

BOREAL BEAVERS (CASTOR CANADENSIS):
HOME RANGE, TERRITORIALITY, FOOD HABITS AND GENETICS
OF A MID-CONTINENT POPULATION

BY

MICHELLE WHEATLEY

A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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Winnipeg, Manitoba

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CHAPTER 8

**DNA FINGERPRINTING OF BEAVERS:
AN ASSESSMENT OF RELATEDNESS**

ABSTRACT

DNA fingerprinting studies of 60 beavers (*Castor canadensis*) showed a mean band sharing coefficient (BSC) among unrelated beavers of 0.36 ± 0.111 , and among known first order relatives of 0.62 ± 0.102 . Beavers of unknown relationship in the population had a mean BSC of 0.40 ± 0.113 , significantly smaller than known first order relatives, but significantly larger than the value for unrelated animals. Further study is needed to determine what role relatedness plays in limiting territorial behaviour.

INTRODUCTION

Beavers (*Castor canadensis*) are semi-aquatic mammals. They live in family groups, often termed colonies. These groups normally consist of the adult pair, the young of the current year (kits) and the young of the previous year (yearlings). The mating pair generally remain together for many years if not for life. Mating takes place in about February, under the ice in regions with ice cover. Kits are born in early June. The young usually leave the natal lodge at about their second birthday, though some may leave as yearlings or remain past their second birthday.

In studying the beaver population in the Wallace Lake region of eastern Manitoba, I found no direct evidence of territorial behaviour (See Chapter 6). I hypothesized 2 explanations for this lack of territoriality: 1) The Wallace Lake fire in 1980 wiped out much of the resident beaver population and left only a few founders for a new population. The offspring of these founders may not have dispersed great distances, but occupied sites near their natal lodge. Territorial behaviour might therefore have been avoided due to the relatedness of adjacent beaver families.; 2) The fire also resulted in an abundant growth of *Populus tremuloides*, a favoured food of beaver. A profusion of food might also reduce the need for expenditure of energy on territorial defence. Alternatively, both these hypotheses might be working in conjunction with one another. To ascertain the likelihood of hypothesis 1, I collected blood and tissue samples from the beavers in a number of lodges throughout the area for DNA fingerprinting, to determine the degree of relatedness present in the beaver population of the Wallace Lake area.

Jeffreys *et al.* (1985a) discovered the presence, in the human genome, of regions of DNA with multiallelic variation and high heterozygosities. These variable regions consist of tandem repeats of

short sequences (minisatellites). They are polymorphic due to allelic differences in the number of tandem repeats (Jeffreys *et al.* 1985a). Using specific restriction endonucleases and probes, it is possible to produce a ladder-like series of bands on x-ray film, representing strands of DNA of different lengths. An individual's array of bands is termed its DNA fingerprint (Lynch 1988).

Burke and Bruford (1987) adapted Jeffrey's method for work with tree swallows (*Tachycineta bicolor*). Since then DNA fingerprinting has been used for a variety of work with both mammals and birds. Most bird studies have been concerned with determining paternity and the likelihood of extra-pair copulations or intraspecific brood parasitism in a variety of species (Quinn *et al.* 1987; Burke *et al.* 1989; Birkhead *et al.* 1990; Morton *et al.* 1990; Rabenold *et al.* 1990; Westneat 1990; Dunn and Robertson 1993; Jones *et al.* 1993; Lifjeld *et al.* 1993). Other studies have examined population structure (Wetton *et al.* 1987; Haig *et al.* 1993). DNA fingerprinting in mammals has also been used to determine paternity in common shrews (*Sorex araneus*) (Tegelstrom *et al.* 1991). However most work on mammals has centred around understanding the relationships and genetic diversity within a population (Faulkes *et al.* 1990; Gilbert *et al.* 1990; Reeve *et al.* 1990; Gilbert *et al.* 1991; Hoelzel and Dover 1991; Wayne *et al.* 1991; Ellegren *et al.* 1993).

In this study I examine patterns of relationship within a local population of beavers, compare the results to similar studies on other mammals and birds and consider whether a high degree of genetic relatedness may be the determining factor in the lack of apparent territoriality in the population.

METHODS

COLLECTION OF SAMPLES

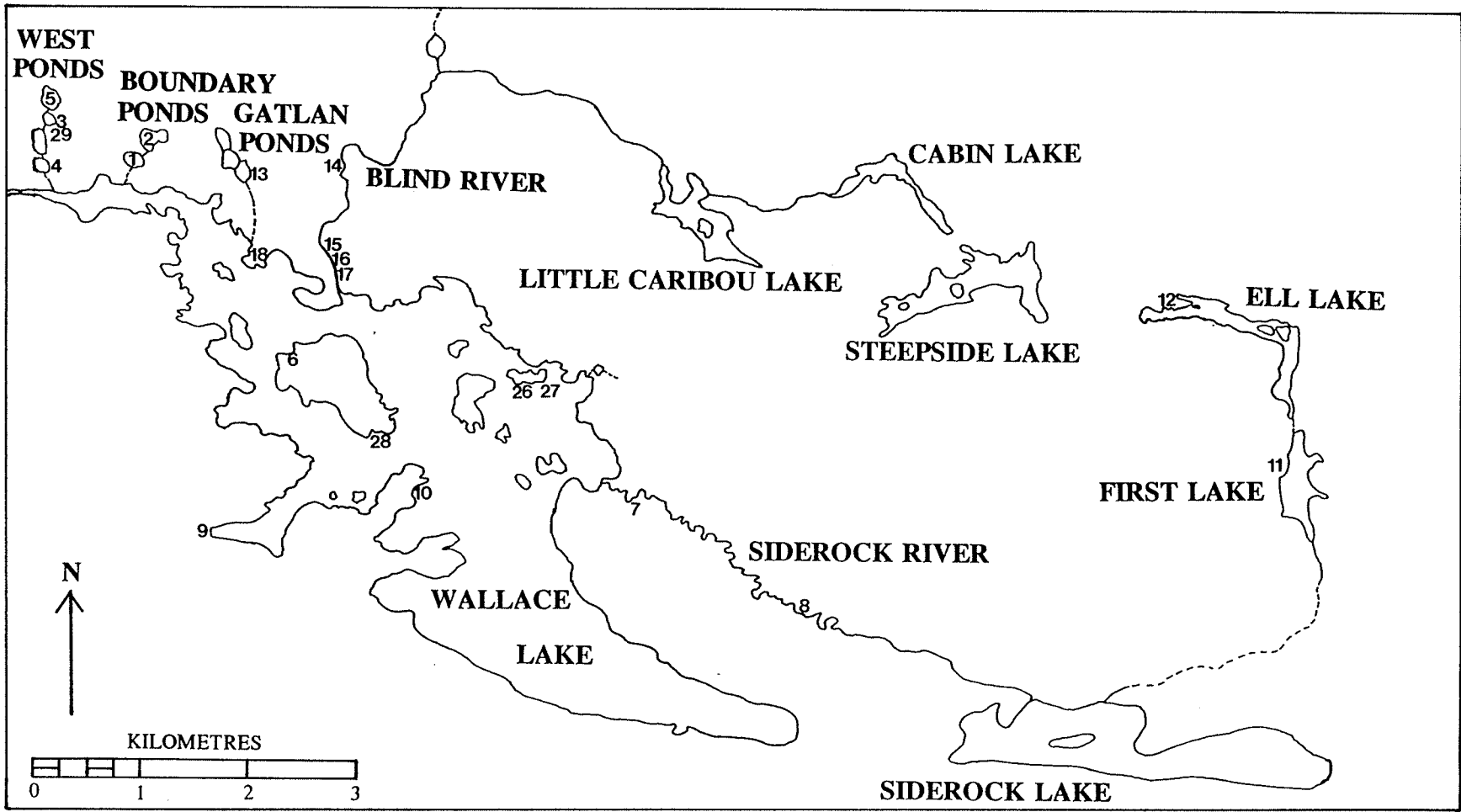
I collected blood and tissue samples from beavers from 28 different lodges. I collected blood samples from beavers live-trapped for radio-telemetry and behavioural studies. I froze blood samples in 5 ml vacutainer tubes after collection. I also collected tissue (muscle) samples from beavers trapped by the local trapper. These were stored in individual freezer bags after collection. Samples from 60 beavers were usable in the DNA analysis. The locations of capture of the beavers are shown in Figure 1.

DNA FINGERPRINTING

DNA profile tests were performed at Therion Corporation (Troy, NY) using the following procedures: DNA was isolated from 1.0 ml of blood using a non-organic extraction technique (Grimberg *et al.* 1989). DNA was isolated from frozen tissue using an organic extraction technique (Sambrook *et al.* 1989). The yield of DNA from each sample was determined by comparison to controls on an agarose gel.

The DNA was cleaved using conditions specified by the supplier with 20 units of restriction endonuclease Hinf I (New England Biolabs, Beverly, MA) per microgram of DNA. Completeness of digestion was monitored by comparison to controls on an agarose gel. Two micrograms of digested DNA from each individual were loaded onto a 1.2 % agarose analytical gel. Molecular weight sizing standards (MWSS) were loaded in up to three lanes so that the samples were bracketed by MWSS. This set of standard DNA fragments of known molecular size is composed of 48 bands ranging from 0.504 to 34.679 kilobase pairs. The gel was run in 40 mM Tris pH 7.8, 1 mM EDTA for a total of 1500 volt-hrs.

Figure 1. Map showing location of capture sites of beavers used for DNA fingerprinting. Numbers refer to family numbers used in coding the samples (See Appendix 5).



The DNA was transferred from the gel to a nylon membrane (Biodyne B, Pall Corporation) using an alkaline transfer technique described by the manufacturer. The membranes were hybridized with an oligonucleotide probe derived from the repeat sequences of bacteriophage M13 (probe OPTTM-12). In a pilot study this probe had been shown to give highly variable DNA profile patterns among "unrelated" beavers. The probe was labelled with ³²P (NEN, Boston) by primer extension (Sambrook *et al.* 1989), and unincorporated nucleotide was removed on a Nuc-Trap column (Stratagene, LaJolla, CA). Hybridizations were carried out at 50°C in 5X SSPE (1X = 150 mM NaCl, 10 mM sodium phosphate, 1 mM EDTA), 2 % SDS, 1 mg/ml herring testes DNA and 1 % PEG for 18 hours. The membranes were washed at 55°C in 2X SSPE, 1 % SDS, covered with plastic and exposed to x-ray film at -70°C for 1 to 5 days.

Analyses of DNA profile patterns were performed using two computer programs designed at Therion Corporation. 1) Using a digitizing pad, band sizes for each individual were determined by comparison to the MWSS within the range of 13.823 to 3.034 kb. 2) A set of matrices were generated that reflected the ratio of bands shared to the total number of bands scored for each pair of individuals using the formula $2N_{AB}/(N_A + N_B)$ where N_A is the number of bands in animal A, N_B is the number of bands in animal B, and N_{AB} is the number of bands shared by both beavers A and B (Wetton *et al.* 1987; Lynch 1990; 1991; Morton *et al.* 1990). This ratio is referred to as the band-sharing coefficient (BSC). In all published reports to date, BSCs (also called the index of similarity, variably termed "D" values (Wetton *et al.* 1987; Morton *et al.* 1990) or "S" values (Lynch 1990; 1991) have exhibited a significant positive correlation with known values of relatedness.

During comparisons to determine band sharing between individuals, bands were considered to be a match when their respective sizes overlapped within a range (called tolerance) of ± 0.45 % of each band size (i.e. the total range is equal to 0.9 % of band size).

Theoretically, higher levels of tolerance can be used since BSC is a relative measure of relatedness among individuals. However, higher tolerances are expected to mask true differences between individuals because as the range of overlap is increased, more bands at different positions will be called matches. (W. Gergits and N. Casna, Therion Corporation, personal communication).

STATISTICAL ANALYSIS

I separated the pairwise BSCs into 4 groups: known first order relatives (parent-offspring or siblings); known non-first order relatives ("unrelated" - fetuses, kits and yearlings from one end of the sampling area compared to fetuses, kits and yearlings from the other end of the sampling area); other members of family groups (1 lodge) whose direct relationship to each other was unknown; and all other comparisons between beavers of unknown relatedness. I subdivided known first order relatives into 4 groups: father to offspring; mother to offspring; siblings of the same year class; and siblings of different year classes.

I computed the mean BSC for each group and also calculated an unbiased estimate of variance for each group with Lynch's (1990) formula:

$$\text{Variance} = \frac{2\bar{S}(1-\bar{S})(2-\bar{S})}{\bar{n}(4-\bar{S})}$$

where \bar{S} = mean BSC for the group
 \bar{n} = mean number of bands scored for the group

This unbiased estimate of variance and standard deviation (square root of variance) circumvents the difficulties associated with conducting parametric statistics on values which are not truly independent. I computed F-tests and t-tests to ascertain if there was any significant difference between BSCs for the different categories outlined above. I also computed histograms of the frequency of BSC values by grouping values in 0.05 increments.

RESULTS

Samples from 60 beavers were usable for band sharing comparisons. The mean number of bands scored per beaver was 16.77 (s.d. = 3.33, N=60, range: 9 to 27).

The mean BSC for all 1770 pairwise comparisons was 0.42 (s.d.=0.113, N=1770, range: 0 to 0.82)(Figure 2). The mean BSC for known first order relatives (parent-offspring, or full siblings) was 0.62 (s.d.=0.102, N=83, range: 0.39 to 0.79). Unrelated animals had a mean BSC of 0.36 (s.d.=0.111, N=72, range: 0.14 to 0.55). Beavers within a lodge of unknown relationship to each other had a mean BSC of 0.598 (s.d.= 0.111, N=32, range: 0.29 to 0.82). The remaining 1583 comparisons between beavers of unknown relatedness had a mean BSC of 0.40 (s.d.=0.113, N=1583, range: 0 to 0.8).

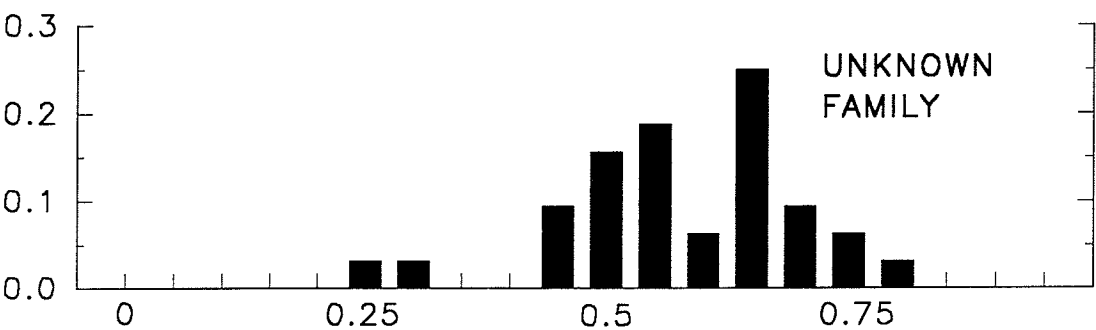
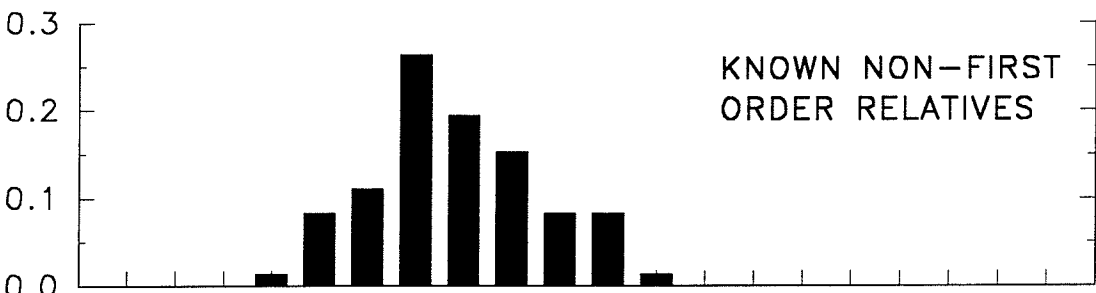
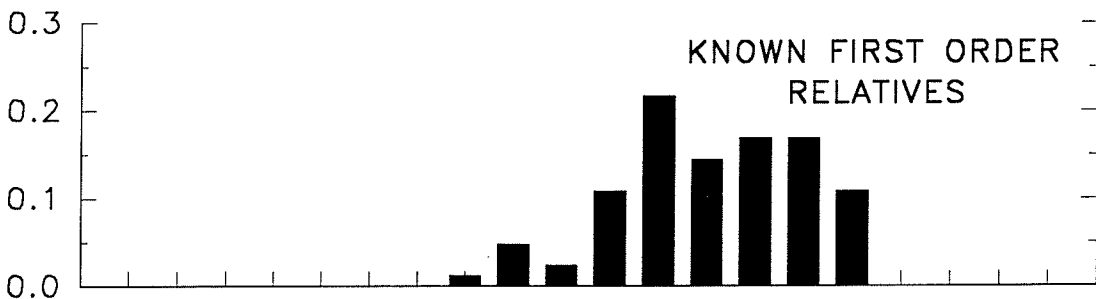
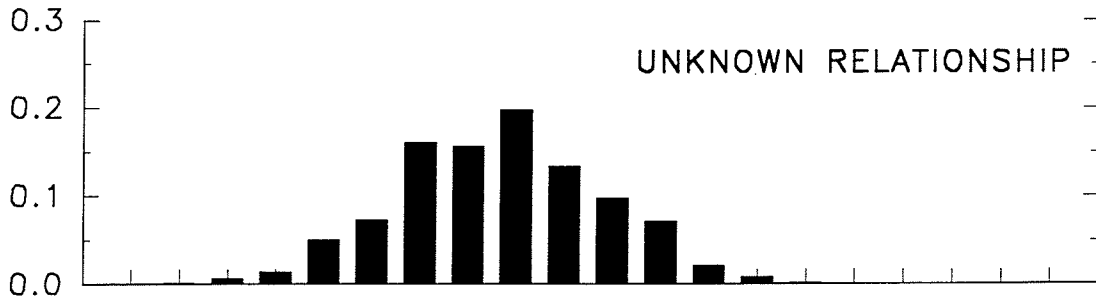
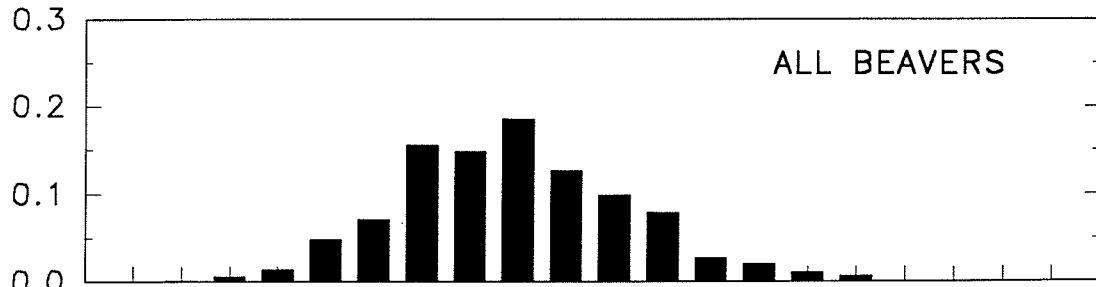
First order relatives had a significantly larger mean BSC than the unrelated group ($t=6.36$, $N=83,72$, $p<0.001$). The unknown group had a significantly smaller mean BSC than known first-order relatives ($t=18.97$, $N=1583,83$, $p<0.001$), and a significantly larger mean BSC than the unrelated group ($t=2.99$, $N=1583,72$, $p<0.01$).

FAMILY

Within the known first order relatives the mean BSC for fathers to offspring was 0.66 (s.d.=0.1, N=7, range: 0.56 to 0.77) and for mothers to offspring was 0.62 (s.d.=0.105, N=24, range: 0.4 to 0.79)(Figure 3). The mean BSC between offspring of the same year class was 0.60 (s.d.=0.11, N=32, range:0.39 to 0.79) and between offspring from different year classes was 0.64 (s.d.=0.104, N=20, range:0.5 to 0.79)(Figure 3).

Figure 2. Histogram of frequency of occurrence of band sharing coefficient values for all beavers (N= 1770); non-cohabiting beavers of unknown relationship (N=1583); known first order relatives (N=83); known non-first order relatives ("unrelated") (N=72); and unknown same lodge residents (N=32).

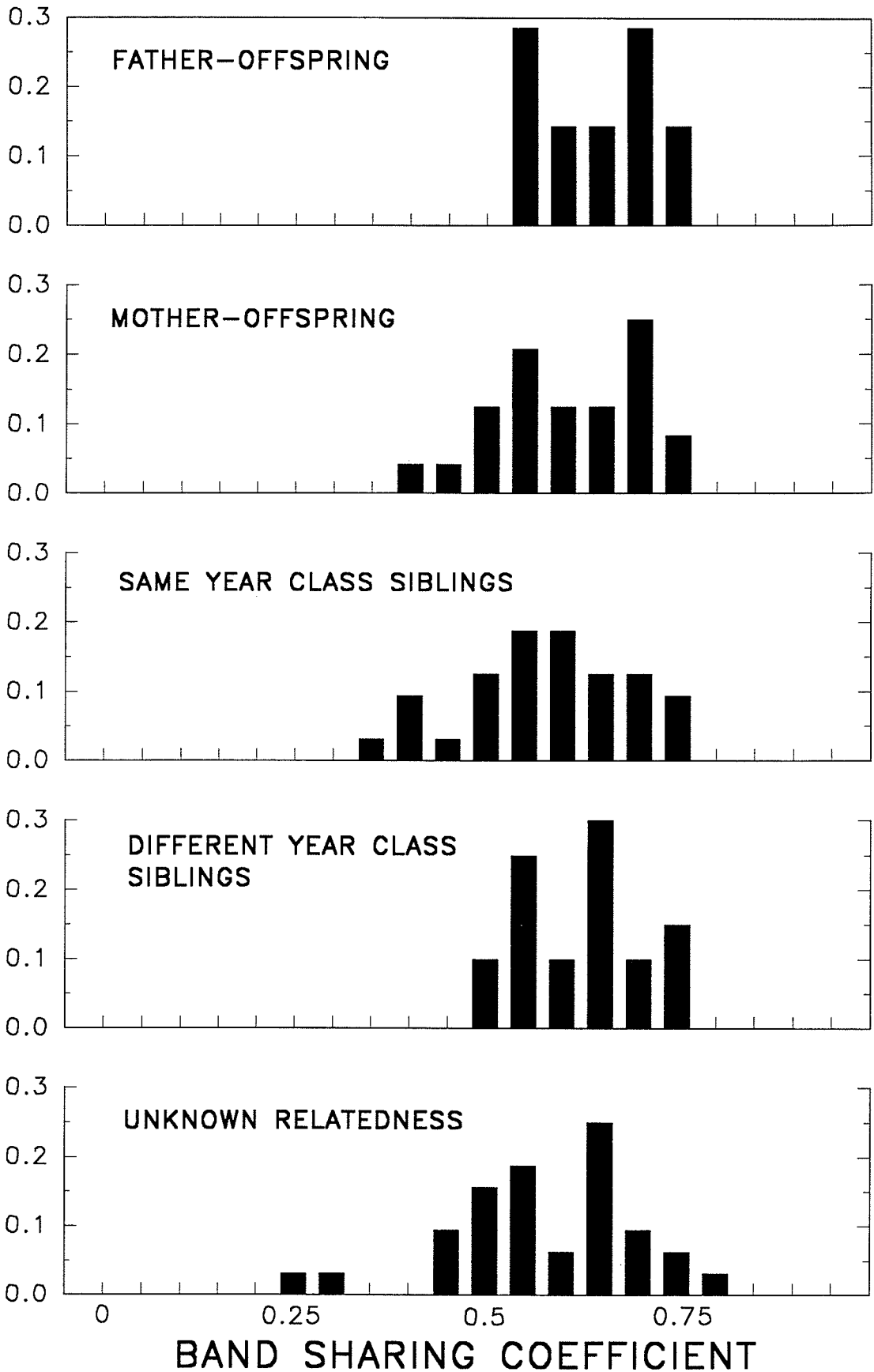
FREQUENCY (PROPORTION OF COMPARISONS)



BAND SHARING COEFFICIENT

Figure 3. Histogram of frequency of occurrence of band sharing coefficient values for beavers living in common lodges: father-offspring (N=7); mother-offspring (N=24); same year class siblings (N=32); different year class siblings (N=20); and beavers of unknown relationship residing in the same lodge (N=32).

FREQUENCY (PROPORTION OF COMPARISONS)



The mean BSCs between mothers and offspring and fathers and offspring were not significantly different ($t=0.924$, $N=24,7$, $p>0.2$). Likewise, the mean BSCs did not differ significantly between siblings of the same year class and siblings of different year class ($t=1.33$, $N=32,20$, $p>0.1$). There were no significant differences in mean BSC between mothers and offspring and same year class siblings ($t=0.699$, $N=32,24$, $p>0.5$); between mothers and offspring and different year class siblings ($t=0.63$, $N=24,20$, $p>0.5$); between fathers and offspring and same year class siblings ($t=1.42$, $N=32,7$, $p>0.1$); or between fathers and offspring and different year class siblings ($t=0.45$, $N=20,7$, $p>0.5$). The beavers resident in the same colony, whose relationships to each other were not known had a mean BSC that was not significantly different from that for the known first order relatives ($t=0.88$, $N=32,83$, $p>0.2$).

DISCUSSION

The beavers showed a mean BSC among known first order relatives of 0.62 and among unrelated beavers of 0.36. The value for first order relatives is lower than for other mammal species previously reported (Table 1). However the *Heterocephalus glaber* (naked mole rat) population had extreme inbreeding (Reeve *et al.* 1990), and the *Panthera leo* (lion) population may also have had inbreeding (Gilbert *et al.* 1991), which will serve to raise the BSC value. Both these populations also demonstrated higher BSC values among unrelated animals (Table 2). The higher the degree of similarity between unrelated members of the population, the more "noise" in the system and the lower the relative value of the BSC for related animals in that population (Lewin 1989). If the value of this background "noise" is subtracted from the value for the related animals, the values for the different species become much more similar. The BSC estimate for unrelated beavers is somewhat intermediate among estimates of other mammal and bird species (Table 2). However, because this is such a recently developed method, there is not an abundance of data available in the literature to which we can compare the beaver results.

The unrelated values are much lower than most of the values for unrelated *Castor fiber* in Sweden, but very similar to the values for Swedish beavers compared to Russian beavers (Table 2). The Swedish sample group, although taken from a population of over 100,000 animals, represent the descendants of 46 successfully reintroduced animals which in turn are descended from less than 100 Norwegian beavers (Ellegren *et al.* 1993). There was likely loss of genetic variability as a result of this bottleneck in the population. However, in the pilot study for the current study, a great deal of similarity was found among the beavers, and the probes for the current study were selected because they showed considerable variability between known unrelated animals. To compare

Table 1. Literature values for mean band sharing coefficients for known first order relatives for several bird and mammal species.

SPECIES	MEAN BSC	AUTHOR(S)
Birds		
<i>Passer domesticus</i>	0.47	Wetton <i>et al.</i> 1987
Mammals		
<i>Panthera leo</i>	0.72 - 0.80	Gilbert <i>et al.</i> 1991
<i>Canis lupus</i>	0.68	Wayne <i>et al.</i> 1991
<i>Heterocephalus glaber</i>	0.88 - 0.99	Reeve <i>et al.</i> 1990
<i>Castor canadensis</i>	0.62	Present paper

Table 2. Literature values for mean band sharing coefficients for unrelated members of several bird and mammal species.

SPECIES	MEAN BSC	AUTHOR(S)
Birds		
<i>Merops apiaster</i>	0.189	Jones et al. 1991
<i>Passer domesticus</i>	0.1 - 0.3	Burke and Bruford 1987
<i>Taeniopygia guttata</i>	0.16 - 0.17	Birkhead et al. 1990
<i>Campylorhynchus nuchalis</i>	0.26 - 0.27	Rabenold et al. 1990
<i>Prunella modularis</i>	0.24	Burke et al. 1989
<i>Progne subis</i>	0.19	Morton et al. 1990
<i>Picoides borealis</i>	0.55	Haig et al. 1993
<i>Passerina cyanea</i>	0.21 - 0.28	Westneat 1990
<i>Tachycineta bicolor</i>	0.25	Lifjeld et al. 1993
Mammals		
<i>Castor fiber</i>	0.23 - 0.55 ¹	Ellegren et al. 1993
<i>Castor fiber</i>	0.77 - 0.89 ²	Ellegren et al. 1993
<i>Heterocephalus glaber</i>	0.42 - 0.84	Reeve et al. 1990
<i>Urocyon littoralis</i>	0.26 - 0.56	Gilbert et al. 1990
<i>Canis lupus</i>	0.31	Wayne et al. 1991
<i>Orcinus orca</i>	0.64	Hoelzel and Dover 1991
<i>Panthera leo</i>	0.49	Gilbert et al. 1991
<i>Homo sapiens</i>	0.08 - 0.28	Jeffreys et al. 1985b
<i>Castor canadensis</i>	0.36	Present paper

¹ Comparison between populations in Sweden and Russia

² Comparison between unrelated animals in Sweden

accurately these beavers to the European beavers, we would have to compare results based on the same probes. Ellegren *et al.* (1993) also reports a complete lack of variability in the Major Histocompatibility Complex (MHC), which plays a role in the immune system. The Russian beavers show only 2 variations from the Swedish beavers at MHC loci (Ellegren *et al.* 1993). Faulkes *et al.* (1990) also found limited polymorphism at MHC loci in *Heterocephalus glaber*, an inbreeding colonial small mammal. The rapid expansion of the beaver population in Scandinavia demonstrates that the animals do not seem to be negatively affected by low amounts of variability in DNA fingerprints and MHCs (Ellegren *et al.* 1993).

The comparison between all animals of unknown relatedness showed that the BSC values were somewhat intermediate between known related beavers and unrelated beavers, but covered the entire range of both. While the latter 2 groups were significantly different from one another, there was overlap (Figure 2). It would be expected that there would be some greater degree of relatedness in the population, but the sample of unrelated was also taken from this same population. I believe this indicates that there is a somewhat higher degree of relatedness among the beavers in some parts of the study area. Further examination of the data, with comparisons to geographic distance, will show what the patterns of relatedness are over the study area.

CONCLUSIONS

Neither of my hypotheses are proven or disproven. The beavers in the Wallace Lake region do not show evidence of inbreeding as a whole, but rather have BSC values for both related and unrelated animals that are within the range of values cited for other mammals and birds. The results do not indicate a high degree of relatedness across the population, but there appears to be some degree of relatedness among non-cohabiting animals. It appears, therefore, that repopulation after the fire may have resulted both from unrelated immigration and limited dispersal of the offspring of the founders. Further study and pairwise comparison between different sites will better illustrate whether relatedness is playing a role in reducing territorial behaviour in the beavers in this area.

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CHAPTER 9

SUMMARY

SUMMARY

Most of the early literature on beavers was very much anecdotal and anthropomorphic. The more recent literature has covered a variety of fields, but the taiga or boreal forest of mid-continent North America has not been well represented in this literature. In this study I sought to gain a better understanding of the beavers living in the taiga.

My first objective was to identify a suitable method of delineating home ranges for beavers. While each of the four methods tested functioned well in specific situations, only the grid cell method gave reasonable estimates in all cases and allowed for analysis of intensity of use of the home range.

Secondly I wished to determine the home range sizes for beavers living in this region, and thirdly habitat, sex, age class and seasonal differences in home range size. Summer home ranges averaged 10.34 ha, fall 3.07 ha and winter 0.25 ha. Core areas were almost always present and usually included the lodge and feeding areas. River beavers had larger home ranges than pond or lake beavers in both summer and fall, while in summer pond home ranges were smaller than lake home ranges. The habitat bordering lakes and ponds is more suited to the growth of favoured beaver foods, such as *Populus tremuloides*, than the habitat bordering rivers. This means that beavers living on the river may have to go farther in search of food than those living in lake or pond habitats. Adult males were active farther from the lodge and had larger home ranges than other family members, while adult females were active closer to the lodge and had smaller home ranges. Home ranges and core areas were larger in summer than in fall, but summer and fall home range sizes were positively correlated. Fall home ranges were centred closer to the lodge than summer home ranges. Beavers appear to use about 25 %

of their home range for about 75 % of their activity. This trend holds across all habitats, age classes, sexes and seasons.

My fourth objective was to assess whether territories are present in this beaver population. I never observed any evidence of territorial behaviour or defense. Some home ranges overlapped and I caught many individual beavers inside home ranges of other individual or family groups. I believe mutual avoidance is the more likely pattern that is followed by these beavers.

My fifth and sixth objectives were to determine feeding habits and the cause of any seasonal variation in these habits. Food habits did vary seasonally, probably as a result of many interacting requirements. The essential requirements appear to be protein and a moderate potassium to sodium ratio. Beavers appear to choose species and parts of trees in order to meet these requirements.

My last objective was to assess the relatedness amongst the beaver population using DNA fingerprinting and determine if relatedness and territoriality are correlated. I found no direct evidence of inbreeding in the population. However, the beavers of unknown relatedness fit between unrelated and known related in their average bands sharing coefficient. Therefore, at least some of the members of the population do not appear to have dispersed a great distance from their natal site, but the relatedness estimates also indicate that there are some unrelated immigrants in the breeding population.

Beavers require both a dwelling - a lodge or bank burrow - and a source of food. Suitable sites for building lodges or burrows will not necessarily coincide with good sources of food. Beavers living in areas with both requirements in close proximity will have smaller home ranges than those who must travel farther from their dwelling to suitable feeding sites. Similarly, the seasonal change in food preferences will result in seasonal differences in home range size.

In my study area, ice cover persists for up to 6 months each year. In the remaining 6 months of open water, beavers must grow, raise young and deposit fat reserves for the winter. These are very different stresses than those faced by beavers residing in more moderate climates. The choices made by beavers in my study area with regard to tree species and harvesting sites appear to maximize protein intake and minimize energy expenditure. In meeting these requirements beavers' home ranges change seasonally, being smaller in the fall when the food pile is being constructed and larger in summer when beavers feed at greater distances from the lodge.

Territorial behaviour is usually a method of defending some resource such as food or living sites. After the 1980 Wallace Lake fire, *Populus tremuloides* became abundant in my study area. If food is abundant, energy expenditure on territoriality would not seem to be necessary. Since beavers appear to be conserving energy by only harvesting trees for the winter food pile from the vicinity of their lodge, it seems unlikely that they would put effort into territoriality when food supplies appear adequate.

Alternatively, or supplementarily, the DNA fingerprinting appears to show that there is at least some degree of relatedness among this population. If this is the case, territories are less likely to be defended against related individuals than against unrelated individuals. The combined effects of relatedness and ample food supply may negate the need for territoriality in this population. If this is the case, I would expect that as relatedness and food supply both decrease with time, territoriality should increase. In the mean time mutual avoidance appears to serve the purpose of separating different beaver families or individuals. Similarly, if territories do occur, home range shape and size may also change in order to be better defended by the owner.

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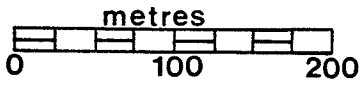
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APPENDIX 1

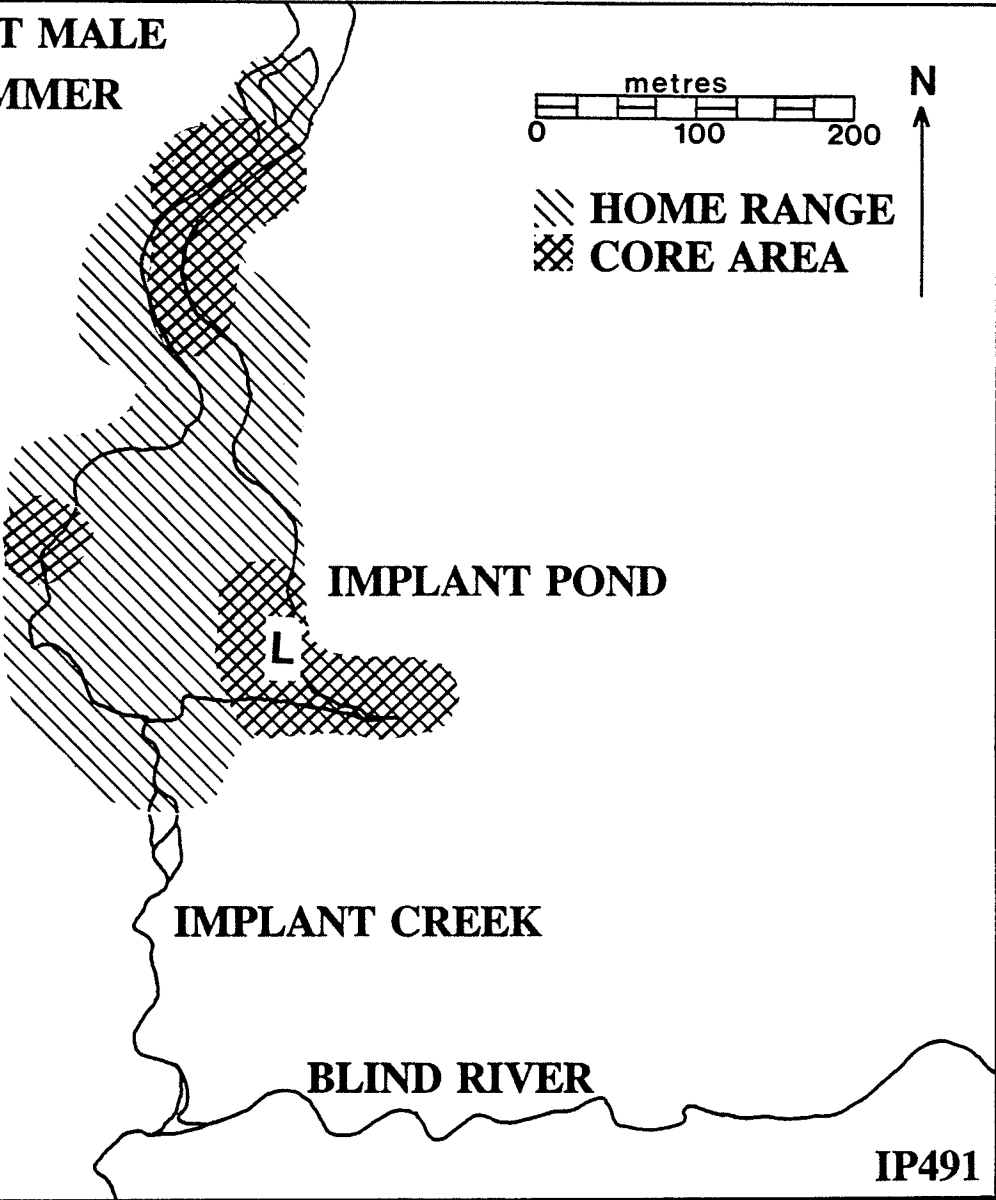
HOME RANGE MAPS

Figure 1. Maps of home range area for beavers in the Implant Pond Family for summer and fall, 1989. L indicates location of the lodge.

**ADULT MALE
SUMMER**

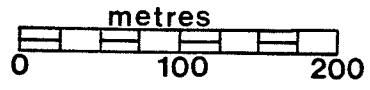


HOME RANGE
CORE AREA

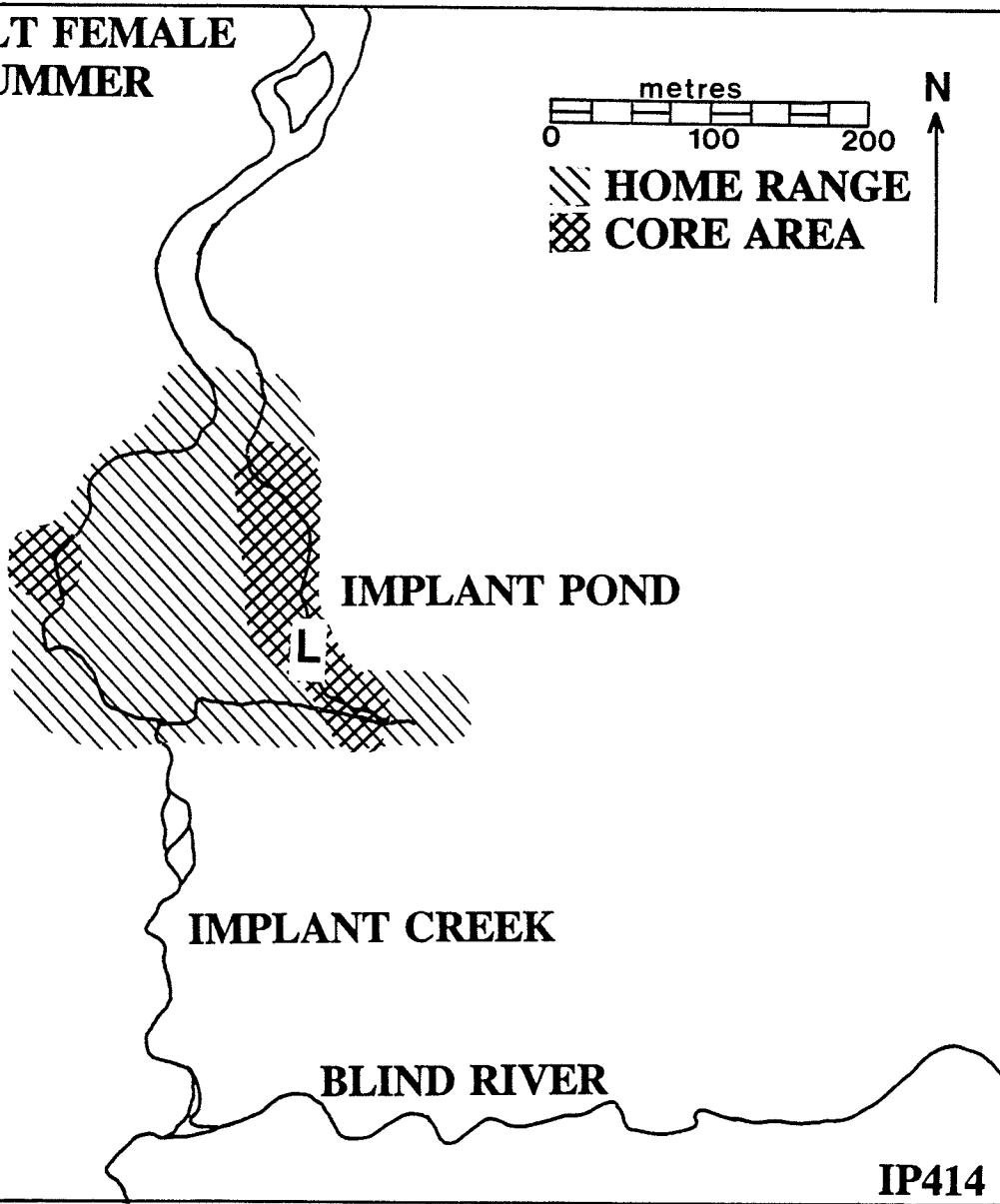


IP491

**ADULT FEMALE
SUMMER**

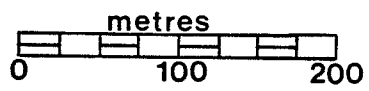


HOME RANGE
CORE AREA

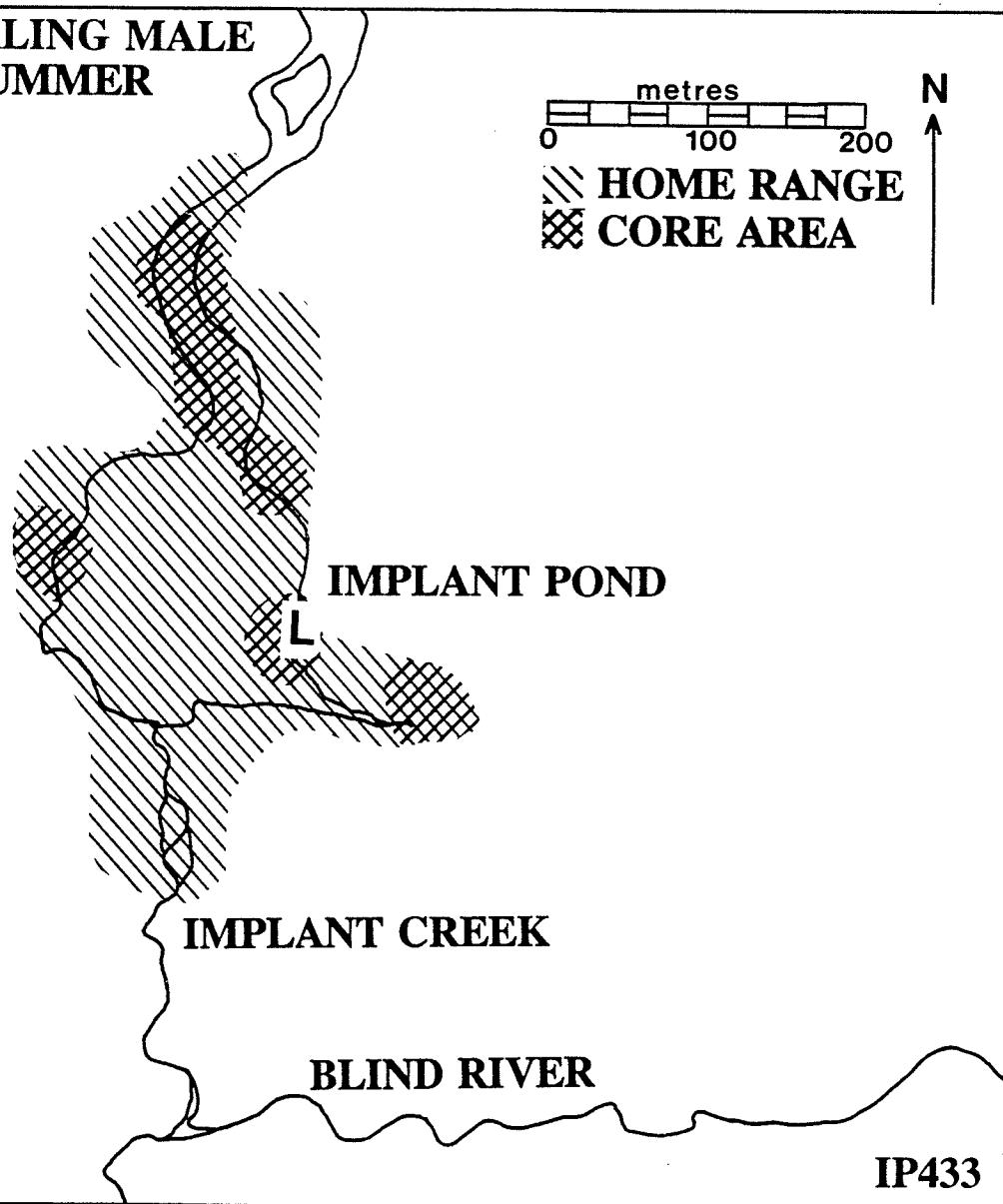


IP414

**YEARLING MALE
SUMMER**

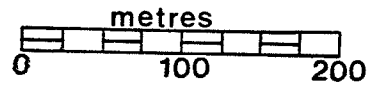


HOME RANGE
CORE AREA

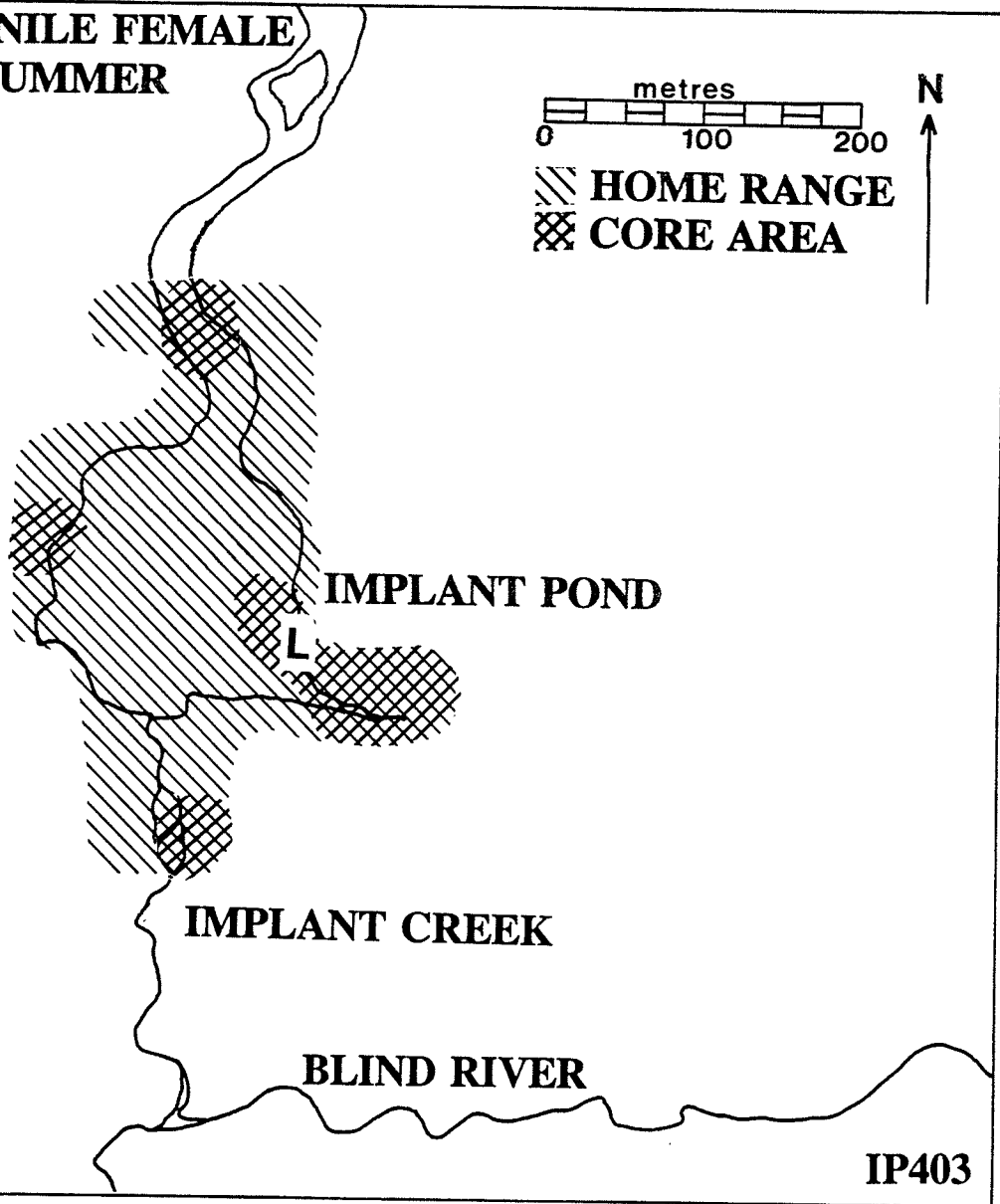


IP433

**JUVENILE FEMALE
SUMMER**



HOME RANGE
CORE AREA

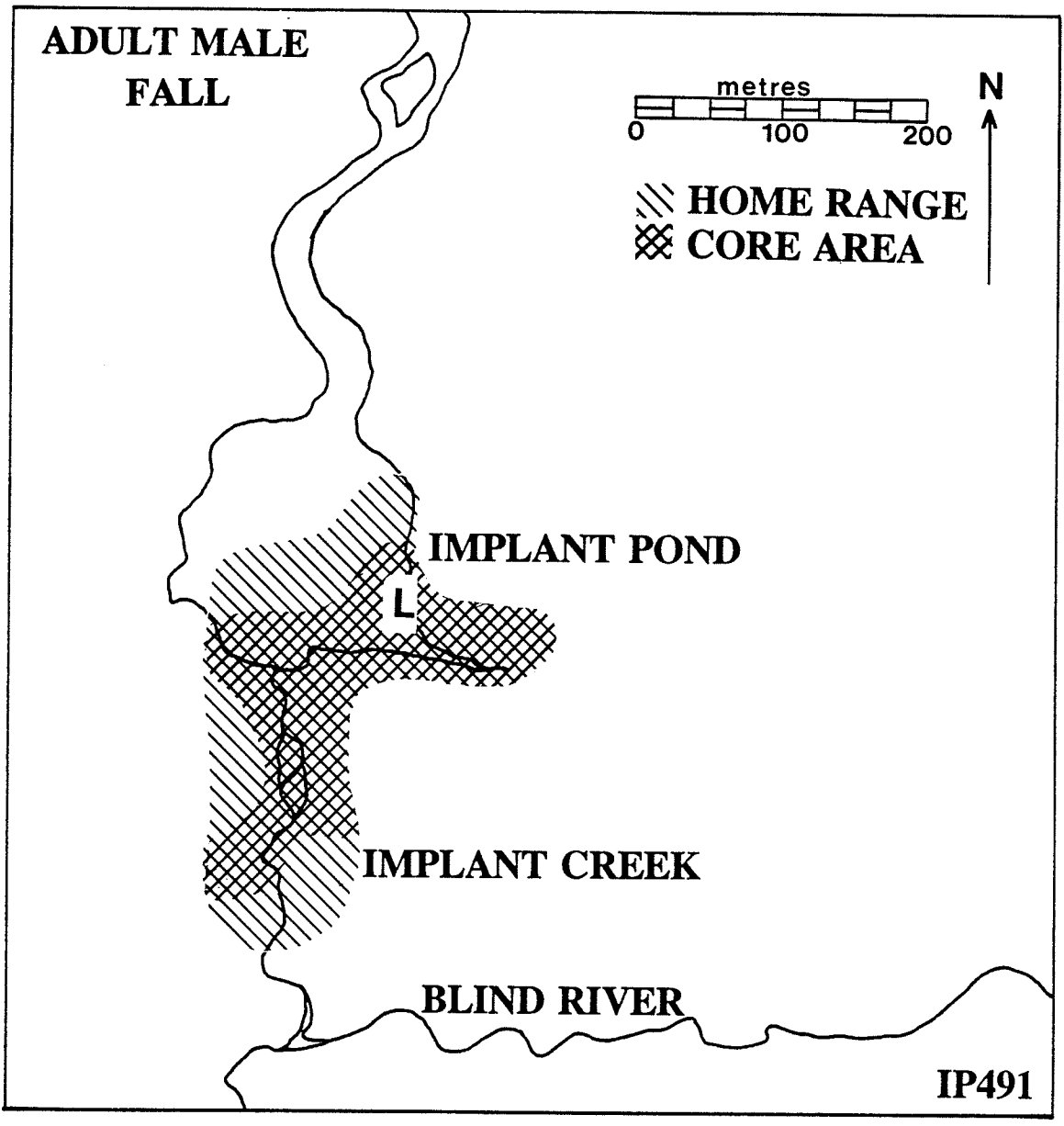


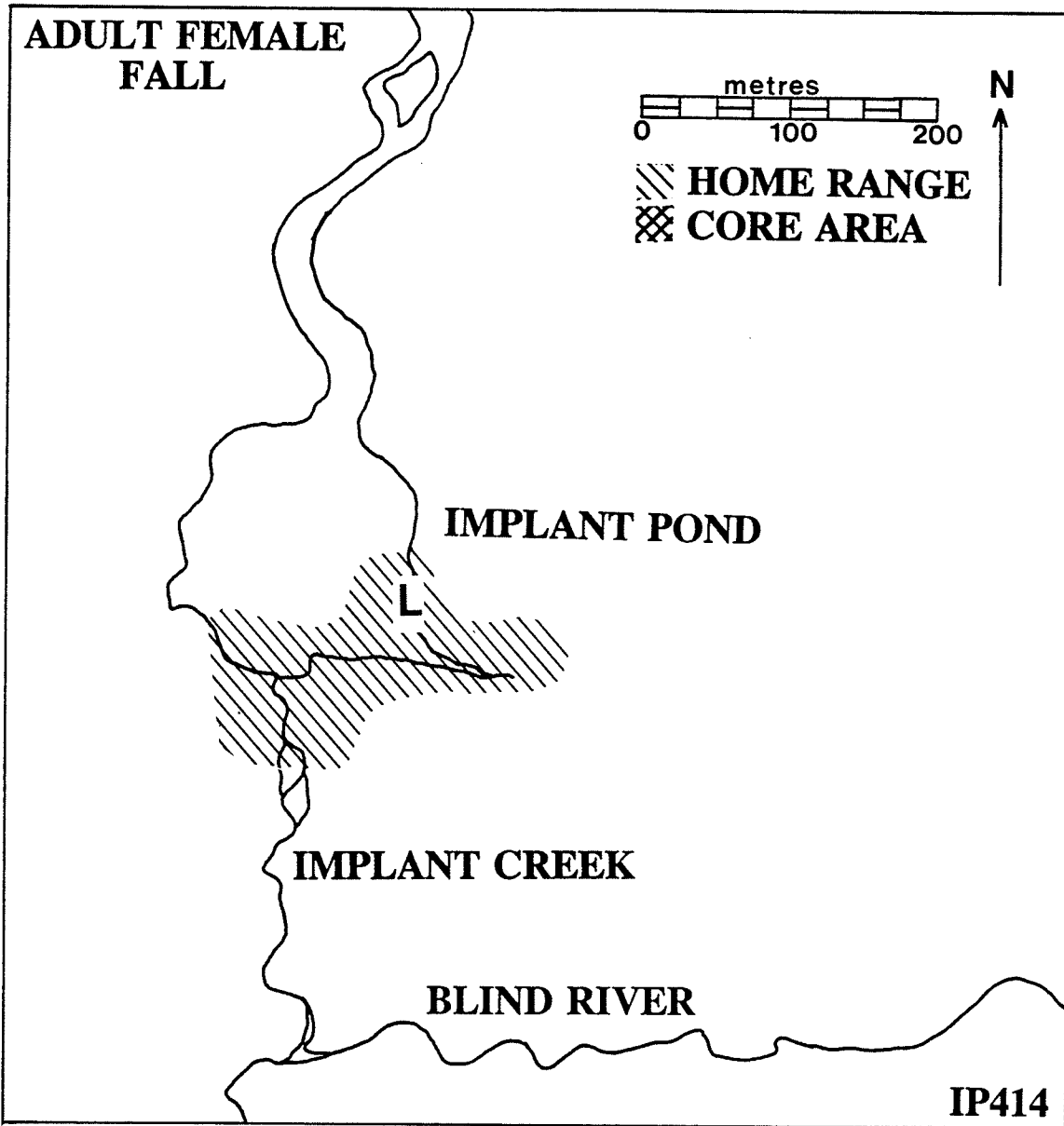
IMPLANT POND

IMPLANT CREEK

BLIND RIVER

IP403





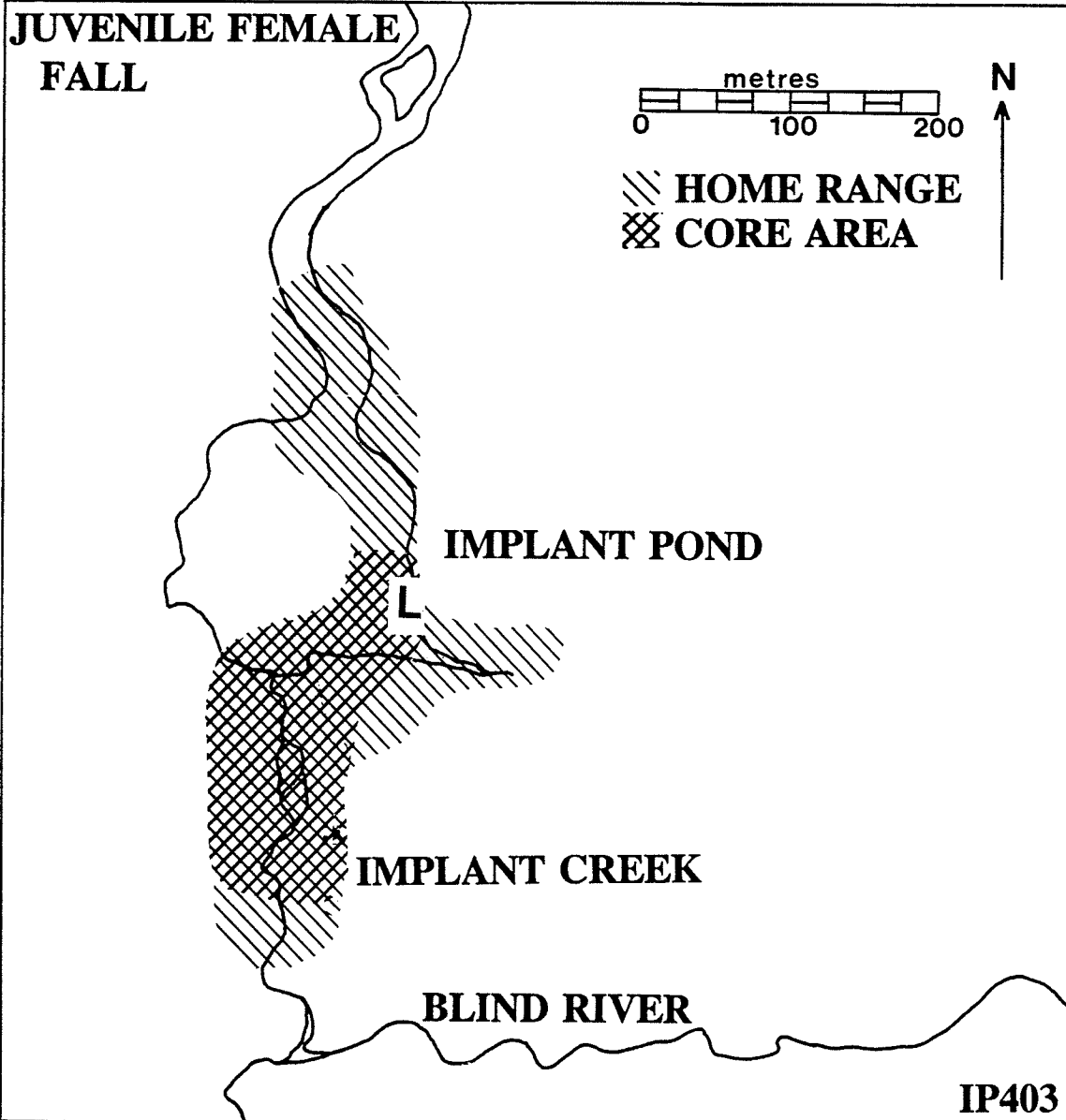
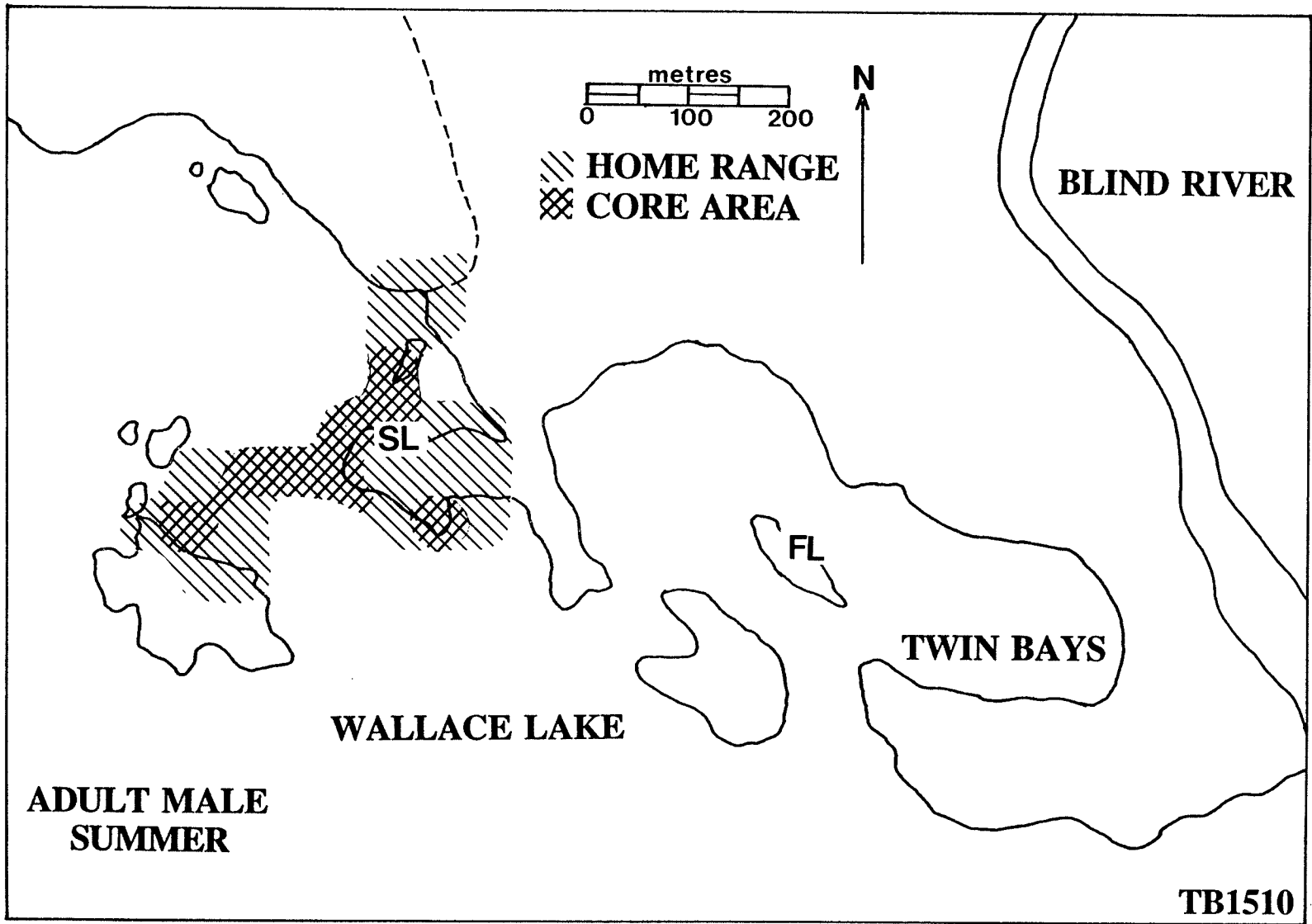
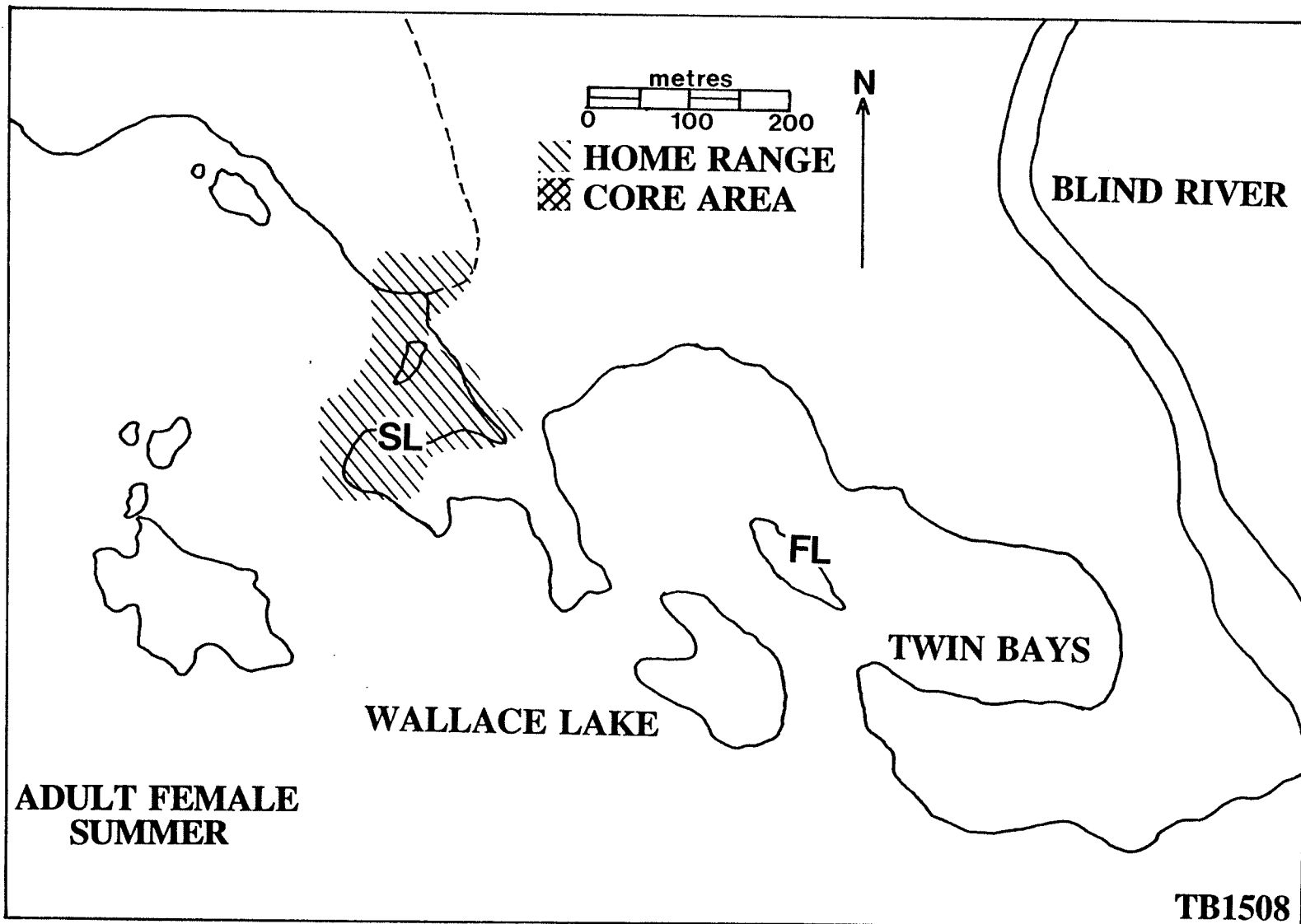
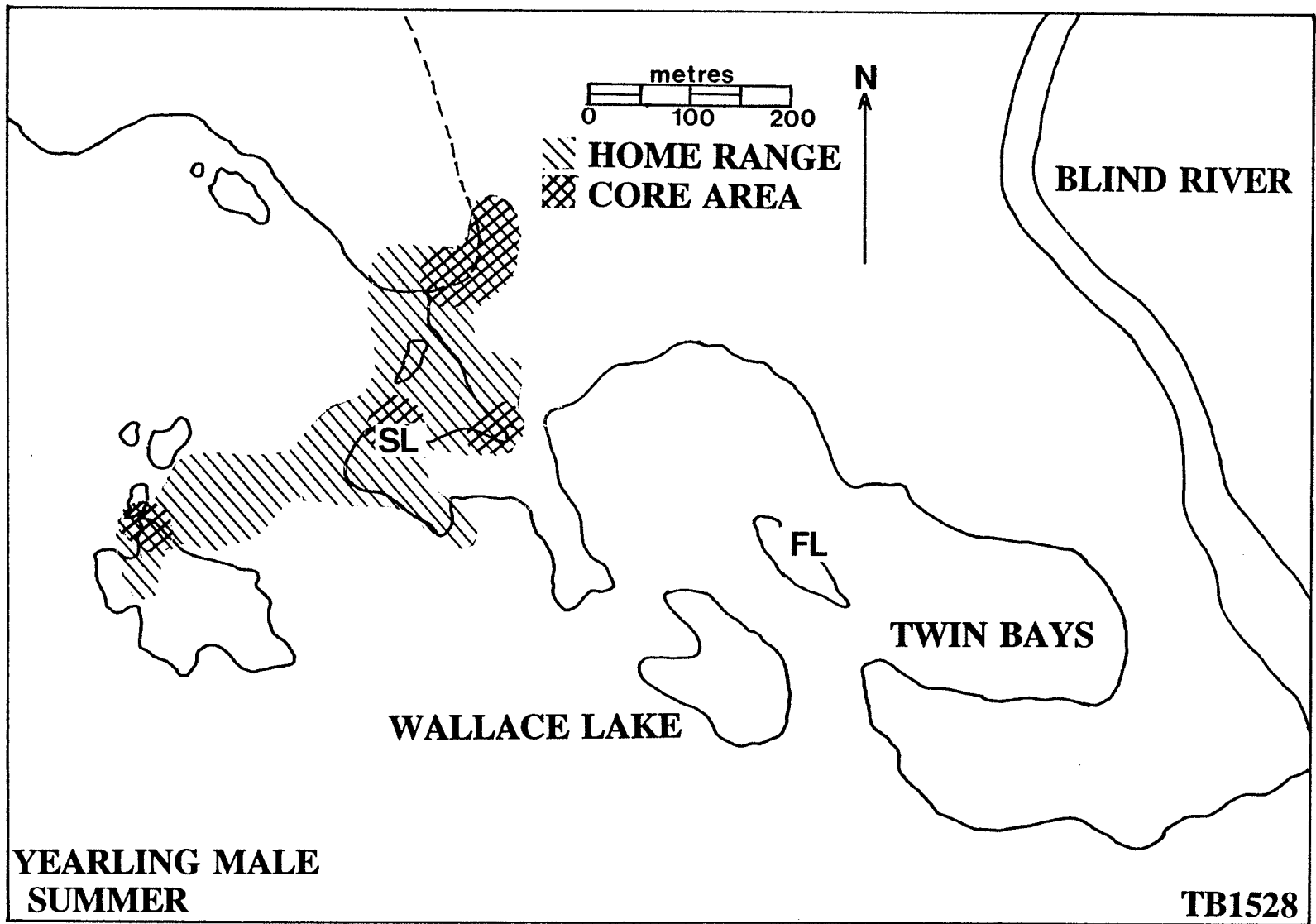
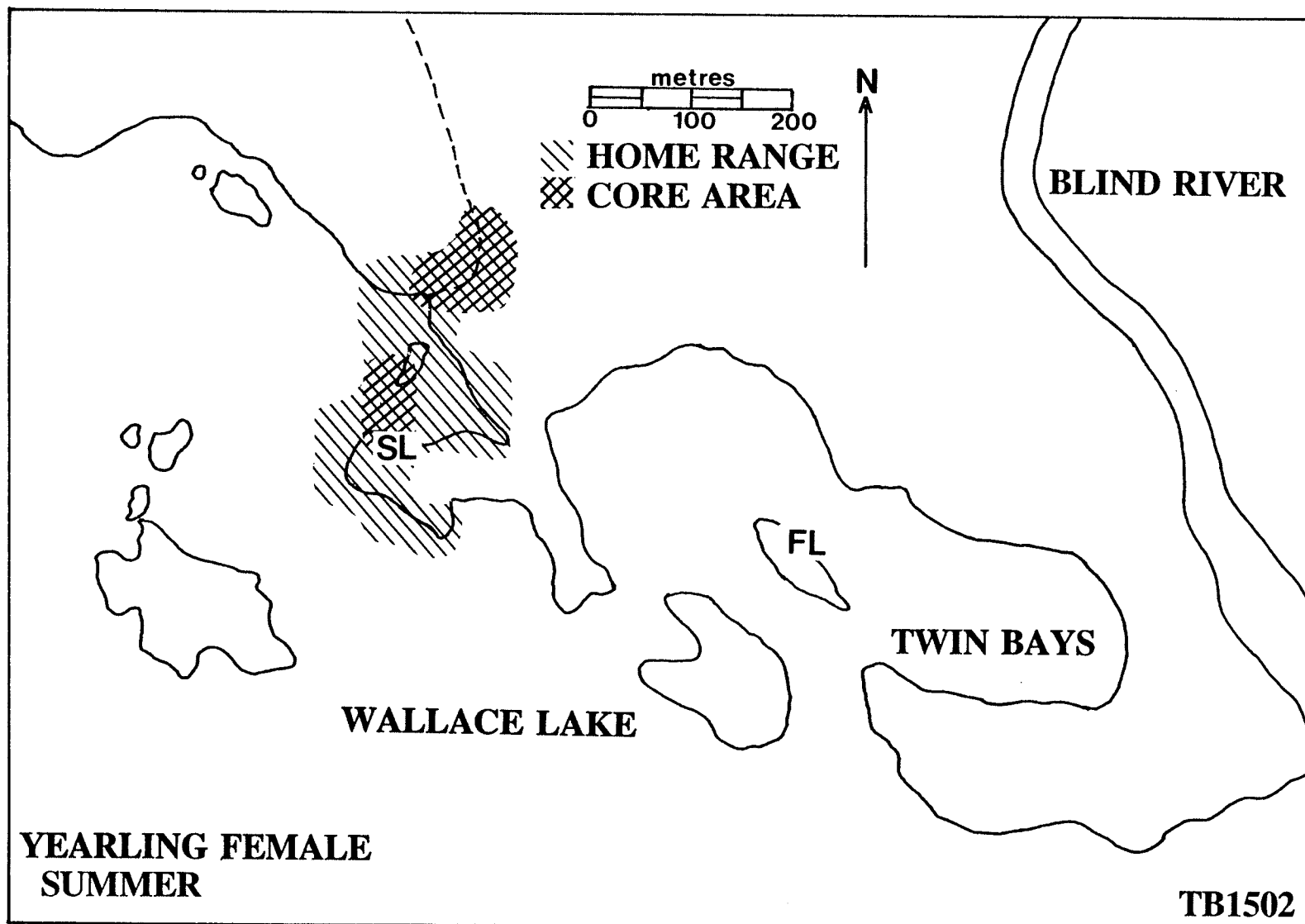


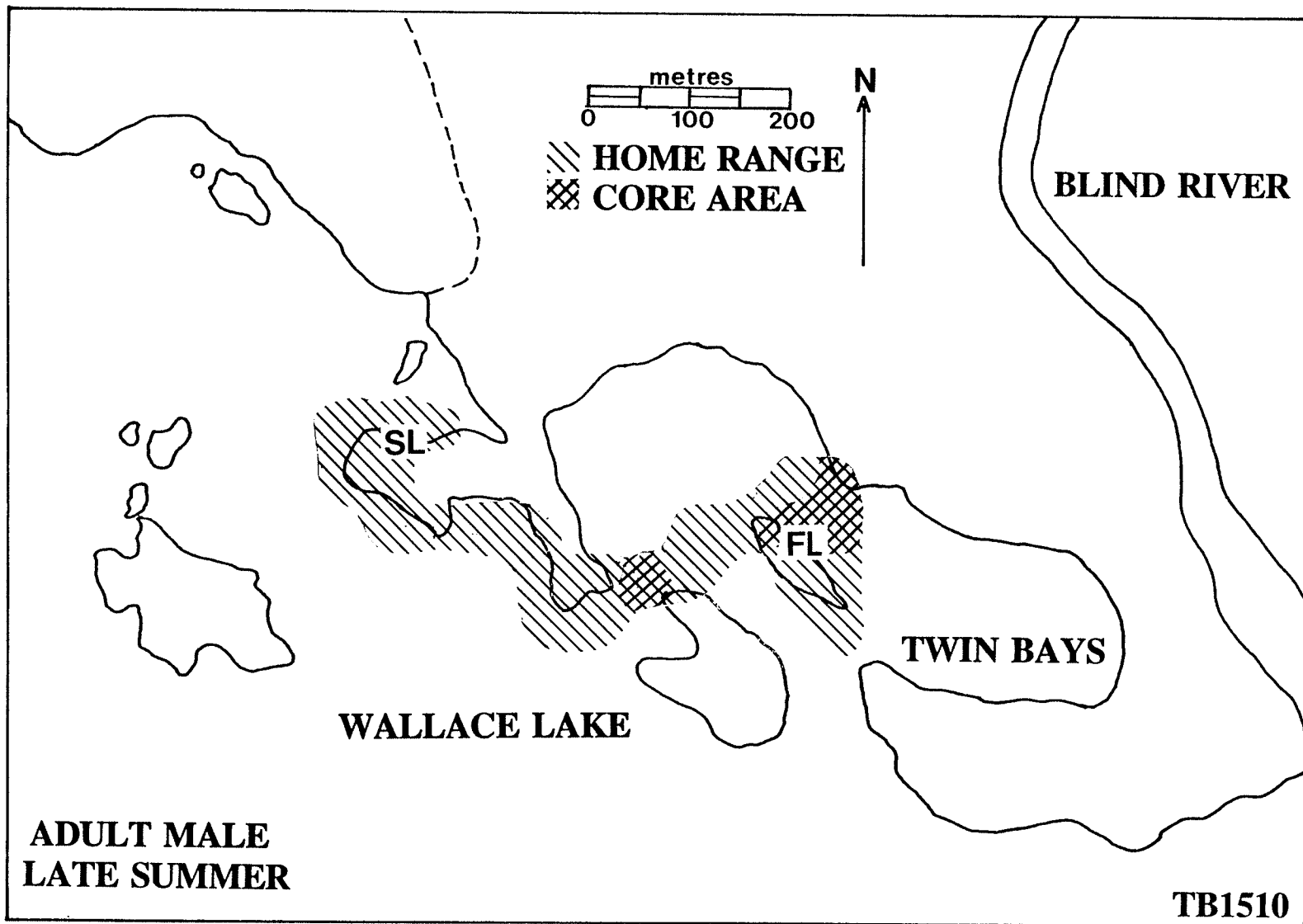
Figure 2. Maps of home range area for beavers in the Twin Bays Family for summer and fall, 1991. L indicates location of the lodge.

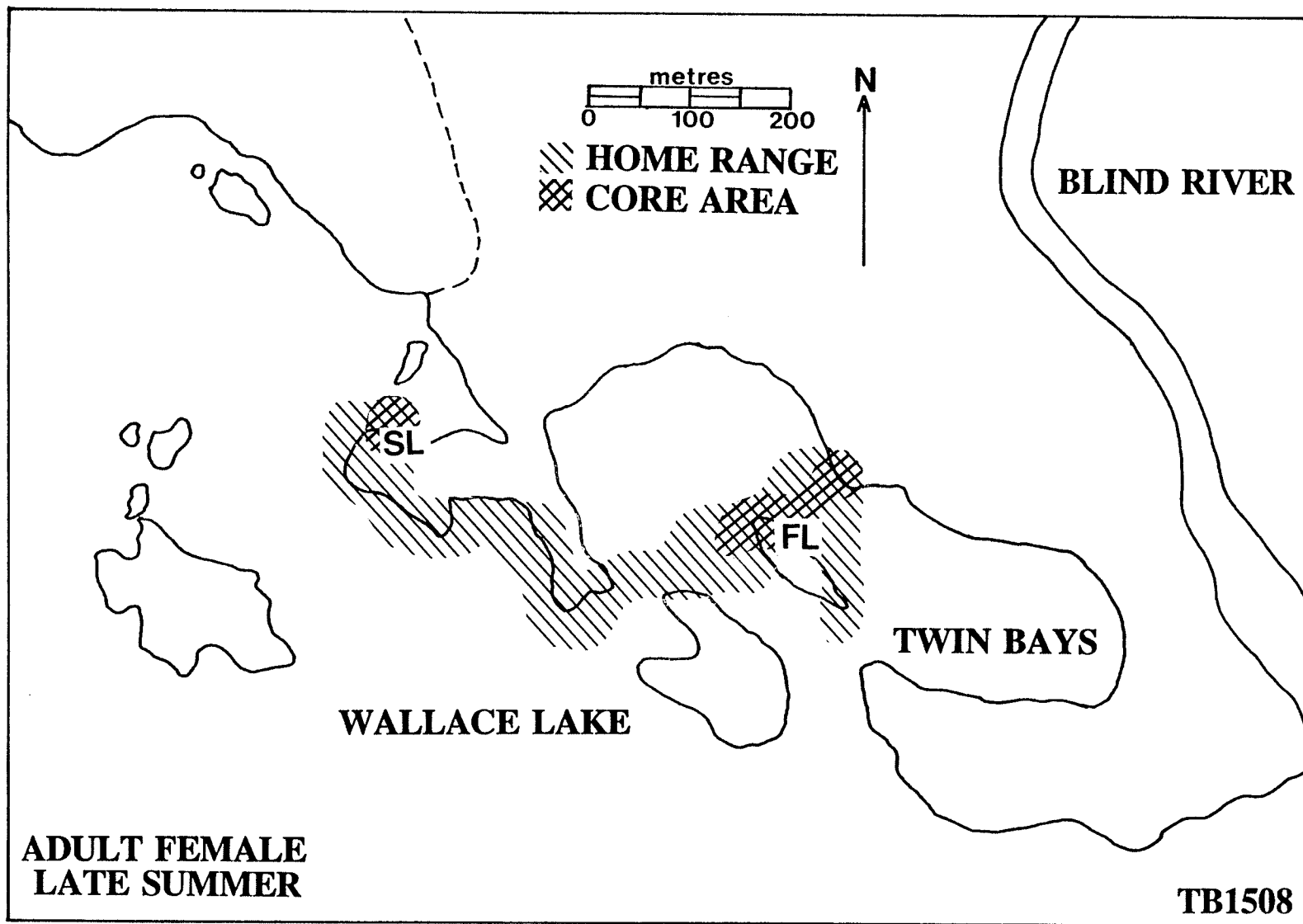


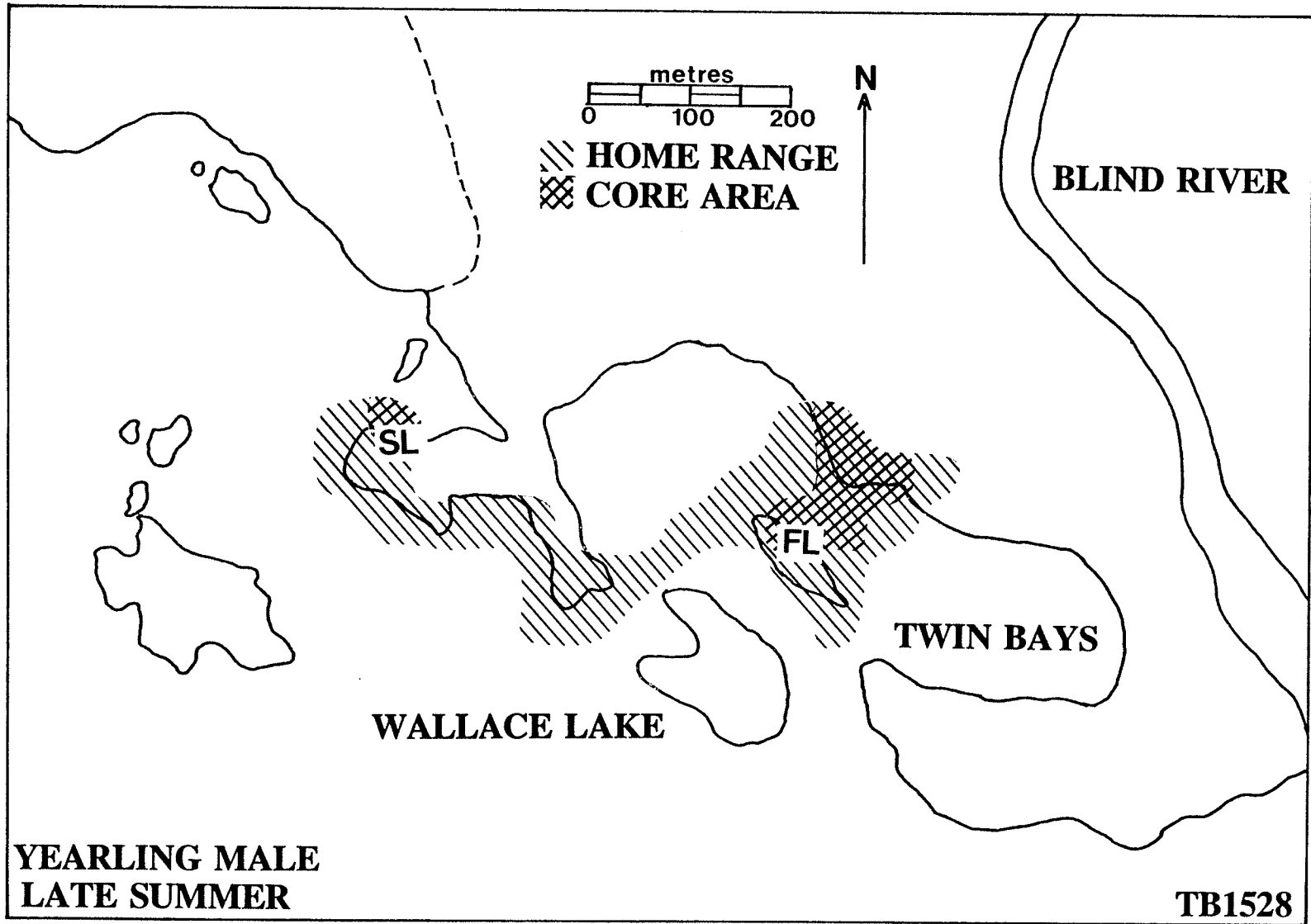


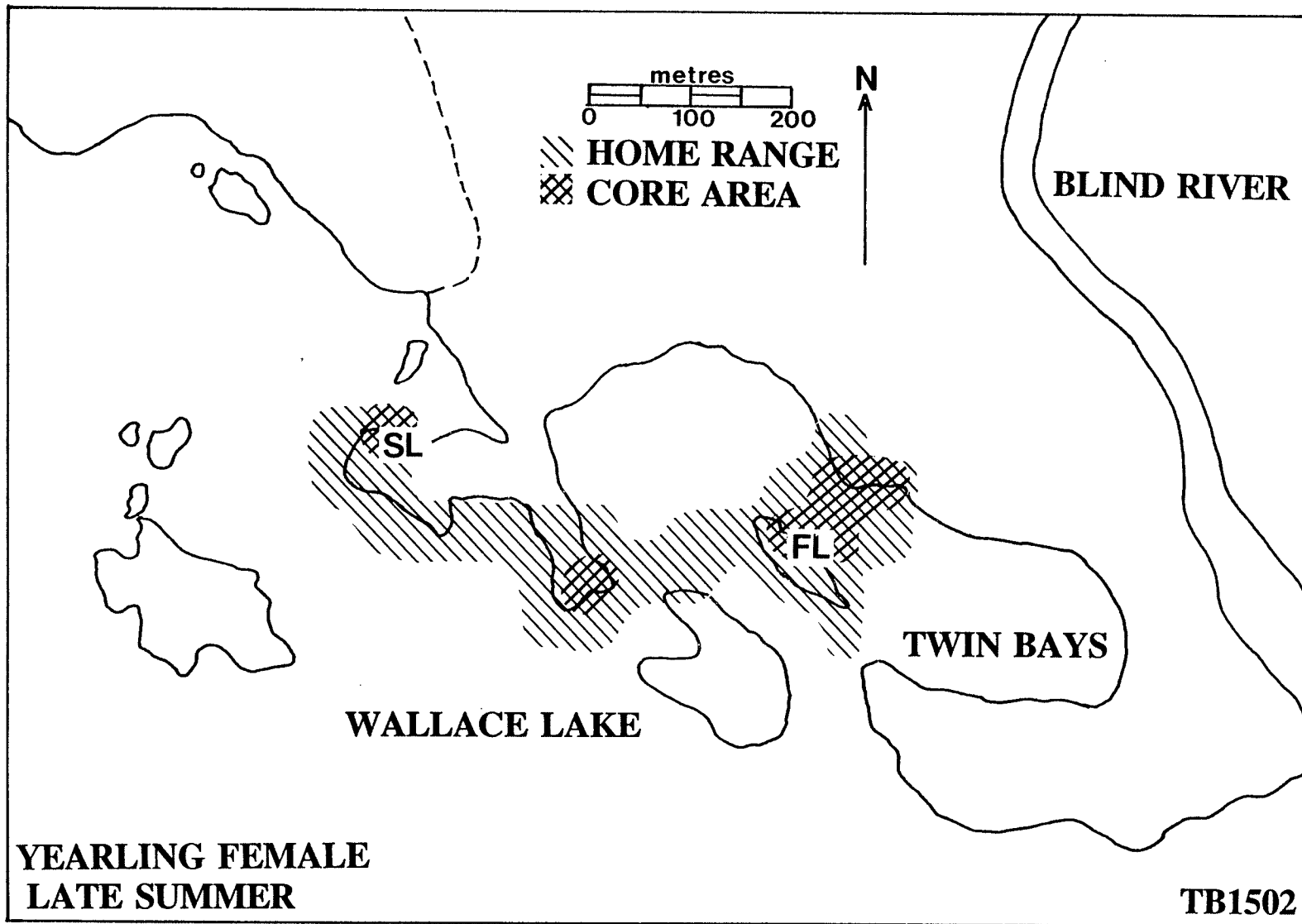


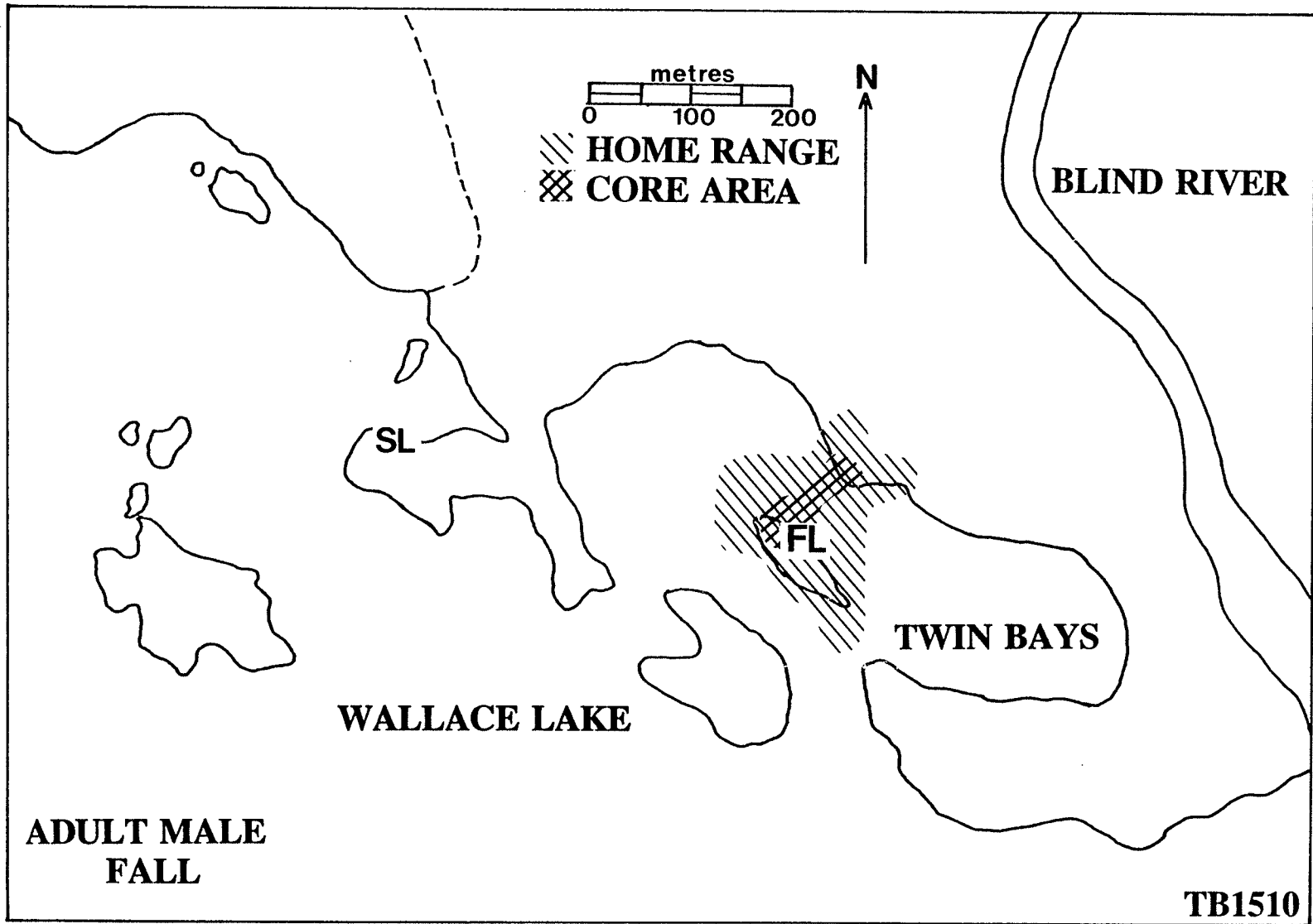


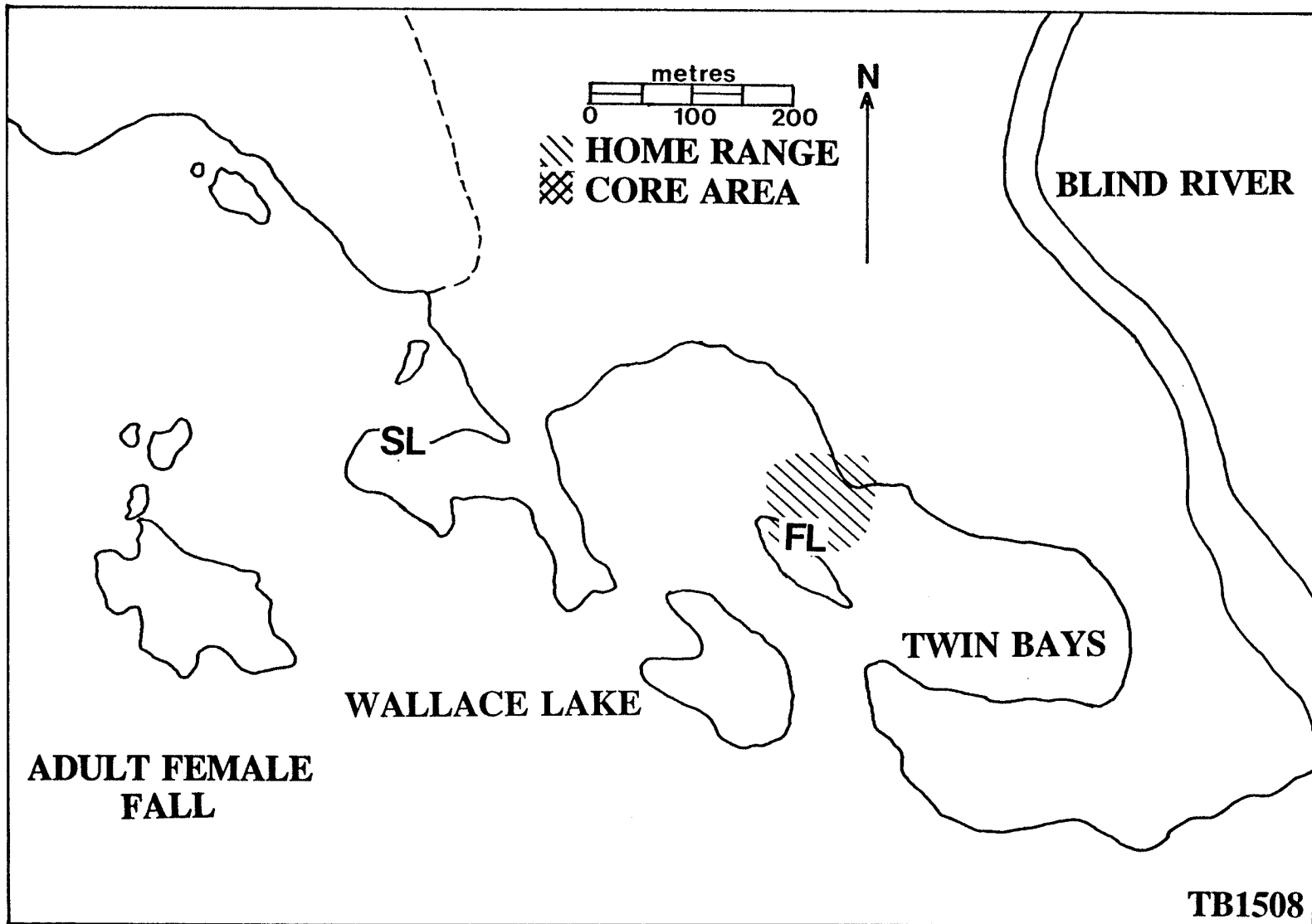


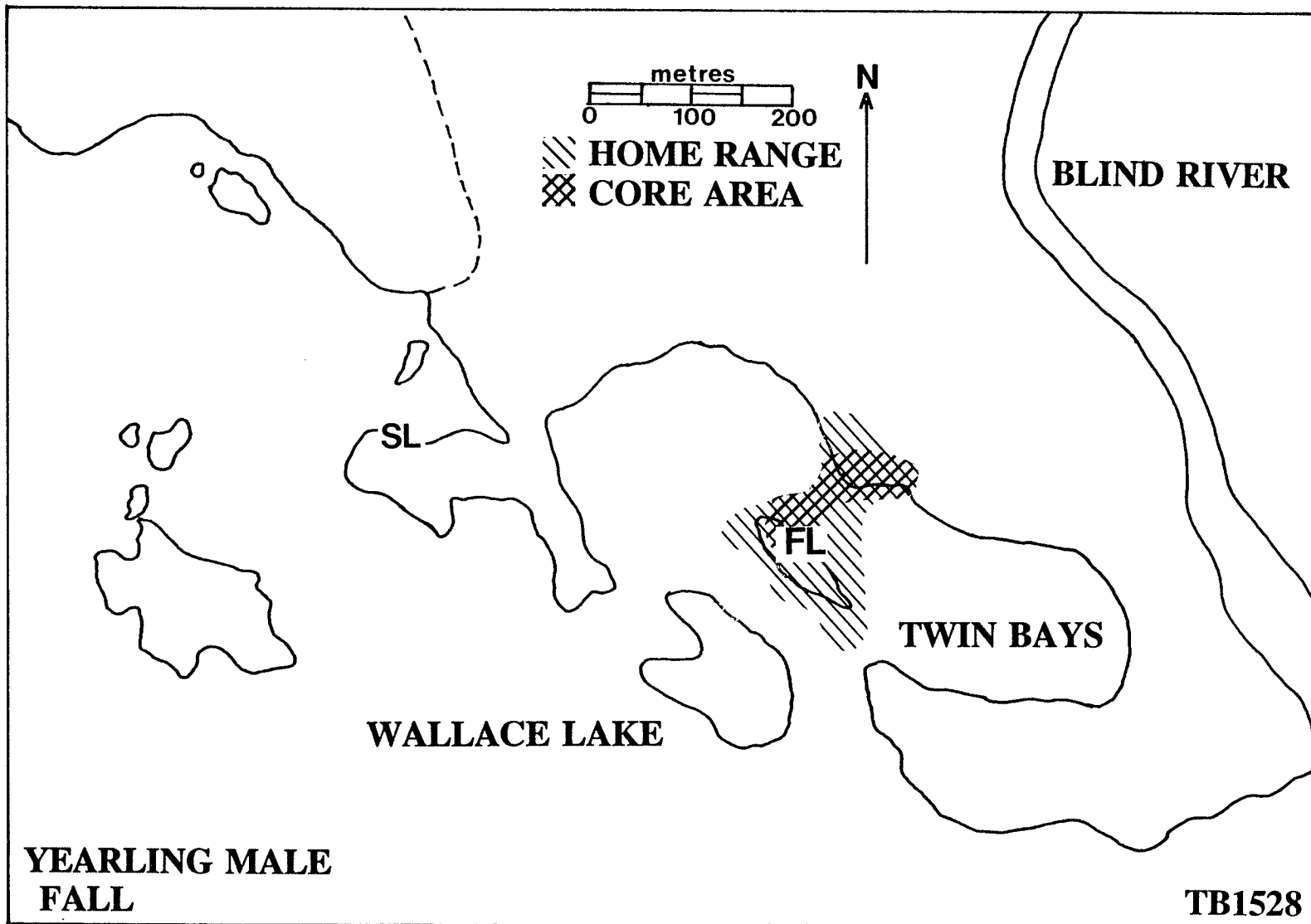


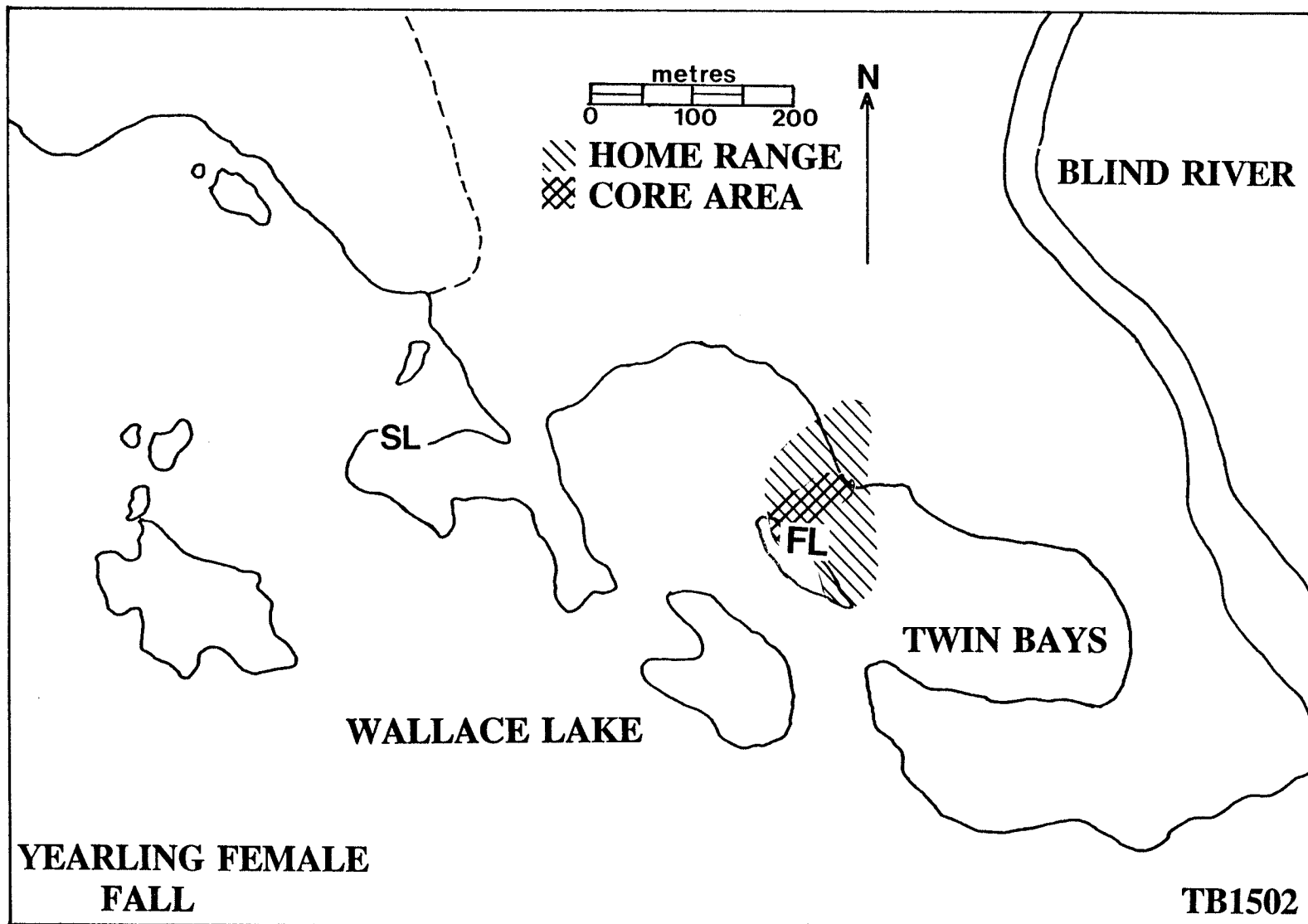


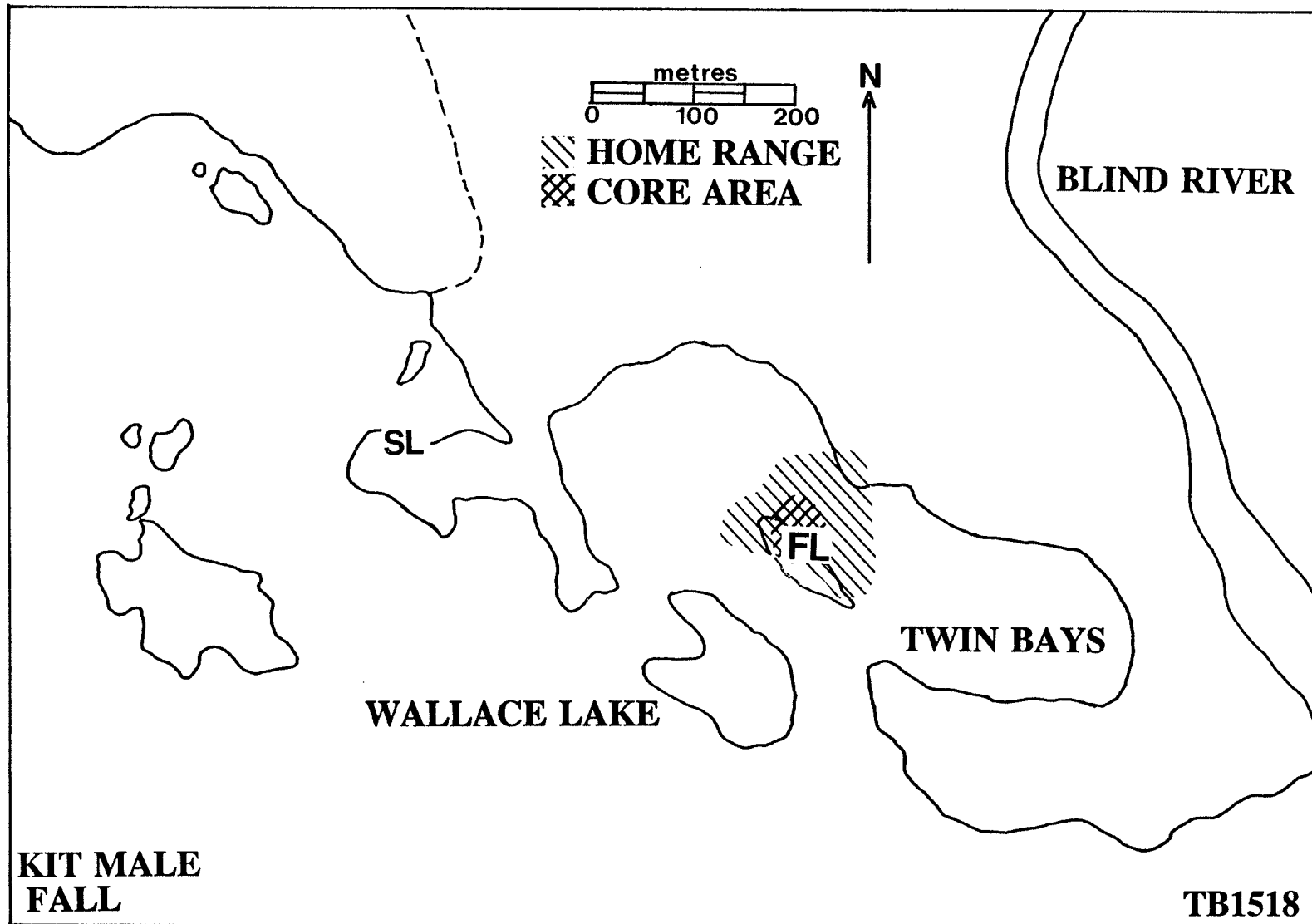


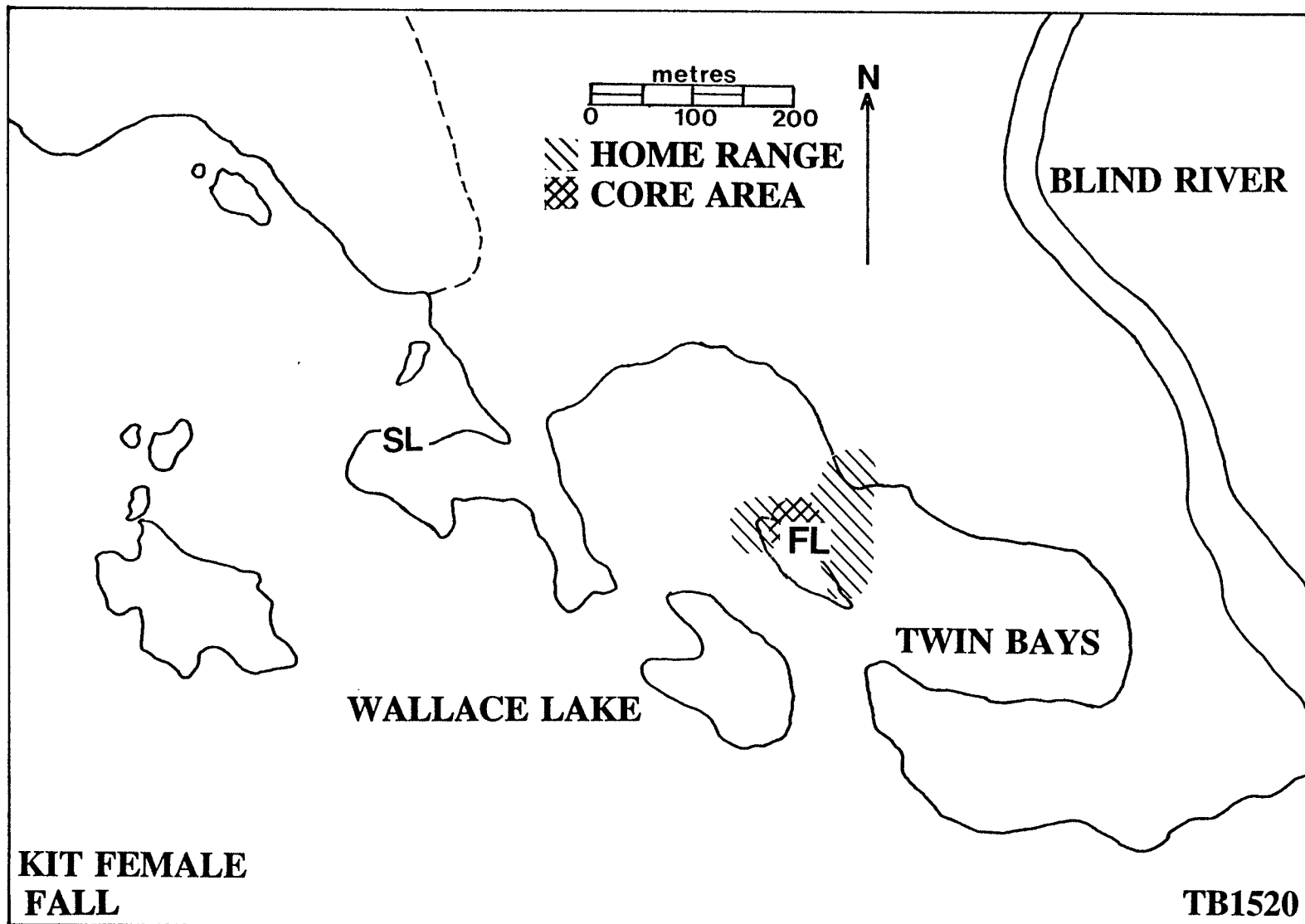












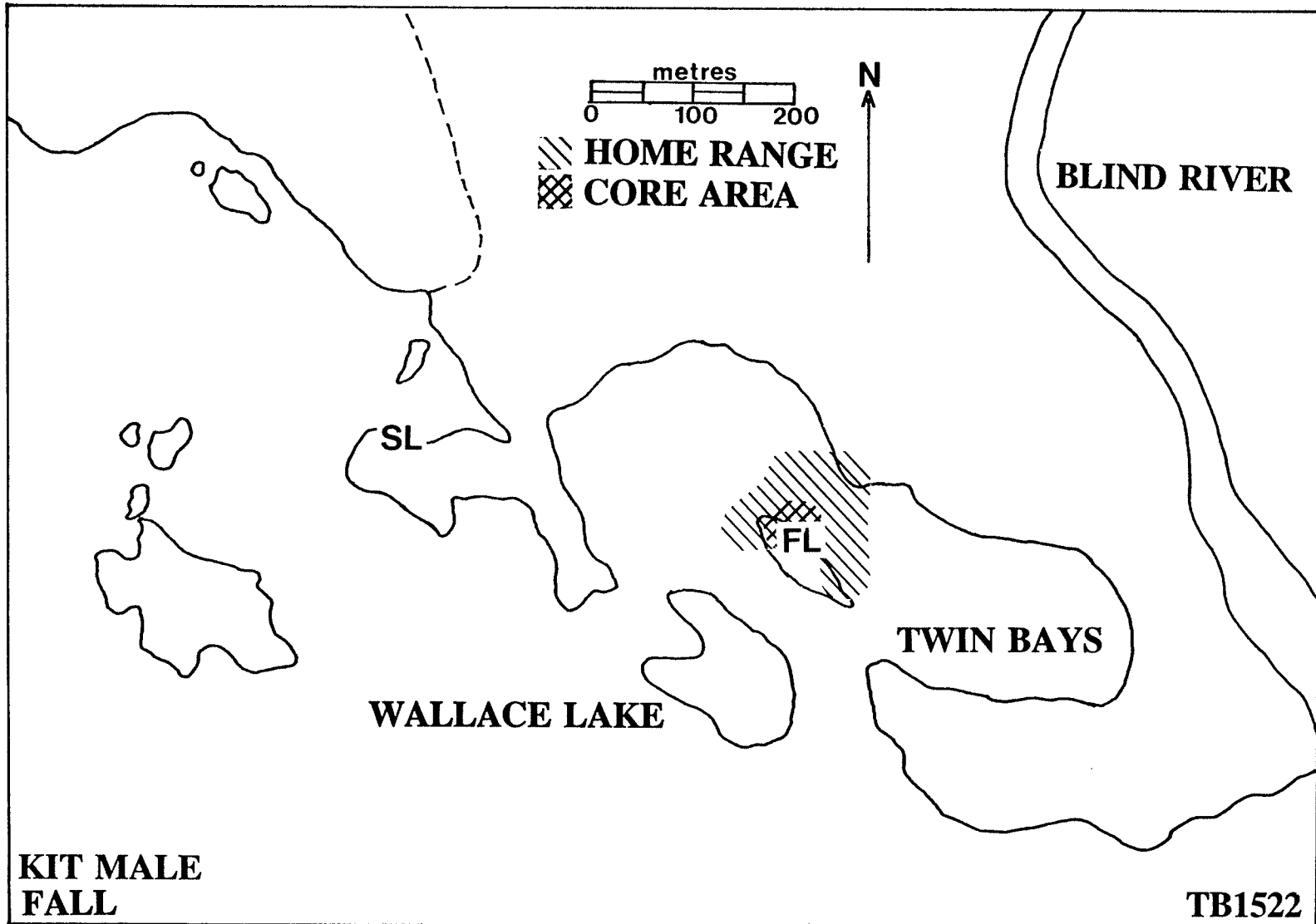
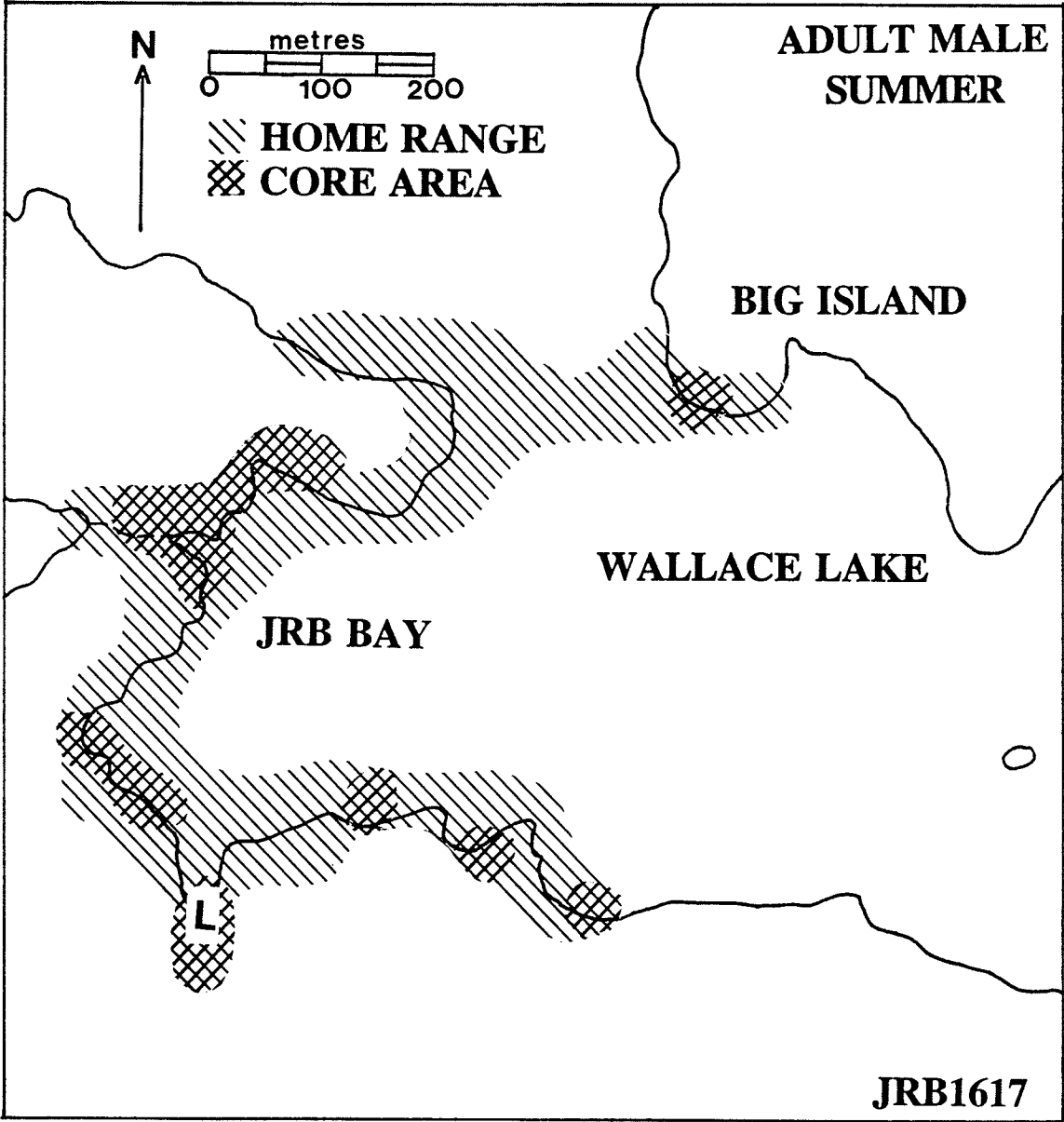
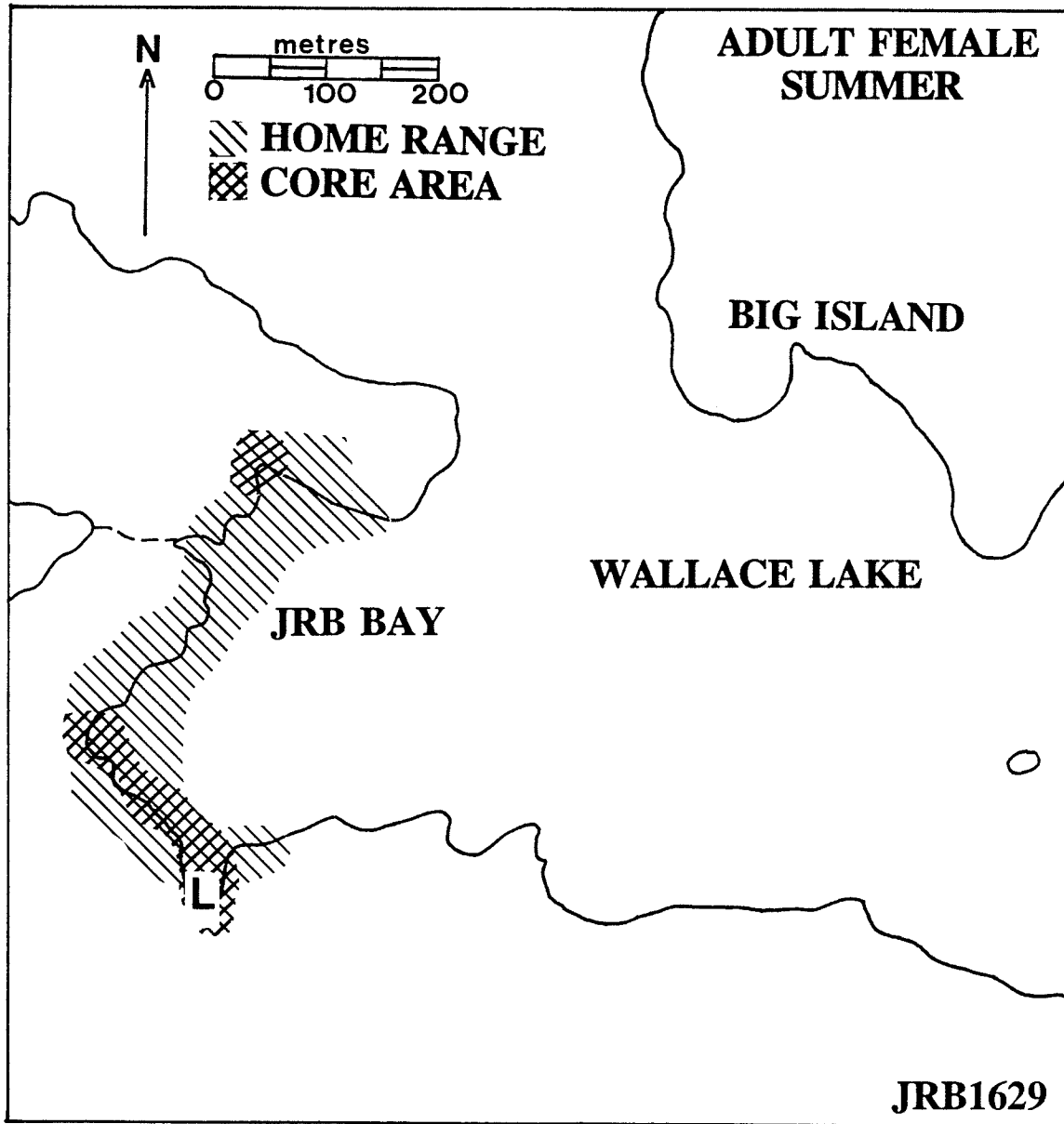
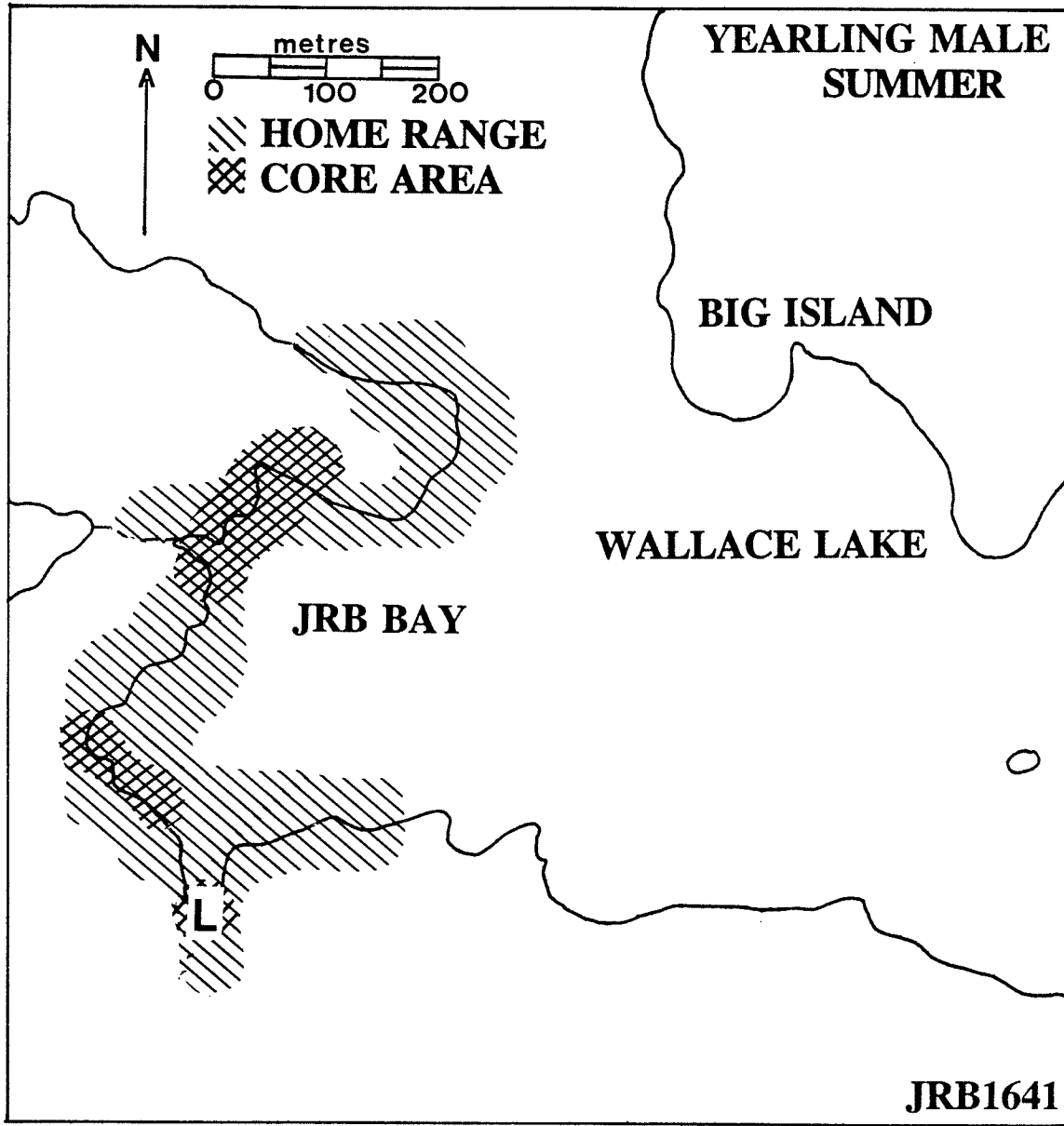
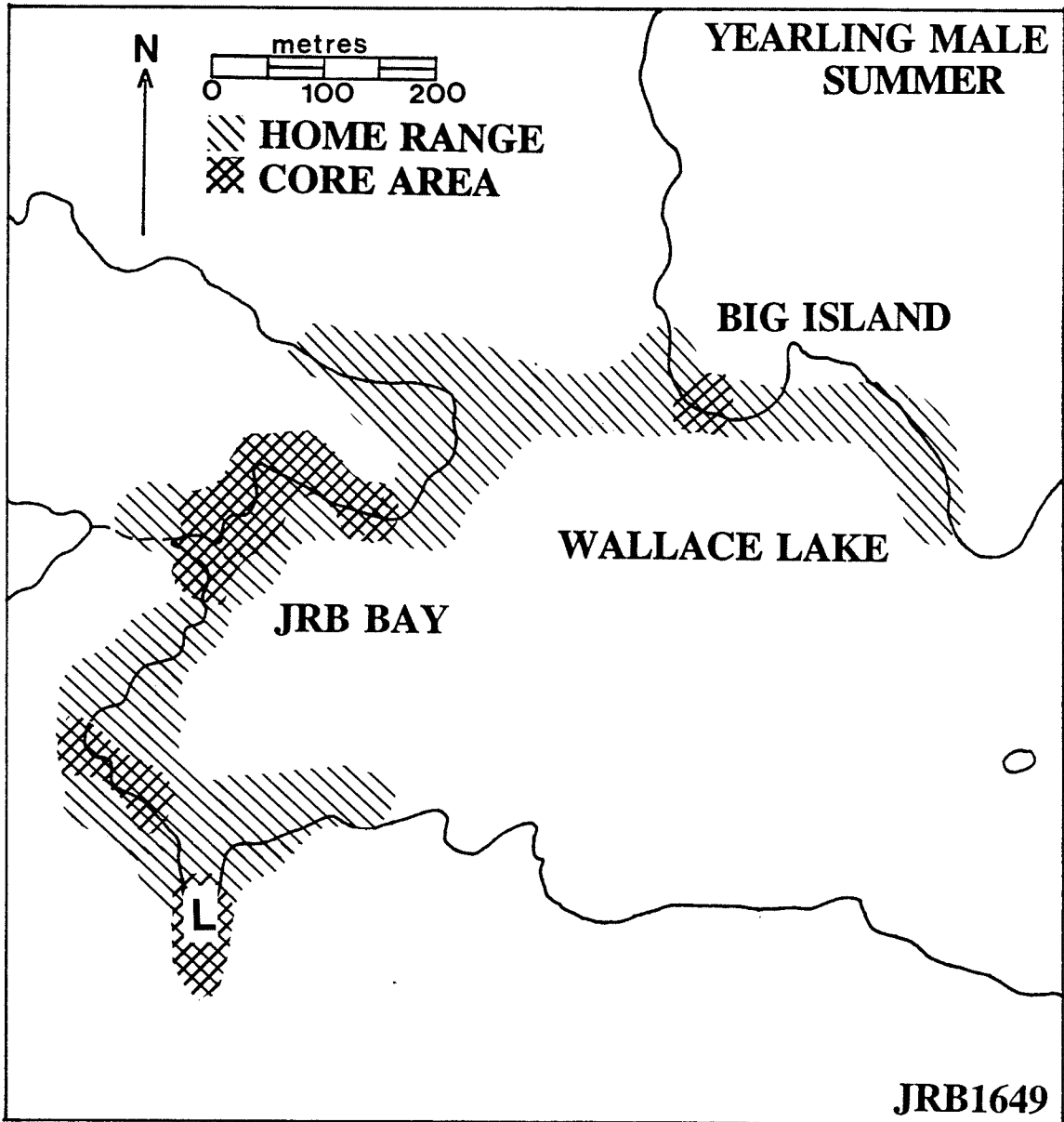


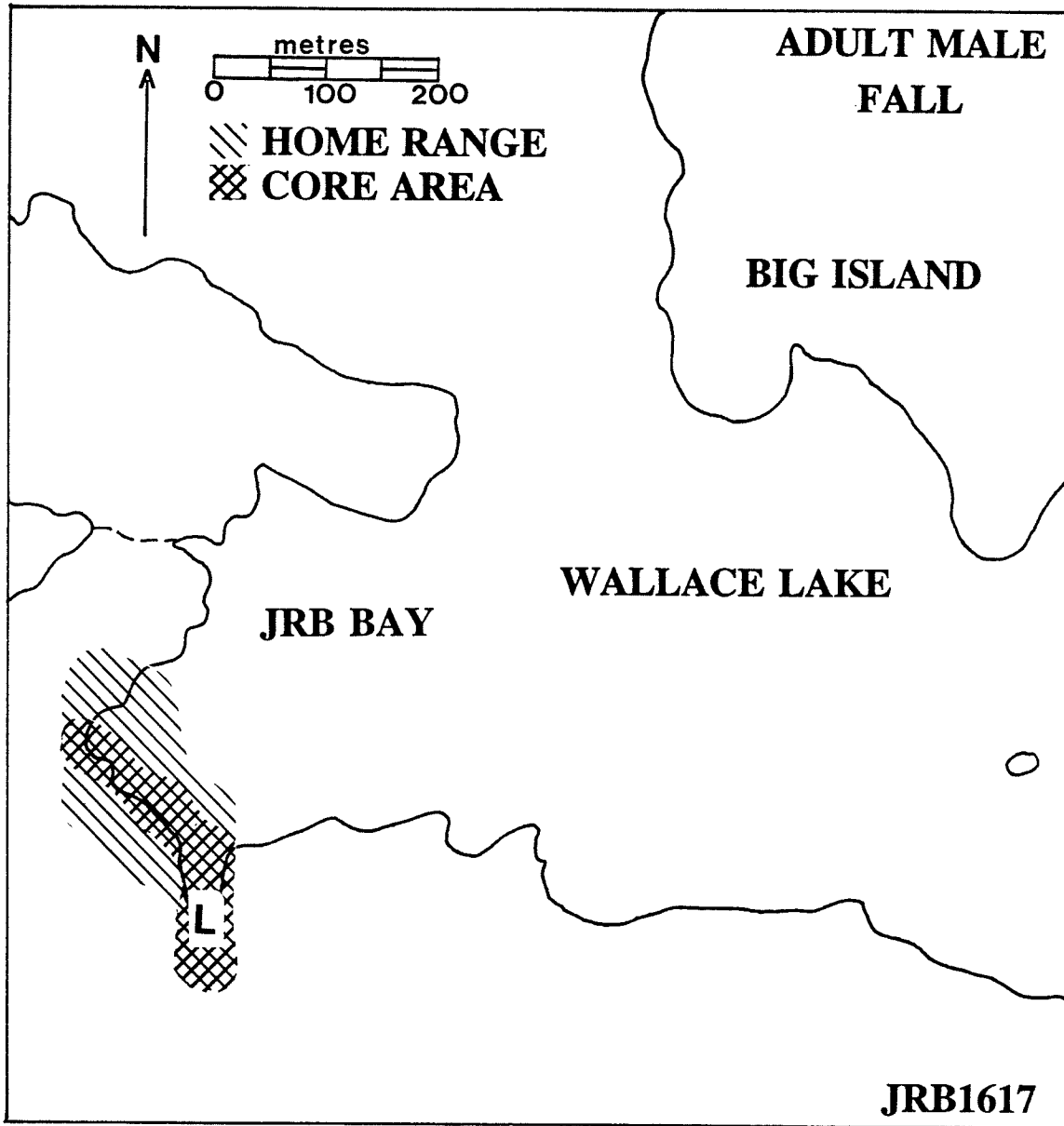
Figure 3. Maps of home range area for beavers in the JRB Family for summer and fall, 1990. L indicates location of the lodge.

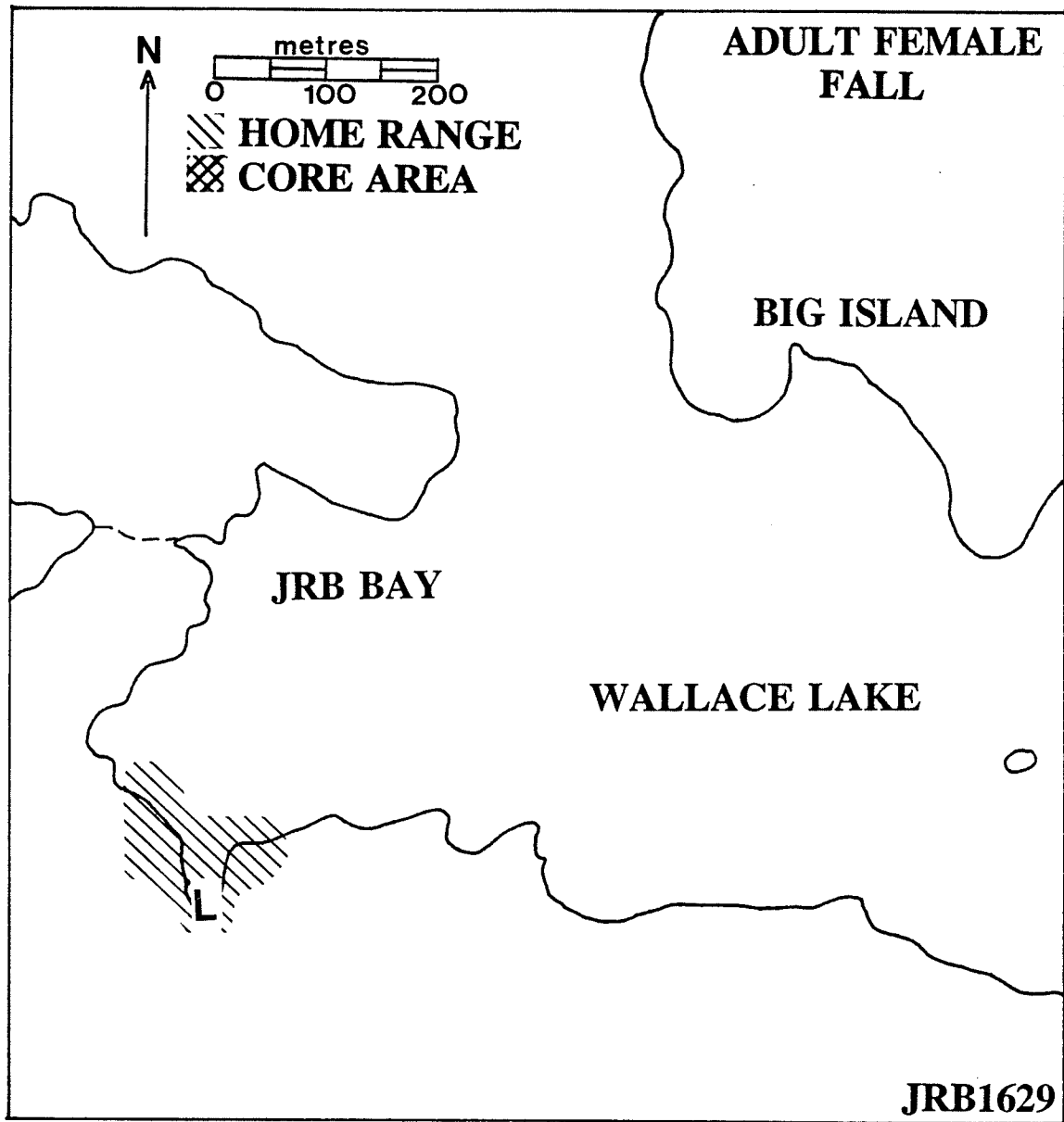


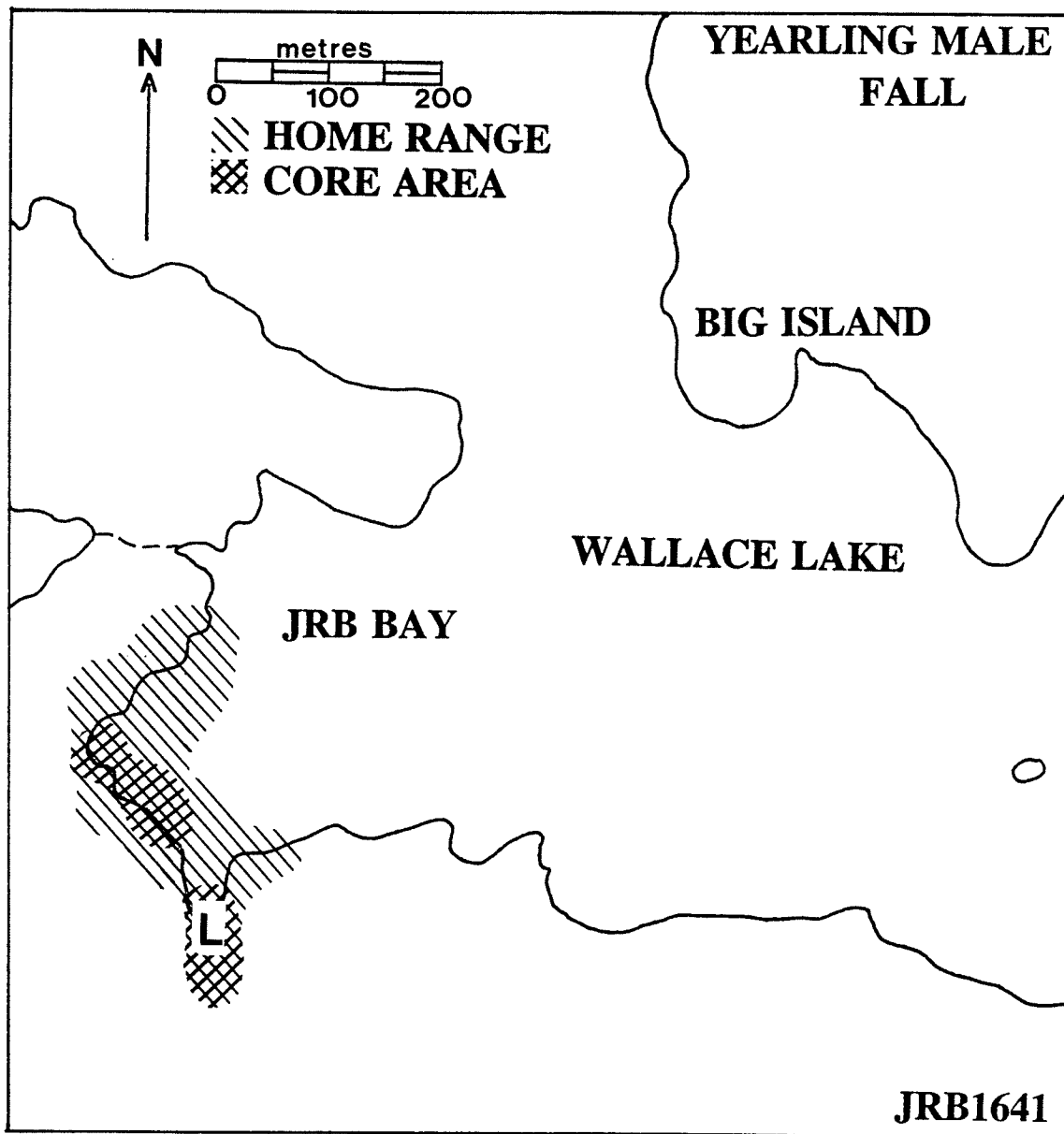












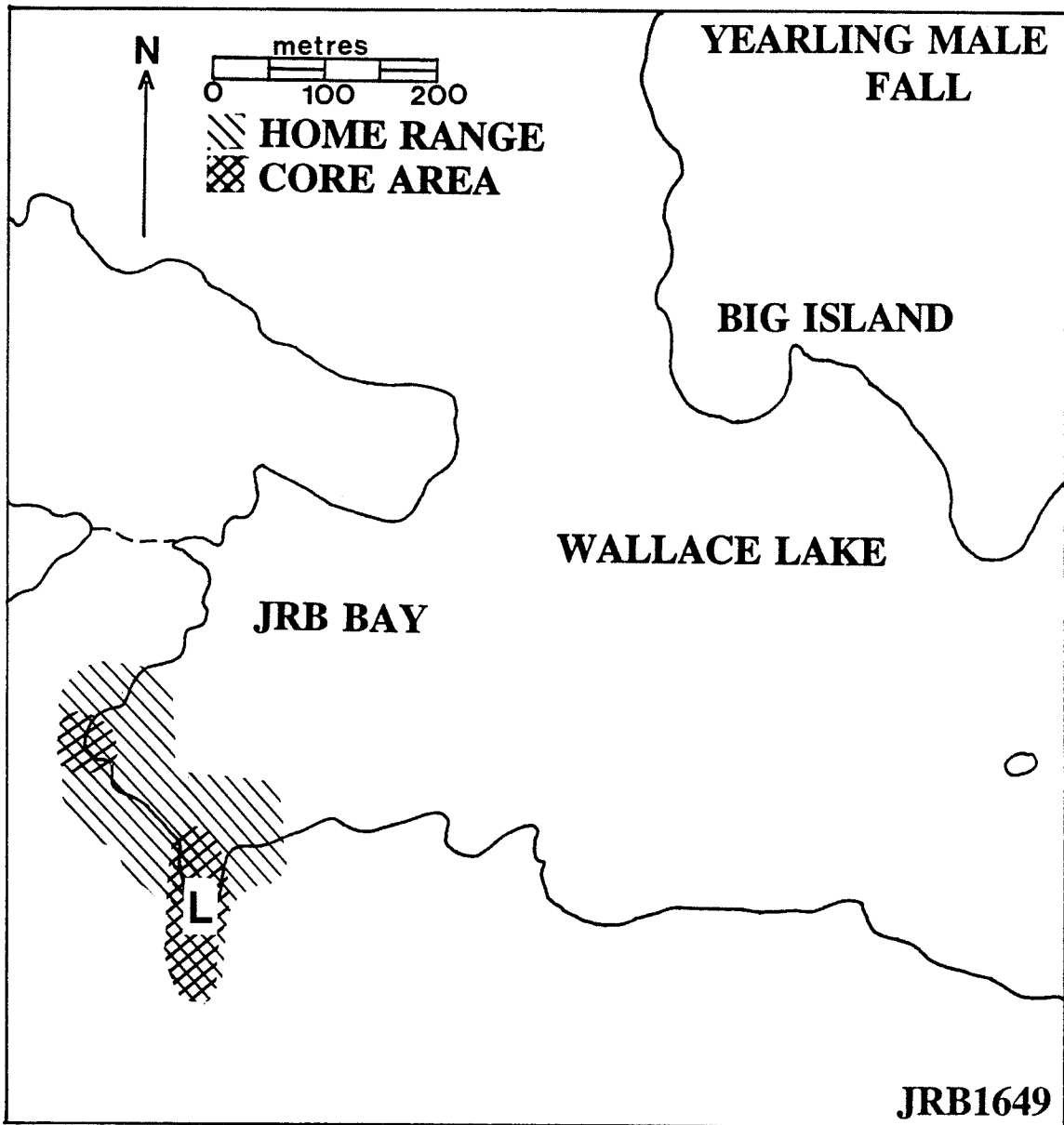
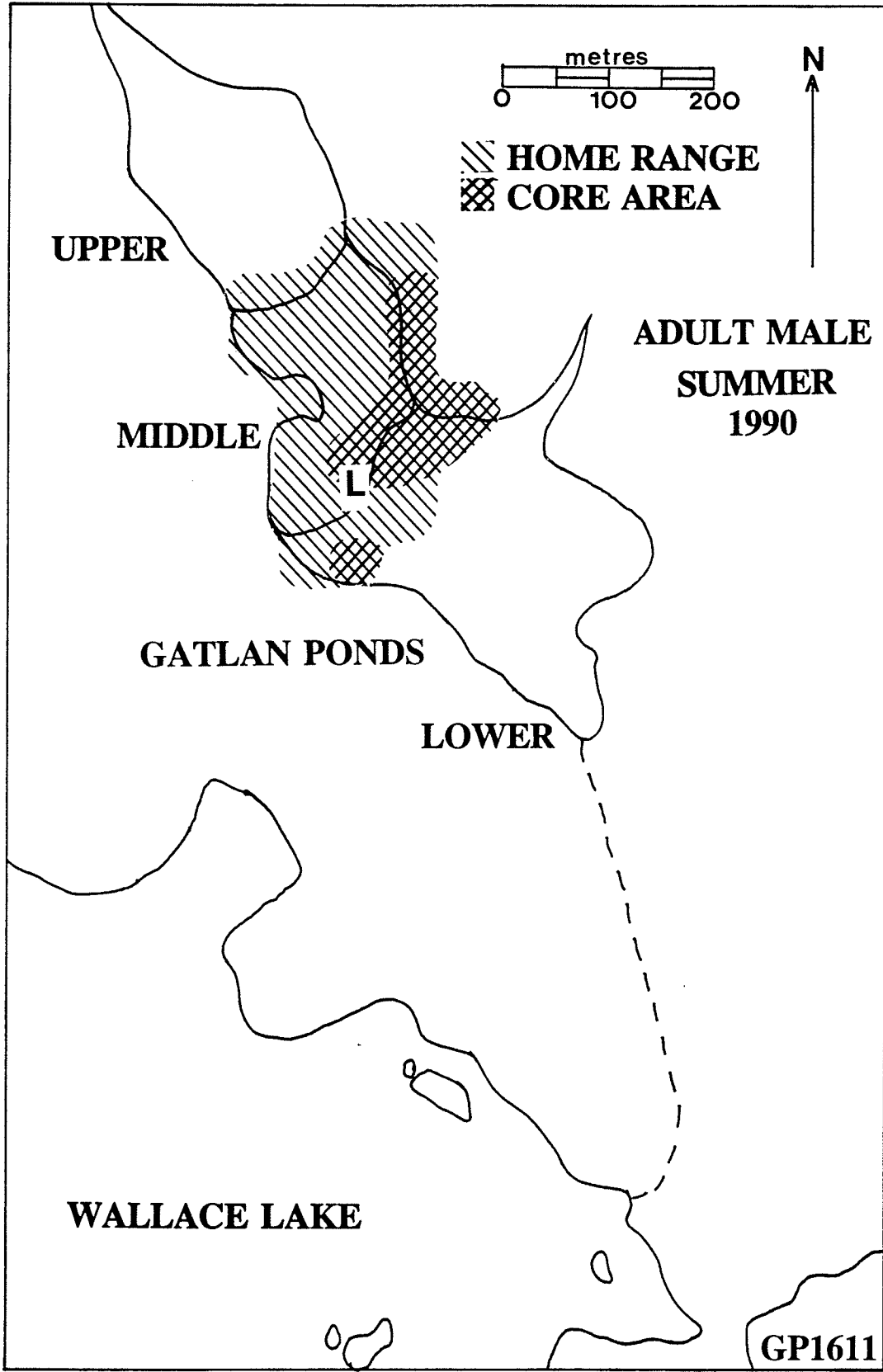
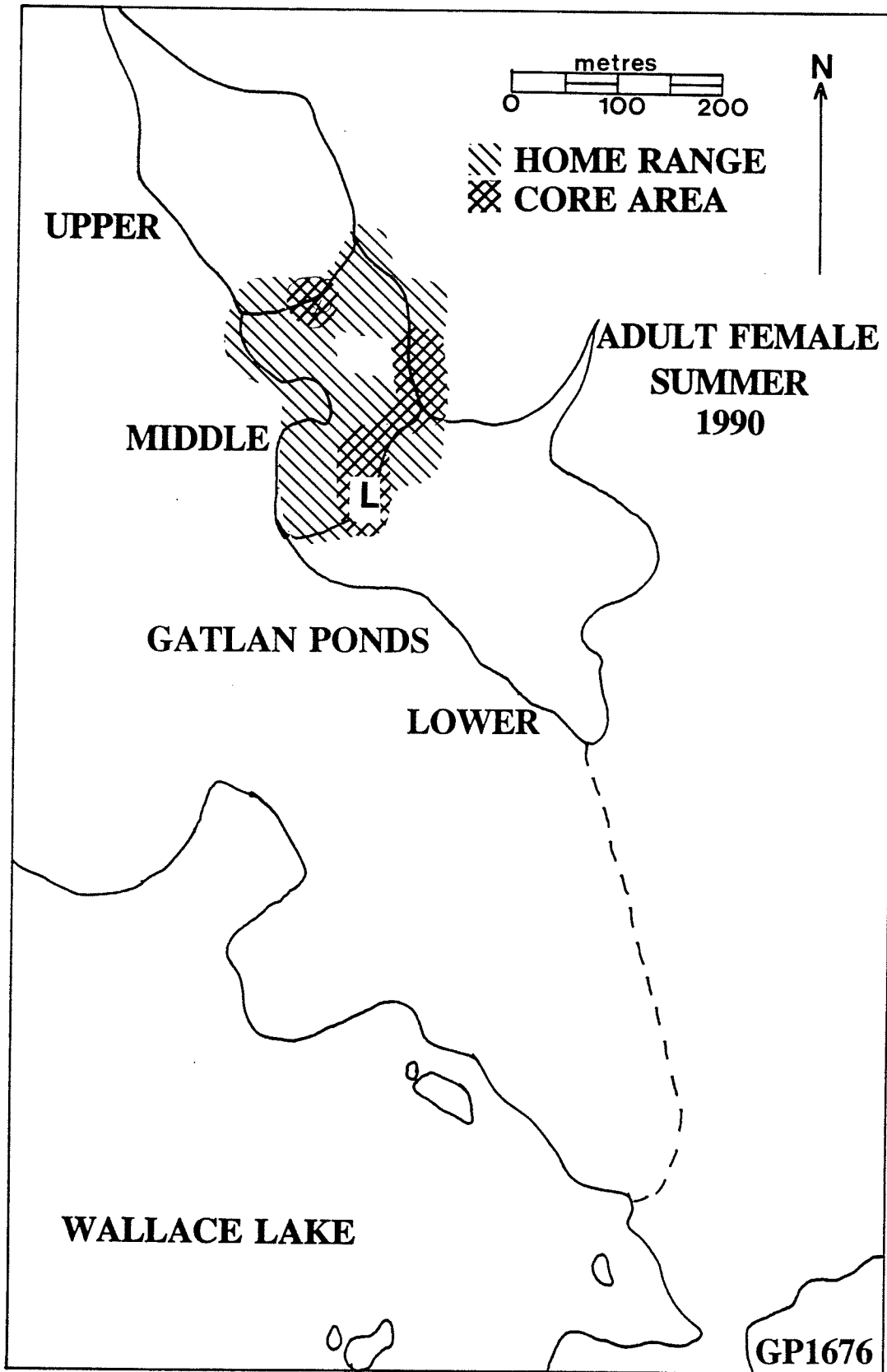
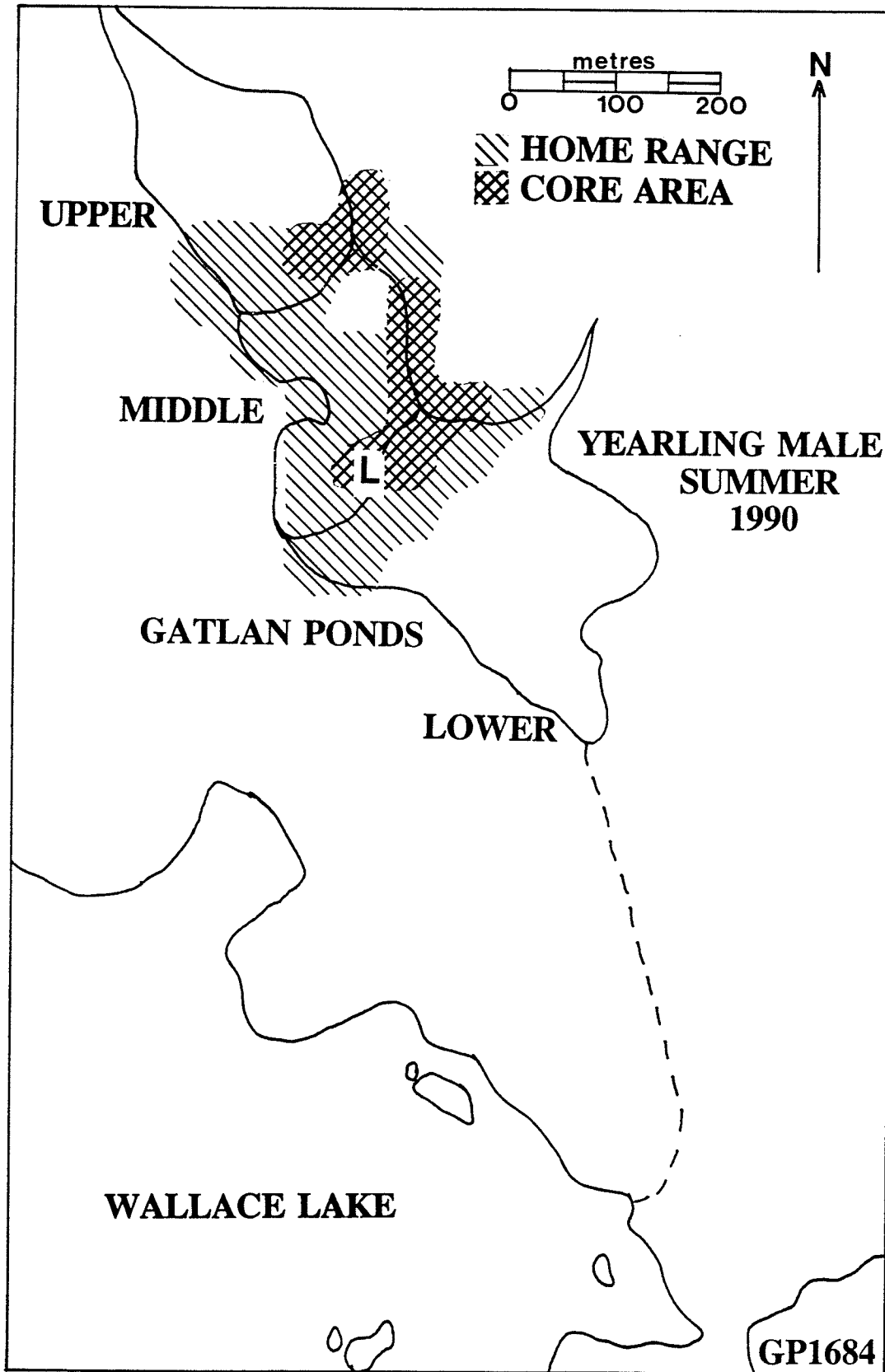
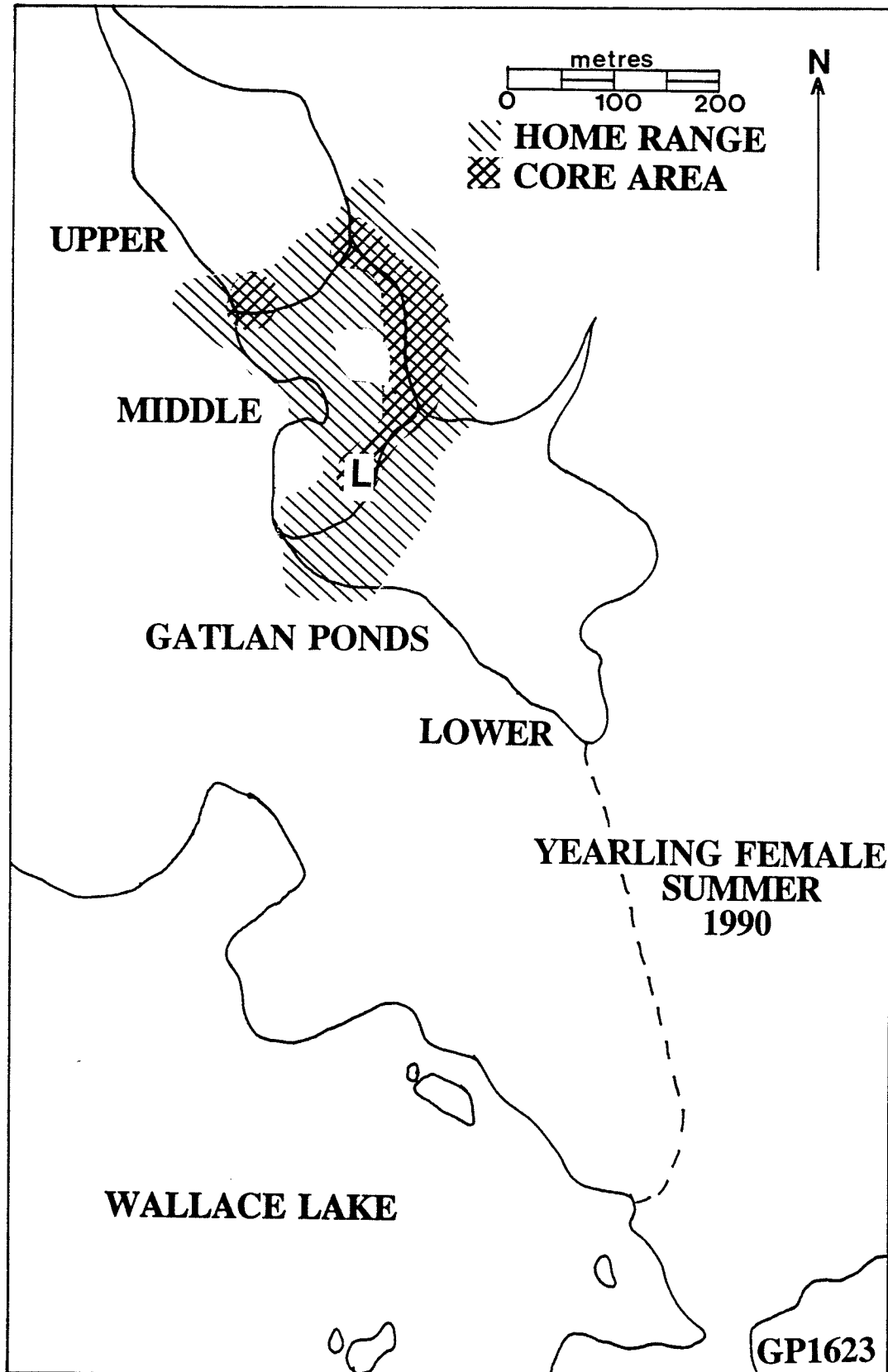


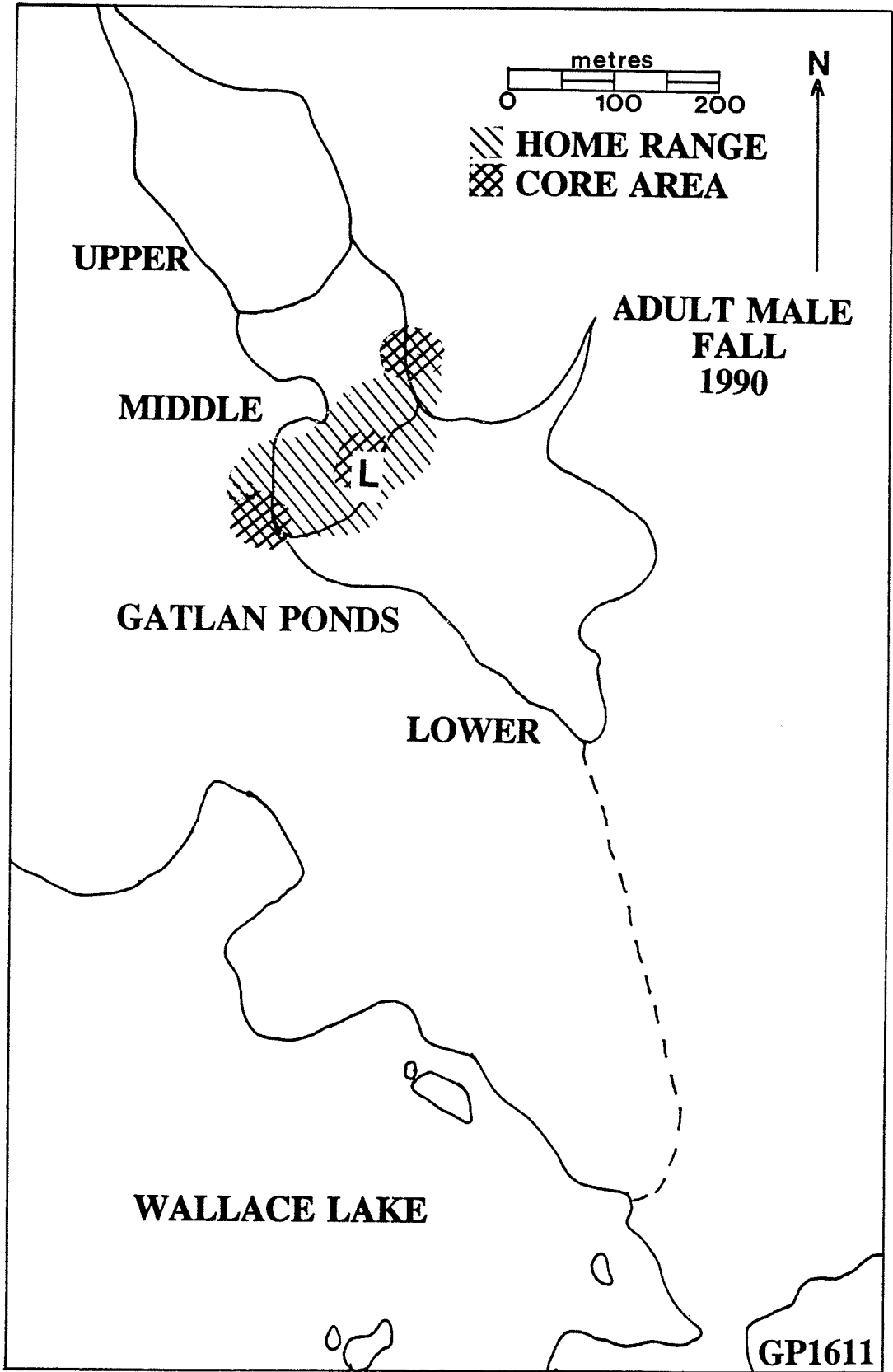
Figure 4. Maps of home range area for beavers in the Gatlan Pond Family for summer and fall, 1990. L indicates location of the lodge.

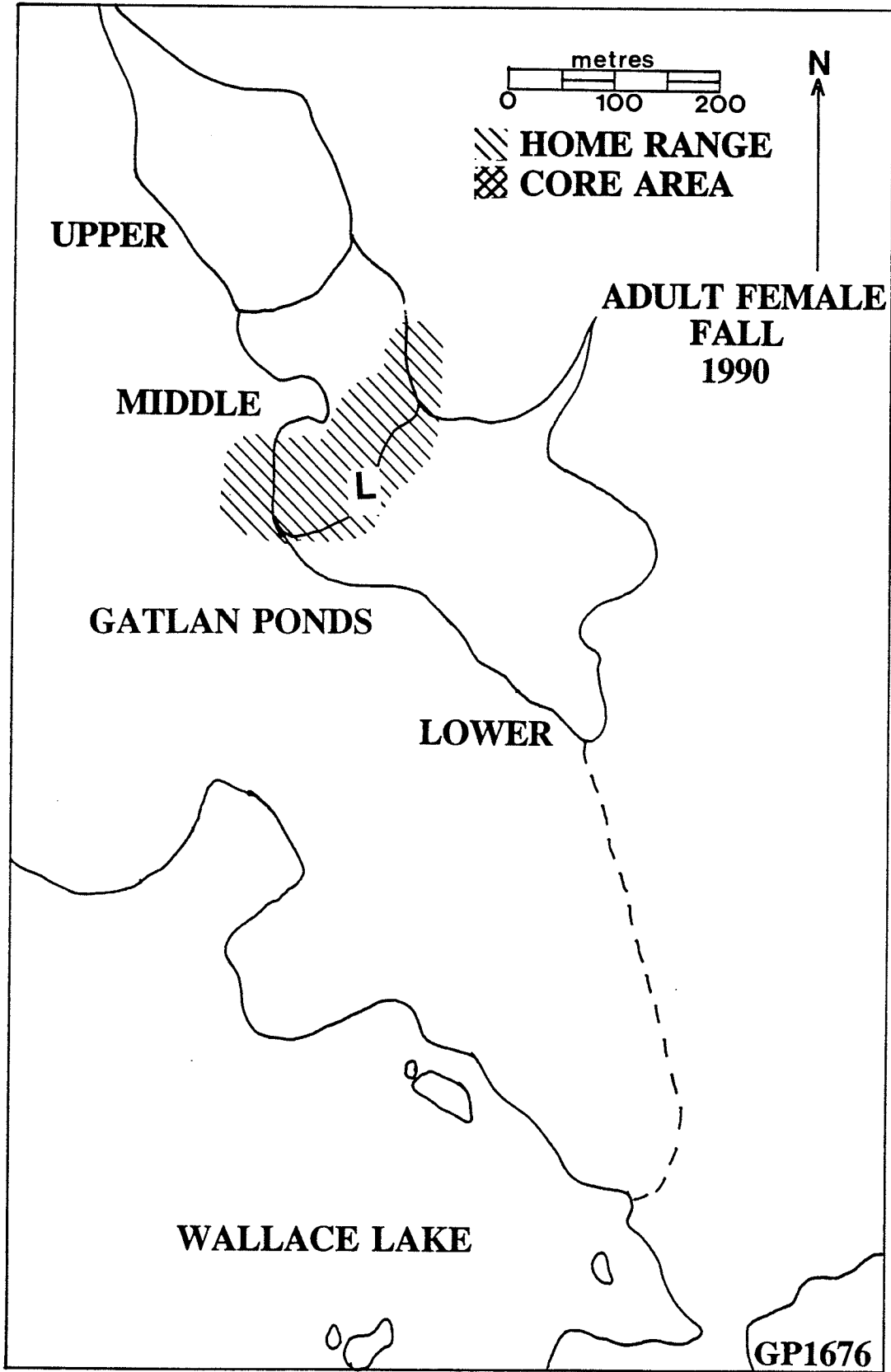












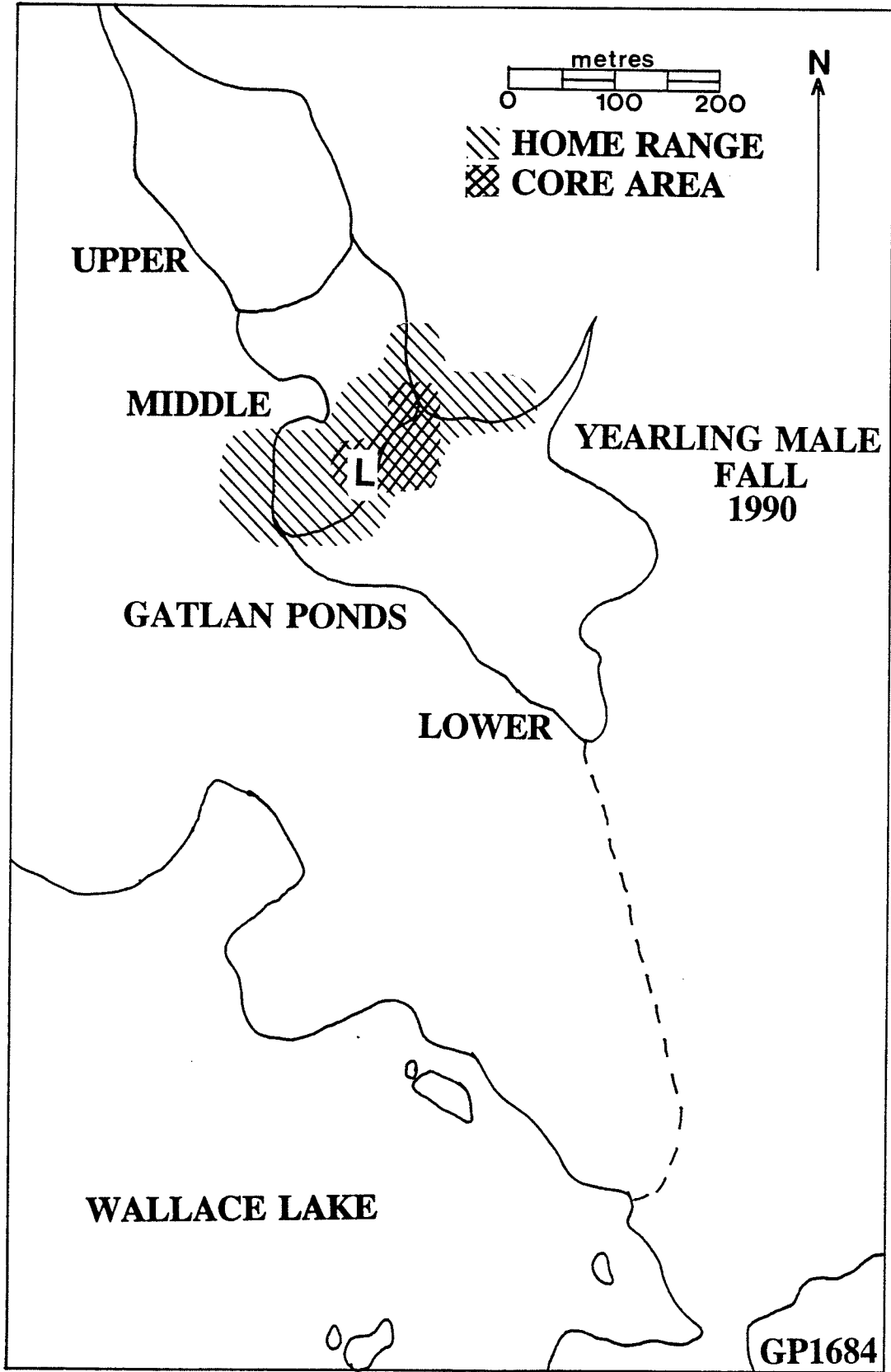
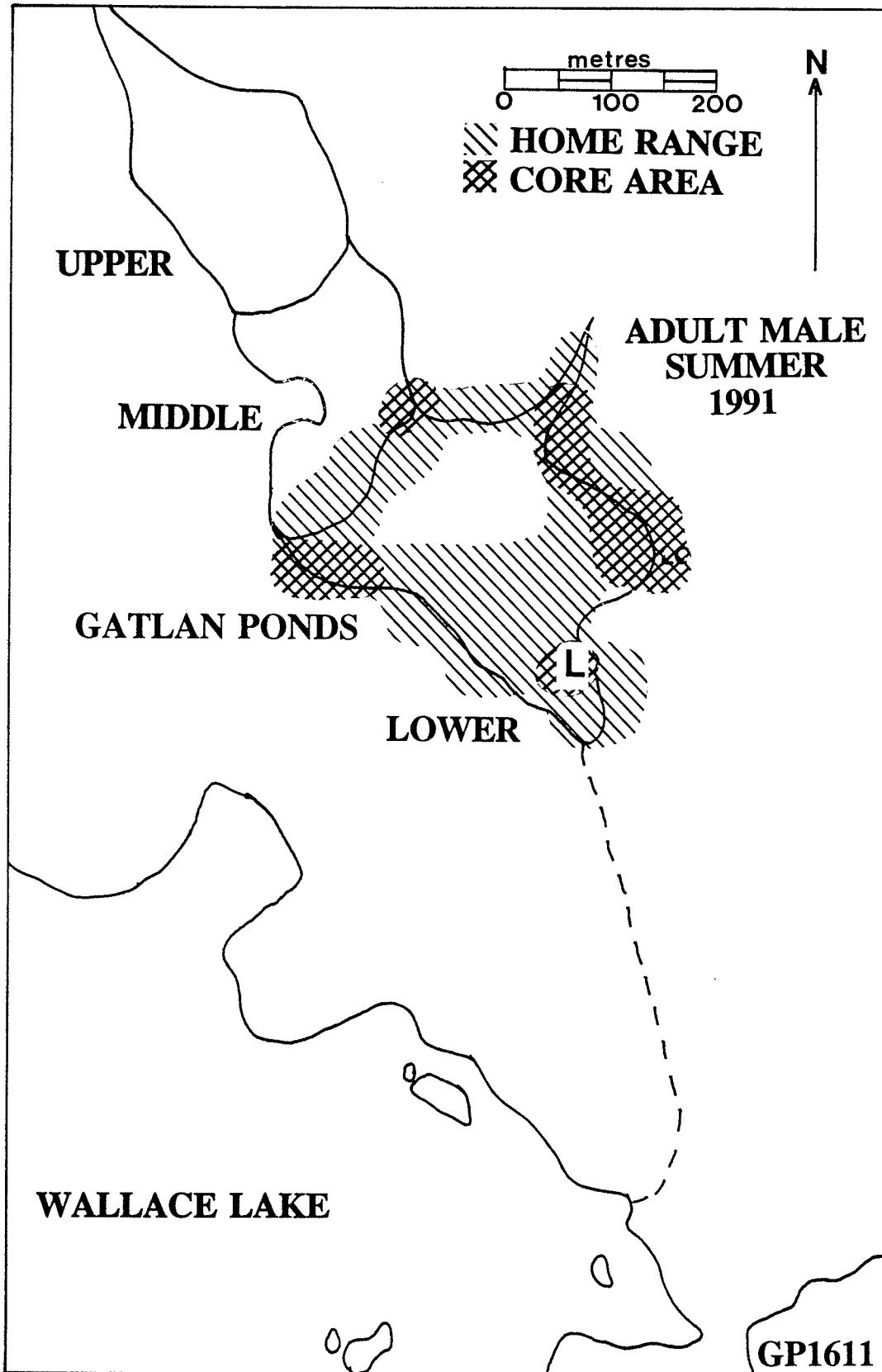
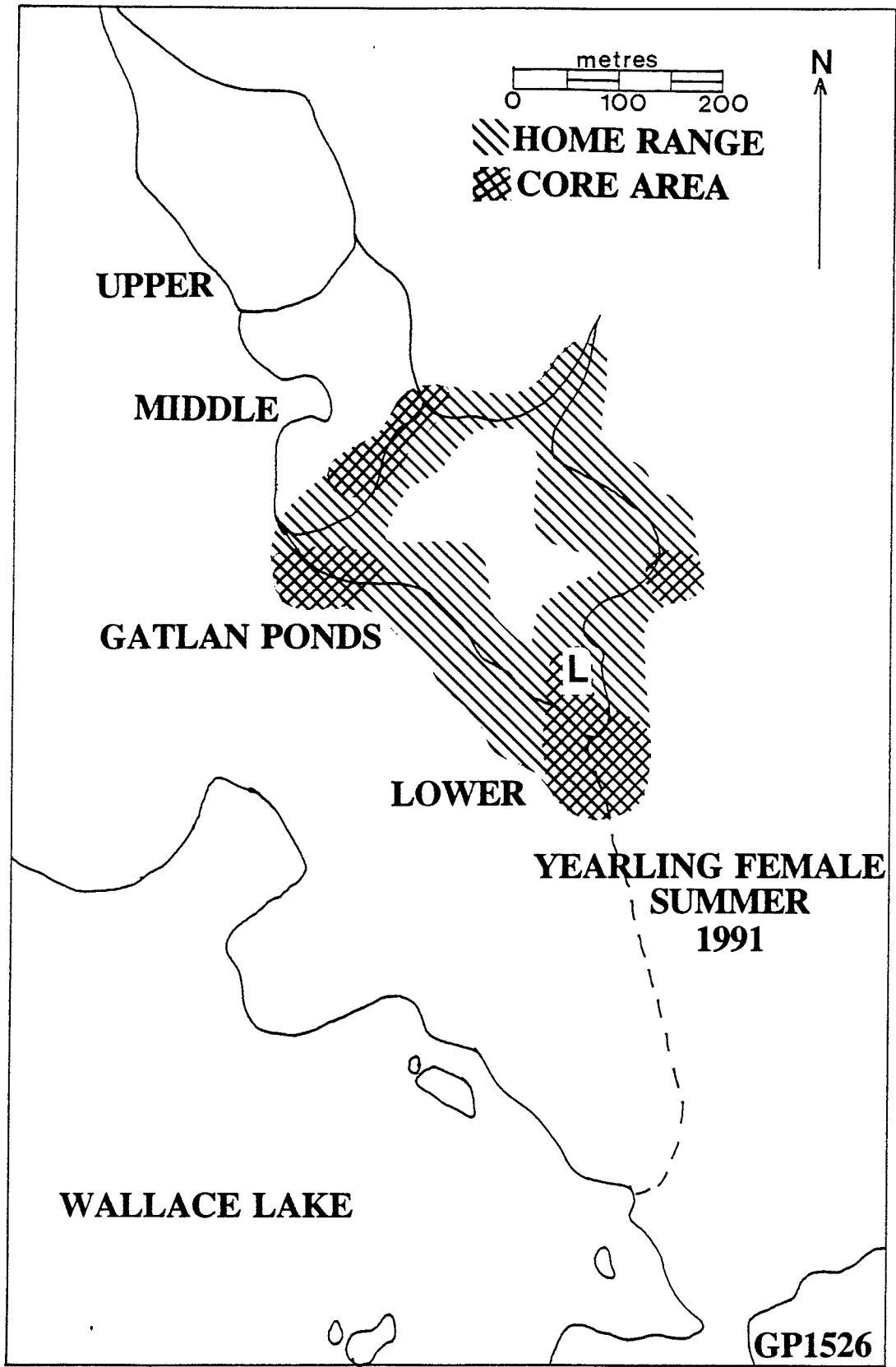
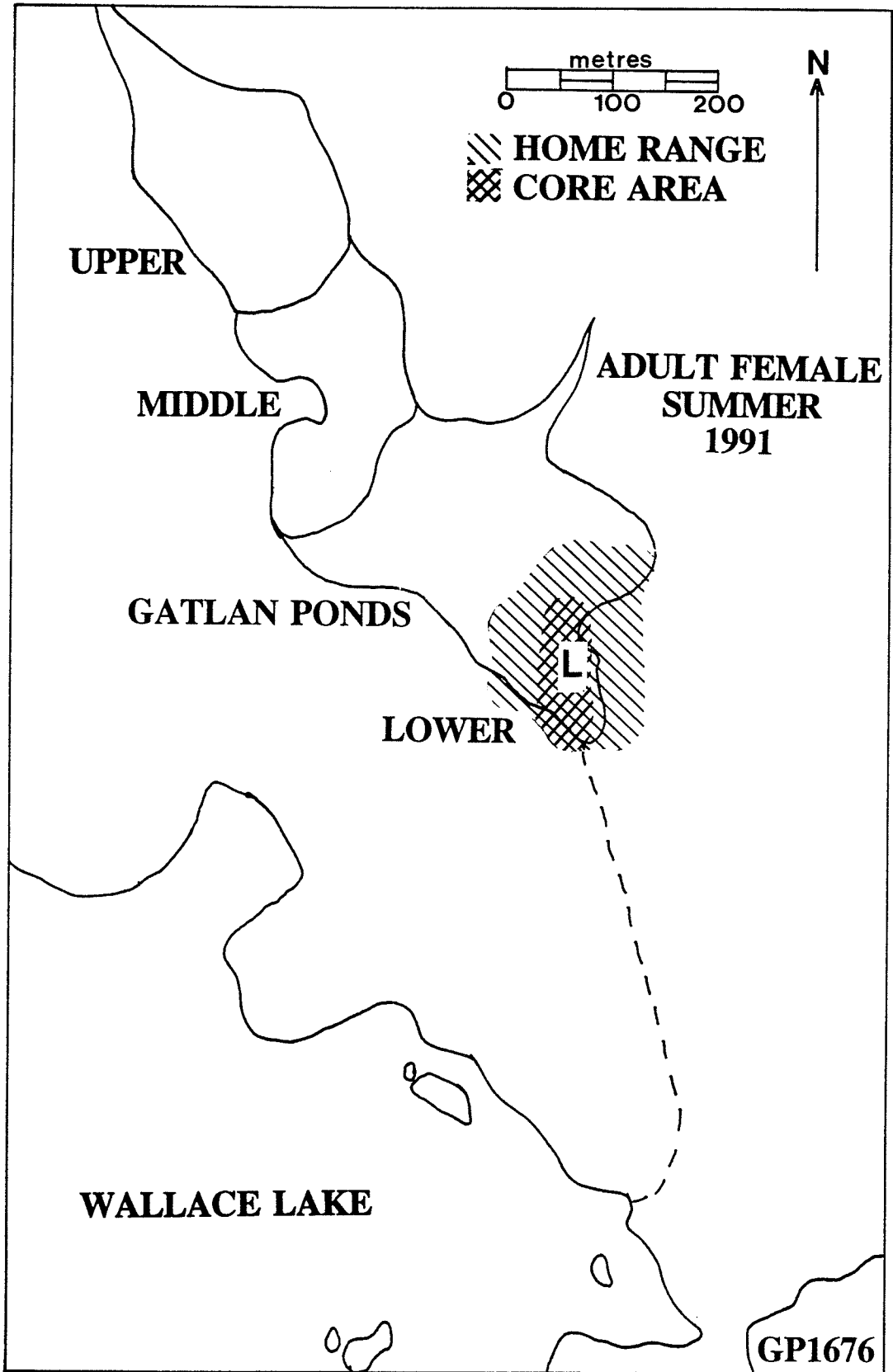
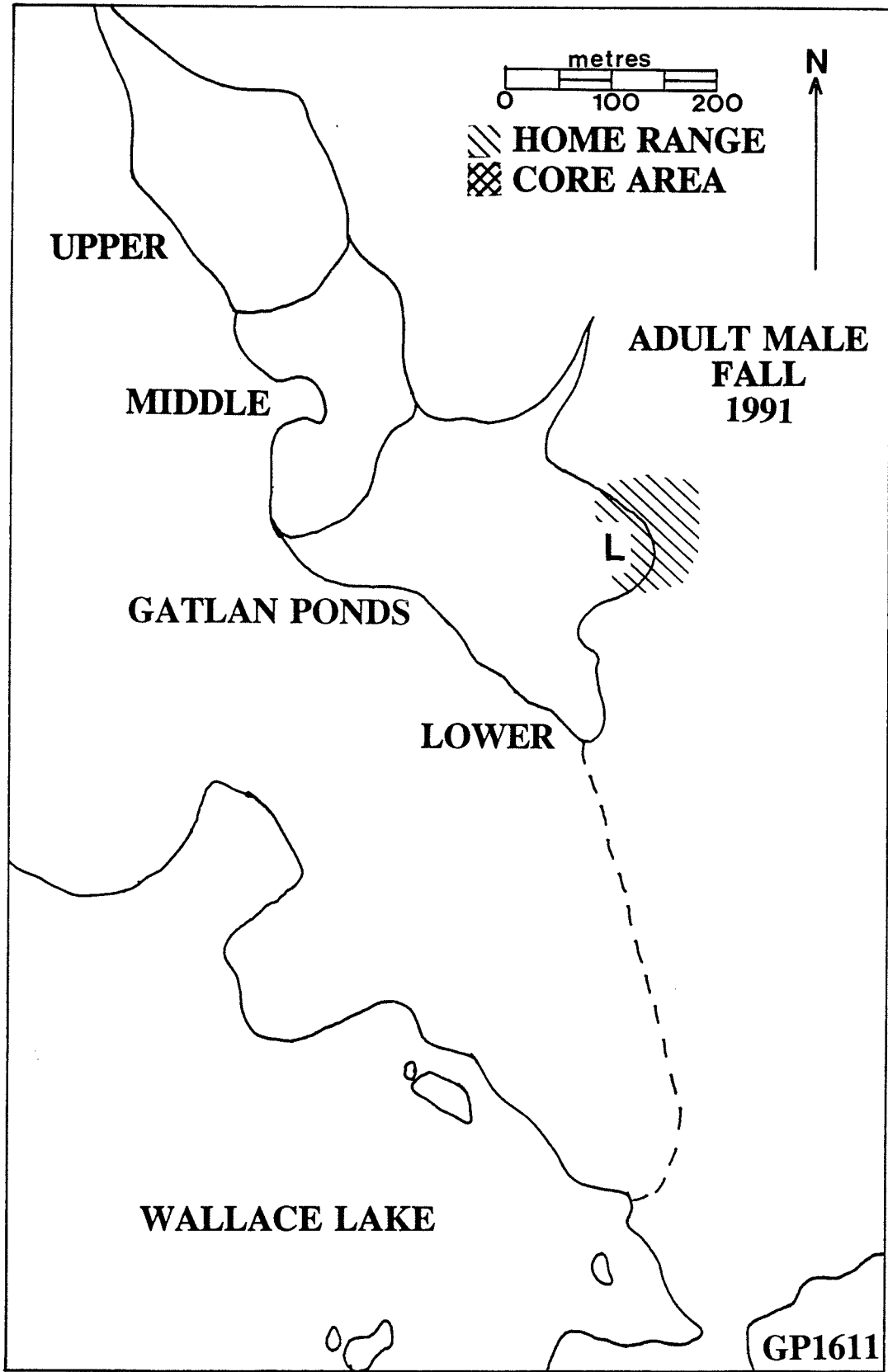


Figure 5. Maps of home range area for beavers in the Gatlan Pond Family for summer and fall, 1991. L indicates location of the lodge.









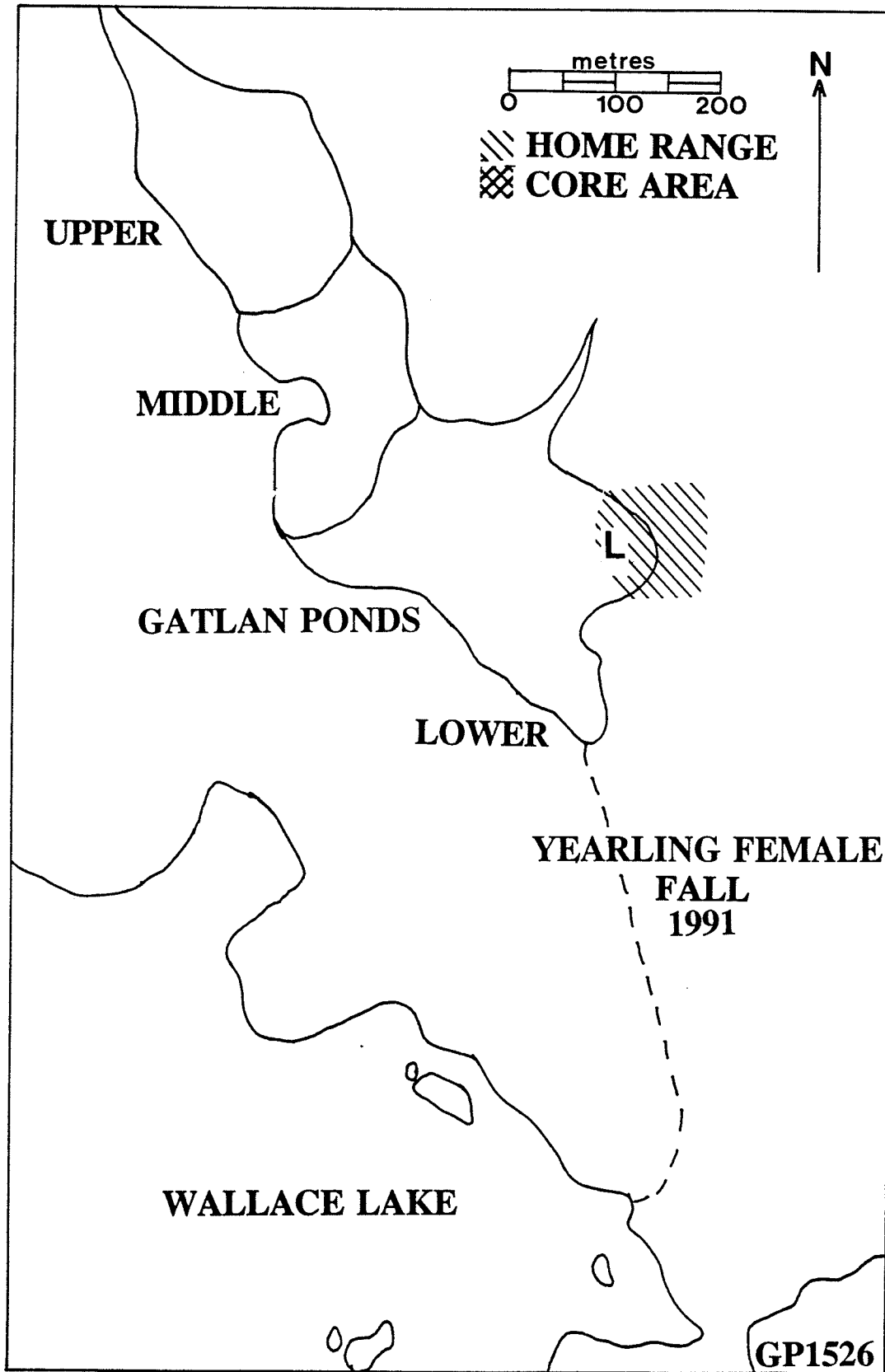
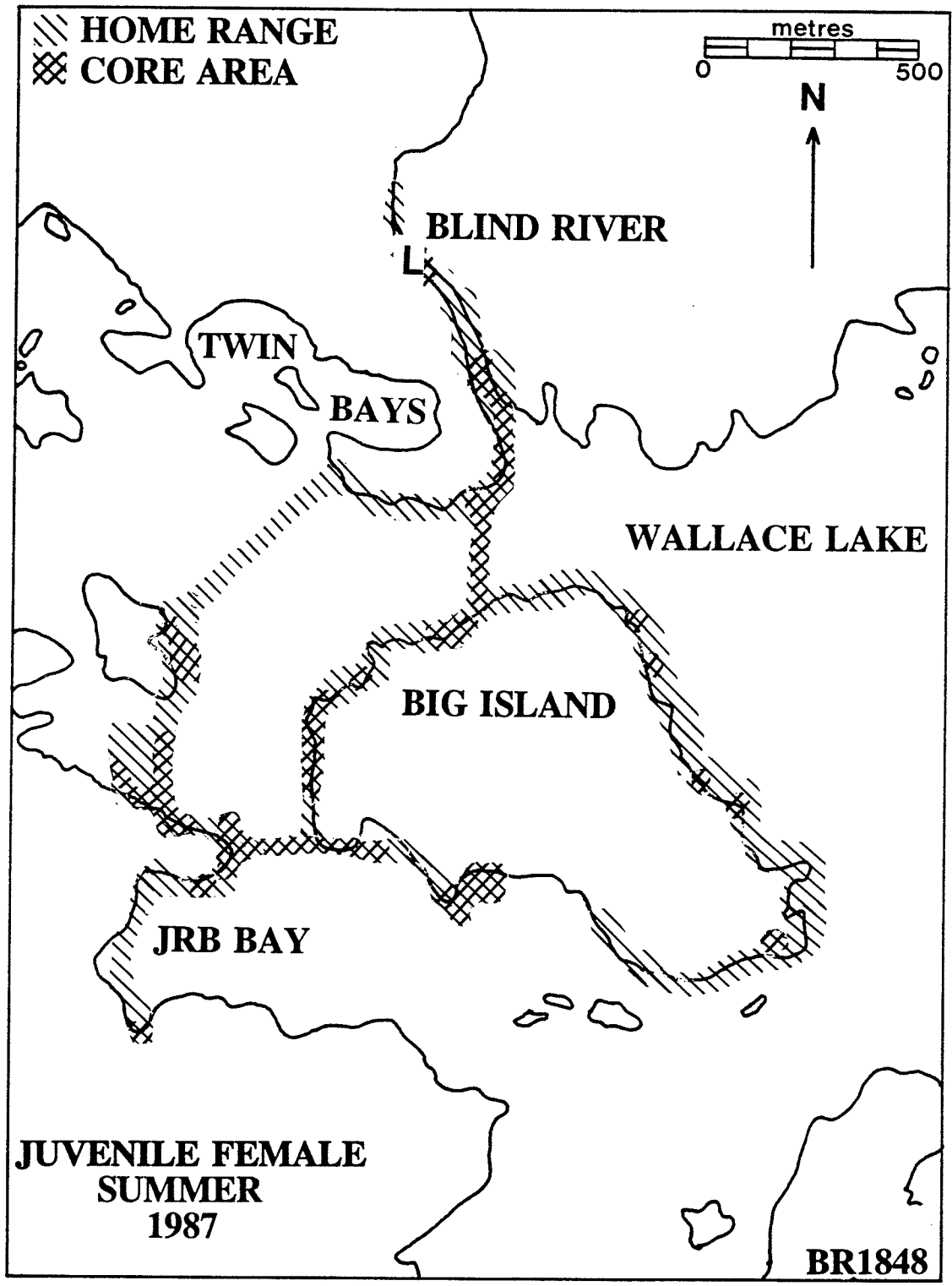
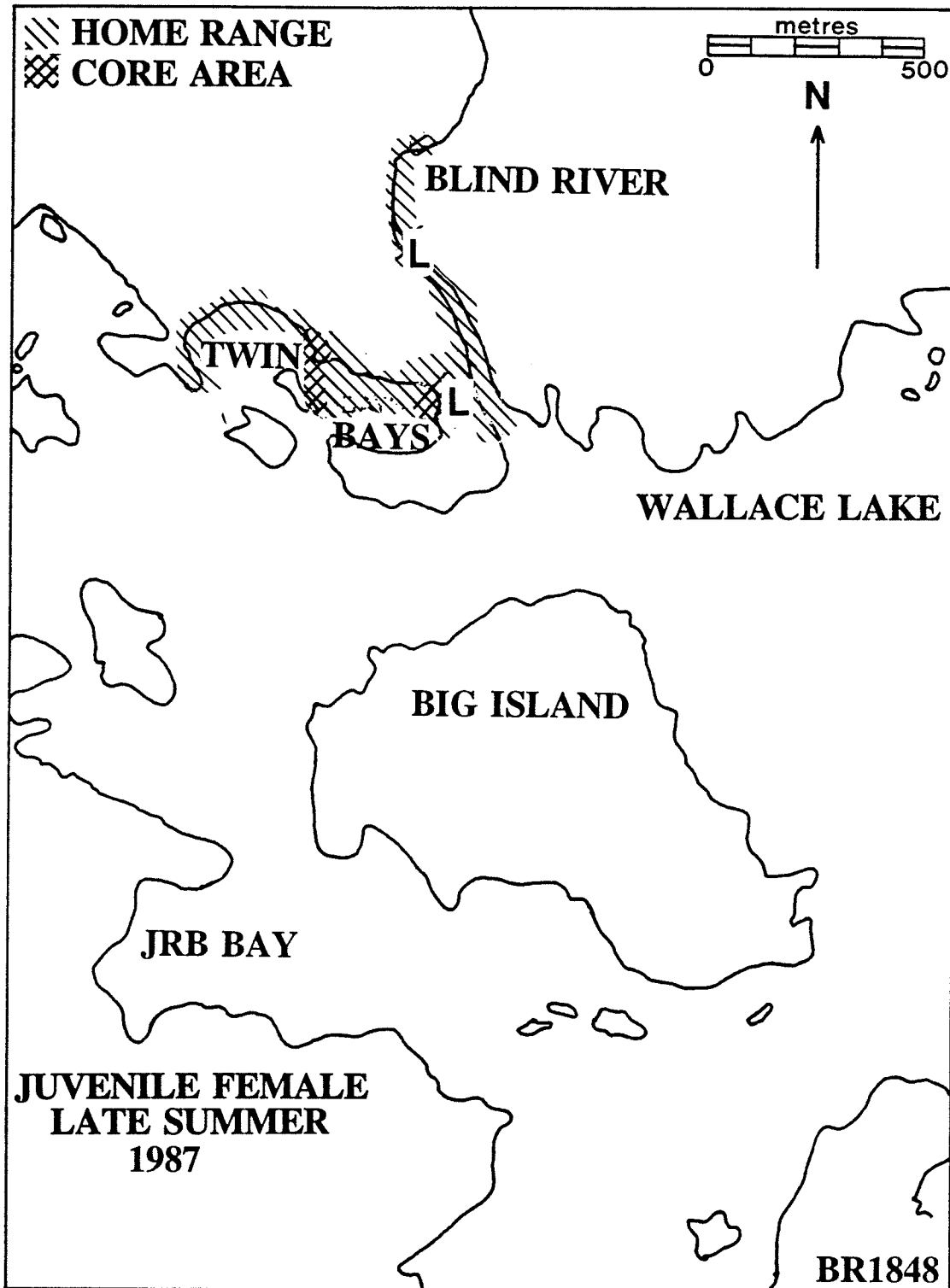
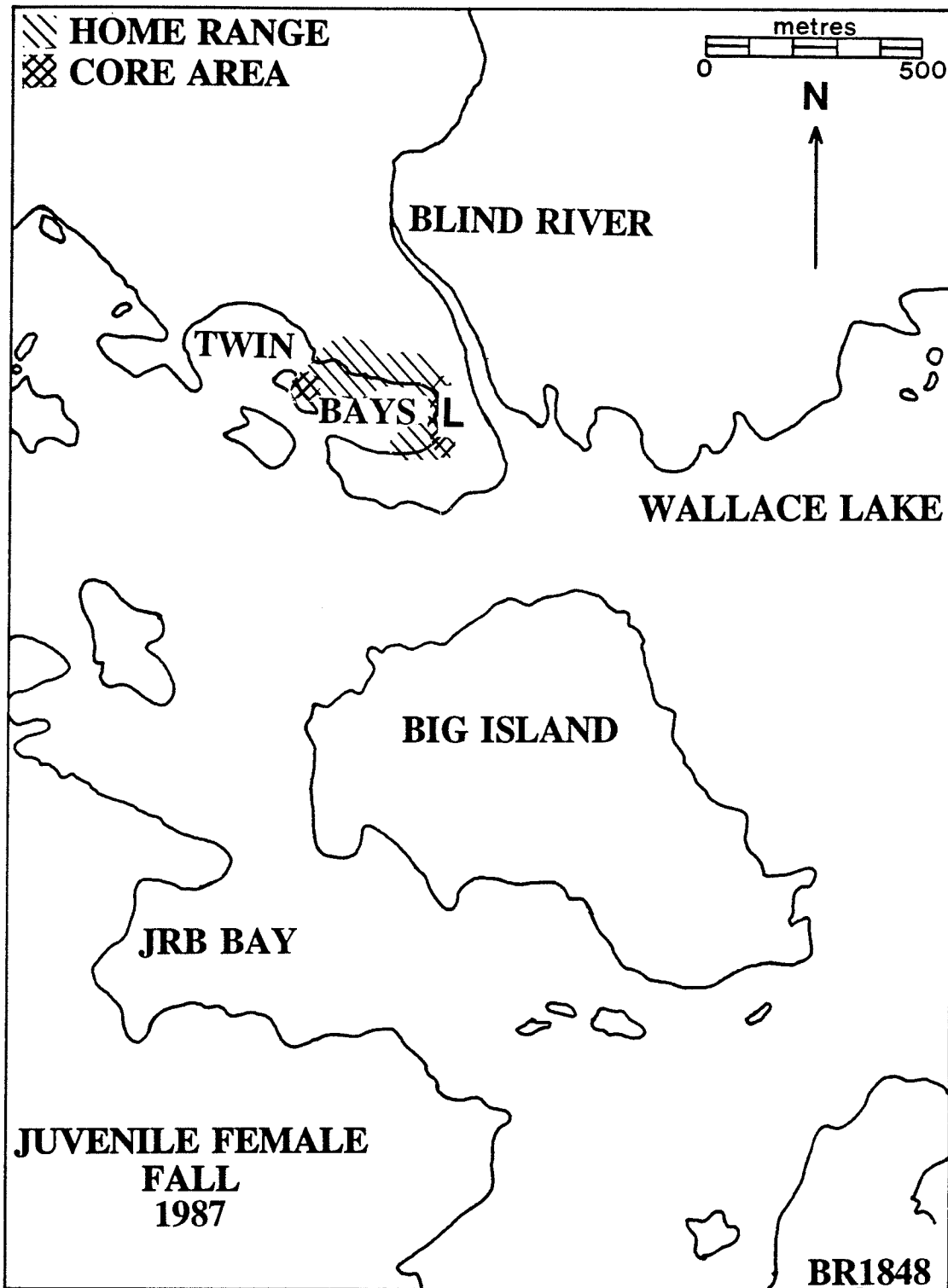
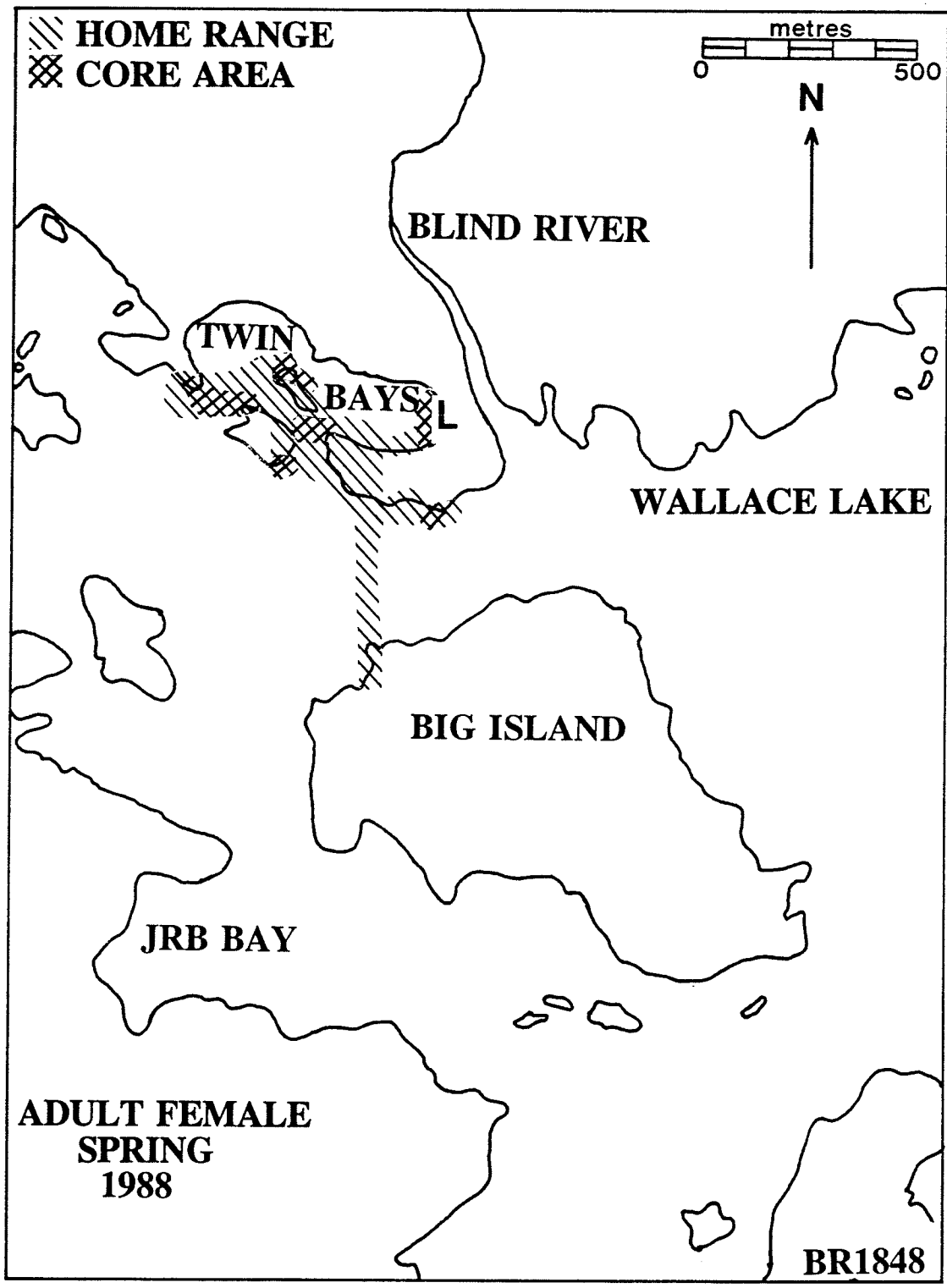


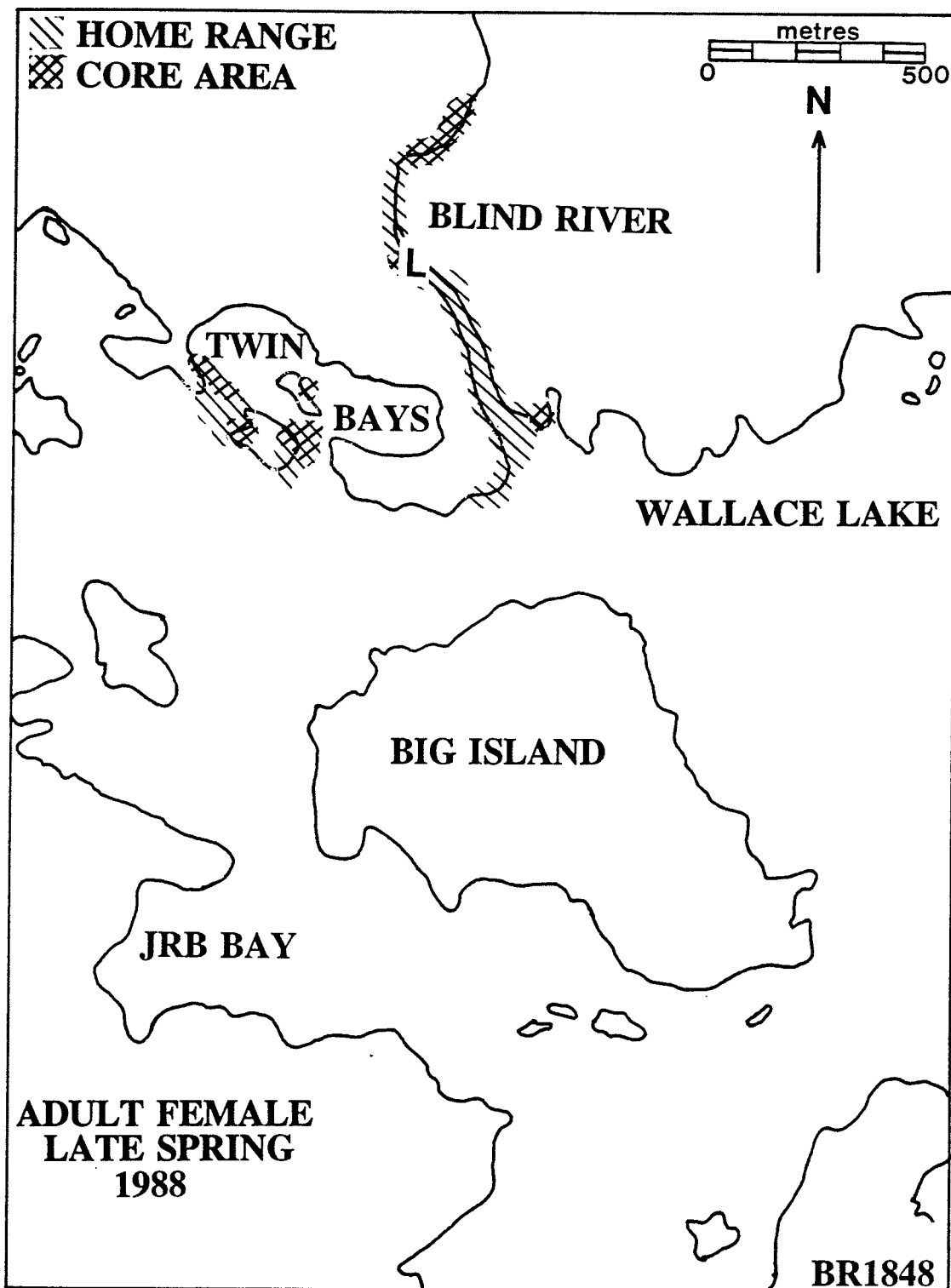
Figure 6. Maps of home range area for beaver BR1848 for 1987, 1988 and 1989. L indicates the location of the lodge.

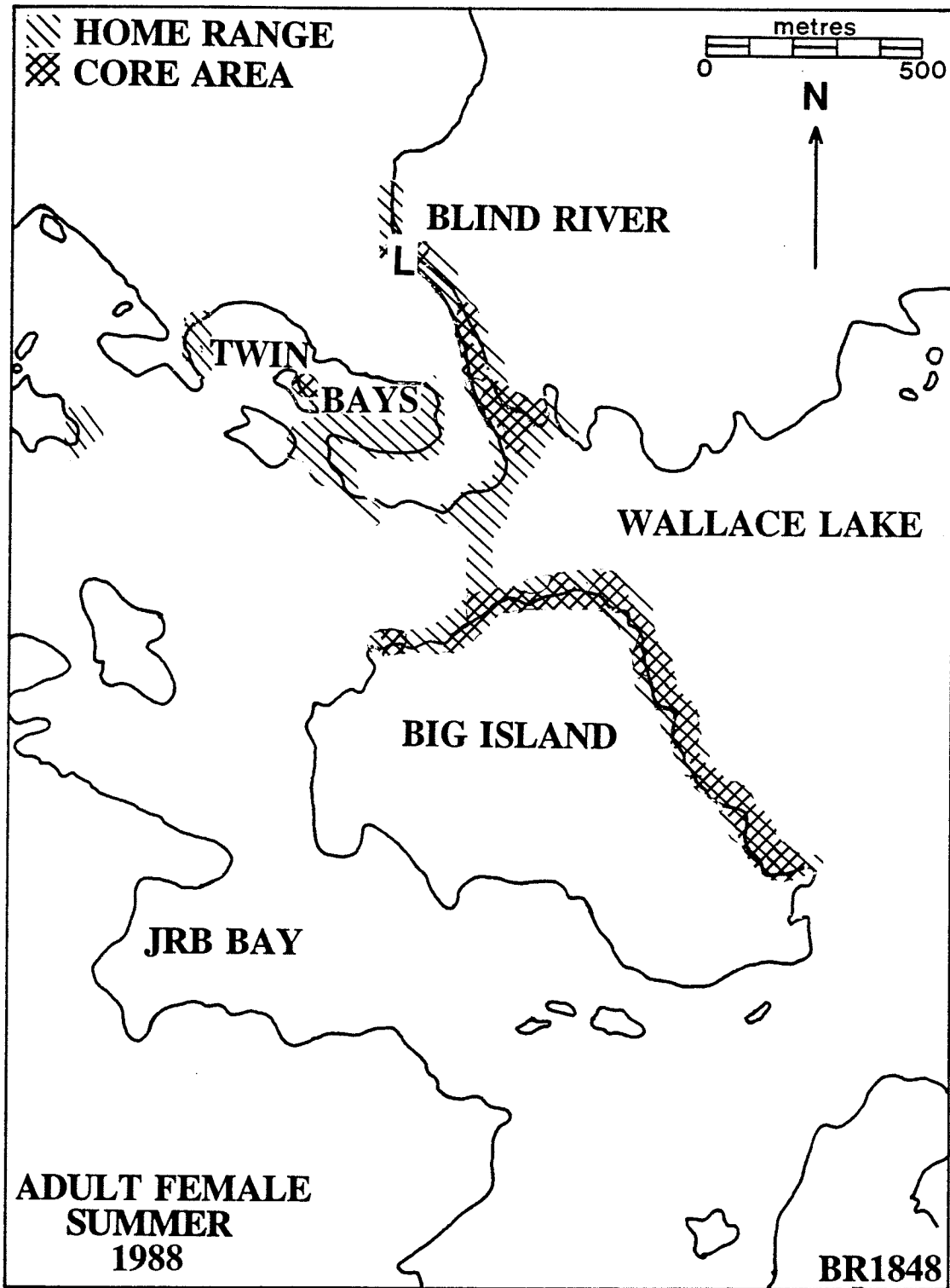


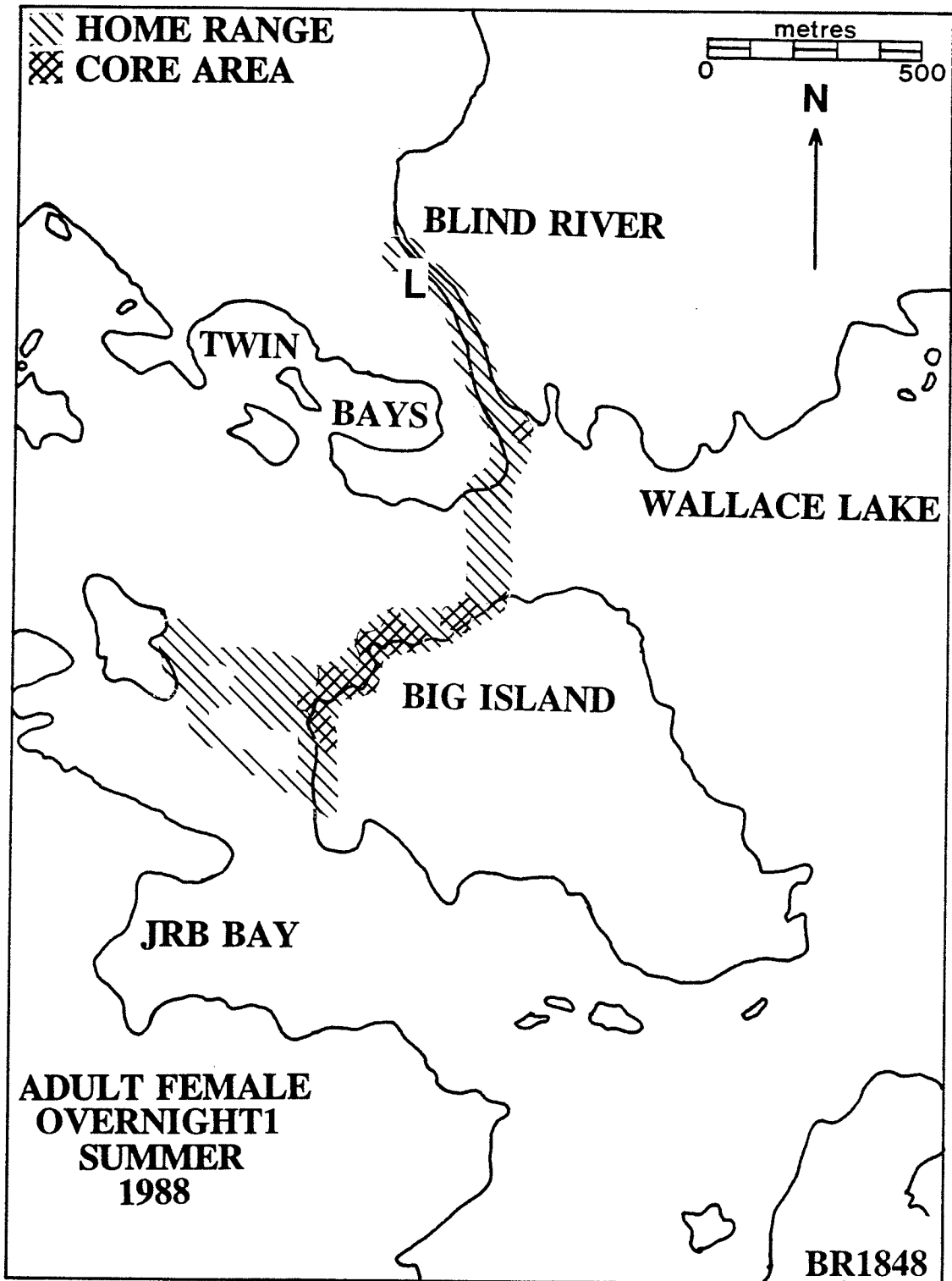


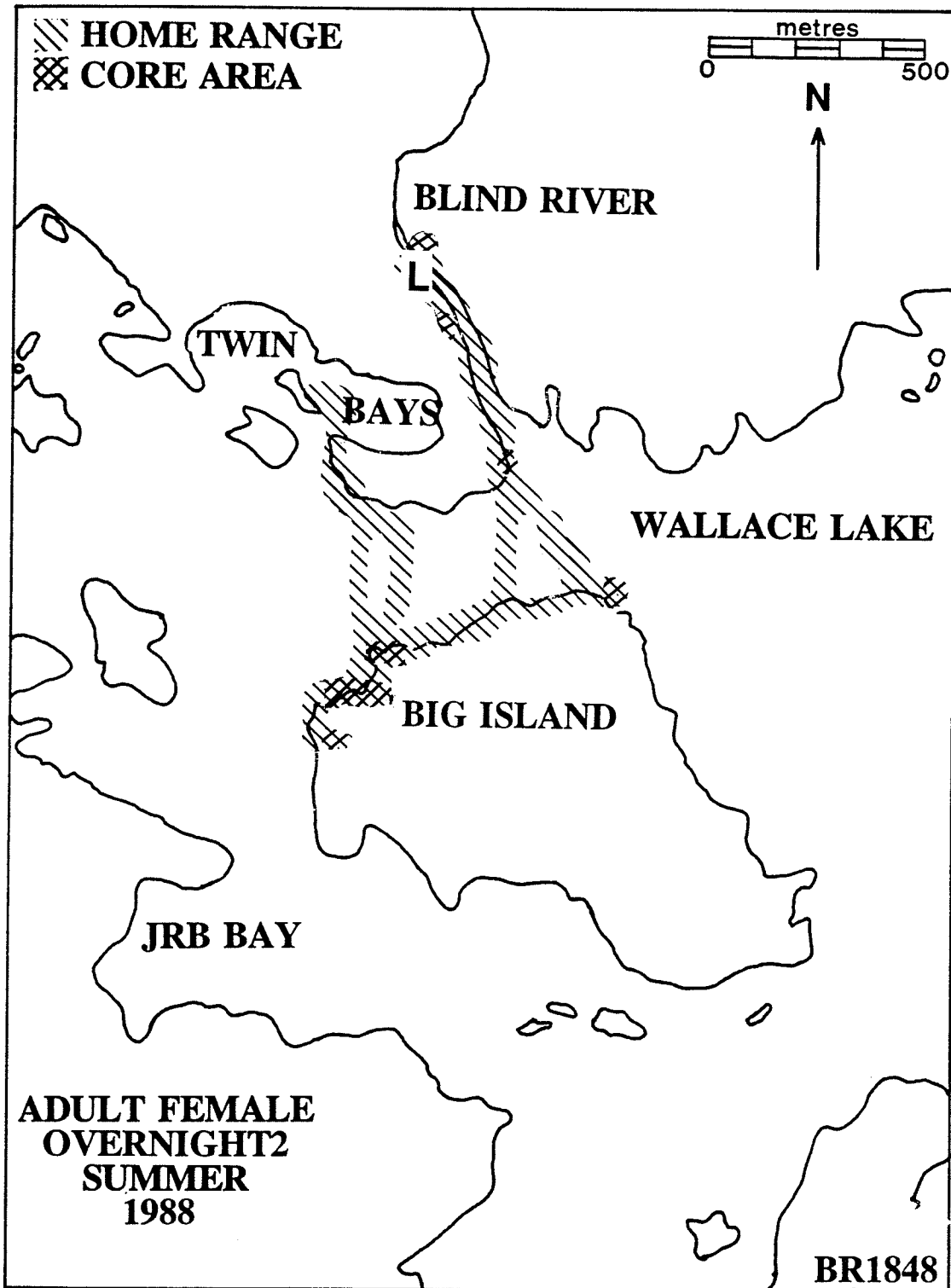


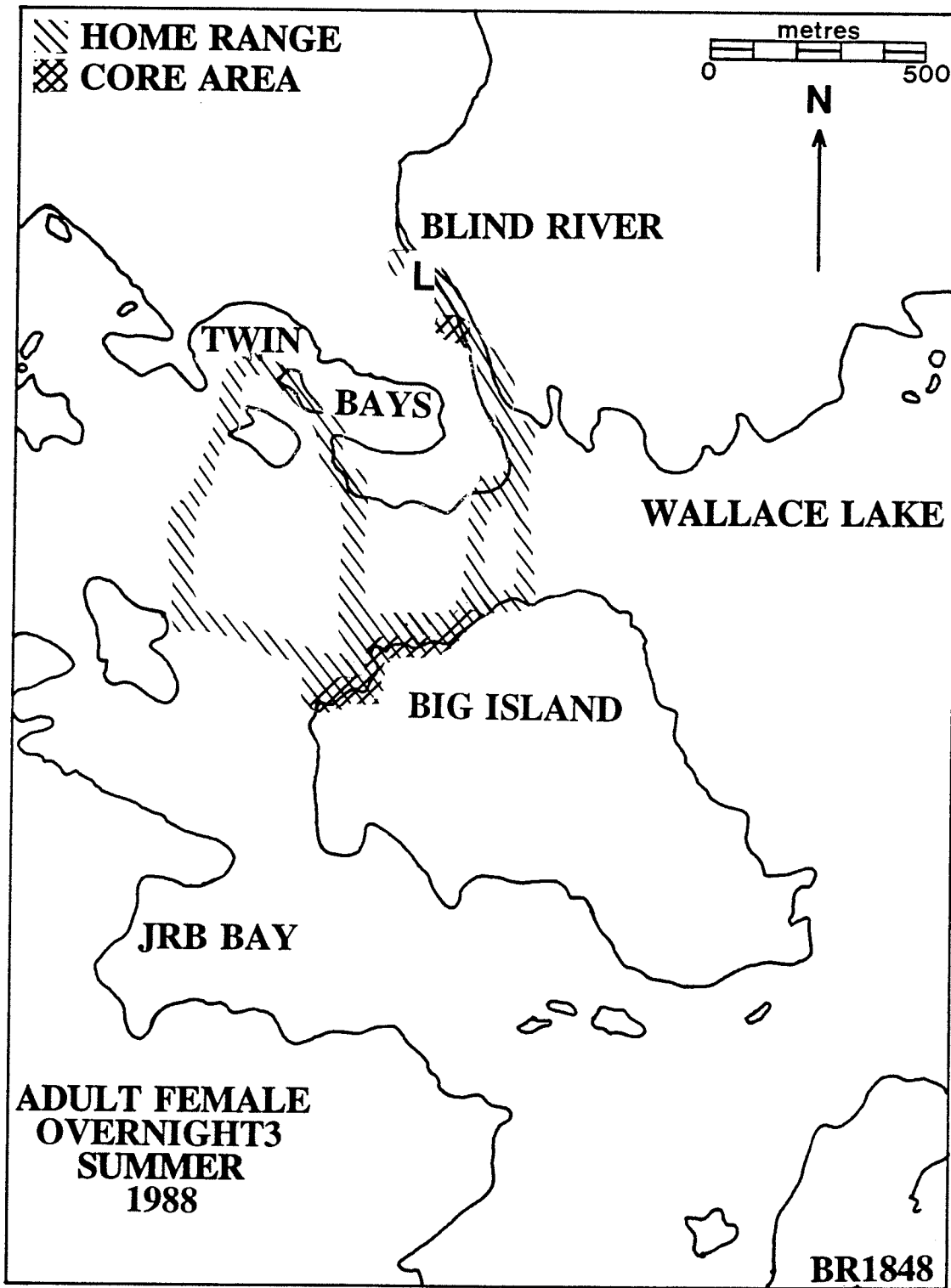


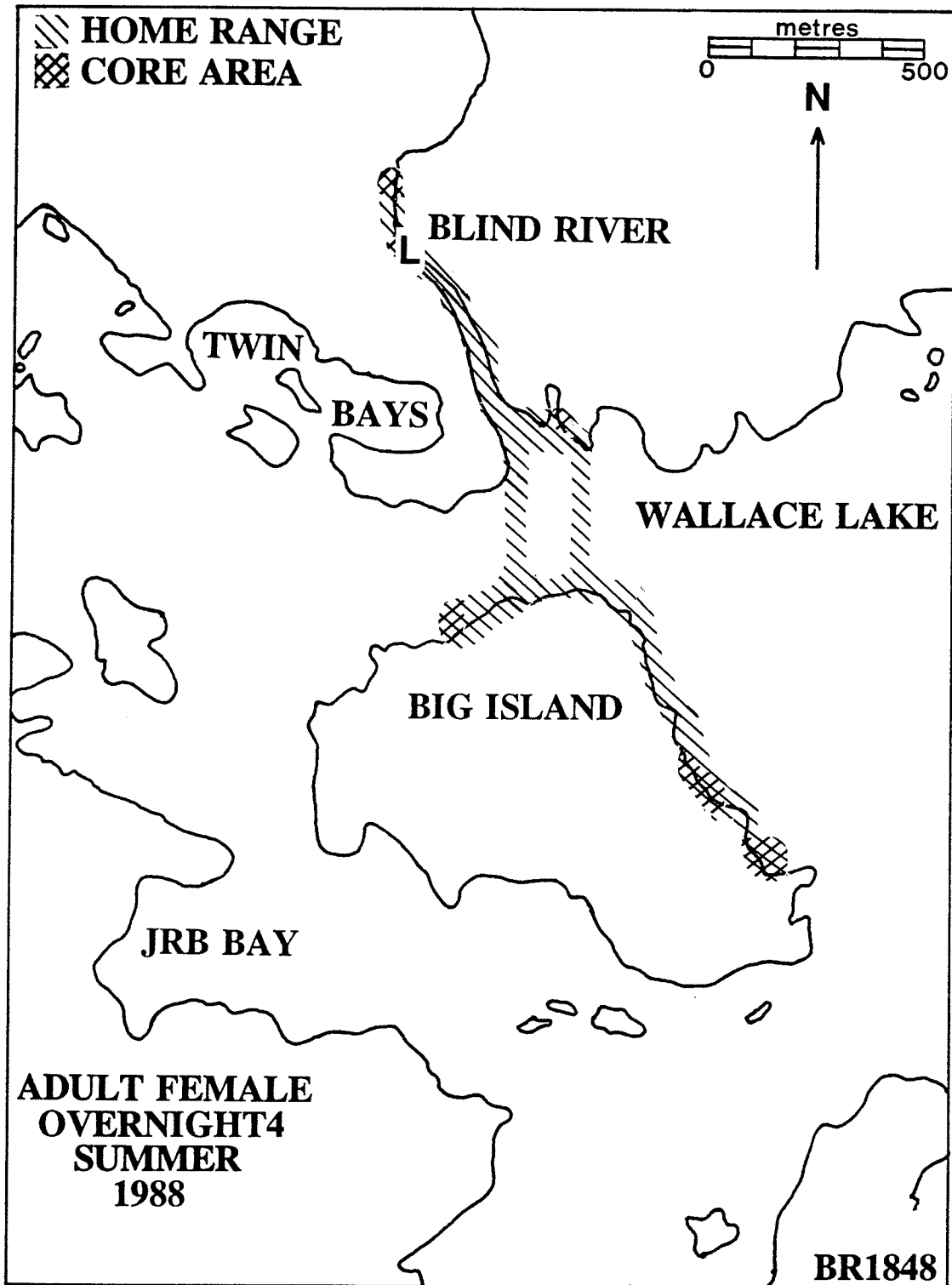


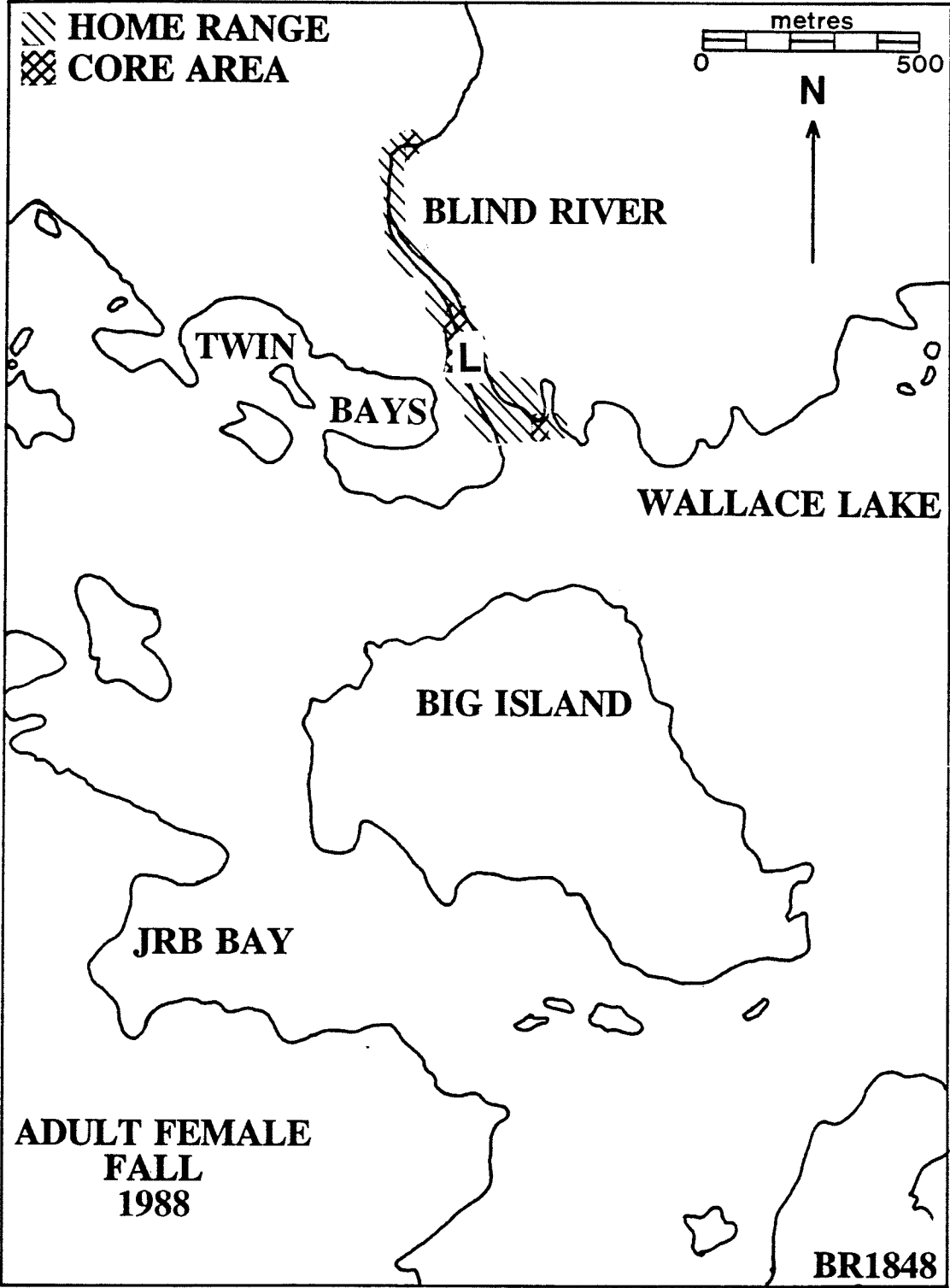












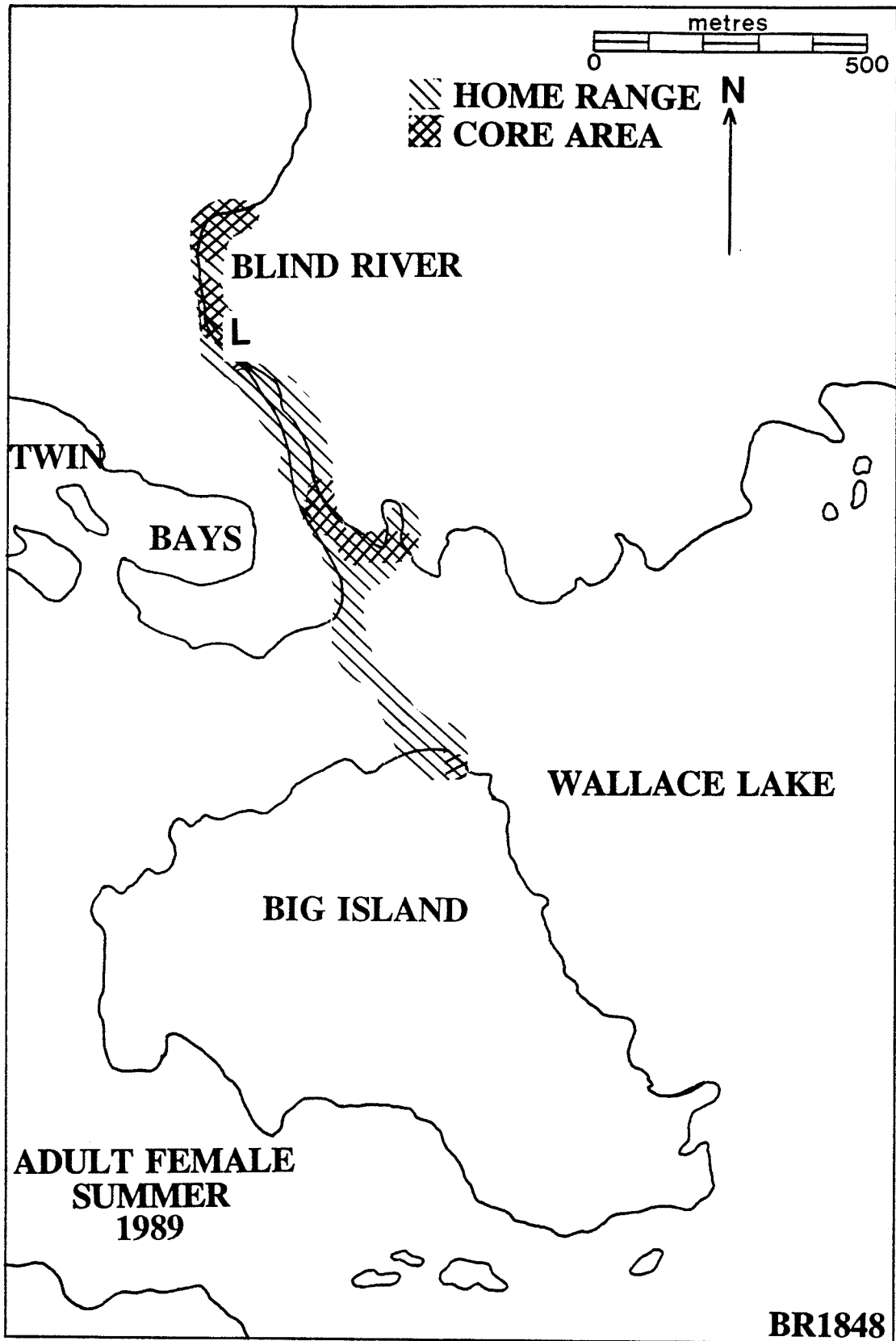


Figure 7. Maps of home range area for beaver BR1844 for summer and fall, 1987. L indicates location of the lodge.

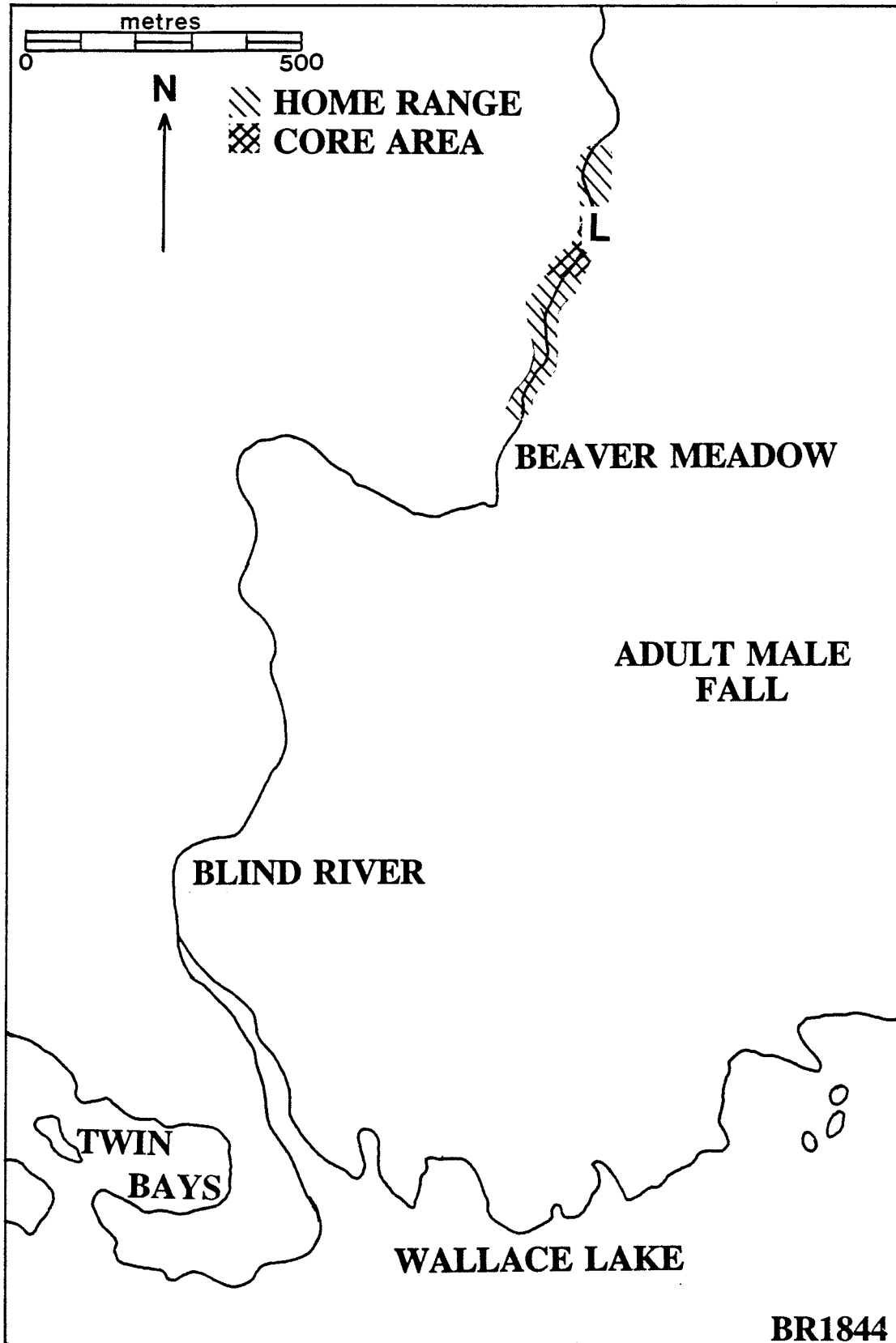
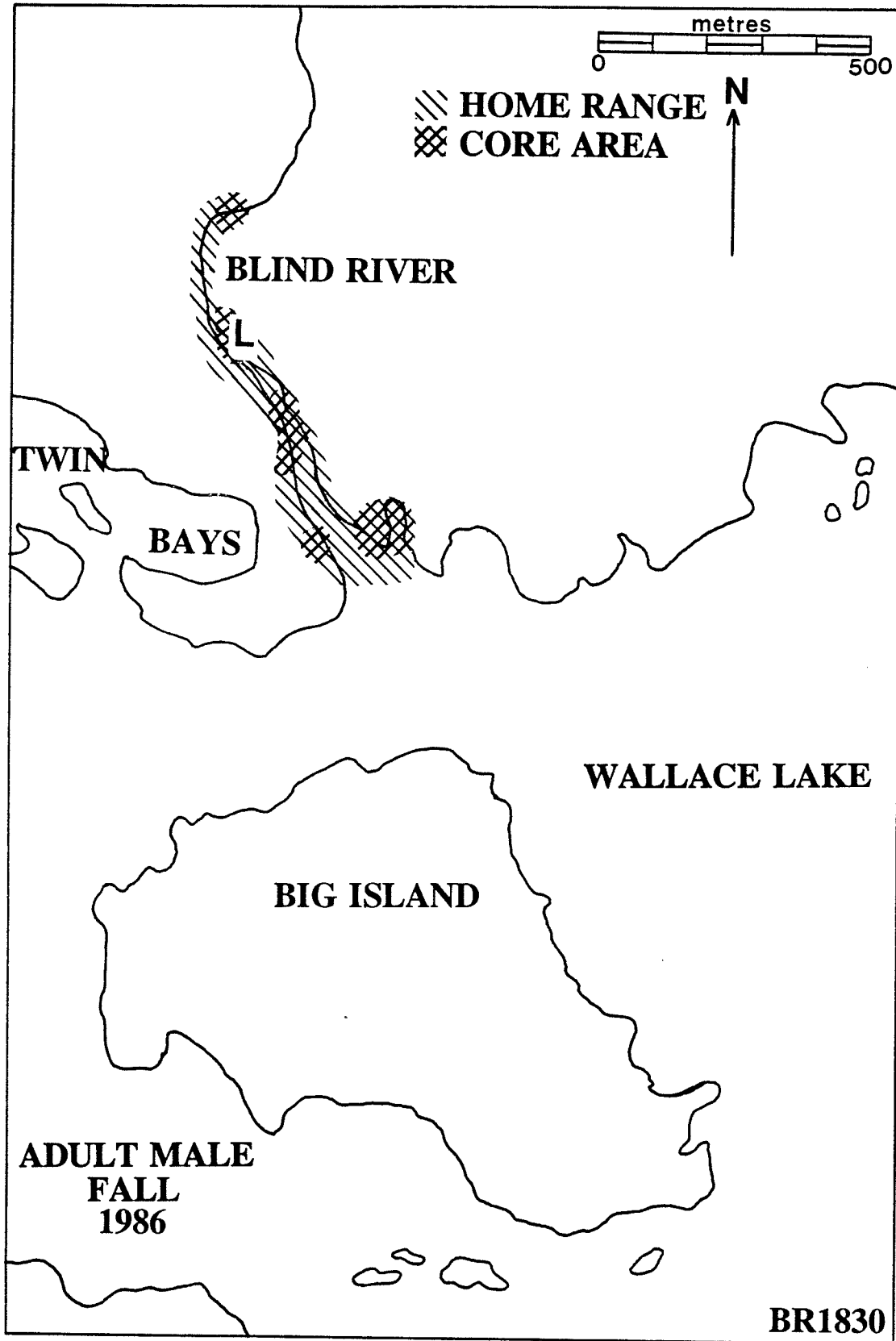


Figure 8. Maps of home range area for beaver BR1830 for fall, 1986 and summer, 1989. L indicates location of the lodge.



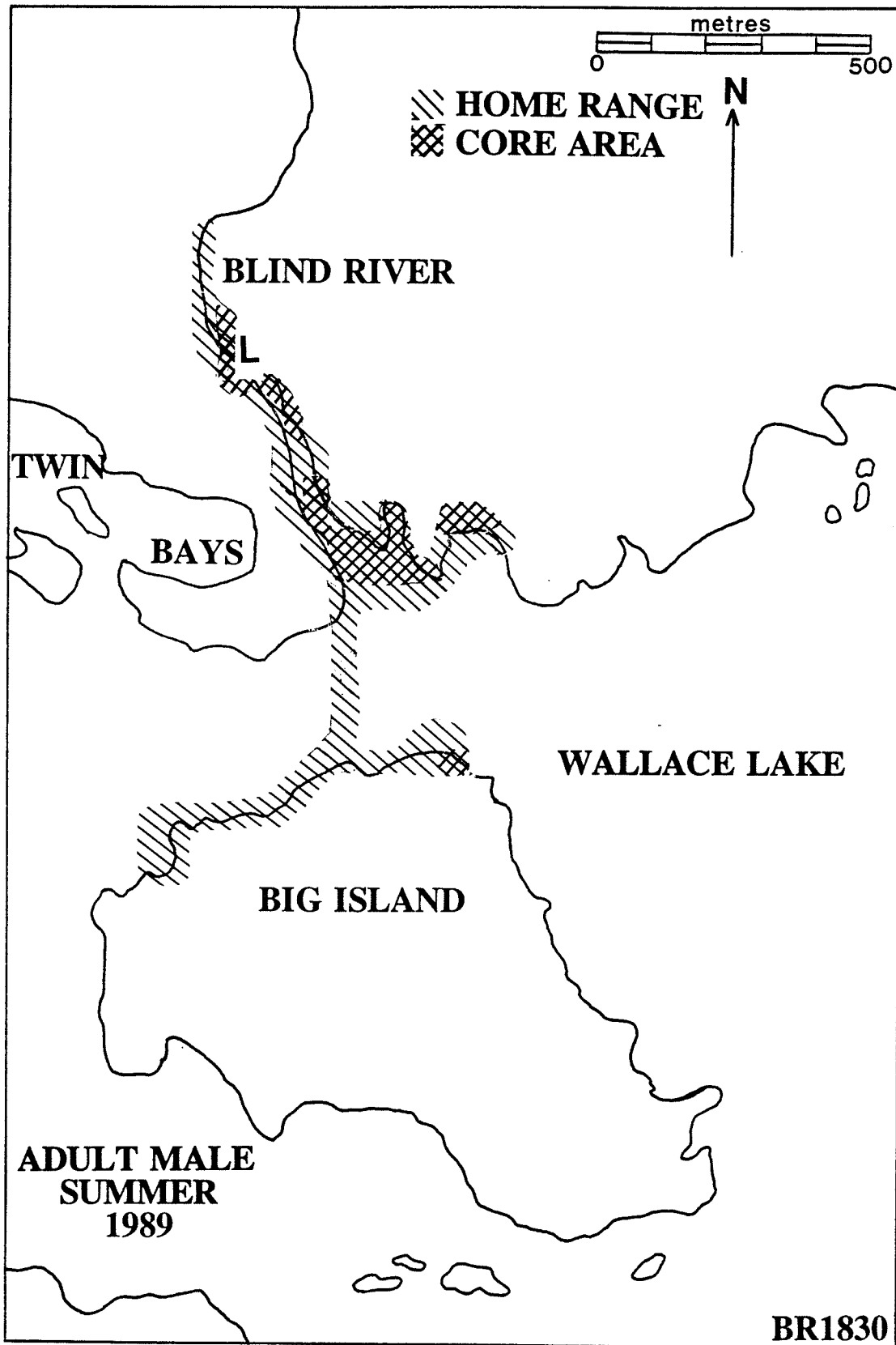
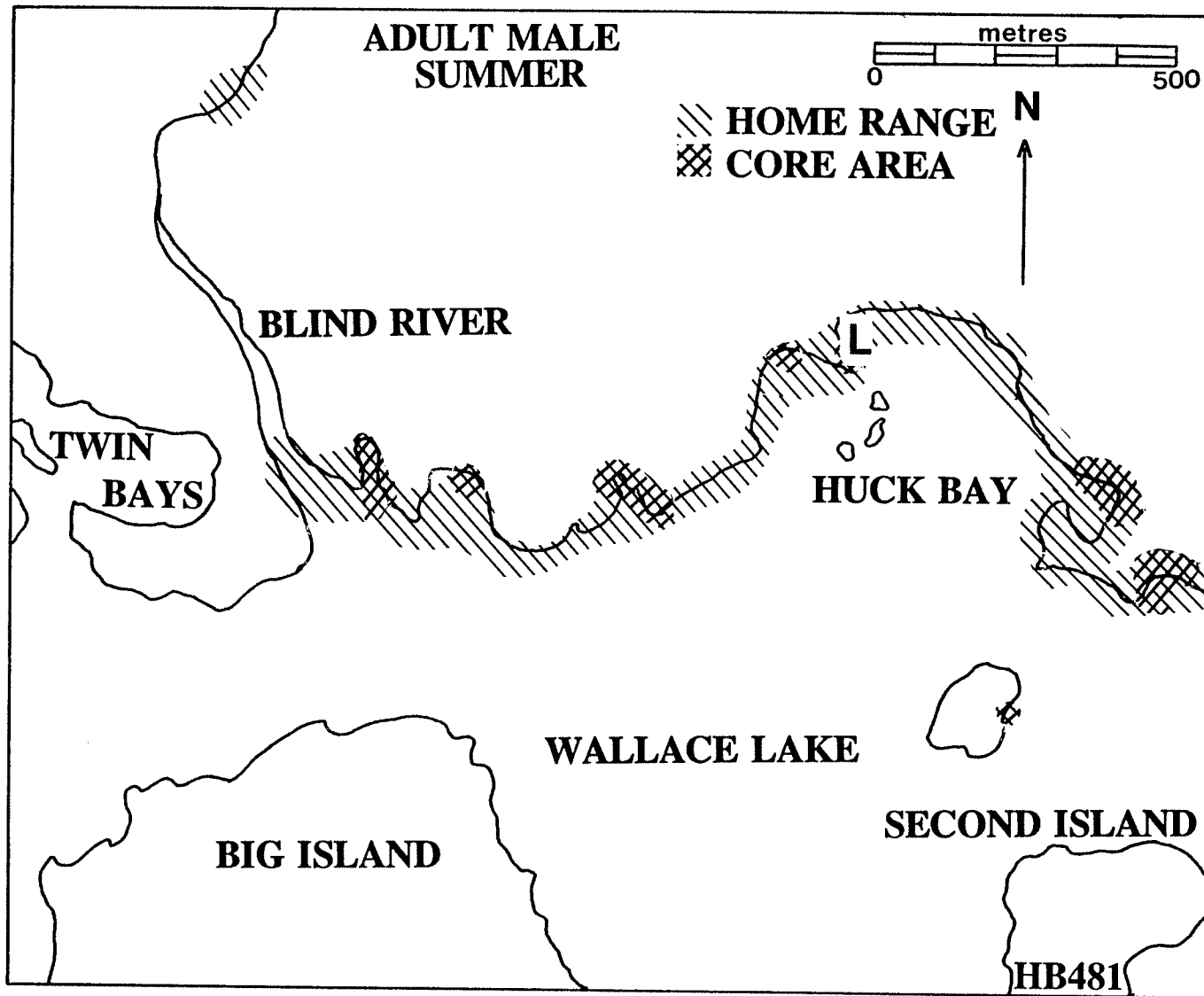


Figure 9. Maps of home range area for beaver HB481 for summer and fall, 1989. L indicates location of the lodge.



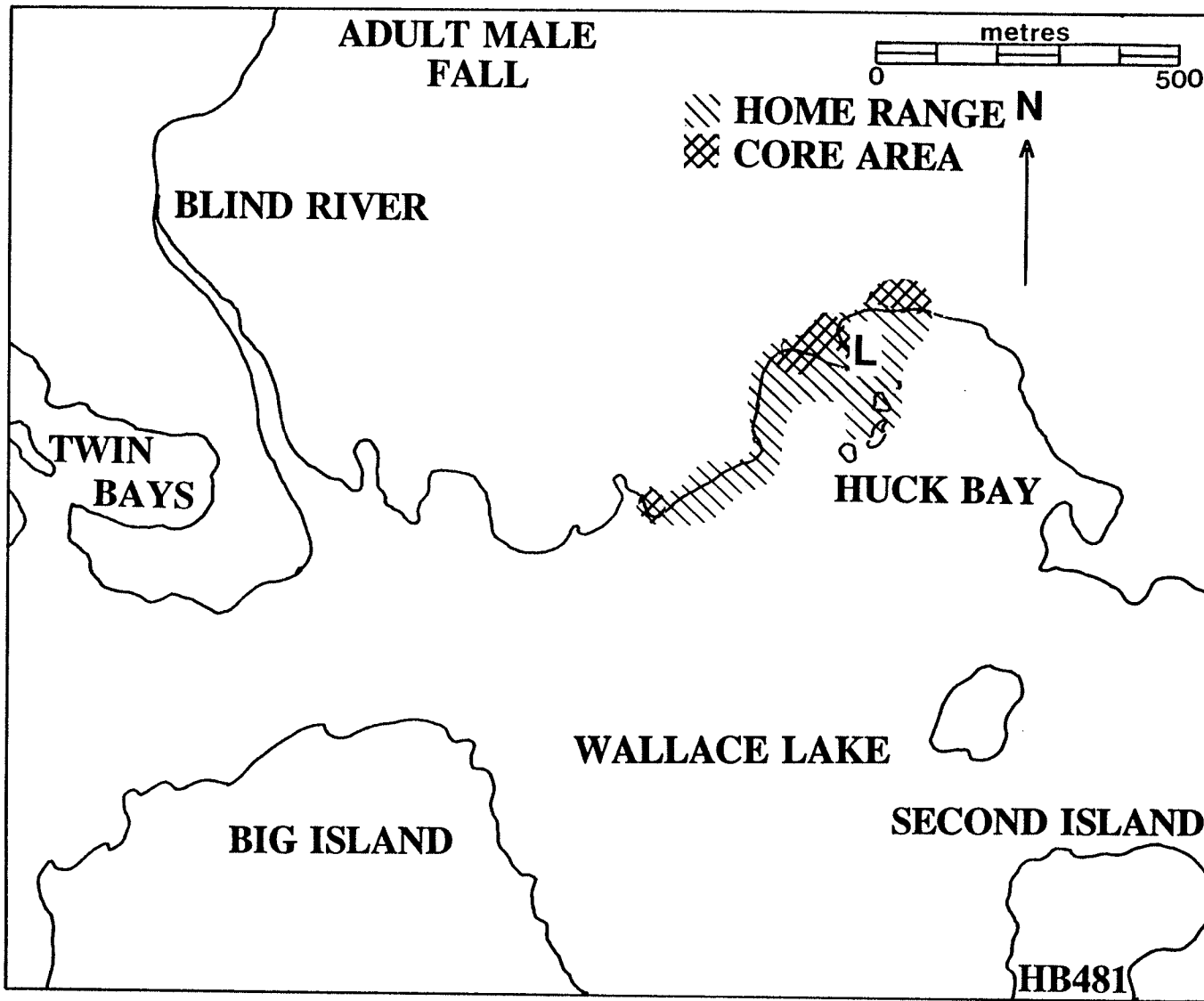
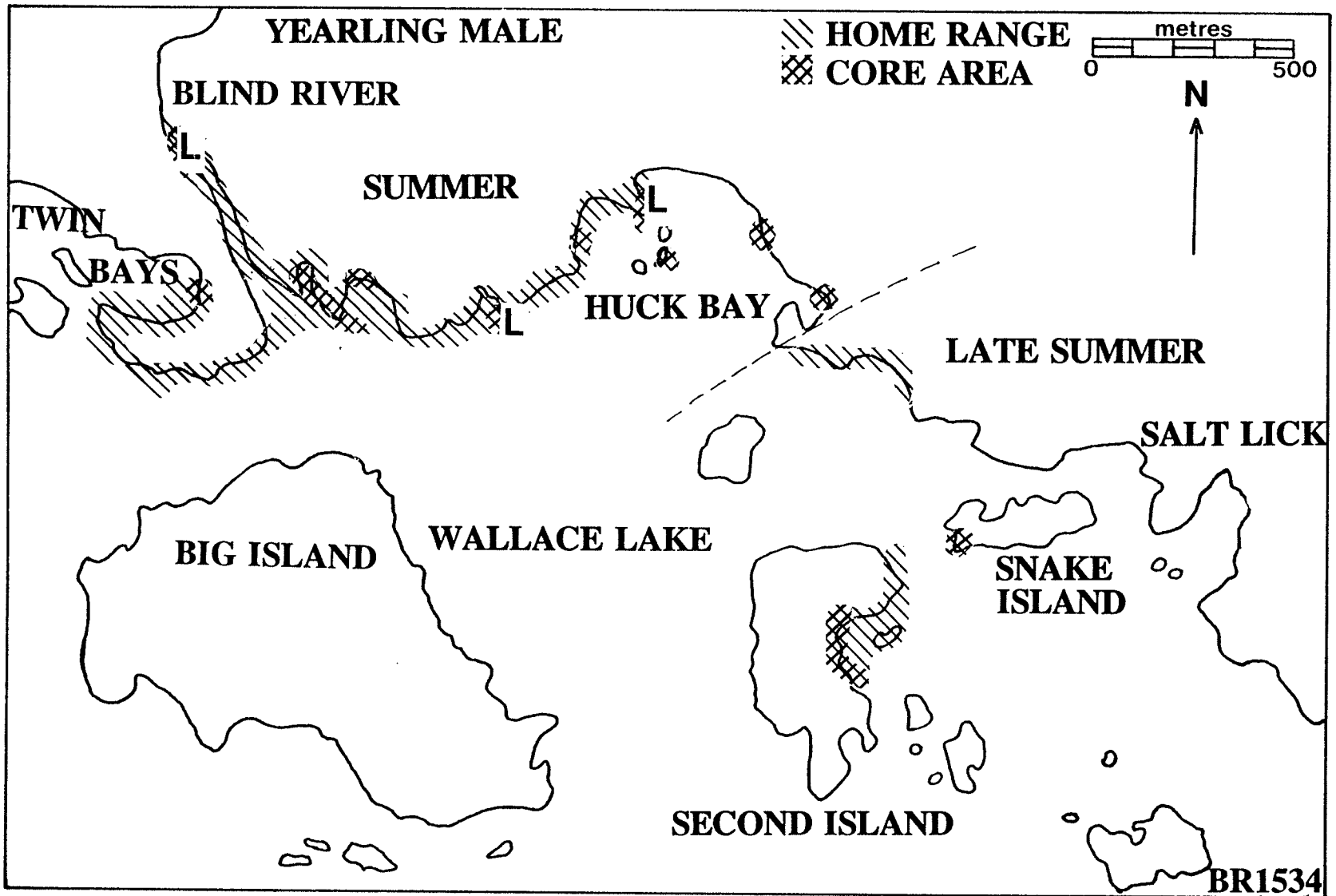


Figure 10. Maps of home range area for beavers BR1534 and BR1524 for summer and late fall, 1991. L indicates location of the lodges.



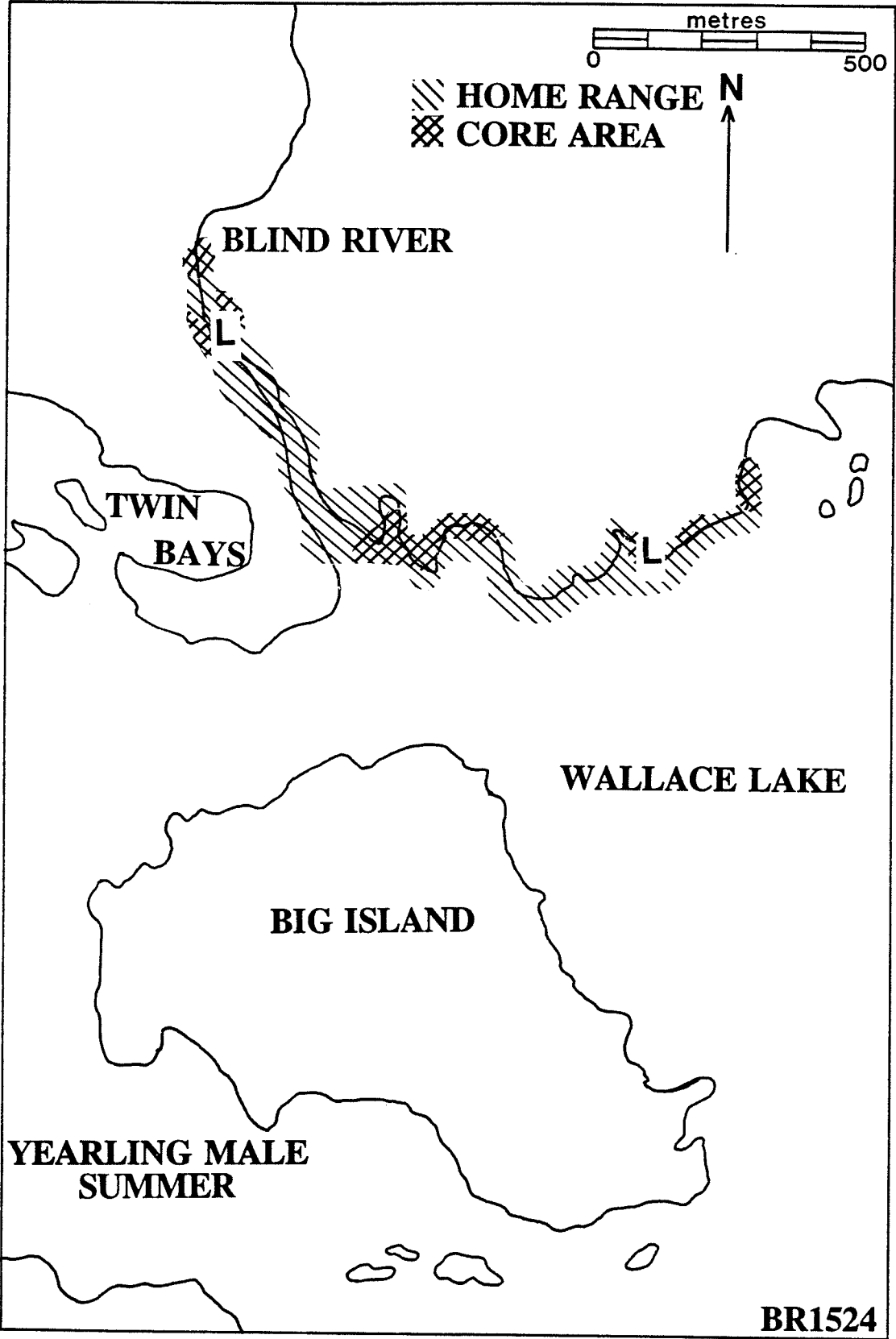
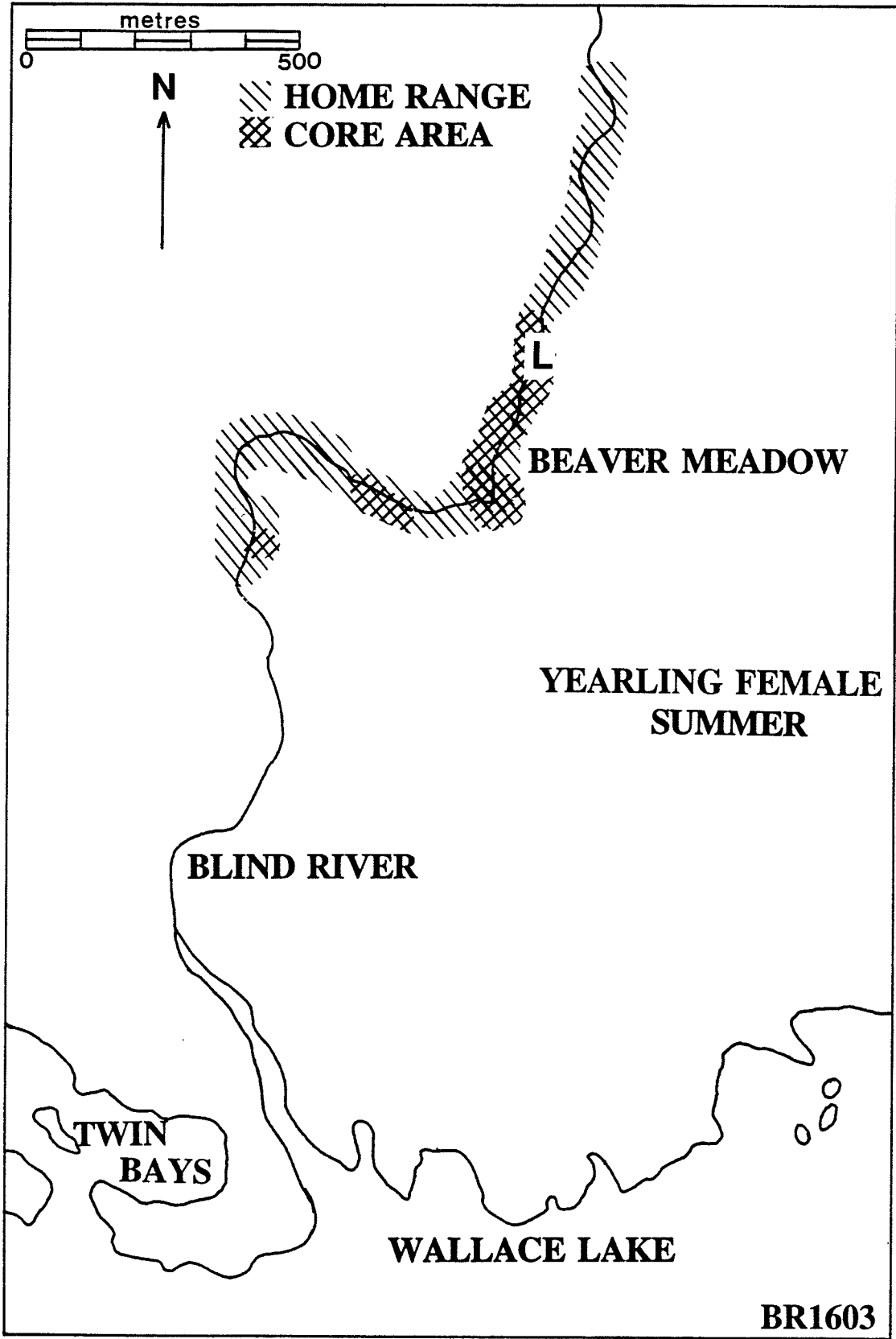


Figure 11. Maps of home range area for beavers BR1603 for summer and fall, 1990. L indicates location of the lodge.



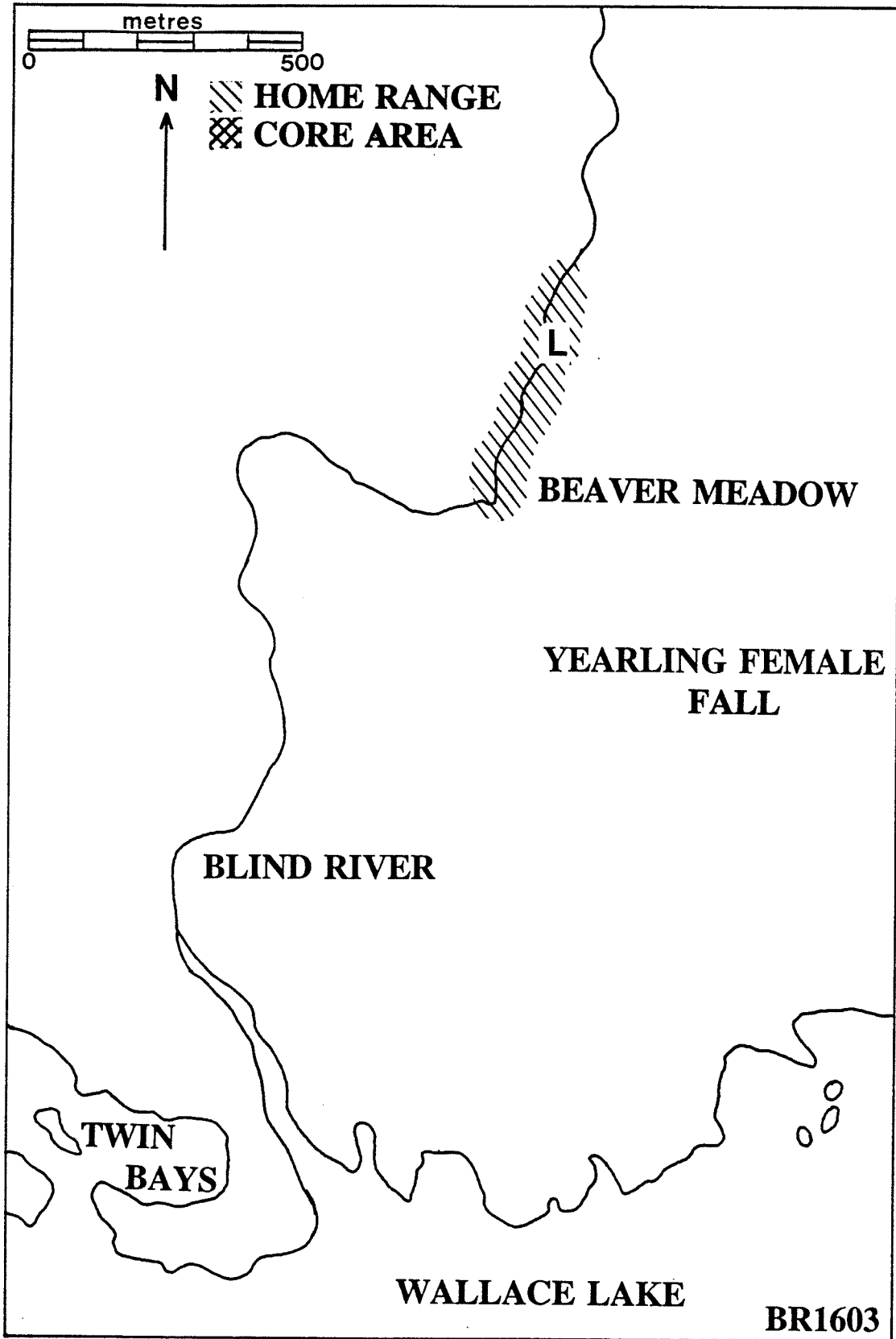
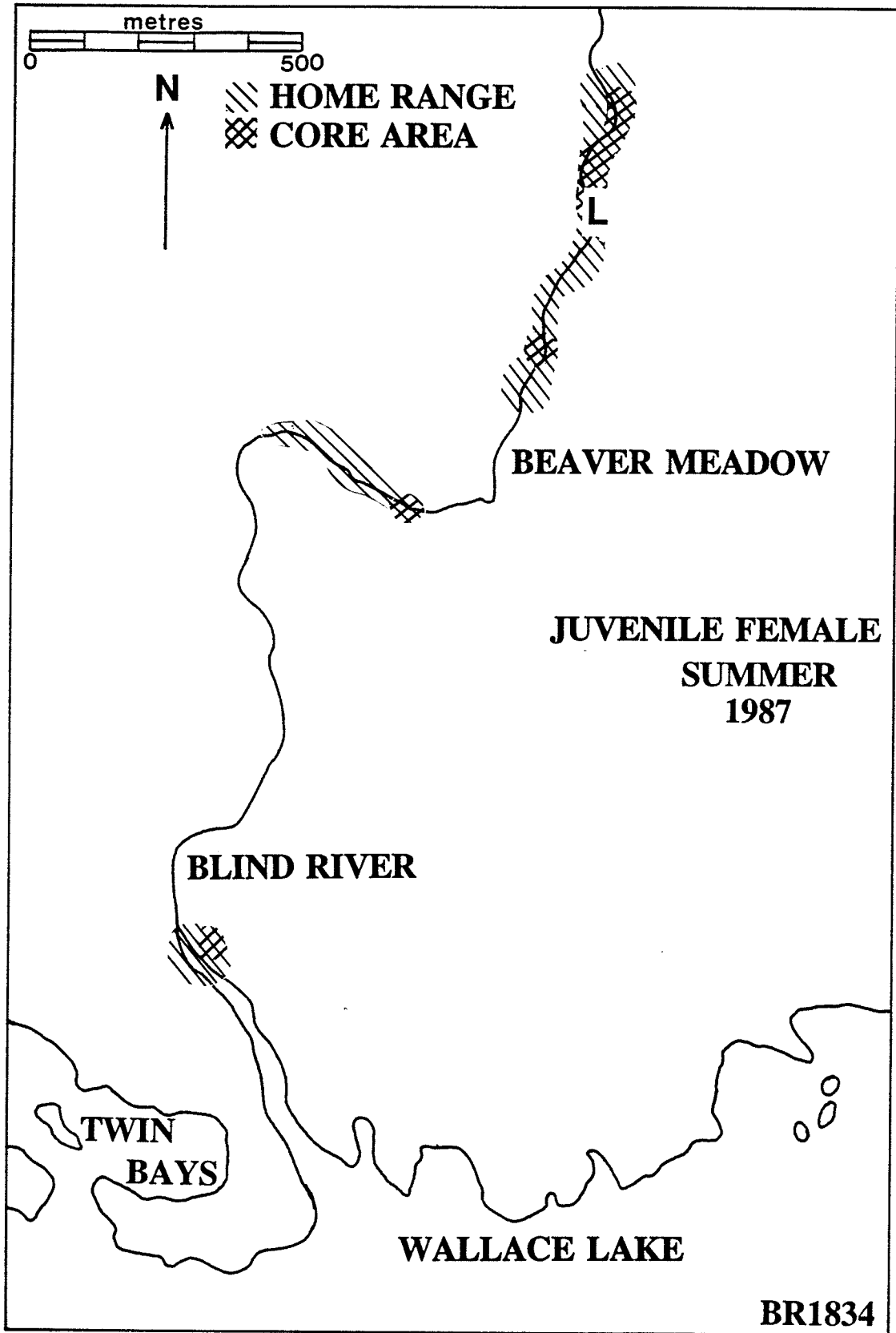
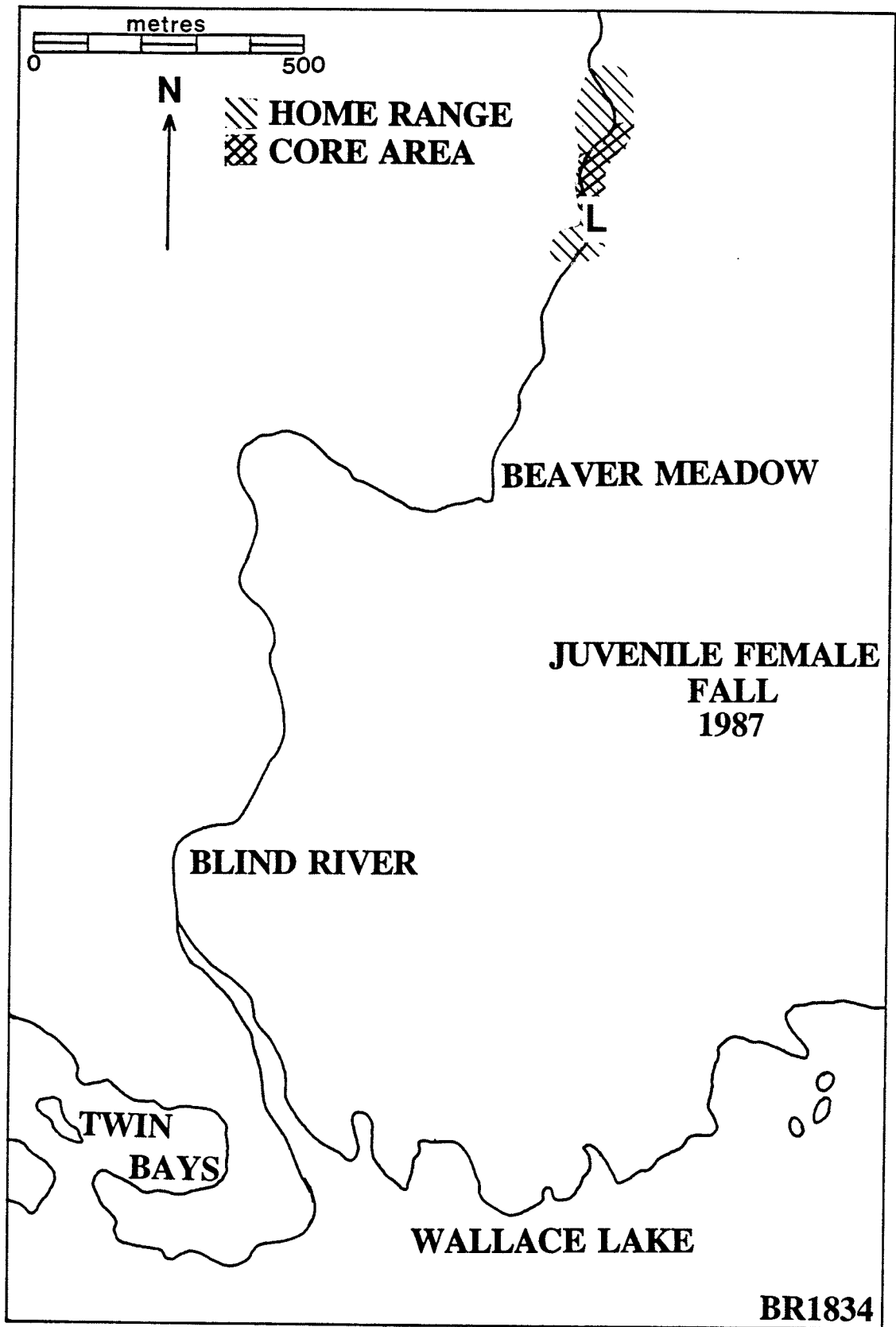
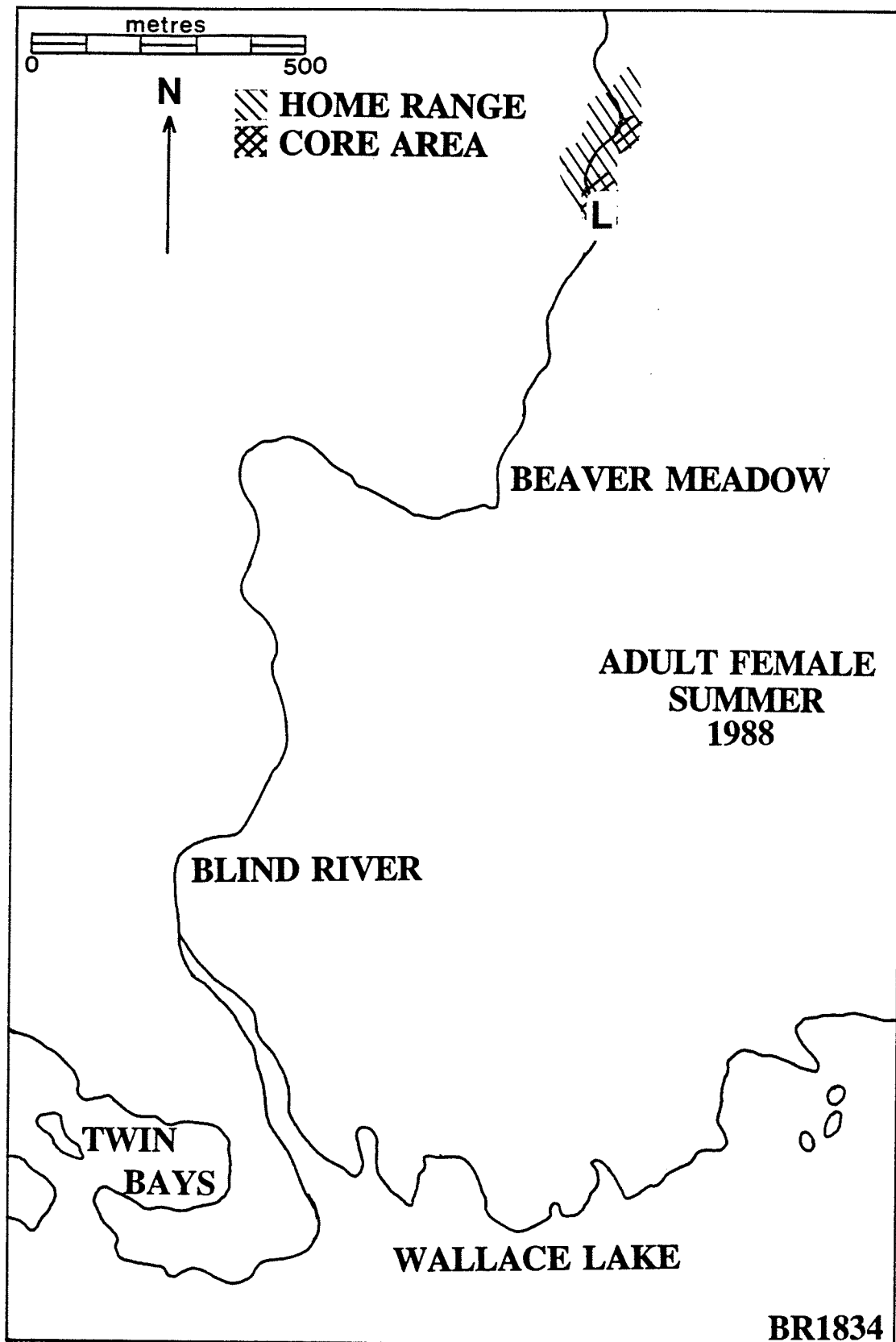


Figure 12. Maps of home range area for beaver BR1834 for summer and fall, 1987 and 1988. L indicates location of the lodge.





BR1834



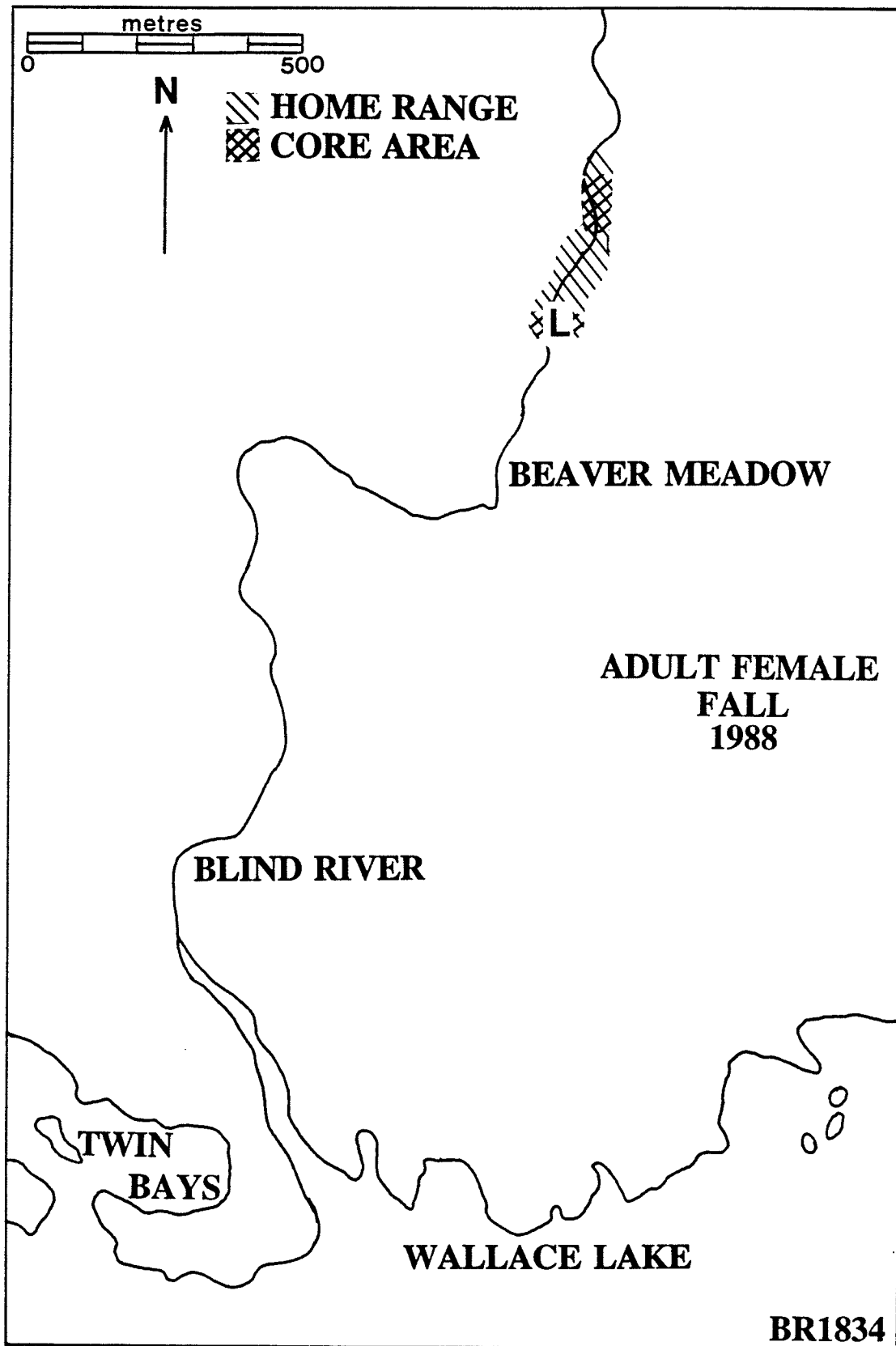
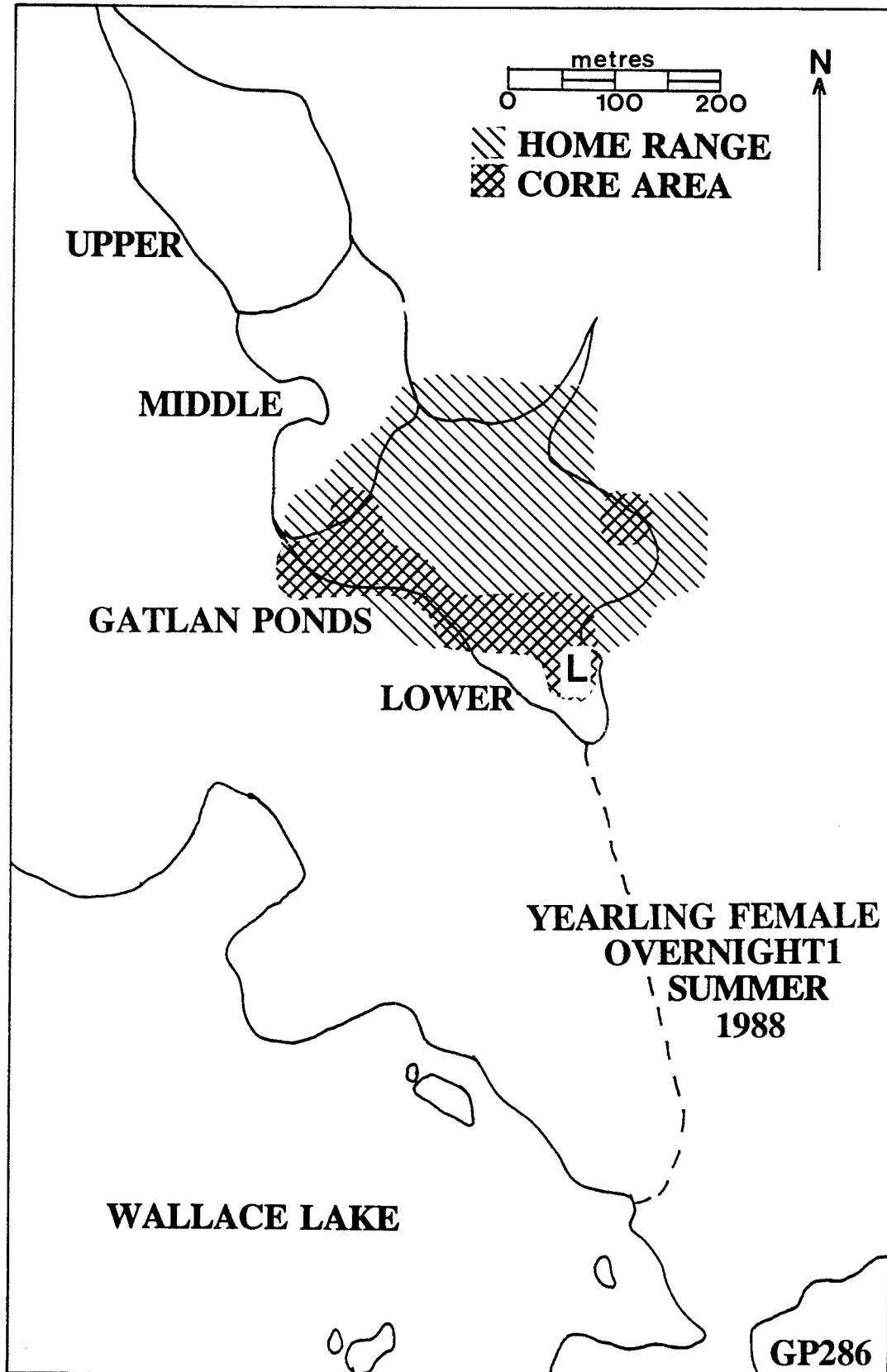
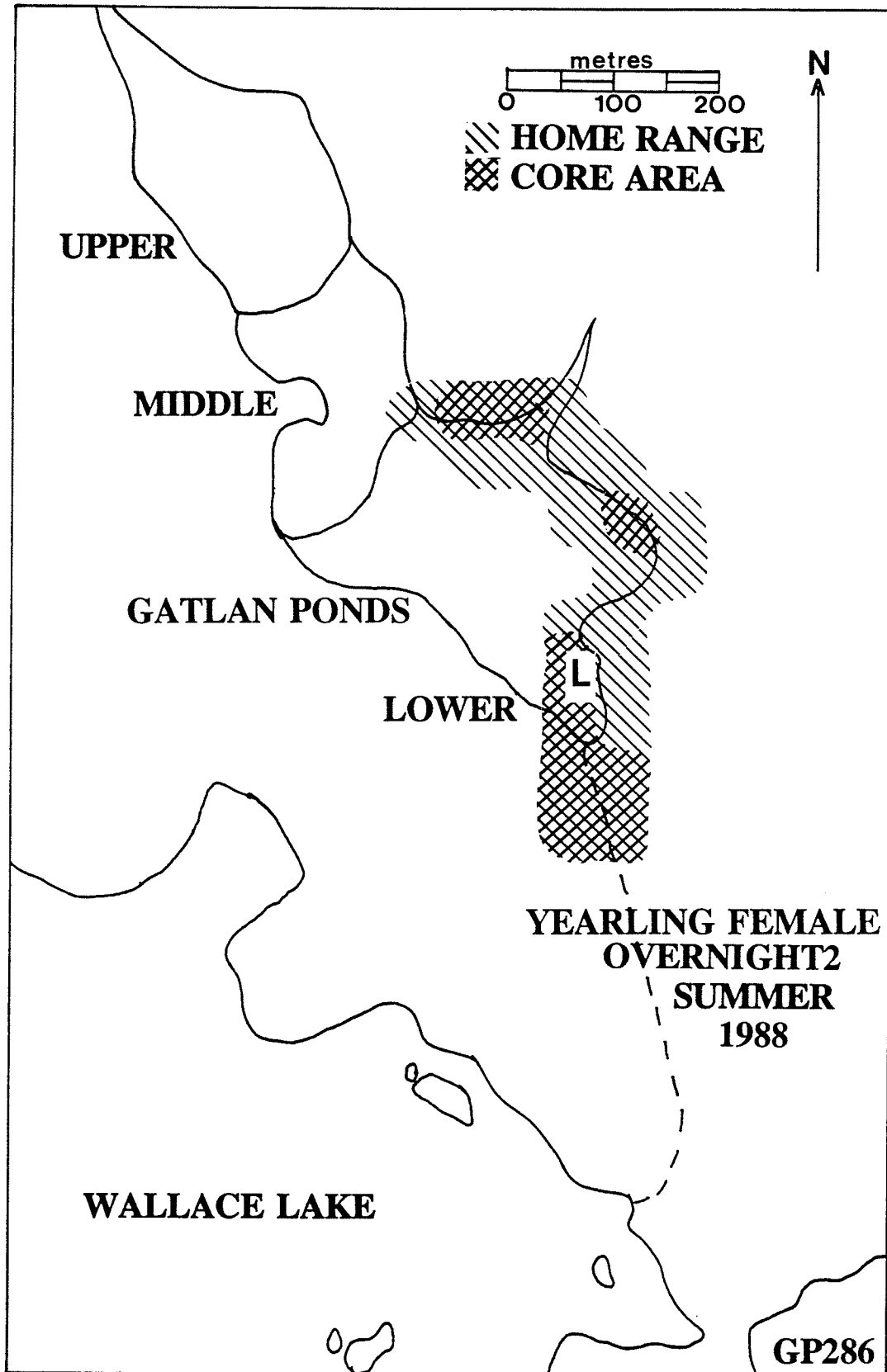


Figure 13. Maps of home range area for beaver GP286 for overnights in summer, 1988, and summer 1989. L indicates location of the lodge.





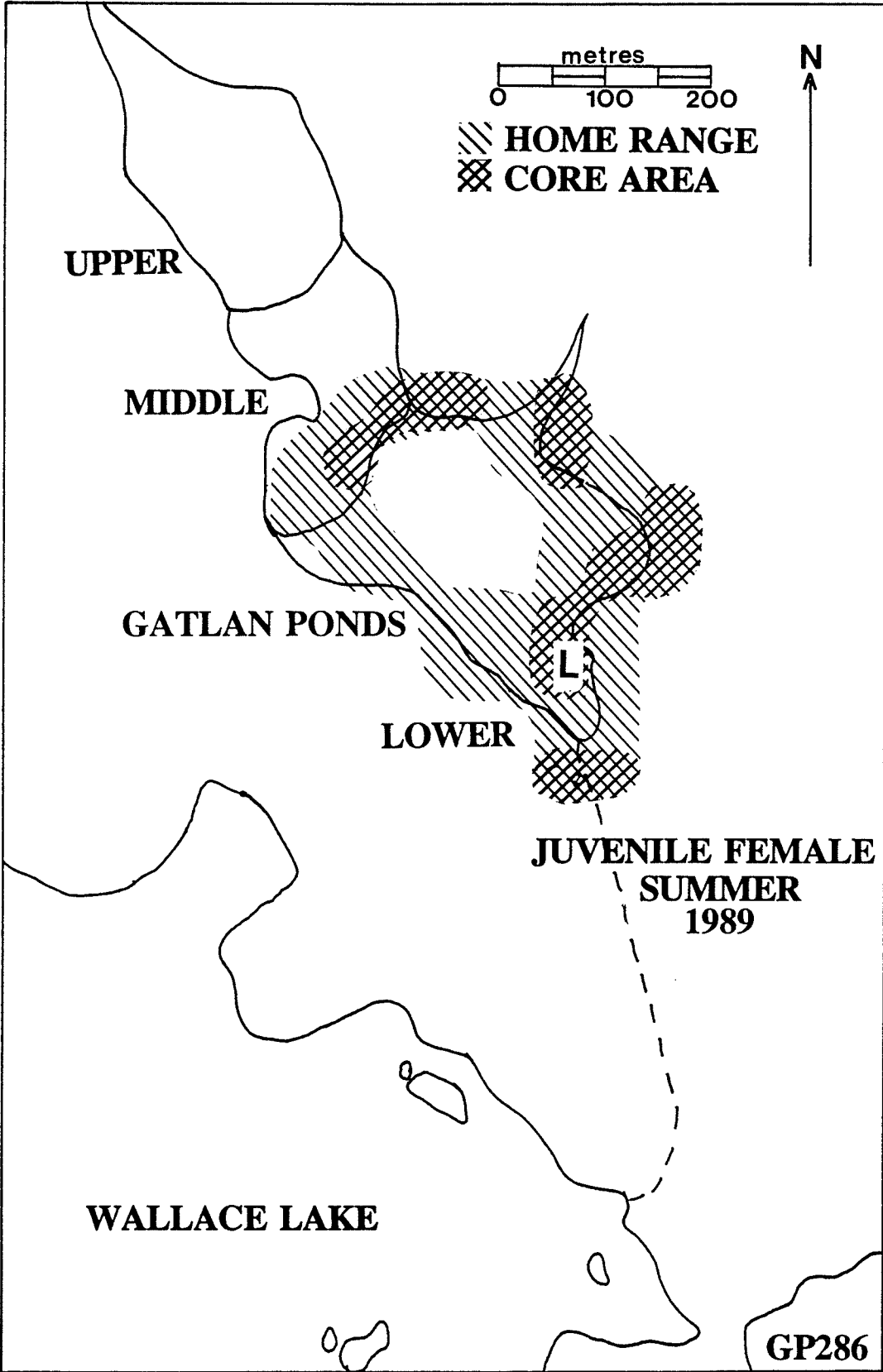
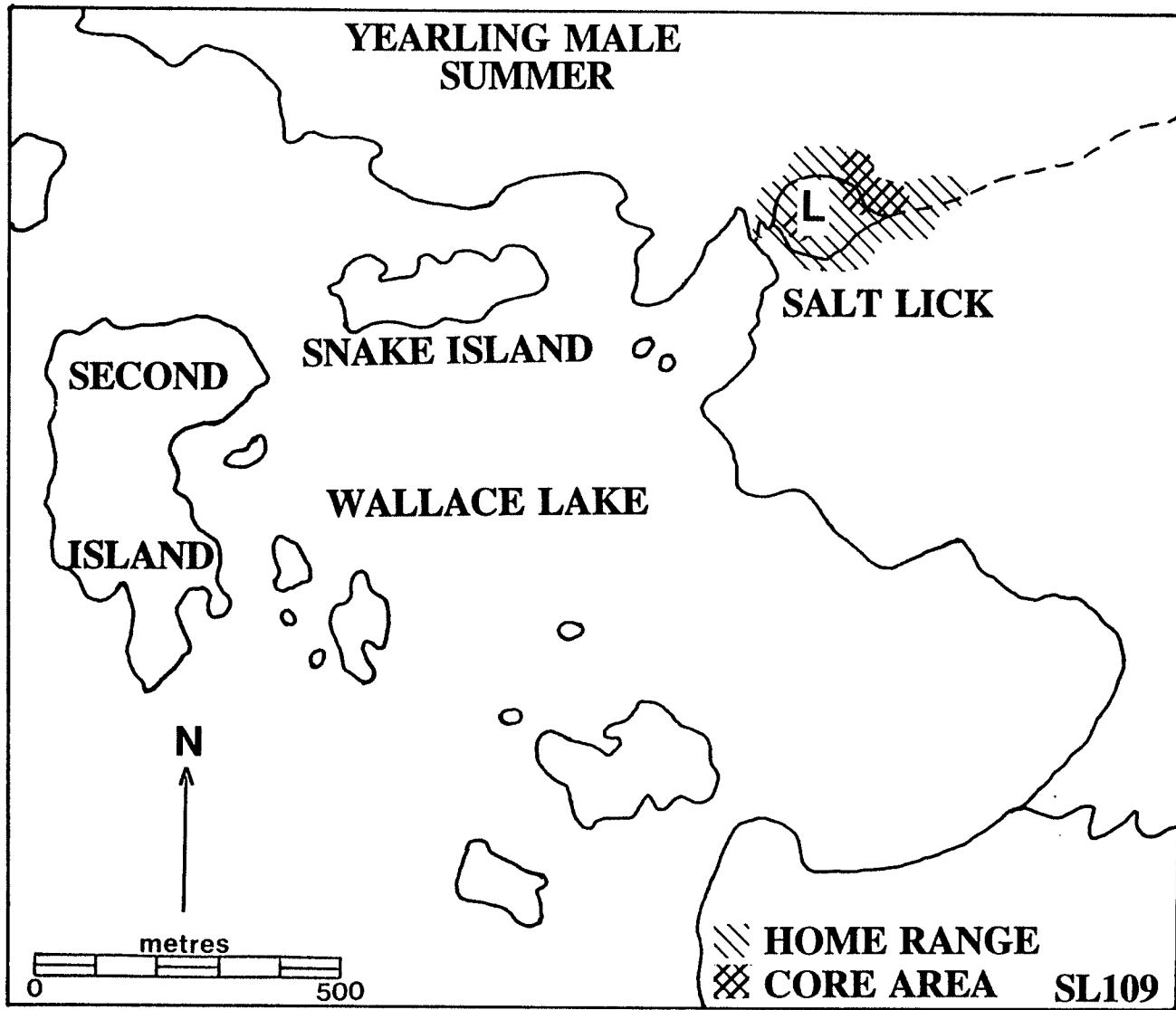
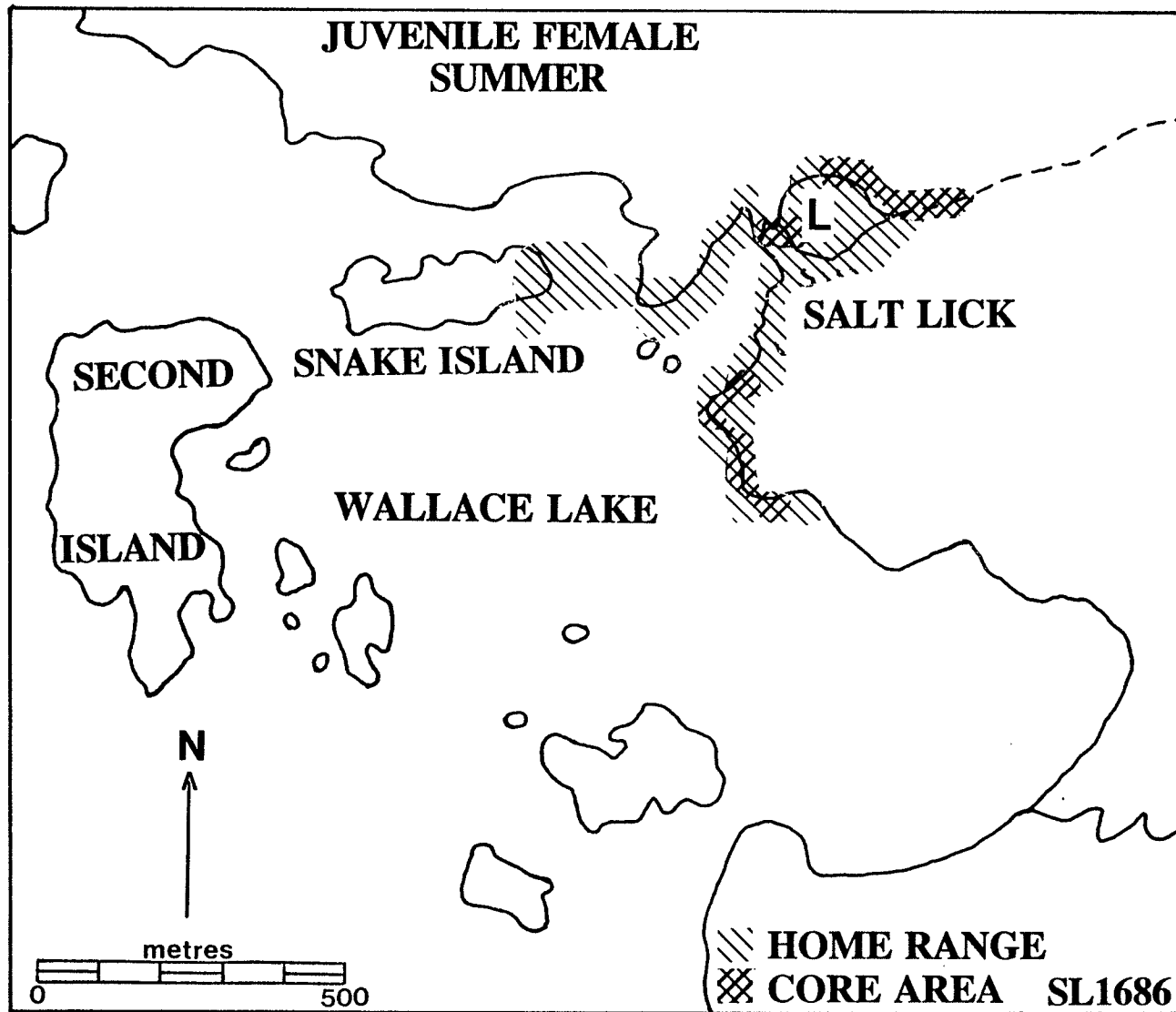
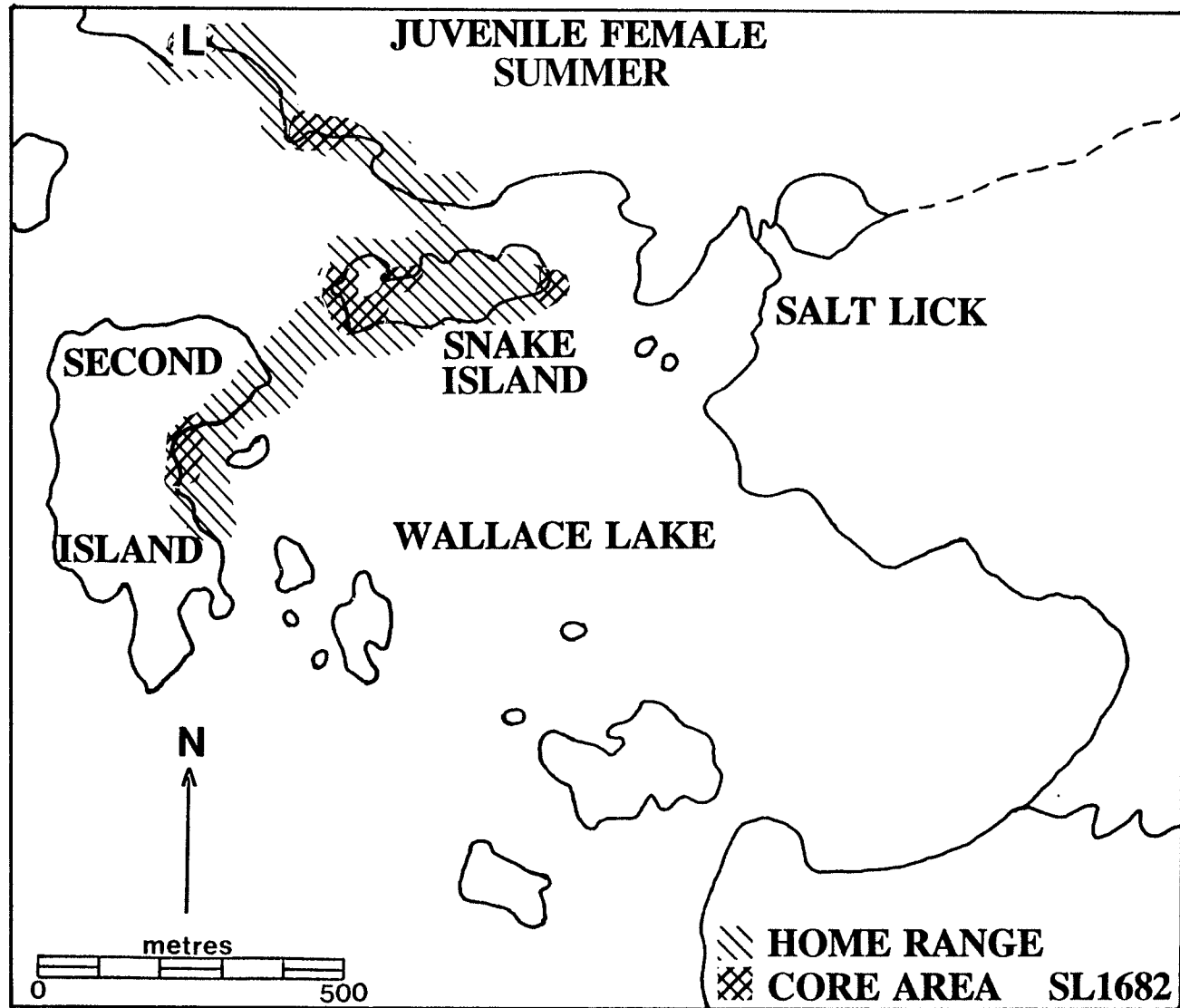


Figure 14. Maps of home range area for beavers SL109, summer, 1989 and SL1686 and SL1682, summer, 1990. L indicates known lodges.



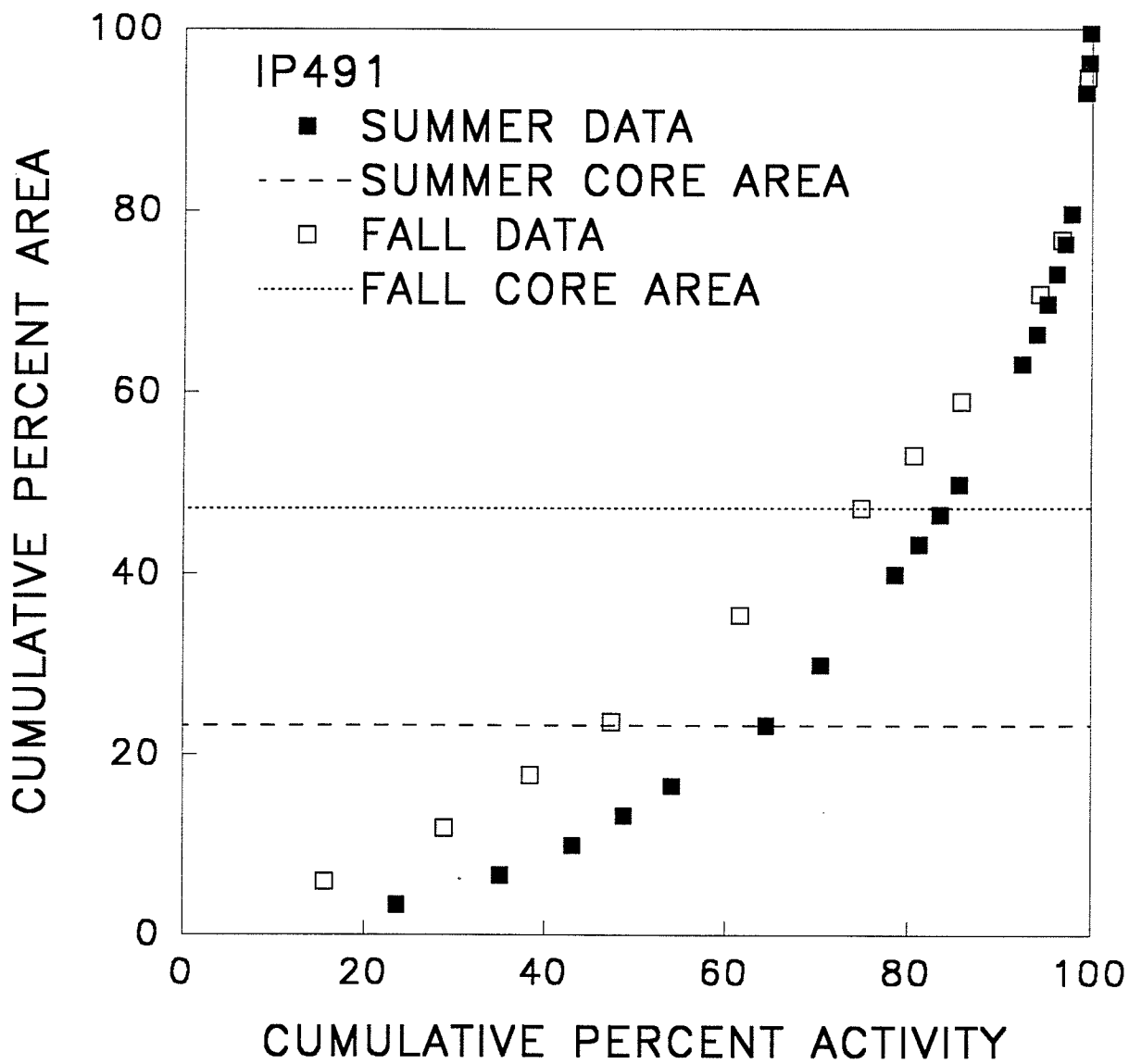


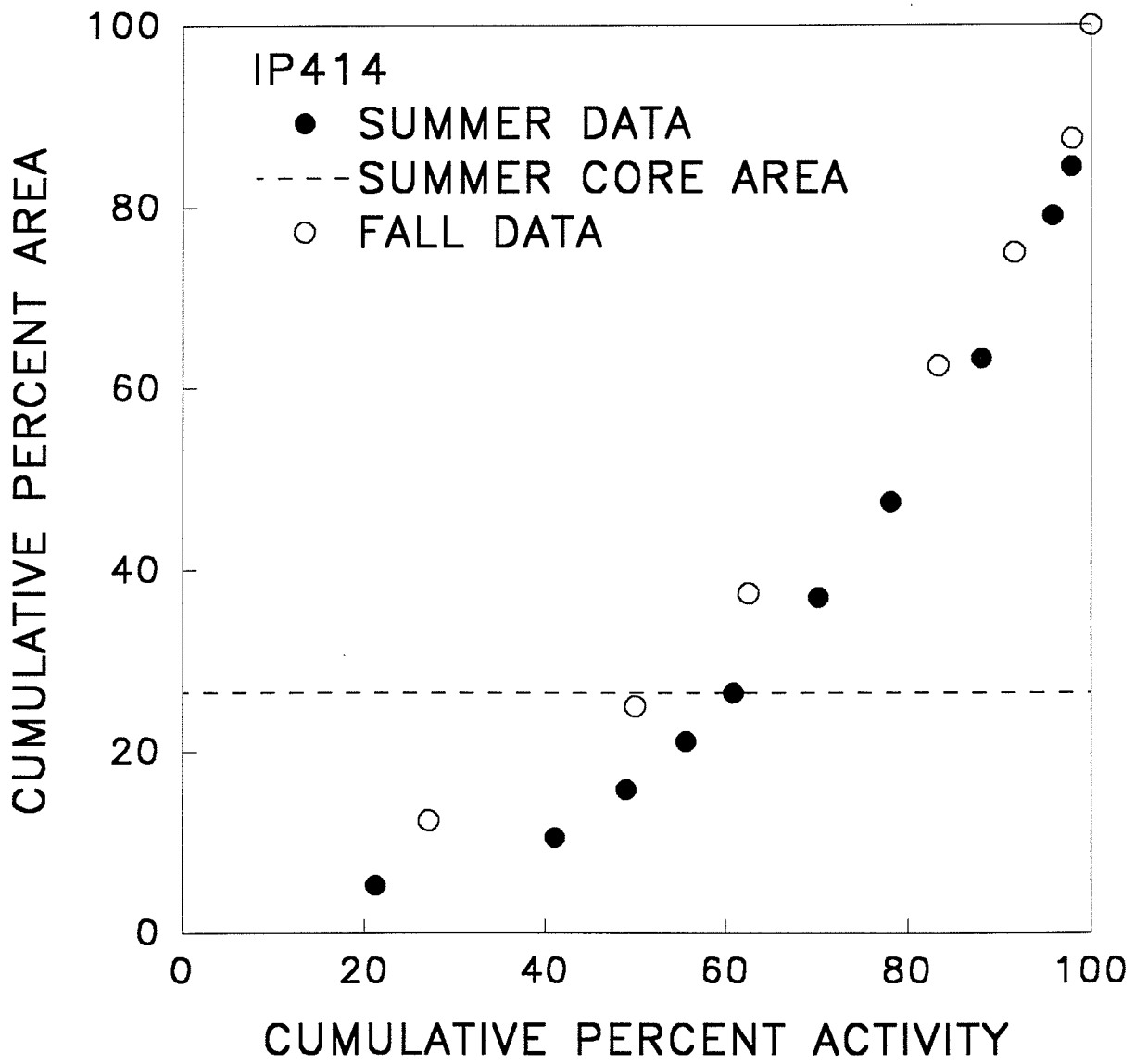


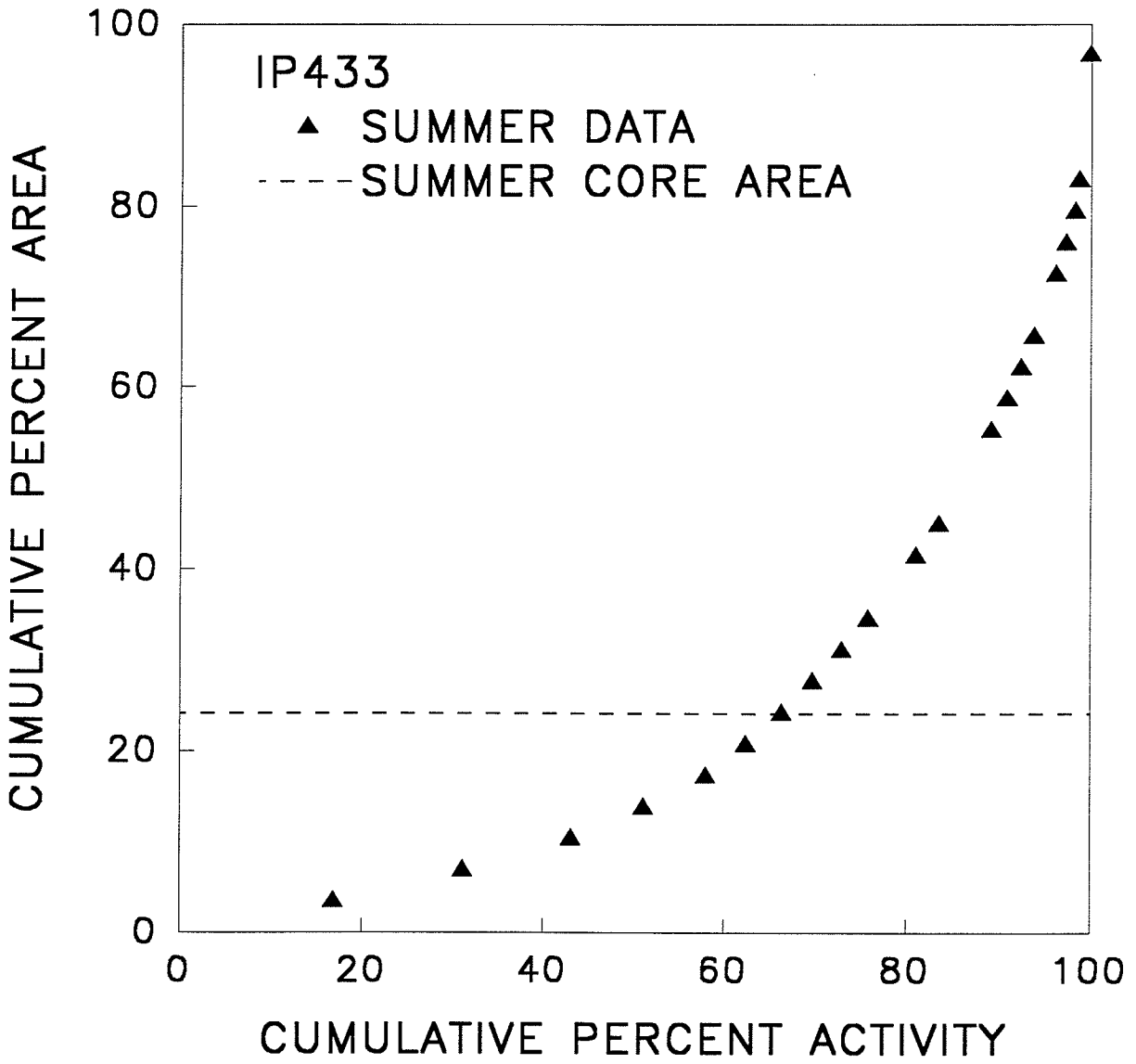
APPENDIX 2

HOME RANGE USE GRAPHS

Figure 1. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Implant Pond Family for summer and fall, 1989.







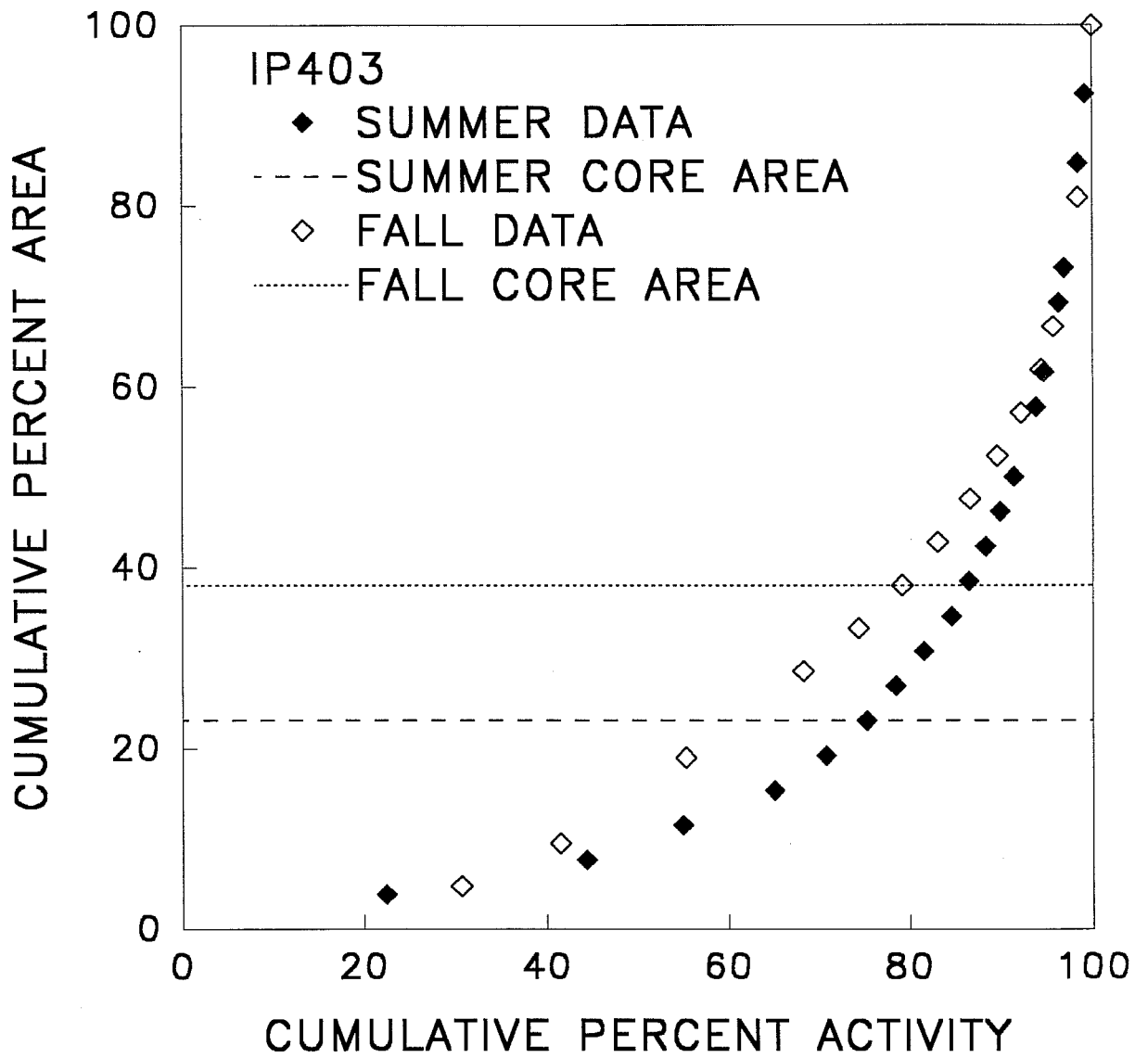
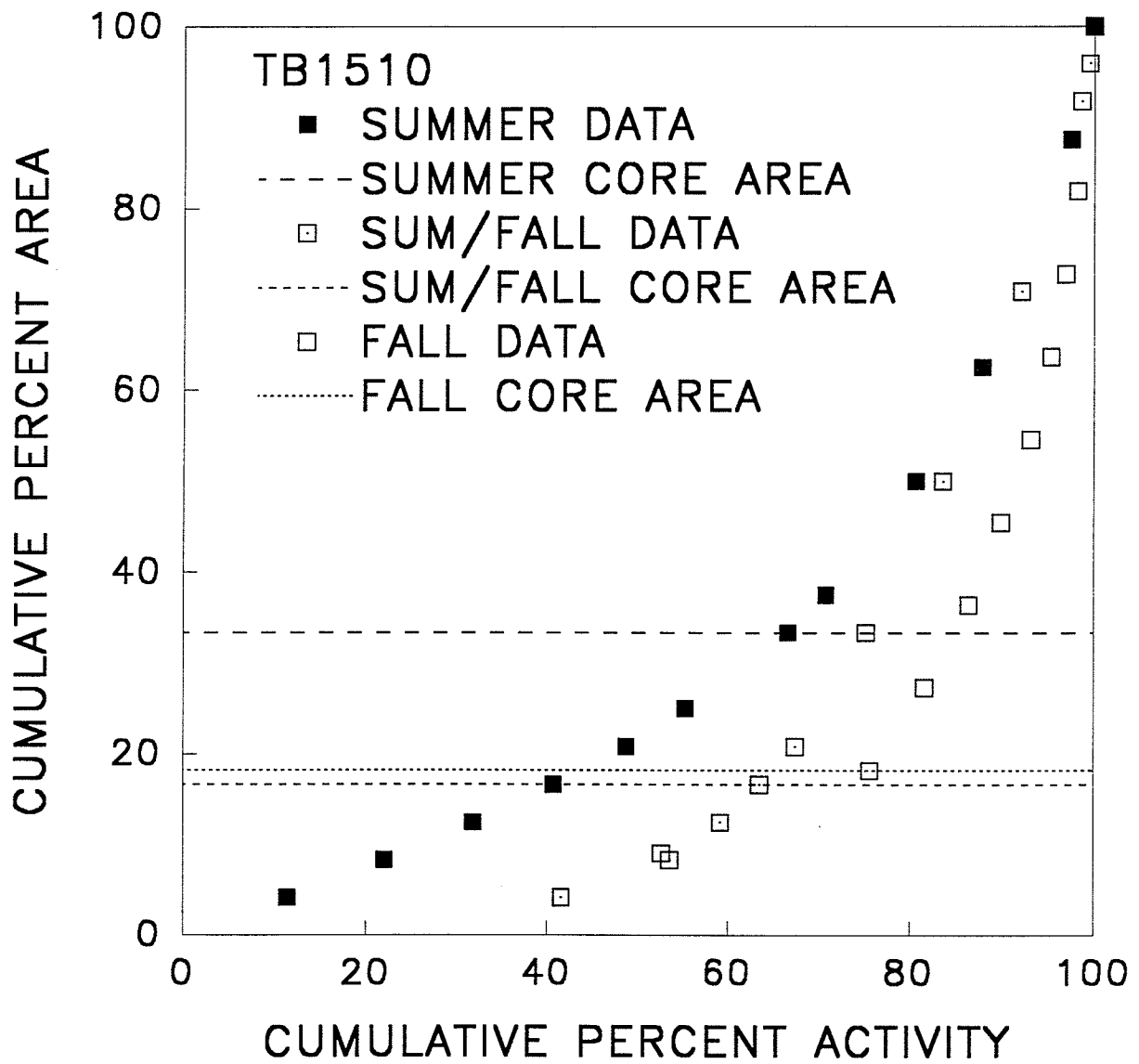
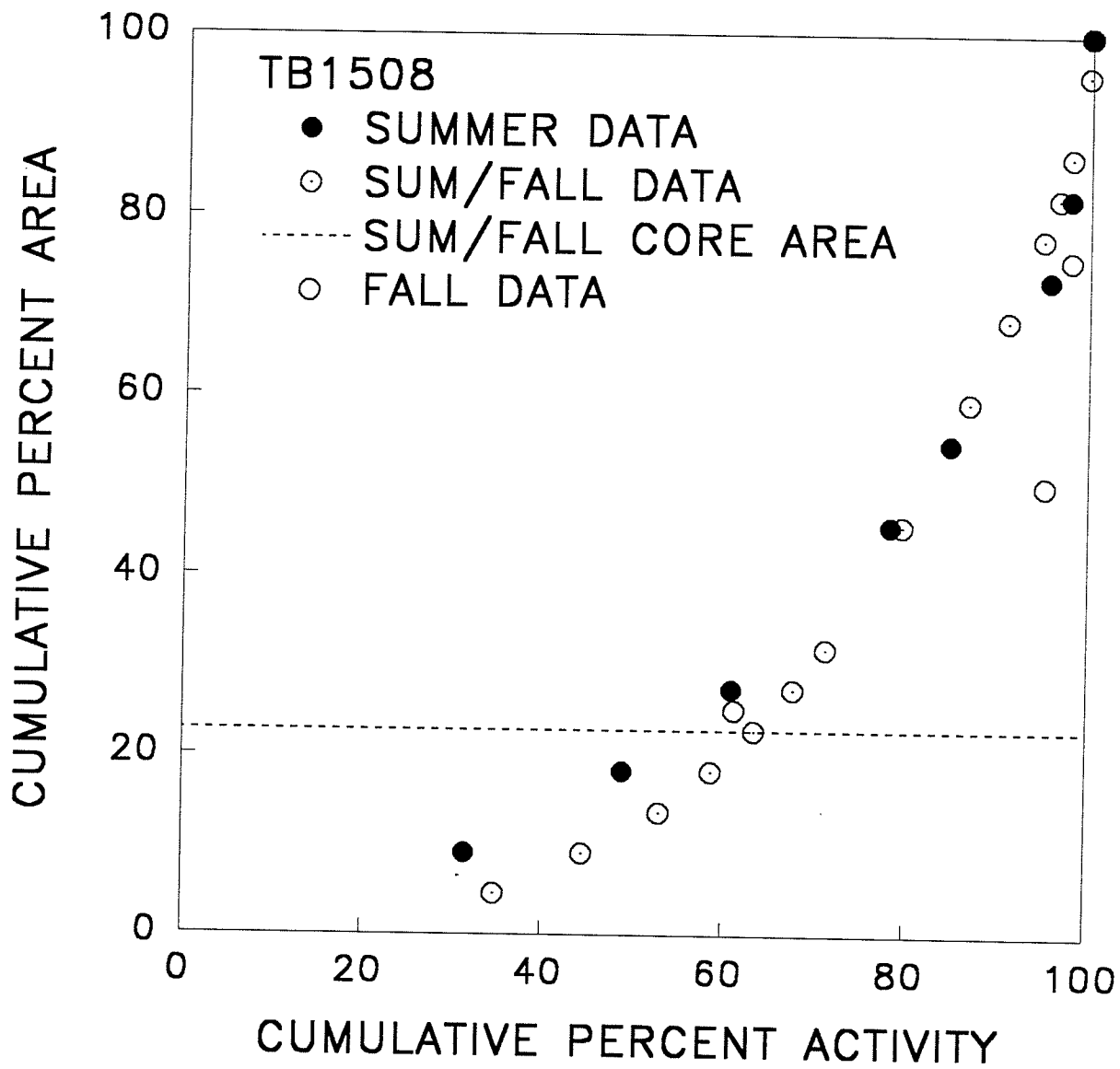
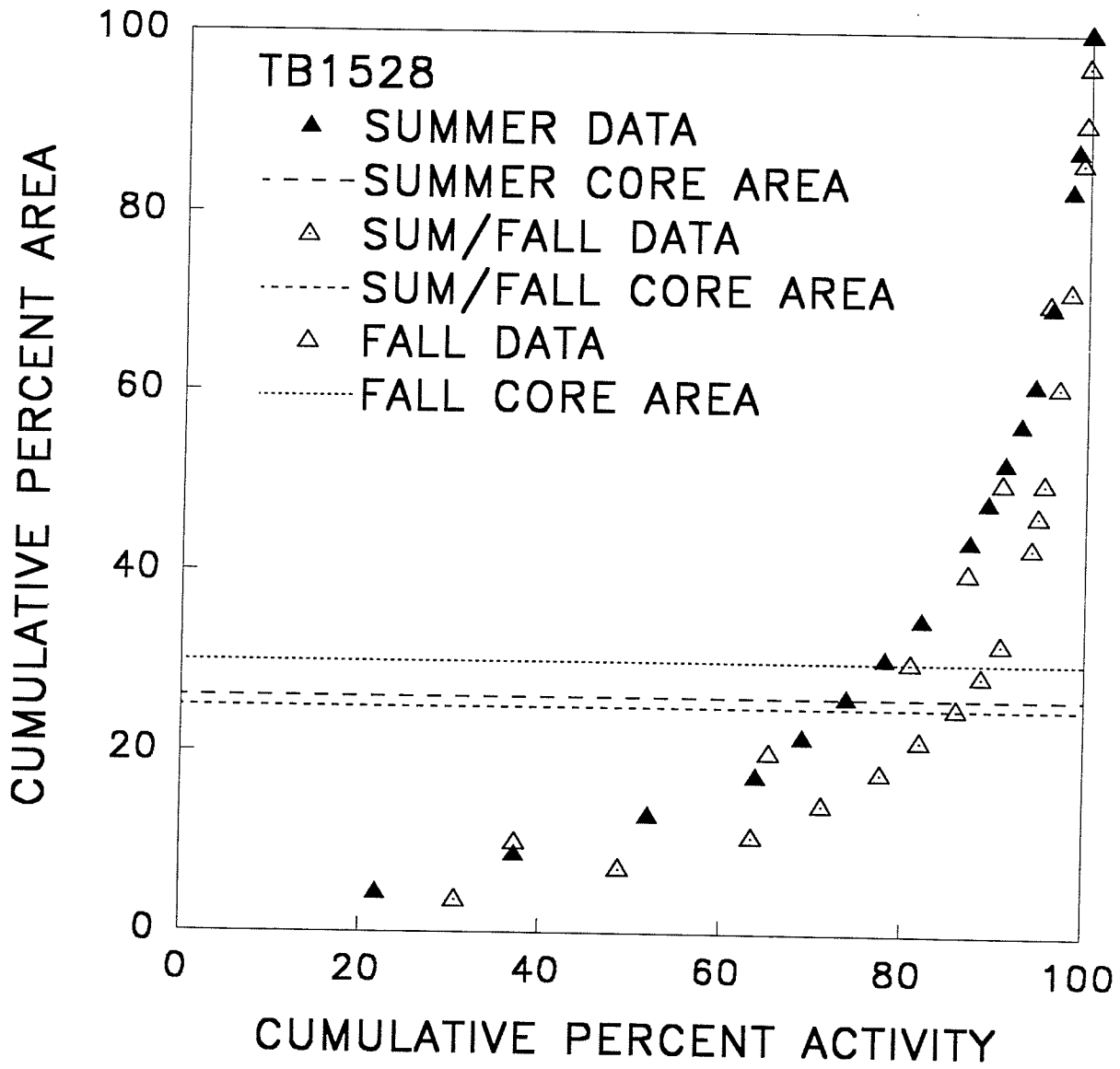
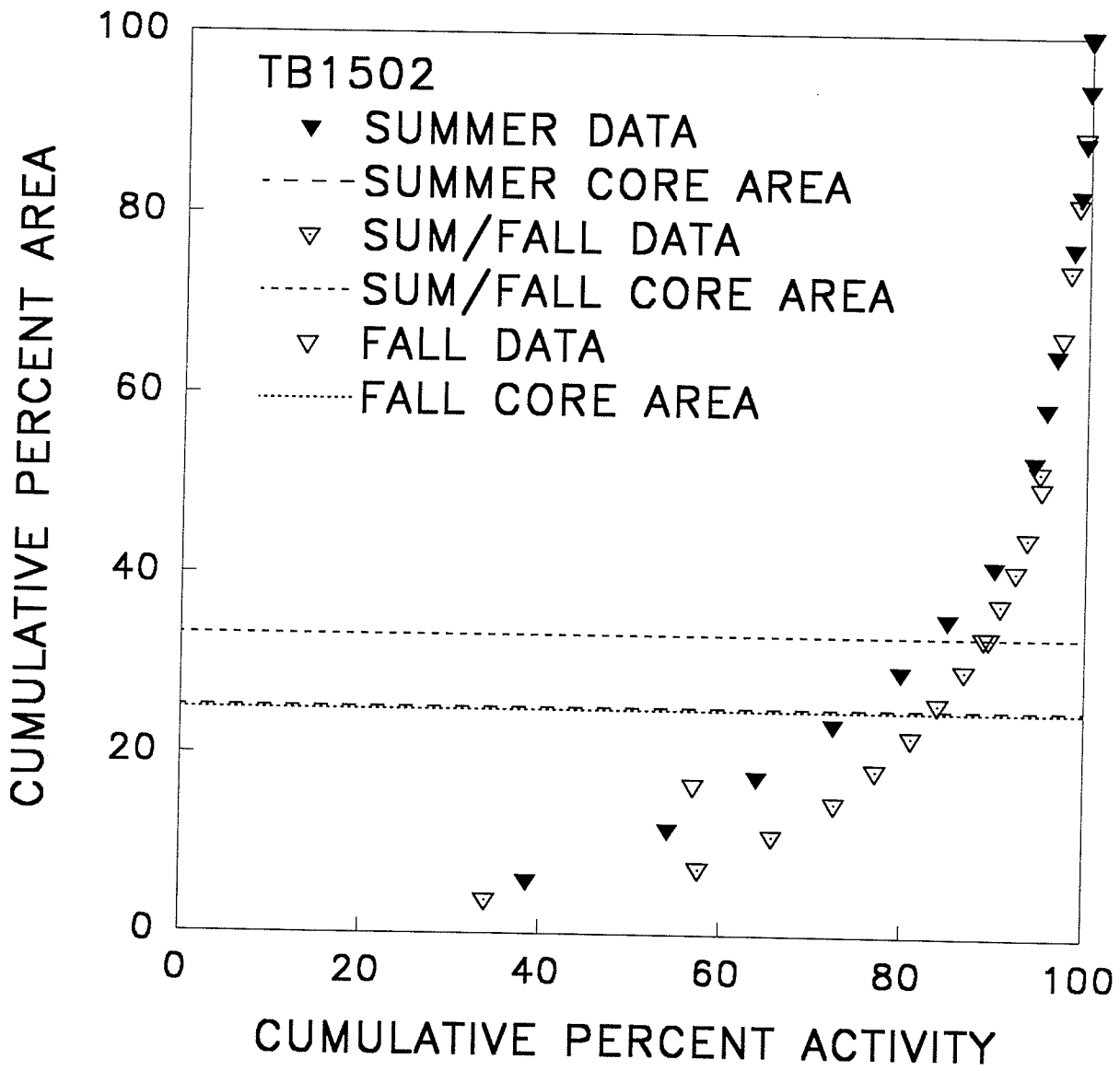


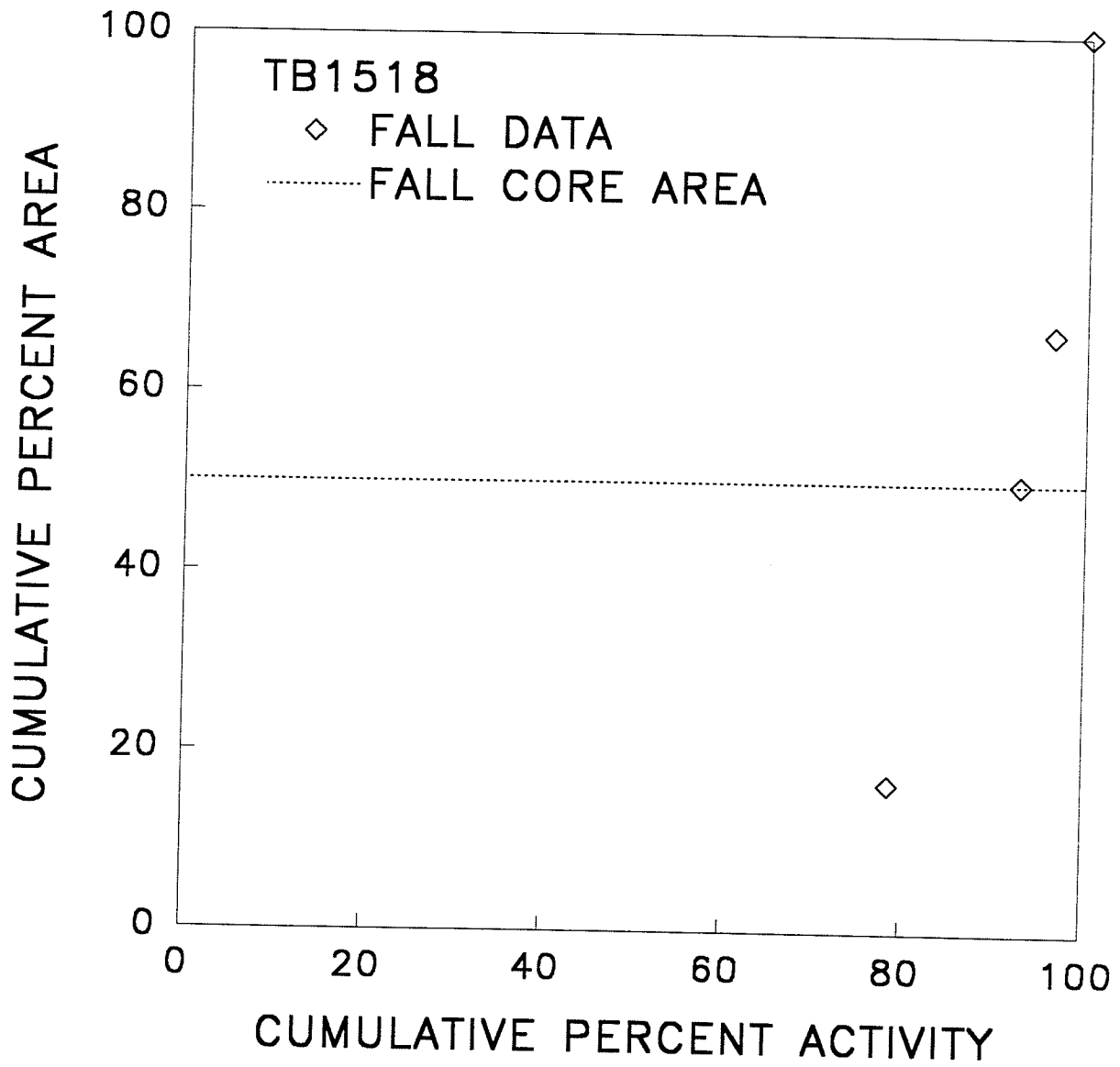
Figure 2. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Twin Bays Family for summer and fall, 1991.

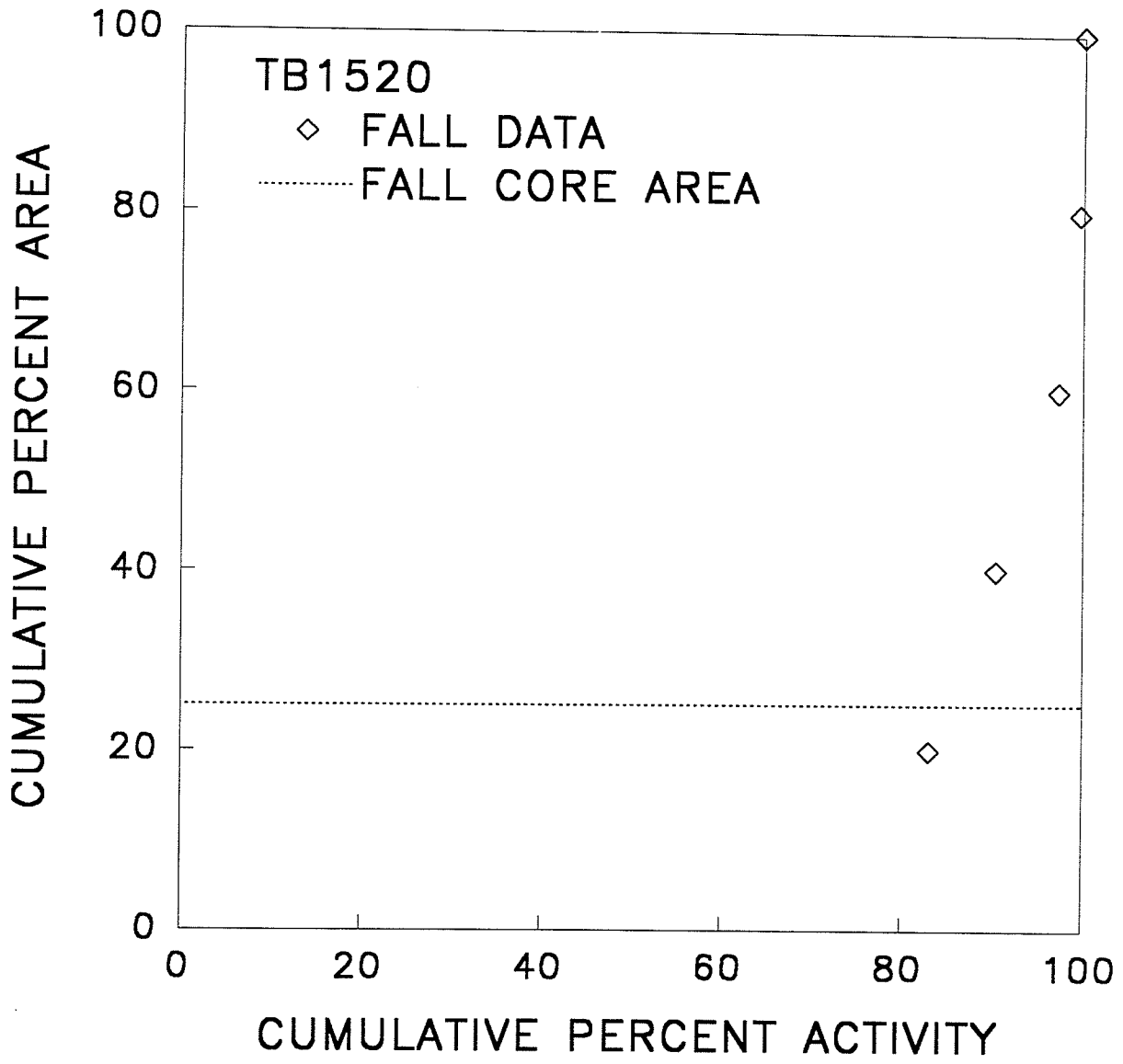












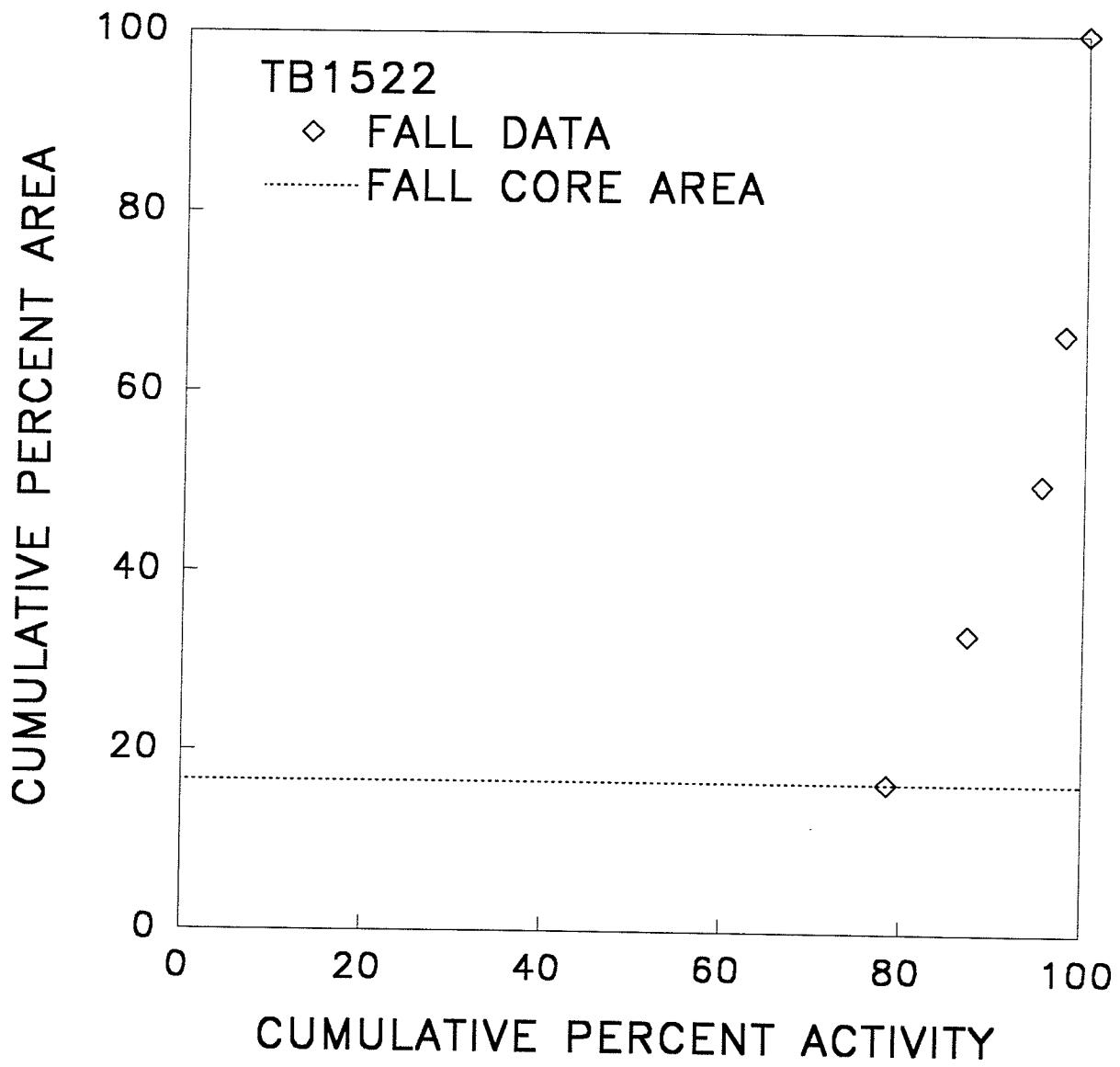
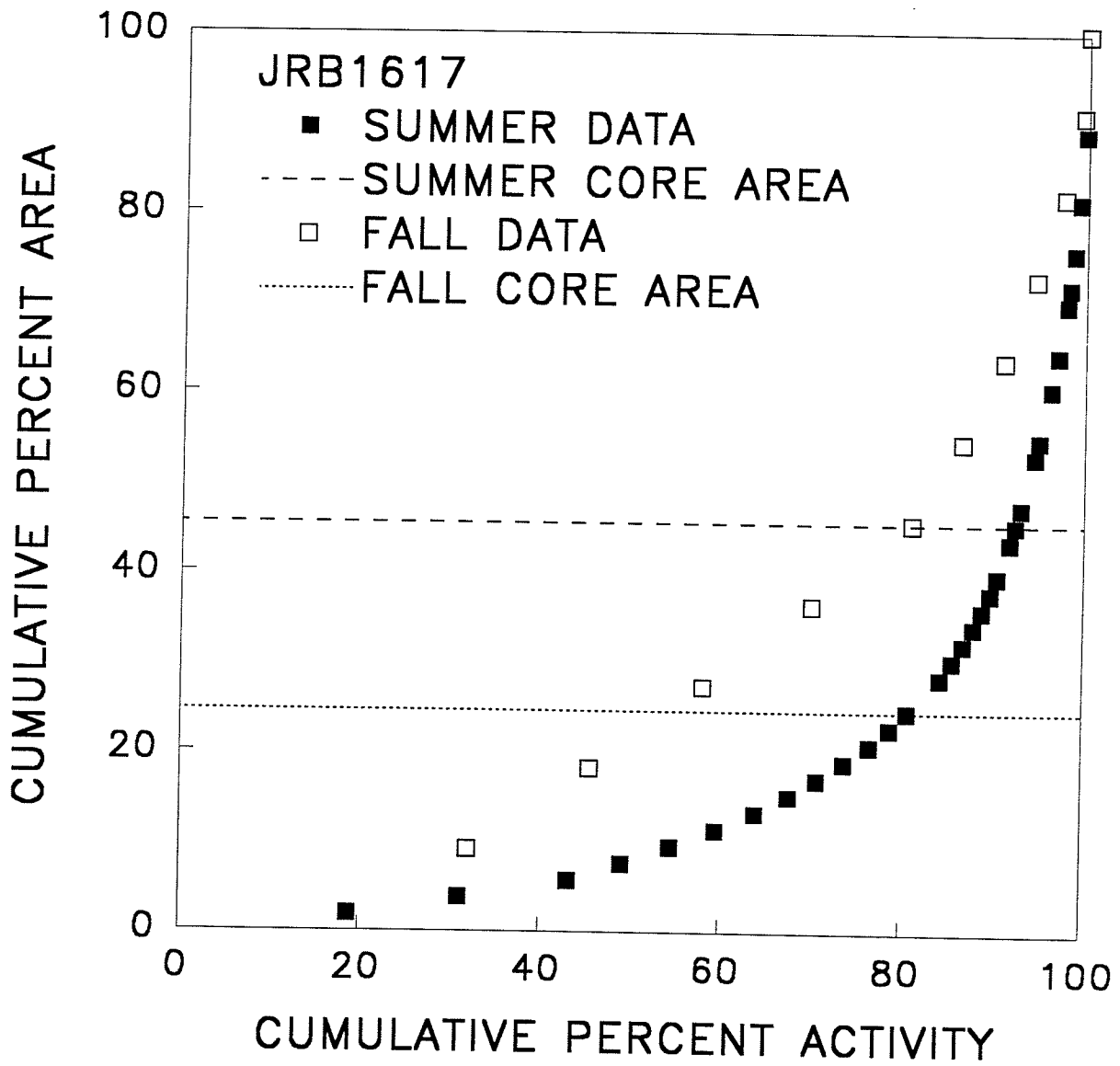
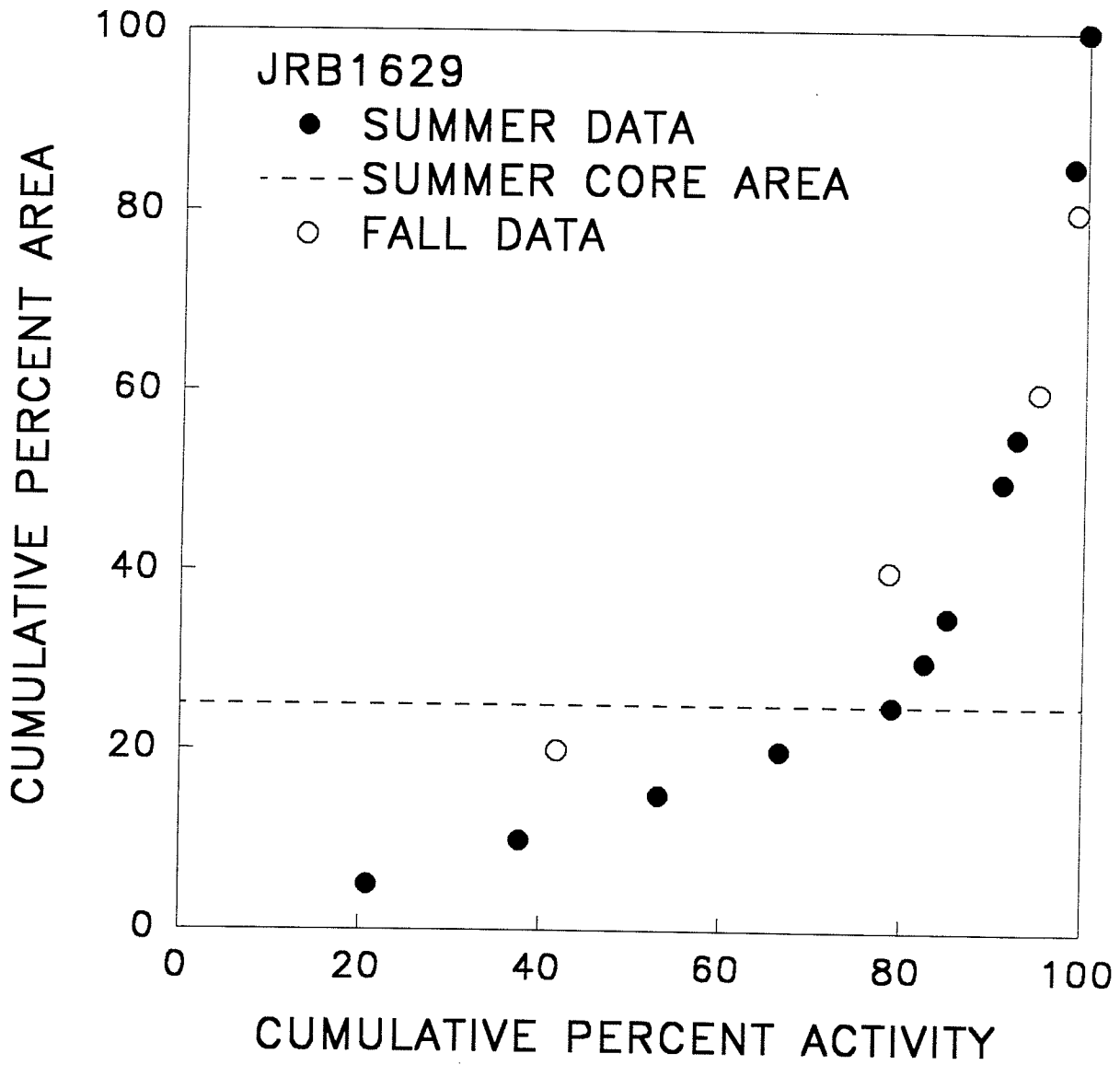
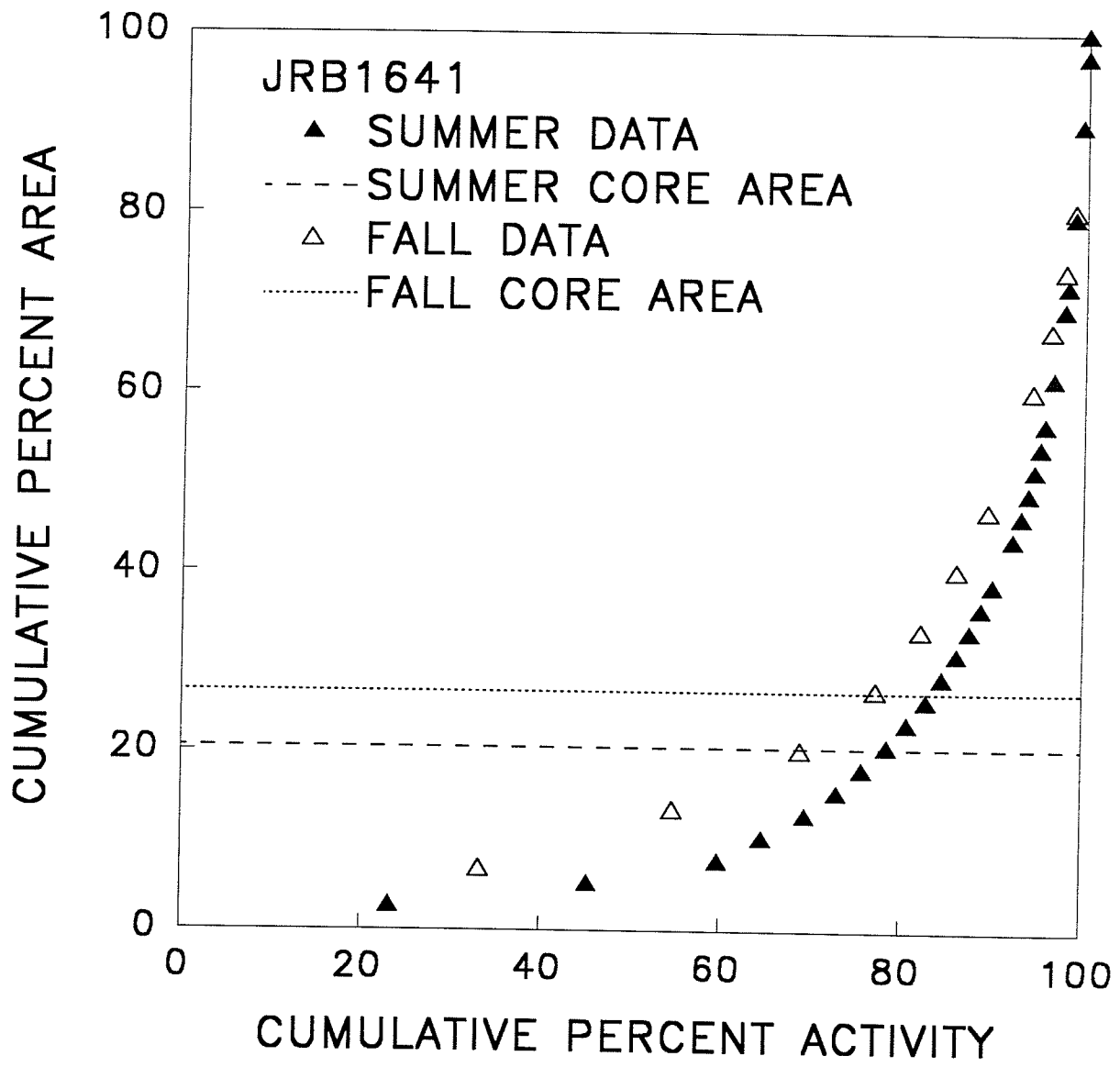


Figure 3. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the JRB Family for summer and fall, 1990.







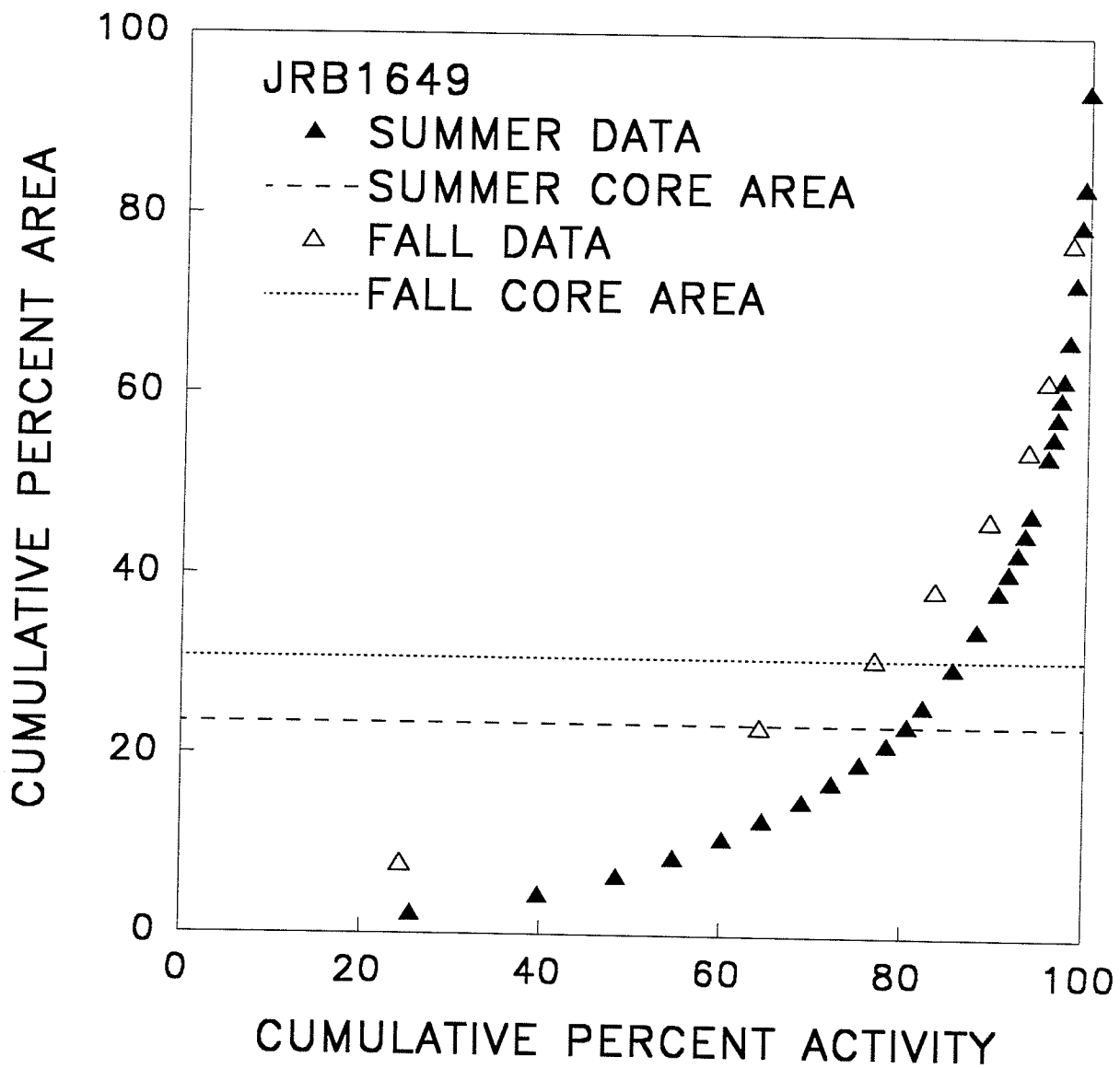
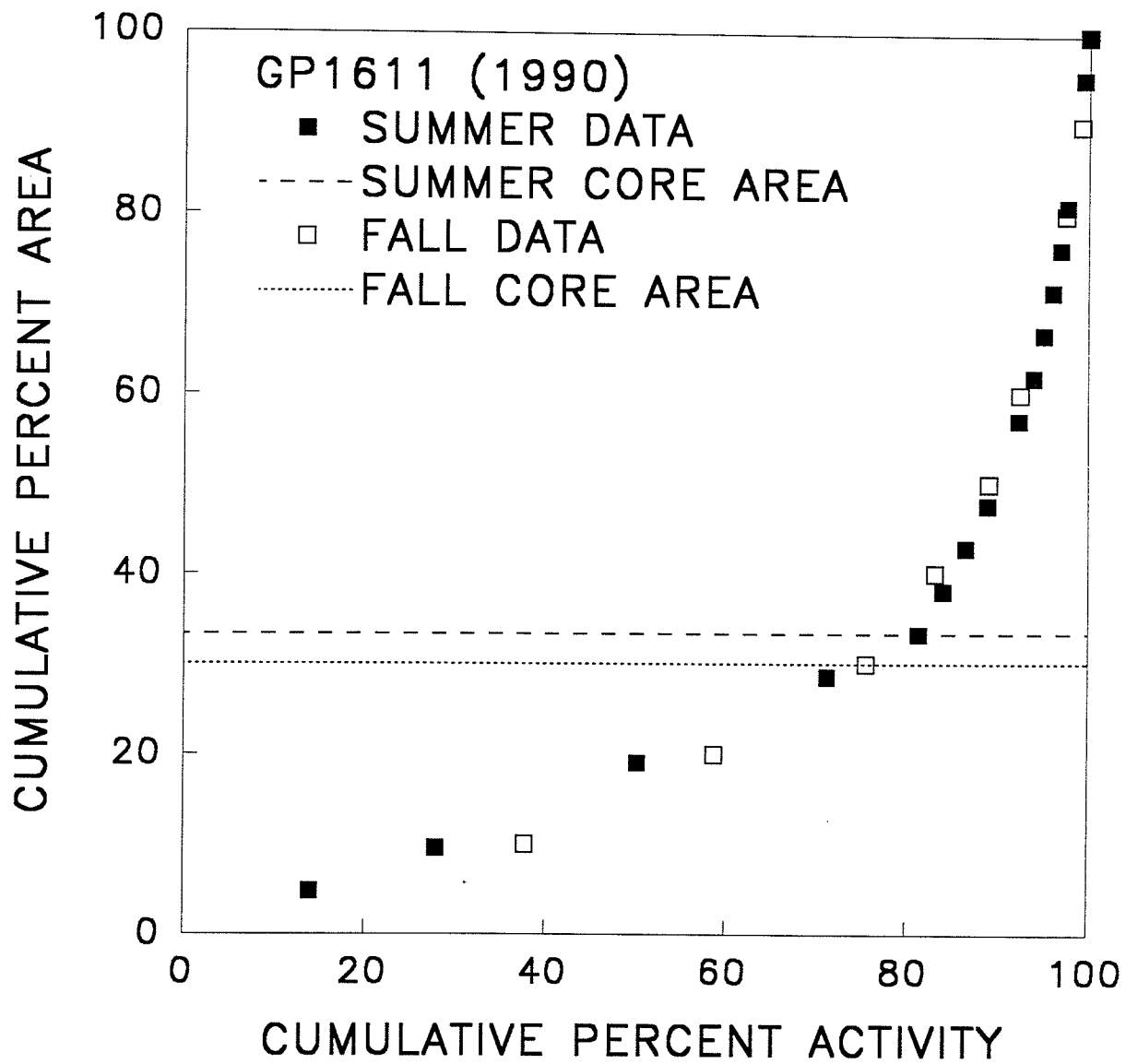
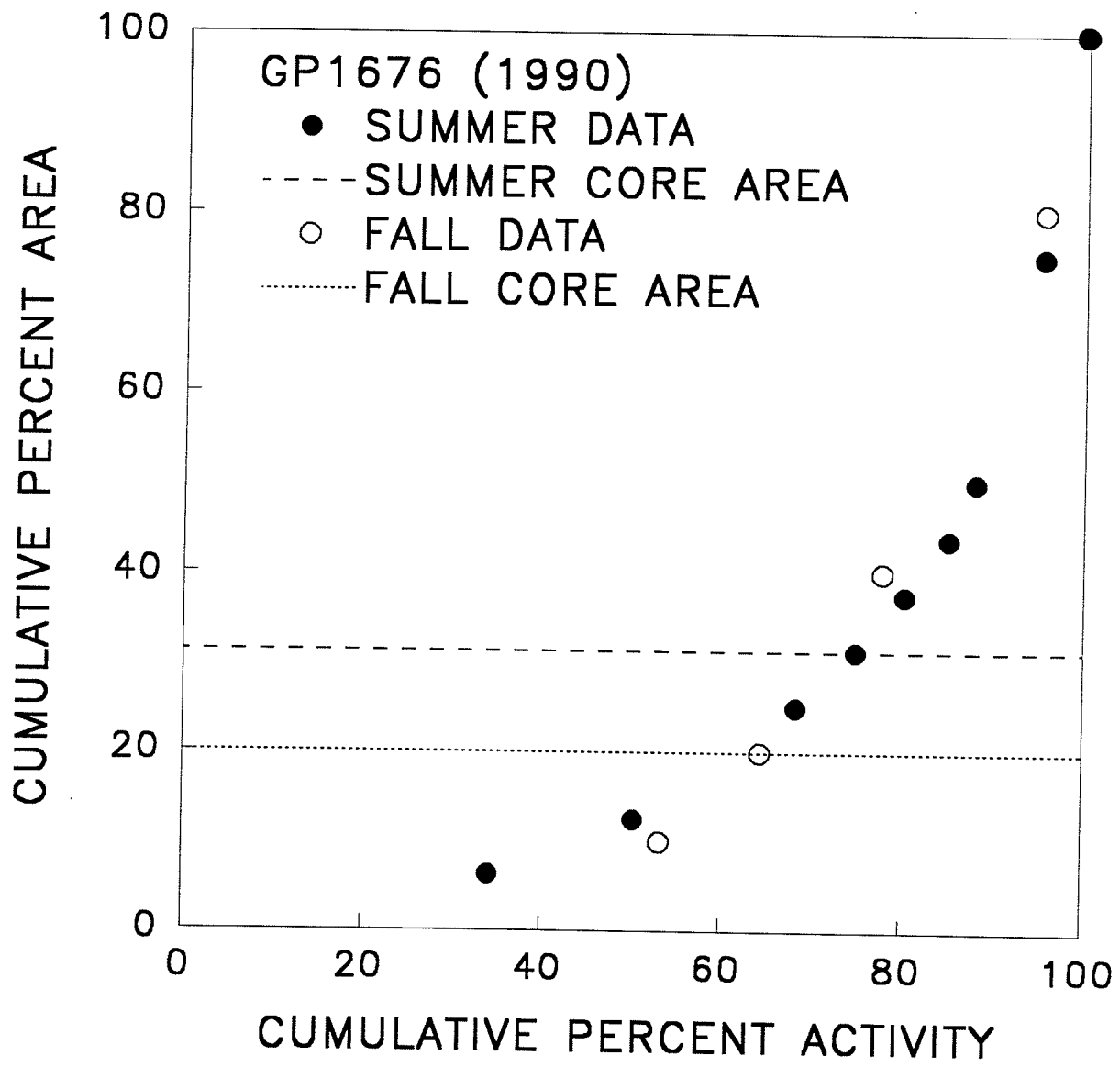
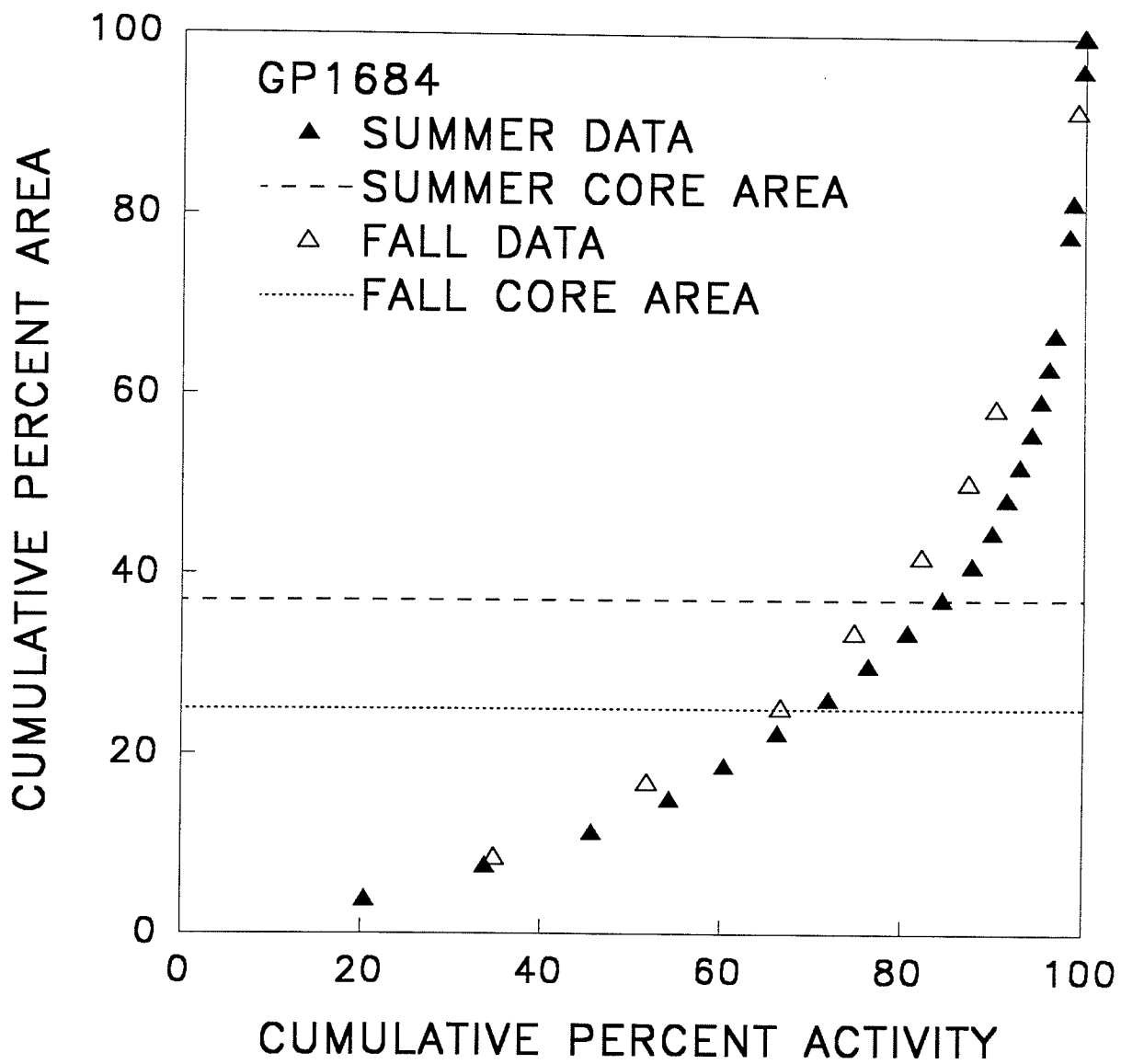


Figure 4. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Gatlan Pond Family for summer and fall, 1990.







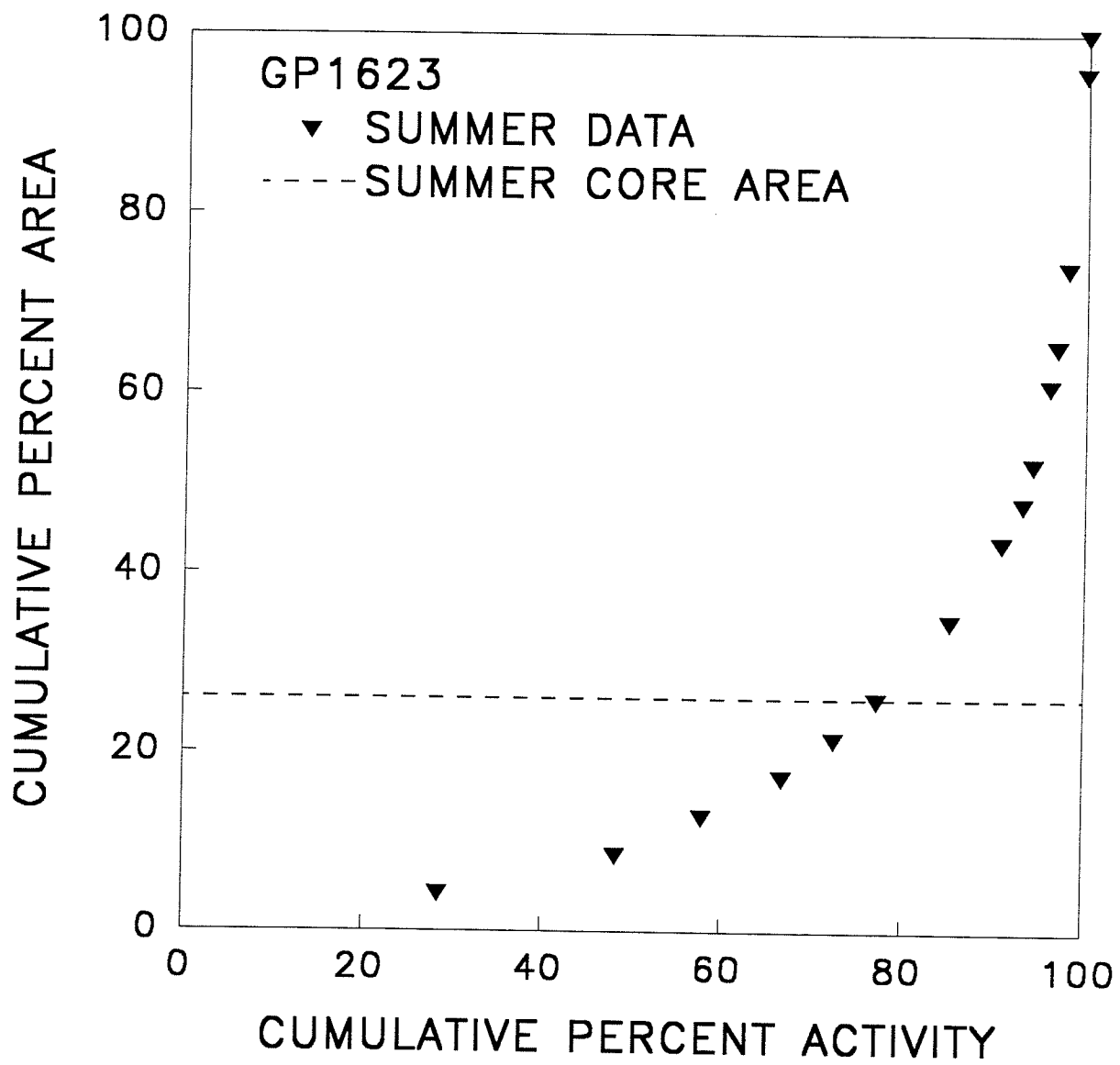
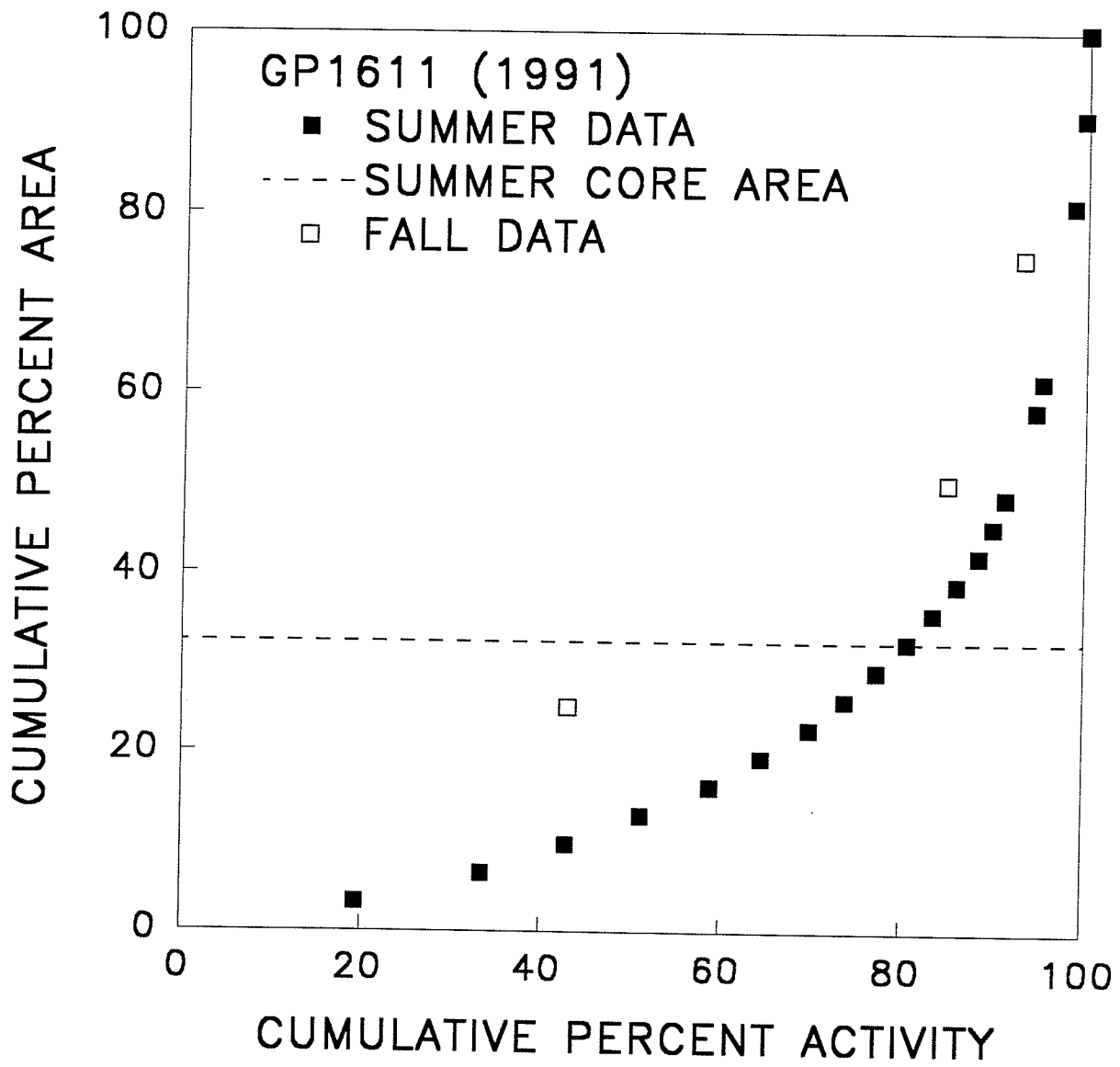
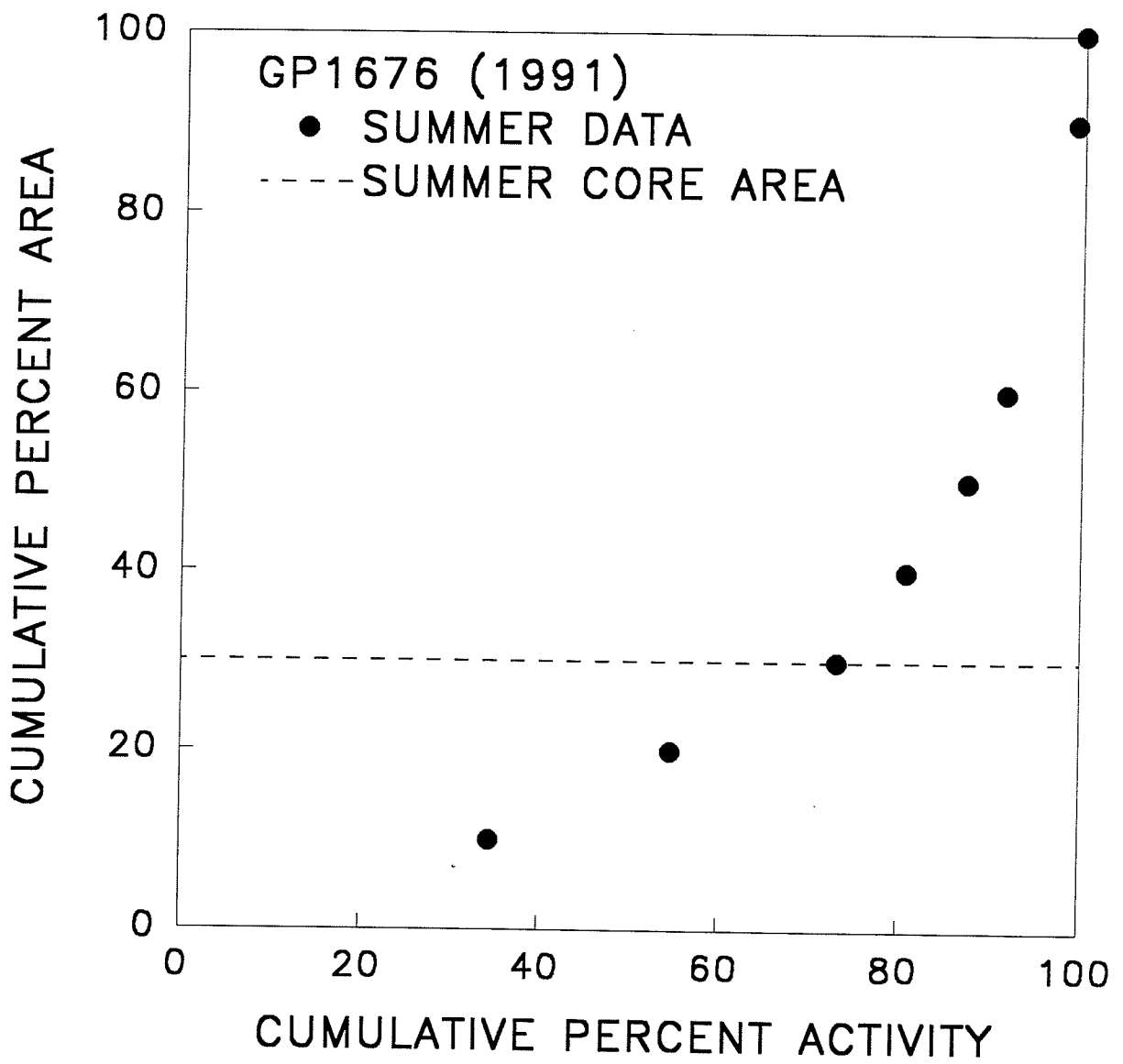


Figure 5. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers in the Gatlan Pond Family for summer and fall, 1991.





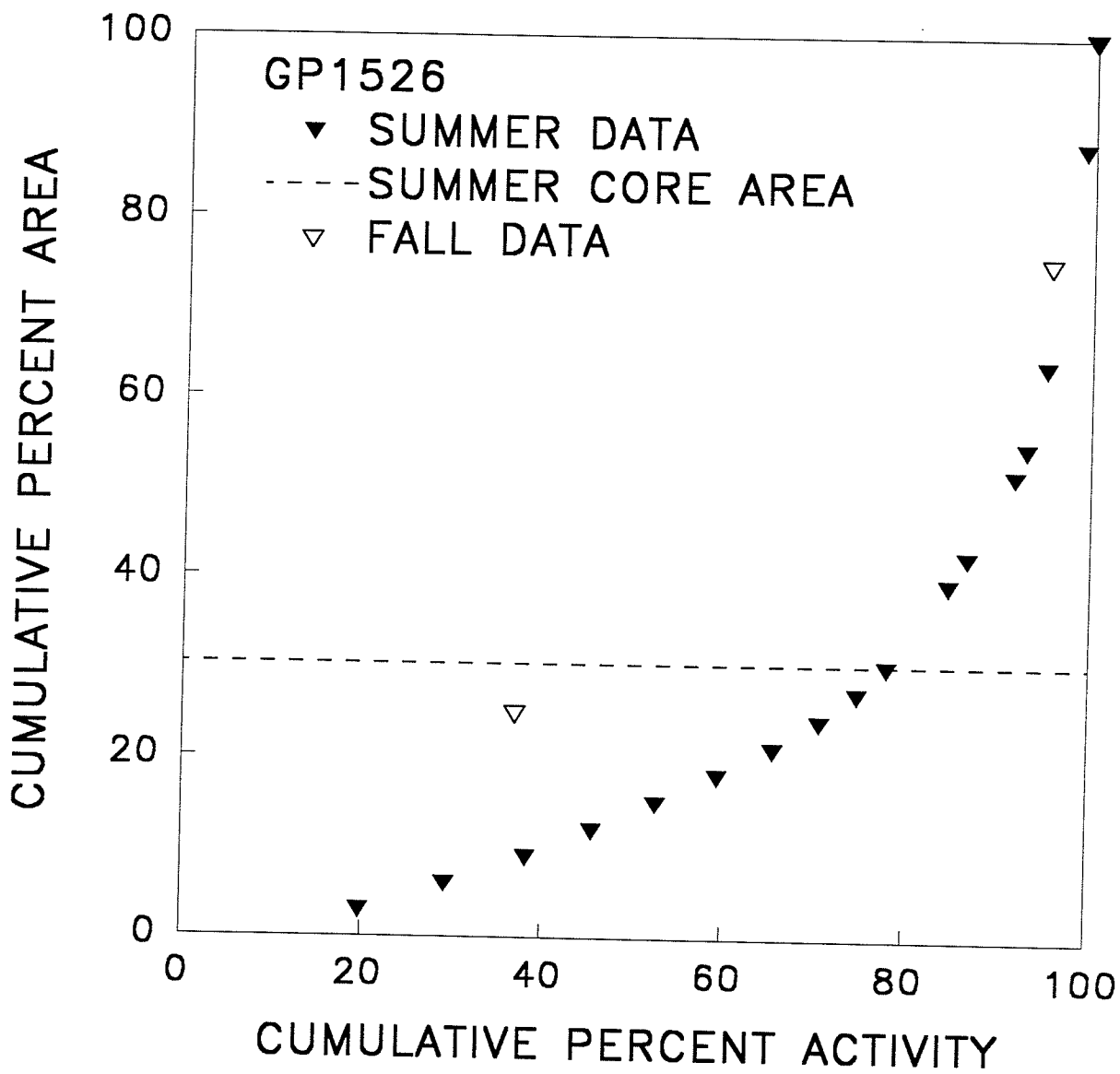
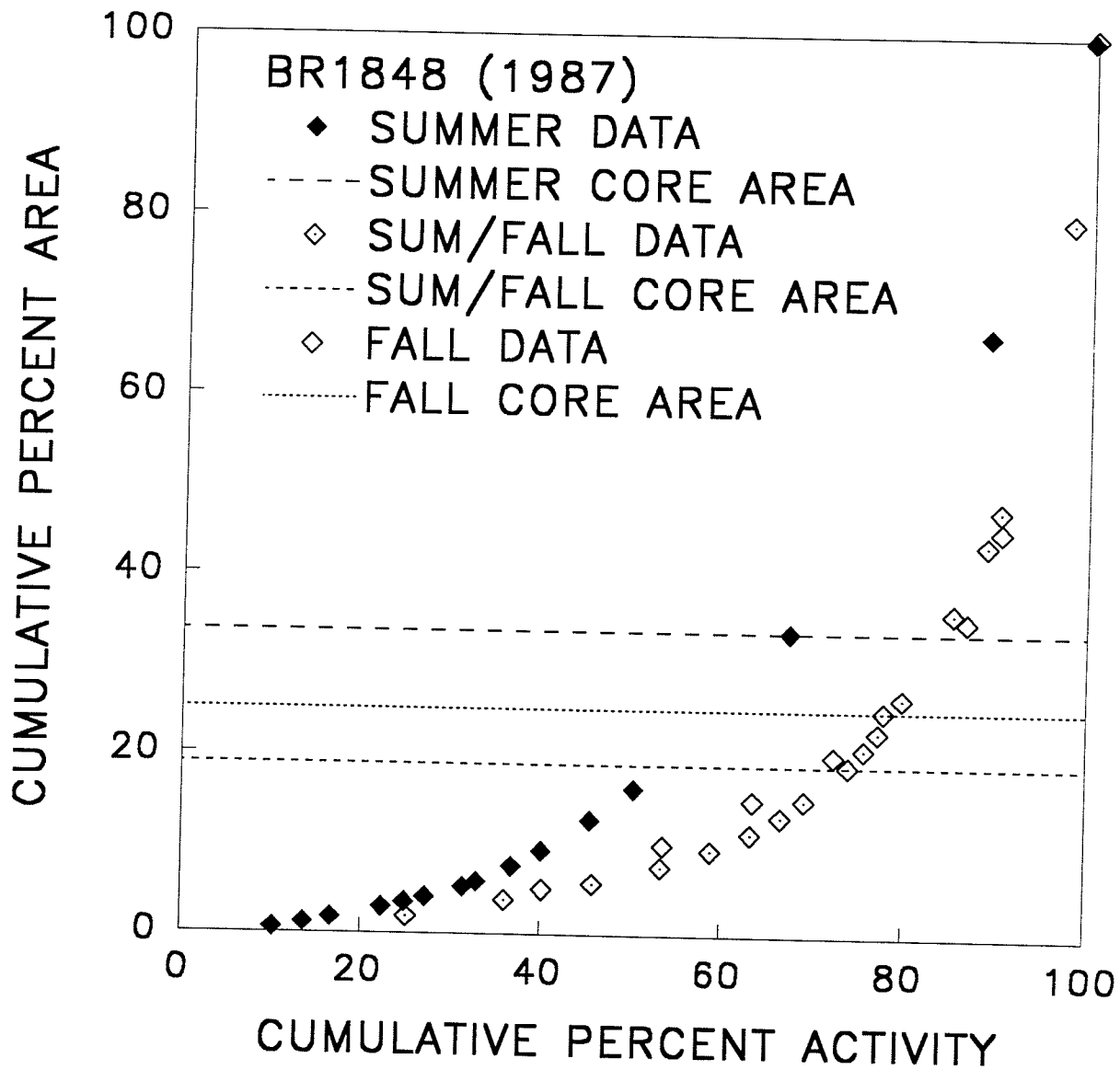
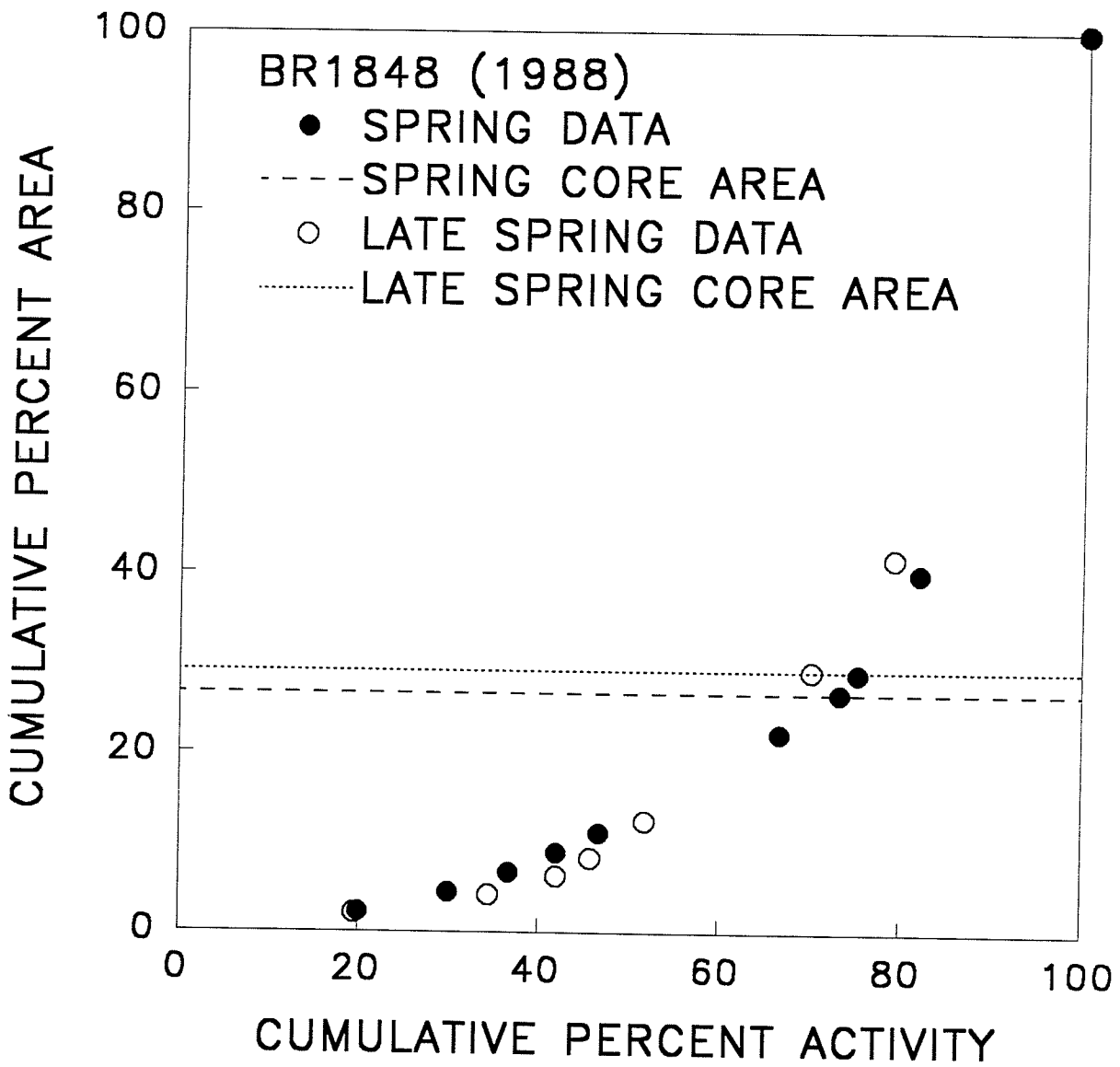
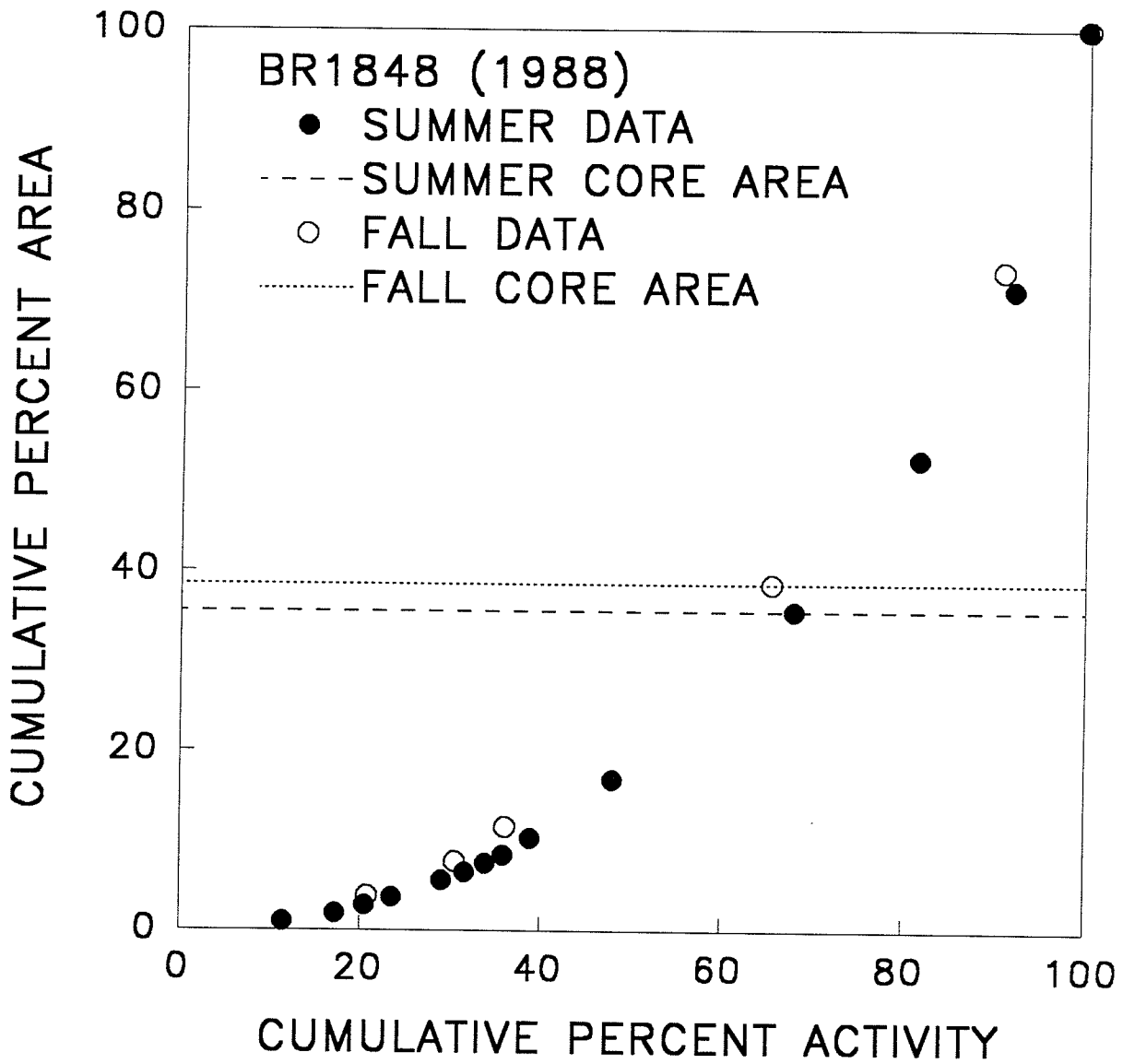
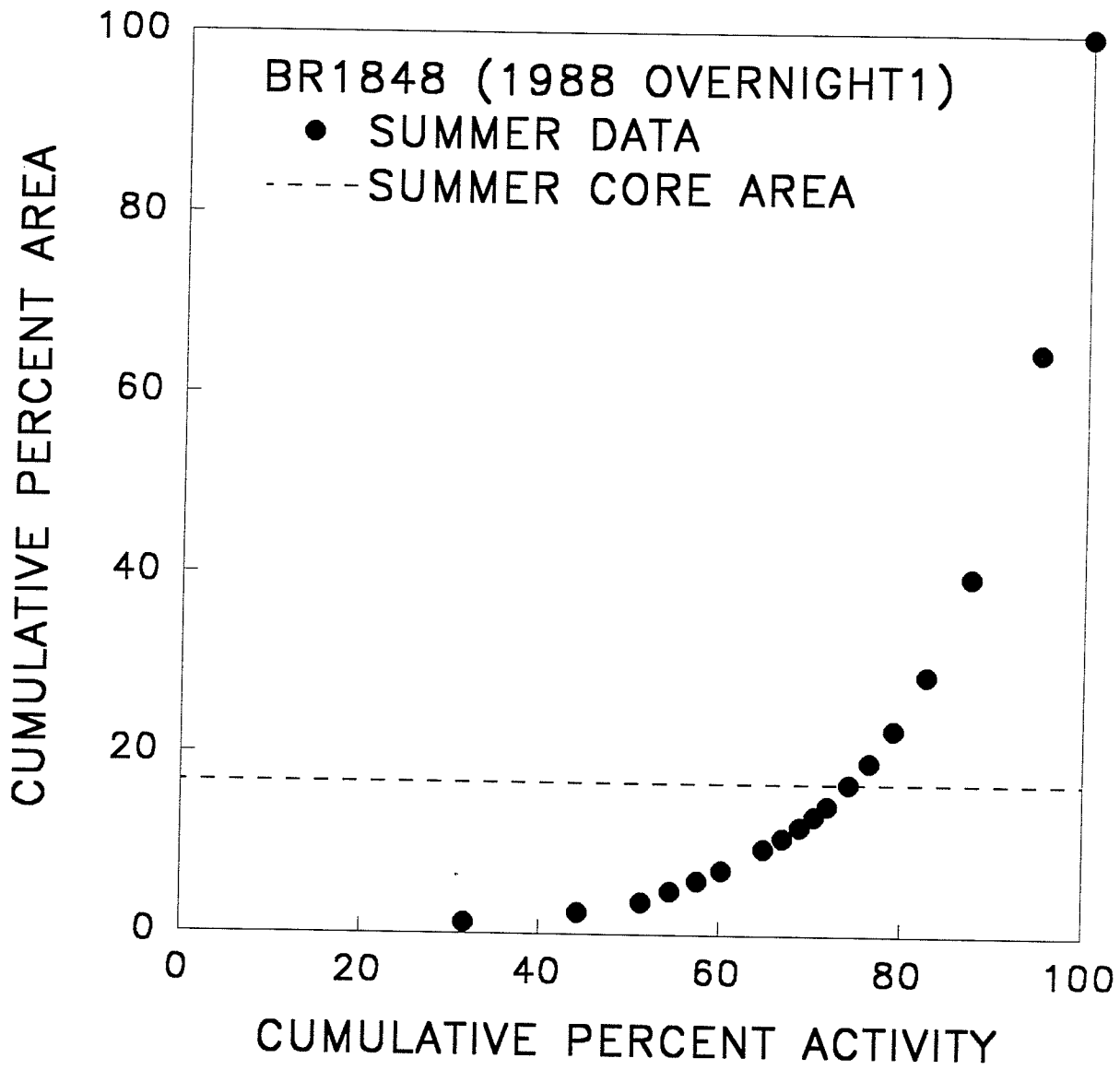


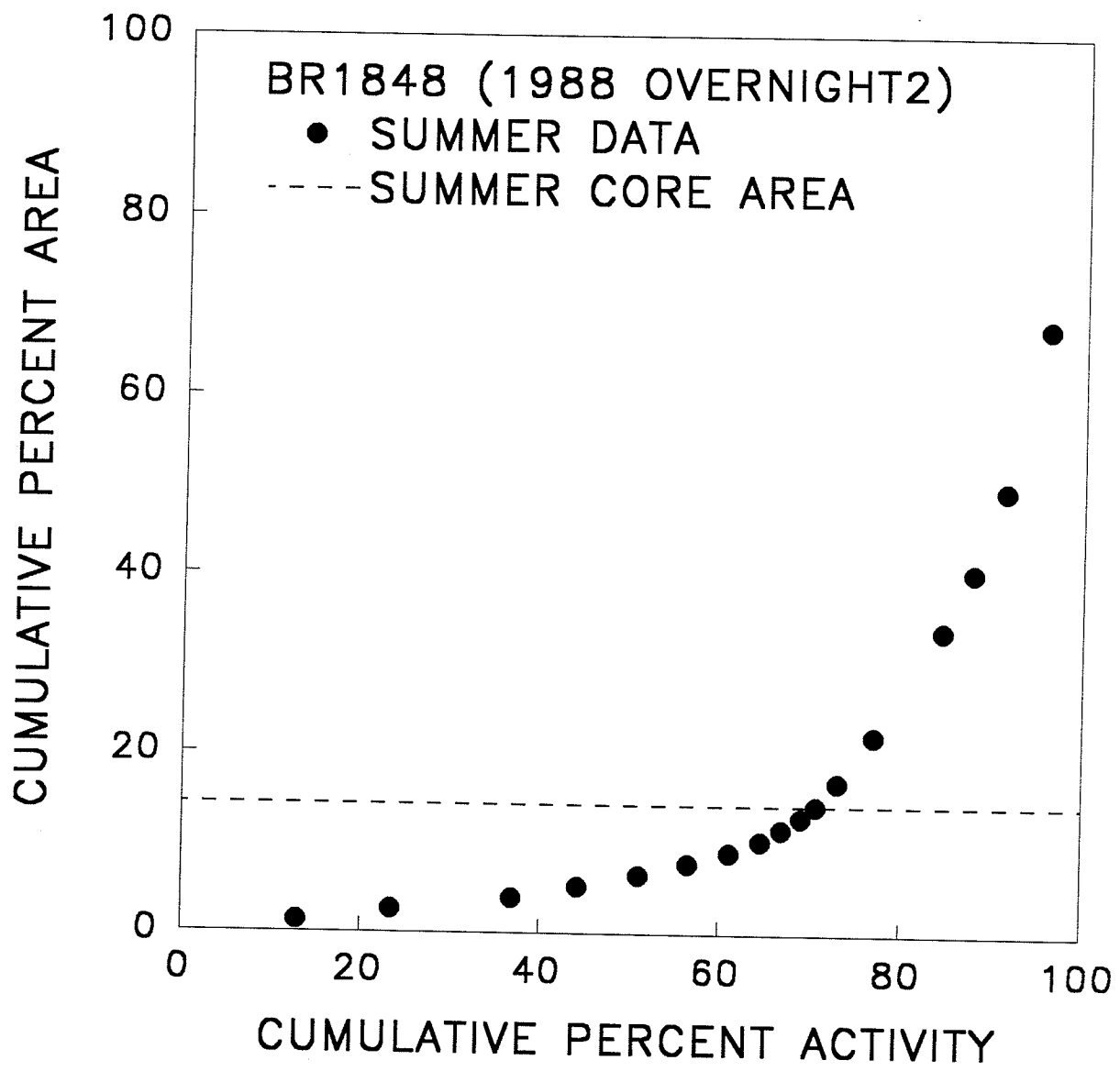
Figure 6. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1848 for 1987, 1988 and 1989.

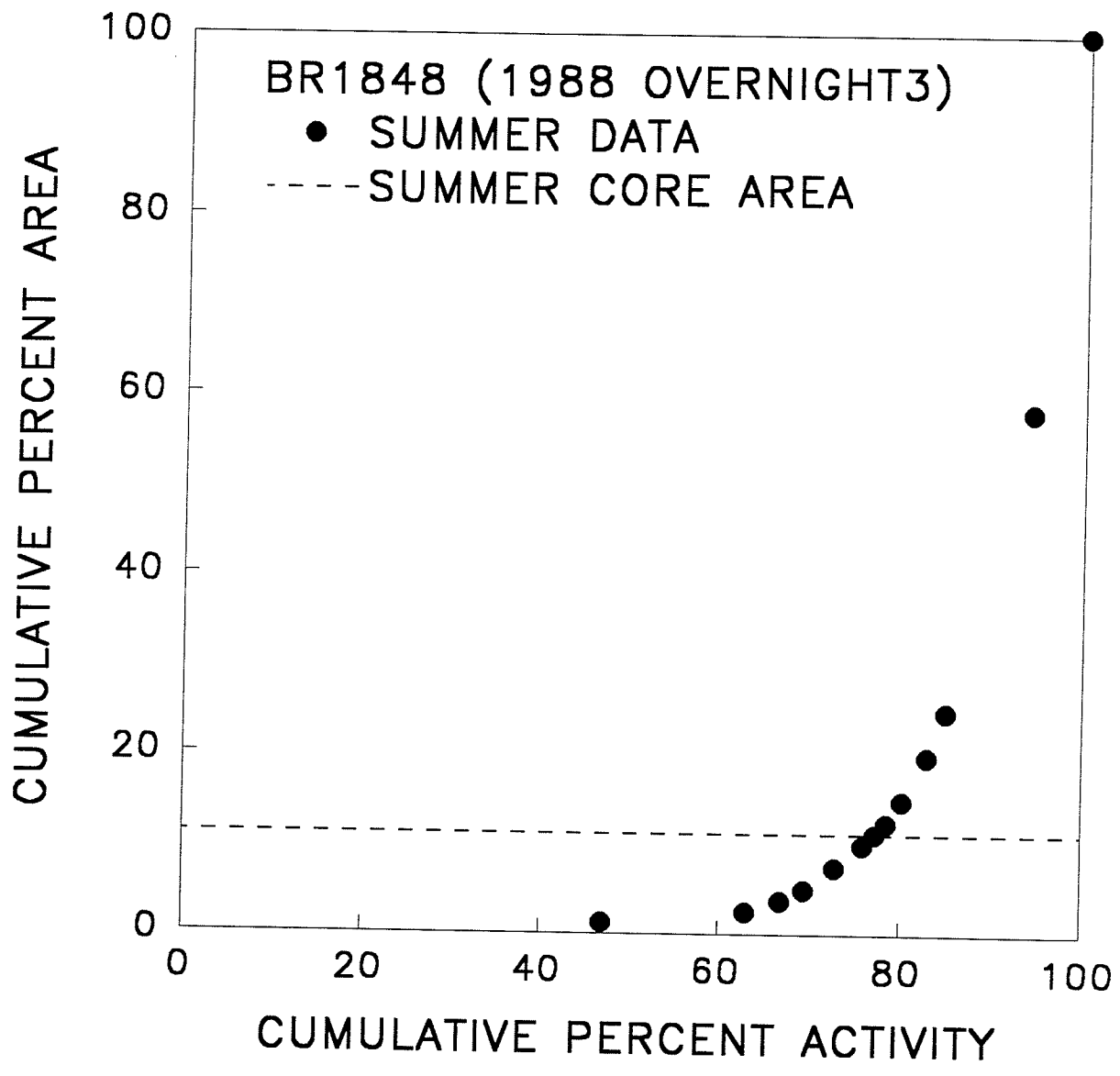


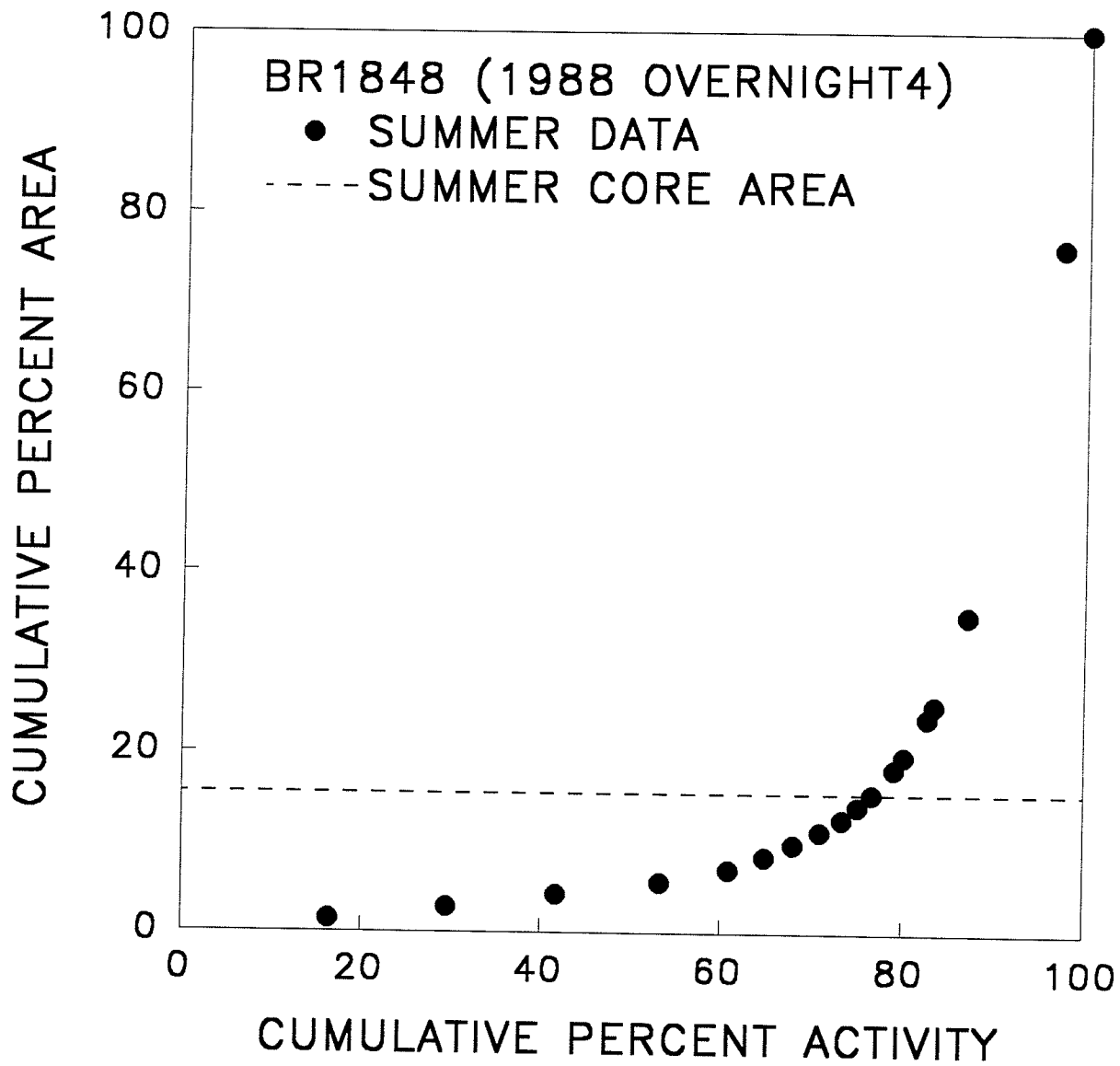












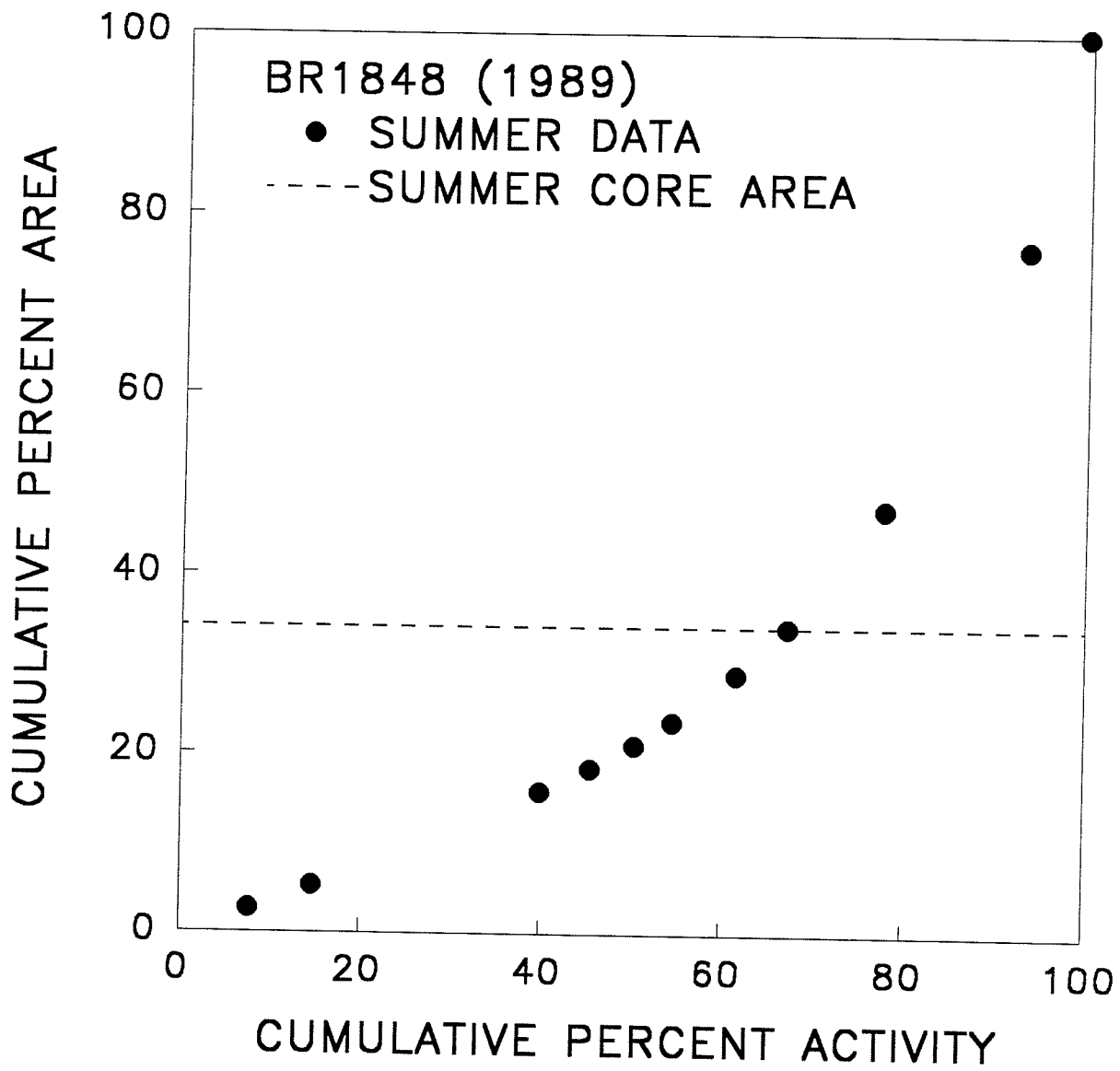


Figure 7. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1844 for summer and fall, 1987.

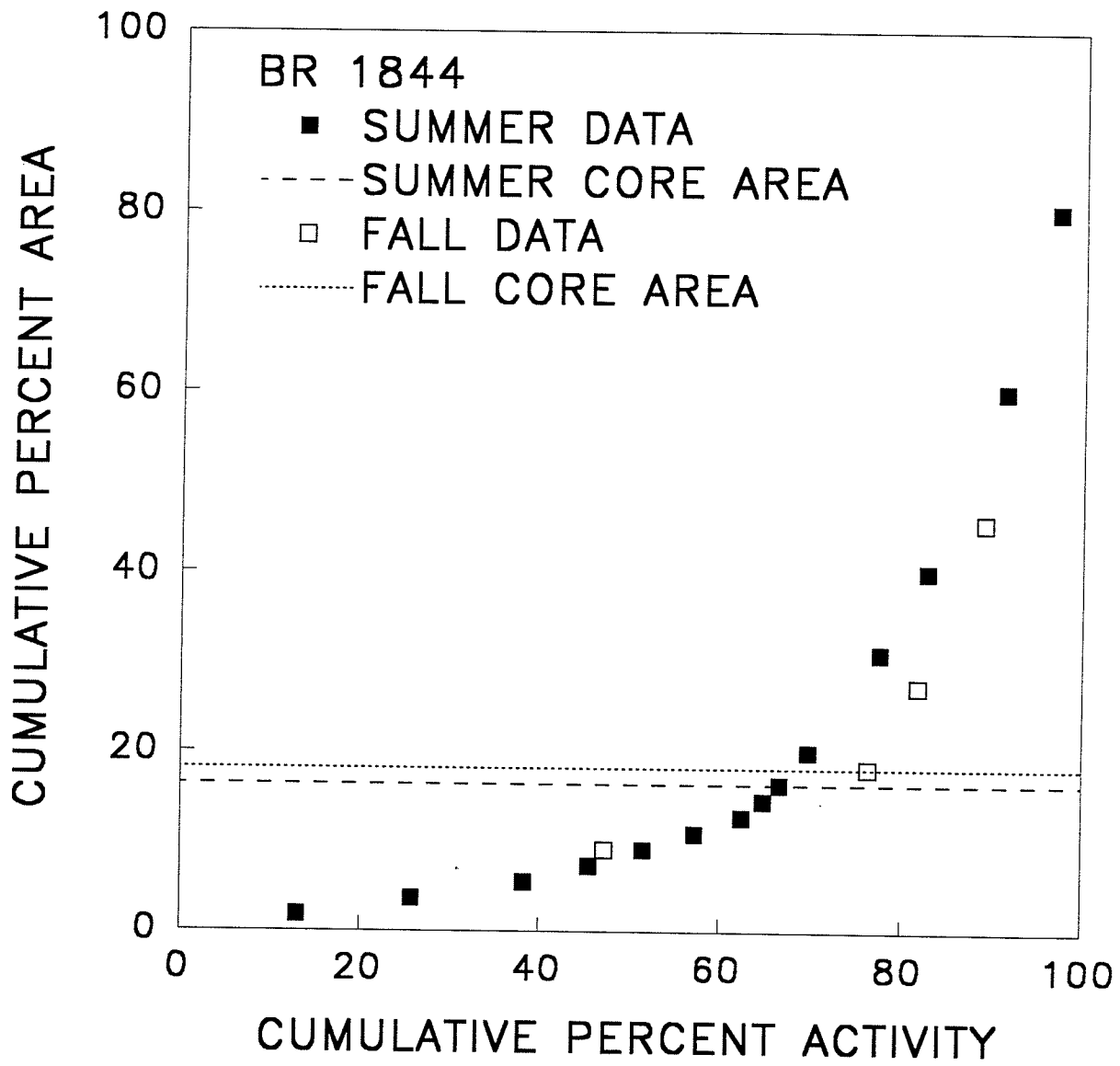
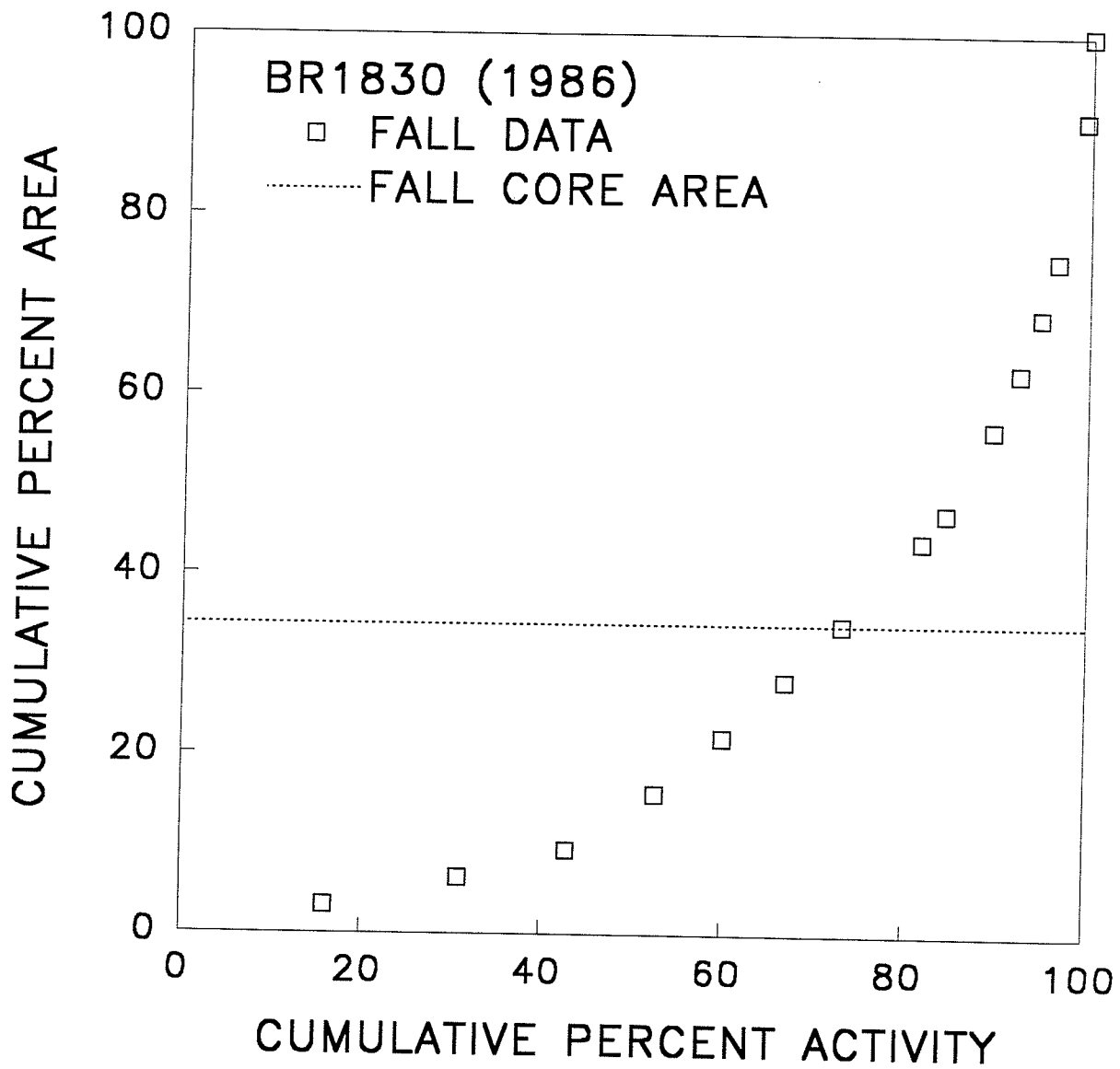


Figure 8. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1830 for fall, 1986 and summer, 1989.



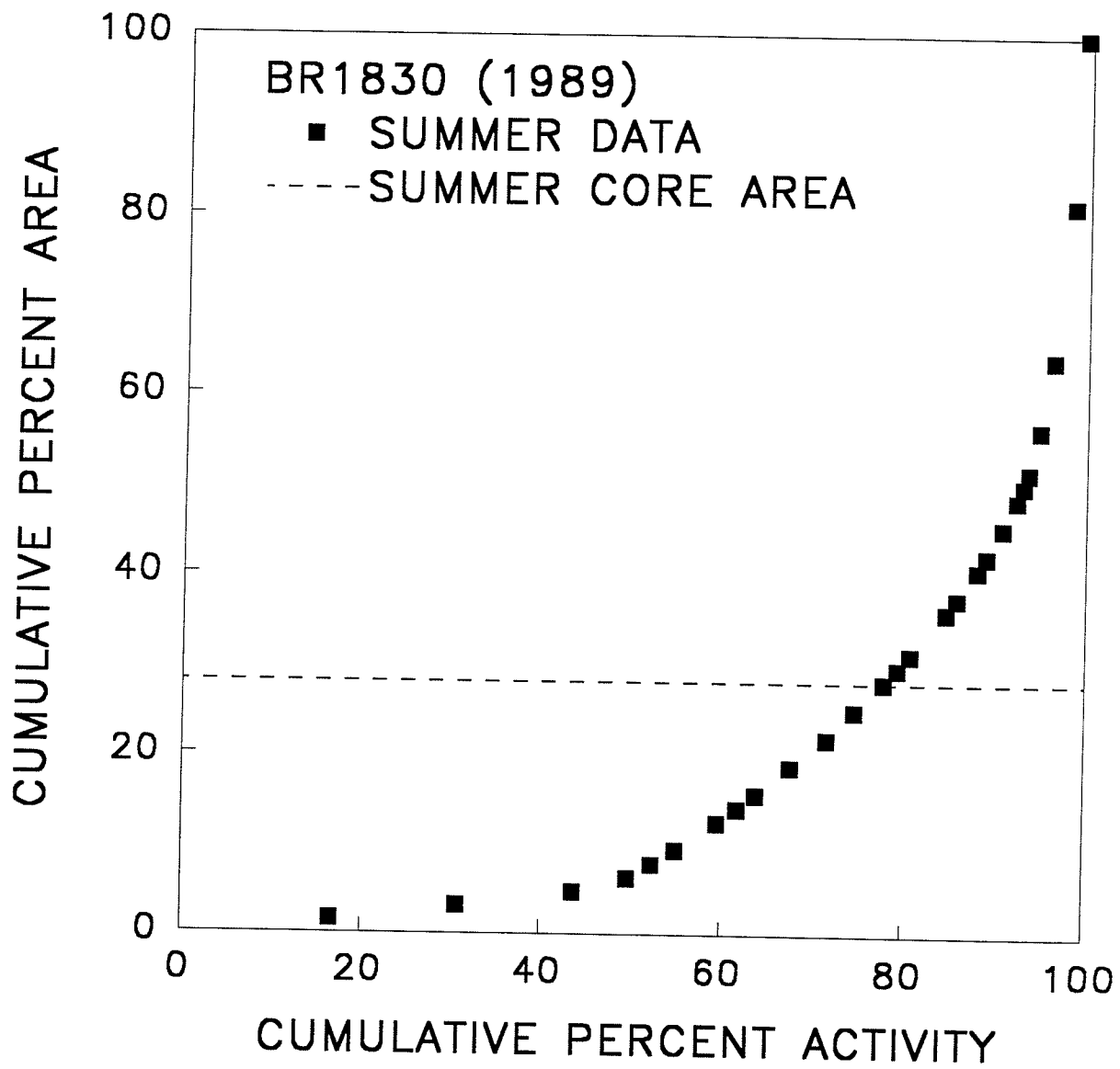


Figure 9. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver HB481 for summer and fall, 1989.

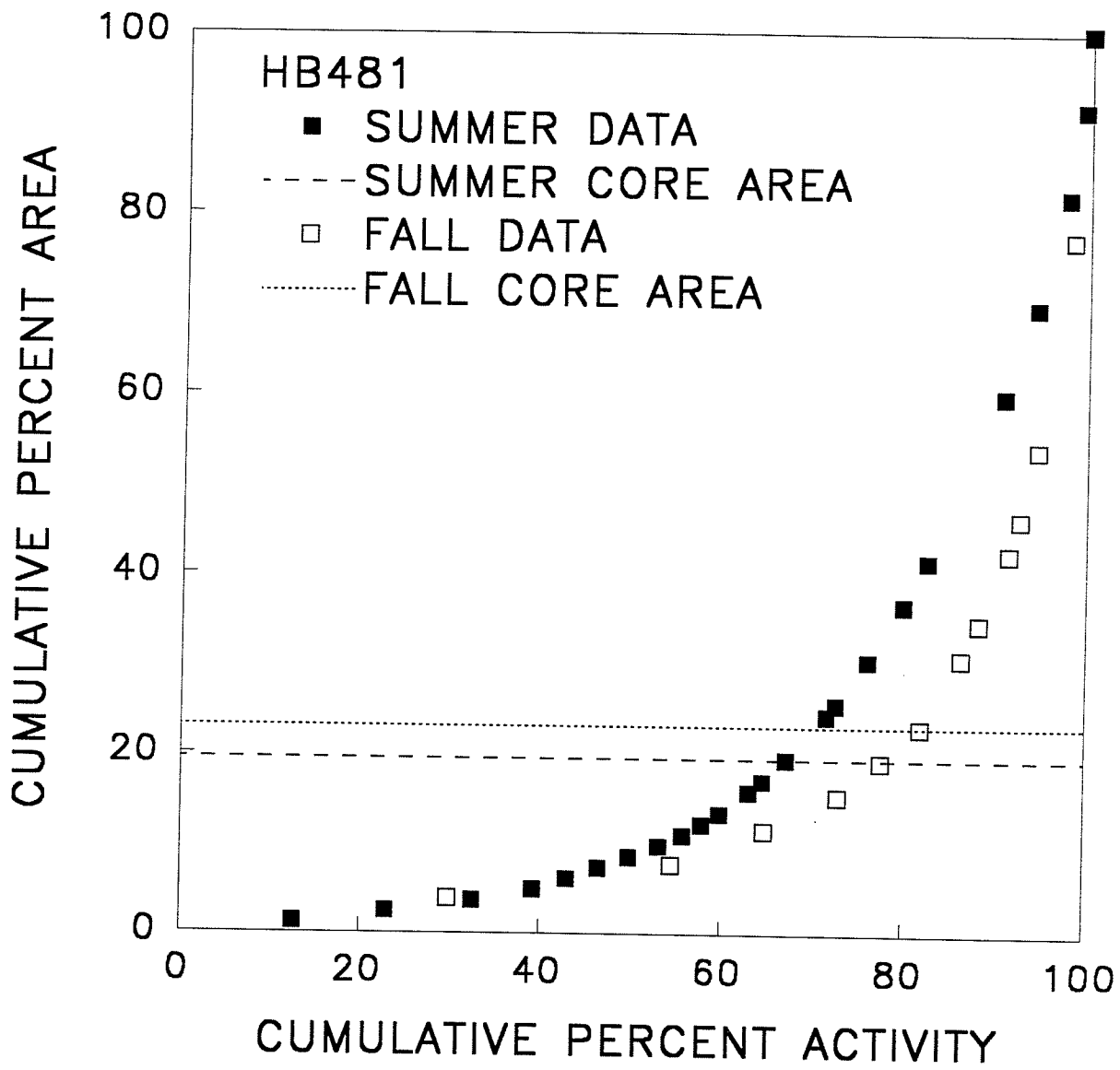
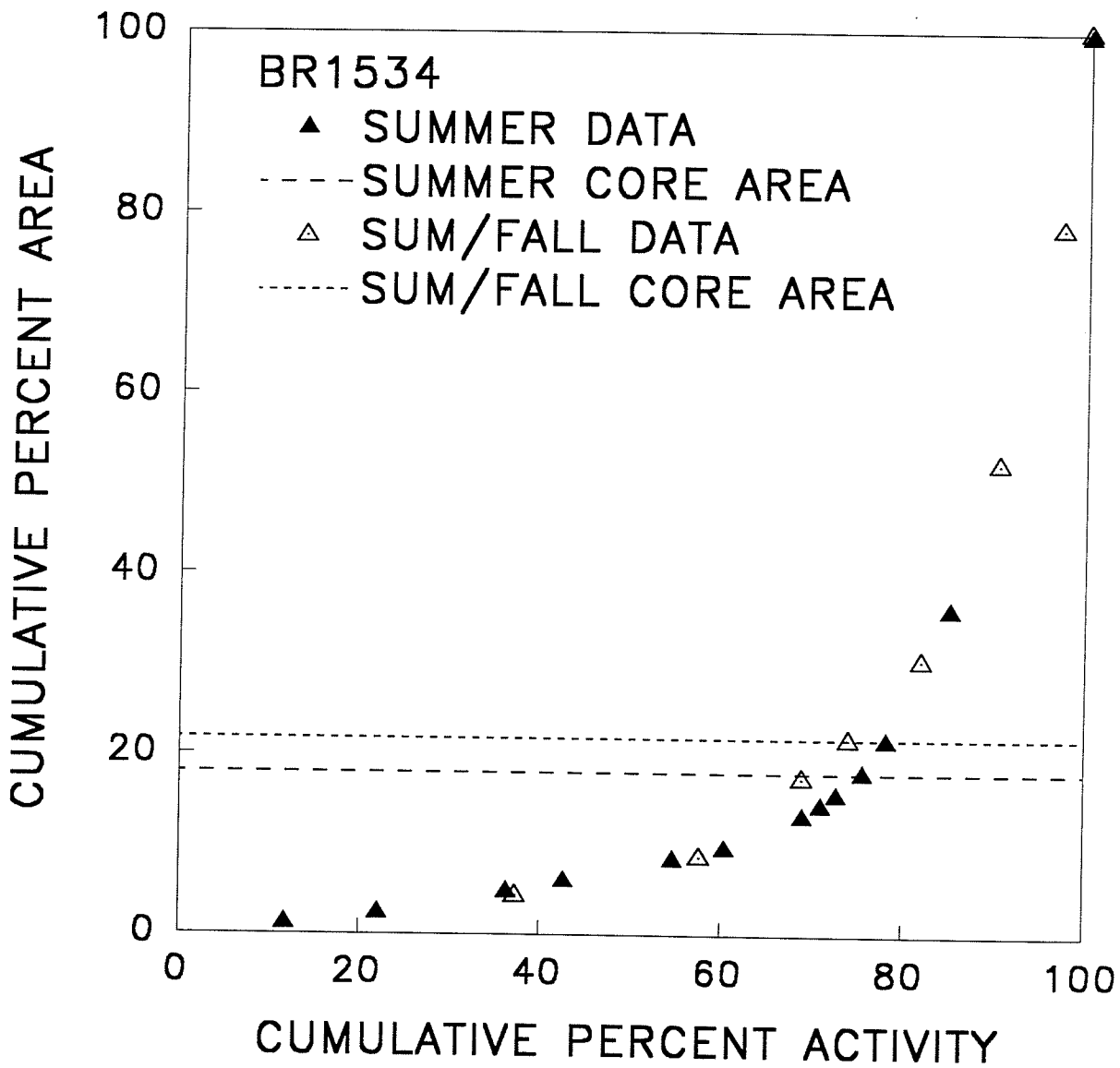


Figure 10. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers BR1534 and BR1524 for summer and late fall, 1991.



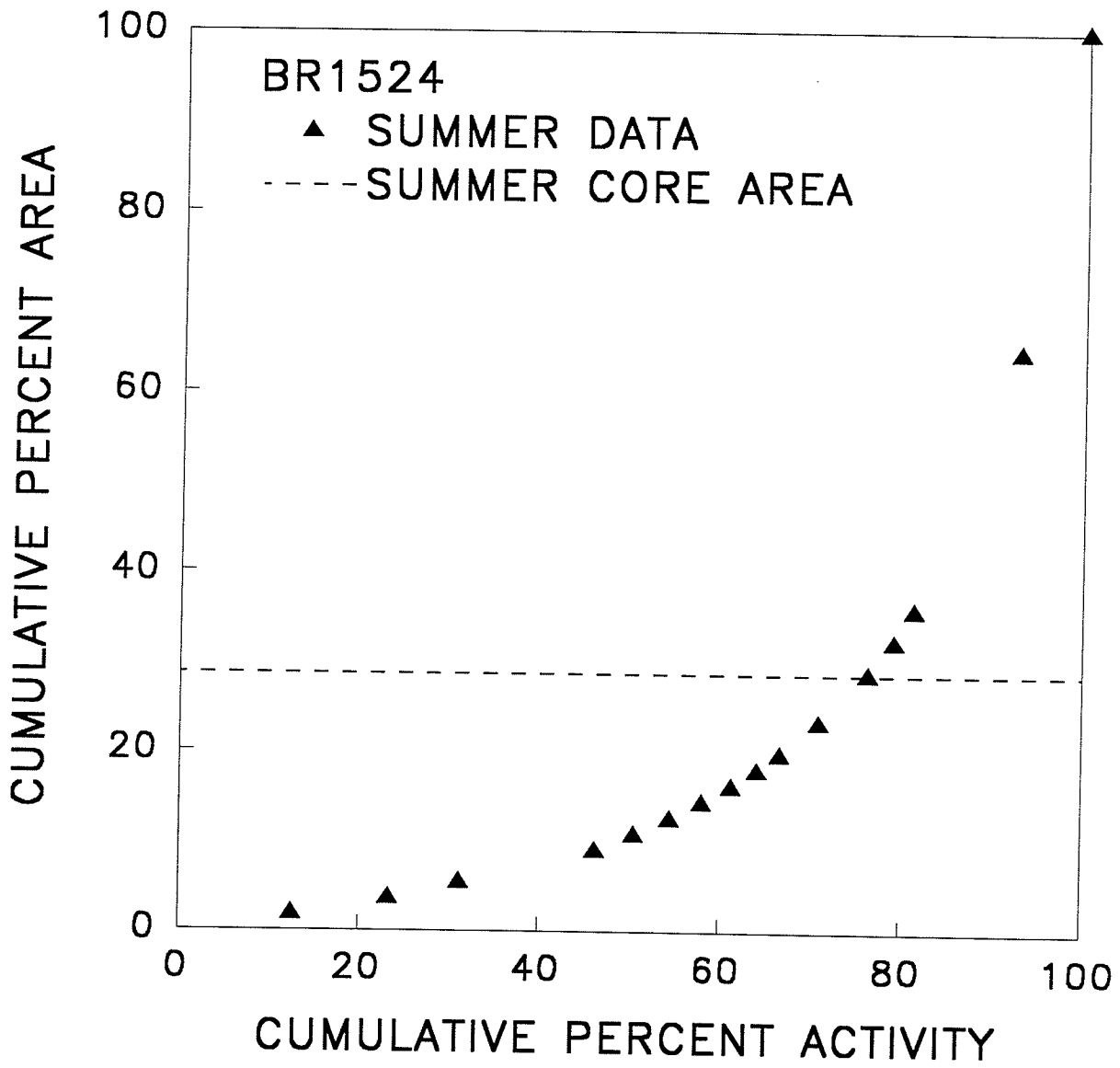


Figure 11. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1603 for summer and fall, 1990.

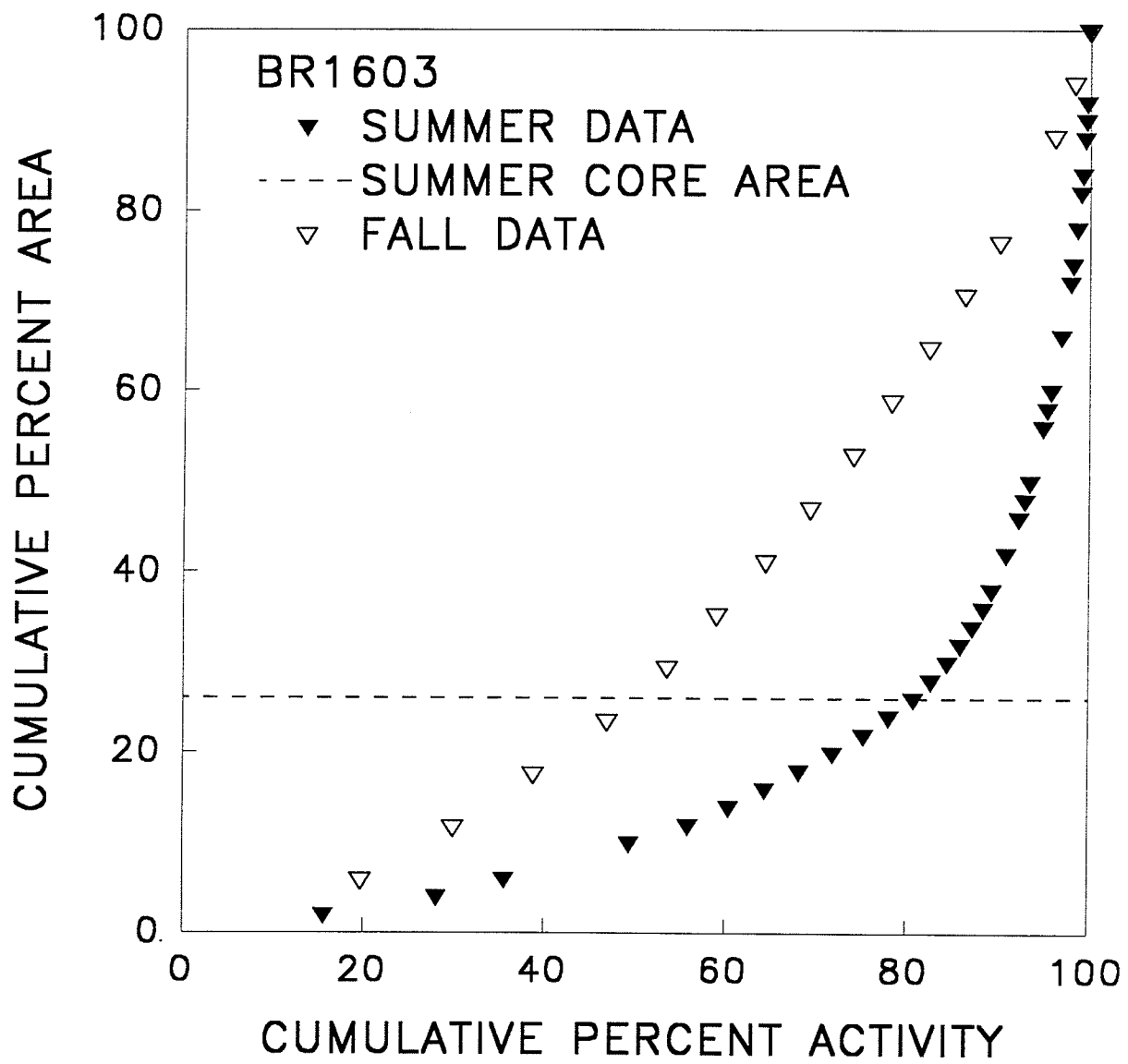
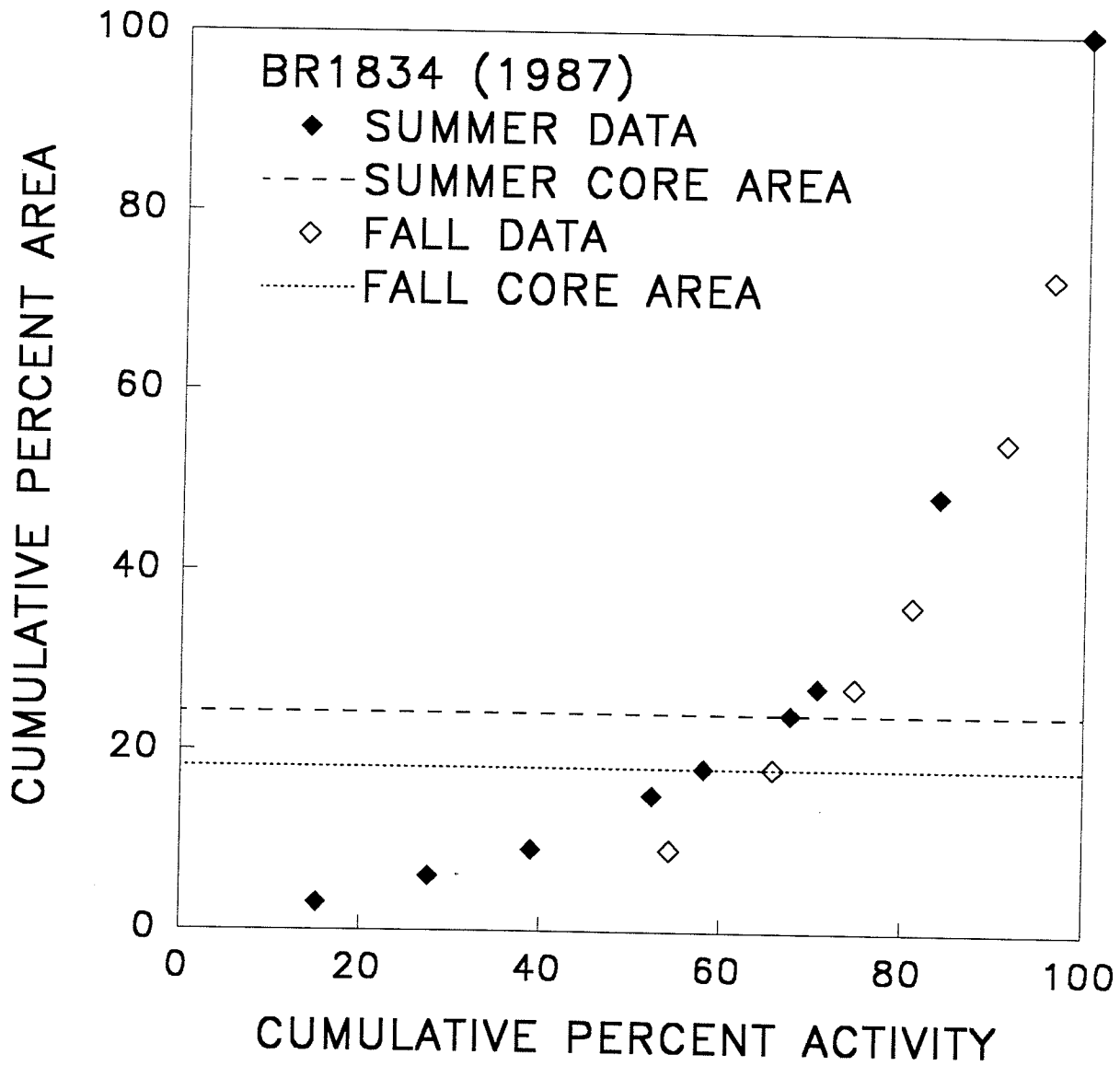


Figure 12. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver BR1834 for summer and fall, 1987 and 1988.



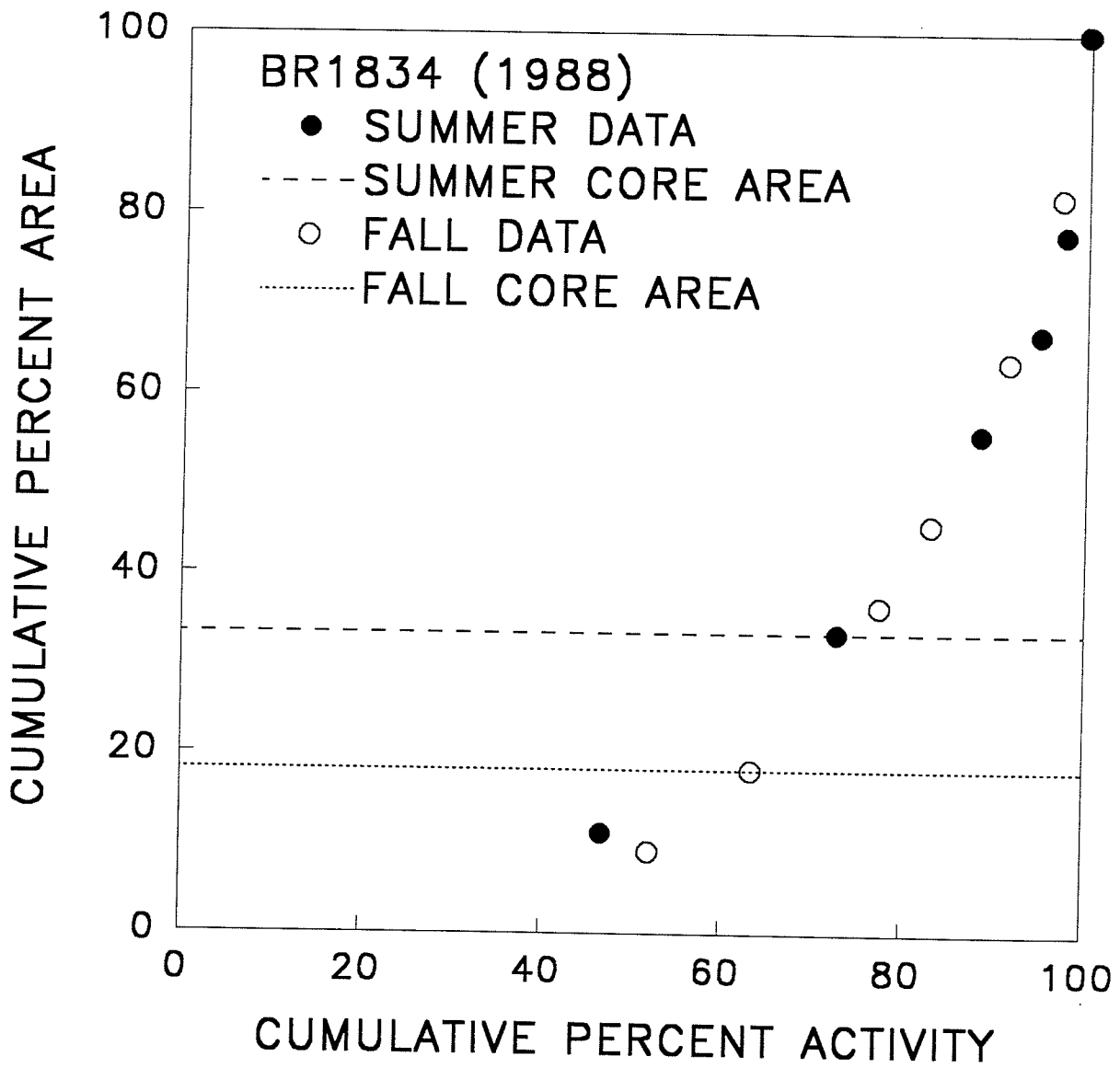
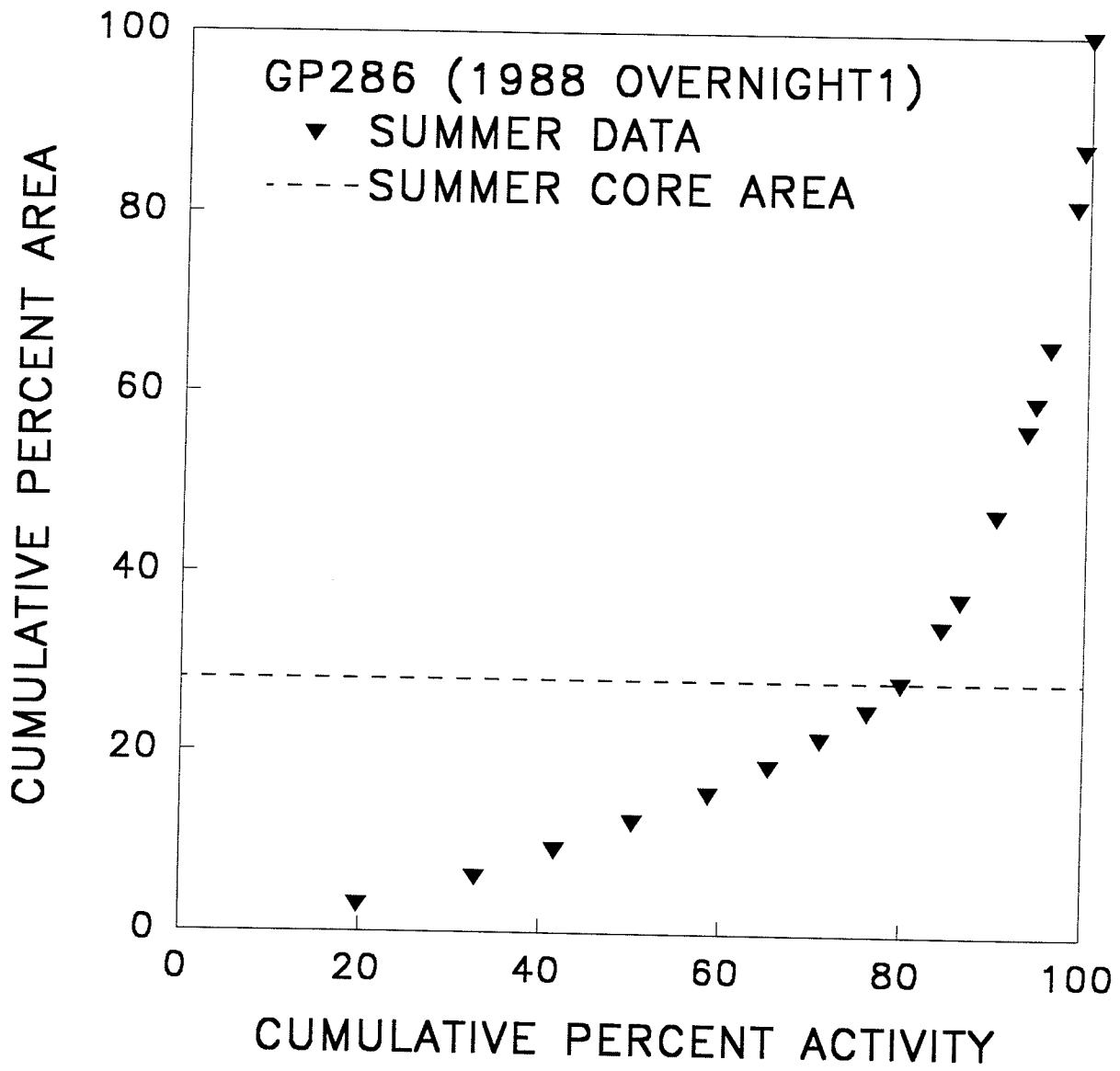
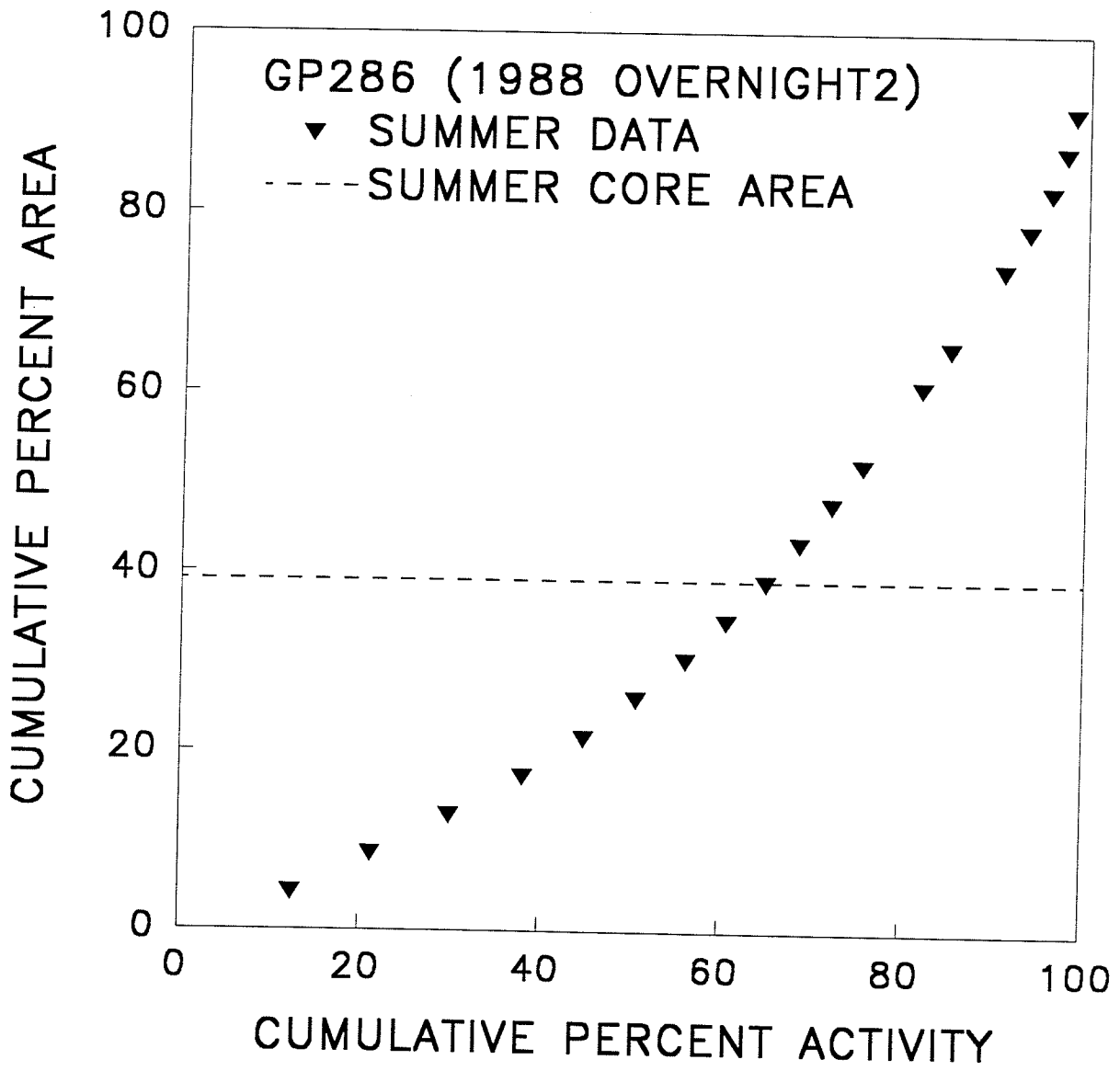


Figure 13. Graphs of cumulative percent of home range area versus cumulative percent of activity for beaver GP286 for overnights in summer, 1988, and summer 1989.





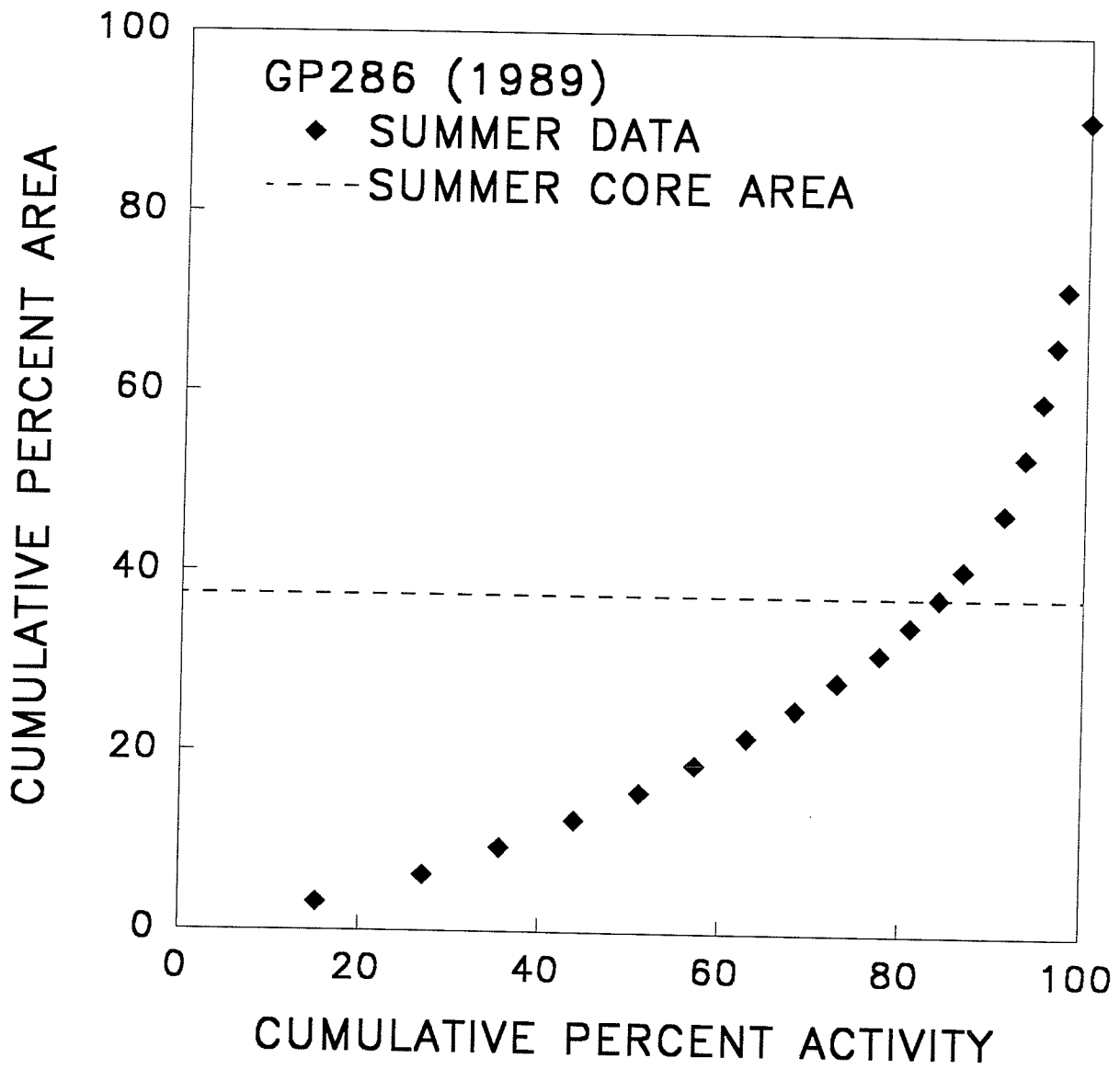
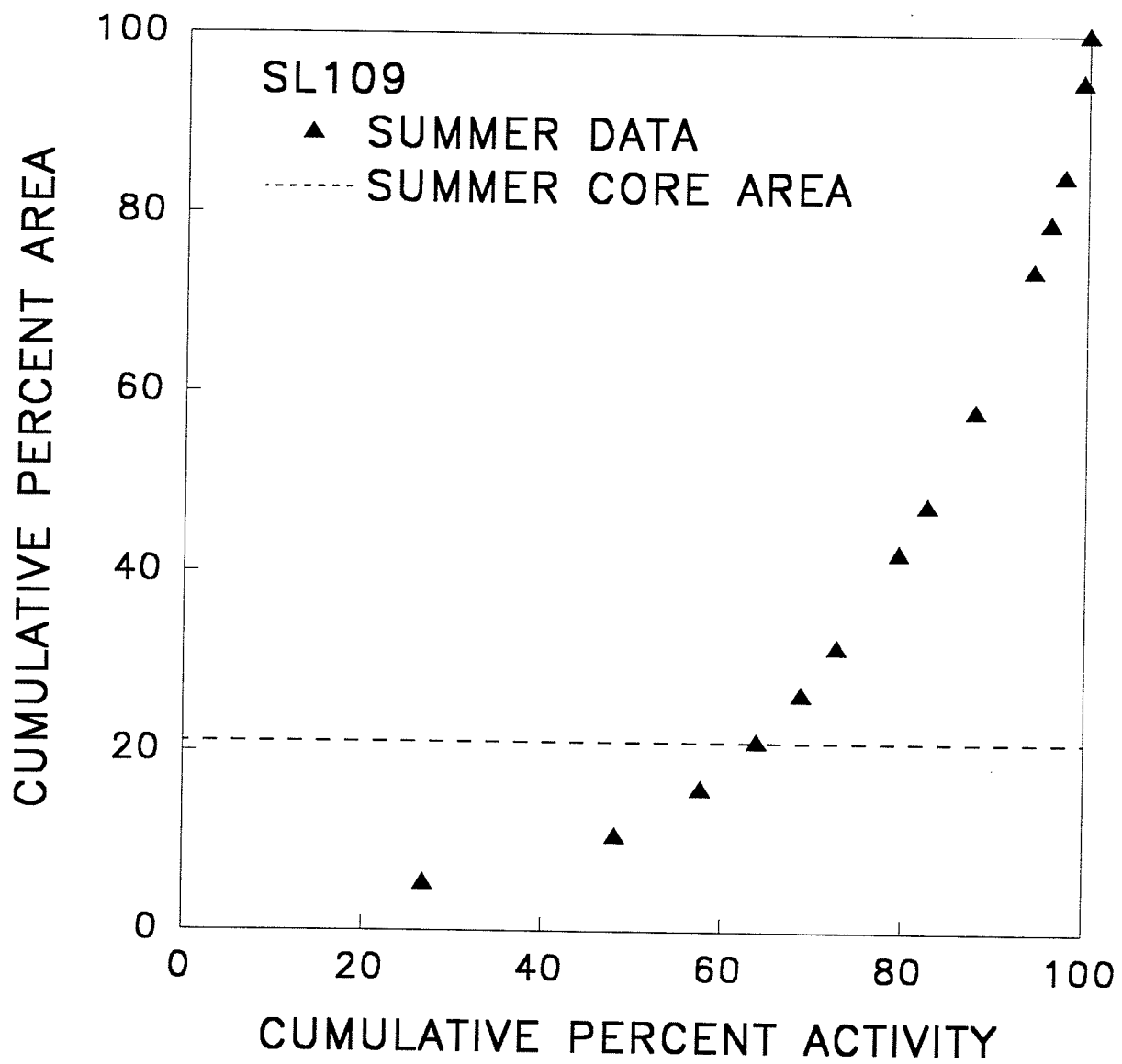
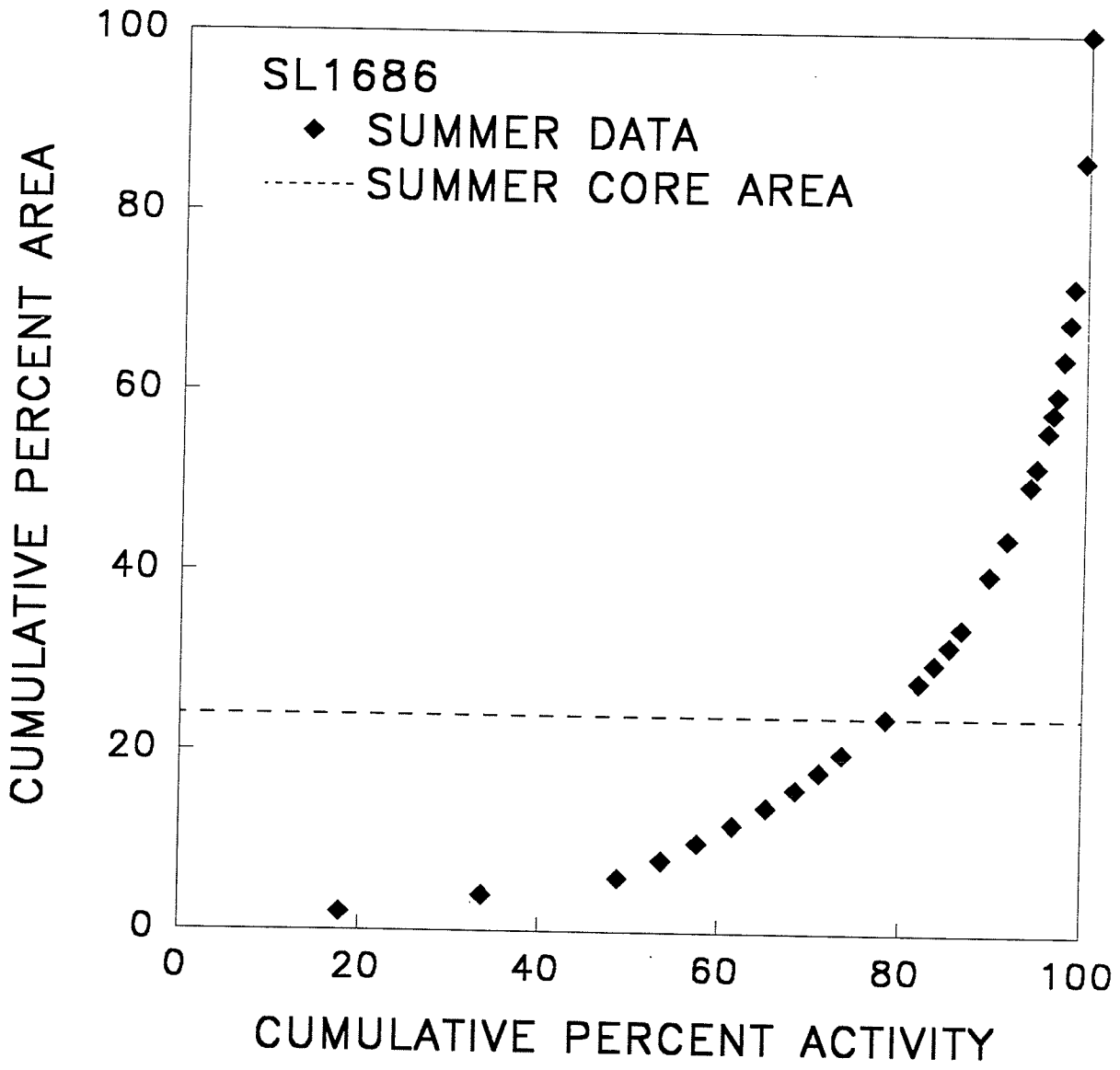
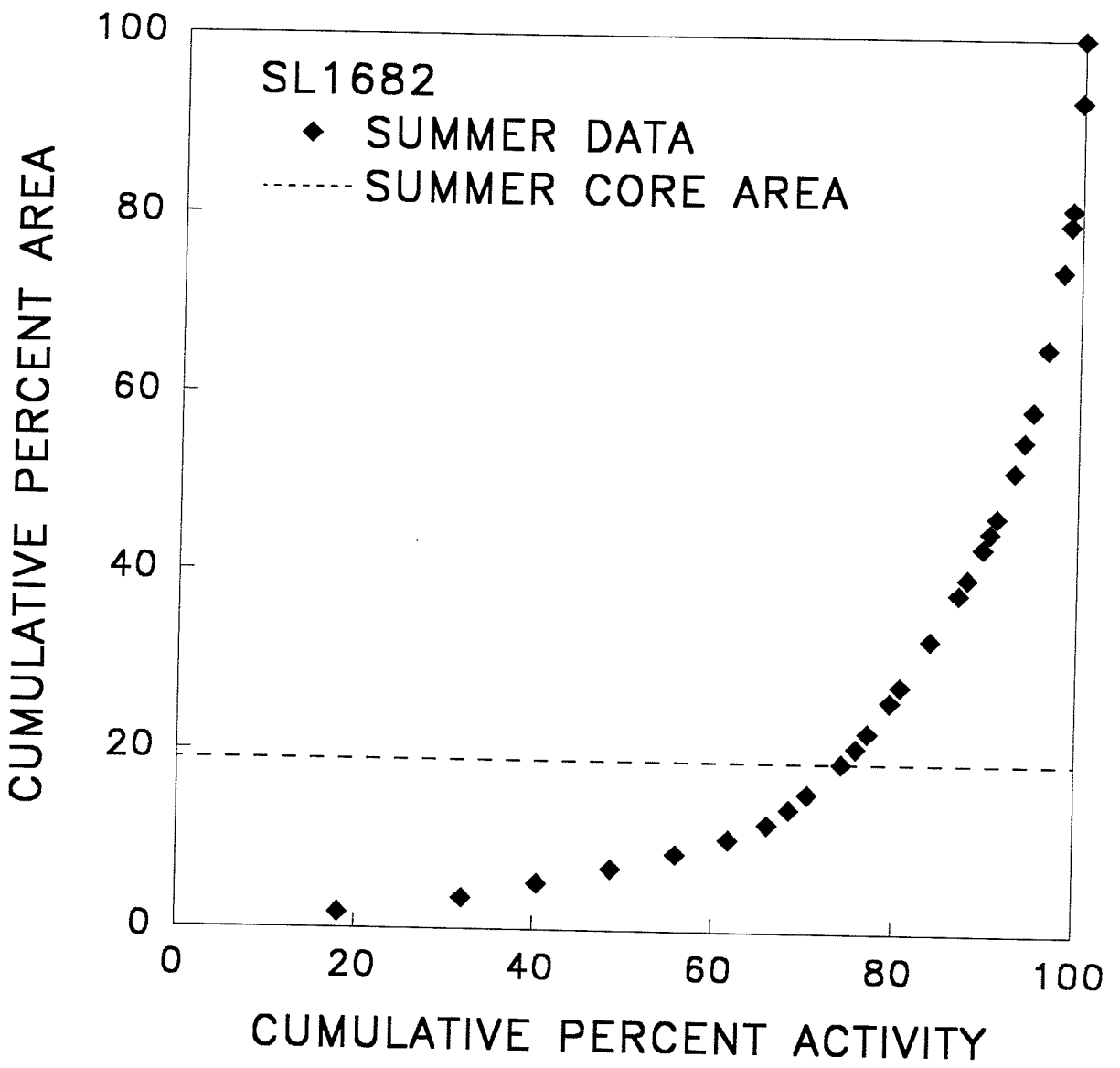


Figure 14. Graphs of cumulative percent of home range area versus cumulative percent of activity for beavers SL109, summer, 1989 and SL1686 and SL1682, summer, 1990.







APPENDIX 3

KOLMOGOROV-SMIRNOV VALUES

Table 1. Values of K (Kolmogorov-Smirnov Statistic) for summer home ranges, p value <0.05 indicates presence of core area.
† 1987, ‡ 1988, † 1989, § 1990, # 1991, * Overnights

BEAVER#	SEX	AGE	K	p	N
IP491	MALE	ADULT	0.413	<0.005	30
IP414	FEMALE	ADULT	0.344	<0.01	19
IP433	MALE	YEARLING	0.422	<0.005	29
IP403	FEMALE	JUVENILE	0.522	<0.005	26
TB1510	MALE	ADULT	0.333	<0.005	24
TB1508	FEMALE	ADULT	0.336	>0.05	11
TB1528	MALE	YEARLING	0.477	<0.005	23
TB1502	FEMALE	YEARLING	0.504	<0.005	17
JRB1617	MALE	ADULT	0.561	<0.005	53
JRB1629	FEMALE	ADULT	0.540	<0.005	20
JRB1641	MALE	YEARLING	0.580	<0.005	39
JRB1649	MALE	YEARLING	0.571	<0.005	47
GP1611 ^s	MALE	ADULT	0.481	<0.005	21
GP1676 ^s	FEMALE	ADULT	0.437	<0.005	16
GP1684	MALE	YEARLING	0.474	<0.005	27
GP1623	FEMALE	YEARLING	0.511	<0.005	23
GP1611 [#]	MALE	ADULT	0.483	<0.005	31
GP1676 [#]	FEMALE	ADULT	0.432	<0.025	10
GP1526	FEMALE	YEARLING	0.477	<0.005	33
BR1848 [†]	FEMALE	JUVENILE	0.337	<0.005	172
BR1848 [‡]	FEMALE	ADULT	0.325	<0.005	107
BR1848 ^{**}	FEMALE	ADULT	0.575	<0.005	83
BR1848 ^{**}	FEMALE	ADULT	0.565	<0.005	77
BR1848 ^{**}	FEMALE	ADULT	0.662	<0.005	81
BR1848 ^{**}	FEMALE	ADULT	0.612	<0.005	71
BR1848 [!]	FEMALE	ADULT	0.330	<0.005	38
BR1844	MALE	ADULT	0.467	<0.005	55
BR1830	MALE	ADULT	0.497	<0.005	64
HB481	MALE	ADULT	0.477	<0.005	82
BR1534	MALE	YEARLING	0.576	<0.005	83
BR1524	MALE	YEARLING	0.477	<0.005	56
BR1603	FEMALE	YEARLING	0.548	<0.005	50

BEAVER#	SEX	AGE	K	p	N
BR1834 [†]	FEMALE	JUVENILE	0.435	<0.005	33
BR1834 [‡]	FEMALE	ADULT	0.395	<0.05	9
GP286 [*]	FEMALE	YEARLING	0.517	<0.005	32
GP286 [*]	FEMALE	YEARLING	0.258	<0.05	23
GP286 [†]	FEMALE	JUVENILE	0.466	<0.005	32
SL109	MALE	YEARLING	0.429	<0.005	19
SL1686	FEMALE	JUVENILE	0.544	<0.005	50
SL1682	FEMALE	JUVENILE	0.553	<0.005	58

Table 2. Values of K (Kolmogorov-Smirnov Statistic) for fall home ranges, p value <0.05 indicates presence of core area.
† 1987, ‡ 1988, † 1989, § 1990, # 1991, * Overnights

BEAVER#	SEX	AGE	K	P	N
IP491	MALE	ADULT	0.277	>0.05	17
IP414	FEMALE	ADULT	0.250	>0.1	8
IP403	FEMALE	JUVENILE	0.411	<0.005	21
TB1510	MALE	ADULT	0.574	<0.005	11
TB1508	FEMALE	ADULT	0.452	>0.1	4
TB1528	MALE	YEARLING	0.508	<0.005	10
TB1502	FEMALE	YEARLING	0.561	<0.025	6
TB1518	MALE	KIT	0.619	<0.005	6
TB1520	FEMALE	KIT	0.631	<0.01	5
TB1522	MALE	KIT	0.618	<0.005	6
JRB1617	MALE	ADULT	0.356	<0.05	11
JRB1629	FEMALE	ADULT	0.385	>0.1	5
JRB1641	MALE	YEARLING	0.505	<0.005	15
JRB1649	MALE	YEARLING	0.463	<0.005	13
GP1611 [§]	MALE	ADULT	0.456	<0.005	10
GP1676 [§]	FEMALE	ADULT	0.444	<0.025	10
GP1684	MALE	YEARLING	0.416	<0.025	12
GP1611 [#]	MALE	ADULT	0.349	>0.1	4
GP1526	FEMALE	YEARLING	0.204	>0.1	4
BR1848 [†]	FEMALE	JUVENILE	0.528	<0.005	20
BR1848 [‡]	FEMALE	ADULT	0.270	<0.025	26
BR1844	MALE	ADULT	0.582	<0.005	11
BR1830	MALE	ADULT	0.387	<0.005	32
HB481	MALE	ADULT	0.588	<0.005	26
BR1603	FEMALE	YEARLING	0.241	>0.1	17
BR1834 [†]	FEMALE	JUVENILE	0.476	<0.005	11
BR1834 [‡]	FEMALE	ADULT	0.452	<0.01	11

Table 3. Values of K (Kolmogorov-Smirnov Statistic) for spring, late spring and late summer home ranges, p value <0.05 indicates presence of core area.
† 1987, ‡ 1988, § 1989, ¶ 1990, # 1991, * Overnights

BEAVER#	SEX	AGE	SEASON	K	P	N
BR1848 [†]	FEMALE	JUVENILE	LATE SUMMER	0.551	<0.005	53
BR1848 [‡]	FEMALE	ADULT	SPRING	0.467	<0.005	45
BR1848 [‡]	FEMALE	ADULT	LATE SPRING	0.411	<0.005	48
BR1534	MALE	YEARLING	LATE SUMMER	0.523	<0.005	23
TB1510	MALE	ADULT	LATE SUMMER	0.468	<0.005	24
TB1508	FEMALE	ADULT	LATE SUMMER	0.407	<0.005	22
TB1528	MALE	YEARLING	LATE SUMMER	0.609	<0.005	28
TB1502	FEMALE	YEARLING	LATE SUMMER	0.588	<0.005	27

APPENDIX 4

CENTROID MAPS

Figure 1. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Summer, Late Summer and Fall, 1987. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male = BR1844, Juvenile Female 1 = BR1834, Juvenile Female 2 = BR1848.

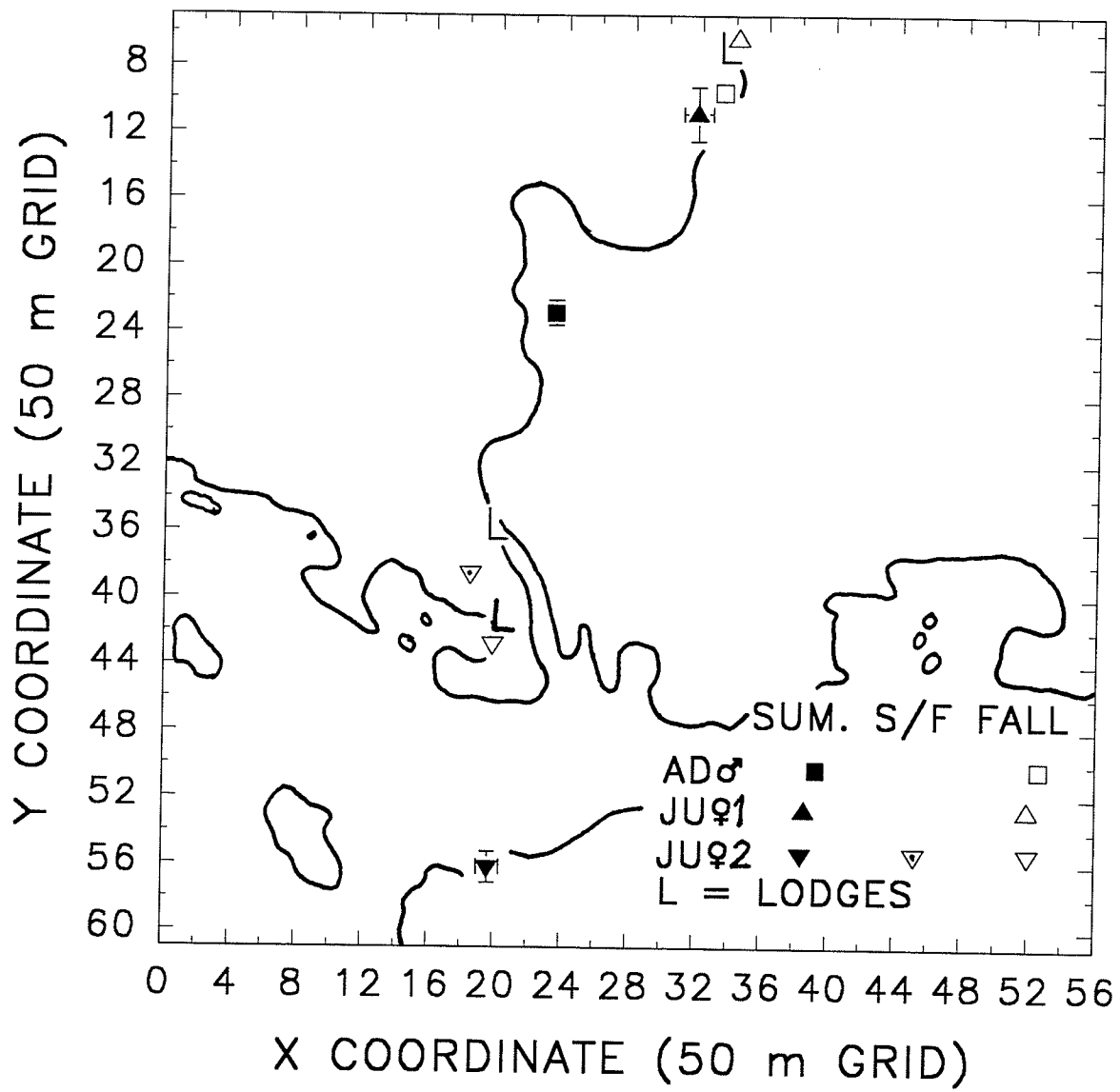


Figure 2. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Spring, Late Spring, Summer and Fall, and Summer Overnights, 1988. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Female 1 = BR1848, Adult Female 2 = BR1834.

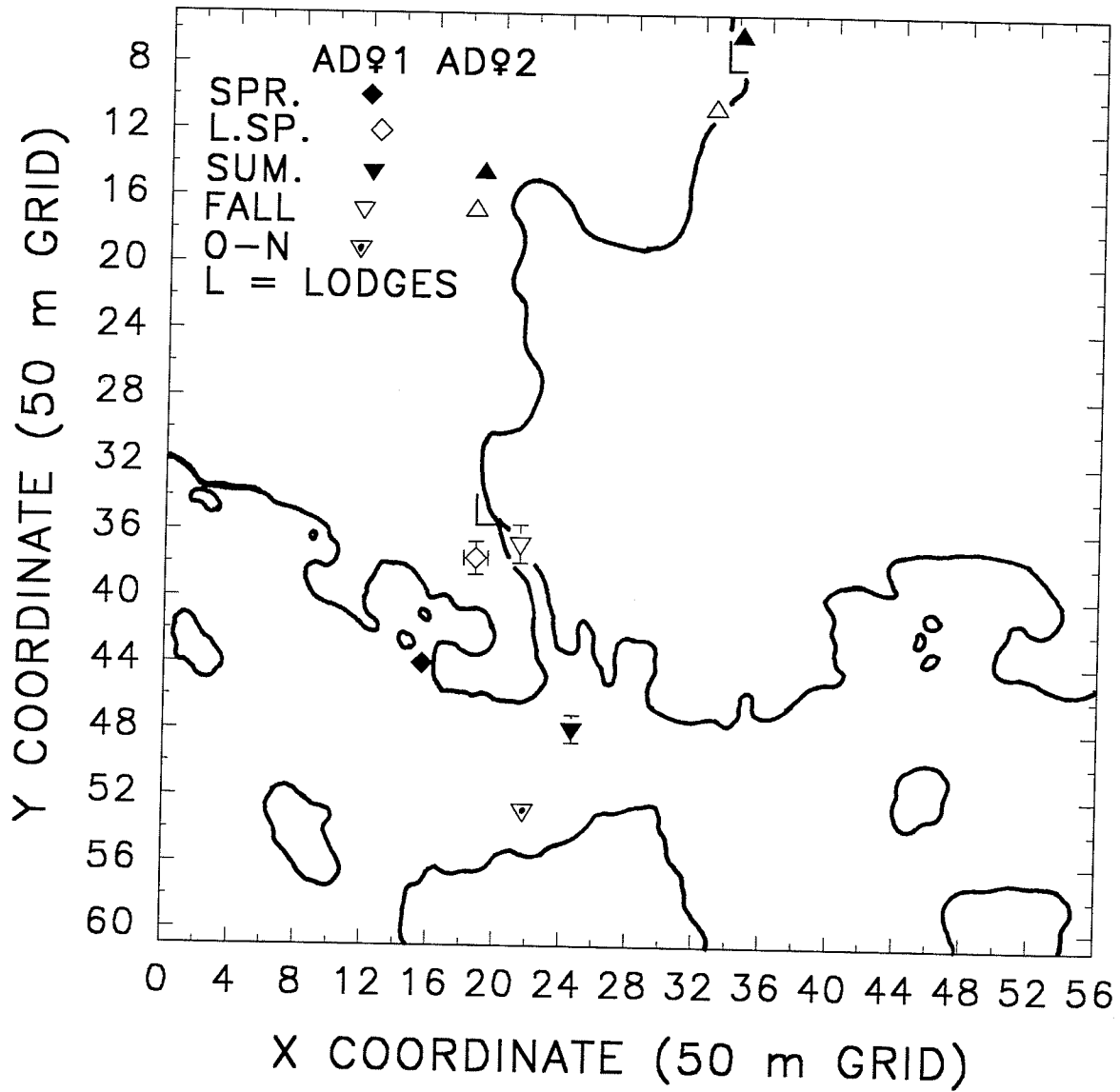


Figure 3. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Summer and Fall, 1989. Centroids are shown ± 2 standard errors in both X and Y directions. Adult Male 1 = BR1830, Adult Female = BR1848, Adult Male 2 = HB481.

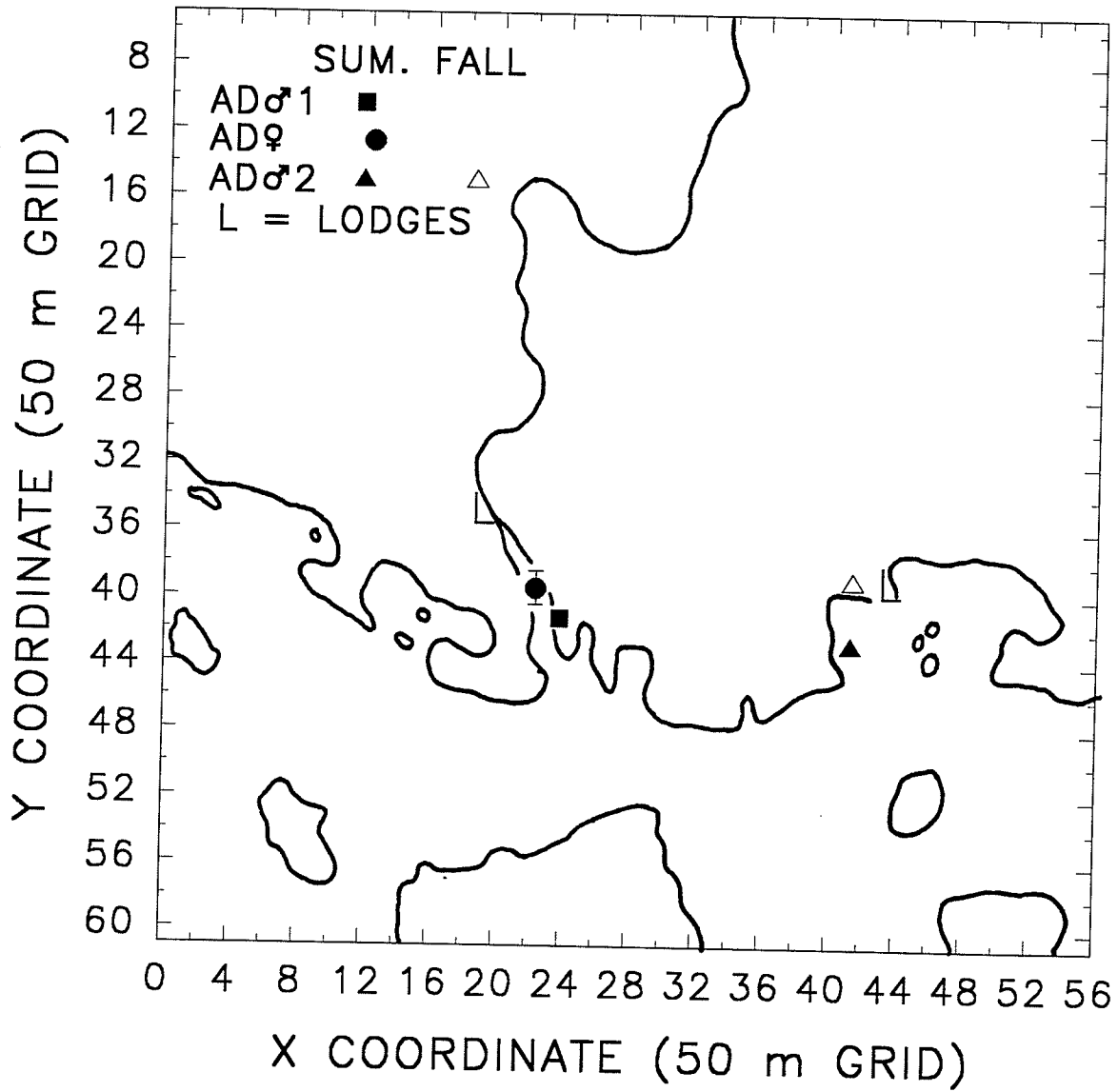


Figure 4. Centroids of activity for beavers living on the Blind River and North Wallace Lake, Summer and Late Summer, 1991. Centroids are shown ± 2 standard errors in both X and Y directions. Yearling Male 1 = BR1534, Yearling Male 2 = BR1524.

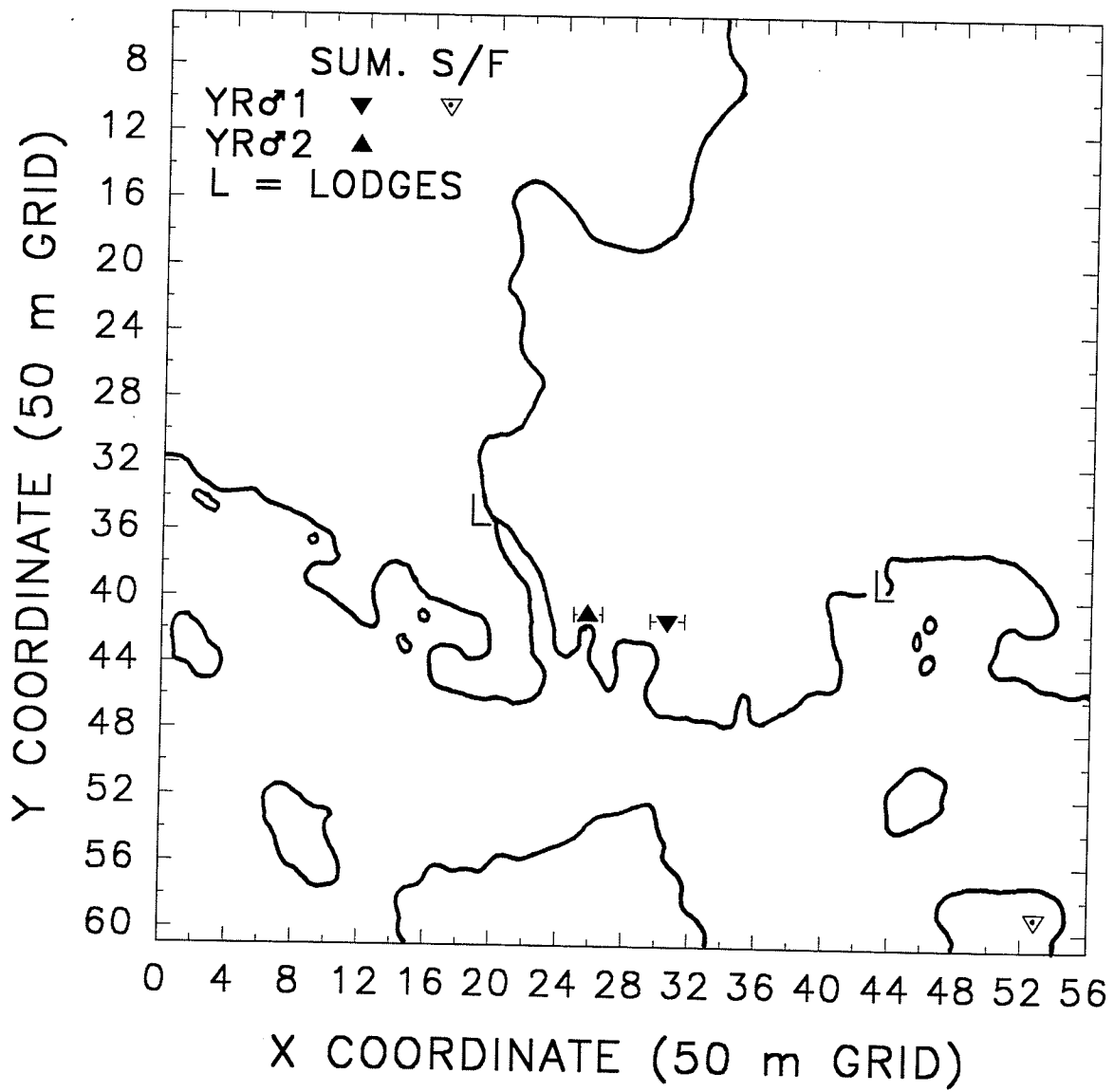


Figure 5. Centroids of activity for beaver BR1603 living on the Blind River, Summer and Fall, 1990. Centroids are shown ± 2 standard errors in both X and Y directions.

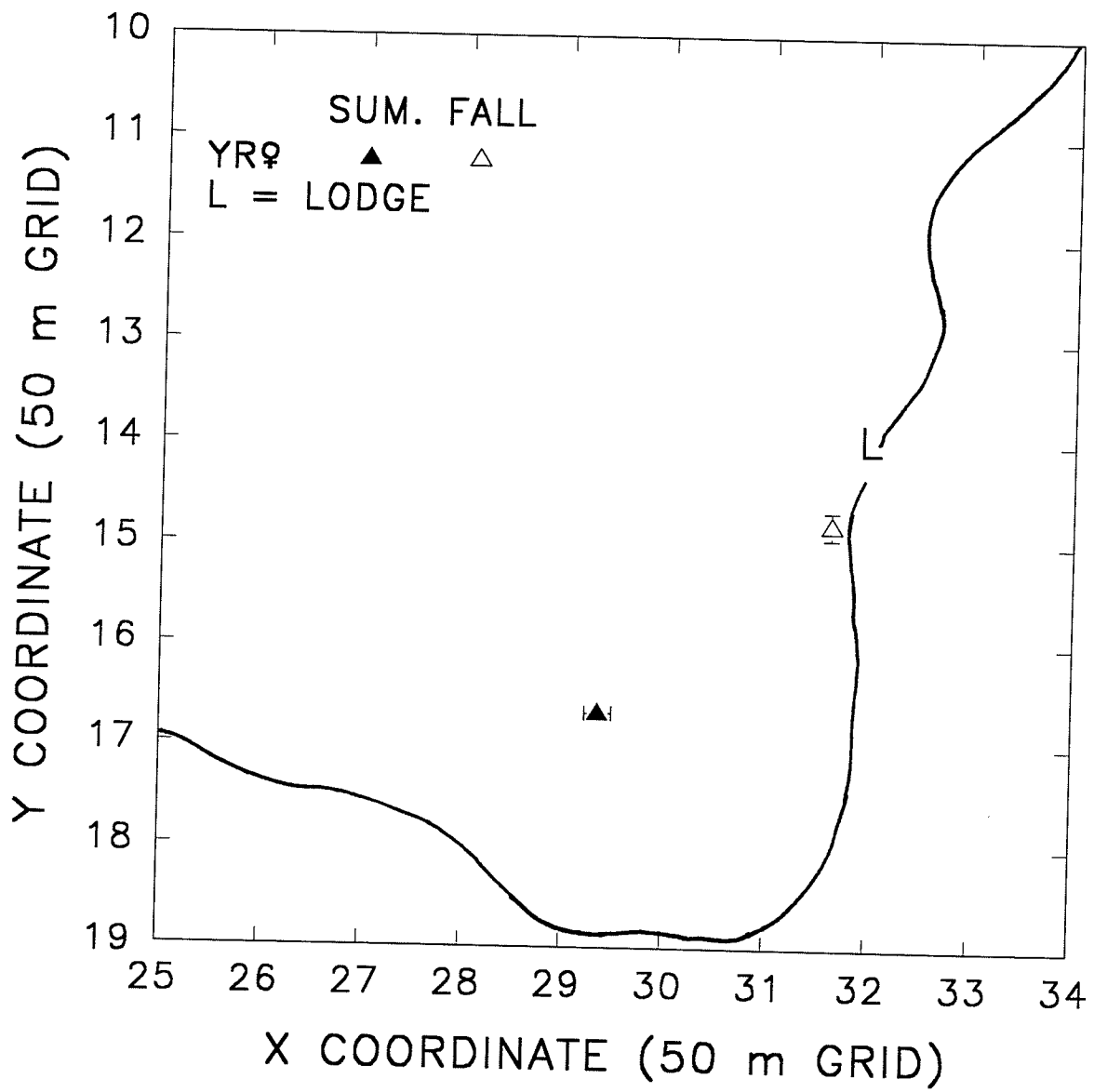


Figure 6. Centroids of activity for beaver BR1848 living on the Blind River and Wallace Lake, Summer and Fall, 1987, 1988, and 1989. Centroids are shown ± 2 standard errors in both X and Y directions.

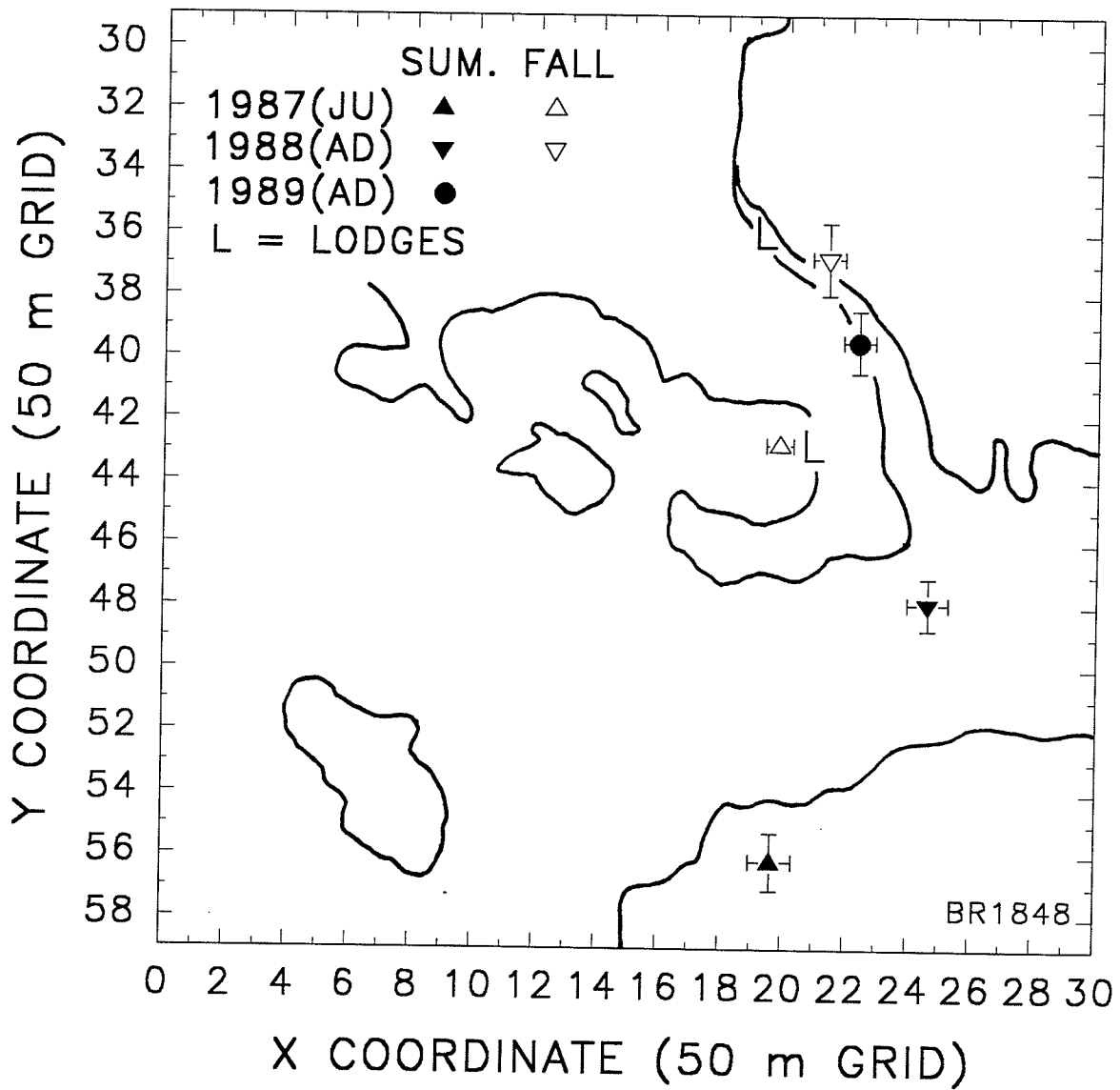


Figure 7. Centroids of activity for beaver BR1834 living on the Blind River, Summer and Fall, 1987 and 1988. Centroids are shown ± 2 standard errors in both X and Y directions.

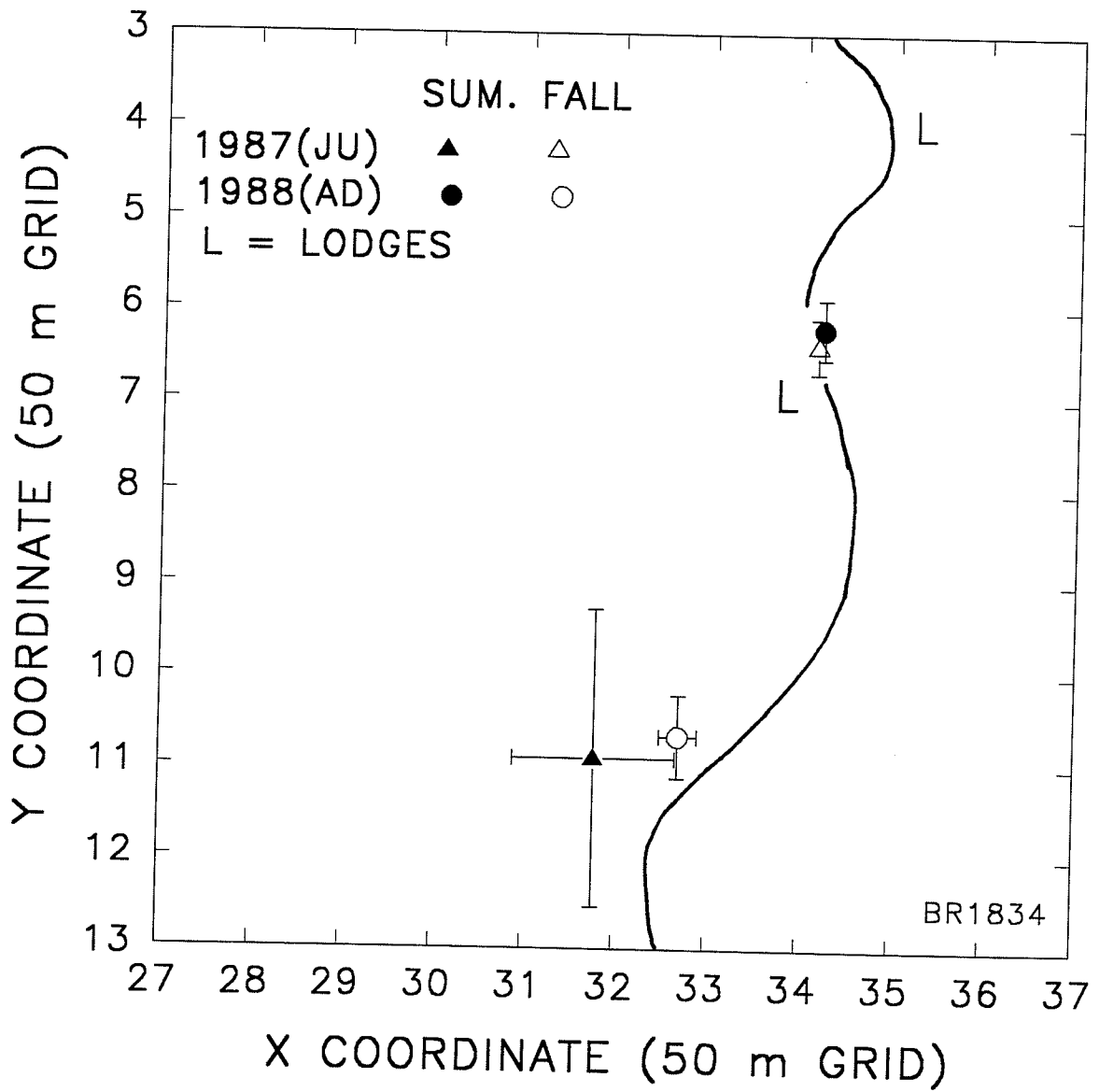


Figure 8. Centroids of activity for beaver GP286, living in Lower Gatlan Pond, Summer (Overnights) 1988 and Summer, 1989. Centroids are shown ± 2 standard errors in both X and Y directions.

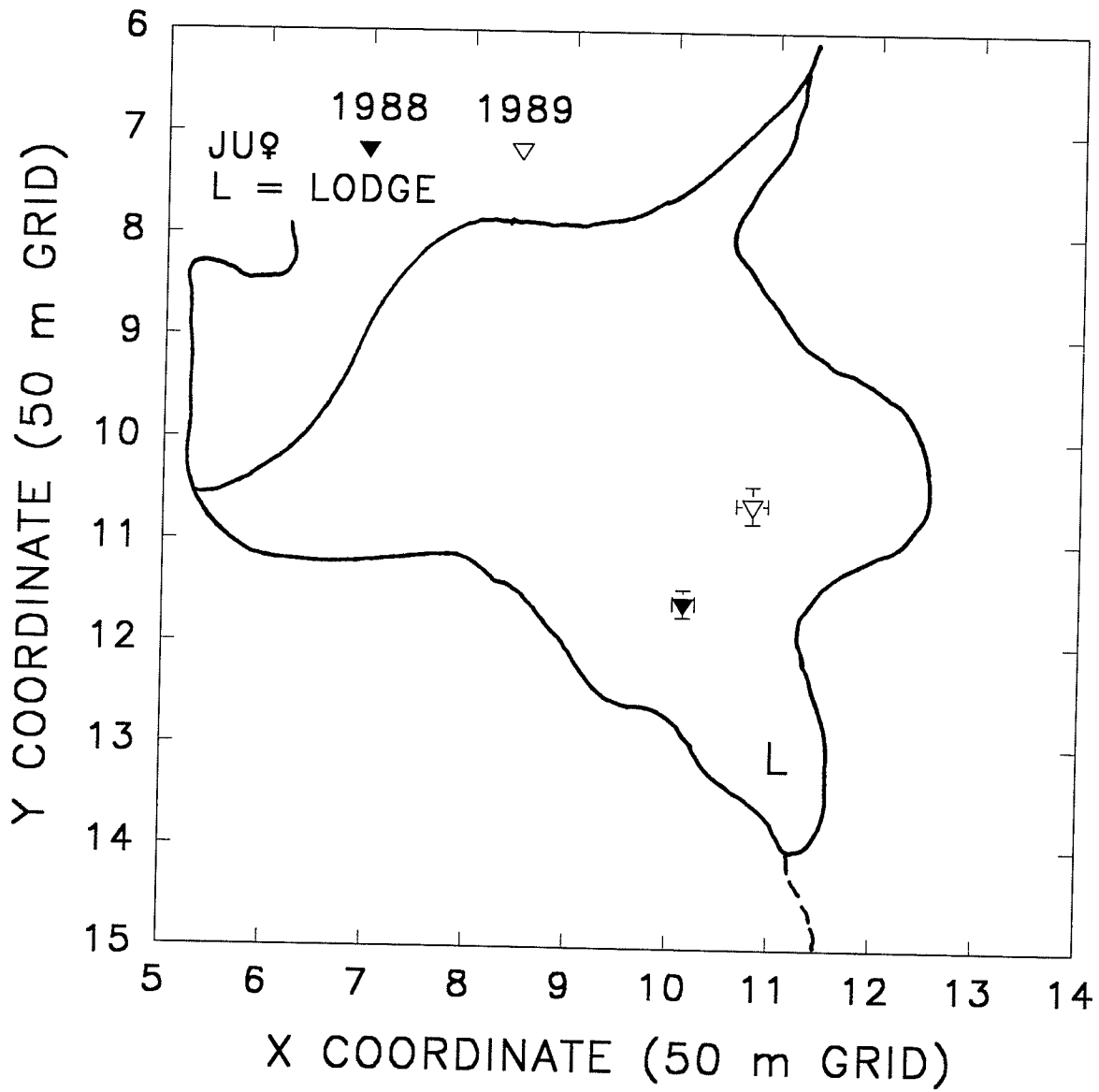
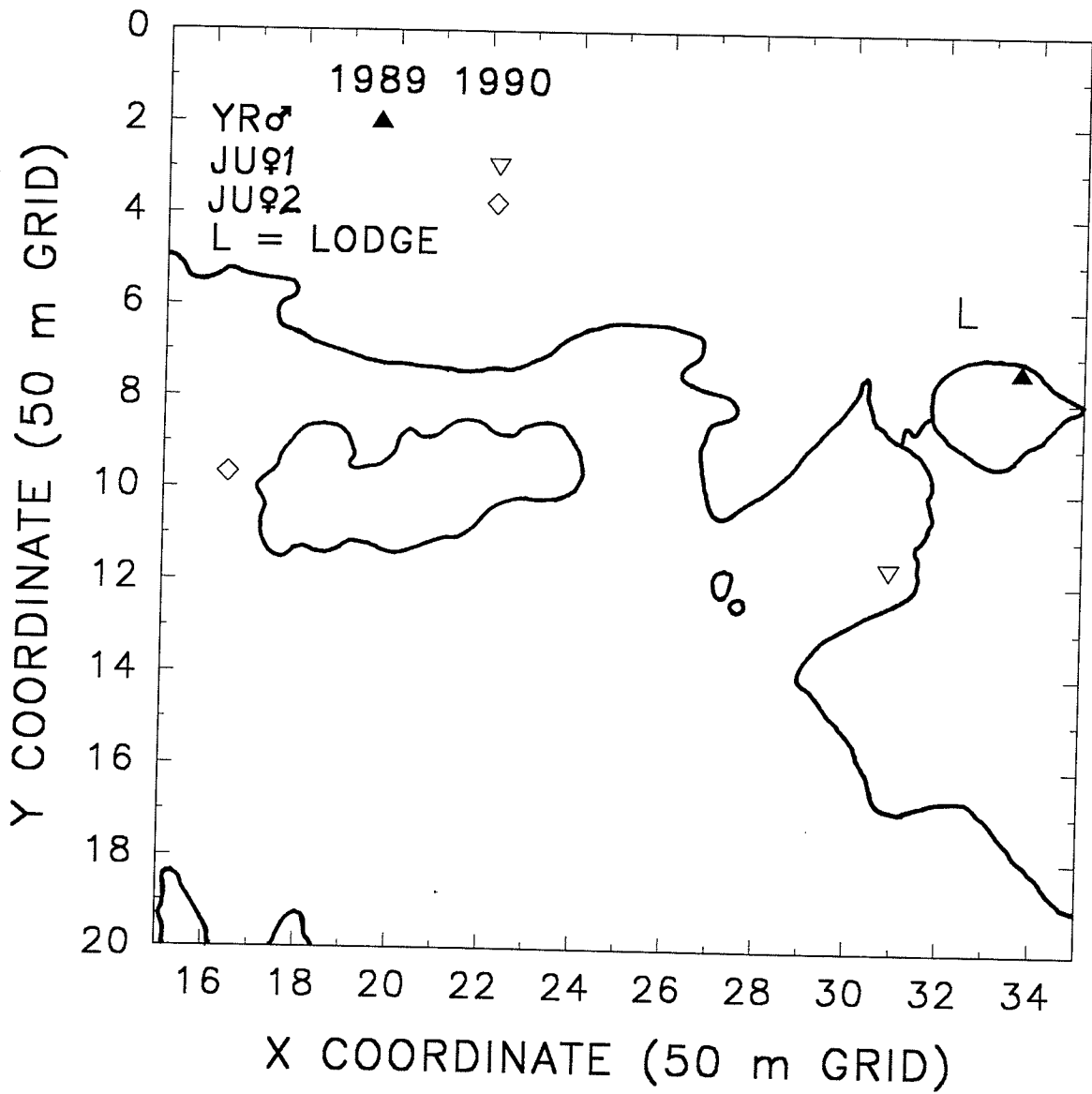


Figure 9. Centroids of activity for beavers living in the vicinity of Salt Lick Pond and Salt Lick Bay. Centroids are shown ± 2 standard errors in both X and Y directions. Yearling Male = SL109, Juvenile Female 1 = SL1686, Juvenile Female 2 = SL1682.



APPENDIX 5

DNA AUTORADIOGRAPHS

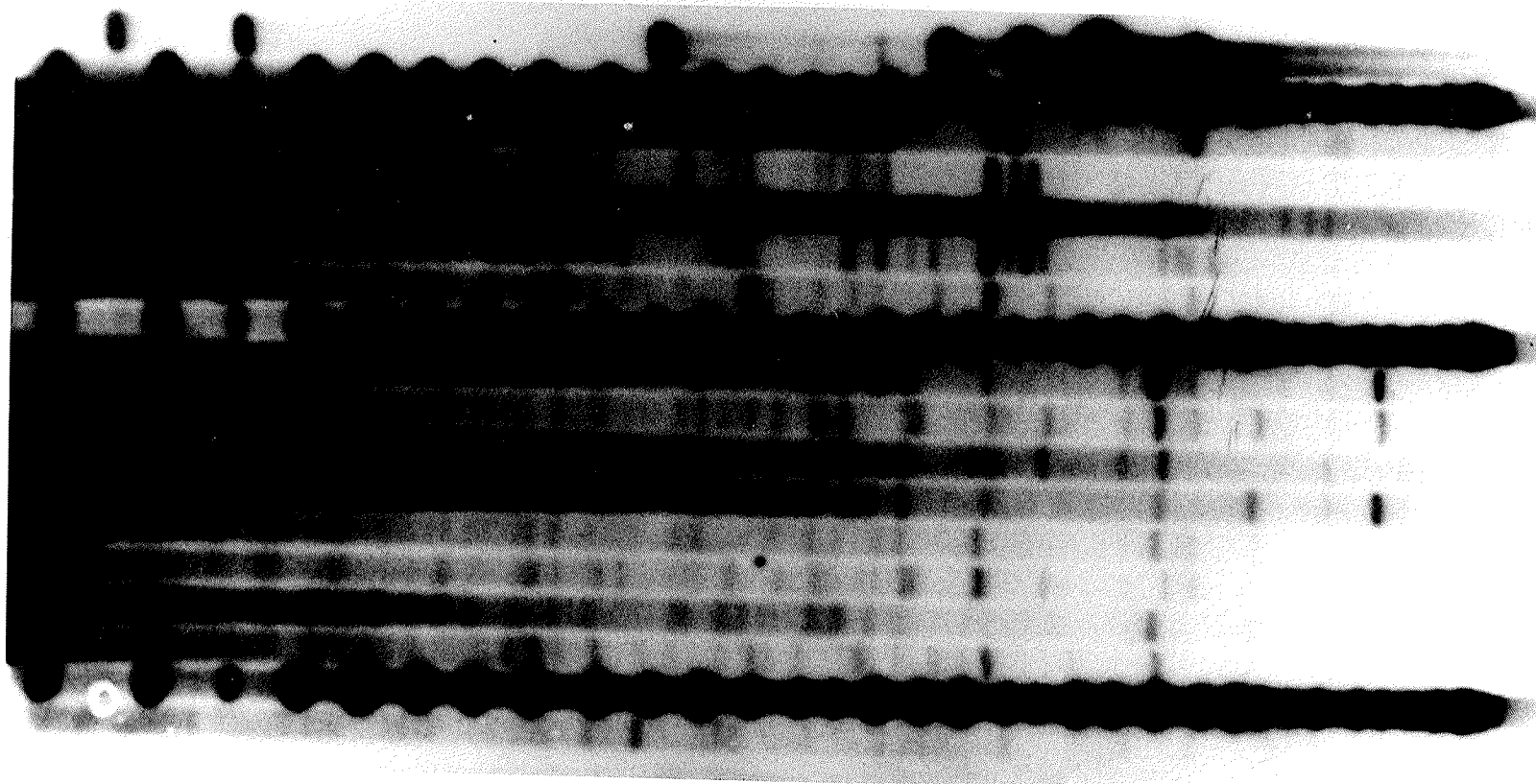
Table 1. Summary of composition of families groups in DNA study. Refer to Figure 1 in Chapter 8 for geographic location of families.

FAMILY NUMBER	ADULTS		TWO-YEAR OLDS		YEARLINGS		KITS		FETUSES
	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	MALE	FEMALE	
1	--	1	--	--	--	1	4	1	--
2	1	--	--	--	--	--	--	--	--
3	--	--	1	--	--	--	--	--	--
4	--	--	1	1	--	--	--	1	--
5	1	1	--	--	--	--	--	--	--
6	--	--	--	--	2	--	--	--	--
7	--	--	1	--	--	--	--	1	--
8	--	--	--	1	--	--	2	--	--
9	--	--	1	--	1	--	--	2	--
10	--	1	--	--	--	--	--	1	5
11	1	--	--	--	--	--	1	--	--
12	--	2	--	--	--	--	1	--	6 ¹
13	1	1	--	--	--	1	--	--	--
15	--	--	--	--	--	1	--	--	--
16	--	--	--	--	1	--	--	--	--
17	--	--	--	1	--	--	--	--	--
18	1	1	--	--	1	1	2	1	--
26	--	--	--	--	--	1	--	--	--
27	--	--	--	--	--	--	--	1	--
28	--	--	--	--	--	--	1 ²	--	--
29	--	1	--	--	--	--	--	--	--

¹ Both adult females were pregnant, each with 3 fetuses, see Wheatley, 1993.

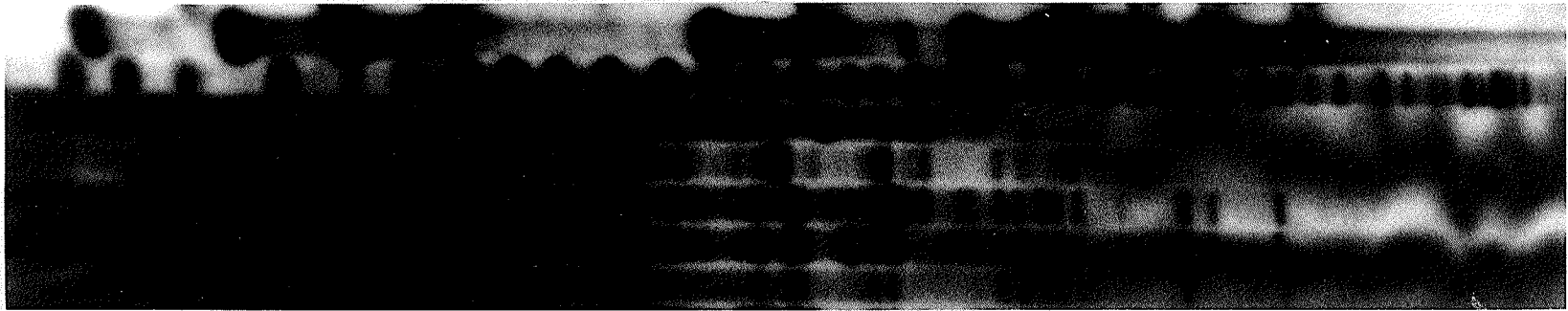
² Sex of fetus undetermined.

Figure 1. Autoradiograph of DNA samples from beavers from families 1, 2, 6, 26, 27 and 28. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit.



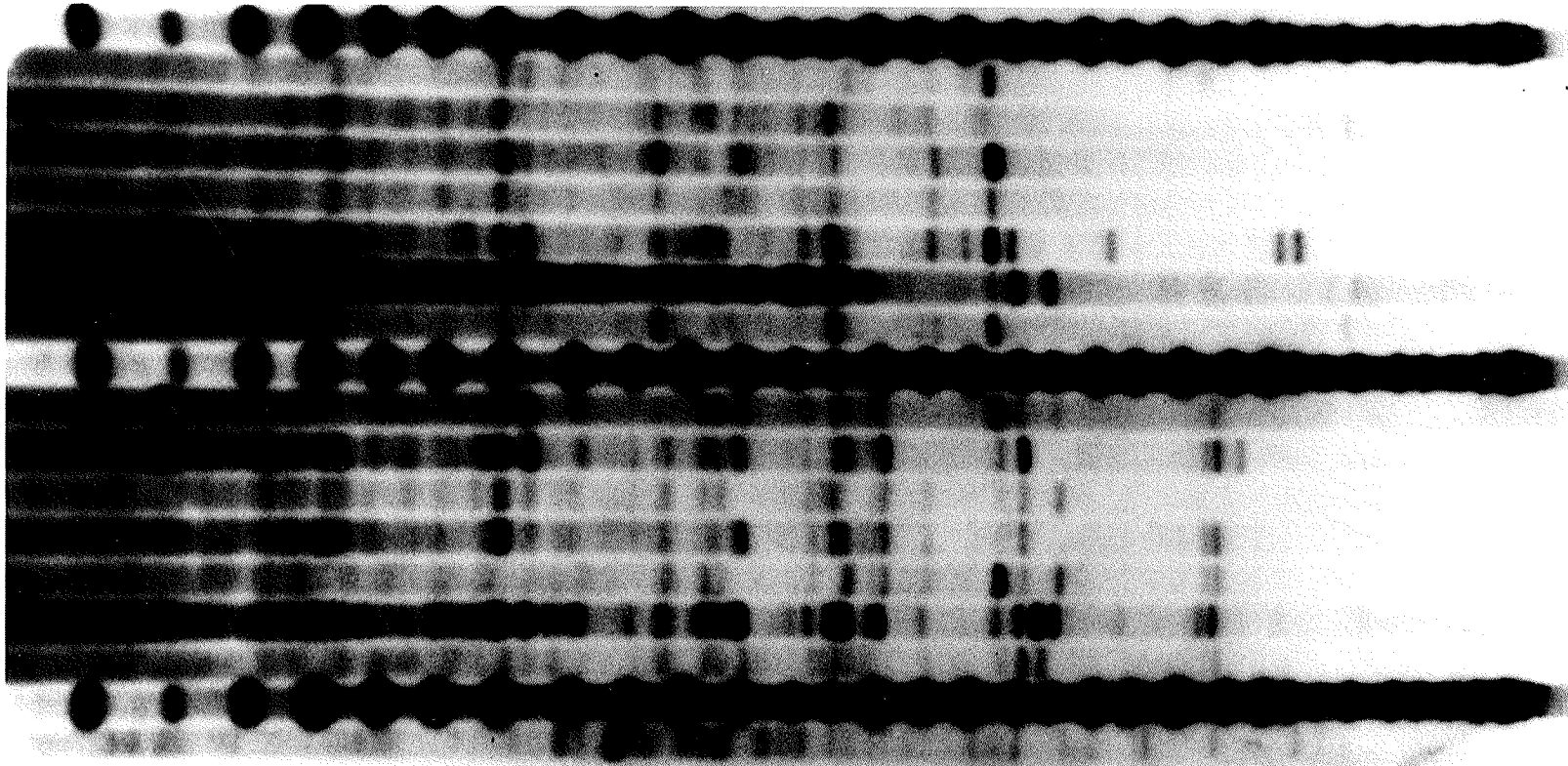
V
M
6▽
6▽
26△
27◆
28◆
M
1●
1◆
1△
1◆
1◆
1◆
1◆
2■
M
H

Figure 2. Autoradiograph of DNA samples from beavers from families 7 and 8. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit.



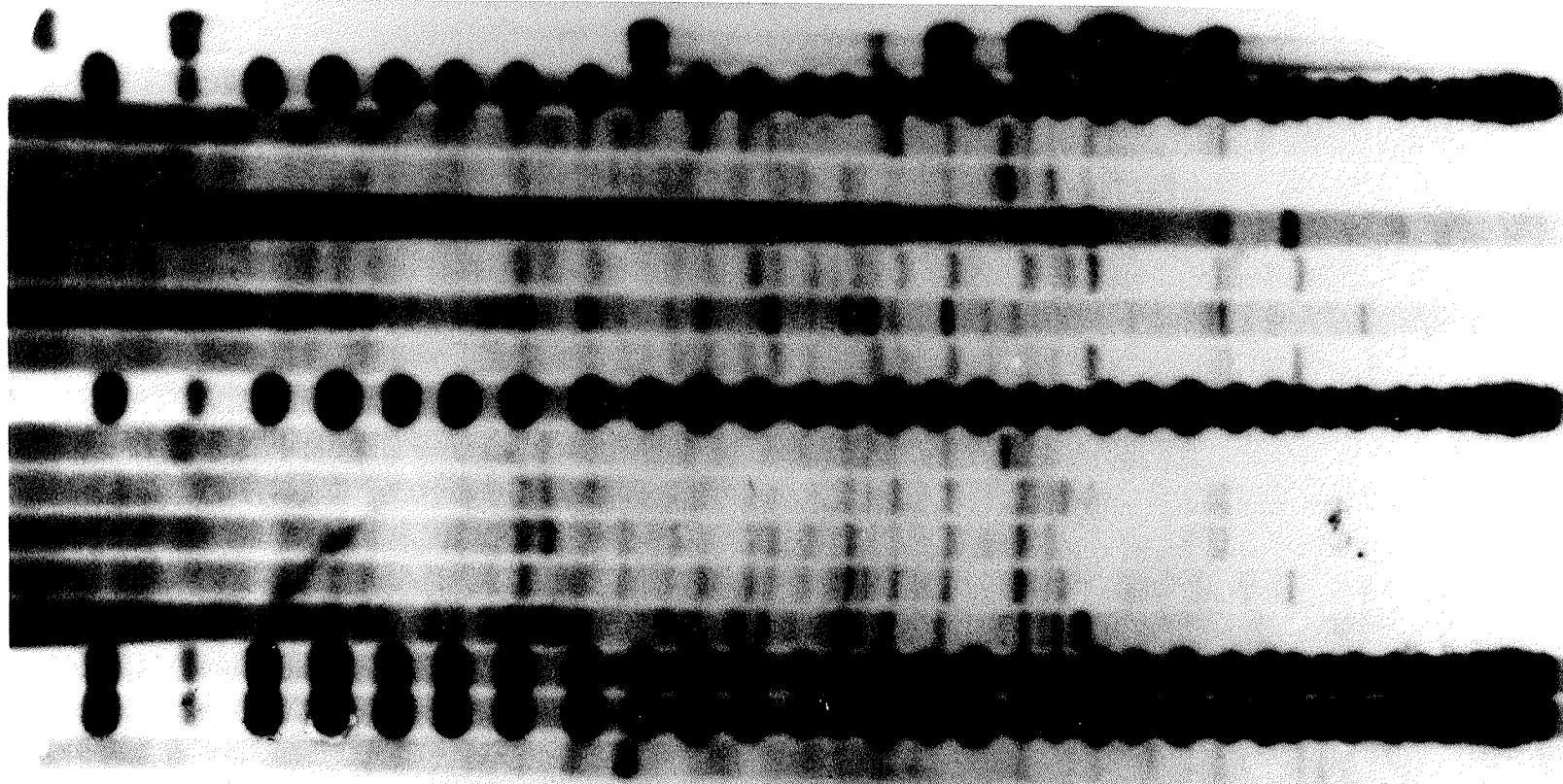
V
M
7▽
7◆
8◆
8◆
8△

Figure 3. Autoradiograph of DNA samples from beavers from families 3, 4, 5, 10 and 29. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit, small open circles = fetuses.



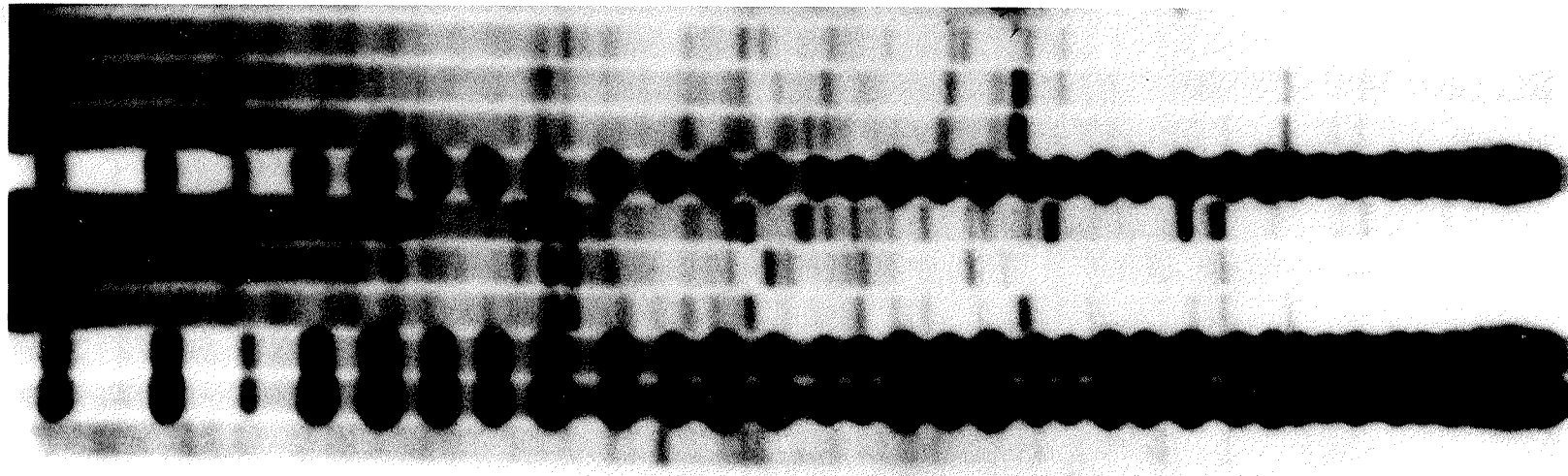
M
3▽
4△
4▽
4◆
5●
5■
29●
M
10●
10◆
10○
10○
10○
10○
10○
M
H

Figure 4. Autoradiograph of DNA samples from beavers from families 11 and 12. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, diamond = kit, small open circles = fetuses.



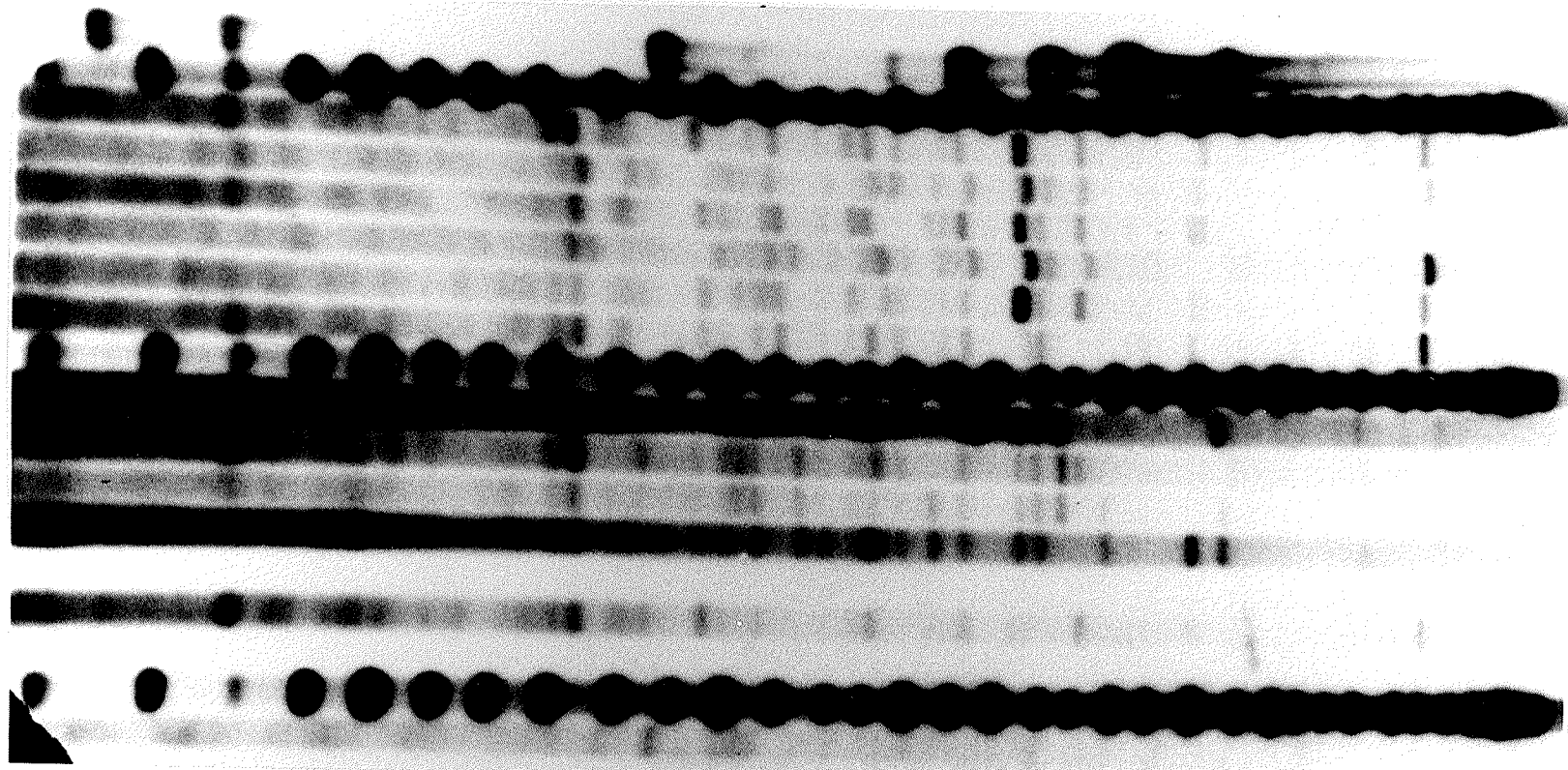
V
M
11■
11◆
12●
12○
12○
12○
M
12●
12○
12○
12○
12◆
M
M
H

Figure 5. Autoradiograph of DNA samples from beavers from families 13, 15, 16 and 17. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male.



13●
13■
13△
M
15△
16▽
17△
M
M
H

Figure 6. Autoradiograph of DNA samples from beavers from families 9 and 18. See Table 1 for summary of family composition, and Figure 1 in Chapter 8 for geographic location of families. V = visual control, M = molecular weight sizing standard, H = human control, square = adult male, circle = adult female, triangle up = yearling or two-year old female, triangle down = yearling or two-year old male, diamond = kit.



V
M
18●
18■
18△
18▽
18◆
18◆
M
9▽
9◆
9◆
9▽
18◆
M
H