plants (sword fern, bracken fern (*Pteridium aquilinum*), forbs, other shrubs, grasses, blackberry (*Rubus* spp.), forage plants (total % cover of sword fern, bracken fern, forbs, and shrubs)) and ground cover (woody debris < 25 cm diameter, organic litter, bare ground) in 12 1-m^2 quadrats. These were placed 4, 7, and 12 m from the plot center in each cardinal direction. The average of the 12 quadrats/plot was used to characterize the plot.

Physical habitat features were slope (%), aspect, whether or not the plot was in a drainage, and two soil measures. Plots in drainages were < 100-m upslope from a perennial water/moisture source. Distance from water was originally measured as a continuous variable and later made categorical to facilitate data interpretation. I measured soil characteristics by taking 3 core-samples 1 m from the plot center. Core samples were 2 to 10 cm deep and were taken by a fixed-weight driven soil core sampler after removing all litter and living vegetation. Bulk density was estimated as the average dry-weight-density (g/cm^3) of the soil core samples after oven drying at 45°C for 48 hr. Soil penetrability was estimated as the average number of fixed-weight blows required to cut each core sample. This was treated as a measure of soil hardness (Jamison and Weaver 1952). Samples were taken only in soils undisturbed by mountain beaver activities. Habitat features were measured June-September 1989 except for soil samples which were taken in August 1990.

Most continuous habitat variables were not normally distributed; the categorical variables (in/out of drainage and aspect) could not be normally distributed. Many of the continuous variables were bimodal or highly skewed with one peak occurring at 0. They were therefore non-normal even after square-root and logarithmic transformations (Shapiro-Wilk statistic $P < 0.05$, Zar 1984: 95-96). I used Chi-square procedures to determine if colonized and non-colonized plots differed from each other with respect to the two categorical variables. Nonparametric 2-factor ANOVAs (Zar 1984: 219-222) were used to determine differences in continuous habitat variables based on the factors stand type and colonized/non-colonized.

I used stepwise logistic regression (SLR) to identify variables that could predict the probability of an 0.05-ha plot being colonized by mountain beaver. SLR is a multivariate discrimination procedure that performs well with categorical data (Press and Wilson 1978) and is appropriate even when the distribution of data is non-normal (Anderson 1972). Candidates for entry into the logistic function included all habitat variables that differed significantly between colonized and non-colonized plots ($P < 0.01$) and an indicator variable for clearcut stand type. There were a total of 17 possible habitat variables and 163 habitat plots. Prior probabilities of group membership were equal to the proportion of observations in each group. Inclusion of variables into the logistic function was allowed at $P < 0.05$ but only variables with $P < 0.01$ were retained. The classification error rate was calculated using a jackknife procedure (Morrison 1976). The jackknife procedure classifies each observation using the logistic function developed from all observations except for the one being classified and yields a less biased assessment of model fit. The relative importance of variables included in the logistic function was determined by taking the ratio of each coefficient to its standard error to standardize coefficient size.

RESULTS

The number of mountain beaver burrows counted along each 50-m transect was highly variable and not predicted by the distance of the transect from the clearcut edge (R^2 = 0.01; *P* = 0.3, Fig 2.1).

Colonized habitat sampling plots (N = 84) differed (*P* < 0.01) from non-colonized plots (N = 79) with respect to 14 of 23 continuous variables (Table 2.1), and both categorical variables (Fig 2.2, 2.3). On average, plots with mountain beaver had more sword fern, shrubs, forbs, wood, and forage plant cover and less grass than plots without mountain beaver. Colonized plots were more likely to be in drainages, and in areas with a northerly aspect. They had a greater volume of large woody debris, more uprooted and big-old stumps, steeper slopes, and softer, less dense soils than non-colonized plots.

Percent cover of small wood and forage plants differed most strikingly between colonized and non-colonized plots. The logistic regression model included these 2 variables and abundance of uprooted stumps, soil penetrability, total volume of large woody debris and whether the plot was in a drainage. Clearcut stand type was also included in the model (Table 2.2). Sixteen of 23 continuous habitat variables differed between 1-year-old and 4- to 5-year-old

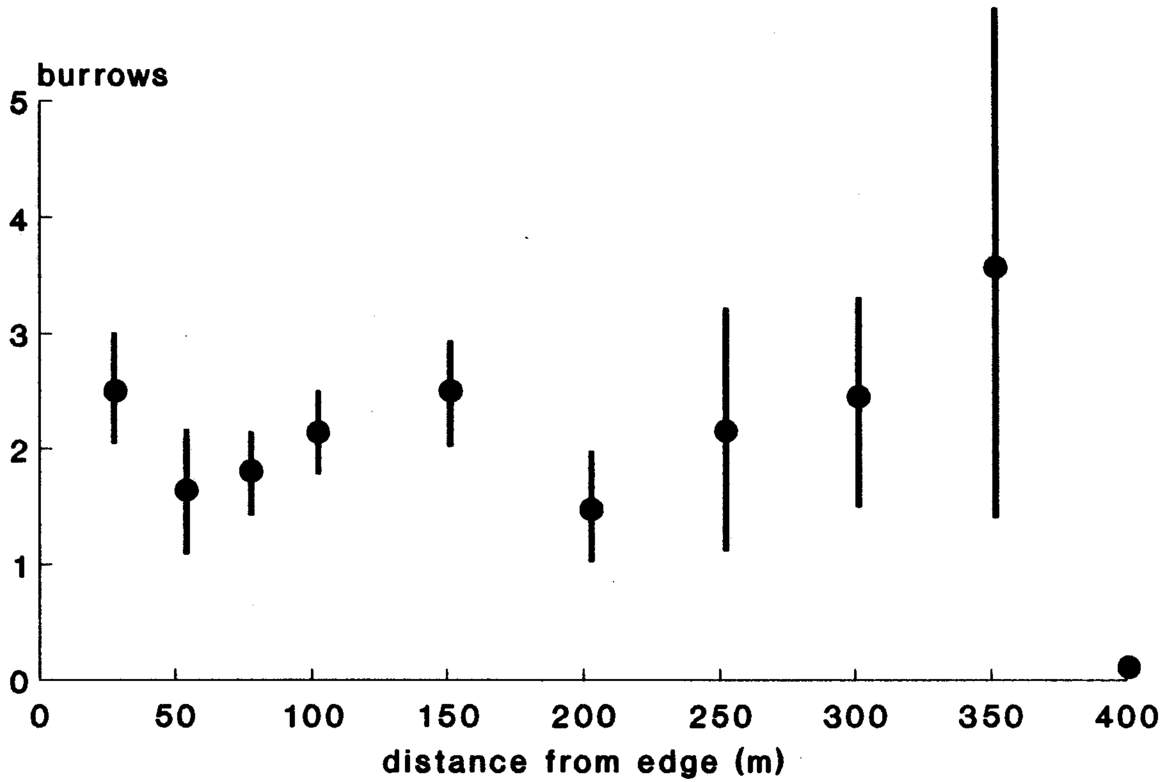

Fig 2.1 Number of Mountain beaver burrows as a function of distance from clearcut edge, Coast Range mountains, Oregon, 1989.

Table 2.1 Mean (SE) values for 23 habitat variables on plots colonized (N = 84) versus not colonized (N = 79) by mountain beaver in the Coast Range mountains, Oregon, 1989-90. Significant differences between colonized and non-colonized plots are denoted by an asterisk. Significant differences between clearcut types are denoted by a T ($P < 0.01$).

variable	1-year-old clearcuts				4- to 5-year-old clearcuts	
	used (N = 39)	not used (N = 41)			used (N = 45)	not used (N = 38)
uprooted stumps (#/plot)	1.9 (0.4)	0.6 (0.1)	*	T	1.2 (0.3)	0.1 (0.0)
new[a] small[b] stumps (#/plot)	2.9 (0.4)	3.7 (0.6)			4.3 (0.5)	4.1 (0.5)
old[c] small stumps (#/plot)	0.2 (0.1)	0.2 (0.1)		T	1.2 (0.2)	0.6 (0.2)
new big[d] stumps (#/plot)	2.7 (0.4)	3.3 (0.4)		T	1.3 (0.2)	1.5 (0.3)
old big stumps (#/plot)	0.8 (0.1)	0.7 (0.1)	*		1.8 (0.2)	0.6 (0.2)
total stumps (#/plot)	8.4 (0.6)	8.5 (0.7)			9.8 (0.7)	6.9 (0.7)
slope (%)	54.1 (2.6)	36.5 (3.6)	*	T	34.3 (2.4)	24.2 (3.3)
shrubs (% cover)	9.8 (1.6)	5.9 (1.3)	*		10.0 (1.6)	7.1 (1.9)
sword fern (% cover)	7.9 (0.9)	4.8 (0.8)	*	T	5.9 (1.3)	2.3 (0.6)
bracken fern (% cover)	0.8 (0.4)	2.1 (1.0)		T	9.3 (1.4)	4.6 (1.1)
grasses (% cover)	3.0 (0.9)	9.7 (2.9)	*	T	17.7 (1.8)	27.7 (2.6)
forbs (% cover)	22.2 (2.2)	15.1 (1.6)	*		21.0 (1.6)	20.7 (2.8)
Rubus spp. (% cover)	0.5 (0.2)	1.9 (0.6)		T	18.4 (2.9)	20.3 (3.4)
wood < 25 cm diam. (% cover)	27.7 (1.8)	17.4 (1.4)	*	T	10.5 (1.2)	4.3 (0.5)
bare ground (% cover)	13.4 (1.8)	19.9 (2.3)		T	3.1 (0.4)	1.9 (0.7)
organic litter (% cover)	17.0 (1.1)	21.7 (1.8)		T	9.7 (0.8)	11.4 (1.1)
forage plants[e]	40.7 (2.6)	27.8 (2.1)	*		46.2 (2.8)	34.7 (3.6)
woody debris 1[f] (m^3/plot)	0.91 (0.24)	0.43 (0.09)	*	T	0.24 (0.08)	0.05 (0.02)
woody debris 2[g] (m^3/plot)	1.74 (0.32)	1.10 (0.22)		T	0.86 (0.17)	0.48 (0.15)
woody debris 3[h] (m^3/plot)	3.47 (0.57)	1.47 (0.31)	*		2.77 (0.36)	0.77 (0.33)
total woody debris (m^3/plot)	6.12 (0.72)	3.00 (0.46)	*	T	3.82 (0.40)	1.30 (0.36)
soil bulk density (g/cm^3)	4.96 (0.13)	5.25 (0.14)	*	T	4.23 (0.15)	4.87 (0.15)
soil penetrability	14.9 (1.4)	25.4 (3.7)	*	T	15.9 (1.4)	40.0 (3.7)

Table 2.1 (continued)

a: decay class 1 or 2
b: < 50-cm diameter
c: decay class 3
d: > 50-cm diameter
e: total % cover of swordfern, bracken fern, forbs, shrubs
f: volume of downed wood > 25 cm diameter decay class 1
g: volume of downed wood > 25 cm diameter decay class 2
h: volume of downed wood > 25 cm diameter decay class 3

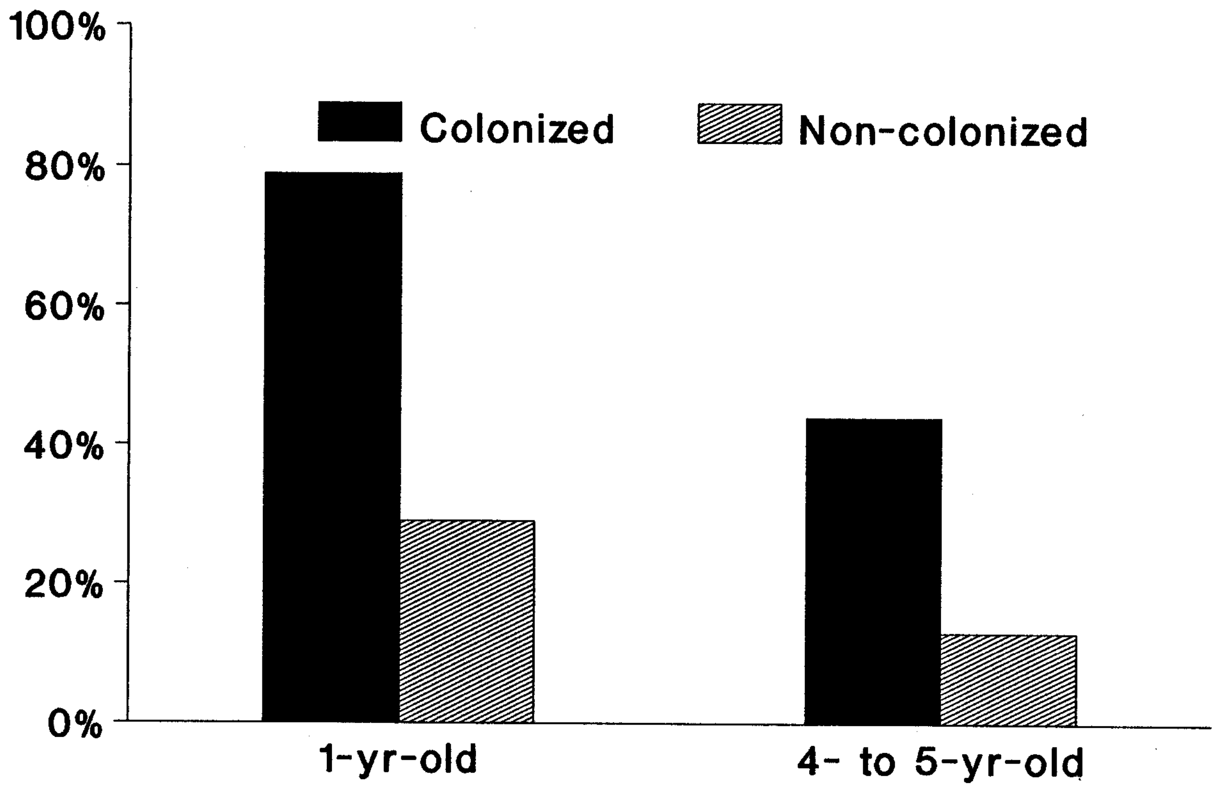

Fig 2.2 Percent of colonized and non-colonized plots in drainages (< 100 m from water), Coast Range mountains, Oregon, 1989.

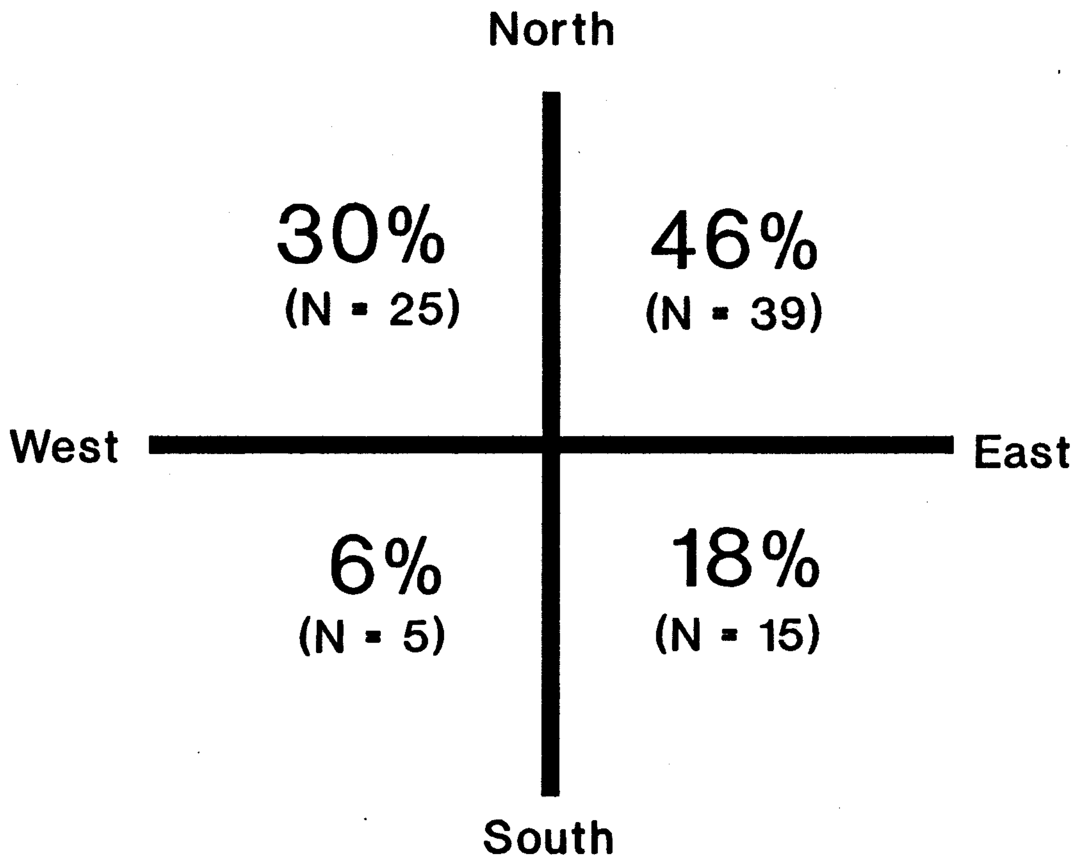

Fig 2.3: Proportion of colonized plots (N = 84) with each of 4 aspects. Non-colonized plots were randomly located with respect to aspect.

Table 2.2 Statistics for habitat variables included in the logistic function predicting mountain beaver recolonization, Coast Range Mountains, Oregon, 1989-90.

variable	coefficient	ratio[a]
intercept	-10.532	......
clearcut type	6.542	1.809
uprooted stumps (#/plot)	0.970	0.885
drainage	3.053	0.833
wood < 25 cm diameter (% cover)	0.221	1.451
soil penetrability[b]	-1.725	-0.683
forage plants[c]	0.930	0.846
total woody debris (m^3/plot)	0.331	0.652

a: ratio of coefficient to its SE.
b: variable was natural log transformed.
c: variable was square root transformed.

clearcuts (Table 2.1); these differences were accounted for by the inclusion of the variable clearcut type.

The logistic function correctly classified 85% of all observations based on a jackknife procedure. Error rates were approximately 15% for both colonized and non-colonized plots. The logistic function performed equally well for the 2 clearcut types.

DISCUSSION

Mountain beaver rapidly recolonized vacant habitat created by trapping. They colonized clearcuts without respect to distance from edge, at least for the size of clearcuts in this study. When mountain beaver were removed from the clearcuts prior to this study, a border area of 100-m was also trapped. Up to 450 m clearly represents no barrier to dispersal over 1 year's time. I suggest that much larger distances may in fact be traveled in search of suitable habitat. Many 1-year-old clearcuts supported population densities in excess of any of the surrounding stands and clearcuts were frequently situated such that only 1 or 2 adjacent stands supported mountain beavers (Hacker, unpublished data). Specific habitat features rather than geographic proximity seemed to determine portions of clearcuts colonized by mountain beaver.

Percent cover of small (< 25 cm diameter) woody debris was the most important microhabitat feature related to colonization by mountain beaver; coarse woody debris volume, and the number of uprooted stumps were also important habitat features selected by colonists. Several researchers had previously made reference to mountain beaver selecting habitat with logging slash (Russell et al. 1989, Neal and Borrecco 1981, Martin 1971) and large woody debris or uprooted stumps (Martin 1971). Mountain beaver nest sites were frequently located under logs, uprooted stumps, or slash accumulations. Their burrows radiated from the activity center utilizing similar structural habitat features. These woody components may provide stability to their unstable and shallow burrows or they may provide a measure of protection from excavation by coyotes (*Canis latrans*) and bobcats (*Felis rufus*), their major predators (Maser et al. 1981).

Mountain beaver colonization was associated with soft, penetrable soils. Fossorial animals certainly affect the soils in which they are found; however, because sampling did not occur in soils with evidence of mountain beaver disturbance, this habitat attribute was probably not caused by the presence of the animals. Softer soils may lend themselves to more efficient burrowing, possibly important to animals that construct extensive tunnel networks (Rhodes and Richmond 1985). Moreover, because soil penetrability is related to soil porosity (Jamison and Weaver 1952), these soils promote water drainage, thus helping to minimize burrow flooding. Adequate soil drainage is thought to be an important feature of mountain beaver habitat throughout their geographic range (Beier 1989, Martin 1971).

Mountain beaver probably selected drainages because they were associated with moist climatic regimes, access to water, and well-drained soils. Mountain beaver are restricted to moist habitats because their kidneys are primitive and unable to efficiently concentrate urine; they require succulent vegetation or surface water daily (Schmidt-Nielsen and Pfeiffer 1970, Nungesser and Pfeiffer 1965). Drainages frequently had little ground-level incident radiation because of topographic and vegetational attributes that encouraged shading. Mountain beaver were more likely to colonize slopes with a northerly aspect, supporting the notion that moist microclimate and the vegetational and/or soil characteristics associated with them are selected as habitat. Drainages were also highly correlated with slope ($r = 0.50$, $P = 0.0001$). Slope may be important in promoting water drainage and in keeping burrows free from standing water (Beier 1989).

Several vegetational variables differed between colonized and non-colonized sites, however only percent cover of forage plants contributed to the logistic function. Various species of shrubs, sword fern, and forbs were the common types of vegetation piled at burrow entrances; bracken fern was also included in the habitat variable "forage plants" because it was purported to be an important mountain beaver food item (Voth 1968). In northern California mountain beaver selected areas that were high in willow (*Salix* spp.), alder (*Alnus* spp.), and fir (*Abies* spp.), suggesting that mountain beaver use succulent vegetation but that the species composition can vary (Beier 1989). My data support this conclusion in western Oregon and suggest that mountain beaver require structural wood and soil features conducive to burrow stability, moist microclimates, and conditions that promote adequate soil drainage. Their food requirements seem to involve quantity rather than specific species, but must include access to evergreen winter food sources such as swordfern and salal.

MANAGEMENT IMPLICATIONS

Clearcuts in the Oregon Coast Range mountains are susceptible to mountain beaver recolonization after direct control measures. This finding is consistent with forest managers' reports of persistent mountain beaver damage to Douglas-fir despite extensive trapping efforts. Mountain beaver colonize moist areas with plentiful wood debris and lush vegetation. Removing populations from 100-m border areas does not deter recolonization. The habitat features included in the logistic model may be useful in predicting areas likely to support populations of mountain beaver (Shugart 1981). Direct control measures can be focused on these areas, or foresters can adopt habitat management strategies aimed at reducing damage either in place of or in addition to trapping efforts.

There are at least 2 approaches to habitat management. Manipulations can reduce habitat suitability for mountain beaver resulting in a reduction in the number of colonists, or provide alternate food sources to minimize tree damage without reducing colonization. Mountain beaver carrying capacity may be reduced by avoiding the creation of downed wood accumulations during tree harvest. In particular, such accumulation should be avoided in conjunction with geographic features that encourage recolonization by mountain beaver. Such features include drainages, northerly aspects, or steep slopes. Recolonization is most likely in areas with greater amounts of small (< 25 cm diameter) woody debris. To avoid such accumulations, managers should ensure that the entire clearcut is broadcast burned. Piling logging debris should be avoided because slash piles are particularly prone to supporting mountain beaver. Moreover, yarding machinery creates uprooted stumps, another habitat feature selected by colonizing mountain beaver. Depression of animal numbers through long-term forage reduction may be impractical in the Oregon Coast Range mountains. Reducing forage availability by setting succession back to an earlier stage would have limited success; in this study 1-year-old clearcuts that were treated with herbicides already supported dense mountain beaver populations. Mountain beaver are opportunistic feeders and thrive at various stages of vegetational succession. Grasses were the only plants that were negatively related to mountain beaver recolonization, probably because % cover of grass was negatively associated with % cover of forage plants. The possibility of reducing mountain beaver recolonization by seeding clearcuts with grasses may be a worthwhile avenue for further research.

Habitat manipulations aimed at reducing damage without affecting animal numbers may have merit. Conifers are not a preferred food source but are consumed when availability of alternate foods is limited, such as during the winter (Voth 1968) and around the time of canopy closure (Neal and Borrecco 1981). Management strategies that emphasize alternate winter food sources may reduce damage to conifers. Efforts to retain sword fern and salal should be made in stands that support these plant species. Low intensity burns will remove small woody debris without destroying the root systems of these forage plants. Seeding forbs or retaining deciduous shrubs in clearcuts would probably not reduce damage because these plants would not be available for consumption during the winter.

Habitat manipulations that provide alternate food sources for mountain beaver may avoid problems associated with reducing habitat suitability by removing coarse woody debris. Increased browsing by deer and elk may result from the removal of woody debris (Swanson 1970, Grisez 1960). Decaying wood is important to many forest species and provides nutrients essential to soil productivity. Forest ecosystems are extremely complex and their health and community structure should be considered in any single species management plan.

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APPENDICES

Appendix A. Location and characteristics of mountain beaver study areas, Coast Range mountains, Oregon, 1989.

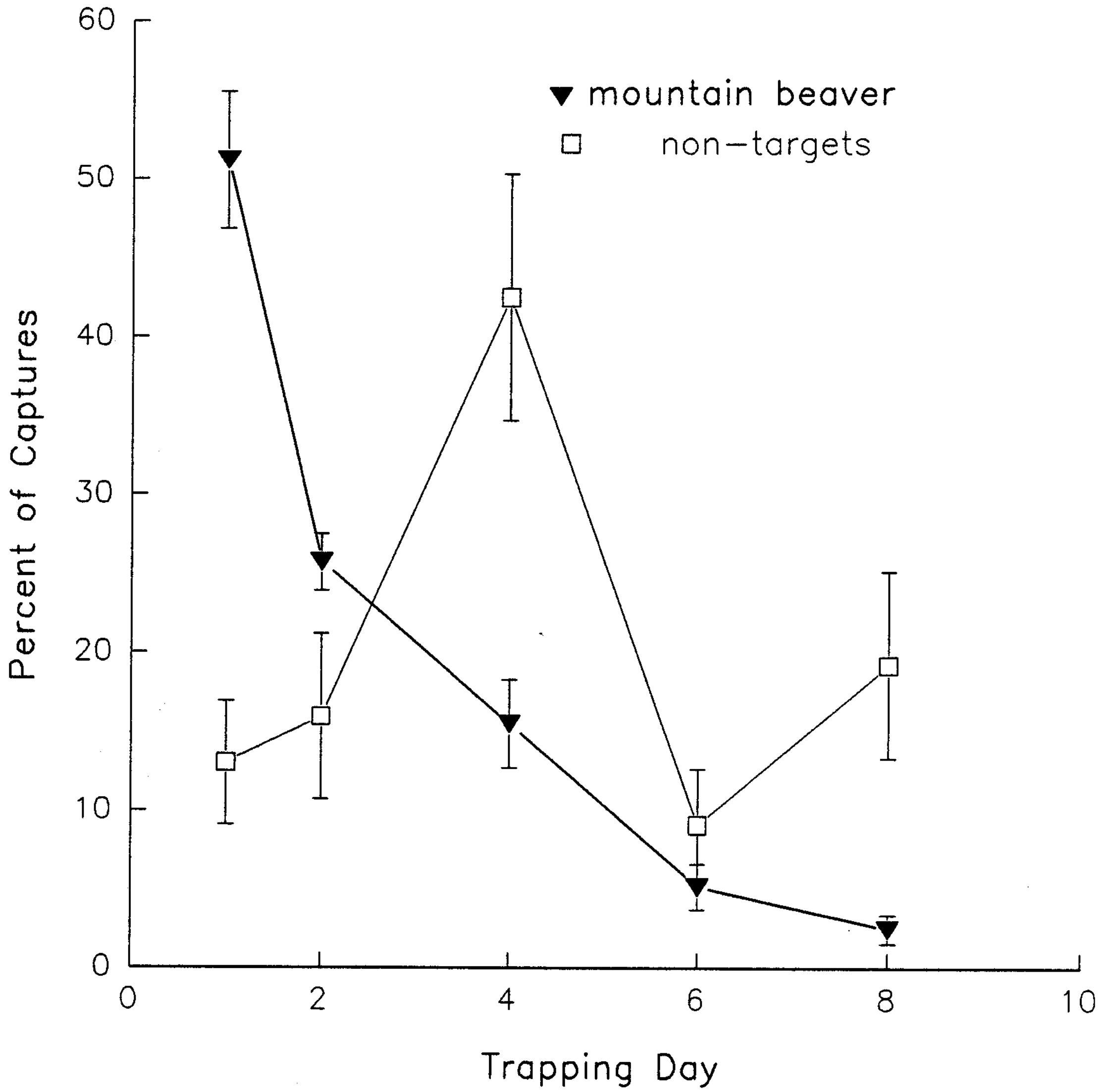
Stand name	Stand #	Type	Location	Ownership	Elev. (m)	aspect	area (ha)
Steere Creek	3	1-yr-old	T10S R8W sect 10	Oregon Dept. of Forestry	200	W	39.4
Bickford	6	1-yr-old	T11S R8W sect 31	Starker Forests Inc.	180	NW	30.0
Crudele Creek	9	1-yr-old	T10S R8W sect 29	Starker Forests Inc.	120	N	12.3
SA1	12	1-yr-old	T9S R8W sect 29	Oregon Dept. of Forestry	215	NW	9.6
Nilsen	1	4- to 5-yr-old	T10S R9W sect 1	Starker Forests Inc.	150	SE	34.8
McIntyre	4	4- to 5-yr-old	T10S R9W sect 33	Starker Forests Inc.	90	W	55.2
Norton Hill	7	4- to 5-yr-old	T10S R9W sect 13	Starker Forests Inc.	305	NW	11.8
Aire King	10	4- to 5-yr-old	T11S R9W sect 36	Starker Forests Inc.	170	E	42.7
Nilsen Forest	2	forest	T10S R9W sect 1	Starker Forests Inc.	150	E	±30
Salmon 1	5	forest	T11S R9W sect 23	Oregon Dept. of Forestry	110	E	±40
Norton Forest	8	forest	T10S R9W sect 13	Starker Forests Inc.	305	E	±40
Salmon 2	11	forest	T11S R9W sect 25	Oregon Dept. of Forestry	120	NE	±60

Appendix B. Herbicide histories of mountain beaver study areas, Coast Range mountains, Oregon.

Stand name	Chemical rate/ acre	Date
Steere Creek	Atrizine (4 lbs)	April 1989
	2,4-D (2 qts)	April 1989
	Accord (2 qts)	Sept. 1990
Bickford	Atrizine (4 lbs)	Spring 1989
	2,4-D (2 qts)	Spring 1989
	Roundup (1.5 qts)	Fall 1989
Crudele Creek	3% Garlon 4 & Diesel	Summer 1991
SA1	Roundup (2 qts)	Sept. 1988
Nilsen	Atrazine (4 lbs)	Spring 1984
	Dowpon (4 lbs)	Spring 1984
	2,4-D (3 qts)	Spring 1987
McIntyre	Atrazine (4 lbs)	Spring 1985
	2,4-D (2 qts)	Spring 1985
	Roundup (1.5 qts)	Fall 1987
Norton Hill	Roundup (1.5 qts)	Fall 1987
	3% Garlon 4 & Diesel	Summer 1991
Aire King	Atrazine (4 lbs)	Spring 1984
	Dowpon (4 lbs)	Spring 1984
	Roundup (1.5 qts)	Fall 1985

Appendix C. Non-target species captured and number of captures on 12 trapping areas totalling 36.3 ha, Coast Range mountains, Oregon, 1990.

Common name	Species name	Number captured
California ground squirrel	*Spermophilus beecheyi*	64
Douglas squirrel	*Tamiasciurus douglasii*	18
mink	*Mustela vison*	5
Townsend's chipmunk	*Tamias towmsendii*	4
shorttail weasel	*Mustela erminea*	2
spotted skunk	*Spilogale gracilis*	2
brush rabbit	*Sylvilagus bachmani*	1
Great Horned Owl	*Bubo virginianus*	1
Fox Sparrow	*Passeralla iliaca*	1



Appendix D. Percent of total captures (SE) by trapping day for mountain beaver and non-target species.