

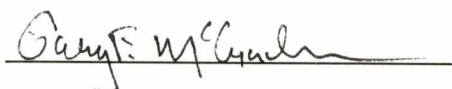
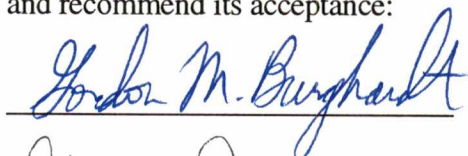
To the Graduate Council:

I am submitting herewith a dissertation by Andrea Bixler entitled "The Striped Skunk: Factors Affecting a Solitary Social System." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Life Sciences.



John L. Gittleman, Major Professor

We have read this dissertation
and recommend its acceptance:



Accepted for the Council:



Associate Vice Chancellor and
Dean of the Graduate School

THE STRIPED SKUNK:
FACTORS AFFECTING A
SOLITARY SOCIAL SYSTEM

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Andrea Bixler
May 1997

DEDICATION

This dissertation is dedicated to my parents,

Ray H. Bixler,
the first professor to teach me that
“nothing in biology makes sense except in the light of evolution,”

and
Marjorie M. Bixler,
who taught me that there is more to life than biology.

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ABSTRACT

Most behavioral ecological research on carnivores has focused on those few (10-15%) species which are social. This dissertation focuses on factors related to social behavior in a solitary carnivore, the striped skunk (*Mephitis mephitis*). I examined home range size and overlap, movement patterns, habitat preferences for home ranges and den sites, genetic variability within skunk populations and the biochemistry of lipids in skunk musk. None of these aspects of skunk biology have been examined extensively or quantitatively before.

Of six variables expected to impact home range size (season, body size, latitude, habitat and number of radio fixes), only the first two showed any effect: skunks have larger home ranges in the spring than in the winter and heavier females have larger home ranges. Movement patterns showed a similar relationship: skunks moved faster in the spring than in the winter. Home range overlap was extensive (up to 100% of an individual's home range) and did not show the pattern of intrasexual territoriality found in most mustelids. There was no clear pattern of habitat preferences in home range and den usage, but there is some indication of a preference for edges. Several examples of communal denning and long-term den use were found, although this was not expected so far south. Genetic variability in striped skunks was comparable to that found in other mammals. Biochemical analysis of lipids revealed a greater number of more diverse and complex compounds than previously found in skunk musk.

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PART ONE
INTRODUCTION

A *social* animal is one that cooperates with other group members to find or defend food, shelter, territories and mates. A *solitary* animal is often found alone and does not cooperate with conspecifics except to mate. However, solitary animals still experience many and varied social interactions (Leyhausen, 1965; Waser and Jones, 1983; Sandell, 1989). Solitary is thus “the opposite not of ‘social,’ but of ‘gregarious’” (Waser and Jones, 1983, p 356). Therefore, “the only mammal one could conceivably speak of as being socially indifferent is a dead one” (Leyhausen, 1965, p 257).

Despite the fact that solitary animals interact socially, their behavior is difficult to study because: 1) direct social interactions are infrequent, 2) indirect social interactions, such as those mediated by vocalizations or scent-marking, are difficult to detect and analyze, and 3) many solitary species, especially solitary carnivores, are also nocturnal, rare and/or dangerous.

Because of the difficulty in observing social interactions in solitary species, social behavior is often studied indirectly by examining spacing patterns. Spacing patterns refer to relative sizes of and amounts of overlap among home ranges, and reflect on a large (spatial) scale those behaviors performed at the individual level (Sandell and Liberg, 1992). Knowledge of spacing patterns can provide information about mating systems, parental behavior, dispersal, feeding ecology and population structure (Sunkist, 1981; Waser and Jones, 1983; Sandell, 1989; Powell, 1994).

Most (85-90%) species in the order Carnivora are solitary, yet behavioral ecological studies of carnivores are almost exclusively of social species (Gittleman, 1989). In this dissertation, I present findings from a study of a solitary carnivore, the striped skunk, *Mephitis mephitis* (family Mustelidae). I focus on spacing patterns and the related subjects of ecology, genetics and the biochemistry of skunk musk.

BIOLOGY OF THE STRIPED SKUNK

There are about 9 species of skunks (subfamily Mephitinae) distributed throughout the New World in almost all available habitat types (Corbett and Hill, 1991; Wade-Smith and Verts, 1982; Wozencraft, 1989). The striped skunk has been studied primarily in the upper mid-western United States and adjacent provinces of Canada because of its importance as a vector of rabies in these areas. Unlike many solitary carnivores, it is slow-moving, non-aggressive, uses small home ranges (see below) and often lives at high population densities (2-9 skunks/km²; Bailey, 1971; Rosatte, et al., 1992). Most researchers have focused on reproduction (in captivity), home range size, movement patterns, denning and diet (in the wild).

Striped skunks mate in late February and March (Wade-Smith and Richmond, 1975) and litters of 2-8 kits are born in May or June (Wade-Smith and Verts, 1982). Kits are weaned at approximately 2 months of age (Stegeman, 1937; Wade-Smith and Richmond, 1975; Wade-Smith and Verts, 1982). Juveniles probably disperse shortly after weaning and breed the following spring, when they are approximately 10 months old (Wade-Smith and Verts, 1982). It is thought that striped skunks usually live less than two years in the wild (Wade-Smith and Verts, 1982), although one study has found a few individuals surviving to five or more years (Chase and Suffolk, 1989).

Winter mortality, combined with variable litter sizes following severe and easy winters, is thought to drive large fluctuations in population density in northern climates (Bjorge et al., 1981). Factors controlling population density in southern areas are unknown but may relate to disease; Wade-Smith and Verts (1982) suggest that the major causes of mortality in striped skunks are epizootics of pneumonia, distemper, leptospirosis and rabies. Skunks are preyed upon by wolves (*Canis lupus*), coyotes (*Canis latrans*), foxes (*Urocyon cinereoargenteus*), badgers (*Taxidea taxus*), mountain lions (*Felis concolor*), bobcats (*Lynx rufus*), black vultures (*Coragyps atratus atratus*), eagles

(unspecified Accipitridae) and owls (unspecified Strigiformes) (Merriam, 1886; Seton, 1929; McIlhenny, 1939; Robinette et al., 1959; McCord, 1974; Garcelon, 1981).

Further information about striped skunks, relevant to specific questions addressed in this study, is discussed below.

ORGANIZATION OF THE DISSERTATION

This dissertation is organized in three parts and an appendix: Part 1) Individual Home Range Size, Movements and Overlap; Part 2) Use of Home Ranges: Habitat and Den Sites; Part 3) Genetic Variability Within A Population of Striped Skunks and Appendix 1) Mechanisms of Home Range Use: The Biochemistry of Skunk Musk. Each section is presented as an independent study and includes an introduction, methods, results, discussion and literature cited. Because of this, there is overlap among some parts.

INDIVIDUAL HOME RANGE SIZE, MOVEMENTS AND OVERLAP. A home range is the area traversed by an animal during its normal daily activities (Burt, 1943). In mammals, variables as diverse as latitude, habitat, sex and weight are known to affect home range size (e.g., Gompper and Gittleman, 1991; Wauters and Dhondt, 1992; Reid et al, 1994). However, few studies have examined these or other variables in relation to home ranges in striped skunks. The home range size of striped skunks (*Mephitis mephitis*) has been determined primarily in prairie and agricultural areas of the American and Canadian mid-west. Values range from 0.11 to 0.31 km² for studies using mark-recapture data and from 2.4 to 5.1 km² for radio tracking work.

Home range overlap is one of the most obvious and important means of examining social behavior in solitary animals (Leyhausen, 1965). There are no quantitative data in the literature on home range overlap in striped skunks, although they are expected to follow patterns of intrasexual territoriality, the most common spacing patterns found in carnivores, including mustelids (Powell, 1979; Sandell, 1989; Balharry, 1993). In part 2, I examine

patterns of intrasexual territoriality, the most common spacing patterns found in carnivores, including mustelids (Powell, 1979; Sandell, 1989; Balharry, 1993). In part 2, I examine the affect of variables such as latitude, habitat, sex and weight on variation in home range size of striped skunks. I also determine patterns of inter- and intrasexual overlap in home ranges.

USE OF HOME RANGES: HABITAT AND DEN SITES. Some mustelids use a diversity of habitats, while others are restricted to a particular habitat type (e.g., otters to rivers and martens to forests). Skunks appear to fall into the former category: "semi-open country; mixed woods, brushland and prairie preferred. . ." (Burt and Grossenheider, 1980, p. 70).

Habitat preferences are indicated by differences in the location of activity (home ranges) or rest (den sites). Home ranges and dens may be selected for thermal conditions, availability of food or cover from predators (e.g., Beier, 1989; Dubuc et al., 1990). Intraspecific variation in habitat preferences may be due to age, sex, season and activity patterns (Andelt and Andelt, 1981; Griffith and Peek, 1989; Leptich and Gilbert, 1989). Habitat preferences in home ranges have not been explicitly studied in skunks, and whether there are differences in habitat use among individuals within a population is not known.

More information is available on den selection, however. Skunks have been reported to show a seasonal dichotomy, using underground dens in winter and aboveground dens in summer (Houseknecht and Tester, 1978), but habitat preferences associated with den usage are not known. Den site selection may be particularly important for striped skunks, since they are nocturnal and may require insulation in cold climates. In northern regions, this solitary carnivore has been observed to overwinter in communal dens of up to 18 females with a single male (Gunson and Bjorge, 1979). Winter denning may be continuous for 30 days at a time in northern Illinois and up to 150 days in Alberta (Gunson

and Bjorge, 1979; Storm, 1972). In part 3, I determine habitat preferences in both home range and den use within a population of striped skunks.

GENETIC VARIABILITY WITHIN A POPULATION OF STRIPED SKUNKS. Genetic variability, represented as average polymorphism (P) and heterozygosity (H), is lower in mammals than in any other class of vertebrates, and vertebrates exhibit lower levels than both plants and invertebrates (mammals: $P=0.147$, $H=0.0359$; vertebrates: $P=0.173$, $H=0.0494$; plants: $P=0.259$, $H=0.0706$; invertebrates: $P=0.397$, $H=0.1123$; Nevo, 1978). Average polymorphism and heterozygosity in mustelids have been reported to be both very low (Simonsen, 1982) and as high as in other mammals (Mitton and Raphael, 1990). None of these studies included polymorphism or heterozygosity values for striped skunk. O'Brien et. al. (1989) used a single skunk among several species in a comparison of mustelid allozymes and found only one heterozygous locus out of 30. In part 4 I provide an estimate of polymorphism and heterozygosity for striped skunks from an allozyme survey.

CONCLUSIONS. In the final part, I briefly summarize the results from each preceding part and then suggest ideas for future study. These range from radio tracking skunks in different habitats and geographic areas to the use of behavioral studies of captive skunks to elucidate the possible communicative value of their musk.

APPENDIX I: MECHANISMS OF HOME RANGE USE: THE BIOCHEMISTRY OF SKUNK MUSK. Skunks produce and spray a noxious substance from paired anal sacs. The liquid is known to be composed of seven major low-molecular weight compounds, six of which contain sulfur (Wood, 1990). Scientists from Darwin (1871) to the present

(Verts, 1967; Wood, 1990) have discussed skunk spray as a mechanism of defense against predators. Only Coues (1877) suggested that it might additionally be used in intraspecific communication, specifically as a sexual attractant. Anal gland secretions are believed to function in this way in many carnivores (Macdonald, 1985). Here, I use a new method of biochemical analysis to examine the lipid content of skunk musk in contrast to the simpler compounds determined by Wood (1990). Information about more complex compounds such as lipids may give new insights into the function of skunk musk.

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PART TWO

INDIVIDUAL HOME RANGE SIZE, MOVEMENTS AND OVERLAP

INTRODUCTION

An individual animal's home range is the area traversed during its normal daily activities (Burt 1943). Measuring home range size and overlap is one of the most obvious and important means of examining social behavior in solitary animals (Leyhausen, 1965). Home range size is influenced by many variables, including diet, latitude, habitat and sex (Gittleman and Harvey, 1982; Buskirk and McDonald, 1989; Sandell, 1989; Gompper and Gittleman, 1991). In addition, estimates of home range size may be affected by the number of radio fixes taken per individual (Bekoff and Mech, 1984; Buskirk and McDonald, 1989). In this part, I explore how these variables influence the home range size of striped skunks (*Mephitis mephitis*, Mustelidae) in Cades Cove, Great Smoky Mountains National Park. In addition, I determine the amount of overlap between home ranges and relate this to patterns of intrasexual territoriality observed in many mustelids (Powell, 1979).

Striped skunks are a model species to examine because they: 1) are widely distributed across North America, 2) are found in virtually all habitat types and 3) are easy to study relative to most carnivores. Even so, many variables affecting spacing patterns in striped skunks have not been tested.

HOME RANGE SIZE. The following factors related to home range size will be examined in this part. It should be noted that these variables are not mutually exclusive and may interact with one another.

Latitude. Individuals living at higher latitudes may be expected to have larger home ranges than individuals of the same species at lower latitudes because they must search larger areas to locate sufficient resources. Gompper and Gittleman (1991) found that in coyotes (*Canis latrans*), black bears (*Ursus americanus*) and bobcats (*Felis rufus*), there was a significant positive relationship between latitude and home range size. However, Buskirk and McDonald (1989) found no relationship between latitude and home range size in a review

of 12 studies on American marten (*Martes americana*). The relationship between latitude and home range size has not been quantitatively examined in skunks, in part because home range measurements are only available from study sites between 40° and 55°N latitude.

Habitat. Home range size has not been found to correlate with habitat across the order Carnivora, perhaps in part because intraspecific variability makes habitat preferences difficult to classify (Gittleman and Harvey, 1982). Even so, single-species studies suggest differences in home range size with habitat [red fox (*Vulpes vulpes*), Ables, 1969; gray fox (*Urocyon cinereoargenteus*), Fuller 1978; coyote, Gese et al. 1988, Person and Hirth, 1991; red squirrel (*Sciurus vulgaris*), Wauters and Dhondt, 1992]. Generally, home ranges were larger when they included habitats with fewer resources or more heterogeneous resources. While no single study of striped skunks has correlated home range size with habitat, comparisons can be made across studies. However, care must be taken since techniques used to determine home range size varied from study to study.

Seasonality. Seasonal differences in home range size are often thought to relate to life history events. In spring, home ranges of males may be larger because they are moving farther in search of mates [spotted skunk (*Spilogale putorius*), McCullough and Fritzell, 1984; kit fox (*Vulpes velox macrotis*), Zoellick and Smith, 1992; least weasel, Jedrzejewska et al., 1995]; during the summer, females may be restricted to the immediate vicinity of a natal den [Franklin's ground squirrels (*Spermophilus franklinii*), Choromanski-Norris et al., 1989; American marten, Katnick et al., 1994]; and, during the autumn, juveniles may move farther as they disperse [coyote, Holzman et al., 1988, Gese et al., 1988 and Person and Hirth, 1991]. However, some studies do not show seasonal differences in home range size [Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), Schoen and Kirchhoff, 1985; Virginia opossums (*Didelphis virginiana*), Sunquist et al.,

1987]. Seasonal patterns have not been examined in striped skunks, since most studies have been short term or have not distinguished home range sizes across seasons.

Sex and Body Size. Home range size increases with body mass because of the increased metabolic needs of the animal (McNab, 1963; Gittleman and Harvey, 1982). Studies examining the correlation between weight and home range size provide conflicting results: larger animals may have larger home ranges [hispid cotton rat (*Sigmodon hispidus*), Spencer et al., 1990], or the correlation may hold true only within a sex [male but not female home range size is positively correlated with weight: fulvous harvest mouse, Spencer and Cameron, 1988; female but not male home range size is positively correlated with weight: American marten, Buskirk and McDonald, 1989].

In sexually dimorphic species, it would be expected that the larger sex would have a larger home range. In addition, males of polygynous species might be expected to expand home ranges to find and attract more females. Males have been found to have larger home ranges than females in a number of studies [wolverine (*Gulo gulo*), Whitman et al., 1986; American marten, Buskirk and McDonald, 1989; river otter (*Lontra canadensis*), Reid et al., 1994]. Others have found no sex differences in home range size [coyote, Gese et al., 1988, Person and Hirth, 1991; moose (*Alces alces*), Leptich and Gilbert, 1989; San Joaquin kit foxes (*Vulpes macrotis mutica*), White and Ralls, 1993] or results the opposite of those expected [coyote, Holzman et al., 1992].

Fuller et al. (1985) found that male skunks weighed significantly more than females in most age classes, but Stout and Sonenshine (1974) did not find any significant dimorphism in weight. Greenwood et al. (1985) found a nonsignificant trend for male striped skunks to have larger home ranges than females. Other studies do not provide body sizes for individual skunks or give home range sizes by sex, so correlations between these variables are difficult to determine.

Number of radio fixes. The estimate of home range size is expected to increase to an asymptote with the number of radio fixes (Bekoff and Mech, 1984; but it may not: coyote, Gese et al., 1988; American marten, Buskirk and McDonald, 1989). Unfortunately, it is not always possible to reach the asymptote because of animal death or equipment failure, and many researchers do not attempt to do so. Few studies of home range in skunks used telemetry (three out of six home range studies) and, although most estimate the number of radio fixes, they are usually not explicit as to the number of fixes used to calculate each individual home range estimate. However, Storm (1972) does specify that there did not appear to be a relationship between length of tracking and size of home ranges in his study.

Other. Age and diet may also be expected to affect home range size (comparative studies, Gittleman and Harvey, 1982; Gompper and Gittleman, 1991; coyote, Gese et al., 1988, Holzman et al., 1992; least weasel, Jedrzejewska et al., 1995; but no age differences in moose, Cederlund and Okarma, 1988). Although other authors have measured home range size of juvenile skunks as well as adults, generally finding juvenile ranges smaller than adult ranges (Bailey, 1971; Storm, 1972; Goldsmith, 1981), I did not have radio collars small enough to safely equip juveniles. I also did not assess diet. Therefore, these factors were not examined in the present study.

MOVEMENTS. Animals move between den sites, feeding grounds, water sources and conspecifics. Length and speed of movement may or may not be reflected by reported home range sizes. Many authors report movements in addition to home range sizes and I do so here for comparative purposes. More researchers have examined movement distances than home range size in striped skunks; this is in part because movements can be

determined by snow-tracking, though mark-recapture and telemetry have also been used. The following variables have been reported to influence mammal movement patterns.

Sex and Season. Season, or an interaction between sex and season, have been reported to influence movement patterns in mammals. Opossums (Allen et al., 1985) move the same distances in spring and summer despite shorter summer nights. Male movements have been found to be greater in the breeding season in Franklin's ground squirrels (Choromanski-Norris et al., 1989), kit foxes (Zoellick and Smith, 1992) and river otters (Reid et al., 1994). Laundre and Keller (1981) found that male coyotes traveled longer distances and females shorter distances per day during the breeding season. However, no sex differences were found in red fox or, in contradiction to the above, in coyote movement patterns (Cavallini, 1992; Holzman et al., 1992; respectively). Zoellick et al. (1989) found no seasonal differences in movements of female desert kit foxes (*Vulpes macrotis arsipus*).

Three studies of striped skunks show that males move farther than females, although this pattern has either not been examined statistically (Storm, 1972; Greenwood et al., 1985) or is not significant (Rosatte and Gunson, 1984). Bailey (1971) found juvenile females moving farther than juvenile males, although the longest movement was by a male. Bjorge et al. (1981) found adult males moving farther than adult females but juvenile females moving farther than juvenile males. Neither of the latter studies reported significance levels. Seasonal trends have also been reported, with skunks moving farther in spring than winter (Sunquist, 1974) and female skunks moving farther during July and August, when they would be weaning their kits, than in May and June, during parturition and lactation.

Habitat. Few studies attempt to correlate movement patterns with habitat type. Palomares and Delibes (1994) found a negative correlation between the distance traveled and the

amount of preferred habitat in European genet (*Genetta genetta*). It is suggested that the habitat was preferred because of availability of feeding and resting sites, and that there was little movement between such sites. A similar relationship has been found in baboons (*Papio* spp.), vervet monkeys (*Cercopithecus aethiops*) and sifakas (*Propithecus verreauxi*; reviewed in Dunbar, 1988). Correlations of movement patterns and habitat type have not been made in striped skunks.

Weight. Larger animals might be expected to move farther in order to obtain more resources, but this hypothesis has not been thoroughly examined. Palomares and Delibes (1994) found a positive relationship between distance traveled by European genet and body mass. Clutton-Brock and Harvey (1977) found a positive relationship between day range length and group weight in a comparative study of 56 primate species. Martin (1981) disputed the relevance of this result to body weight *per se* and, in separate analyses of arboreal and terrestrial primates, found no relationship between day range length and body size. Such correlations have not been tested in striped skunks.

Weather. Weather conditions could influence movements. This has only been examined directly by Greenwood et al. (1985), who found decreased skunk movements during extreme wind-chill conditions. However, several authors have found that weather variables influence trap success, presumably because they influence food availability and thus skunk movement. Bailey (1971) captured significantly more skunks during periods of decreasing barometric pressure, but found no correlation between captures and precipitation, fog, sky cover, winds or temperature. Verts (1967) found no relationship between minimum temperature and trap success. Kinlaw et al. (1995) trapped significantly more spotted skunks on colder, cloudier nights, and found significant relationships (the direction of which were not specified) between trap success and maximum temperature the

previous day, dew point and barometric pressure. They found no significant relationship between captures and precipitation or wind.

Age. An animal's age may influence how far it moves. In coyotes and European genets, adults move longer distances than juveniles, although the result was significant only for genets (Holzman et al., 1992; Palomares and Delibes, 1994, respectively). Juveniles have been reported both to move longer distances (Gunson and Bjorge, 1979; the result is significant in Bjorge et al., 1981) and shorter distances than adults (Verts, 1967; Bailey, 1971; Storm, 1972). These conflicting results may have to do with whether long-distance juvenile dispersals were included in the data. Since juvenile skunks were not radio collared in my study, I do not examine age differences in movement patterns.

HOME RANGE OVERLAP. Many carnivores, especially felids and mustelids, are thought to exhibit a pattern of intrasexual territoriality in which males maintain territories exclusive of other males and females maintain territories exclusive of other females, but male and female territories overlap (Powell, 1979; Sunquist, 1981). Powell (1979) suggested that skunks (both striped and spotted) exhibit a variation of intrasexual territoriality in which males maintain exclusive territories but females do not. This hypothesis was based solely on evidence that there is never more than one male present (but up to 18 females, Gunson and Bjorge, 1979) in a communal winter den. Powell suggested that females may maintain some sort of loose-knit organization, a hypothesis that has gained further support from the finding that females may move in groups from one den to another during and between winters (see Part 3; also, Gunson and Bjorge, 1979). Across mustelids, Powell found a correlation between increasing levels of carnivory, sexual dimorphism, elongation (calculated as average male body length divided by the cube root of average male body weight) and intrasexual territoriality. Striped and spotted skunks

are less carnivorous, less sexually dimorphic and less elongate than other mustelids, and they appear to be less intrasexually territorial as well (Powell, 1979). There are no quantitative data in the literature on home range overlap in striped skunks and the qualitative suggestions conflict (Bailey, 1971; Gunson and Bjorge, 1979; Goldsmith, 1981).

In light of the above variables, I present data on striped skunks in relation to three patterns: 1) differences in home range size associated with latitude, habitat, season, body size, sex and number of radio fixes; 2) individual movement patterns related to sex, season, weight, weather and habitat; and 3) home range overlap between and within the sexes.

METHODS

Study area. Cades Cove is located in Blount County, Tennessee in the northwest portion of Great Smoky Mountains National Park (approximately 35°35'N, 83°51'W to 35°37'N, 83°46'W). It includes a campground, picnic area, ranger station, personnel living quarters and the Cades Cove Loop Road (Figure 2-1). The Loop Road encloses approximately 8 km². This area of rolling hills and fields is grazed by horses and cattle as well as native fauna and is mowed twice each summer. Many historical structures in this area are maintained by the Park Service and are well-trafficked by visitors; these seldom show signs of use by terrestrial wildlife. However, several abandoned hay barns contain burrows. The altitude of the area within the Loop Road is approximately 600 m. Outside the Loop Road the terrain is steeper, grading to an altitude of 800 m or more, and covered with cove-hardwood forest. Cades Cove is visited by more than two million tourists each year, who frequently leave litter edible to wildlife. Further information about the natural history of Cades Cove can be found in Komarek and Komarek (1938), Whittaker (1956), and Goldsmith (1981).

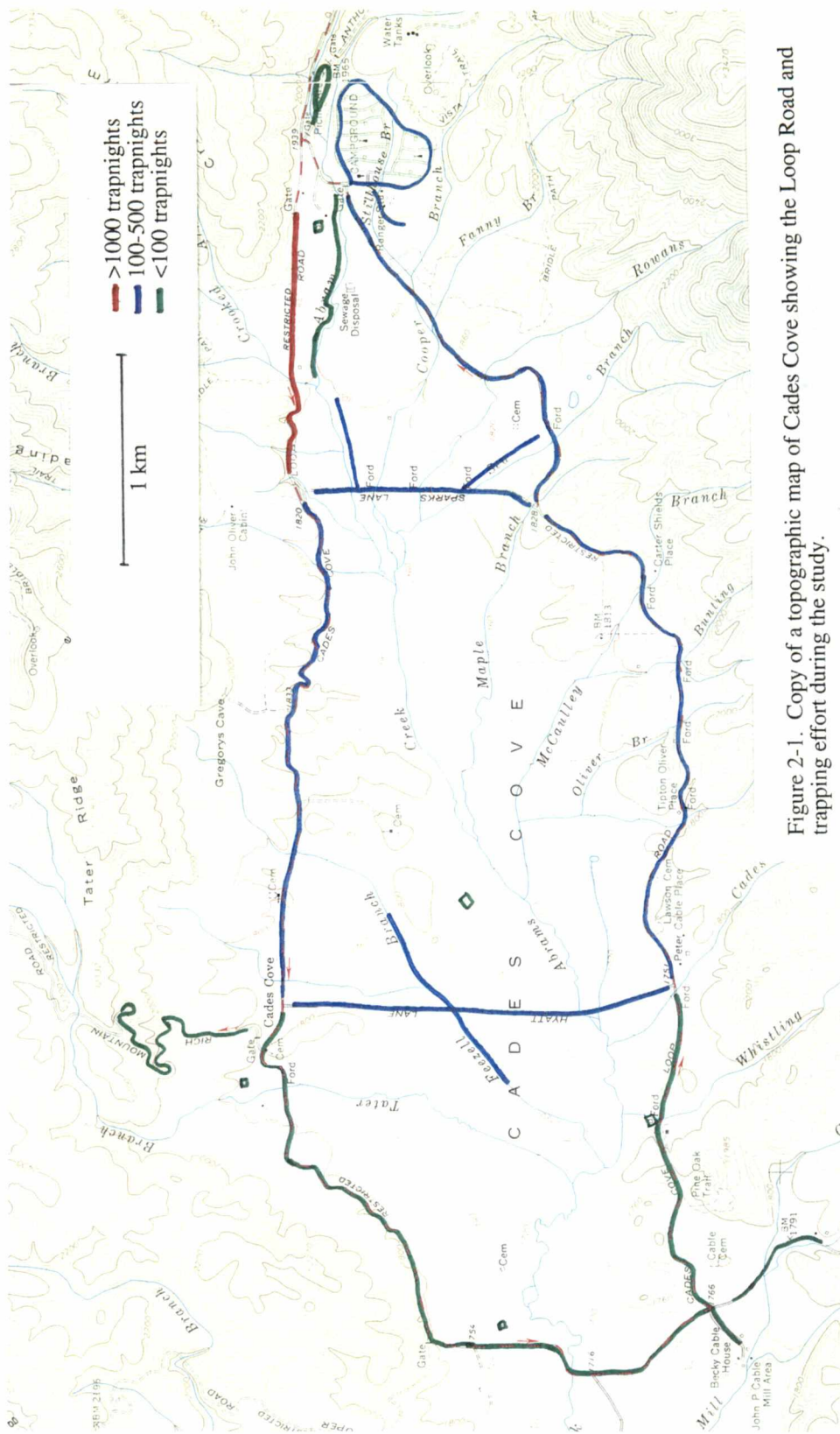


Figure 2-1. Copy of a topographic map of Cades Cove showing the Loop Road and trapping effort during the study.

Trapping. Trapping was conducted from mid-January 1993 through March 1995 and February through mid-April 1996. Tomahawk traps #105 were set shortly after dusk and checked just before dawn each day for a total of 3416 trapnights (from one to 42 traps/night, mode=10 traps/night). Traps were baited with oil-packed tuna and most were set along the Loop Road either in culverts or in the woods nearby (Figure 2-1). The majority of traps were set at the east end of the Cove for two reasons: 1) to reduce travel time when there were many tourists and 2) to ensure the possibility of identifying overlapping home ranges since traps were set in areas of previous trap success. Traps were also set in the picnic area, campground and near personnel housing. Captured skunks were anesthetized with a 4:1 mixture of ketamine hydrochloride and xylazine (Rosatte and Hobson, 1983; Servin and Huxley, 1992; R. Greenwood, pers. comm.). Sex, canine length, head-body length, tail length and weight of all trapped individuals were recorded.

Home range analysis. A total of 15 skunks (nine male and six female) were radio collared. Telemetry packages produced by ATS (Isanti, MN) weighed approximately 53 g and had a flexible whip-type antenna of about 15 cm. The battery was designed to last 1 yr.

Each radio-collared animal was located at least 14 times (see Table 2-1). Location data were analyzed using the minimum convex polygon and percent overlap functions of Wildtrak II Home Range Analysis for the Macintosh (Todd, 1995). With Wildtrak II, it is also possible to compute different home ranges for each season.

Latitude. Latitude for Cades Cove was estimated from the USGS topographic map. Latitudinal data for other studies were taken from the original publication or estimated from *Goode's World Atlas* (Espenshade and Morrison, 1986).

Table 2-1. Home range size (HR) and associated variables for 15 striped skunks: sex, weight, habitat type and the number of radio fixes used to calculate the home range size. Habitat was measured as described in the methods, and is here presented as the proportion of forest habitat in a home range.

SKUNK	SEX	WT (kg)	HABITAT	#FIXES	HR (km ²)
19	male	1.65	0.194	51	1.693
23	male	2.20	0.170	14	0.190
27	female	1.20	0.655	19	0.747
40	male	1.75	0.602	22	0.833
72	male	1.40	0.436	32	2.668
74	male	2.45	0.364	62	0.580
90	male	1.65	0.613	24	0.602
95	male	2.15	0.417	64	0.925
98	female	2.15	0.445	157	1.355
DG60	female	1.25	0.589	96	0.537
LB143	female	1.20	0.780	136	0.295
P169	male	1.75	0.352	25	2.407
P174	female	1.55	0.457	230	1.049
R2	male	2.50	0.333	137	0.896
Y98	female	2.65	0.486	186	1.267

Habitat. A USGS topographical map of the Cades Cove Quadrangle was scanned into a Macintosh computer using Ofoto software. The map was transferred to Aldus SuperPaint, where the habitat was classified as forest or field, represented by different colors. Plant species found in forest habitat are listed in Table 2-2a. Field habitat was that area which is mowed regularly and included those species listed in Table 2-2b. Home range maps created in Wildtrak were overlaid on the habitat map (this is shown in Figure 2-2). PV-Wave (Version 6.1) software was used to count the number of pixels of each color (habitat type) within each home range outline.

Habitat was then examined in three ways: 1) The absolute area of forest habitat (AAFor) and field habitat (AAFie) within each home range was analyzed in relation to home range size, sex and weight. 2) The absolute area of forest was converted to a proportion of forest available (PFA) for each home range. The proportion of field available is not reported since it is the inverse of PFA. 3) The proportion of times that each skunk was located in forest habitat (PLF) is also reported. The proportion of locations in field habitat is the inverse of PLF and is not given.

Weather. Maximum and minimum temperatures and precipitation are recorded daily shortly after sunrise at a weather station near the Cades Cove Ranger Station. Barometric pressure data were obtained from the National Climatic Data Center for the nearest location (Knoxville, TN, approximately 50 miles NW of Cades Cove).

Movements. Movements were calculated when three or more consecutive locations, each less than 2 hrs. after the previous, were available for an individual. Since fixes were not obtained on a systematic time schedule, distance moved was divided by time between first and last fix to obtain speed (m/min).

Table 2-2a. Plant species typical of forest habitat in Cades Cove (Whittaker, 1956; Radford et al., 1968; Wofford, 1989).

Scientific Name	Common Name
Trees	
<i>Tsuga canadensis</i>	Eastern hemlock
<i>Tilia heterophylla</i>	Basswood
<i>Acer saccharum</i>	Sugar maple
<i>Aesculus octandra</i>	Yellow buckeye
<i>Betula allegheniensis</i>	Silver birch
<i>Liriodendrom tulipifera</i>	Tulip poplar
<i>Fagus grandifolia</i>	American Beech
Shrubs	
<i>Euonymus americanus</i>	Strawberry bush
<i>Lindera benzoin</i>	Common spicebush
<i>Hydrangea arborescens</i>	Wild hydrangea
<i>Rhododendron maximum</i>	Rosebay rhododendron
<i>Leucothoe editorum</i>	Dog hobble
Herbs	
<i>Eupatorium rugosum</i>	White snakeroot
<i>Cimicifuga racemosa</i>	Black cohosh
<i>Impatiens pallida</i>	Pale touch-me-not
<i>Laportea canadensis</i>	Wood nettle
<i>Trillium erectum</i>	Red trillium
<i>Aster divaricatus</i>	Heart leaved aster
<i>Dryopteris carthusiana</i>	Spinulose wood-fern
<i>Deparia acrostichoides</i>	Silvery glade fern
<i>Viola spp.</i>	Violets
<i>Stellaria pubera</i>	Giant chickweed
<i>Tiarella cordifolia</i>	Foamflower
<i>Galium triflorum</i>	Bedstraw
<i>Euonymus obovatus</i>	Running euonymus

Table 2-2b. Genera likely to be found in field habitat in Cades Cove (DeSelm et al., 1994). Only genera that include three or more species found in Cades Cove are listed here.

Genus Name

Agrostis
Andropogon
Aristida
Bromus
Calamagrostis
Chasmanthium
Danthonia
Elymus
Eragrostis
Glyceria
Muhlenbergia
Panicum
Paspalum
Poa
Sphenopholis

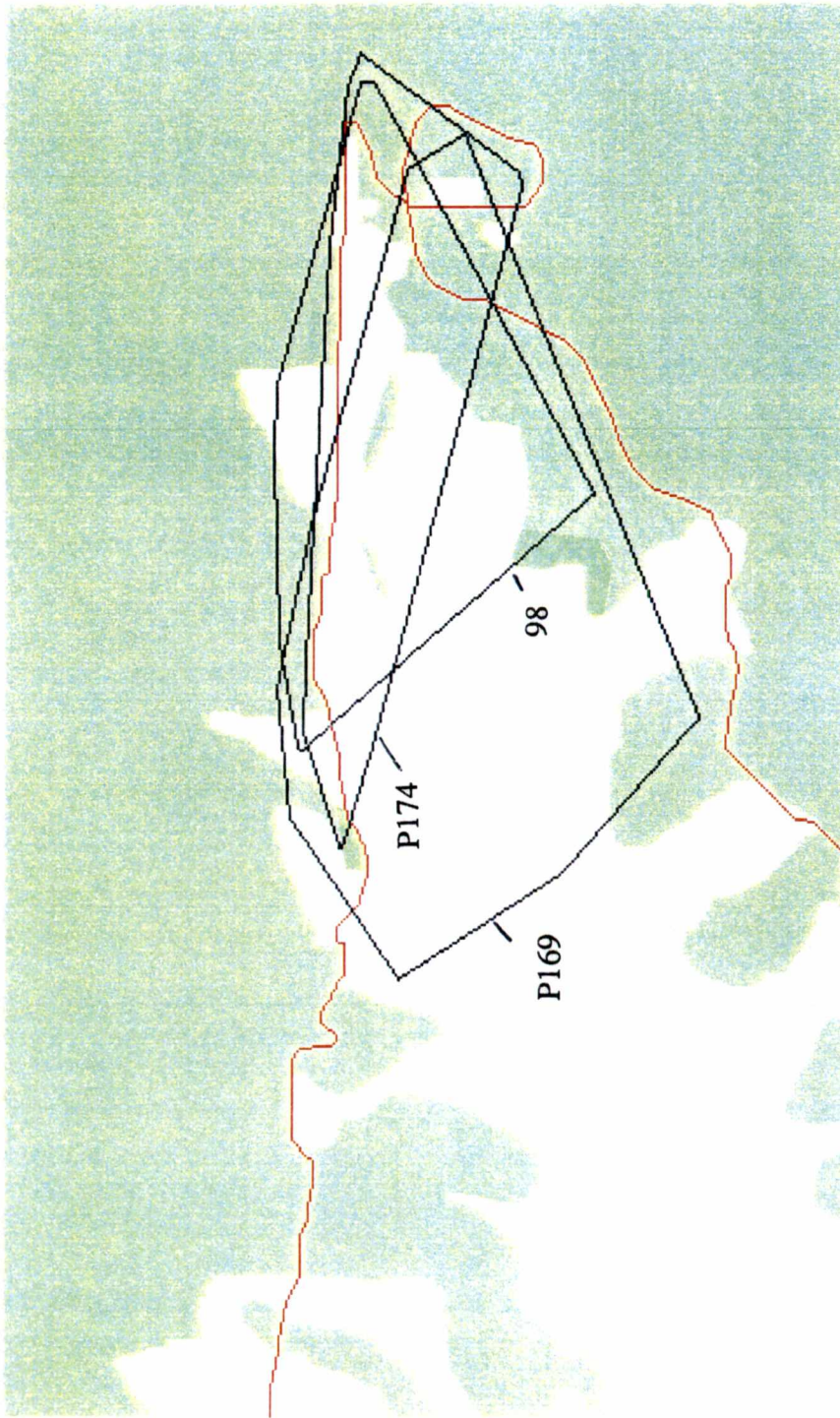


Figure 2-2. The 15 striped skunk home ranges on a habitat map of Cades Cove. Forest habitat is represented by green and field habitat by white. Home ranges are outlined in black. The paved Cades Cove Loop Road is shown in red along with the outline of the campground area (to the right of the page. North is toward the binding. a) This map shows the home ranges of three skunks that were first trapped in 1993: male P169 and females P174 and 98.

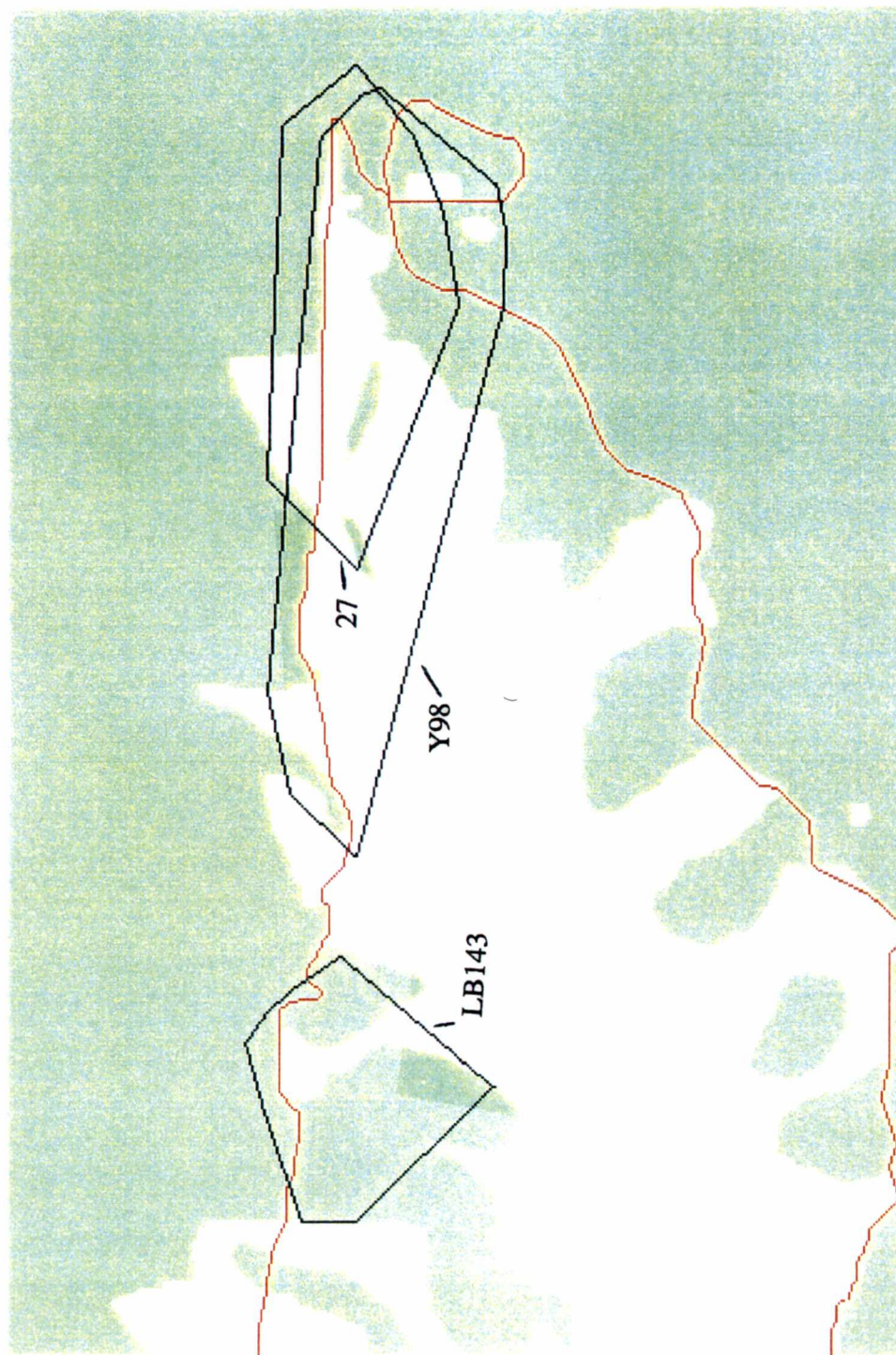


Figure 2-2 (continued). b) This map shows the ranges of three females, 27, LB143 and Y98.

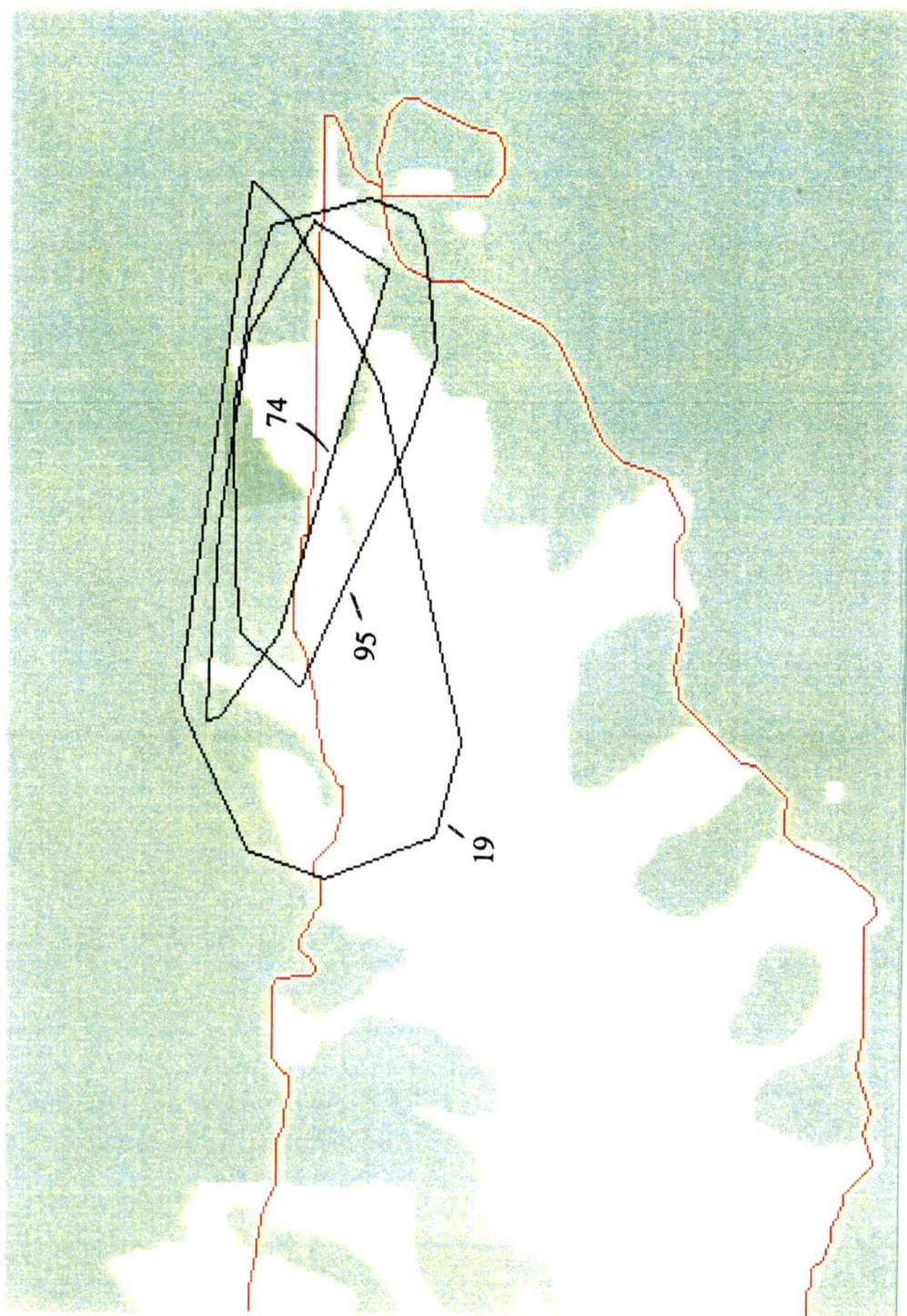


Figure 2-2 (continued). c) This map shows the ranges of three males, 19, 74 and 95.

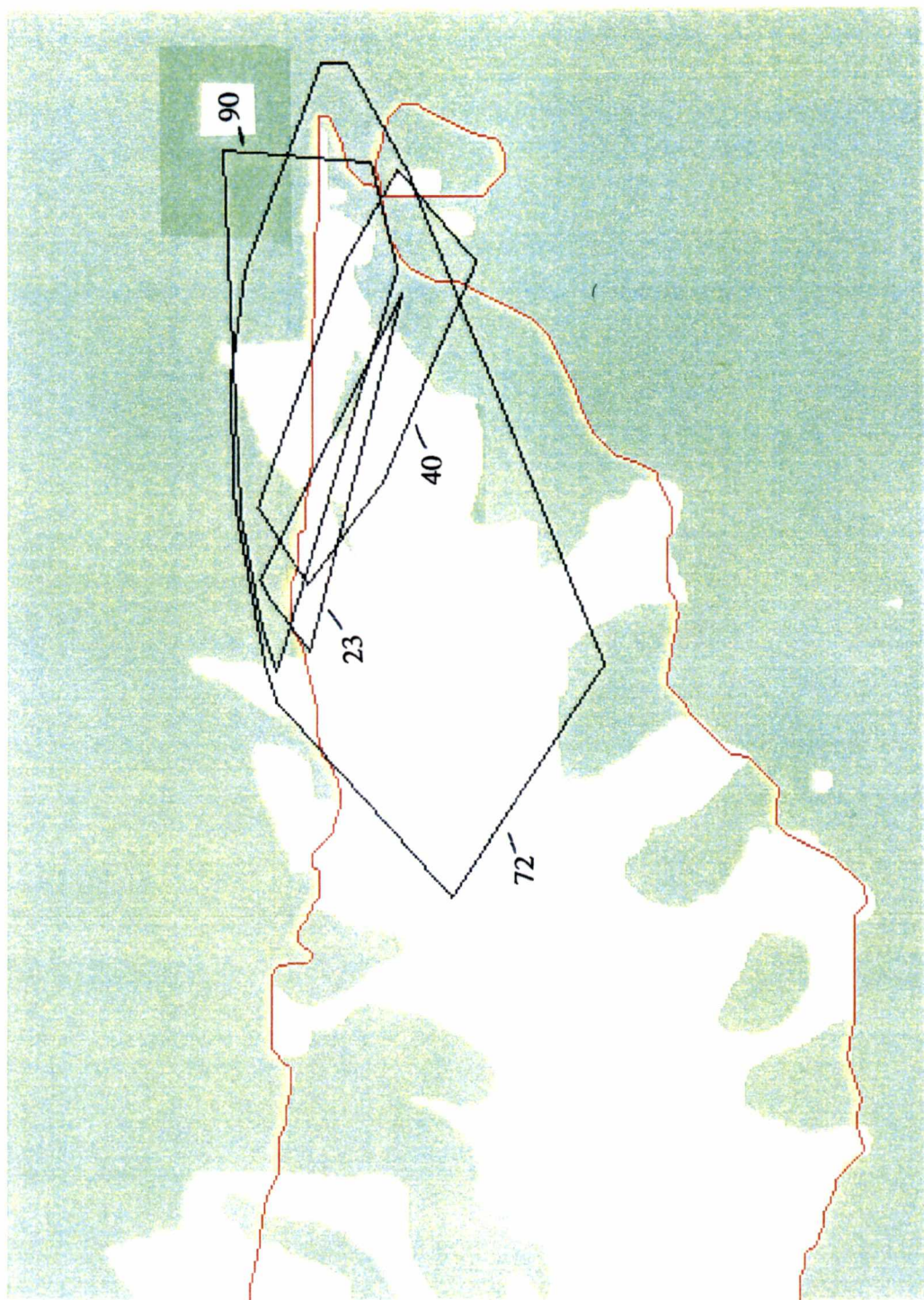


Figure 2-2 (continued). d) This map shows the ranges of four males, 23, 40, 72 and 90.

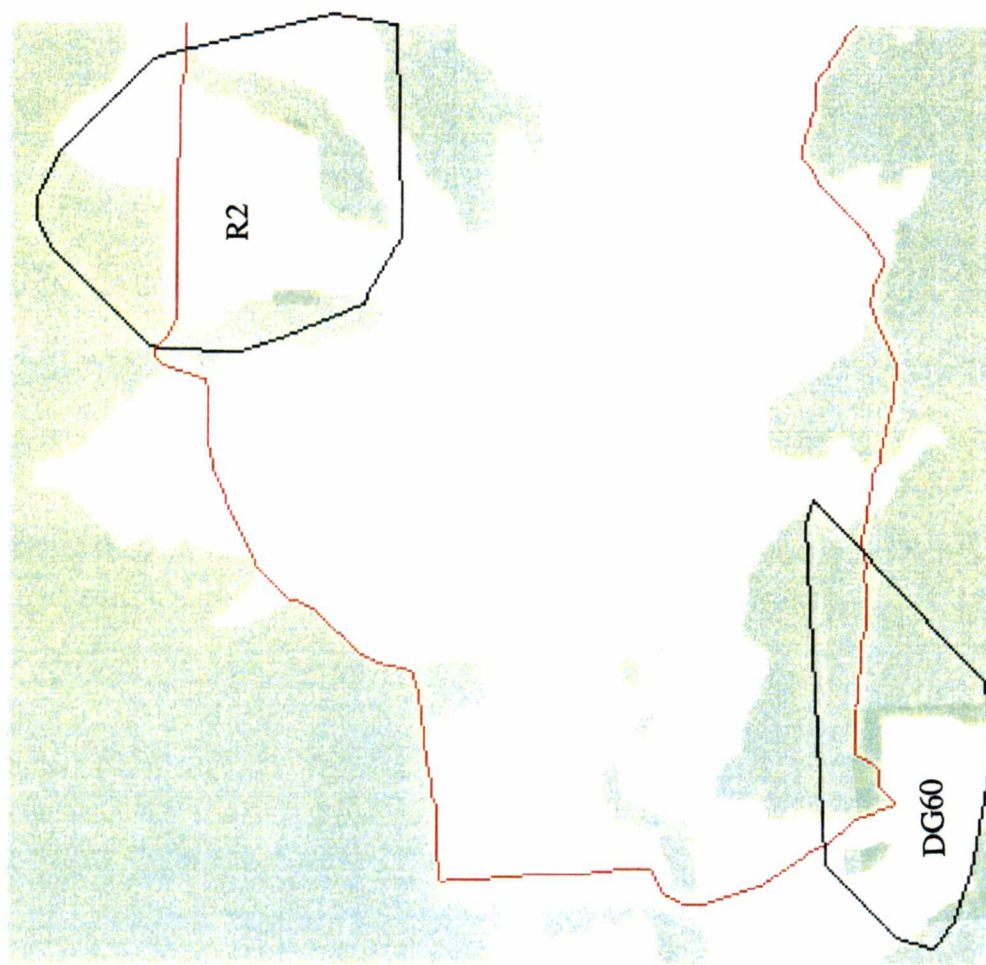


Figure 2-2 (continued). e) This map shows the range of male R2 and female DG60. The right edge of this map overlaps the left edge of the maps shown in Figure 2-2 a-d.

Overlaps. Percent overlaps of pairs of home ranges were calculated using Wildtrak II Home Range Analysis for the Macintosh. The methods of Madison (1980) were used to determine whether the observed patterns of home range overlap differed from random. To do this, the following procedure was used for each pair of overlapping home ranges: One range was held constant while the other was rotated a random number of degrees around its center of activity. This was repeated 1000 times. The overlap was measured each time to give an expected distribution of overlaps, and the observed overlap was compared to the simulated distribution.

RESULTS

Trap success (the number of skunks caught divided by the number of trapnights) varied by year. Forty-three skunks were trapped in 1993 (3.24% trap success) and 13 in 1994 (1.14% success) but none were trapped in 1995 or 1996 (see Figure 2-3). The number of captures of non-target species also dropped over the course of the study: in 1993 I caught 31 raccoons (*Procyon lotor*) and three opossums; in 1994, eight raccoons and one opossum; in 1995, 10 raccoons and zero opossums; in 1996, eight raccoons and one opossum. Trap success also varied by month. In 1993 and 1994, 43% of the captures were made in February (see Figure 2-4). Notably, 84% of the skunks captured in February were male.

There was a significant correlation between trap success and temperature (see Figure 2-5a-b; maximum temperature: $r^2=0.084$, $N=206$, $P<0.0001$; minimum temperature: $r^2=0.086$, $N=206$, $P<0.0001$; when the 0% trap success values are removed, the r^2 increases (see Figure 2-5c-d): maximum temperature: $r^2=0.247$, $N=33$, $P=0.0028$; minimum temperature: $r^2=0.226$, $N=33$, $P=0.0044$). There was no relationship between precipitation and trap success (Figure 2-5e-f; $r^2=0.003$, $N=206$, $P=0.8207$; without 0% values, $r^2=0.008$, $N=33$, $P=0.6174$). Trap success was positively correlated with

Table 2-3. Habitat preferences of 15 radio-collared striped skunks. For each individual, its sex and home range size (HR) are given, along with the absolute amount of forest habitat within its home range (AAFor, in pixels), the absolute amount of field habitat within its home range (AAFie, in pixels), the proportion of forested area to total area available within its home range (PFA) and the proportion of times that each skunk was located in forest habitat (PLF).

SKUNK	SEX	HR	AAFor	AAFie	PFA	PLF
19	m	1.693	4466	18517	0.194	0.529
23	m	0.190	443	2162	0.170	0.643
27	f	0.747	6504	3429	0.655	0.579
40	m	0.833	6579	4356	0.602	0.818
72	m	2.668	15921	20555	0.436	0.688
74	m	0.580	2844	4970	0.364	0.774
90	m	0.602	5167	3263	0.613	0.833
95	m	0.925	5204	7265	0.417	0.750
98	f	1.355	8175	10207	0.445	0.545
DG60	f	0.537	4442	3102	0.589	0.198
LB143	f	0.295	3028	854	0.780	0.920
P169	m	2.407	11709	21528	0.352	0.640
P174	f	1.049	6489	7719	0.457	0.713
R2	m	0.896	4056	8108	0.333	0.175
Y98	f	1.267	8217	8691	0.486	0.849

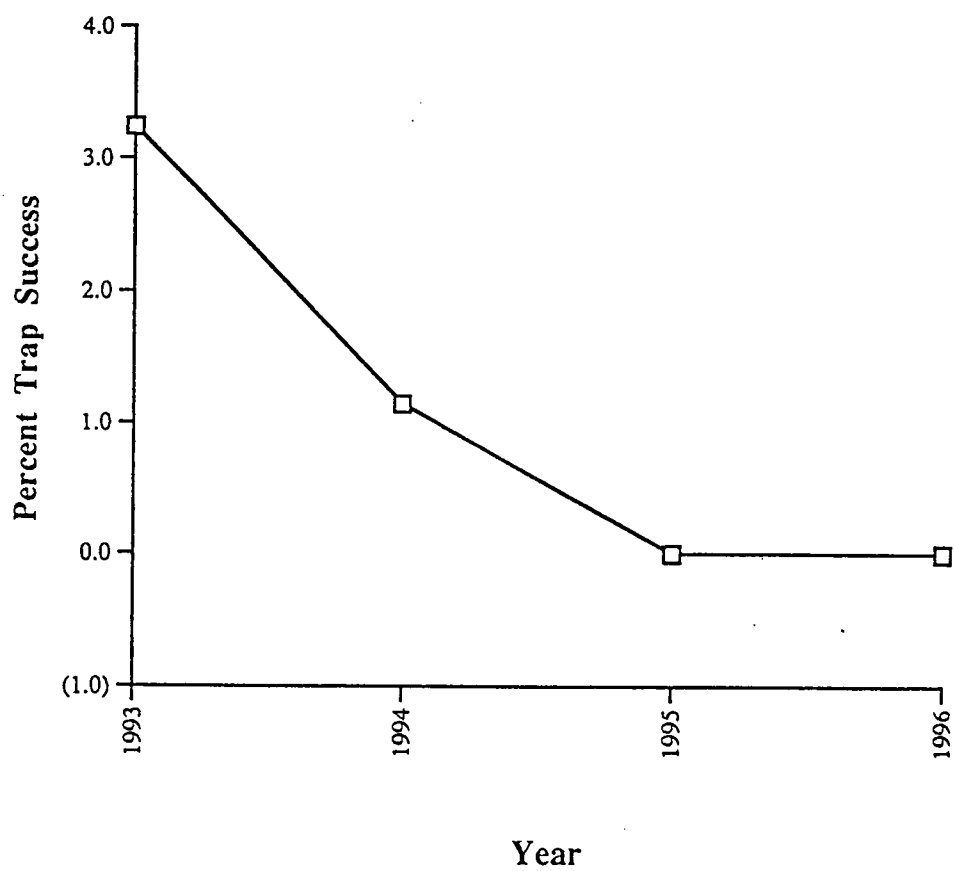


Figure 2-3. Annual trap success, calculated as the number of skunks trapped divided by the number of trapnights, for 1993-1996.

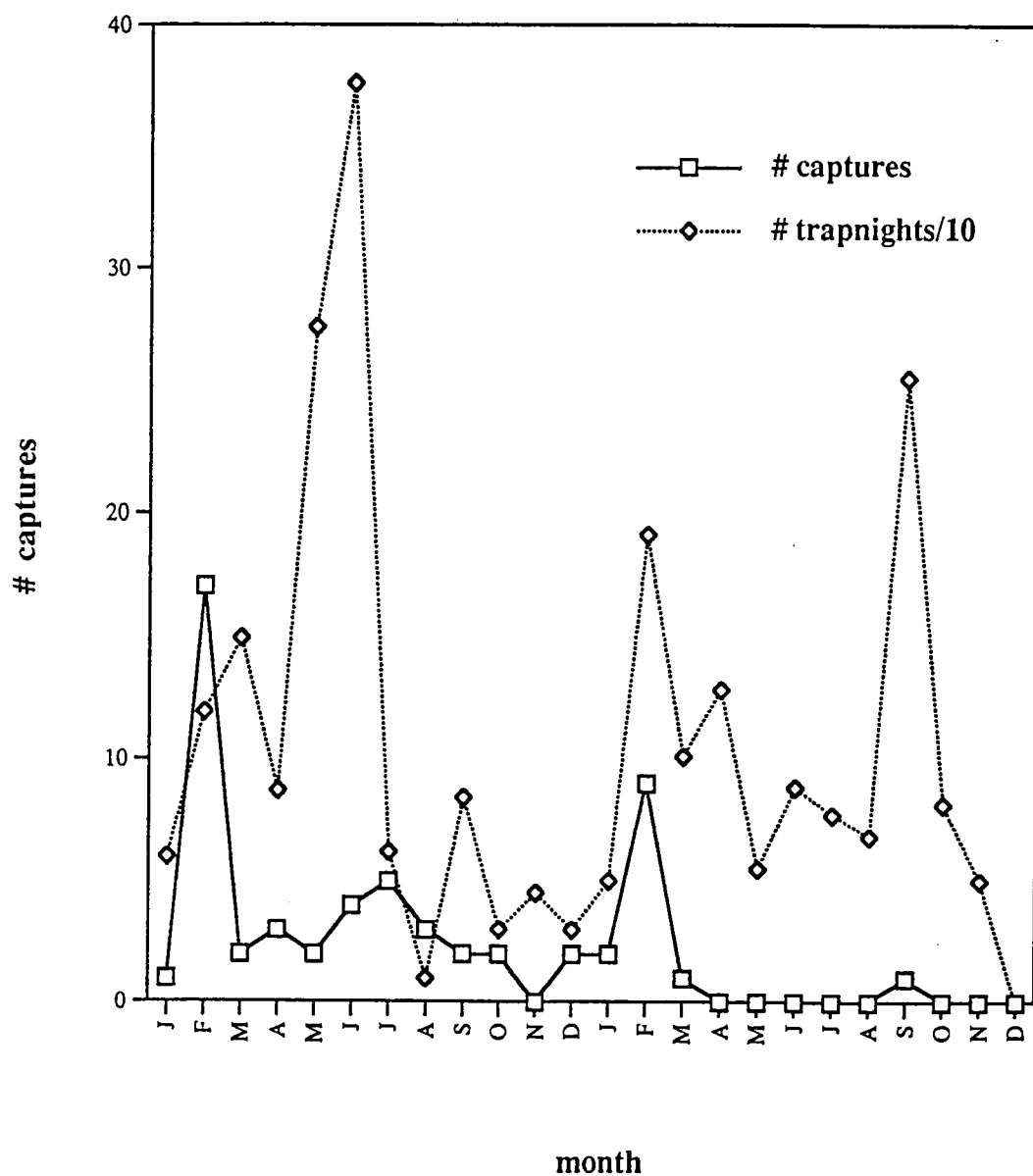


Figure 2-4. Number of trapnights (divided by 10 for ease of graphing) and number of skunk captures each month of 1993 and 1994. Forty-three percent of the 58 skunks trapped were trapped in February.

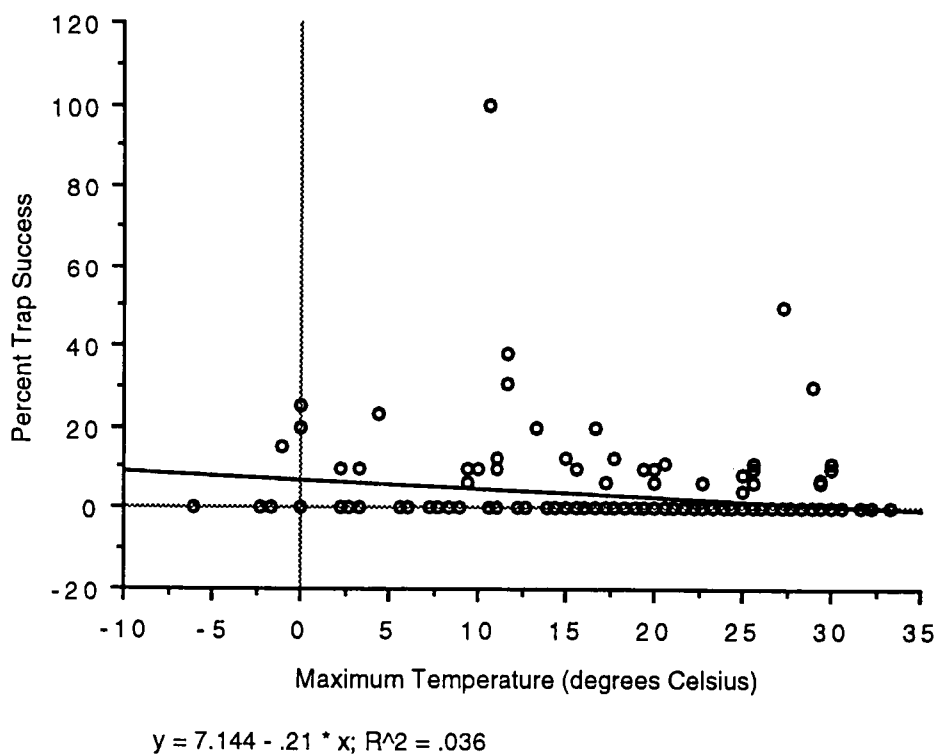


Figure 2-5. Skunk trap success regressed against various climatic variables. a) Trap success vs. maximum temperature.

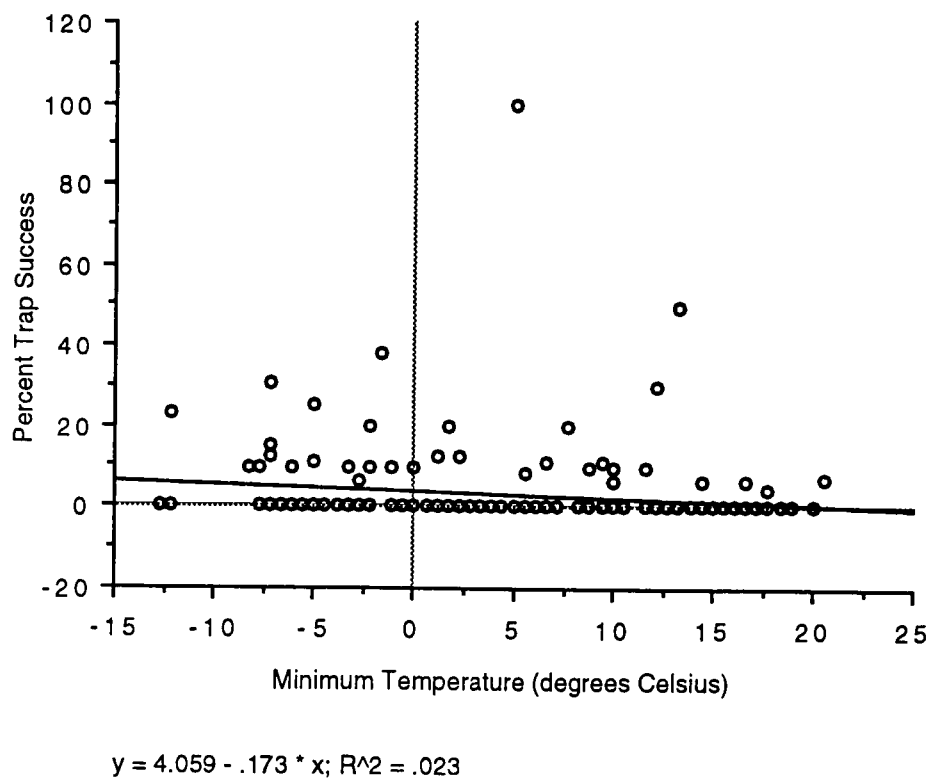
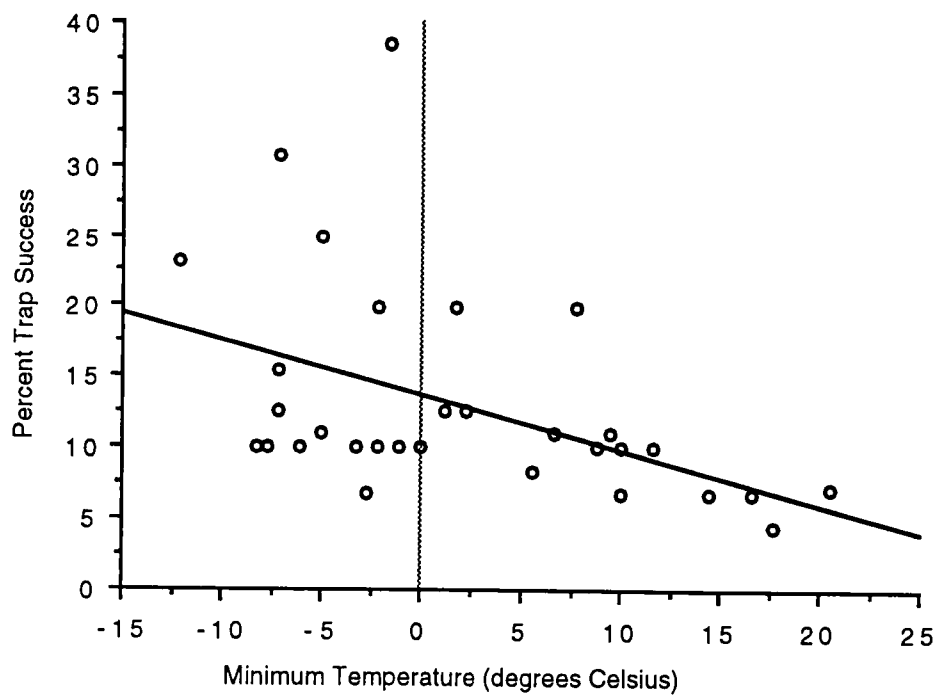


Figure 2-5 (continued). b) Trap success vs. minimum temperature.



$$y = 13.685 - .386 * x; R^2 = .194$$

Figure 2-5 (continued). c) Trap success vs. maximum temperature, not including 0% values.

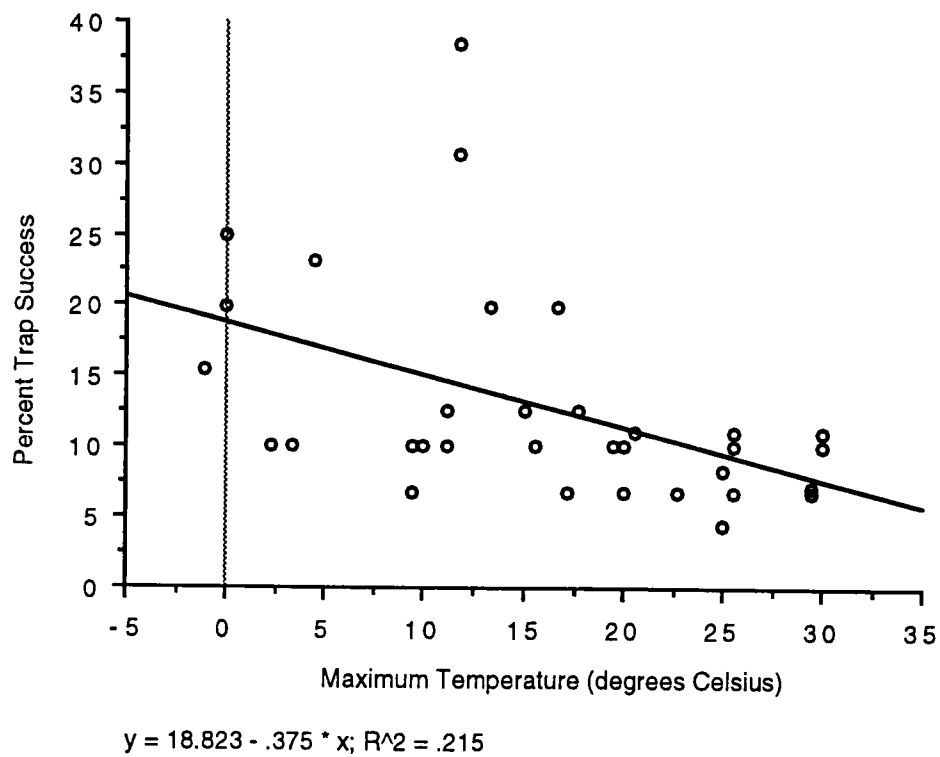


Figure 2-5 (continued). d) Trap success vs. minimum temperature, not including 0% values.

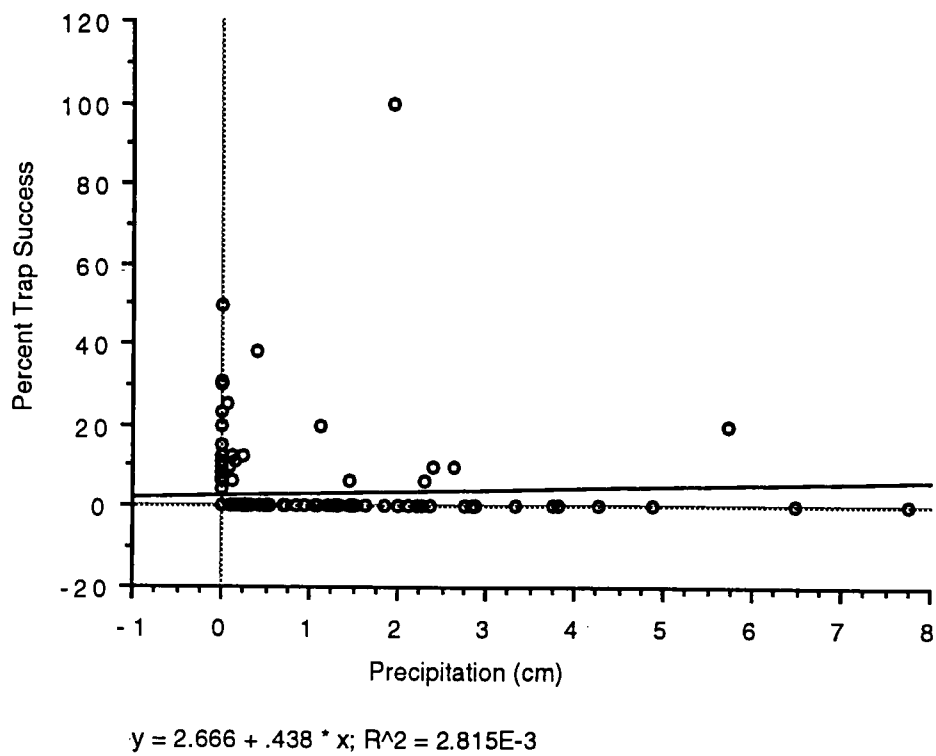


Figure 2-5 (continued). e) Trap success vs. precipitation.

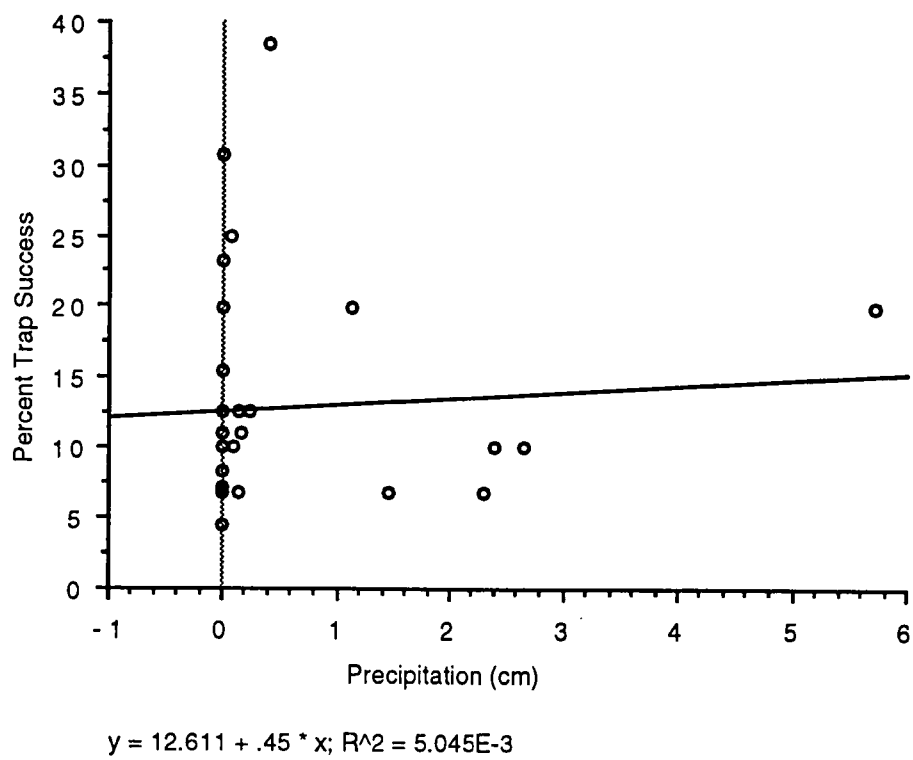


Figure 2-5 (continued). f) Trap success vs. precipitation, not including 0% values.

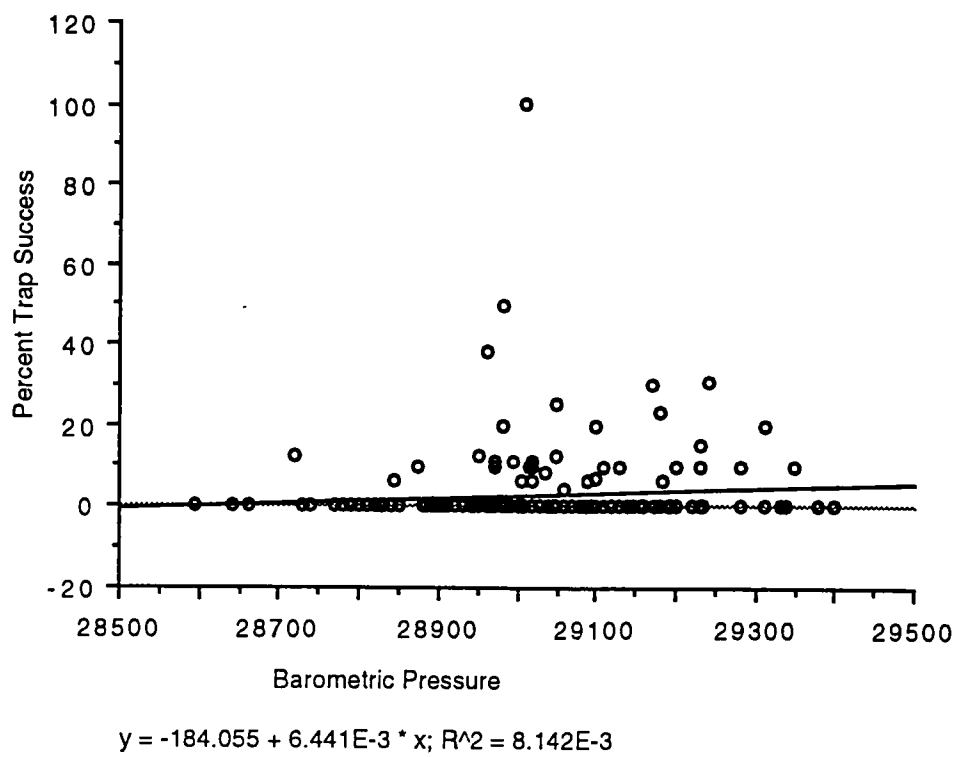


Figure 2-5 (continued). g) Trap success vs. actual barometric pressure.

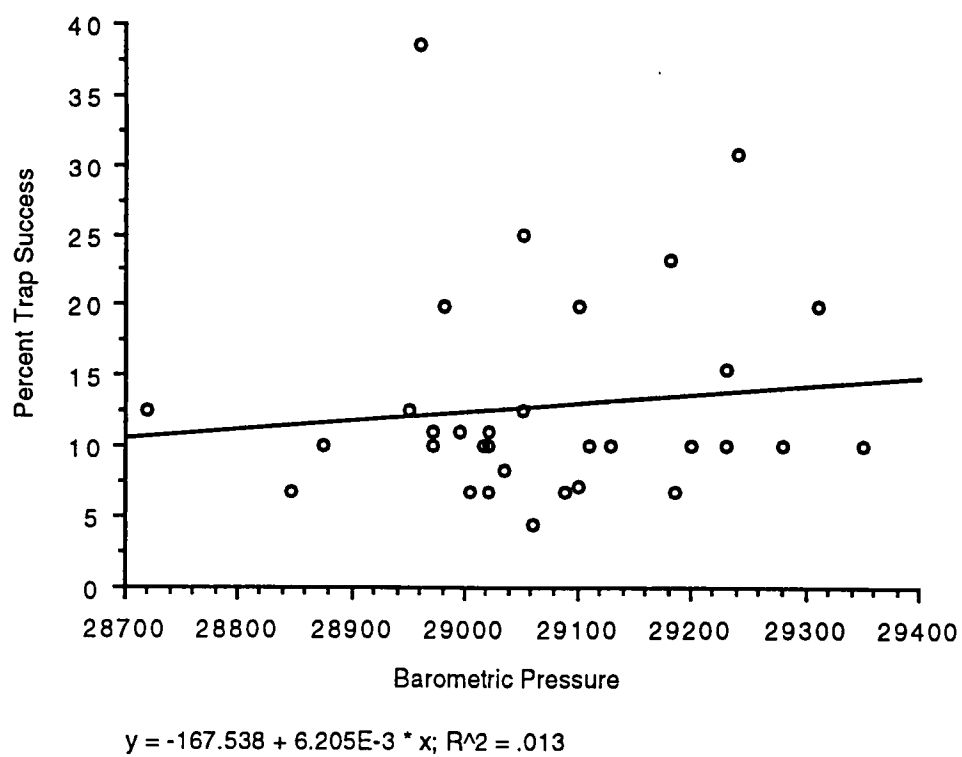


Figure 2-5 (continued). h) Trap success vs. actual barometric pressure, not including 0% values.

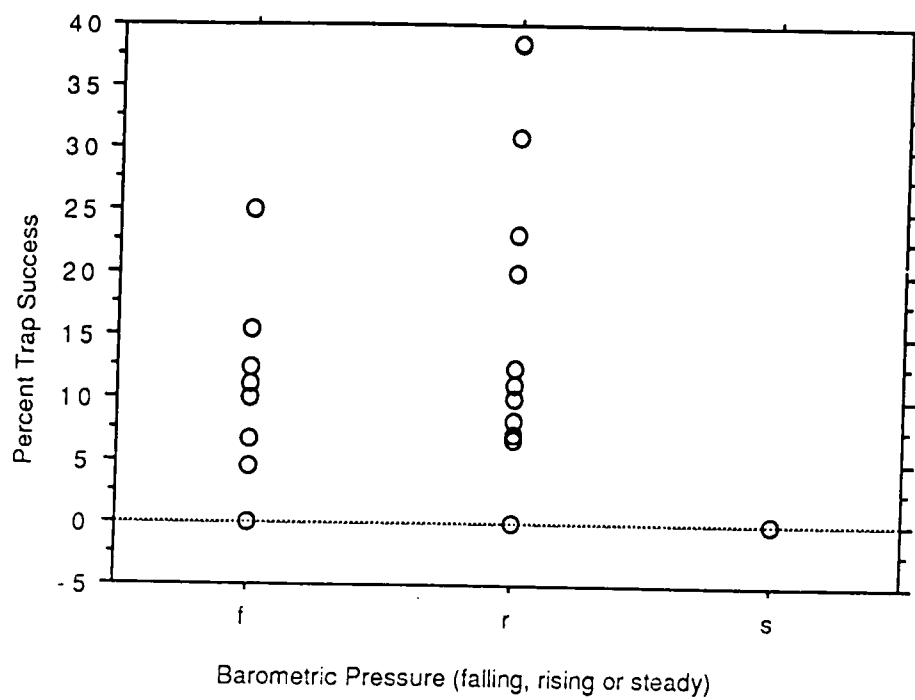


Figure 2-5 (continued). i) Trap success vs. a categorical representation of barometric pressure.

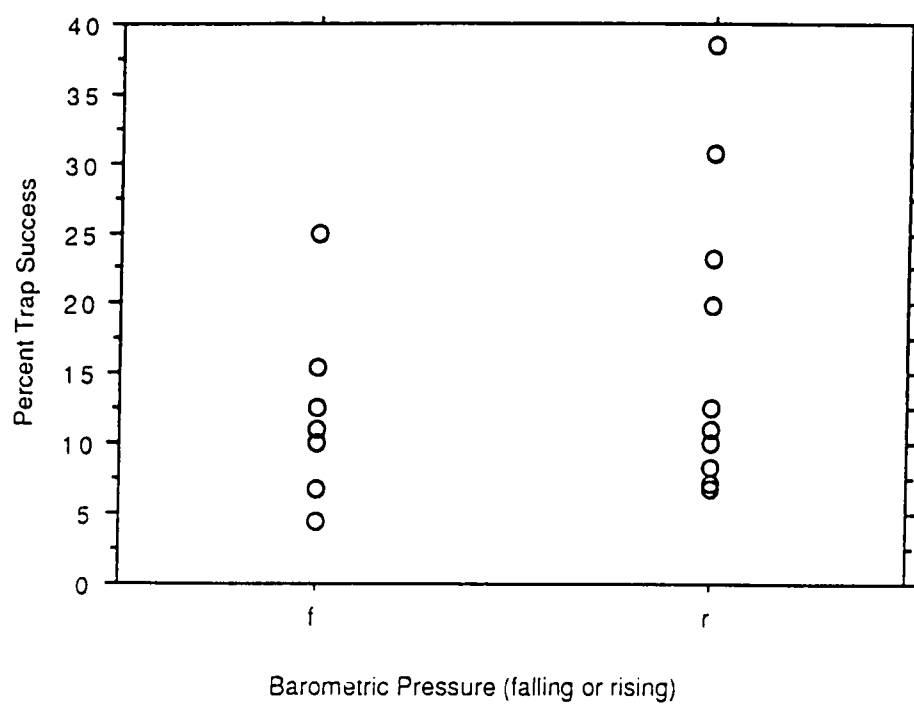


Figure 2-5 (continued). j) Trap success vs. a categorical representation of barometric pressure, not including 0% values.

barometric pressure recorded the day the trap was set, but only when 0% values were included (see Figure 2-5g-h; $r^2=0.023$, $N=206$, $P=0.0301$; without 0% values, $r^2=0.010$, $N=33$, $P=0.5795$). Trap success was positively related to rising barometric pressure (see Figure 2-5i-j; $F=3.173$, $d.f.=2$, $P=0.0439$, but not when 0% values are removed: $F=0.720$, $d.f.=1$, $P=0.4026$).

HOME RANGE SIZE. Home ranges calculated for 15 striped skunks averaged 1.08 km^2 (range: 0.190-2.668). Table 2-1 lists the home range size of each skunk along with variables relevant to this study. Figure 2-2 presents all 15 home ranges in relation to each other and Cades Cove.

Latitude. There is insufficient variation in latitude within this study to examine its effects on home range size. Therefore comparisons are made to other studies. Figure 2-6 shows the relationship between latitude and average home range size for four studies, including this one, that used telemetry (Storm, 1972; Rosatte and Gunson, 1984; Greenwood et al., 1985). There is a trend for home ranges to be larger at higher latitudes but it is not significant ($r^2=0.116$, $N=8$, $P=0.4097$).

Habitat. All home ranges contained both forest and field habitat (Table 2-3, Figure 2-2). Home range size was significantly positively correlated with the absolute amount of forest (AAFor; $r^2=0.789$, $N=15$, $P<0.0001$) and the absolute amount of field (AAFie; $r^2=0.930$, $N=15$, $P<0.0001$) habitat. The proportion of forest available in each home range (PFA) ranged from 0.17 to 0.78 (mean=0.46). The proportion of locations of each skunk in forest habitat (PLF) varied from 0.18-0.92 (mean=0.64). There was no correlation between PLF and home range size across individuals ($r^2=0.088$, $N=15$, $P=0.2821$). Females alone showed a negative relationship between home range size and PFA, but this

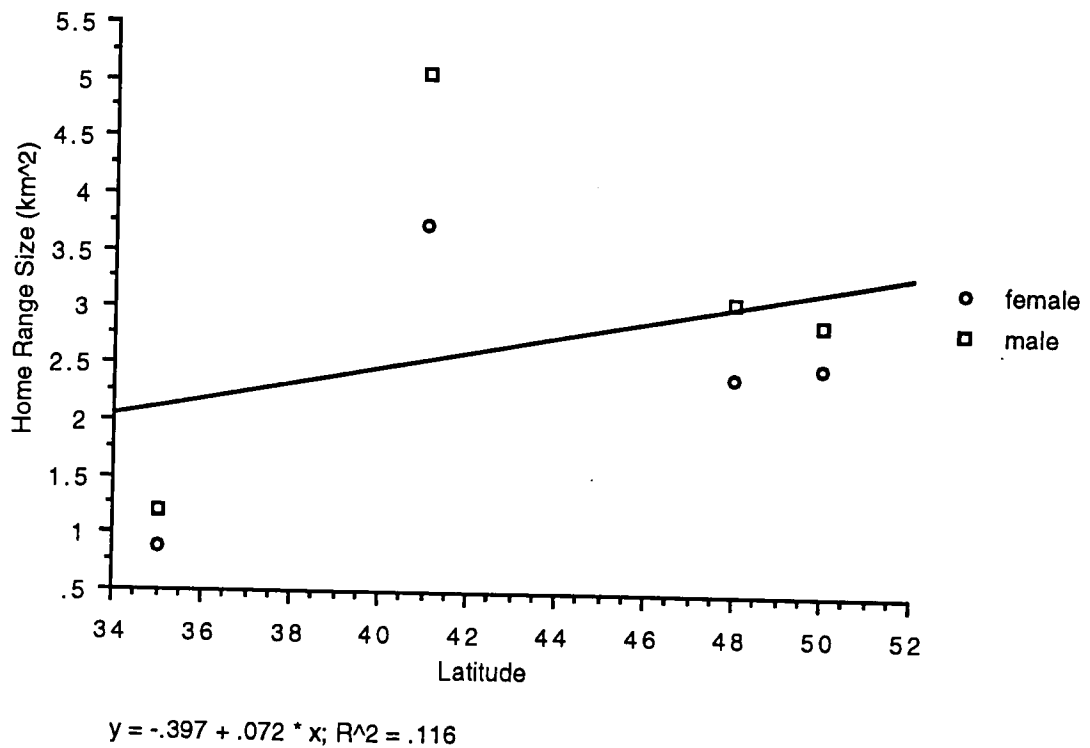


Figure 2-6. Skunk home range size and latitude reported from four studies that used telemetry. The studies are, from lower to higher latitudes: southeastern TN (this study), northwestern IL (Storm, 1972), ND (Greenwood et al., 1985) and southern Alberta, Canada (Rosatte and Gunson, 1984).

was due to one female, LB143 (all females: $r^2=0.825$, $N=6$, $P=0.00123$; without LB143: $r^2=0.683$, $N=5$, $P=0.0846$). PLF was not significantly related to home range size ($r^2=0.001$, $N=15$, $P=0.8998$).

Seasonality. Home ranges were first compared among seasons (spring, summer, fall, winter) by pooling all individuals and years. Table 2-4a lists average home range sizes for each season. An ANOVA indicated no significant differences among seasons ($F=1.987$, $d.f.=3$, $P=0.1351$). However, t-tests for each pair of seasons indicated that spring ranges were significantly larger than winter ranges (see Table 2-4b; $t=2.304$, $d.f.=19$, $P=0.0327$). For males alone, this relationship was nearly significant but for females alone it was not ($t=2.069$, $d.f.=12$, $P=0.0608$; $t=1.100$, $d.f.=5$, $P=0.3214$, respectively).

Few (from two to six) skunks were tracked for two or more consecutive seasons. Home ranges of these individuals were analyzed in a paired t-test, and yielded the same results as the unpaired t-tests. Skunks used larger home ranges in spring 1994 than in winter 1993-94 ($t=-2.696$, $d.f.=13$, $P=0.0430$).

Sex and Body Size. For all skunks trapped, males were significantly larger than females for three measures (see Table 2-5): weight ($t=2.370$, $d.f.=38$, $P=0.0230$), head-body length ($t=3.585$, $d.f.=39$, $P=0.0009$) and canine length ($t=3.329$, $d.f.=31$, $P=0.0023$). Females had significantly longer tails than males ($t=3.534$, $d.f.=39$, $P=0.0011$). For those 15 skunks that were radio collared, there were significant differences in only two measures: males were longer in head-body length ($t=2.195$, $d.f.=13$, $P=0.469$) and females had longer tails ($t=3.116$, $d.f.=13$, $P=0.0082$); there were no significant differences in weight ($t=1.09$, $d.f.=13$, $P=0.3633$) or canine length ($t=1.709$, $d.f.=13$, $P=0.1182$).

Table 2-4a. Average home range sizes of skunks in spring (March-May), summer (June-August), fall (September-November) and winter (December-February). Only spring and winter were significantly different (unpaired t-test, ignoring year: $t=2.304$, $p=0.03$).

Season	HR (km ²)	N
Spring	0.613	11
Summer	0.621	10
Fall	0.328	6
Winter	0.255	10

Table 2-4b. Average home range sizes of skunks in spring, summer, fall and winter (defined as above). Consecutive seasons in which fewer than two animals were radiotracked were not included in the analysis. Using a paired t-test comparing seasons within years, the only significant pair was spring-winter ($t=-2.696$, $P=0.0430$).

Skunk	Spr93	Sum93	Fall93	Win93	Spr94	Sum94
<u>Males</u>						
19				0.5681	1.5810	
40				0.1898	0.7384	
72					0.9194	2.0152
74				0.2700	0.4110	0.0008
95				0.1644	0.7857	0.6990
R2	0.3634	0.6047	0.3848	0.0554		
<u>Females</u>						
98			0.1176	0.2408	0.9074	1.1208
DG60		0.1789	0.3595			
LB143	0.1250	0.4460				
P174		0.2456	0.7414	0.0321		
Y98		0.6182	0.2556	0.2543	0.0678	0.2832

Table 2-5. Average measurements of male and female skunks with range in parentheses. CL=length of canine in mm (many were chipped or broken, and those are not included here), Wt=weight in kg, HBL=length from tip of nose to base of tail in cm, TL=length from base of tail to end of last caudal vertebra in cm.

Measurement	avg.	Male range	N	avg.	Female range	N	P
CL	6.8	5.0-8.5	23	5.3	3.5-8.0	10	0.0023
Wt	2.1	1.25-2.95	29	1.7	1.0-2.65	11	0.0230
HBL	41.8	35-47	30	38.2	34-42	11	0.0009
TL	20.7	18-26	30	23.9	17.5-28	11	0.0011

There were no sex differences in home range size ($t=1.09$, d.f.=13, $P=0.30$) or correlations between home range size and weight ($r^2=-0.0047$, $N=15$, $P=0.8075$; see Figure 2-7a) across all individuals. However, for females alone, there was a significant positive relationship between home range size and body weight (see Figure 2-7b; $r^2=0.71$, $N=6$, $P=0.0351$). For males, the relationship was the opposite: there was a trend for smaller males to have larger home ranges (see Figure 2-7c; $r^2=0.415$, $N=9$, $P=0.0612$). There were no significant relationships between home range size and other measures of size (head-body length: $r^2=0.010$, $N=15$, $P=0.7394$; tail length: $r^2=0.040$, $N=15$, $P=0.4954$; canine length: $r^2=0.045$, $N=15$, $P=0.5323$).

Number of radio fixes. Skunks were located between 14 and 230 times each. This variability was due to how many times I was able to locate an individual after it was fitted with a collar; seven skunks were killed during the course of the study, two by antifreeze poisoning (confirmed by necropsy at the University of Tennessee School of Veterinary Medicine) and the others presumably by predation (in four cases, the collar and fur or bones were found and in one case the collar was found with deep gashes thought to be those of raptor talons). Additionally, three collars were found without remains. Four skunks disappeared with no trace and one collar was located to the same den for several weeks before it ceased transmitting. These figures are not surprising given the short life expectancy of skunks in the wild (see Part 1). There was no correlation between the number of times an individual skunk was located and its calculated home range size ($r^2=-0.10$, $N=15$, $P=0.72$). To insure that repeated locations of females near their presumed dens were not obscuring this correlation, repeated fixes in the same location were deleted from all data sets. There was still no relationship between the number of fixes and home range size ($r^2=0.0002$, $N=15$, $P=0.9632$).

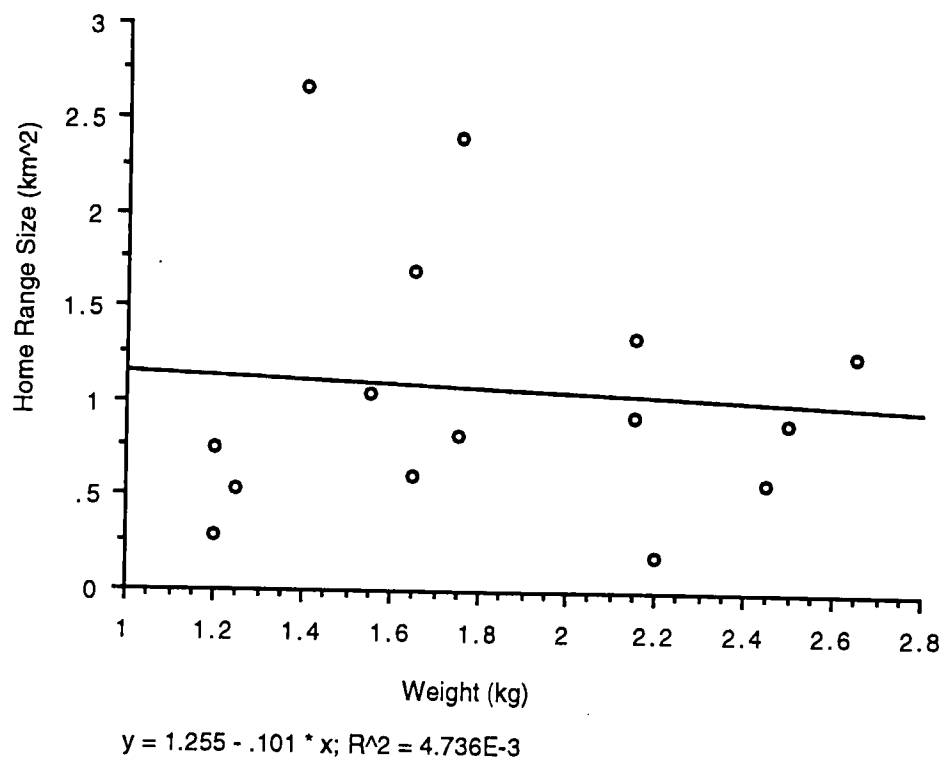
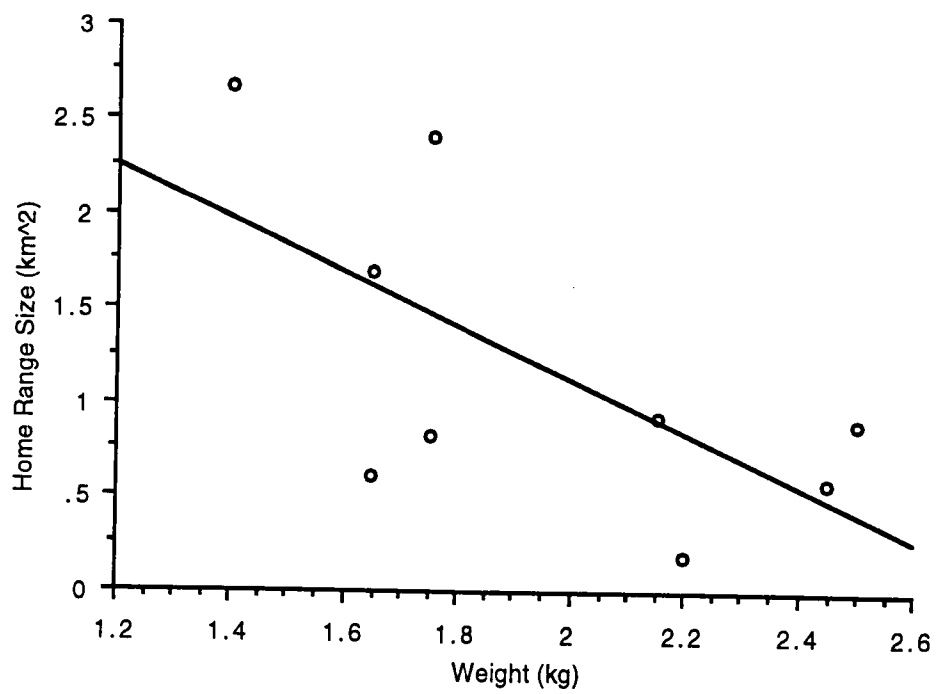


Figure 2-7. Home range size regressed against weight. a) all skunks.



$y = 3.961 - 1.42 * x; R^2 = .415$

Figure 2-7 (continued). b) males only.

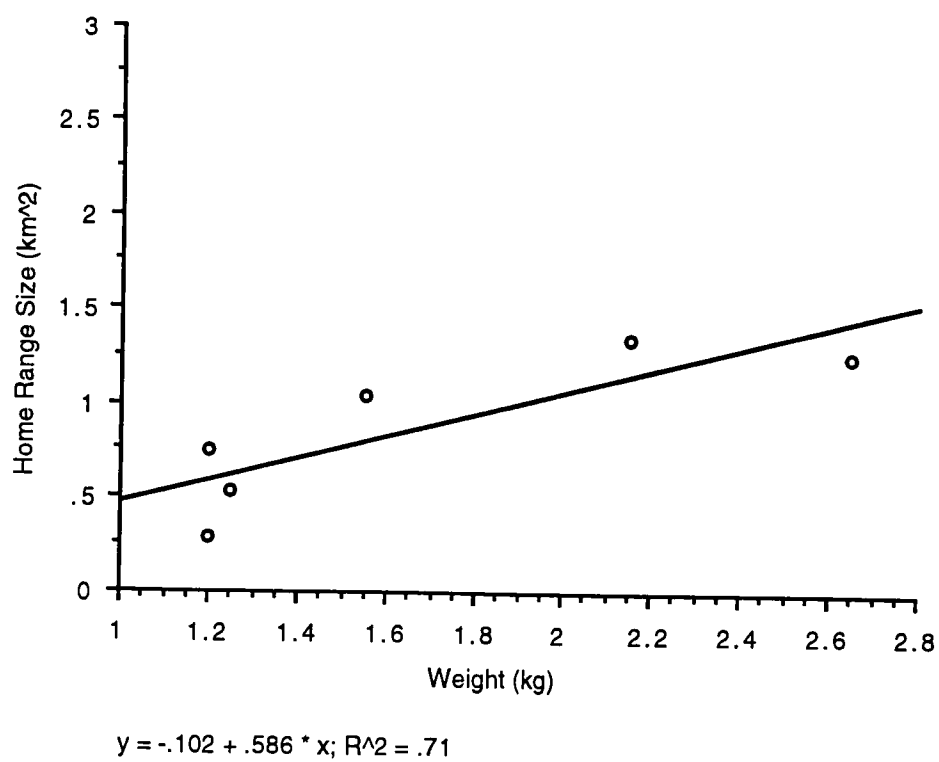


Figure 2-7 (continued). c) females only.

MOVEMENTS. There were 27 instances of movements by 12 skunks over periods of 15-325 min. Speed ranged from 0.8-44.6 m/min. Movements were categorized by individual, sex, season, habitat and time of day, but there were too many missing cells for a multivariate analysis. When each variable was analyzed separately, the following were significant: individual ($F=15.209$, $d.f.=11$, $P<0.0001$), sex (males moved faster, $F=6.467$, $d.f.=1$, $P<0.0176$) and season (skunks moved faster in spring and winter than in summer or fall, $F=12.741$, $d.f.=3$, $P=0.0001$). However, the significance of the variable sex was due to one male, P169, with two movements of 23.8 and 44.6 m/min (without P169, $F=2.901$, $d.f.=1$, $P=0.1020$). Removal of P169 did not affect the significance of other variables. There was a negative correlation between weight and movement speed for males but no relationship between these variables for females (Figure 2-8; males: $r^2=0.576$, $N=8$, $P=0.0290$; females: $r^2=0.017$, $N=19$, $P=0.5920$). The correlation for males became nonsignificant with the removal of either of two males, P169 or 72. The only weather variable which affected movement speed was minimum temperature: skunks moved faster when it was colder (Figure 2-9; $r^2=0.452$, $N=27$, $P=0.0179$; maximum temperature: $r^2=0.265$, $N=27$, $P=0.1813$; precipitation: $r^2=0.115$, $N=27$, $P=0.5689$; barometric pressure: $F=0.282$, $d.f.=1$, $P=0.6018$). To prevent pseudoreplication, I reanalyzed the patterns found to be significant using average values for each skunk. This caused one change in the results: no longer was there a significant correlation between weight and movement speed for males ($r^2=0.551$, $N=6$, $P=0.0911$; weight vs. speed for females: $r^2=0.113$, $N=6$, $P=0.5140$; minimum temperature vs. speed: $r^2=0.526$, $N=12$, $P=0.0076$).

OVERLAP. Twelve home ranges all overlapped each other by 1.4 to 100% (Figure 2-2). Three other home ranges were spatially separated from these 12 and each other. Overlaps were significantly greater (randomization test, $P\leq 0.05$) than would be expected by chance for seven pairs (three male-male and four male-female pairs). No home range overlap was

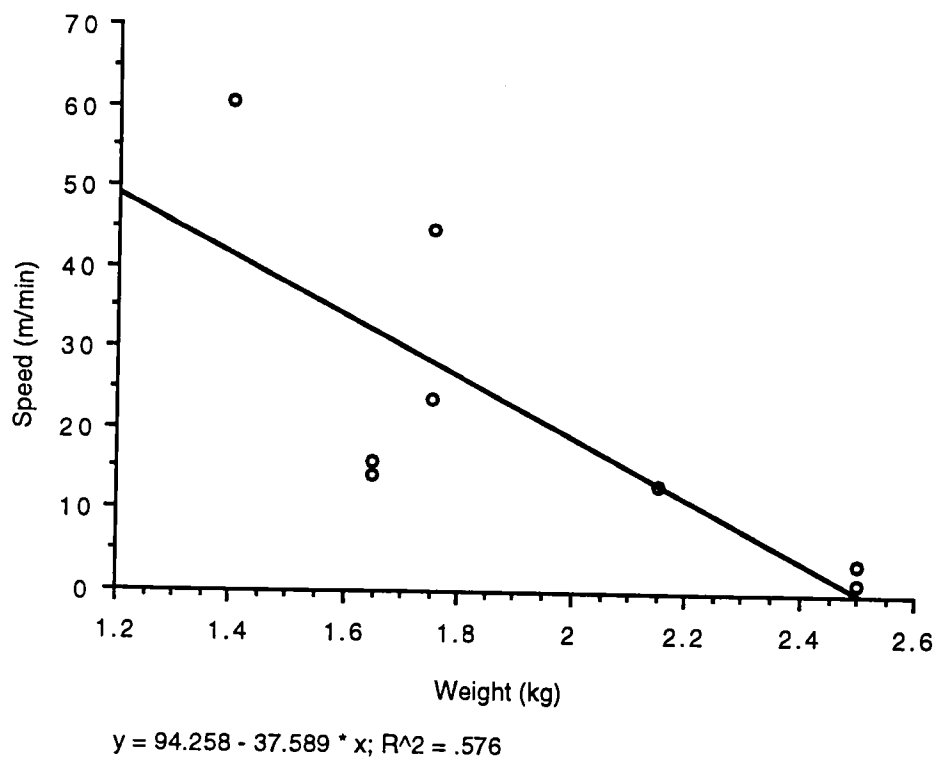


Figure 2-8. Skunk movement speed regressed against weight. a) males.

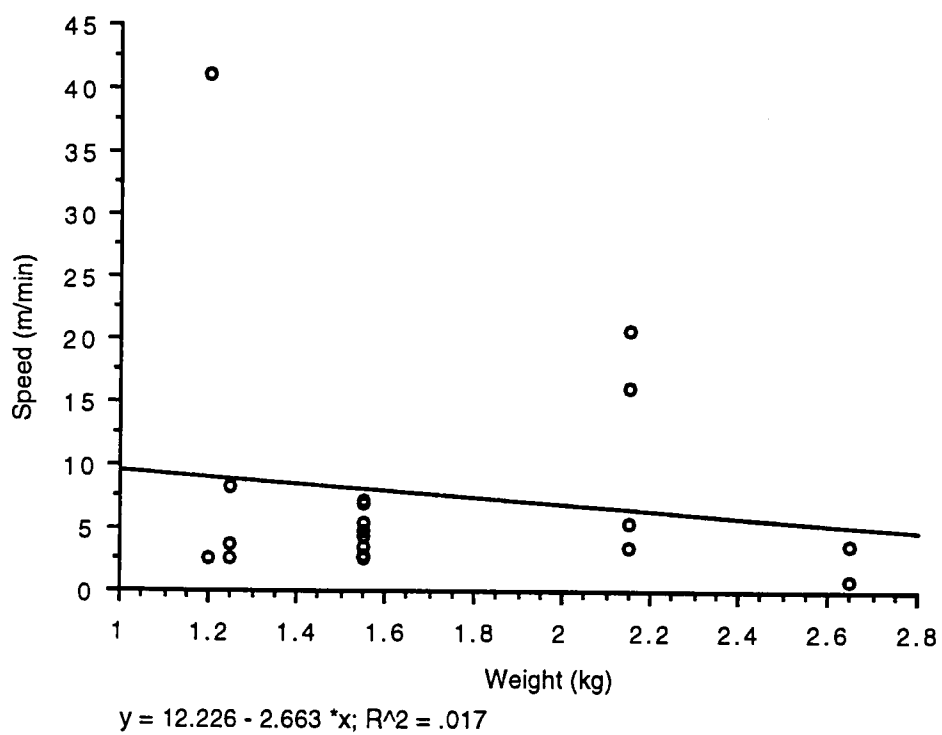


Figure 2-8 (continued). b) females.

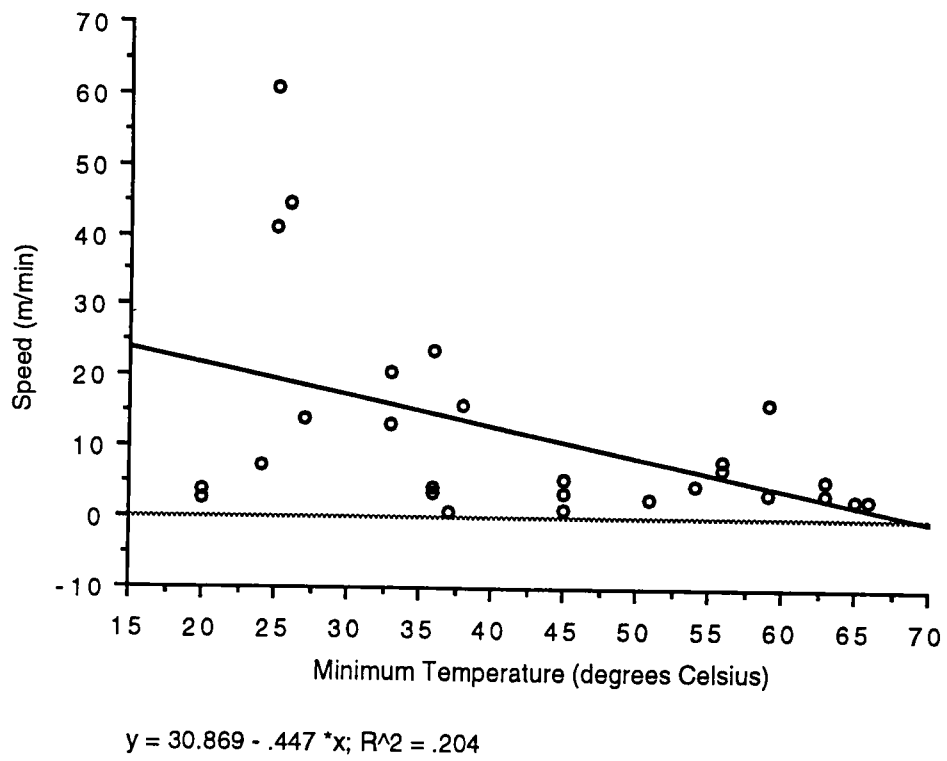


Figure 2-9. Skunk movement speed regressed against minimum temperature.

significantly smaller than expected by chance. Percent overlaps (arcsin transformed) were compared by sex for each individual; none was significantly different (for 12 t-tests, $0.054 < t < 2.149$, d.f.=10, $0.9583 < P < 0.0601$). There was a nonsignificant trend for larger skunks to have greater overlaps ($r^2=0.278$, $N=12$, $P=0.0784$). For females, this relationship was not significant ($r^2=0.051$, $N=4$, $P=0.7749$) but for males it was ($r^2=0.624$, $N=8$, $P=0.0197$).

DISCUSSION

Home range size is significantly related to season (ranges are larger in spring than in winter) and weight (larger females have larger home ranges). The other variables examined, latitude, sex, habitat and number of fixes, were not significantly associated with home range size. Movement speed was significantly related to season (skunks moved faster in winter and spring than summer and fall) and temperature (skunks moved faster when it was colder). However, movement speed was not significantly related to sex, habitat or time of day. Home ranges overlapped extensively, with no apparent inter- or intrasexual differences.

Trap success dropped markedly over the four years of the study. This did not appear to be due to increasing trap shyness of skunks, since in addition to the 56 captures, there were 43 recaptures. Also, recaptures of skunks increased from 17 in 1993 to 25 in 1994; one skunk was recaptured in early 1995. There was no evidence of disease in the population. The apparent population crash was probably due to weather conditions: a blizzard in March 1993 and a flood in March 1994. Two such events, occurring during consecutive breeding seasons of a species with a life expectancy of only about two years could decimate a population.

HOME RANGE SIZE

Table 2-6 summarizes the results of seven studies including this one which examined home range size in striped skunks. Variables examined in this study are included in the Table; notably absent is weight, which was reported in only one of the other six studies and then as monthly averages not divided by sex (Goldsmith, 1981). Studies of home range size that used mark-recapture, or used telemetry only for locating dens, indicate much smaller home ranges. Mark-recapture usually yields fewer locations from which to compute home ranges and home range size is consequently smaller. Using locations of dens alone excludes data on actively moving skunks, thereby also reducing home range size. The home ranges reported in this study are the smallest of the telemetry studies; this is also the only study in partially forested habitat and is at the lowest latitude. The largest reported home ranges are from Illinois (Storm, 1972), which is also the only study besides this one to radio track skunks in the spring; this may be important since I found larger home ranges in the spring and summer than in the fall and winter. It is obvious from the summary Table that more data are needed on skunk home ranges in the south and west, and from more diverse habitats.

The only variable analyzed in this study that seems to affect home range size is season, with significantly larger home ranges in the spring than winter. When data are analyzed for each sex alone, only males reveal a nearly significant trend for larger home ranges in spring than winter. This is probably due to the fact that skunks den for long periods of time in the winter, but in the spring males begin actively searching for mates and both sexes for food (Storm, 1972; Gunson and Bjorge, 1979). Skunks may also have more difficulty moving around during the winter when there is snow on the ground (Sunquist, 1974), as do other mammals (Cederlund and Okarma, 1988). Despite their presumed greater energy expenditure searching for mates, in this study, males that were

Table 2-6. Home range sizes of striped skunks (*Mephitis mephitis*) observed in this study and reported in the literature. Most studies did not give values for juveniles. Technique: MR=mark-recapture, O=observation, T=telemetry, with the number of fixes per animal as reported in the paper or estimated from the description of methods, DT=location of dens only (not moving animals) by telemetry; Season: S=spring (March, April, May) U=summer (June, July, August), F=fall (September, October, November), W=winter (December, January, February). Most studies considered skunks to be juveniles only in the fall and winter of their first year.

Reference	Locality & Latitude	Habitat	Technique	Season	Home Range Size in km ² (sample size)			
					Adult Males	Adult Females	Juvenile Males	Juvenile Females
Shirer & Fitch 1970	NE KS 39°N	prairie	DT	SUFW	0.117 (1)	0.272 (2)		
Bailey 1971	NW OH 41°N	marsh	MR	SU	0.308 (3)		0.292 (2)	
Storm 1972	IL 40°N	farmland	T (1-428)	SUFW	5.06 (2)	3.74 (5)	2.80 (6)	2.32 (13)
Goldsmith 1981	SE TN 35°N	wooded campgrnd	MR, O	UFW	0.156 (5)	0.243 (9)	0.275 (1)	0.100 (2)
Rosatte & Gunson 1984	S Alberta 50°N	prairie	T (40-60)	UFW	2.9 (14)	2.5 (14)		
Greenwood et al. 1985	ND 48°N	farmland	T (22-35)	U	3.08 (15)	2.42 (24)		
This study	SE TN 35°N	forest, field	T (14-230)	SUFW	1.199 (9)	0.875 (6)		

trapped during the spring weighed more than males trapped in the winter (see Table 2-7, $t=2.115$, $d.f.=25$, $P=0.0445$).

The relationship between weight and home range size differed for the sexes: larger females showed significantly larger home ranges, as would be expected due to the increased energetic needs of a larger animal. However, in males, the correlation was negative. It is possible that since these 15 skunks were not sexually dimorphic in weight, the relationship between weight and home range size is obscured. An additional factor compromising this analysis is that most skunks were only trapped once, and the weight obtained at that time was the only one available. However, skunks may vary significantly in weight from one season to another (see Table 2-7; Fuller et al., 1985; Schowalter and Gunson, 1982) and home range could vary accordingly. Analyzing home range size in relation to other measures of size (canine length, tail length and head-body length) eliminates this problem, but still yields no significant pattern.

Striped skunk home range size did not correspond with latitude. There was little difference between home range size in this study at the southernmost latitude, and in southern Alberta at the northernmost latitude (Rosatte and Gunson, 1984). This could be due to the fact that the latitudes were not sufficiently separated. The latitudinal range summarized in this study was approximately 15° , while the latitudinal range in Gompper and Gittleman (1991), who found a significant relationship in three other carnivore species, was 33° . Work currently being carried out in Texas (L. Baker, pers. comm.) should provide much-needed low latitude data.

An additional factor that was predicted to reflect larger home ranges in the north is habitat type: study sites used by Storm (1972), Rosatte and Gunson (1984) and Greenwood et al. (1985) were primarily agricultural. The mixed forest-field habitat of Cades Cove was hypothesized to provide greater resources (see below), and thus allow smaller home range sizes than the mostly cultivated lands at the other study sites. Other

Table 2-7. Weights (kg) of skunks during different seasons with sample sizes in parentheses. Spring=March, April, May, Summer=June, July, August, Fall=September, October, November, Winter=December, January, February. t- and P-values are given for male-female comparisons within seasons; the only significant difference between seasons within a sex was between spring and winter for males; males that were trapped in the spring weighed significantly more than males trapped in the winter ($t=2.115$, $d.f.=25$, $P=0.0445$).

Sex	Spring	Summer	Fall	Winter
Male	2.22 (17)	--	1.88 (2)	1.83 (10)
Female	1.54 (4)	1.82 (3)	2.15 (1)	1.47 (3)
t	-2.412	--	--	-1.493
P	0.0261			0.1635

studies of skunks in non-agricultural habitat cannot be compared to this one because they did not use telemetry, and home range sizes reported from mark-recapture are much smaller (Bailey, 1971; Goldsmith, 1981).

In general, there is a wide range of individual differences in the amounts of different habitats within home ranges. The absolute amounts of forest and field habitat (AAFor and AAFie) correlate with home range size in part because of geometry (if the home range size increases, so must the amount of one or both habitats within it). However, it also suggests that skunks are not choosing one habitat over the other. The fact that the proportion of forest habitat did not correlate with home range size was surprising. Home ranges in areas of greater resource abundance would be expected to be smaller, since an animal's energetic needs are more easily met. However, Cades Cove may be relatively uniform in resources, preventing any noticeable correlation between these variables. Additionally, it seems possible from trapping data (Stout and Sonenshine, 1974) and den preferences (Part 3, this study), that the most important habitat for a skunk is forest-field edges. Therefore, their home range size and location may maximize not forests or fields but the edge between the two. If a skunk expands its home range to include ecotones (edges), there would be no relationship between home range size and the proportion of a single habitat type in the home range. Questions relating to habitat are explored more fully in Part 3.

Perhaps the most surprising finding in this part is that home range size did not correlate with the number of fixes used to calculate home ranges, a finding common to most studies (see Bekoff and Mech, 1984 for review, but see Gese et al., 1988; Buskirk and McDonald, 1989). My results could be due to what is shown in Figure 2-10. For this female, had I stopped locating her after 50 fixes I would have obtained the same home range size had I stopped tracking her after 160 fixes. Many of the skunks I tracked showed similar stepwise patterns of home range increase with increasing number of fixes; a

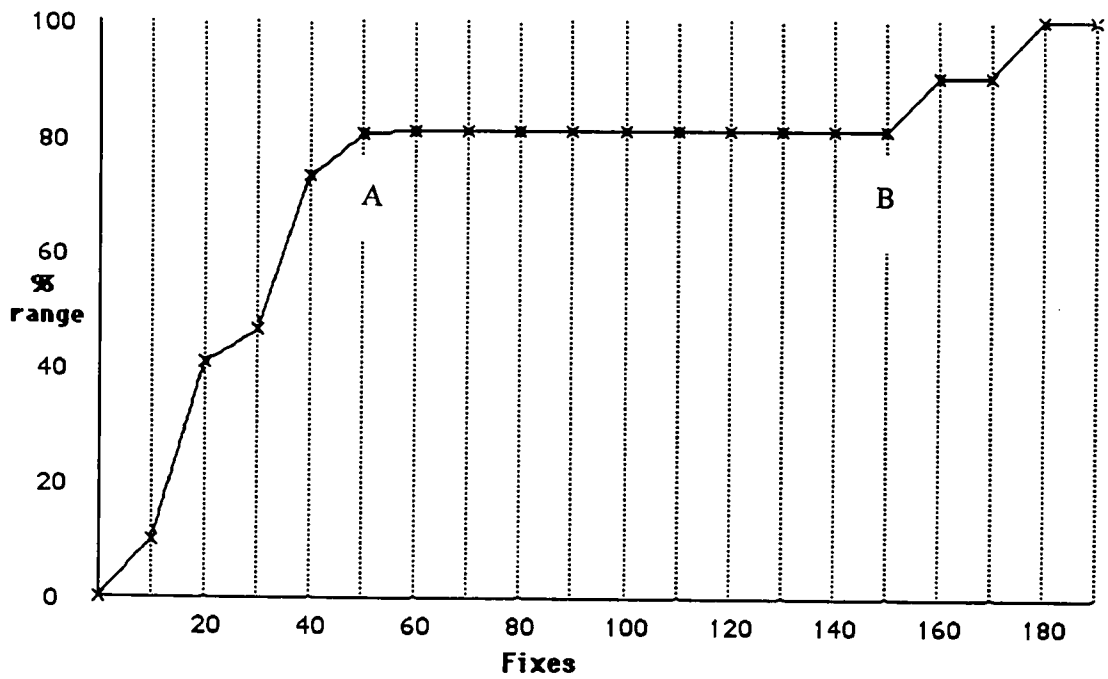


Figure 2-10. Graph of % total home range size against cumulative number of fixes for one skunk. Note that if radiotracking had ceased at point A or point B, the home range estimate would have been the same despite a threefold difference in the number of fixes.

cessation of tracking at different stages in the stepwise pattern for different animals could lead to a lack of relationship between the number of fixes and home range size. Another possible explanation for this lack of relationship is that there is not enough variability in these small home ranges to discover such a correlation, especially with such a small sample size.

MOVEMENTS

It is difficult to compare movements reported here with those from other studies. Other authors reported distances traveled without consideration of time spent moving. In order to analyze movements by sex, season, habitat, weight and weather, I standardized them as distance traveled over time. The only reported value for skunk movement speeds is from MacLulich (1936), who estimated speeds of two skunks from his car speedometer as he followed them down the road! The speeds he gives range from 161.7-241.7 m/min. These are much higher than those calculated in this study, which ranged from 0.8-44.6 m/min.

Movement speeds were greater in spring and summer than fall and winter. This is consistent with other data from this study indicating that males are actively searching for mates in spring: 1) Trap success was highest in February and most skunks caught then were males. 2) Five males trapped in spring 1993 and one trapped in spring 1994 had recent puncture wounds, one of which was a pair of holes consistent with a skunk's canines in diameter, depth and distance apart; this suggests males were fighting for mates. 3) Home range size was larger in spring than in winter.

Although the significant sex difference in movement speed was due to one male, P169, males moved faster than females on average. Skunks also moved faster when it was colder.

OVERLAPS

Home ranges overlapped extensively between and within sexes. This does not follow the predicted pattern of intrasexual territoriality common in other Mustelidae (Powell, 1979). There are at least two possible explanations. First, there are unusually abundant food resources in Cades Cove, which includes natural forest, mowed fields, barns, and a campground/picnic area. Eleven of the 12 skunks with extensively overlapping home ranges included the campground/picnic area within their home ranges. On at least three occasions, skunks were observed eating food brought into the Park by people. The availability and importance of such foods were not examined, but they must influence the spatial patterns of individual skunks and in turn contribute substantially to the amount of overlap observed in home ranges. Another study of a carnivore (red fox) in a residential area found increased overlap in home ranges and attributed it to availability of food scraps or garbage (Cavallini, 1992).

The lack of sexual dimorphism in weight of the 15 radio-collared skunks could also indicate why there is such extensive overlap in home ranges. Powell suggested that degree of sexual dimorphism and of intrasexual territoriality are related across carnivore species. Since the radio-collared skunks were not dimorphic, they may not have been sexually mature and therefore not yet maintaining intrasexual territories. However, this seems unlikely for several reasons: 1) Skunks mature and can mate during their first spring, at less than one year of age. Based on size, all radio-collared skunks were at least that old. 2) One radio-collared female was trapped with a litter of five and two other females were thought to have litters based on the fact that they spent 2-4 weeks localized in one small area, probably near a natal den, in early summer. The observation that males were moving long distances in February and moving from one den to another (see details in Part 3) indicates that they were also sexually active. 3) Other skunks were trapped or sighted in the

same area as the 12 overlapping home ranges and it is unlikely they were also all immature or had exclusive home ranges.

Powell also noted a correlation between degree of intrasexual territoriality and degree of elongation. It is unclear whether such a correlation would hold within a population, but it is interesting to note that average elongations for 30 male skunks in Cades Cove and the nine radio-collared male skunks were larger than that reported by Powell [3.3 and 3.4 vs. 2.7 (estimated from a figure in Powell, 1979)]. This finding is contrary to Powell's.

Future work with skunks should emphasize non-agricultural habitat, using larger sample sizes and more radio locations per individual. Accurate measures of age and diet would be helpful in analyzing home range size in relation to other variables. Dietary analyses could also address questions related to home range overlap in different habitats.

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PART THREE

USE OF HOME RANGES: HABITATS AND DEN SITES

INTRODUCTION

Members of the Mustelidae are found on every continent except Antarctica and Australia. Reflecting this vast geographic range, mustelids use a diversity of habitats including tundra, savanna, semi-desert, tropical rainforest, rivers and oceans. Individual mustelid species may be limited in their habitat preferences (such as otters to rivers or oceans and martens to forests) or they may be flexible in their preferences, as are skunks. Habitat preferences may be revealed by where animals are active (home ranges) or where they sleep (den sites). Locations and use of den sites may be particularly important for nocturnal species like skunks which must hide during inactive periods of the day and, despite low metabolic rates (Knudsen, 1979), are found in cold climates up to 60°N latitude. In the following sections, I describe variables known to influence habitat preferences in mammals in general and striped skunks (*Mephitis mephitis*) in particular.

HABITAT. Mammals are known to select habitats because of weather and thermal conditions or availability of den sites, food, or cover from predators (see Table 3-1 for a non-exhaustive list of references). Intraspecific differences in habitat preferences may be due to age, season or activity patterns (Table 3-2). Across carnivores, size differences are generally not found among habitat types (Gittleman, 1985). Likewise, differences in habitat selection due to body size are not generally noted within species. However, this variable could correlate with age and/or sex and therefore may be of importance.

There are differences in habitat use of striped skunks between populations (Wade-Smith and Verts, 1982); however, only four studies have analyzed habitat preferences within populations of skunks. These studies examined various habitats using different techniques and their results are sometimes contradictory; however, they indicate a general trend toward a preference for field habitat. For example, Verts (1967, in Illinois) trapped more skunks in areas with fewer woodlots and located radio-collared skunks more often

Table 3-1. Some factors known to affect habitat choice in mammals. Note some species appear in more than one category. Also, in some cases, categories are interrelated; for example, fishers show habitat preferences based on availability of den sites which offer concealment from predators.

Factor	Species	Reference
weather or thermal conditions	moose (<i>Alces alces</i>)	Cederlund and Okarma, 1988
	mountain beavers (<i>Aplodontia rufa</i>)	Beier, 1989
	river otters (<i>Lontra canadensis</i>)	Reid et al., 1994
	American marten (<i>Martes americana</i>)	Buskirk et al., 1989
availability of den sites	Franklin's ground squirrels (<i>Spermophilus franklinii</i>)	Choromanski-Norris et al., 1989
	mountain beavers	Hacker and Coblenz, 1993
	coyotes (<i>Canis latrans</i>)	Andelt and Andelt, 1981
	fishers (<i>Martes pennanti</i>)	Arthur et al., 1989
	desert kit foxes (<i>Vulpes macrotis arsipus</i>)	Zoellick et al., 1989
	black bears (<i>Ursus americanus</i>)	Hellgren et al., 1991
availability of forage or prey	elk (<i>Cervus elaphus</i>)	Edge et al., 1988
	mountain beavers	Hacker and Coblenz, 1993
	river otters	Dubuc et al., 1990
	red foxes (<i>Vulpes vulpes</i>)	Macdonald, 1980
	coyote	Andelt and Andelt, 1981
	fishers	Arthur et al., 1989
	black bears	Unsworth et al., 1989; Hellgren et al., 1991
availability of cover from predators	mountain beavers	Beier, 1989
	mule deer (<i>Odocoileus hemionus</i>)	Griffith and Peek, 1989

Table 3-2. Factors known to cause intraspecific differences in habitat preference in mammals. Studies which have not found these variables to affect habitat choice are listed with the notation "no effect."

Factor	Species	Reference
age	martens (<i>Martes americana</i>)	Buskirk et al., 1989;
	river otters (<i>Lontra canadensis</i>)	Reid et al., 1994
sex	moose (<i>Odocoileus hemionus</i>)	Leptich and Gilbert, 1989
	black bears (<i>Ursus americanus</i>)	Hellgren et al., 1991
(no effect)	polecats (<i>Mustela putorius</i>)	Lode, 1994
season	coyotes (<i>Canis latrans</i>)	Andelt & Andelt, 1981; Person & Hirth, 1991
	black bears	Unsworth et al., 1989
(no effect)	mule deer (<i>Odocoileus hemionus</i>)	Griffith and Peek, 1989
activity patterns	coyotes	Andelt & Andelt, 1981; Person & Hirth, 1991
	black bears	Unsworth et al., 1989

than expected in cornfields. Storm (1972, also in Illinois) located radio-collared skunks more often in hayfields than cornfields. Stout and Sonenshine (1974, in Virginia) found that skunk captures were concentrated in old fields and young second-growth deciduous forest. Rosatte et al. (1992, in metropolitan Toronto) found that capture success decreased across the following habitats: field>industrial>commercial> residential>groomed-grass>forested-park.

DENS. In addition to movement and home range patterns, habitat preferences can also be studied in relation to den sites. Mammals tend to adopt den sites based on availability, accessibility and ease of maintenance, or effectiveness of predator detection or avoidance (Table 3-3). Den sites are probably important to skunks for protection from predators as well as for insulation from extremes of heat and cold (Mutch and Aleksasuk, 1977; Gunson and Bjorge, 1979).

Studies of habitat preferences for den sites vary greatly in methods and results. Skunks have been reported to prefer dens near water (Selko, 1938; Allen and Shapton, 1942; Storm, 1972), in hardwood or mixed growth forest (Dean, 1965), on limestone outcrops (Shirer and Fitch, 1970), or in corn and hay fields (Storm, 1972). It must be noted that different authors may have categorized habitats within their study sites differently. They also used different techniques to quantify habitat preferences. Therefore, the reported results may be less contradictory than they seem at first.

Striped skunks den communally during the winter, at least at higher latitudes; this is thought to be important for thermoregulation (Mutch and Aleksasuk, 1977; Gunson and Bjorge, 1981). However, there is at least one report of communal denning from farther south (Texas). Cuyler (1924) claims to have found a winter den in which, "I could see at least twelve pairs of eyes" (p 182). Skunks also den for extended periods of time (up to 150 days in Alberta, Gunson and Bjorge, 1981). Reports from lower latitudes are difficult

Table 3-3. Factors known to influence choice of den sites in mammals.

Factor	Species	Reference
availability	Franklin's ground squirrels (<i>Spermophilus franklinii</i>)	Choromanski-Norris et al., 1989
	river otters (<i>Lontra canadensis</i>)	Dubuc et al., 1990
	black bears (<i>Ursus americanus</i>)	Hellgren et al., 1991
accessibility and ease of maintenance	mountain beavers (<i>Aplodontia rufa</i>)	Hacker and Coblenz, 1993
ease of predator detection and avoidance	coyotes	Andelt and Andelt, 1981
	fishers	Arthur et al., 1989
	desert kit foxes	Zoellick et al., 1989
	(<i>Vulpes macrotis arsipus</i>)	

to interpret; both Cuyler (1924) and Stout and Sonenshine (1974, Virginia) state that skunks do not den for long periods during the winter. Habitat selection would undoubtedly make a difference in the thermal environment of winter dens, but this has not been studied except in a marsh (Mutch, 1977).

In this part, I determine whether striped skunks exhibit habitat preferences in home range and den use. I also examine intrapopulational differences in habitat and den use in relation to sex, season and body size. Examples of communal denning are also noted for comparison to data from populations inhabiting higher latitudes.

METHODS

Study area. Cades Cove is located in Blount County, Tennessee in the northwest portion of Great Smoky Mountains National Park (approximately 35°35'N, 83°51'W to 35°37'N, 83°46'W). It includes a campground, picnic area, ranger station, personnel living quarters and the Cades Cove Loop Road (Figure 3-1). The Loop Road encloses approximately 8 km². This area of rolling hills and fields is grazed by horses and cattle as well as native fauna and is mowed twice each summer. Many historical structures in this area are maintained by the Park Service and are well-trafficked by visitors; these seldom show signs of use by terrestrial wildlife. However, several abandoned hay barns contain burrows. The altitude of the area within the Loop Road is approximately 600 m. Outside the Loop Road the terrain is steeper, grading to an altitude of 800 m or more, and covered with cove-hardwood forest. Cades Cove is visited by more than two million tourists each year, who frequently leave litter edible to wildlife. Further information about the natural history of Cades Cove can be found in Komarek and Komarek (1938), Whittaker (1956), and Goldsmith (1981).

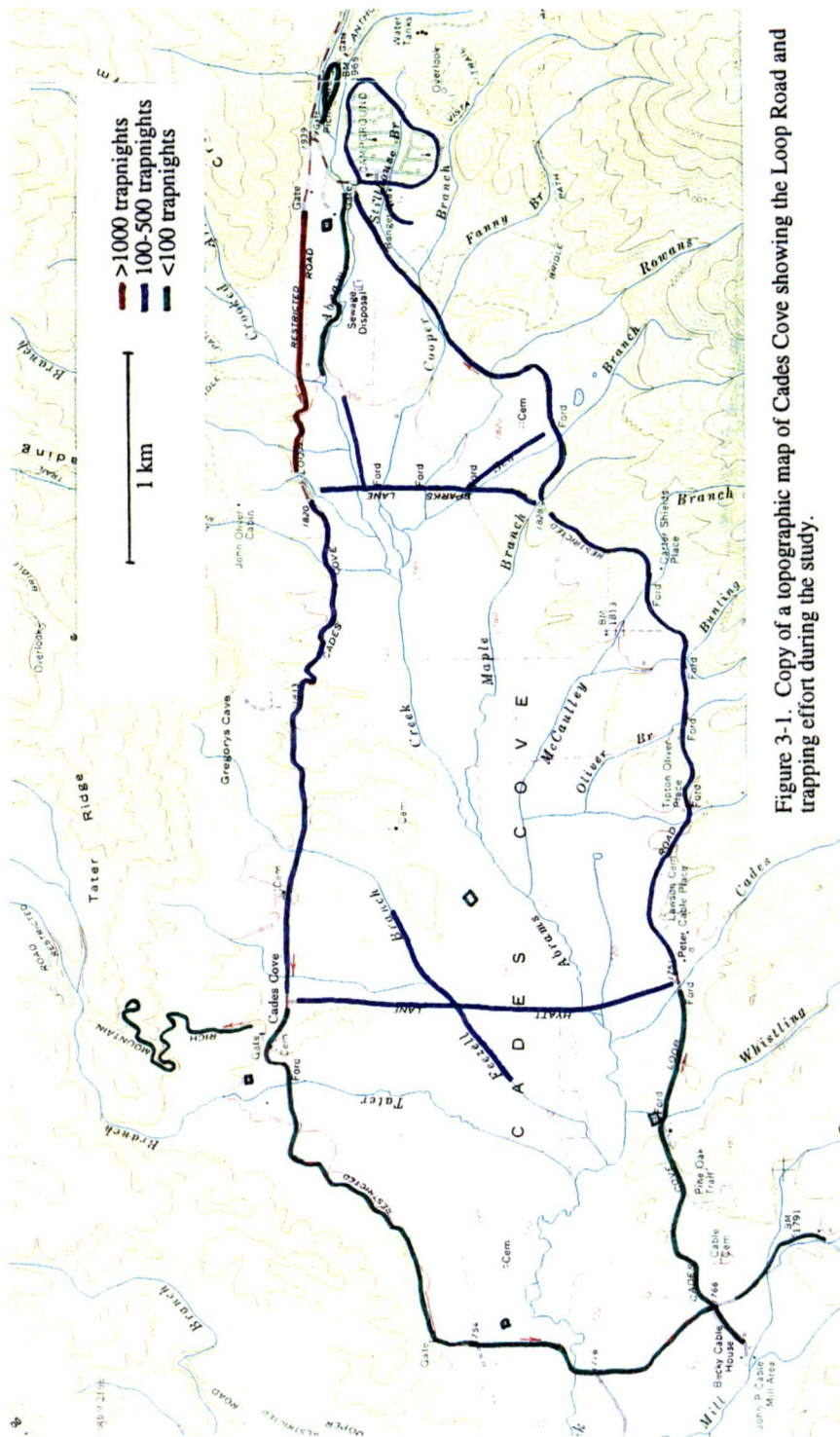


Figure 3-1. Copy of a topographic map of Cades Cove showing the Loop Road and trapping effort during the study.

Trapping. Trapping was conducted from mid-January 1993 through March 1995 and February through mid-April 1996. Tomahawk traps #105 were set shortly after dusk and checked just before dawn each day for a total of 3416 trapnights (from one to 42 traps/night, mode=10 traps/night). Traps were baited with oil-packed tuna and most were set along the Loop Road either in culverts or in the woods nearby (Figure 3-1). The majority of traps were set at the east end of the Cove for two reasons: 1) to reduce travel time when there were many tourists and 2) to ensure the possibility of identifying overlapping home ranges since traps were set in areas of previous trap success. Traps were also set in the picnic area, campground and near personnel housing. Captured skunks were anesthetized with a 4:1 mixture of ketamine hydrochloride and xylazine (Rosatte and Hobson, 1983; Servin and Huxley, 1992; R. Greenwood, pers. comm.). Sex, canine length, head-body length, tail length and weight of all trapped individuals were recorded.

Home range analysis. A total of 15 skunks (nine male and six female) were radio collared. Telemetry packages produced by ATS (Isanti, MN) weighed approximately 53 g and had a flexible whip-type antenna of about 15 cm. The battery was designed to last 1 yr.

Each radio-collared animal was located at least 14 times (Table 3-4). Location data were analyzed using the minimum convex polygon and percent overlap functions of Wildtrak II Home Range Analysis for the Macintosh (Todd, 1995). With Wildtrak II, it is also possible to compute different home ranges for each season.

Habitat. A USGS topographical map of the Cades Cove Quadrangle was scanned into a Macintosh computer using Ofoto software. The map was transferred to Aldus SuperPaint, where the habitat was classified as forest or field, represented by different colors. Those species found in forest habitat are listed in Table 3-5a. Field habitat was that area which is mowed regularly and included those species listed in Table 3-5b. Home range maps

Table 3-4. Home range size (HR) and associated variables for 15 striped skunks: sex, weight, habitat type and the number of radio fixes used to calculate the home range size. Habitat was measured as described in the methods, and is here presented as the proportion of forest habitat in a home range.

SKUNK	SEX	WT (kg)	HABITAT	#FIXES	HR (km ²)
19	male	1.65	0.194	51	1.693
23	male	2.20	0.170	14	0.190
27	female	1.20	0.655	19	0.747
40	male	1.75	0.602	22	0.833
72	male	1.40	0.436	32	2.668
74	male	2.45	0.364	62	0.580
90	male	1.65	0.613	24	0.602
95	male	2.15	0.417	64	0.925
98	female	2.15	0.445	157	1.355
DG60	female	1.25	0.589	96	0.537
LB143	female	1.20	0.780	136	0.295
P169	male	1.75	0.352	25	2.407
P174	female	1.55	0.457	230	1.049
R2	male	2.50	0.333	137	0.896
Y98	female	2.65	0.486	186	1.267

Table 3-5a. Plant species typical of forest habitat in Cades Cove (Whittaker, 1956; Radford et al., 1968; Wofford, 1989).

Scientific Name	Latin Name
Trees	
<i>Tsuga canadensis</i>	Eastern hemlock
<i>Tilia heterophylla</i>	Basswood
<i>Acer saccharum</i>	Sugar maple
<i>Aesculus octandra</i>	Yellow buckeye
<i>Betula allegheniensis</i>	Silver birch
<i>Liriodendrom tulipifera</i>	Tulip poplar
<i>Fagus grandifolia</i>	American Beech
Shrubs	
<i>Euonymus americanus</i>	Strawberry bush
<i>Lindera benzoin</i>	Common spicebush
<i>Hydrangea arborescens</i>	Wild hydrangea
<i>Rhododendron maximum</i>	Rosebay rhododendron
<i>Leucothoe editorum</i>	Dog hobble
Herbs	
<i>Eupatorium rugosum</i>	White snakeroot
<i>Cimicifuga racemosa</i>	Black cohosh
<i>Impatiens pallida</i>	Pale touch-me-not
<i>Laportea canadensis</i>	Wood nettle
<i>Trillium erectum</i>	Red trillium
<i>Aster divaricatus</i>	Heart leaved aster
<i>Dryopteris carthusiana</i>	Spinulose wood-fern
<i>Deparia acrostichoides</i>	Silvery glade fern
<i>Viola spp.</i>	Violets
<i>Stellaria pubera</i>	Giant chickweed
<i>Tiarella cordifolia</i>	Foamflower
<i>Galium triflorum</i>	Bedstraw
<i>Euonymus obovatus</i>	Running euonymus

Table 3-5b. Genera likely to be found in field habitat in Cades Cove (DeSelm et al., 1994). Only genera that include three or more species found in Cades Cove are listed here.

Genus Name

Agrostis
Andropogon
Aristida
Bromus
Calamagrostis
Chasmanthium
Danthonia
Elymus
Eragrostis
Glyceria
Muhlenbergia
Panicum
Paspalum
Poa
Sphenopholis

created in Wildtrak were overlaid on the habitat map (this is shown in Figure 3-2). PV-Wave (Version 6.1) software was used to count the number of pixels of each color (habitat type) within each home range outline.

Habitat was then examined in three ways: 1) The absolute area of forest habitat (AAFor) and field habitat (AAFie) within each home range were analyzed in relation to home range size, sex and weight. 2) The absolute area of forest was converted to a proportion of forest available (PFA) for each home range. The proportion of field available is not reported since it is the inverse of PFA. PFA was analyzed in relation to home range size, sex, weight and season. 3) The proportion of times that each skunk was located in forest habitat (PLF) is also reported. The proportion of locations in field habitat is the inverse of PLF and is not given. PLF is analyzed in relation to home range size, sex and weight.

Dens. Use of a den by a skunk was determined by 1) direct observation of an individual entering a den or 2) localization of a radio-collared individual in a den. The habitat surrounding each den was categorized as forest, field or forest-field edge. Forest and field habitat types were defined as above. Edges were defined as 1) less than 15 m (by pacing) from both forest and field or 2) along a road through the middle of forest habitat. Distance of a given den from water (up to 100 m) was also measured. Sex of known inhabitants of a den and the season of den use were recorded.

RESULTS

Habitat. Results are reported first in relation to 1) absolute amount of forest (AAFor) and absolute amount of field (AAFie) within the home range, 2) the proportion of forest available (PFA) within the home range and 3) the proportion of locations that were in forest habitat (PLF; see Table 3-6). Home range size increased significantly with both AAFor

Table 3-6. Habitat preferences of 15 radio-collared striped skunks. For each individual, its sex and home range size (HR) are given, along with the absolute amount of forest habitat within its home range (AAFor, in pixels), the absolute amount of field habitat within its home range (AAFie, in pixels), the proportion of forested area to total area available within its home range (PFA) and the proportion of times that each skunk was located in forest habitat (PLF).

SKUNK	SEX	HR	AAFor	AAFie	PFA	PLF
19	m	1.693	4466	18517	0.194	0.529
23	m	0.190	443	2162	0.170	0.643
27	f	0.747	6504	3429	0.655	0.579
40	m	0.833	6579	4356	0.602	0.818
72	m	2.668	15921	20555	0.436	0.688
74	m	0.580	2844	4970	0.364	0.774
90	m	0.602	5167	3263	0.613	0.833
95	m	0.925	5204	7265	0.417	0.750
98	f	1.355	8175	10207	0.445	0.545
DG60	f	0.537	4442	3102	0.589	0.198
LB143	f	0.295	3028	854	0.780	0.920
P169	m	2.407	11709	21528	0.352	0.640
P174	f	1.049	6489	7719	0.457	0.713
R2	m	0.896	4056	8108	0.333	0.175
Y98	f	1.267	8217	8691	0.486	0.849

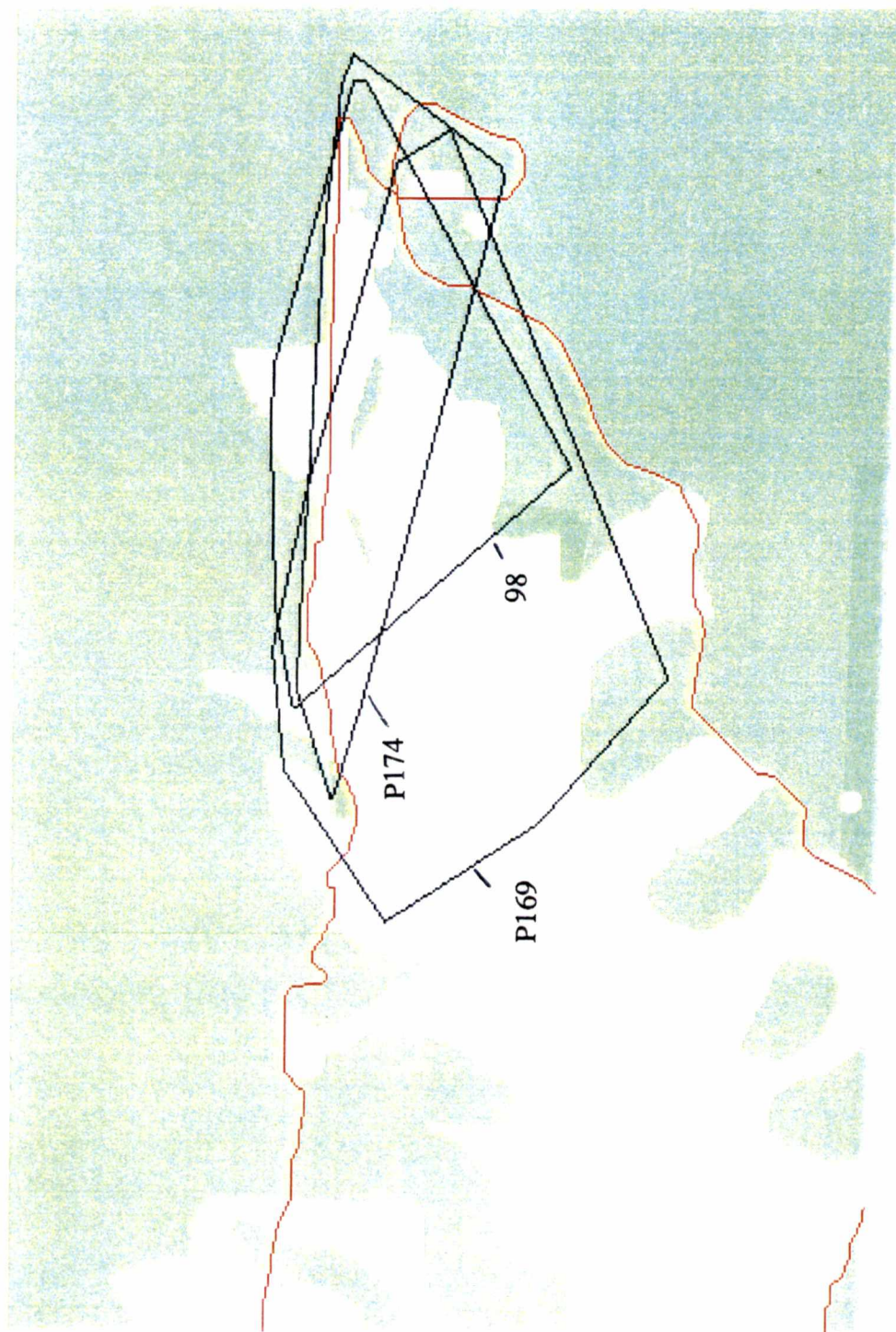


Figure 3-2. The 15 striped skunk home ranges on a habitat map of Cades Cove. Forest habitat is represented by green and field habitat by white. Home ranges are outlined in black. The paved Cades Cove Loop Road is shown in red along with the outline of the campground area (to the right of the page. North is toward the binding. a) This map shows the home ranges of three skunks that were first trapped in 1993: male P169 and females P174 and 98.

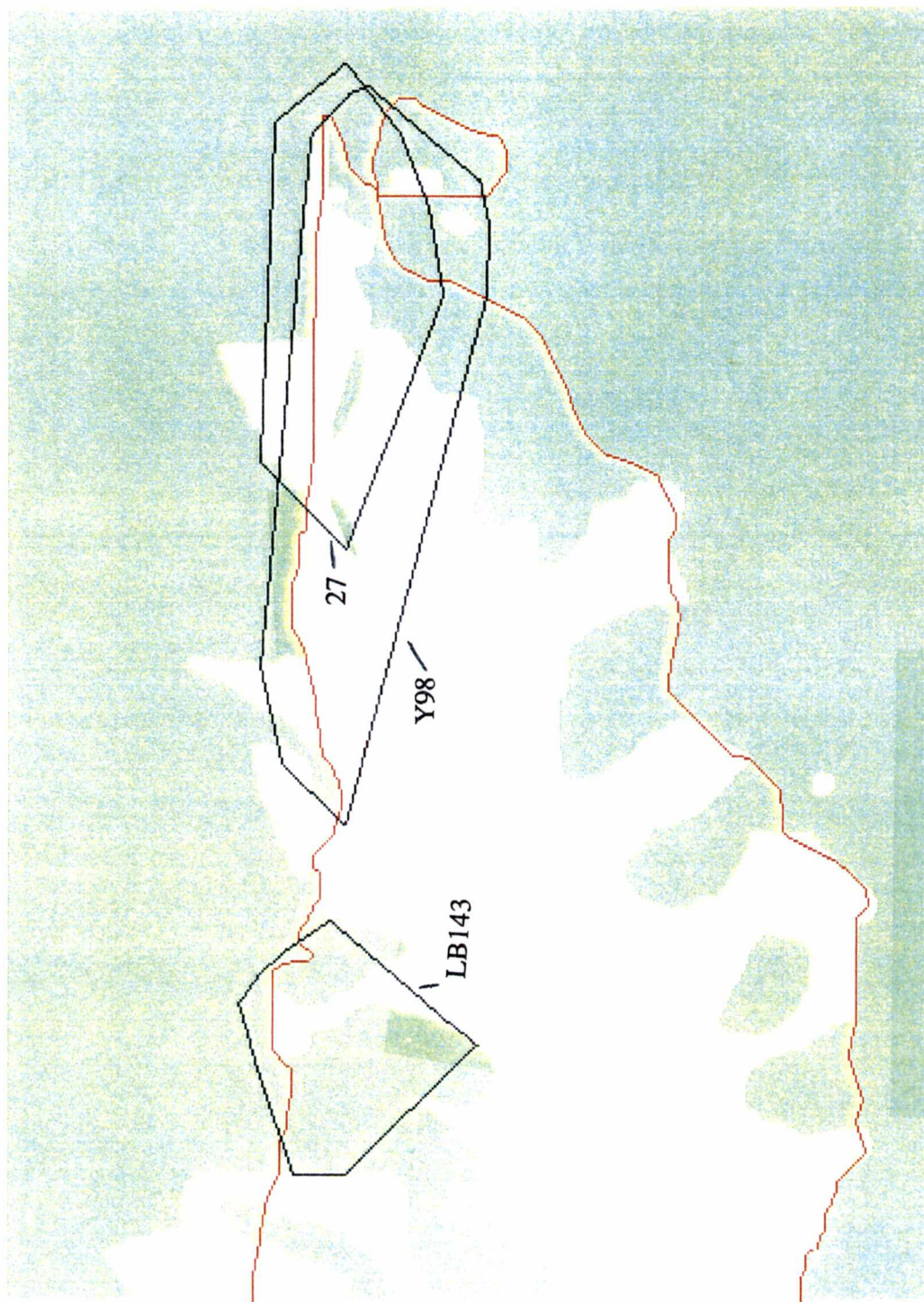


Figure 3-2 (continued). b) This map shows the ranges of three females, 27, LB143 and Y98.

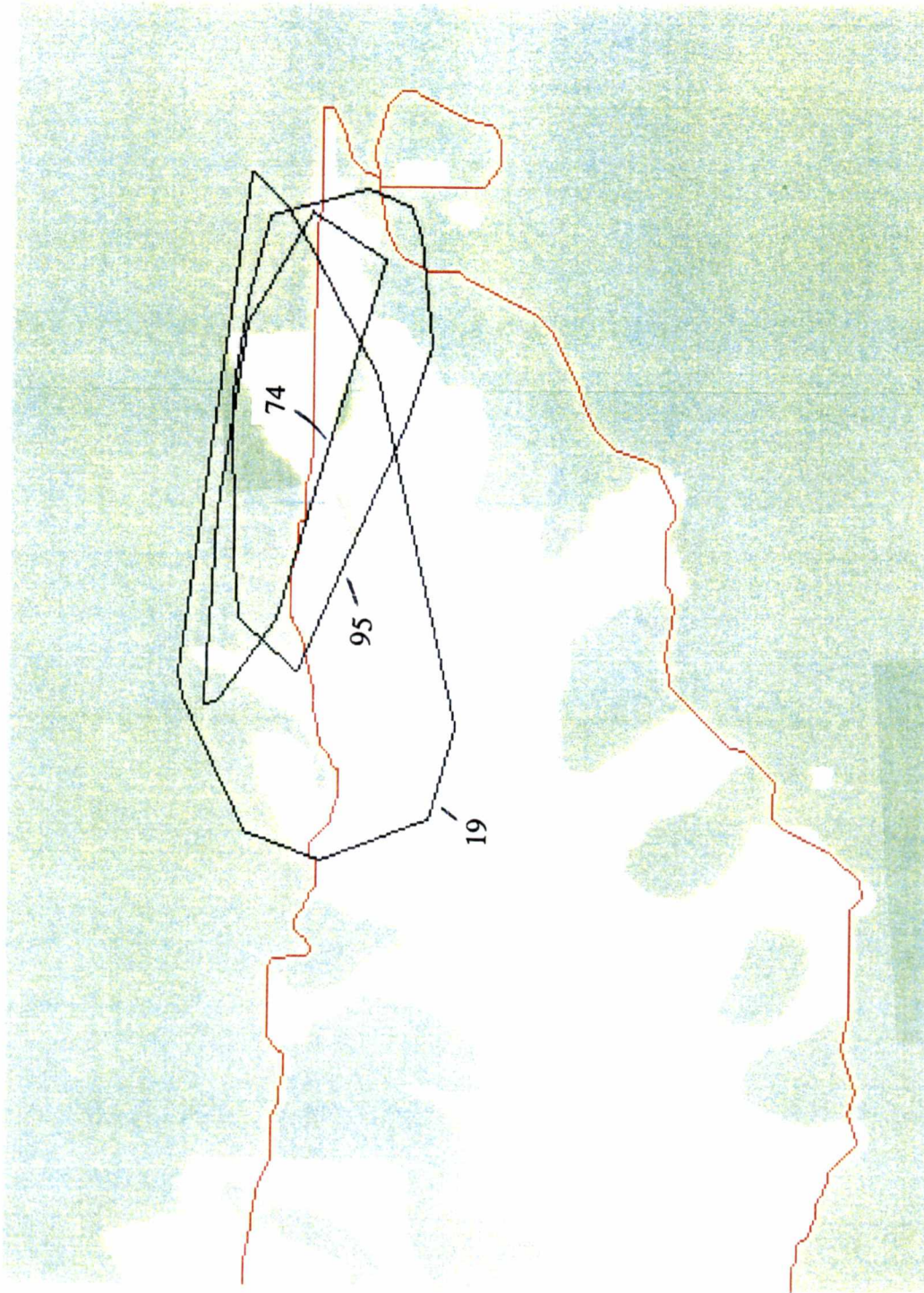


Figure 3-2 (continued). c) This map shows the ranges of three males, 19, 74 and 95

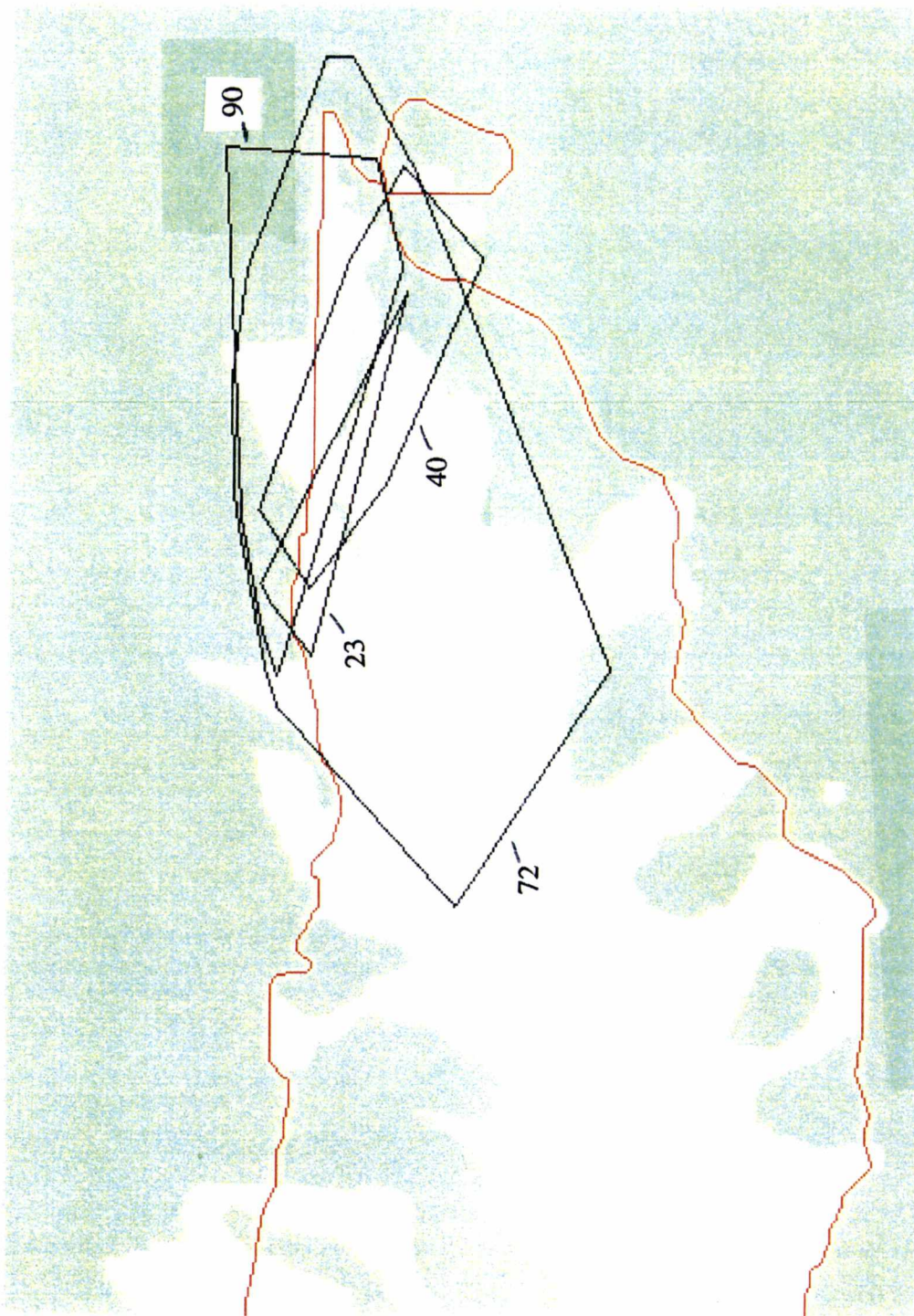


Figure 3-2 (continued). d) This map shows the ranges of four males, 23, 40, 72 and 90.

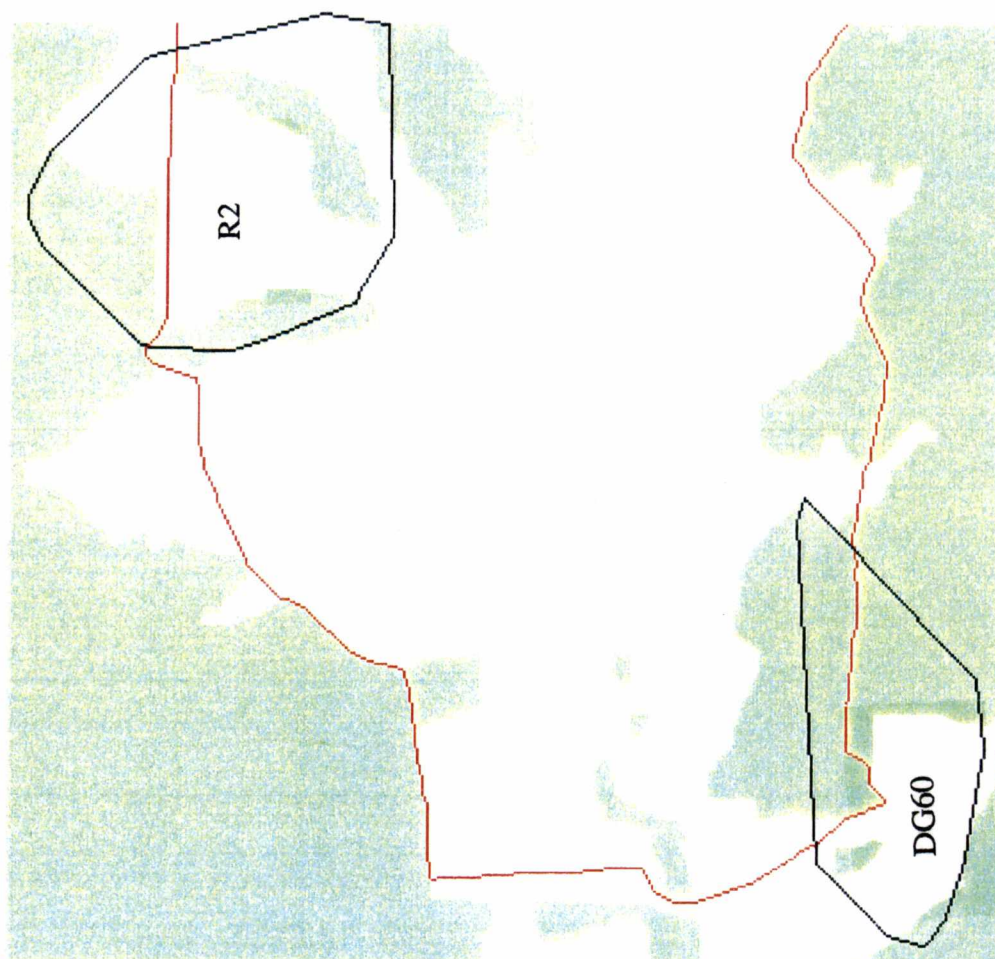
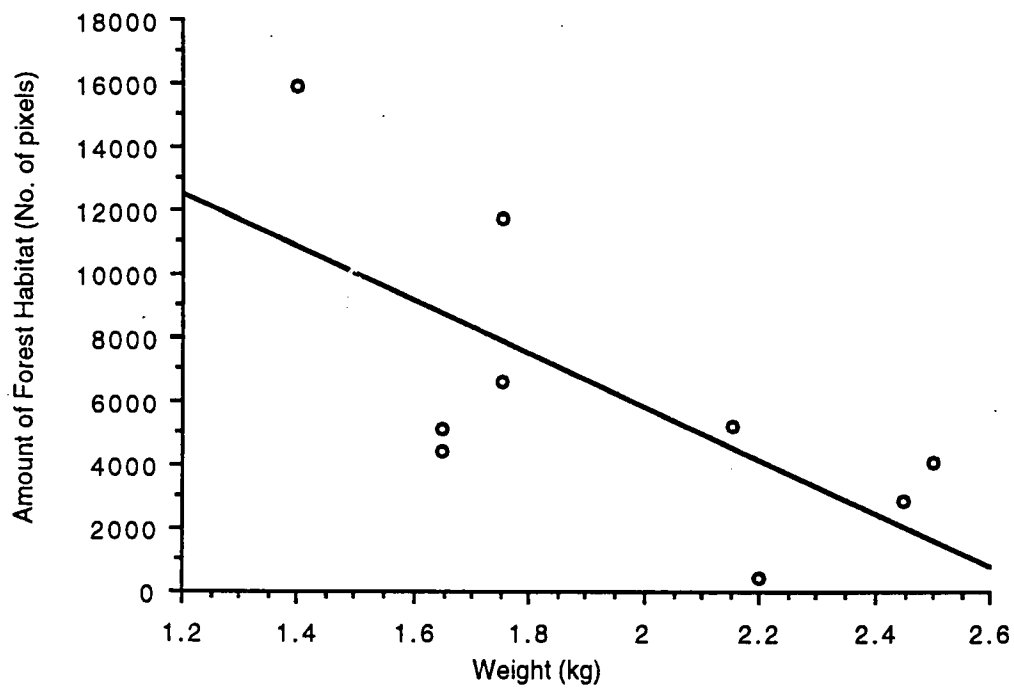


Figure 3-2 (continued). e) This map shows the range of male R2 and female DG60. The right edge of this map overlaps the left edge of the maps shown in Figure 3-2 a-d.

and AAFie (forest: $r^2=0.789$, $N=15$, $P<0.0001$; field: $r^2=0.930$, $N=15$, $P<0.0001$). AAFor and AAFie were not significantly related to sex of the individual (forest: $t=-0.059$, $d.f.=13$, $P=0.9535$; field: $t=-1.275$, $d.f.=13$, $P=0.2245$). The relationship between AAFor, AAFie and weight were contradictory by sex: males showed a nonsignificant negative relationship between weight and the amount of field habitat (3-3a; $r^2=0.308$, $N=9$, $P=0.1211$) and a significant negative relationship between weight and the amount of forest habitat (Figure 3-3b; $r^2=0.476$, $N=9$, $P=0.0397$) whereas females showed a significant positive relationship between weight and the amount of field habitat (Figure 3-3c; $r^2=0.725$, $N=6$, $P=0.0314$) and a nearly significant positive relationship between weight and the amount of forest habitat (see Figure 3-3d; $r^2=0.652$, $N=6$, $P=0.0519$).

PFA ranged from 0.17 to 0.78 (mean=0.46; see Table 3-6 and Figure 3-4). There was no significant relationship between PFA and home range size ($r^2=0.088$, $N=15$, $P=0.2821$). Females alone showed a significant negative relationship between PFA and home range size, but this was due primarily to the influence of LB143 (with LB143: $r^2=0.895$, $N=6$, $P=0.0123$; without LB143: $r^2=0.683$, $N=5$, $P=0.0846$). There was a tendency for female skunks to show a higher PFA than males, but this was also due primarily to LB143 (with LB143: $t=2.362$, $d.f.=13$, $P=0.0344$; without LB143: $t=1.832$, $d.f.=12$, $P=0.0918$). Overall, heavier animals had significantly lower PFAs ($r^2=0.297$, $N=15$, $P=0.0357$), but within each sex there was no significant relationship between weight and PFA (males: $r^2=0.114$, $N=9$, $P=0.3734$; females: $r^2=0.521$, $N=6$, $P=0.1055$). This could be due to the opposing trends of sex with AAFor and AAFie mentioned above. There was no relationship between PFA and season ($F=1.111$, $d.f.=3$, $P=0.3624$).

PLF ranged from 0.175-0.920 (mean=0.644, see Table 3-6 and Figure 3-5), yielding a significantly higher proportion of forest when measured by counting locations than when measured as amount of habitat available within the home range ($t=3.062$,



$$y = 22537.693 - 8368.585 * x; R^2 = .476$$

Figure 3-3. The relationship between various habitat measures and weight. a) Weight and AAF_{For} for males.

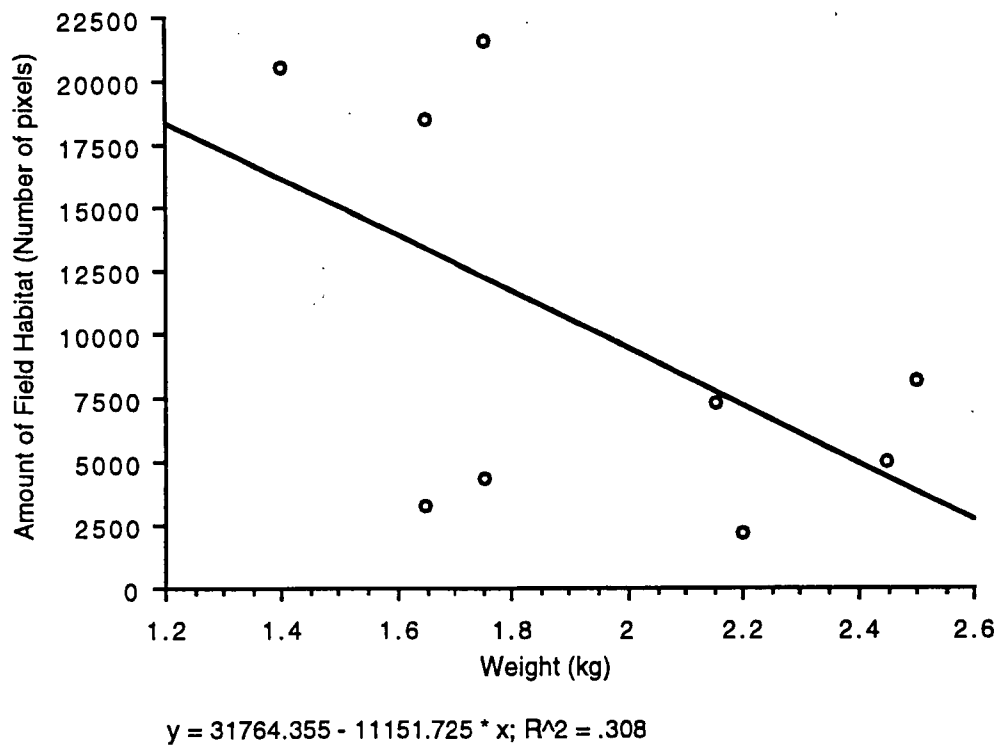
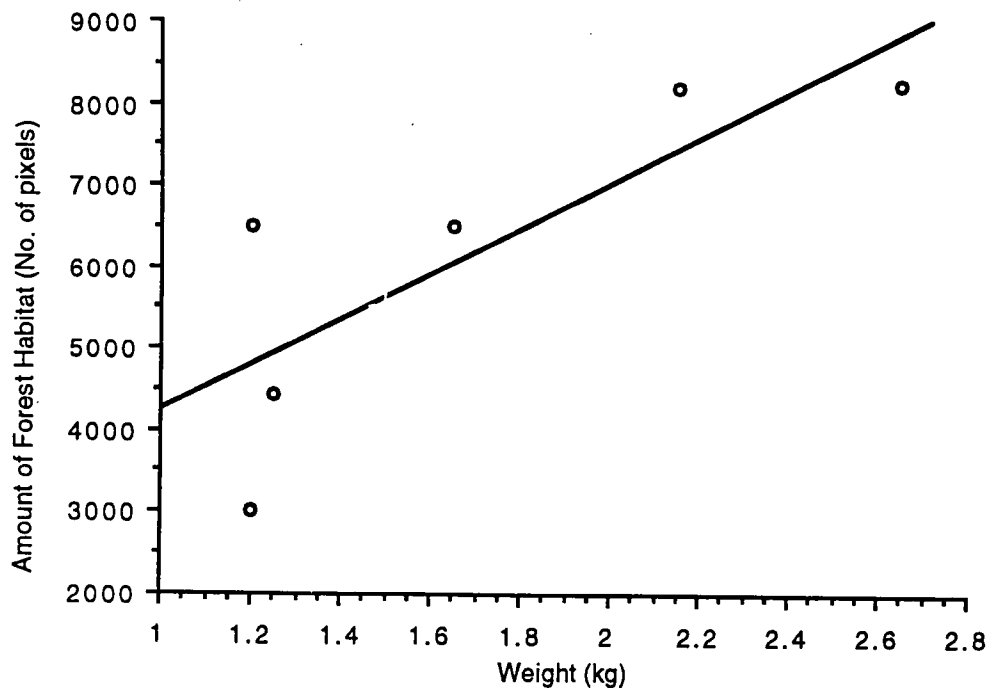


Figure 3-3 (continued). b) Weight and AAFie for males.



$$y = 1479 + 2770.396 * x; R^2 = .652$$

Figure 3-3 (continued). c) Weight and AAF_{For} for females.

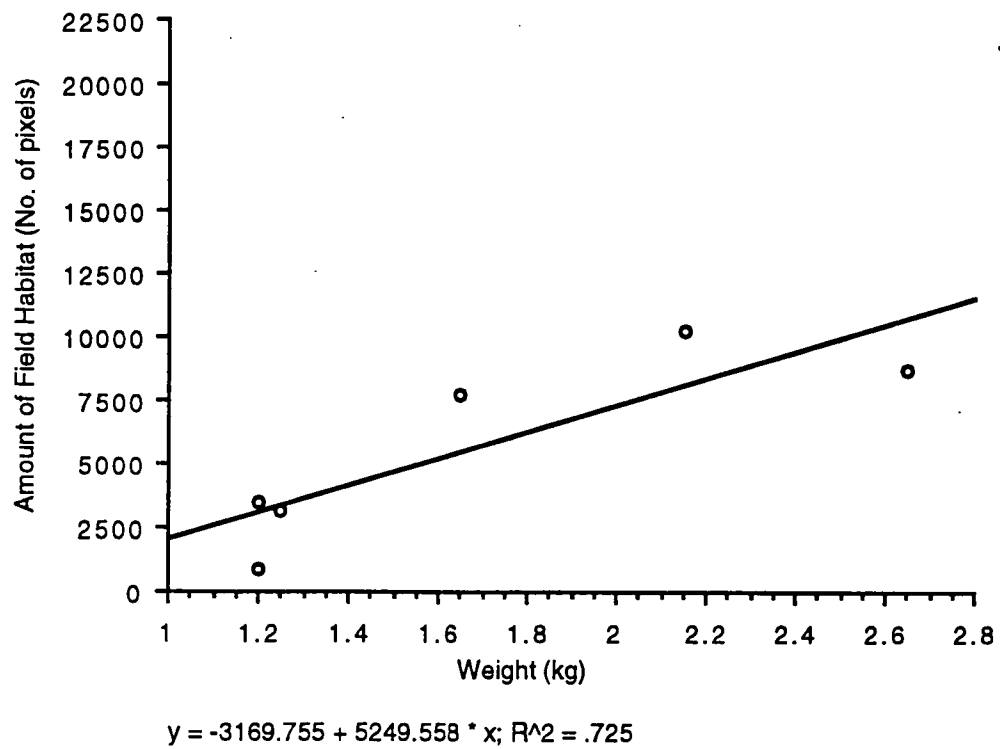


Figure 3-3 (continued). d) Weight and AAFie for females.

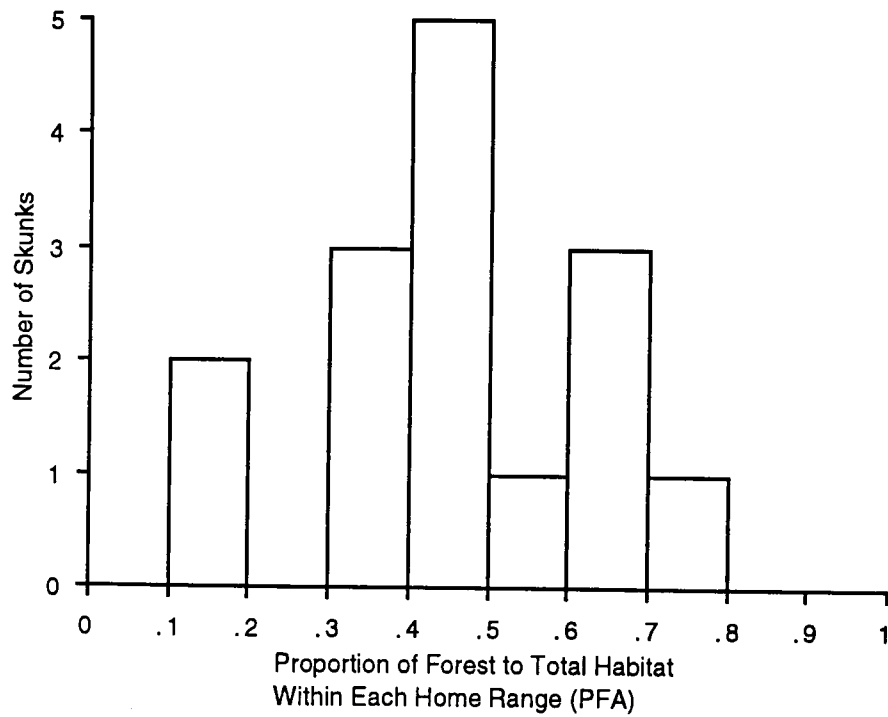


Figure 3-4. Frequency histogram showing the numbers of individual skunks with different PFAs.

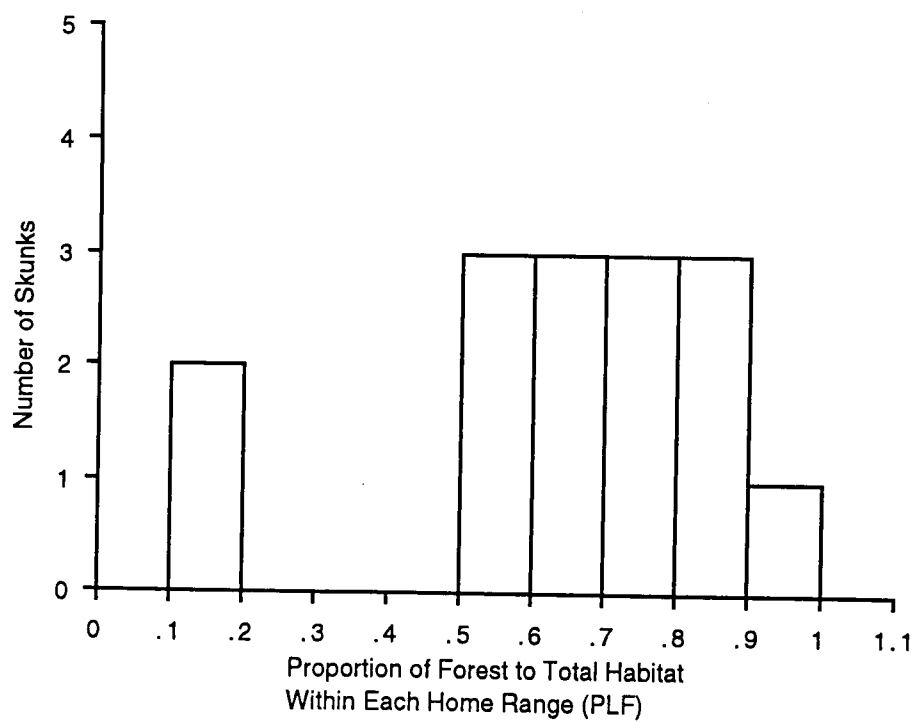


Figure 3-5. Frequency histogram showing the numbers of individual skunks with different PLFs.

d.f.=28, $P=0.0042$). There were no significant relationships between PLF and home range size, sex or weight.

Eleven individuals were located in the campground at least once, ranging in proportion from 0.01 to 0.42 (mean=0.14). No relationship was observed between the proportion of times an individual was located in the campground and home range size ($r^2=0.076$, $N=15$, $P=0.4119$). Females whose home range included part of the campground had significantly larger home ranges than those not including the campground ($F=10.140$, d.f.=1, $P=0.0334$); the relationship was not significant for males ($F=1.611$, d.f.=1, $P=0.2449$). There was no sex difference in the percent of locations of skunks in the campground ($F=0.449$, d.f.=1, $P=0.5197$) nor was there a seasonal difference in use of the campground by the sexes ($\chi^2=2.444$, d.f.=3, $P=0.4856$). Figure 3-2 shows all 15 home ranges in relation to each other and the habitat of Cades Cove.

Dens. Twenty of 29 (69%) dens were in forest-field edges, five (17%) were in forest and four (14%) were in fields (see Figures 3-6 and 3-7). Of the dens classified as edge habitat, seven (35%) were in riparian zones, four (20%) were near roads and one (5%) was near both. There were no differences in habitat type of dens by sex or season of year ($\chi^2=2.25$, d.f.=2, $P>0.5$; $\chi^2=7.37$, d.f.=6, $P>0.1$ respectively). Distance of dens from water was not significantly related to sex, season or habitat type ($F=1.649$, d.f.=1, $P=0.2117$; $F=0.889$, d.f.=3, $P=0.4858$; $F=0.607$, d.f.=2, $P=0.5526$, respectively) and there were no interactions among these variables and distance to water.

Habitat types of dens varied within individuals. Three skunks that were each located at between five and seven dens used dens in more than one habitat. For example, female Y98 was located at five dens, three of which were in edge habitat and two in forest. Four skunks that were each located at two or three dens used only edge habitat.

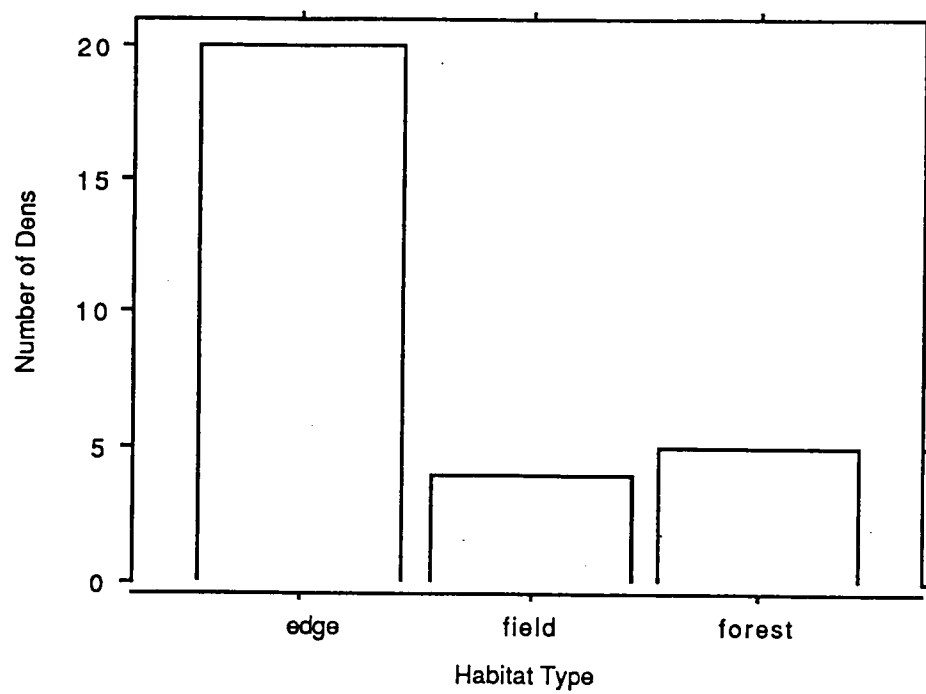


Figure 3-6. The numbers of skunk dens located in different habitat types.

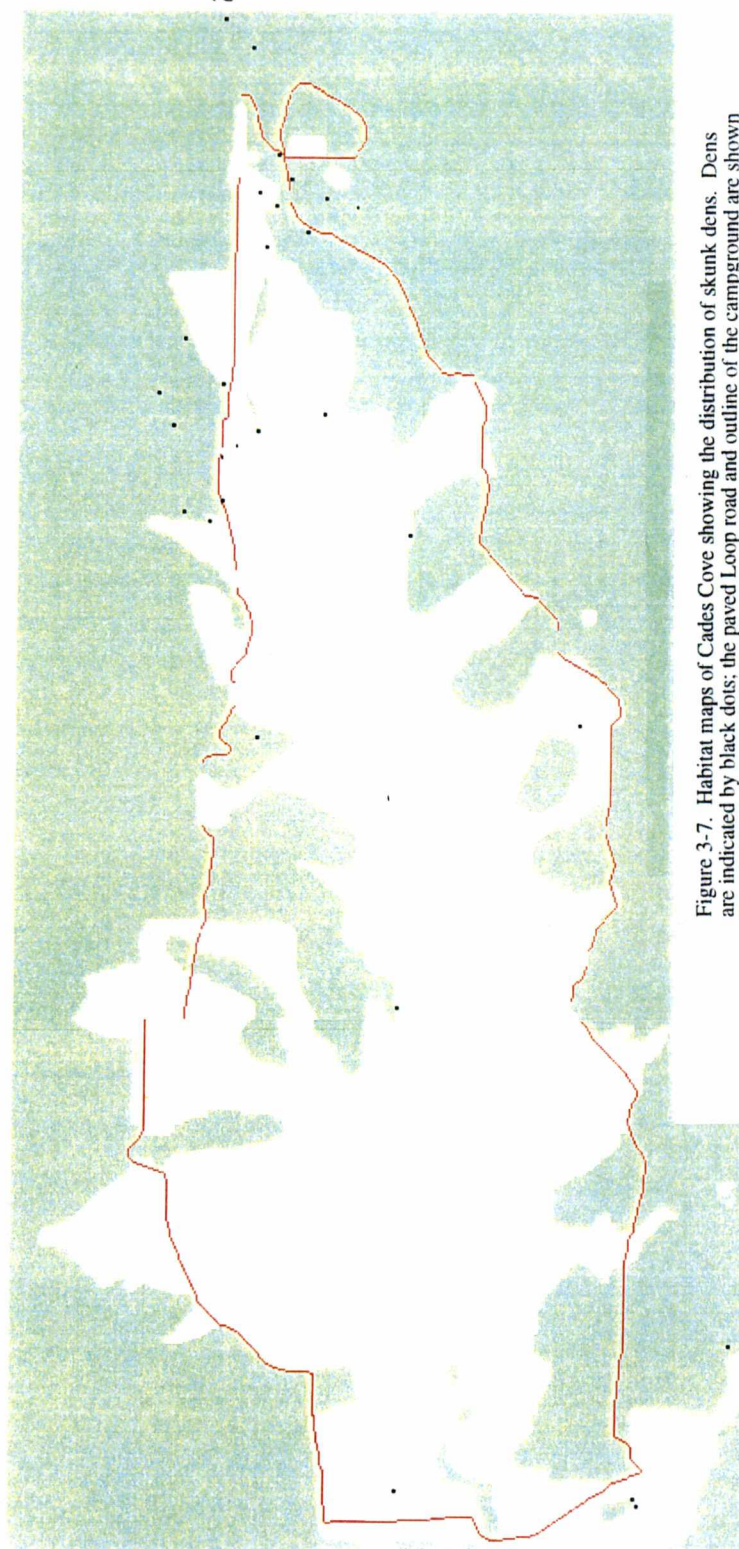


Figure 3-7. Habitat maps of Cades Cove showing the distribution of skunk dens. Dens are indicated by black dots; the paved Loop road and outline of the campground are shown in red. North is toward the binding.

During the winters of 1993 and 1994, there were three instances of communal denning and four cases of skunks remaining in dens for more than 20 days. Although these observations were opportunistic and prohibit statistical analysis, they are worth mentioning for comparison to previous work. The three instances of communal denning are as follows:

- 1) Two females (Y98 and P174) denned together under an unused horse barn in a field (Den #30) in mid-January. They subsequently moved, together, to Den #25.

- 2) Den #25, located in forest habitat, was occupied by a male (74) and two females (Y98 and P174) during late January and early February 1994. The two females were known to have been using this den before the male was first trapped there; all three animals were located at Den #25 off and on through the end of February.

- 3) Den #5 was used at various times by one female and two males. Female 98 was known to be in Den #5 simultaneously with male 19 during early and mid-February and with male 40 on 17 February. The observation of 19 and 40 in Den #5 the same day was probably due to my interference and it apparently resulted in some aggression: 19 was captured in a trap approximately 200 m from Den #5 on the night of 16 February. This apparently gave 40 access to the den. When 19 was released on the morning of 17 February, he was observed to go into the den; shortly thereafter I smelled skunk spray and observed 40 leaving the den.

Female 98 was not present in the den on three other occasions when other skunks were present (11 February when male 23 was located there, 20 February when male 74 was trapped next to the den entrance and 26 February, when an unknown skunk was seen at the den entrance).

Three dens were used by skunks for more than 30 days in the winter. Since skunks were not radio tracked continuously, I cannot discount the possibility that they

entered and left the dens while I was not present. Exact dates of radio tracking for these animals are listed in Table 3-7. Observations of extended den use are as follows:

1) Female 98 was in Den #5 every time she was located between 16 November 1993 and 8 February 1994 (up to 86 days). She was also found in this den several days in February and on 26 March, although she was known to have used another den on 9 February.

2) On 21 January, both Y98 and P174 were located at Den #25. P174 was identified there on all occasions until 23 February (up to 34 days); she and one of her offspring from the previous year, male 23, were found dead of antifreeze poisoning in another den on 25 February.

3) Female DG60 was known to be in Den #18 between 22 November 1993 and 8 March 1994 (up to 107 days).

DISCUSSION

Habitat analyses indicate skunks utilize both forest and field. Although the significant positive relationships between amount of forest and home range size and amount of field and home range size are due in part to geometry (if the home range size increases, so must the amount of habitat within it), they may also indicate that skunks are not choosing one habitat over the other. There is some indication that skunks prefer forest-field edges (see below; Stout and Sonenshine, 1974) and expansion of home ranges may occur along such ecotones. Verts (1967) found that striped skunk home ranges are elongate in shape, attributing this to long, straight-line movements between dens and hunting grounds. Home ranges in this study are on average 2.5 times longer than they are wide, and 10 out of 15 ranges parallel a forest-field ecotone or riparian zone (Figure 3-2).

Categorization of habitat types within a home range polygon (represented by PFA) probably underestimates the use of forest habitat (represented by PLF). There are two

Table 3-7. Dates (during late 1993 and early 1994) skunks were located by telemetry to dens.

Den #	Individual	Dates
5	Female 98	Nov 16, 21, 22, 25, 26, Dec 2, 9, 13, 14, 15, 17, 19, 20, Jan 9, 10, 11, 12, 26, 27, Feb 5, 10, 13, 14, 15, 16, 17, 18, 19
	Male 19	Jan 5, 9, 16, 17, 18, 19, 23, 24, 26
13	Male 19	Jan 30, Feb 2,3,4,9,10,11,13
18	Female DG60	Nov 22, 26, Dec 2, 9, 13, 15, 17, 20, Jan 9, 11, 13, 27, Feb 5, 9, 12, 19, Mar 8
25	Female P174	Jan 21, 22, 26, 27, 28, 29, 31, Feb 1, 2, 3, 4, 5, 6, 9, 10, 11, 13, 15, 16, 17, 18, 19, 23
	Female Y98	Jan 21, 22, 26, 27, 28, 29, 31, Feb 1, 2, 3, 4, 5, 6, 9, 10, 11, 15, 16, 17, 18
	Male 74	Jan 28, 29, 30, Feb 2, 3, 4, 6, 10, 11, 13, 15, 16, 17, 18, 19, 23, 24, 25, 26, Mar 2, 8

possible, non-exclusive reasons for this: 1) The habitat structure of Cades Cove is essentially a large field surrounded by forest, so two locations in forest habitat on opposite sides of the Cove would lead to inclusion of all the intervening field habitat, thus artificially increasing the percentage of the field habitat in the polygon. 2) Skunks are selectively active in forest habitat as opposed to fields. This may seem contradictory to the above suggestion that skunks select ecotones, but error in both radio tracking skunks and assigning habitat types to locations from a topographic map make it difficult to determine how much of what was categorized as forest habitat might be edge habitat. The preference of skunks for forest could be due to a number of factors, including availability of food, cover and dens. These are discussed in turn below.

Food. Availability of food for this omnivore would have to be determined quantitatively by small mammal trapping, insect abundance measures (e.g., sweep-netting, Berlese funnel) and measures of mast and soft mast production. These data are unavailable from other studies and were not collected in the present work. Genovesi et al. (1996) studied stone martens (*Martes foina*), opportunistic hunters that will also feed on fruits and berries, in habitat similar to that of the present study (divided into forested, forested rural and rural). Within one population, they found significant differences in diet between habitats but no apparent habitat preference. This may be indicative of the case for striped skunks.

Cover. Cover such as fallen logs and stumps is more prevalent in the forest but the tall grass in the fields might be equally protective for a mid-size mammal. Selko (1938) emphasized the importance of vegetation shielding the entrance of the den. However, it is also possible that skunks rely not on cover for predator protection, but on their supposedly warning coloration and chemical defense (Darwin, 1871; Verts, 1967; Rosatte, 1987; Walton and Lariviere, 1994).

Dens. There are at least three possible relationships between habitat preferences for dens and habitat preferences for home ranges. It is impossible to distinguish among them based

on these data. 1) Locations of dens may be an important factor drawing skunks into forested areas since most dens were located on forest-field edges. 2) Skunks may be drawn to dens in forest-field edges because of their high use of forest habitat. 3) Skunks may simply use available dens. Based on appearance, at least 14 of the 29 dens were believed to have been dug originally by woodchucks, a species which prefers forest-field edges (Barbour and Davis, 1974).

At this time, it appears that skunks prefer ecotones for den sites and perhaps for home ranges, since home ranges are elongate along edge areas. However, I cannot determine for what reasons edges are preferred.

It was expected that those skunks including part of the campground in their home range would have smaller home ranges because of the increased food availability (e.g., Gittleman and Harvey, 1982). However, the opposite was found for females, and there was no relationship for males. This may indicate that females increase their home range size or shift the area of their home range in order to include the campground area because it is such a rich food source. This relationship may also be because females feed at one end of their home ranges and den at the other end (Verts, 1967). Goldsmith (1981) found that females had a significantly larger percent of their home ranges in the campground than males or juveniles did. My data do not show this pattern. This could be due simply to the fact that Goldsmith's study focused on the campground area.

Reports of skunks denning communally and denning for long periods of time are common at northern latitudes: Gunson and Bjorge (1979) found 19 skunks in one den in the Alberta-Saskatchewan border area and suggested that the *minimum* period of denning one severe winter was 143-150 days. Storm (1972) reported one female who stayed in a single den 62 consecutive days in northwestern Illinois. It is not clear how these authors recorded "continuous" denning. Both used some combination of radio- and snow tracking; Storm (1972) states that he located individuals by telemetry every 10 to 20 minutes for 3 to

4 hour periods but Gunson and Bjorge (1979) do not specify their tracking regime. It is therefore difficult to determine how accurate these estimates of continuous denning are. My *ad libitum* tracking regime may be no worse than those of Storm (1972) and Gunson and Bjorge (1979), and may therefore yield comparable information.

Reports from farther south are few and less informative: near Austin, TX, "skunks are abroad all winter except for brief cold periods," (Cuyler, 1924, p 181) and "Virginia's milder winters do not restrict activity to" the extent they do farther north (Stout and Sonenshine, 1974, p 143). Therefore, it is interesting to find skunks in Tennessee possibly denning for periods of up to 107 days, and denning in communes of at least three animals. This could be due to the colder climate of the mountains.

All data on communal denning and extended periods of denning are from November 1993 to February 1994. This was the coldest winter during the study (average minimum temperature in January 1994: -6°C, average minimum temperature in January 1993, 1995 and 1996: -2 to 0°C). However, snowfall in January-March was lower that year (1993: 114 cm, 1994: 27 cm, 1995: 28 cm, 1996: 110 cm).

It is also noteworthy that two females (Y98 and P174) apparently denned together in one location for several days, and then moved together to another den. Gunson and Bjorge (1979) also found some of the same skunks together in dens in different years. It is not known whether these two females were related, but in addition to sharing two dens, they overlapped home ranges by an area equivalent to 93% of P174's total range and 77% of Y98's range.

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PART FOUR

GENETIC VARIABILITY IN STRIPED SKUNKS

INTRODUCTION

According to a comprehensive review by Nevo (1978), average polymorphism (P) and heterozygosity (H) across mammals are the lowest of any class of vertebrates, and vertebrates exhibit lower levels than both plants and invertebrates (mammals, 46 species: $P=0.147$, $H=0.0359$; vertebrates, 135 species: $P=0.173$, $H=0.0494$; plants, 15 species: $P=0.259$, $H=0.0706$; invertebrates, 93 species: $P=0.397$, $H=0.1123$).

There has been a great deal of debate concerning how genetically variable different groups of mammals are (Wooten and Smith, 1985; Hartl et al., 1988; Mitton and Raphael, 1990). Carnivores purportedly show low levels of genetic variability (e.g., Bonnell and Selander, 1974; Simonsen, 1982; Baccus et al., 1983; O'Brien et al., 1983; for discussion and exceptions, see Fisher et al., 1976; Hartl et al., 1988; Mitton and Raphael, 1990; Merola, 1994). Hartl et al. (1988) have disputed the claim that carnivores in general are not genetically variable, but agree that some carnivore species show low levels of heterozygosity and polymorphism.

Within carnivores, members of the family Mustelidae are thought to show low levels of polymorphism and heterozygosity, with most species in the range of 0-10% polymorphism and 0-3.3% heterozygosity (see 4-1). However, all but one of the zero values are from a single study (Simonsen, 1982) and higher values have been found for the same species by other researchers (Hartl et al., 1988; Evans et al., 1989). Two species have levels well above the average for mammals (least weasel (*Mustela nivalis*), $P=0.225$, $H=0.064$, Hartl et al., 1988; American marten (*Martes americana*), $P=0.33$, $H=0.17$, Mitton and Raphael, 1990).

Only one study has ever examined skunk allozymes; O'Brien et al. (1989) used the kidney of a single striped skunk in a molecular systematic study of black-footed ferrets (*Mustela nigripes*). They found one heterozygous locus out of 30 presumptive loci. Therefore, no extensive study has been made of genetic variability within any skunk

Table 4-1. Levels of genetic variability reported for Mustelidae. N=number of individuals, Loci=number of loci examined, H=average heterozygosity, P= polymorphism. Those values of H marked with an asterisk were calculated from raw data given in the reference; all other values are those reported by the author of the paper cited.

Species	Tissue	N	Loci	H	P	Reference
Zorilla (<i>Ictonyx striatus</i>)	blood, skin	1	36	0.028*	--	O'Brien et al., 1989
American marten (<i>Martes americana</i>)	blood, liver	10	24	0.17	0.33	Mitton and Raphael, 1990
Beech marten (<i>Martes foina</i>)	muscle, liver	121	15	0	0	Simonsen, 1982
"	organs, muscle	3	31	0.057	0.019	Hartl et al., 1988
Pine marten (<i>Martes martes</i>)	muscle, liver	2	15	0	0	Simonsen, 1982
European badger (<i>Meles meles</i>)	muscle, liver	5	15	0	0	Simonsen, 1982
"	organs, muscle	2	31	0.014	0.029	Hartl et al., 1988
"	blood	170	23	--	0.087*	Evans et al., 1989
Striped skunk (<i>Mephitis mephitis</i>)	kidney	1	30	0.033*	--	O'Brien et al., 1989
"	blood	15	28	0.038	0.11	this study, Cades Cove pop'n
	blood	8	28	0.040	0.11	this study, Knoxville pop'n
	blood	2	28	0.036	0.11	this study, Iowa pop'n
Stoat (<i>Mustela erminea</i>)	muscle, liver	39	15	0	0	Simonsen, 1982
"	organs, muscle	3	31	0.033	0.075	Hartl et al., 1988
Black-footed ferret (<i>Mustela nigripes</i>)	blood,skin,12 organs	46		0.008	0.02	O'Brien et al., 1989
"	saliva	22	3	0	0	Kilpatrick et al., 1986
Least weasel (<i>Mustela nivalis</i>)	muscle, liver	13	15	0	0	Simonsen, 1982
"	organs, muscle	19	31	0.064	0.225	Hartl et al., 1988
Polecat (<i>Mustela putorius</i>)	muscle, liver	24	15	0	0	Simonsen, 1982
"	organs, muscle	16	31	0.029	0.100	Hartl et al., 1988

species. Such research is important at the current time as background for a number of taxonomic questions, including whether skunks belong in the family Mustelidae (Dragoo, 1996) and for the above-mentioned problems regarding heterozygosity in mustelids. In this part, I present the first allozyme electrophoresis data on average polymorphism and heterozygosity in a population of the striped skunk, *Mephitis mephitis* (Mustelidae).

METHODS

Collection. Samples came from three populations: Cades Cove, Great Smoky Mountains National Park, TN (N=16), Knoxville, TN (N=7) and Dubuque, IA (N=2). I trapped skunks in Cades Cove and Dubuque; those from Knoxville were trapped by VarmintBusters, an animal control agency. All skunks were anesthetized with a 4:1 mixture of ketamine hydrochloride and xylazine (Rosatte and Hobson, 1983; Servin and Huxley, 1992; R. Greenwood, pers. comm.). I obtained 0.5-2.0 ml blood from each animal by cutting into the quick of the claw and collecting the blood that dripped out in a vacutainer containing EDTA. Bleeding was stopped with application of Stiptik powder. Samples were kept on ice until plasma and red blood cells could be separated; both fractions were frozen at -80°C.

Allozyme analysis. All enzyme systems were resolved using horizontal starch-gel electrophoresis. Methods generally followed those used in the laboratory of Dr. Gary McCracken, University of Tennessee, and Selander et al. (1971). Blood fraction, buffer systems, proteins and sample sizes are as follows: for red blood cells, morpholine citrate buffer, LDH I, II, III, IV, V (N=21) and GPI (N=21); tris versene borate buffer, general protein (N=17). For plasma, Tris-HCl buffer, NP (N=25), TO (N=25), and XDH (N=25); morpholine citrate buffer, MDH (N=25), PGDH (N=25), α GPD I, II, III (N=25) and Hb (N=24); tris versene borate buffer, SOD (N=25), ALD (N=25), α NA I, II, III, IV

(N=25) and ADH (N=25); tris citrate pH 8.0 buffer, MEP (N=25) and HBDH I, II (N=25); lithium hydroxide buffer, DIA (N=25); Poulik buffer, PEP (N=23).

RESULTS

Polymorphisms were present at four of 28 presumptive loci examined. Allele frequencies for each of these are given in Table 4-2. One of the polymorphisms (GP) represented a fixed difference between the Iowa population and the two Tennessee populations; therefore, further discussion focuses on the other three polymorphic loci, MDH, Hb and PEP.

There were no significant deviations from HW for the polymorphic loci in Cades Cove or Knoxville; the Iowa population was excluded due to small sample size (see Table 4-3).

No alleles were present in either of the Tennessee populations that were not present in the other, nor were there significant differences between the genotype frequencies in the two Tennessee populations (MDH: $\chi^2=3.127$, d.f.=1, $P=0.0770$; Hb: $\chi^2=0$, d.f.=1, $P>0.9999$; PEP: $\chi^2=0.109$, d.f.=1, $P=0.7409$).

There were two presumed mother-offspring pairs in the data set. Individual P174 was trapped with her son, 23, in Cades Cove and K1 was trapped with her son, K2, in Iowa. P174 and 23 differed in two out of three polymorphic loci for which they were examined; K1 and K2 were identical at all four polymorphic loci.

Average heterozygosity and polymorphism are, respectively: Cades Cove, 0.038 and 0.11; Knoxville, 0.040 and 0.11; and Iowa, 0.036 and 0.11.

DISCUSSION

Striped skunks show levels of polymorphism and heterozygosity consistent with other studies of mustelids (see Table 4-1) and mammals (Nevo, 1978). Caution must be

Table 4-2. Allele frequencies for the polymorphic loci found in a genetic study of striped skunks.

Locus	Allele	<u>Frequency and Sample Size</u>				Iowa	N
		Cades Cove	N	Knoxville	N		
GP	a	0.00	8	0.00	7	1.00	2
	b	1.00		1.00		0.00	
MDH	a	0.69	16	0.36	7	0.50	2
	b	0.31		0.64		0.50	
Hb	a	0.07	15	0.07	7	0.00	2
	b	0.93		0.93		1.00	
PEP	a	0.46	14	0.36	7	0.00	2
	b	0.54		0.64		1.00	

Table 4-3. Observed genotype frequencies (Obs) and genotype frequencies based on Hardy-Weinberg expectations (Exp) for individuals from the Cades Cove and Knoxville populations. There were no polymorphisms in the Iowa population.

Locus	Genotype	Cades Cove		Knoxville	
		Obs	Exp	Obs	Exp
MDH	AA	8	7.62	0	0.91
	AB	6	6.94	5	3.23
	BB	2	1.54	2	2.87
		$\chi^2=0.26$		$\chi^2=2.14$	
Hb	AA	0	0.74	0	0.03
	AB	2	1.95	1	0.91
	BB	13	12.97	6	6.05
		$\chi^2=0.74$		$\chi^2=0.05$	
PEP	AA	2	2.96	1	0.91
	AB	9	6.96	3	3.26
	BB	3	4.08	3	2.87
		$\chi^2=1.2$		$\chi^2=0.05$	

taken in interpreting these results, since relatively few loci (28) and even fewer individuals (17-25) were examined. The following discussion relates the genetic findings reported in this study to what is known about other mustelids and carnivores.

It has been suggested that carnivore species are less genetically diverse because they have low effective population sizes due to their position on the food chain (Baccus et al., 1983). Nevo (1978) supported this argument by suggesting that, across vertebrate taxa, generalists carry higher levels of variability than do specialists. If this pattern holds true within lower taxonomic groupings, as Hartl et al. (1988) suggest, then within the class Mustelidae, omnivorous species such as the skunks should have higher levels of genetic variability than the more specialized weasels. All of the species listed in Table 4-1 are more carnivorous than skunks except the zorilla (*Ictonyx striatus*) and European badger (*Meles meles*). Excluding these two species, and averaging those non-zero values of P and H from studies using more than one individual, there is no indication of a relationship between genetic variability and dietary specialization. For the more specialist weasels, $P=0.11$ and $H=0.05$ whereas for the more generalist skunk, $P=0.014$ and $H=0.04$.

Population structuring, due to polygamy, could also lower the effective population size and cause a decrease in genetic variability (Bonnell and Selander, 1974; Pimm et al., 1989). Unfortunately, although it is believed that striped skunks are polygamous, the only evidence for this is from captive studies (Wight, 1931; Verts, 1967) and nothing is known about mate choice or reproductive success in this species. Therefore, it is difficult to determine whether mating system affects genetic variability in striped skunks.

Several studies (Bonnell and Selander, 1974; Ryman et al., 1977; Packer et al., 1981; O'Brien et al., 1983; Pemberton and Smith, 1985) have suggested that low levels of genetic variability present today are due to past population bottlenecks. Data on past density fluctuations in the populations I sampled are not available. However, other studies have noted large shifts in skunk population density over short periods of time (Stout and

Sonenshine, 1974; Fuller and Kuehn, 1985). Suggested causes for these shifts include disease epizootics and severe winter weather (Gunson and Bjorge, 1981; Wade-Smith and Verts, 1982). I believe the latter may have caused a decline in population density in Cades Cove during the course of my study (see Part 2). An additional possible cause of population fluctuation peculiar to Cades Cove is a striped skunk removal (Great Smoky Mountains National Park has maintained no record of this action, but Park officials agree that approximately 80 striped skunks were removed from the campground area in about 1988; K. DeLozier, pers. comm.; E. Wanrow, pers. comm.). Crucial to understanding the genetic implications of a bottleneck are the effective population size prior to the event, the length of the population reduction and the speed of recovery of population size (Nei et al., 1975). Again, none of this information is available for the sampled populations. However, it is apparent that skunks have the ability to quickly increase in numbers (Fuller and Kuehn, 1985; litter size averages eight, Wade-Smith and Verts, 1982) and therefore rapidly recover from a bottleneck.

Population fragmentation is also known to reduce genetic variability (Pimm et al., 1989; Wayne and Koepfli, 1996). Notable examples are the Gir Forest lions (*Panthera leo*, O'Brien et al., 1987), Florida panther (*Felis concolor*, Roelke et al., 1993) and Isle Royale wolves (*Canis lupus*, Wayne et al., 1991). However, it is not always clear what constitutes a population; Wathen et al. (1985) found unusually high levels of genetic variation in black bears (*Ursus americanus*) in Great Smoky Mountains National Park and suggested that this could be because the entire Southern Appalachian region might comprise one black bear population. It is possible that the forested areas surrounding Cades Cove, form a partial dispersal barrier to skunks. Possible dispersal barriers within the Knoxville population are unknown. There is no evidence from genotype frequencies or other data that Knoxville is genetically separated from Cades Cove, or that there is fragmentation within these populations.

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PART FIVE
CONCLUSIONS

SUMMARY

In this study, I examined 1) the relationship of morphological and ecological variables with striped skunk spacing patterns and movements; 2) habitat preferences in home ranges and den sites; 3) genetic variability within populations of skunks and 4) the biochemistry of lipids in skunk musk.

Of six variables expected to impact home range size (season, body size, latitude, habitat, sex and number of radio fixes), only the first two showed any significant effect. Home ranges were smaller in the winter than in the spring, and larger females had larger home range sizes. The former effect is apparently due to skunks leaving their winter dens to search for food and mates in the spring. The latter is not immediately explicable, but could relate to methodology (the sample of skunks radio collared), seasonal fluctuations in the weight of skunks or energy requirements.

The data on movement patterns are consistent with those on home range size. Striped skunks appear to be moving faster as well as utilizing larger home ranges in the spring than in the winter.

Home range overlap was extensive (up to 100% of an individual's home range) and did not show the expected pattern of intrasexual territoriality. I cannot tell whether this is due to abundant resources at the study site, the unusual sample of skunks radio collared or some other factor.

There was no clear pattern of habitat preference in home range and den usage, but there is some indication of a preference for ecotones. All skunks included both forest and field habitats within their home ranges, and many of these ranges were elongated parallel to forest-field ecotones. The majority of den sites were located in edge areas as well. The relationships between habitat preference and weight or sex were either contradictory or not significant. Interestingly, several examples of communal denning and long-term den use were found, despite expectations that this would not occur so far south.

Genetic variability in the striped skunks was similar to that found in most other populations of mustelids and other carnivores. There were no differences in genotype frequencies between two populations studied.

Biochemical analysis of skunk musk focusing on lipids yielded sixty compounds, including polar, neutral and glycolipids. This is a larger number and a more diverse array of compounds than those found previously. There were individual differences in the presence and quantities of lipids, but no explanation for why such differences occur.

SUGGESTIONS FOR FUTURE WORK

Several lines of future work may originate from this dissertation. It is obvious that little is known of striped skunk home range size, especially in certain geographical areas (the south and west U.S.) and habitats (forest, arid and urban). Researchers attempting to fill in these gaps should take pains to radio track skunks throughout the year, and should analyze their data with respect to such variables as weight, sex and habitat. Factors that were apparently not important in this study could prove pertinent under other circumstances or with larger sample sizes.

These same suggestions apply to research on striped skunk movements, since we have very little idea what variables affect their movements. To study this, it would also be beneficial to obtain radio locations of skunks on a set time schedule, e.g., every 15 min, throughout the night. Direct observations could be used to determine when skunks were moving and when they were resting.

Home range overlap in this study was extensive and apparently random, but that could be due to the abundant anthropogenic food sources in the study area. A comparison of my results with data from a more pristine setting would be very interesting. Concurrent research on food availability and scat analysis is an additional factor that would improve such a study.

As mentioned above, any future analysis of habitat use in striped skunks should consider other habitats. This type of research would also benefit from a study site less influenced by people, although skunk habitat use in an urban area has not been studied before and should yield results useful at an applied level. Since dens are of such importance to this animal, and we know that denning behavior varies seasonally (communal in winter but solitary or mothers with kits the rest of the year), an analysis of variables important in den selection during different seasons ought to be interesting. This, again, would require a larger sample size, and a study that lasts throughout the year.

Greater understanding of striped skunk genetics may benefit us in related taxonomic discussions such as whether skunks are mustelids or a separate family (mephitids, Dragoo, 1996). Knowledge of skunk genetics also allows us to ask interesting questions at an individual level, such as whether variations in skunk musk correlate with differences in relatedness. This might be expected if musk is used to communicate individual identity.

My research, and that of Wood (1990), clearly indicates that skunk musk could be used in communication. Aside from further chemical analyses, research on this subject might best be conducted in a captive setting (in an area isolated from people). Such studies should examine any reactions to and preferences for the musk of one skunk by another. This may vary by sex, reproductive status, age and dominance of both individuals involved. In addition, it is important to discover whether skunks possess any glands besides the anal glands that could be important in chemocommunication. Such glands, if they exist, have been overlooked, for obvious reasons. Comparative studies of the phylogenetically unrelated, but morphologically and behaviorally similar zorilla (*Ictonyx striatus*) could shed light on the function and evolution of skunk musk. Such information would also relate to discussions of aposematic coloration: Do individuals with greater concentrations of smelly compounds look different from those that produce less offensive

odors? Of course, before this can be tested, it must be known whether an individual's musk changes over time.

Furthering our knowledge of the striped skunk would be of benefit from scientific and applied standpoints. This species is both common (throughout its range) and unique (in its biology) and should no longer be neglected as a research animal.

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APPENDIX ONE

**MECHANISMS OF HOME RANGE USE: THE BIOCHEMISTRY OF
STRIPED SKUNK MUSK**

INTRODUCTION

Two non-mutually exclusive explanations have been proposed for the function of skunk musk. Most scientists [from Darwin (1871) to Verts (1967) and Wood (1990)] have discussed musk as a mechanism of defense against predators. Only Coues (1877, p 214) suggested that it might additionally be used in intraspecific communication: the relation of skunk spray "to the perpetuation of the species, though overshadowed by its exaggeration into a powerfully effective means of preservation of the individual, is evidently the same as in other species of *Mustelidae*, each one of which has its own emanation to bring the sexes together. . ." The relatively large size of the olfactory bulb of skunks (Gittleman, 1991) and behavioral studies indicating that olfaction is important in their foraging behavior (Nams, 1991), suggest that skunks could use odor for communication among conspecifics.

The study of skunk musk has a long history, and some aspects of its biochemistry are well known (Aldrich, 1896; Aldrich and Jones, 1897; Stevens, 1945; Anderson and Bernstein, 1975; Anderson et al., 1982; Wood, 1990). Most recently, Wood (1990) used gas chromatography and other methods to identify seven major compounds in the musk of striped skunks (*Mephitis mephitis*). These include three thiols (of which (E)-2-butene-1-thiol is the most repulsive smelling), three thioacetates and one alkaloid.

Wood's (1990) method of dissolving musk in diethyl ether for gas chromatography allows for the identification of simple organic molecules. The sulfur compounds identified in this manner are probably those that smell offensive to potential predators. However, skunk musk may also contain lipids, some of which would not dissolve in this solvent. These lipids may serve a different function in musk than the molecules that dissolve in ether and may be important in conspecific communication (Gawieniowski, 1977).

Parallel work by Decker et al. (1992) involved analysis of lipid components in the anal glands of three mongoose species. Anal sac secretions of mongooses had previously been analyzed using hexane solvents, which only reveal straight-chain hydrocarbons.

Decker et al. revealed more complex compounds which they hypothesized to be the communicative portion of the scent.

In this part, I compare the results of a lipid analysis of skunk musk to those of the more traditional analysis of Wood (1990).

METHODS

Collection. Anal gland secretions were collected from six anesthetized skunks obtained from VarmintBusters, an animal control agency in Knoxville, TN. Sterilized cotton swabs were inserted into the anus, withdrawn and immediately placed in Teflon-lined screw-capped test tubes. Tubes were frozen at 5°C until analyses could be performed. Control swabs were waved in the air 1-2 m away from the skunks (no skunk had sprayed during the process) and then inserted in test tubes and frozen as above. Samples 1 and 2 were from male skunks; sex was not recorded for the other samples.

Materials. Solvents were chromatographic grade quality purchased from J. T. Baker Chemicals Co., Phillipsburg, NJ. Derivatizing agents were purchased from Supelco, Inc., Bellefonte, PA, Applied Science, State College, PA, Aldrich, Inc., Milwaukee, WI, Sigma Chemical Co., St. Louis, MO and Pierce Chemical Co., Rockford, IL.

Extraction, Lipid Isolation and Analysis. Methods generally followed Decker et al. (1992) and are shown schematically in Figure A-1. Anal gland secretions were extracted with a modified Bligh and Dyer solvent system (White et al., 1979). The aqueous phase underwent acid hydrolysis and TMS-derivitization before analysis by GC/MS. Total lipid was applied to the top of a silicic acid column and washed sequentially with 5 ml of chloroform, acetone and methanol to elute non-polar, glyco- and phospholipids,

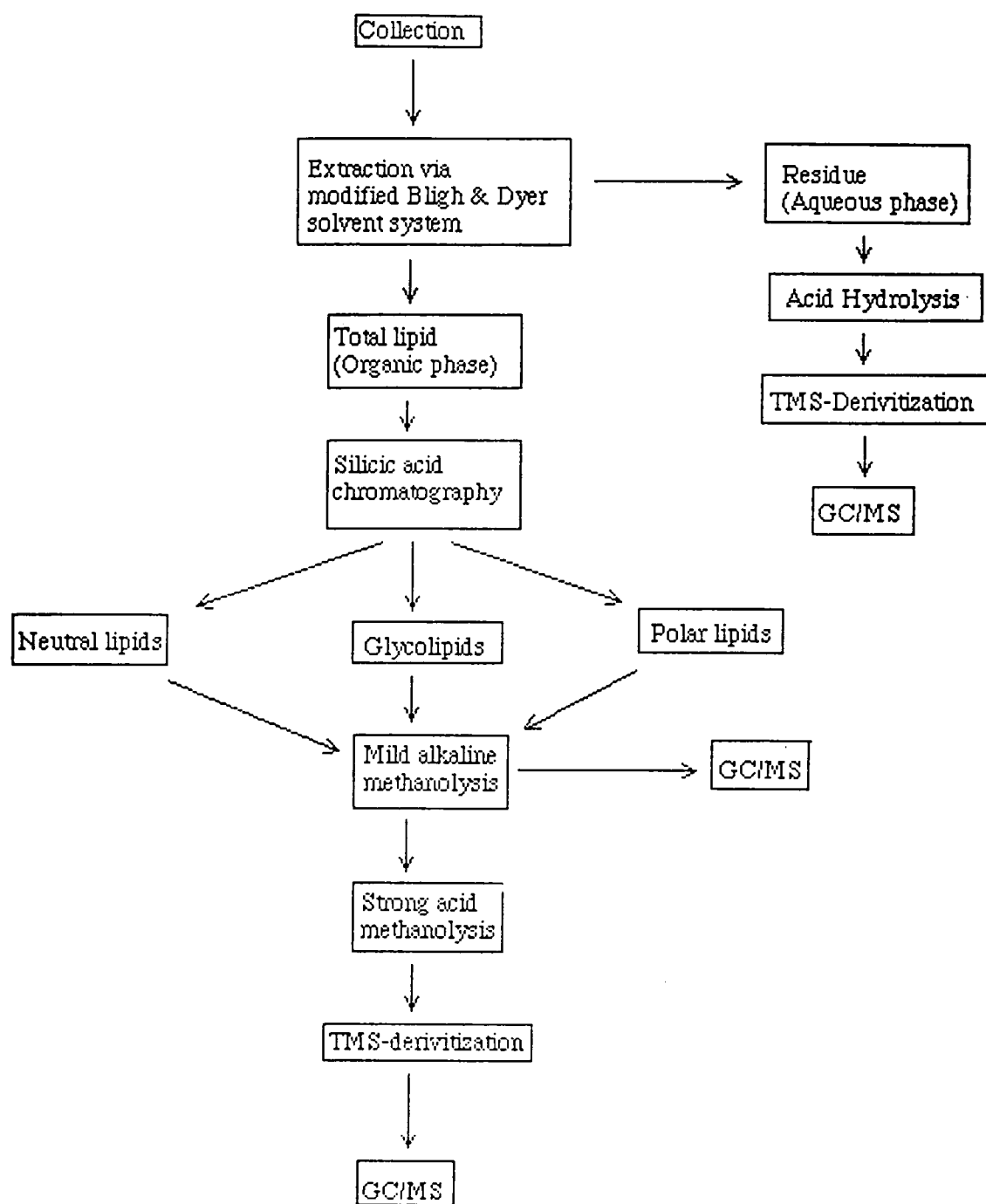


Figure A-1. A flow diagram of the biochemical procedures used in a study of skunk musk.

respectively. Each fraction underwent mild acid methanolysis, after which part of it was analyzed by GC/MS and part underwent strong acid methanolysis and TMS-derivitization before GC/MS analysis.

RESULTS

Compounds determined from transesterification are listed in Table A-1. Twenty-one compounds were revealed in the polar lipid fraction; 13 are prokaryotic in origin, 6 are eukaryotic and 2 are aromatic, which could originate from prokaryotes or eukaryotes. Of the 29 neutral lipids, 9 are prokaryotic, 16 eukaryotic and 4 aromatic. The 18 glycolipids include 7 compounds of prokaryotic origin and 11 eukaryotic ones.

Acid hydrolysis yielded no additional compounds; this was because the controls contained such high concentrations of components. Only compounds present in the experimentals and not in the controls were identified.

DISCUSSION

Sixty different compounds, including polar, neutral and glycolipids, were identified from skunk musk. Sequential elution by chloroform, acetone and methanol led to the discovery of a larger number of compounds, and more diverse and complex compounds than those found by Wood (1990). I found individual differences in occurrence of compounds in the musk, as did Wood (1990).

Relatively few compounds were determined from skunk anal gland secretions as compared to mongooses. There are three possible non-exclusive reasons for this. 1) The three mongoose species [dwarf mongoose (*Helogale parvula*), meerkat (*Suricata suricatta*), and kusimanse (*Crossarchus obscurus*)] were social and are known to use scent-marking in a variety of situations (Decker et al., 1992). Skunks are solitary and are not known to release anal sac secretions except when threatened by potential predators (Wade-Smith and

Table A-1. Results of the biochemical analysis of skunk musk. Compounds are divided into polar, neutral and glycolipids and the quantities of each compound are given in % moles.

Compound	Samples					
	1	2	3	4	5	6
POLAR LIPIDS						
12:0	0.49	0.90	0	0	0	0
14:0	2.92	1.72	3.48	2.42	1.85	1.54
i15:0	0.91	0	1.36	0	1.319	1.37
a15:0	0.54	0	0	0	0	0
15:0	1.00	0	0	0	0.78	2.19
16:1w9c	0	1.37	0	0	3.09	0
16:1w7c	1.76	1.03	4.83	1.70	1.54	0
a17:0	0.74	0	0	0	0	0
cy17:0	4.05	0	0	0	0	0
17:0	0.97	2.72	0	0	0	0
18:1w7c	7.13	5.54	2.60	3.01	4.30	3.18
19:1w6c	1.00	0	0	0	0	0
cy19:0	2.76	0	0	0	0	0
<i>Total</i>						
<i>Prokaryotic</i>	24.28	13.28	12.27	7.13	12.76	8.29
16:0	39.28	22.76	40.61	36.30	21.58	36.46
poly18	0	0	0.83	3.36	10.23	0
18:2w6	8.26	8.29	4.49	2.52	2.64	3.15
18:0	14.84	11.35	35.37	33.86	26.39	42.14
poly20	0	0	0	3.53	8.55	0
<i>Total</i>						
<i>eukaryotic</i>	75.09	56.05	87.73	92.87	87.24	91.71
phenol-a	0.63	4.05	0	0	0	0
phenol-b	0	7.83	0	0	0	0
<i>Total</i>						
<i>aromatics</i>	0.63	11.88	0	0	0	0

Table A-1 (continued).

Compound	Samples					
	1	2	3	4	5	6
NEUTRAL LIPIDS						
14:0	0.56	0.52	2.83	0	0	2.15
15:0	0	0.78	9.00	1.10	2.72	5.62
a15:0	0.75	0	0	0	0	1.67
15:0	4.19	0.26	0	0	1.29	8.96
3OH14:0	0.57	0	0	0	0	0
16:1w9c	1.82	2.73	0	1.61	3.33	0
16:1w7c	4.69	0.73	10.62	0	2.25	3.95
17:0	2.69	0.87	0	1.53	0	3.64
18:1w7c	0.63	5.26	0.93	3.66	5.30	0
<i>Total</i>						
<i>prokaryotic</i>	15.90	11.15	23.39	7.89	14.89	25.99
16:0	13.66	12.09	133.45	12.18	10.74	21.69
18:3w6	0.57	0	0	0	0	0
18:2w6	0.97	2.94	1.09	0.87	1.54	1.28
18:3w3	3.83	2.00	0	0	0	0
18:1w9c	3.93	18.54	3.12	16.67	24.99	4.20
18:0	7.00	15.86	12.95	36.68	16.96	10.47
20:0	2.27	1.83	6.18	5.91	3.84	4.17
21:0	1.37	0.36	0.90	1.26	0	0
22:0	1.71	0.98	2.44	3.19	2.08	2.33
23:0	0.53	0	0	0.52	0	0
24:0	0.83	0.85	0.88	1.24	0	1.03
squalene	0	0.36	0	0	0	0
sterol-1	2.94	0	0	0	0	0
sterol-2	1.31	0	0	0	0	0
cholesterol	0	6.98	2.97	2.89	3.65	4.74
stigmasterol	0	1.20	0	0	0	0
<i>Total</i>						
<i>eukaryotic</i>	40.92	64.00	63.97	81.38	63.79	49.92
aromatic						
phenanthrate	0.90	4.00	0	0	0	0
phenol-a	1.68	0.65	0	0	0	0
phenol-b	0.44	0	0	0	0	0
<i>Total</i>						
<i>aromatics</i>	3.02	4.65	0	0	0	0

Table A-1 (continued).

Compound	Samples					
	1	2	3	4	5	6
<u>GLYCOLIPIDS</u>						
14:0	0.89	0	0	0	0	1.62
a15:0	0	0	0	0	0	1.41
15:0	1.86	0	0	0	0	3.44
3OH14:0	0.52	0	0	0	0	0
16:1w7c	1.93	0	0	0	0	1.68
a17:0	1.21	0	0	0	0	2.42
17:0	1.93	0	0	0	0	2.51
<i>Total</i>						
<i>prokaryotic</i>	8.34	0	0	0	0	13.09
16:0	29.62	0	0	0	0	21.80
18:2w6	3.86	0	0	0	0	2.15
18:1w9c	4.50	0	0	0	0	6.93
18:0	25.75	0	0	0	0	27.86
20:0	0.85	0	0	0	0	11.64
21:0	1.97	0	0	0	0	0
22:0	0	0	0	0	0	5.44
sterol-1	10.13	0	0	0	0	2.71
sterol-2	2.71	0	0	0	0	2.95
cholesterol	1.21	0	0	0	0	0
stigmasterol	9.80	0	0	0	0	1.83
<i>Total</i>						
<i>eukaryotic</i>	90.41	0	0	0	0	83.31

Verts, 1982) or in intraspecific aggression (pers. obs.; D. G. Weller, pers. comm.). The few compounds identified from skunk spray may indicate an adaptation to produce only those compounds crucial for defense or, conversely, the many compounds of the mongooses may represent an adaptation to provide detailed information in intraspecific communication. 2) Variability of compounds identified in mongoose secretions could be due to environmental factors not relevant in skunks. For instance, 11 additional compounds noted in dominant but not subordinate dwarf mongooses could result indirectly from a dominance hierarchy. 3) The acid hydrolysis yielded very little or no material in the experimental samples that was not in the controls. This may indicate that lipids from the environment (e.g., from the collector's hands or on the swabs themselves) contaminated the samples. Future studies should circumvent this problem by using a syringe or Teflon swab, pre-cleaned with solvent, to collect samples for storage in pre-cleaned tubes. Use of a syringe would also allow for capture of volatile compounds which are undoubtedly important in skunk spray, but which would be lost when the swab was removed from the skunk and transferred to the test tube.

Many compounds of prokaryotic origin were apparent in each fraction. It is unlikely that samples became contaminated after they were collected since they were stored in Teflon-lined screw-capped tubes on ice until they could be frozen. It is possible that there was bacterial contamination on the swabs or tubes; they were sterilized before use but lipids could have remained. A more likely possibility is that bacteria were picked up from the anal region of the skunk; these could be bacteria associated with the gut or anal sacs (as in red foxes (*Vulpes vulpes*), Albone et al., 1974; or small Indian mongooses (*Herpestes auropunctatus*) Gorman, 1976). Wood (pers. comm.) thought that some of the variation between samples of skunk spray in his study (Wood, 1990) could be due to bacterial action between the time of death of the skunks and removal of the sample.

The origin of the aromatic compounds in the neutral and polar lipid fractions is uncertain, but these odoriferous compounds are consistent with an origin in skunk spray. Although the sex of 4 skunks was not determined, the two known to be male (samples 1 and 2) show lipid profiles very different from each other. While this does not rule out sex differences in skunk spray lipids, it suggests that sex differences might be obscured by individual differences. This was also suggested by Wood, who found that individual differences were greater than interspecific differences (Wood, pers. comm.; Wood et al., 1991; Wood et al., 1993).

In this study, it was not possible to test hypotheses about the possible communicative function(s) of skunk musk because of problems mentioned above. However, further work could resolve whether there are differences in skunk musk between the sexes or between estrous and anestrus females. This would be expected if, as Coues (1877) suggested, musk plays a role in skunk mating behavior.

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VITA

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