THE UNIVERSITY OF MANITOBA

The Ecology and Distribution of

Mustela <u>frenata</u> <u>longicauda</u> Bonaparte

and its Relationships to Other

<u>Mustela</u> spp. in Sympatry

by

Robert Lloyd Gamble

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ROBERT LLOYD GAMBLE

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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ABSTRACT

Data were obtained for <u>Mustela</u> spp. from May 1977 to
December 1978 on habitat utilization from 24,583 trap nights,
winter track analysis, and description of capture sites of
specimens secured by trappers in southern Manitoba. <u>M</u>. <u>frenata</u>
prefers late seral stages in close proximity to water in which
prey species diversity is greatest. <u>M</u>. <u>erminea</u>, the short-
tailed weasel, selects early successional communities. <u>M</u>.
<u>rixosa</u> was found in wet meadow and grassland communities.
Habitat selection in weasels is a function of the availability
of prey. Under optimal conditions sociability in <u>M</u>. <u>frenata</u>
may define distribution. In areas of sympatry <u>M</u>. <u>frenata</u> will
displace other weasel species by means of interference inter-
actions.

Gut (n = 203) and scat (n = 95) analyses and laboratory
feeding trials revealed that long-tailed weasels are generalists
and short-tailed weasels are specialists. Weasel hunting sets
partition resources by means of the proportion of prey species
consumed. Diet in weasels is a function of the frequency of
occurrence and biomass of prey species.

Long-tailed weasels form aggregations in optimal habitat.
These animals occupy common home ranges and share in a common
gene pool or "deme". Demetic units are likely patrilineal
groupings. In sub-optimal habitat, spacing in <u>M</u>. <u>frenata</u> is
a function of availability of prey. Home ranges are established
accordingly. Interference interactions between <u>M</u>. <u>frenata</u> and
<u>M</u>. <u>erminea</u> are less in sub-optimal habitat than areas in which

<u>M</u>. <u>frenata</u> establishes social units.

Populations of <u>M</u>. <u>erminea</u> are more transient during high vole years. Home ranges are established when resources are limiting. Home ranges are not exclusive to conspecifics.

Long-tailed weasels are crepuscular but will adjust activity in relation to their prey. Male <u>M</u>. <u>frenata</u> hunt mid-sized prey above the snow surface while females are subnivean in activity. Male <u>M</u>. <u>erminea</u> move freely over the snow surface using aŋmaŋa and rodent ventilator shafts for access to the subnivean space, and hence, prey species. Female <u>M</u>. <u>erminea</u> most often use subnivean runways to capture voles.

Long-tailed weasels are characterized by highly variable modes of social organization, ranging from solitary and transient individuals to gregarious and stable groups. Males share parental care with females. Males are dominant to all other sex or age classes except possibly pregnant or oestrous females. Parental investment was observed in <u>M</u>. <u>erminea</u> but is less frequent than <u>M</u>. <u>frenata</u>.

Male <u>M</u>. <u>frenata</u> are sexually mature at two years of age judging from baculum development and weight. Juvenile female <u>M</u>. <u>frenata</u> rarely breed in their first summer. Spring breeding may occur in this age class. Adult female <u>M</u>. <u>frenata</u> exhibit delayed implantation.

Baculum weights and morphology can be used in ageing male <u>M</u>. <u>frenata</u>.

The northern-most distribution of M. frenata longicauda in western Canada is the transition zone adjacent to the Boreal Forest. Distribution is a function of prey species diversity and of the proximity to water. Waterways may provide access corridors to suitable habitat.

A thorough examination of M. frenata and a cursory examination of M. erminea revealed that 100 per cent parasitism by Skrjabingylus nasicola occurred in both hosts. Cranial damage was significantly greater in pooled samples of M. erminea than in pooled samples of M. frenata. In M. frenata damage varied with sex and age. The percentage of infestation and damage is a function of diet and the relative humidity of the microenvironment. Circumstantial evidence suggests that rodents, shrews, amphibians and reptiles are paratenic hosts for S. nasicola.

ACKNOWLEDGEMENT

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INTRODUCTION

Little comprehensive field work has been done on the long-tailed weasel, Mustela frenata, despite numerous studies throughout North America. Many hypotheses and theories have been postulated, often from inadequate data, and applied to all North American subspecies. M. frenata subspp. vary both in size and morphology which often governs the physical capabilities of the predator in procuring prey.

Resource partitioning is a major determinant of the diversity of coexisting species within a community. Mustela species frequently occur in hunting sets (Rosenzweig 1966) which are structurally similar. Generally, two species can not coexist unless they exploit their environment differently (Hardin 1960). Researchers often suggest that in sympatry, weasel hunting sets compete for resources. M. erminea like M. frenata exhibits morphological variation. This variation, in a similar manner, should affect this species' life history strategy.

My study presents information on habitat utilization, food habits, home ranges, activity, reproduction, longevity, parasitism, distribution and social behaviour for M. f. longicauda. Similarly M. erminea is reviewed in terms of resource partitioning.

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CHAPTER I

Distribution and habitat selection in

Mustela frenata longicauda, the

long-tailed weasel and M. erminea richardsoni,

the short-tailed weasel.

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ABSTRACT

Data were obtained for Mustela spp. from May 1977
to December 1978 on habitat utilization, home ranges and
activity from 24,583 trap nights, winter track analysis, radio
telemetry, and descriptions of capture sites of specimens
secured by commercial trappers in Manitoba. M. frenata
prefers late seral stages in close proximity to water in
which prey species diversity is greatest. M. erminea,
the short-tailed weasel, selects early successional stages.
M. rixosa was found in wet meadow and grassland communities.
Habitat selection in weasels is a function of the availability
of prey. Under optimal conditions, sociability in M. frenata
may define distribution. In areas of sympatry M. frenata
will displace other weasel species by means of interference
interactions.

Long-tailed weasels form aggregations in optimal habitat
and are social. These animals occupy common home ranges
and share in a single gene pool or "deme". Long-tailed
weasels are characterized by highly variable modes of social
organization, ranging from solitary and transient individuals
to gregarious and stable groups. Populations of M. erminea
are more transient during high vole years. Home ranges are
established when resources are limiting.

INTRODUCTION

Many ecological studies centre around competitive interactions and community structure (Smartt 1978). Community structure is, in part, the result of resource partitioning. Food type, habitat and activity are dimensions along which species partition their resources (Schoener 1974).

The main objective of this study is to examine resource partitioning in two sympatric carnivores, Mustela frenata longicauda Bonaparte and M. erminea richardsoni Bonaparte in terms of distribution and habitat selection. To understand community dynamics one must quantify resource utilization among community members.

Predators often coexist in hunting sets with other predators of similar morphology and hunting abilities (Rosenzweig 1966). The principle of competitive exclusion states that coexisting species must differ in their ecological requirements to prevent competitive exclusion (Pianka 1974). In weasel hunting sets, each species has specialized on some interval of the resource axis; such an interval may be a coexistence stabilizing force (Rosenzweig 1966).

MATERIALS AND METHODS

Study area

Preliminary live trapping studies were conducted in four Manitoba localities from May to July 1977 - Melbourne (49°51'N 99°10'W), Pratt (49°42'N 98°55'W), Treherne (49°37'N 98°40'W) and Delta (50°10'N 98°22'W) - in order to locate sites suitable for mark and recapture. Delta was selected and trapped from July 1977 to December 1978. Delta is situated within the east-west transition zone and contains flora and fauna native to both types (Simpson 1964). Southern Manitoba is characterized by warm summers, cold winters and moderate seasonal precipitation. The mean July and January temperatures for the region over 30 years are 19.8°C and -17.2°C respectively. Mean annual precipitation is 560 mm with an annual snowfall of 154.8 cm. The annual snowfree period normally extends from April 10 to November 5 (Atmospheric Environment Service).

Two sites were selected at Delta: (1) the Oxbow community consisting of 90 hectares of woodland, 125 hectares of farmland and 185 hectares of old field succession, prairie and wet meadows (Fig. 1) and (2) the beach ridge-marsh wet meadow encompassing 50 hectares of sand beach, jetsam and wooded ridge and 150 hectares of marsh and wet meadows (Fig. 2).

The dominant species in the Oxbow woodland were oak
(<u>Quercus</u> <u>macrocarpa</u>), elm (<u>Ulmus</u> <u>americana</u>), ash (<u>Fraxinus</u>
<u>campestris</u>), Manitoba maple (<u>Acer</u> <u>negundo</u>) and poplar
(<u>Populus</u> <u>tremuloides</u>) (Evans 1972; Kgorba 1980). The Oxbow
woodland border had an extensive shrub layer which includes
hawthorne (<u>Crataegus</u> spp.) hazelnut (<u>Corylus</u> spp.), plums,
pin cherry and chokecherry (<u>Prunus</u> spp.) raspberry (<u>Rubus</u>
<u>strigosus</u>), wild rose (<u>Rosa</u> spp.), snowberry (<u>Symphoricarpos</u>
<u>occidentalis</u>) and saskatoon (<u>Amelanchier</u> <u>alnifolia</u>). The
understory consisted of herbaceous plants. The wet meadows
consisted chiefly of spangle-top (<u>Scholochloa</u> <u>festucacea</u>),
sow thistle (<u>Sonchus</u> spp.) and wild barley (<u>Hordeum</u> <u>jubatum</u>).
The grassland communities consisted of a variety of grasses,
snowberry, raspberry and wild sunflower (<u>Helianthus</u> spp.)
Old field successional communities differed from 'prairie'
simply by the presence of domestic cultivars (ie. white clover).
Farmland was divided into two categories: (1) seasonal crops
under tillage and (2) hayland (alfalfa and clover).

The dominant species of the wooded ridge were Manitoba
maple, green ash, peach-leaved willow (<u>Salix</u> <u>amygdaloides</u>)
and sandbar willow (<u>S.</u> <u>interior</u>) with an extensive herb layer
(MacKenzie 1979). The marsh consisted of reeds (<u>Phragmites</u>
<u>communis</u>), cattails (<u>Typha</u> <u>latifolia</u>) and bulrush (<u>Scirpus</u> spp.)

Trapping and handling

Data on habitat selection and activity were attained through live trapping and radio telemetry. Three kinds of traps were initially used: (1) Sherman-type traps, (2) Tomahawk live traps (models 201 and 202) and (3) Burt wooden treadle traps (45 cm x 15 cm X 15 cm and 60 cm x 20 cm x 20 cm) (Burt 1940, Mosby 1955). Burt live traps were most suitable and were used for the duration of the study. Tomahawk traps (model 201) were suitable for summer work but were not used in the winter because of their metal structure which facilitates heat loss. Nesting material was placed within traps. Baits, including microtines, scuirids, leporids, beef kidney and liver and fish were used in conjunction with weasel scent and/or weasel scats. Baits were replaced as needed. Traps were checked twice daily (after sunrise and before sunset). Trapping was conducted in all months but not uniformly in all areas. Traps were closed on days in which the weather was prohibitive (e.g. windchill > 2300 watts m^{-2} or during severe rain showers). Traps were placed on natural runways (i.e. brush piles, along the sides of roads or ditches, transition zones (edges), culverts, and fencelines (Musgrove 1951; Rust 1968, Erlinge 1974).

The ridge and marsh-wet meadows were live trapped with 7,422 trap nights from July 1977 to July 1978, while Oxbow was trapped with 13,853 trap nights between July and December 1977 and May and December 1978.

Weasels were held temporarily in aquaria before and after anaesthesia. Live prey, water and bedding were provided. Weasels were put in a pillow case in which they were restrained. Sernylan (phencyclidine hydrochloride - Bio - ceutic Laboratories, Inc.) was administered (0.2 mg/100 g bodyweight) in the upper hind leg by using a one ml syringe. Animals were weighed, measured (total length, tail length, hind foot and ear length) and marked by toe clipping, ear notching and ear tagging (size #1 National Band and Tag Co.). Ear tagging was discontinued as tags annoy the animal and were frequently torn off. The technique of photographing the ventral surface of the body suggested by Linn and Day (1966) was found to be unsatisfactory for individual identification in weasels. Recaptured individuals were identified and weighed (gross weight - tare weight = net) within the trap. Each animal was released at the site of capture.

Movements of M. frenata were monitored with telemetry from August to November 1978. An SM1 transmitter and model LA12 (AVM) receiver were used. The transmitter's tuning wire and antenna were approximately 15 and 20 cm respectively. A 1.4 volt battery served as an energy source, giving a signal life of 30 to 60 days. Batteries were checked prior to installation. A three element hand-held yagi antenna was used to receive the signal. Advantage was taken of any available

elevation. Triangulation provided a fix on an individual
and by using signal strength the animal could be approached
to within 5 m. Readings were recorded twice daily.

The radio transmitter was attached to a deerhide vest
which in turn was attached to the animal in a manner that
did not hinder movement of the weasel (Fig. 3). The unit
was placed between the shoulder blades. The tuning wire
was positioned anteriorly around the neck within the confines
of the vest. The antenna ran posterior to the margin of
the vest, circled the abdomen and was allowed to protrude
posteriorly (Fig. 4). The vest was sewn ventrally with
nylon line and excess material removed. Total weight of
the entire package never exceeded 17 g.

Tracking

Winter track surveys were made to determine habitat
utilization and movement for one season in 1977-78.

RESULTS

Five long-tailed weasels Mustela frenata, 59
short-tailed weasels, M. erminea, one least weasel,
M. rixosa and two mink, M. vison were trapped in 1977
and 20 long-tailed weasels, 39 short-tailed weasels, five
least weasels and two mink in 1978. Only six short-tailed
weasels and two long-tailed weasels were recaptured more
than once in 1977 and 14 short-tailed weasels and 10
long-tailed weasels in 1978. In total 22 individual
long-tailed weasels were captured 45 times and 78
short-tailed weasels 163 times. Recaptures of both species
were predominantly males.

Figures 5 and 6 indicate the capture sites for M.
frenata at Oxbow for 1977 and 1978. Recaptures were included
in the site count when an animal had not been captured at
the site previously in a given year. In total 32 captures
were made at 12 sites.

Figure 7 depicts the capture sites of other Mustela spp.
for 1977-78 at Oxbow. Thirty-one short-tailed weasels were
captured 40 times at 29 sites. Captures of M. rixosa and M.
vison were single events.

Forty-seven short-tailed weasels, two long-tailed
weasels, three least weasels and one mink were trapped on
the beach ridge and in the marsh-wet meadow from July 1977
to July 1978. One male long-tailed weasel resided in the

vicinity of the field station from June 1977 to April 1978
(Fig. 8). Occupation did not persist for the entire period,
rather, he would disappear from the immediate vicinity for
periods up to two months. Abandonment was observed both in
summer and winter. A female long-tailed weasel reoccuppied
the site in May 1979 and remained until her death in April
1980. She did not exhibit periods of transience as had
the male. The second long-tailed weasel, a transient male,
caught in early June 1978, died of trap fatigue during a
violent storm.

Data collected by mark and recapture techniques for
short-tailed weasels on the ridge were sufficient to provide
density estimates for the snow-free periods: August - November
1977 and April - July 1978. An 11.2 hectare section of the
beach ridge had a density of 2.6 ermine per hectare including
transients in 1977 or a density of 0.9 ermine per hectare for
residents. The density estimate for 1978 was 0.5 ermine per
hectare for residents. No transients were present.

A reliable density estimate for the marsh and wet meadow
could not be calculated due in part to the nature of cover
and the subjective placement of traps. Nevertheless weasel
populations were lower (2 and 8 per 150 hectares) in the
marsh and wet meadows relative to those observed on the
beach ridge.

From November to March wind-blown snow progressively accumulates on the north face of the ridge resulting in weasels moving to the leeward side including the marsh and meadows. Here, snow accumulates over the vegetation as a thick mat (Fig. 9) resulting in the formation of snow caves readily accessible to _Mustela_ spp.

Figure 10 depicts the distribution of five male ermine during the winter of 1977-78 and is characteristic of home ranges exhibited by other males in this area. Females were repeatedly caught at one site, which, judging from track analysis, was their centre of activity. Most female activity was subnivean within snow caves and rodent tunnels. A female which was repeatedly caught on the snow surface had a home range of 5 hectares. Home ranges occupied by males at this time ranged from 8 to 28 hectares. One female, after snow melt, was found residing in an abandoned ground squirrel hole in which she later reared a minimum of two offspring. Male A (Fig. 10) frequented the den and may have been assisting in parental care judging from capture records and scat deposition.

Males A, B, D, and R overlap in home ranges extensively. All four were caught repeatedly at site D_1. A, B and C on one occasion were caught within a radius of 100 meters from one another. The resident male long-tailed weasel was also foraging in the immediate area. No area was mutually exclusive from conspecifics though females confined activity to relatively localized areas.

Figure 11 presents the distribution of three males
which established residency on the ridge from May - July
1978 in addition to males A and C. K had established
residency at Oxbow from August to October 1977. If K's
home range is considered in entirety for both 1977-78,
K would occupy a minimum area of 260 hectares.

Figure 12 and 13 outline the distribution of 6 female
long-tailed weasels. Females were less mobile than males and
occupied a minimum area of 7 hectares and a maximum of 62
hectares. Females are relatively localized in their movements
but areas of occupation are not mutually exclusive.

Figure 14 outlines the distribution of 3 male M. frenata.
The ranges of 4 other males overlap with those depicted.
Ranges appeared to be shared and not mutually exclusive. Male
M and N on occasion were in direct contact. Male M was
more localized in his movements in contrast to male N which
moved freely within the group range. M and N were present
in both 1977-78. Male M was reared in a den (Fig. 15) in
which N participated in parental care. Another adult
resident male (2^{+} years) occupied an area which coincided with
male N. This male also was caught at the den in which N
provided parental care. The remaining males moved freely
within the occupied area.

Figure 15 depicts the distribution of M. frenata at
Oxbow determined by radio telemetry, capture records, and sight-
ings. Sixty-nine per cent of all weasel activity occurred

within a transition zone 100 m on either side of Blind
Channel. The remaining activity was along ecotonal
boundaries. Few records of movements in a homogeneous
environment were noted. Most movement was confined to the
south-east side of the woodland. Distances from free standing
bodies of water did not exceed 700m.

Table 1 describes trap sites at which commercial
trappers caught long-tailed weasels in southern Manitoba.
Fifty-nine per cent. of captures were associated with water,
16% with woodlands and 3% with grasslands. Twenty-two
per cent. of captures were made in disturbed habitat.

Tracking

Winter track surveys were not rewarding in that weasels,
particularly females, were chiefly subnivean. Snowshoeing and
skiing over grasslands, meadows and marshes collapses the
cavities (snow caves) formed by snow accumulation and
disrupts the habitat. Mustela spp. tend to follow ski trails
over the surface which may confuse home range data. Sexual
dimorphism in Mustela spp. and overlap in size makes track-
ing data unreliable. Snow conditions were such that few
days were suitable for field observations.

DISCUSSION

Long-tailed weasels are site tenacious as suggested
by: (1) their activity being confined to a discrete part
of the Oxbow community, (2) the frequency of their captures
at a particular site increasing in relation to intensity of
occupation, and (3) their movements channelling through
relatively defined sites (Fig. 5, 6, 12-15). Musgrove
(1951) observed that long-tailed weasels often channelled
through relatively defined sites and coined the term
"funnelling" for this effect.

Male-male spacing was similar to male-female spacing,
suggesting males move freely within their shared range
irrespective of other males (p. 100). Simms (1979)
suggested that spacing is a product of the availability of
prey in weasels, and hence, habitat. At Oxbow, habitat
immediately adjacent to that occupied seemed similar
in respect of the availability of prey, the proximity of
water and cover, yet was infrequently used. Spacing in
long-tailed weasels in optimal habitat would seem to be a
function of their sociobiology (Chapter III).

Female long-tailed weasels are localized in their
distribution but home ranges are not contiguous since ranges
overlap and are not mutually exclusive. Spacing in females is
the result of the trophic niche they occupy (primarily a

small mammal predator) and their role in reproduction

(Ralls 1977, Erlinge 1979). Females do not appear

antagonistic towards each other (p. 82) but rarely come

into contact.

I suggest that long-tailed weasels in optimal habitat

establish demes (a local population of potentially inter-

breeding individuals) and are social (Chapter III). Genetic

homogeneity of the demetic population could only be

maintained within a patriarchy as weasels are promiscuous

(Skinner 1927, Hall 1951, and Erlinge 1979). In the

current study males appeared to be related. Young disperse

from the den site in August with females sometimes moving

outside the group range (Fig. 13). This would seem to be

the mechanism of gene flow between demes though supernumeraries

of either sex may be evicted when resources (food and/or space)

become limiting (Wobeser 1966, Smith 1974, and Powell 1979).

Sexual dimorphism can influence expulsion because females

are considerably smaller ($\bar{x}$ = 212 g and would be disadvantaged

in an aggressive encounter with a male ($\bar{x}$ = 394 g). Within

populations smaller animals tend to be subordinate (Turner

and Iverson 1973: Erlinge 1979).

Long-tailed weasels will occupy other suitable habitat

(Fig. 8) but are subjected to changes in social behaviour

with respect to their environment. Variation in the sociality

of carnivores can often be traced to differences in their food

particularly in regards to size of available prey, spatial

distribution of prey and its temporal or seasonal distribution

(Kruuk 1976; Bekoff and Wells 1980).

Most animal characteristics are the product of

inherited predisposition and the environment. Long-tailed

weasels are solitary in areas of low species diversity

such as the beach ridge-marsh wet meadow. Resources on

the ridge would seem to be limiting in terms of numbers

of M. frenata they can support, though ranges are stable over

time. As in coyotes (Bekoff and Wells 1980), long-tailed

weasel populations seem to consist of solitary to gregar-

ious and transient to stable groups.

Throughout its range in southern Manitoba long-tailed

weasel appear to confine activity to the proximity of water

in association with successional communities or ecotones in

which prey diversity is greatest (table 1). At Delta,

long-tailed weasels showed a preference for borders. Rarely

did M. frenata frequent homogeneous habitat. Wobeser (1966)

and Simms (1979) both observed M. f. novaboracensis occupied

advanced seral stages. Glover (1942) suggested that M. f.

novaboracensis prefers an environmental type with a fairly

dense understory. Soper (1964) found M. f. longicauda occupied

short grass plains and the more northern prairies and parkland

but list M. f. longicauda as being typical of the transition

zone which coincides with the Aspen Parkland area.

Historically southern Manitoba comprised a transition

between the tall grass prairie and Boreal Forest and was
termed Aspen Parkland (Bird 1930, Bird 1961, Kiel et al
1972). Aspen Parkland developed as an irregular mosaic
of aspen groves and rough fesque parks mainly on poorly
drained till. Marshes, sloughs and pot hole lakes are
prominant features of this community. Both the theoretical
and applied ecological literature supports the contention
that heterogeneity can be related to faunal richness
(MacArthur 1972, Telfer 1974, Merriam 1978). With the
destruction of Aspen Parkland by agriculture (Merriam 1978)
on the prairies, M. frenata populations have declined such
that in Manitoba and Saskatchewan it is now a threatened
species and probably the same is true in Alberta. In
Manitoba, waterways provide the only habitat in a successional
state suitable for continued existence.

Extralimital records from Alberta in the Canadian zone
(Soper 1964) and Manitoba at The Pas, occur in isolated stands
of parkland within the Boreal Forest or Taiga which provide
prey species diversity necessary for M. frenata.

Few ermine established residency in the Oxbow community.
Resident short-tailed weasels normally occupied home ranges
immediately adjacent to those held by M. frenata. M. erminea
would invade areas abandoned or rarely used by long-tailed
weasels. It would seem long-tailed weasels repress ermine
through interference interactions. The only resident
ermine recorded within the range occupied by M. frenata was
a large (192 g) mature adult male (S. Manitoba $\bar{x}$ = 162 g).

Similarly a large male M. rixosa was trapped within this area. Powell (1979) suggested that a dominant-subordinate hierarchy may exist between M. frenata and M. erminea. There may also be a similar relationship between the smallest member, M. rixosa.

On the beach-ridge long-tailed weasels did not appear to influence the distribution of ermine except in the immediate vicinity of the field station. Here the resident long-tailed weasel hunted in and around the buildings exclusively.

The beach-ridge and, in winter the marsh-wet meadows provided suitable habitat for ermine. Home ranges were not mutually exclusive for either residents or transients. Transients were not necessarily subordinate animals. Some of the largest males were transient particularly in the fall (August, September). Home ranges were rarely occupied in males for more than four months. Possibly, as was the case with K, home ranges are a temporary entity. Perhaps territories are established in M. erminea males only when resources are limiting. Transients were most frequently captured in 1977 when vole populations were high; in 1978, a low vole year, few transient ermine were recorded. Seton (1929) and Erlinge (1974) reported similar observations.

Resident ermine would remain and hunt for variable lengths of time in restricted parts of their ranges. Erlinge (1977) observed a similar relationship and suggested

uneven habitat use was due to variation in prey abundance.
During the snow free period populations of microtines were
higher on the ridge than the marsh-wet meadows. Weasel
populations were distributed accordingly. In winter,
weasels adjusted their distribution to the leeward side
of the ridge and into the marsh-wet meadow. This adjustment
corresponded to changes in vole distribution and accessability.
M. e. richardsoni did not partition resources in areas of
overlap by temporal spacing.

Ermine exhibit a preference for early successional
communities (Erlinge 1977, Simms 1979 and Gamble) in which
distribution appears to be a function of prey availability.
(Robina 1960, Erlinge 1977 and Gamble). These communities
usually contain more prey species which are cyclic. Advanced
seral stages such as the Oxbow community are suitable but are
generally occupied by M. frenata.

Females of both species spend more time hunting in
tunnels than do males. Erlinge (1979) observed a similar
occurrence in M. erminea. Males in my study were frequently
caught on the snow surface and provided most of the data
on winter movements. High male to female ratios from commercial
trap returns or track counts are often reported (Bangs 1896,
Hamilton 1933; Hall 1951; de Vos et al 1959; Wobeser 1966;
Simms 1979). Both methods are dependent upon the amount of
time spent by weasels on the snow and as such are questionable
(Simms 1979). This opinion concurs with my own observations.

Male short-tailed weasels capture microtines in
ventilator shafts or use aŋmaŋa (space formed between a
drift and obstruction causing it) as entrances to the
subnivean environment (i.e. pukak layer = fragile columnar
basal layer of snow on the ground). Simms (1979) suggested
that female M. erminea,because of their body dimensions,
have direct access to microtine tunnels whereas access
is restricted in males. Observations in the marsh,
wet-meadows and grassland do not concur with this belief
of restricted access due to size since snow caves found
in these cover types are equally accessible to all
Mustela spp. Further,female M. frenata ($\bar{x}$ = 212 g) are on
the average larger than male M. erminea yet are more
subnivean judging from capture and dietary records (Gamble).
Inter- and intraspecifically, sexual preferences in
foraging strategies or behaviour would seem equally
important to that of size. In addition Wobeser (1966) and
Fitzgerald (1977) both suggest M. frenata is a capable
digger and will often burrow through snow cover after prey.

M. frenata appears somewhat confined to the close
proximity of water. Clark (1978) similarly found that the
black-footed ferret, M. nigripes,was confined to prairie
dog towns within a mean of 700 m. $\pm$ 400 from permanent water
and associated meadows. Hall (1951) proposed that in desert
areas, though suitable rodents were present, the

absence of water to drink was a limiting factor in the
distribution of M. frenata. Weasels consume the blood and
body fluids from their prey (Bridges 1961). Lapping
blood, perhaps, is a means of water replacement lost through
metabolic activity. Due to the high surface to mass ratio
of weasels, heat loss and accompanying water loss are high
(Brown and Lasiewski 1972, Iverson 1972; Moor 1977).
Perhaps in the smaller Mustela spp., M. erminea and M.
rixosa, replacement is achieved through predation and
percipitation but in the larger species, M. frenata and
M. nigripes, these sources are not entirely satisfactory.
M. frenata uses water courses in daily activity and perhaps
these water courses are a mechanism of dispersal.

Although trapping procedures were not entirely
appropriate for M. rixosa, my results plus field station
records did suggest this species preferred grasslands and
wet meadows. Records of this species' occurrence on the
ridge are from the south side (willow cover) bordering the
marsh. At Oxbow one male was found within the woodland but
was within 100 meters of the channel. M. rixosa appeared
to occupy areas in which M. frenata and M. erminea were
absent or widely spaced.

CONCLUSION

Distribution of weasels is related to prey abundance indicating food is the main factor in habitat selection. Primarily due to its generalist diet, Mustela frenata prefers advanced seral stages or ecotones where prey species diversity is greatest. In contrast, M. erminea occupies early successional stages that consist of cyclic prey species.

In areas of sympatry M. frenata restricts the distribution of M. erminea and M. rixosa by interference interactions. Segregation between M. frenata and M. erminea is more pronounced in advanced seral stages (i.e. the Oxbow community) than in early successional stages (i.e. beach ridge-marsh wet meadow) primarily due to the sociobiology (dominance) of M. frenata.

Short-tailed weasels did not occupy areas which were mutually exclusive; rather home ranges overlapped considerably with conspecifics. Temporal spacing did not appear to be in operation. M. erminea males were more sedentary during a low vole year than in a year of vole abundance. Perhaps, in low vole years, it is critical for this species to partition resources and territorial defence might be the final product.

Females of both species were more subnivean in the winter than males. Subnivean activity in weasels is a function both of size and sexual preference in foraging behaviour. Subnivean activity is one means by which weasels partition resources.

M. frenata, not unlike the black-footed ferret, is confined to the close proximity of water due partially to metabolic demands. M. frenata uses waterways in daily activity, and perhaps these waterways are a means of dispersal. Waterways provide ecotonal environments suited to the mode of existence of this species.

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Figure 1   Oxbow community

Woodlands (deciduous)   Old field succession

Marsh   Farmland(hay)

Wet meadows   Farmland(under tillage)

Prairie   Phragmites (seasonally dry)

Figure 2   Beach-ridge – Marsh communities

Sand beach   Wet meadows   Prairie

Wooded ridge   Marsh   ▬▬▬ Boundary (study site)
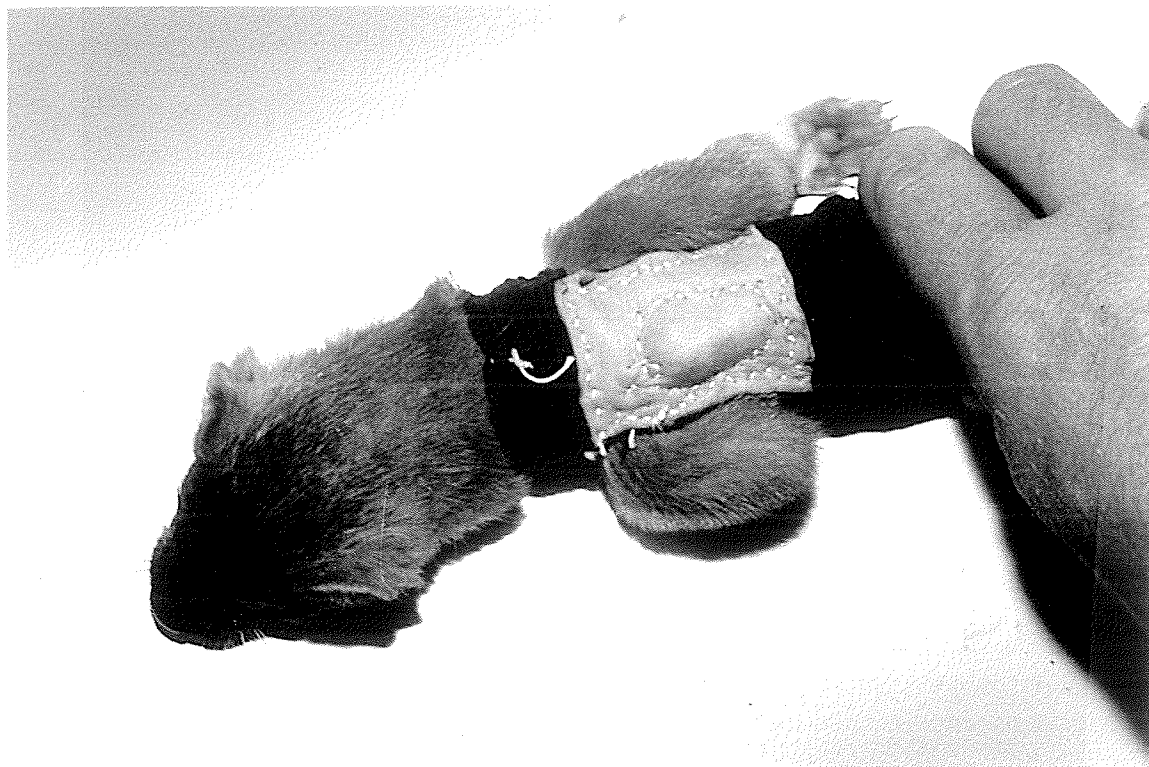
Figure 3. Dorsal view of radio transmitter and vest of
          deerhide and corduroy attached to a male
          long-tailed weasel.

Figure 4.   Lateral view of transmitter and deerhide vest
            showing antenna   trailing posteriorly.
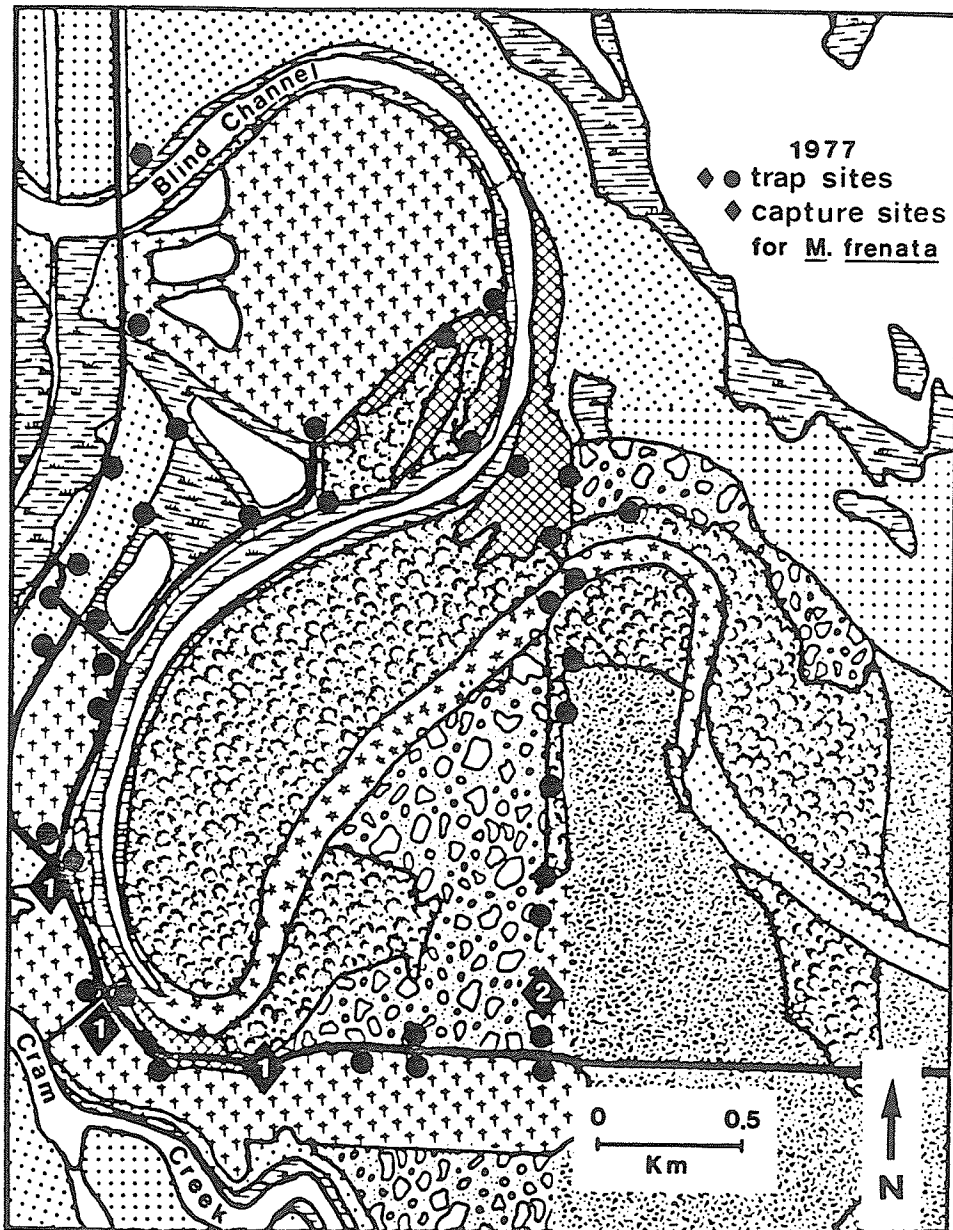
Figure 5. Oxbow study area showing trap sites
and capture sites for M. frenata in
1977. Numbers in the diamonds indi-
cate number of captures.
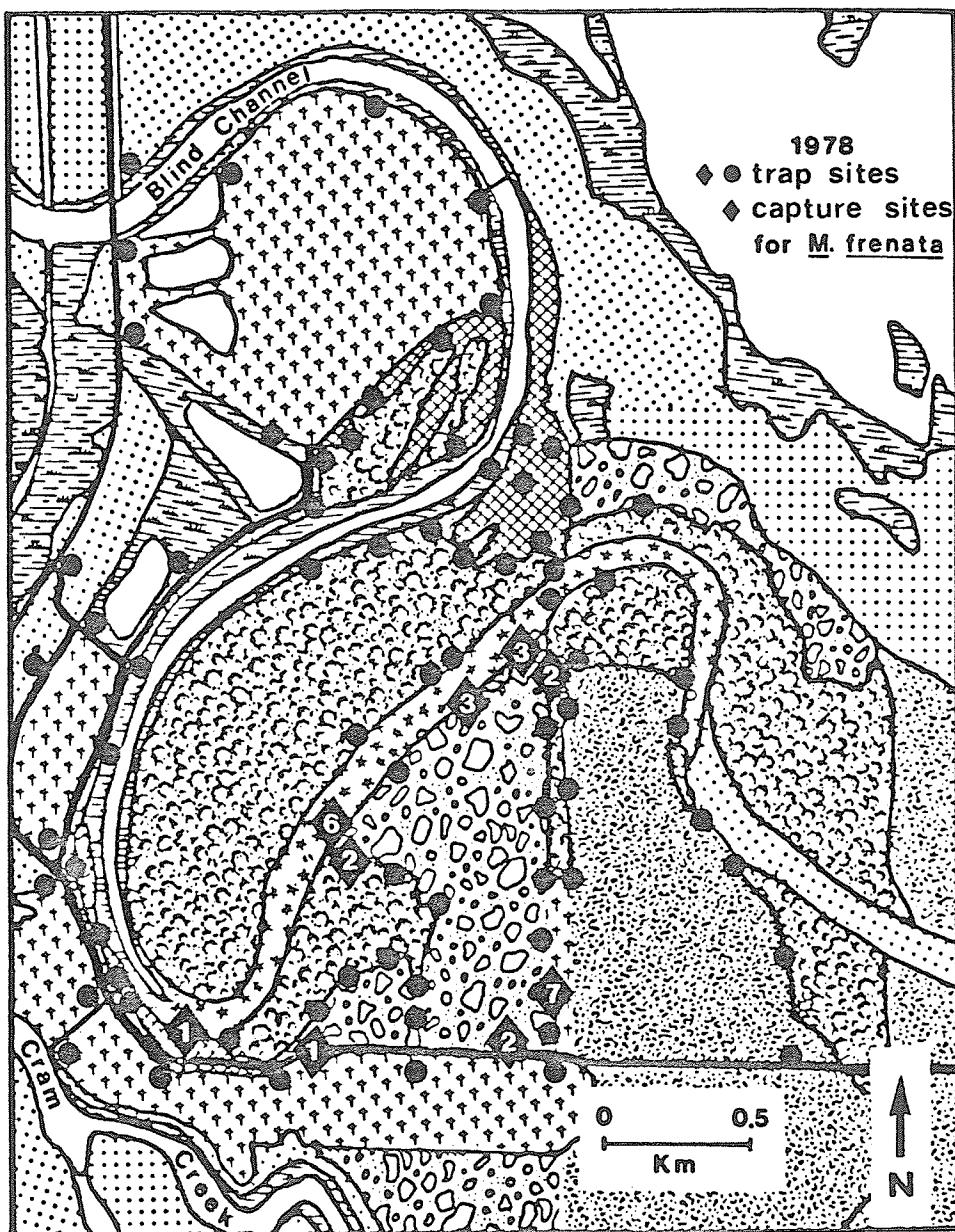
Figure 6. Oxbow study area showing trap sites
and capture sites for M. frenata in
1978.
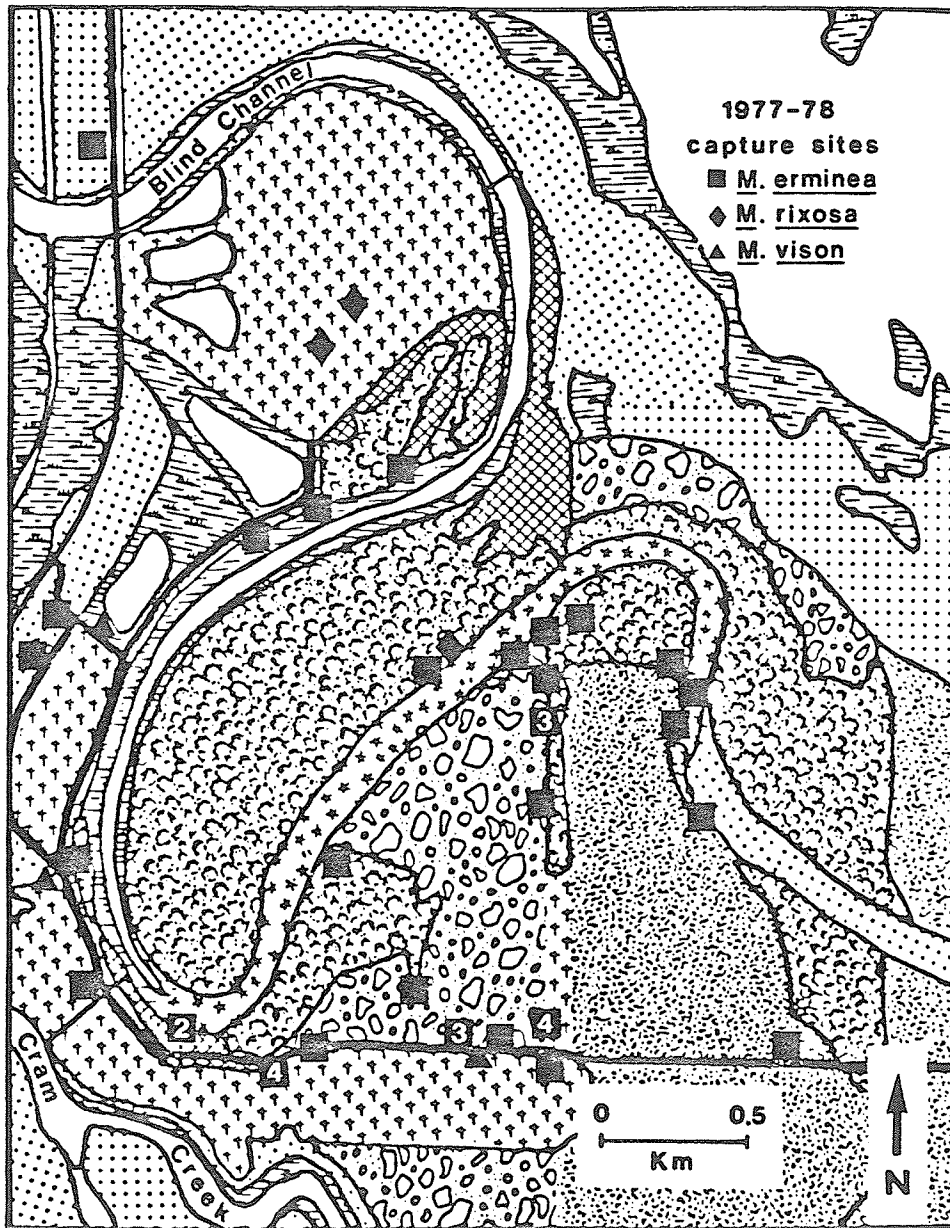
Figure 7. Oxbow study area showing capture sites
for Mustela erminea, M. rixosa and
M. vison in 1977 and 1978.
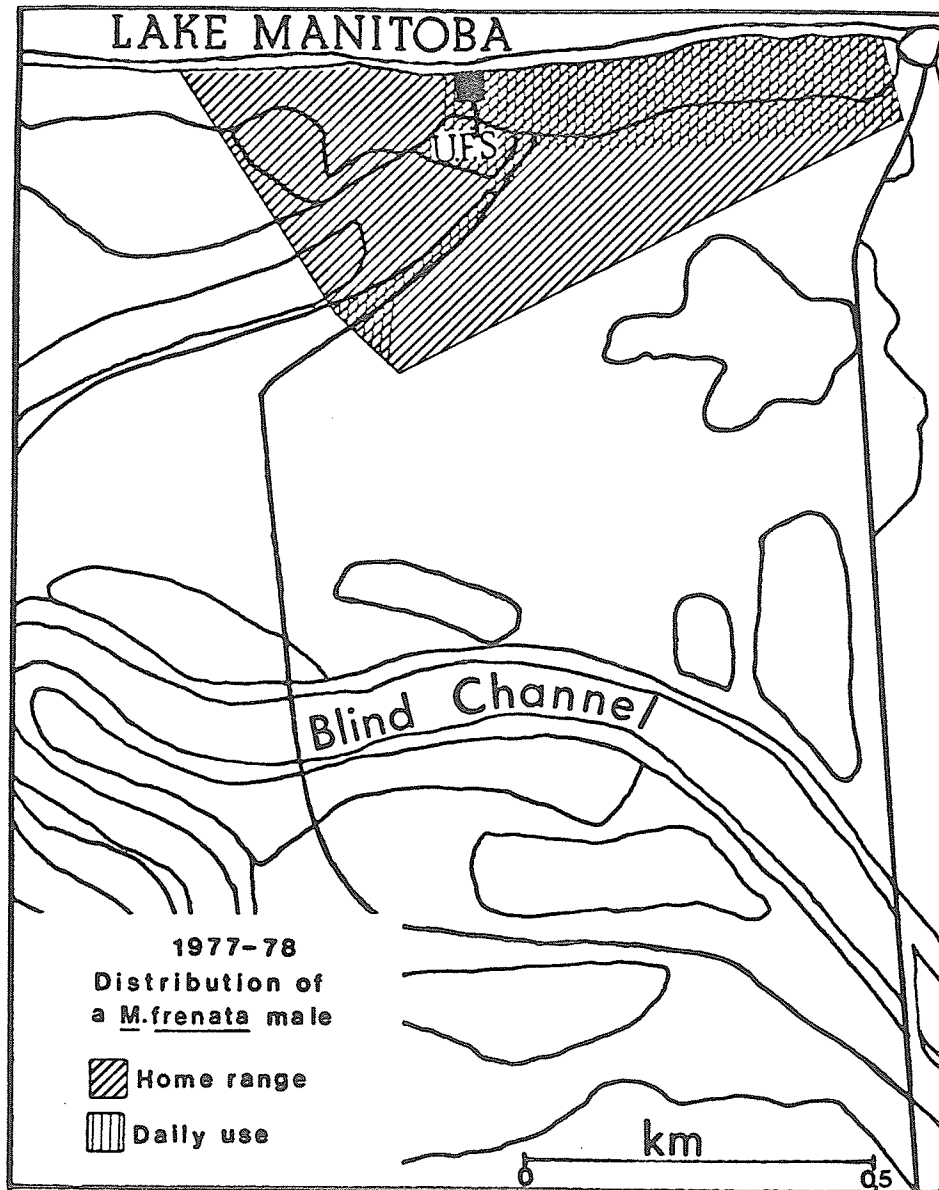
Figure 8. Home range (33 ha.) of a M. frenata
male as determined by live trapping
and visual observations. Its center
of activity extended along the beach
ridge and winter road leading to the
University Field Station.

Figure 9. Progression of snow accumulation and formation
of snow caves in the Delta study area.
A. Early snowfall is trapped on the upper
portion of the phragmites creating large snow
caves at the bases. These caves may range
from 0.2 to 1.5 m in height.

B. and C. show dive holes of long-tailed weasels
leading down to the snow caves later in the
winter. These holes are used throughout the winter.

A

B

C
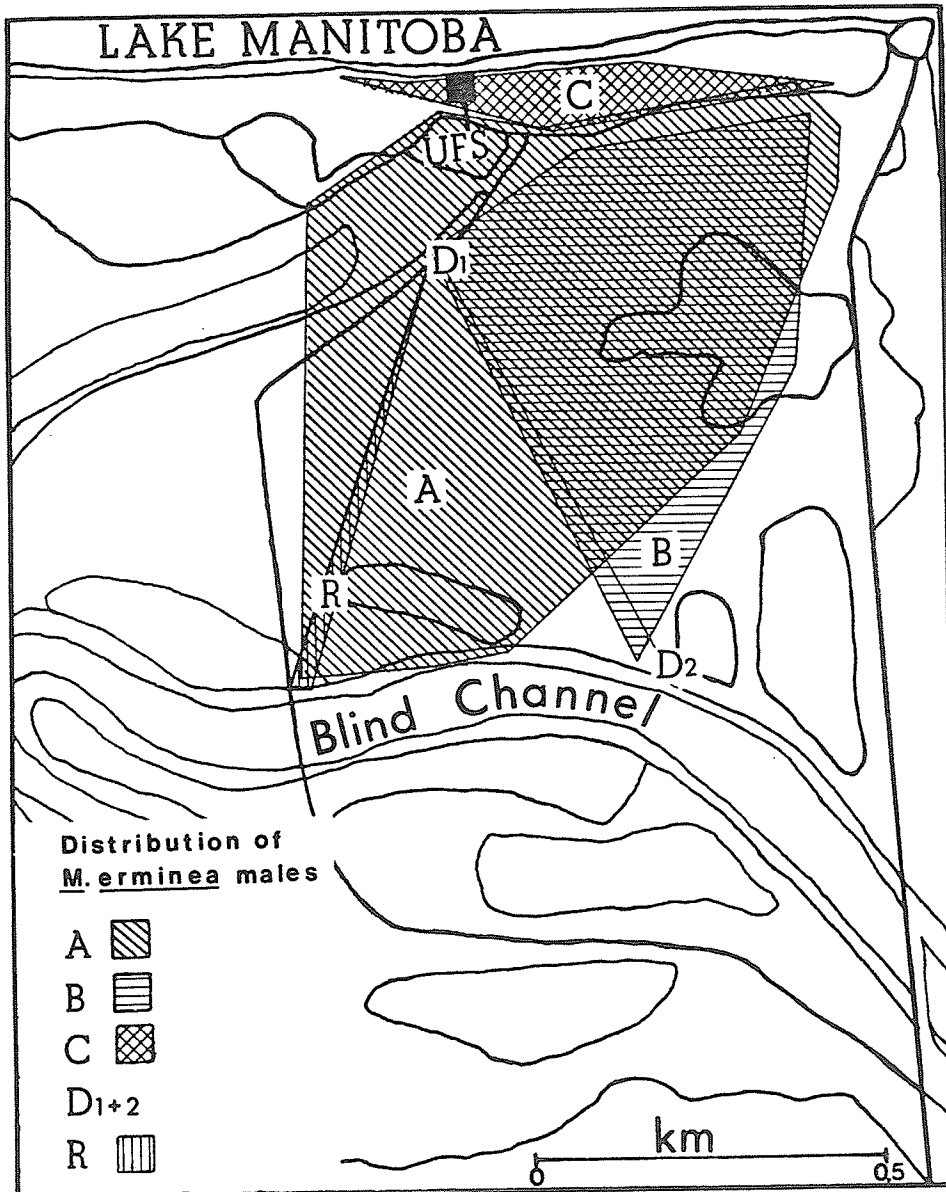
Figure 10. Home ranges of five male <u>M. erminea</u>
as determined by live trapping during
the winter (1977-78). Weasel D which
was trapped 7 times, was captured only
at sites D_1 and D_2.
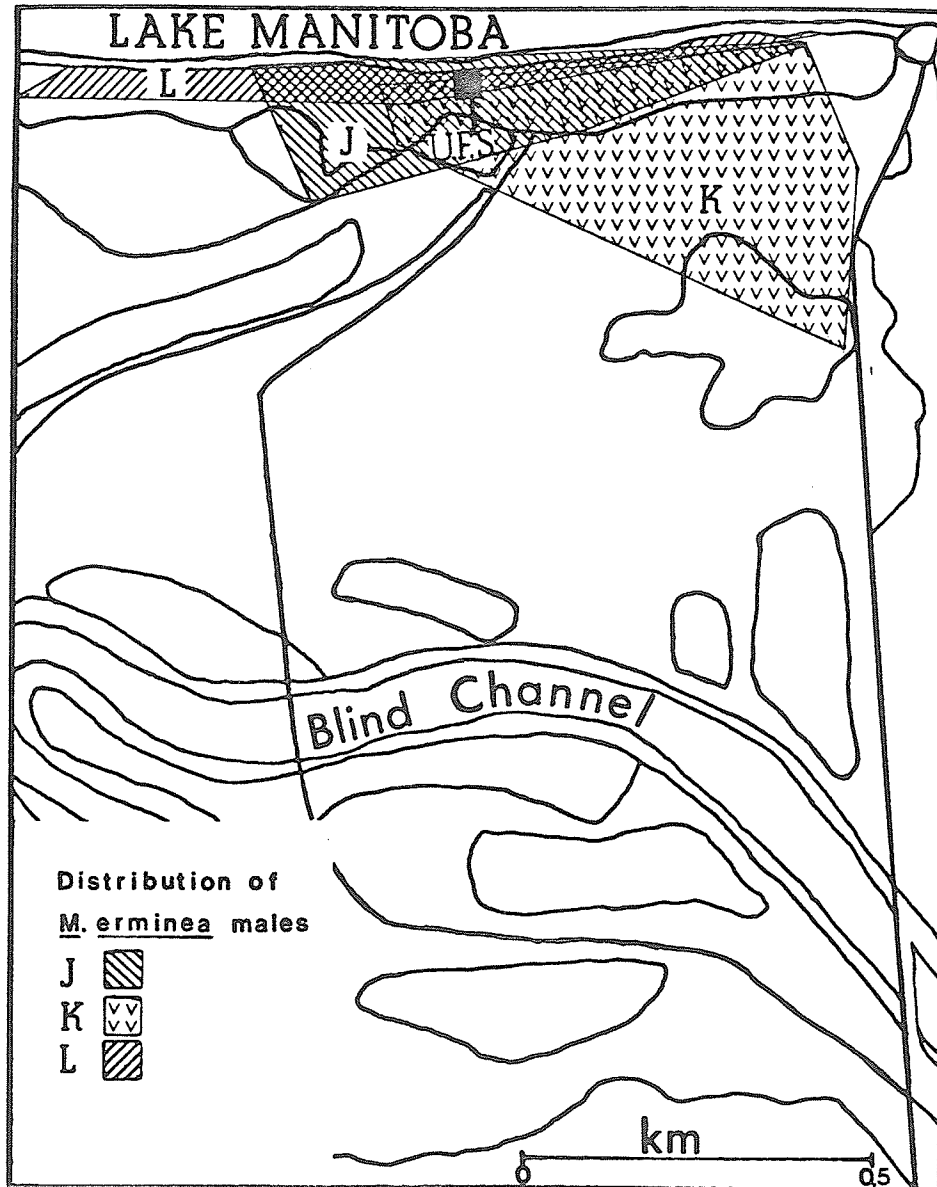
Figure 11. Home ranges of three male M. erminea
as determined by live trapping in the
summer of 1978.
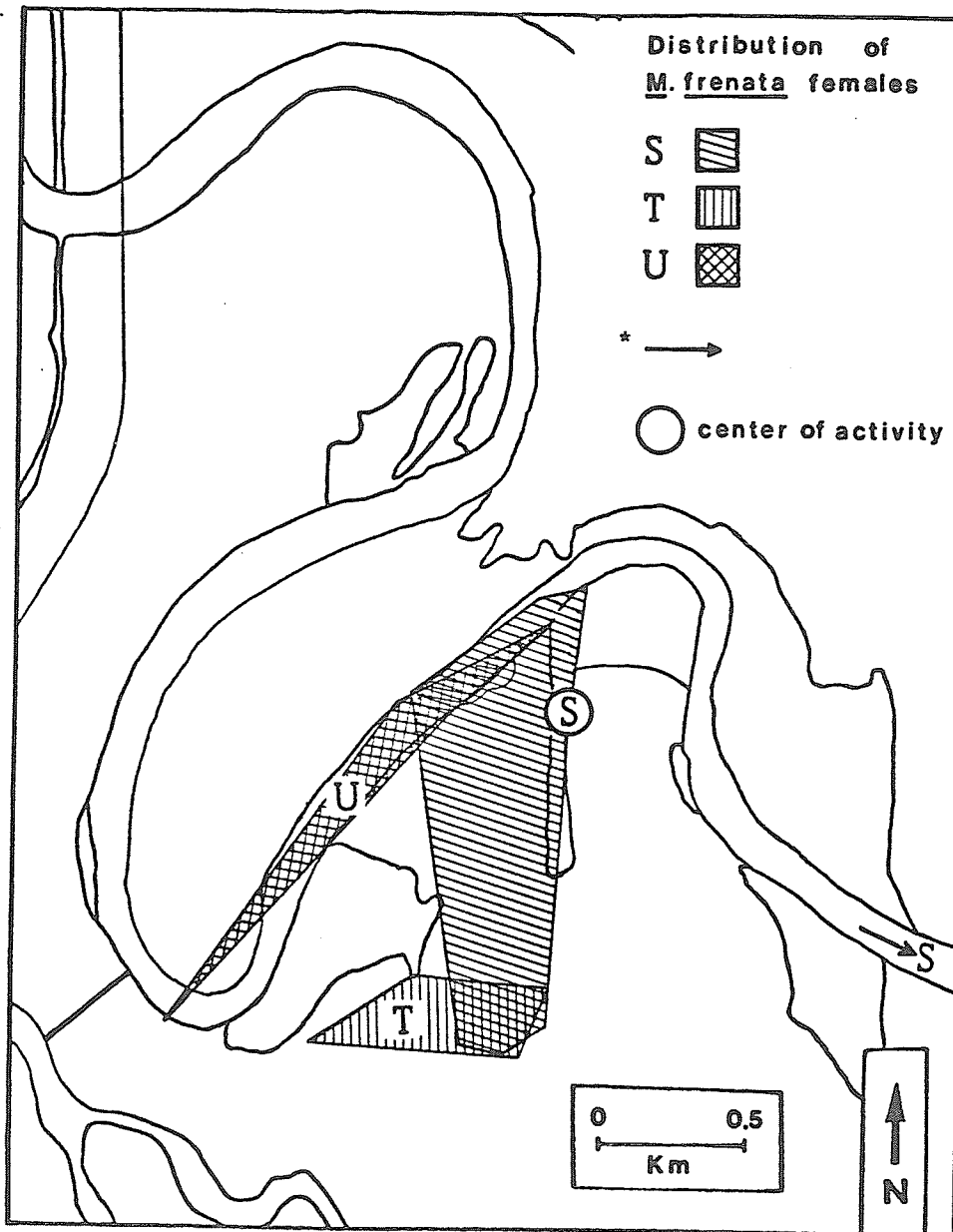
Figure 12.   Home ranges of three female M. frenata
            as determined by trapping and radio
            telemetry in 1978. Center of activity
            indicates a den site. The arrow on the
            Blind Channel indicates the route female
            S used in dispersing from the study area.
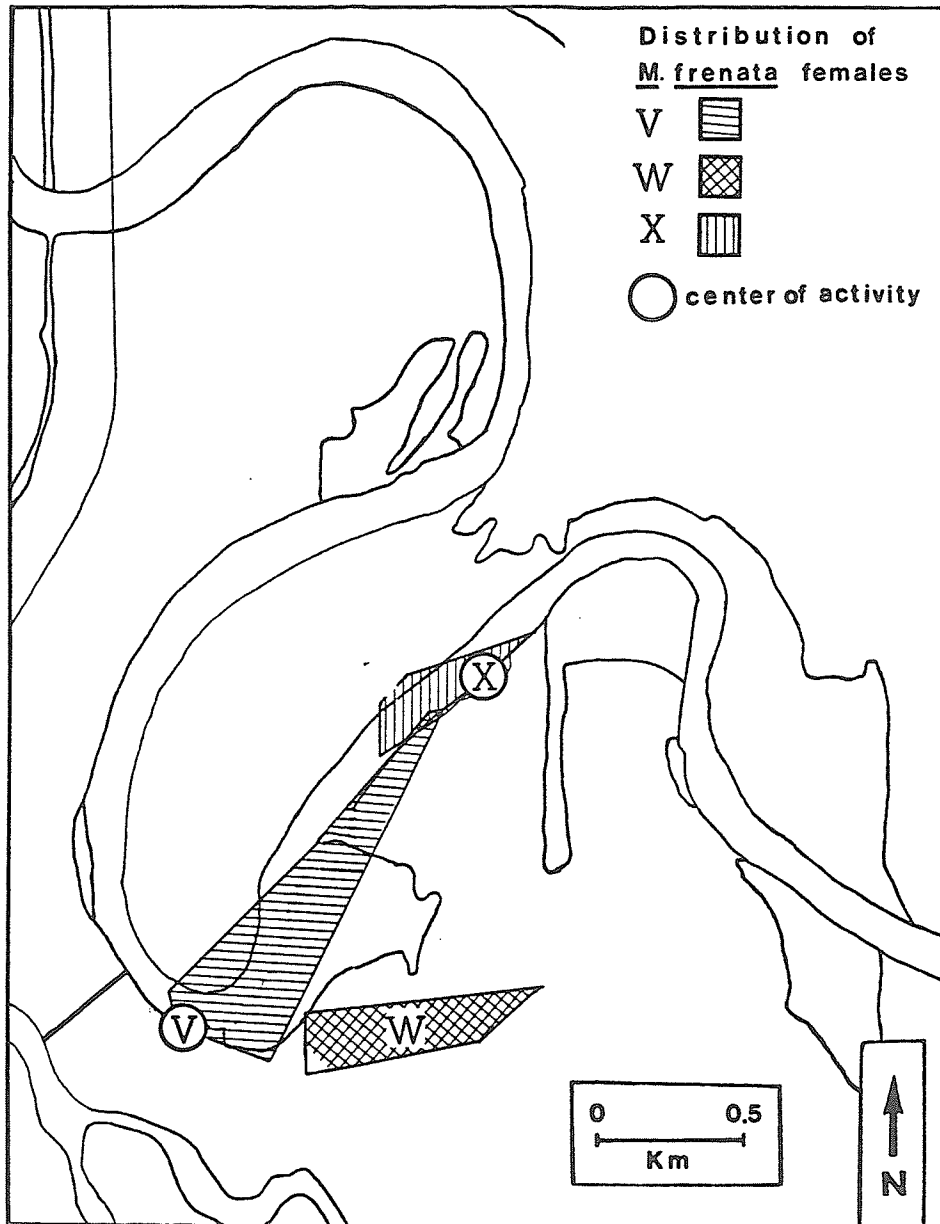
Figure 13. Home ranges of three female M. frenata
as determined by trapping and radio
telemetry in 1978. Center of activity
indicates a den site.
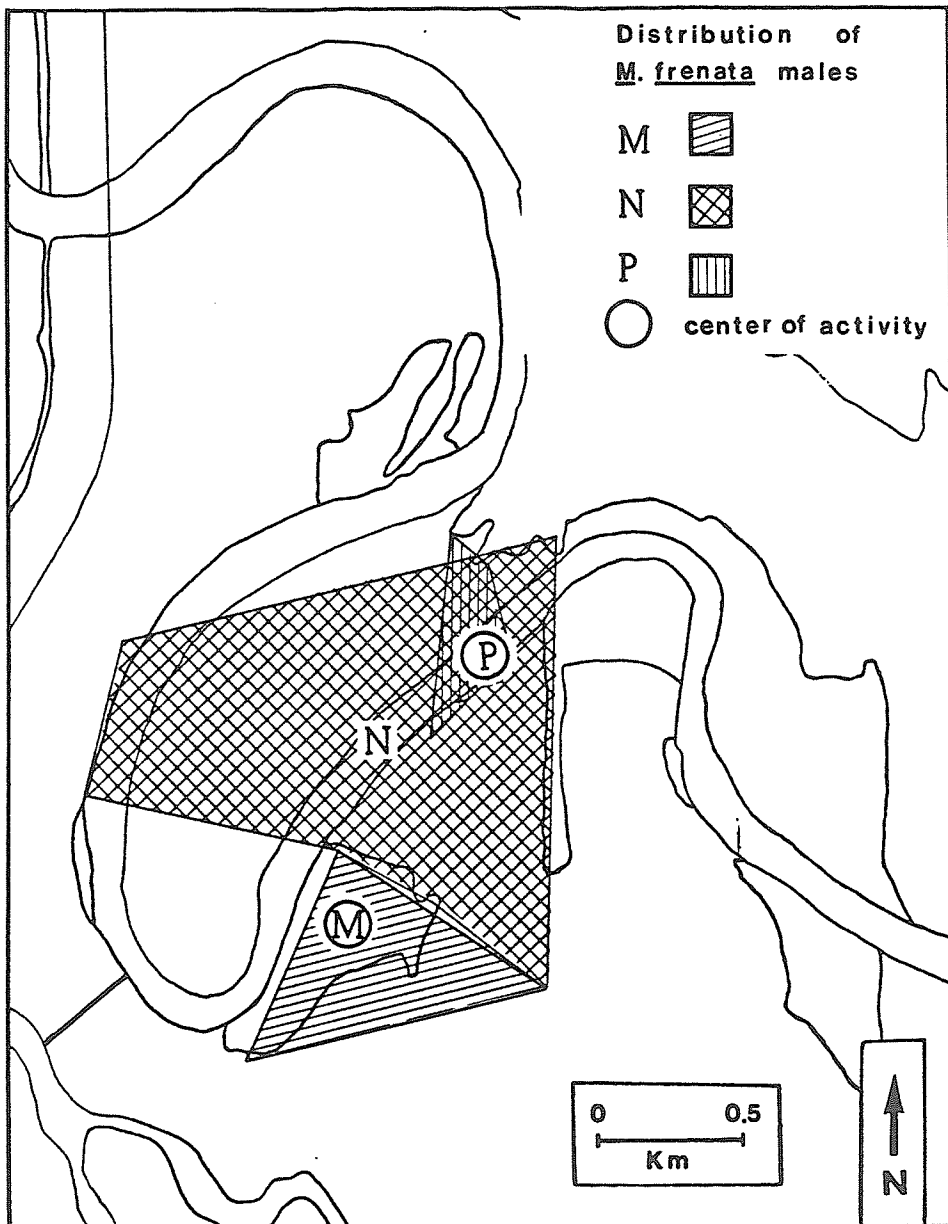
Figure 14. Home ranges of three male M. frenata
as determined by trapping and radio
telemetry. Center of activity indi-
cates movement is localized in this
area and a den site is probable.
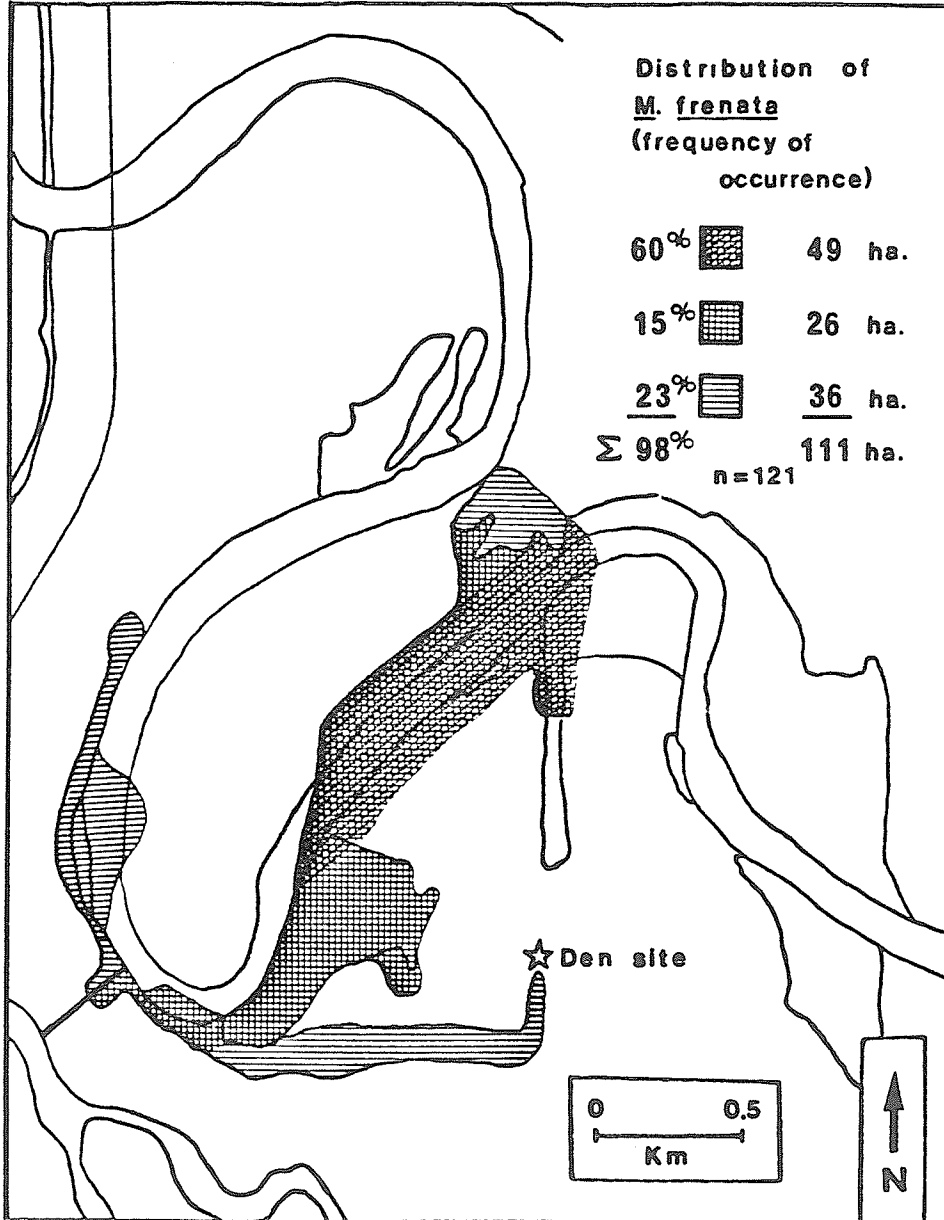
Figure 15- Site tenacity of M. frenata within the
Oxbow community. Heavy shaded areas
are those areas most intensively used.

Table 1. Description of trap sites of long-tailed weasels
caught by commercial trappers in southern Manitoba.

Trappers' description of site	N	$\leq$	Habitat type
creek or river bottoms, lake shores	42		associated
willow stands in conjunction with meadows	7	69	with
mink runs, muskrat houses, marsh & sloughs	20		water
bulldozed piles, dugouts, culverts	17	26	disturbed
farmland and farmyards	9		
poplar ravine, poplar and shrub bluffs	7		
oak and poplar	2	18	woodland
spruce and oak	9		
prairie	3	3	grassland

CHAPTER II

Food habits of <u>Mustela</u> <u>frenata</u> <u>longicauda</u>,

the long-tailed weasel, and <u>M</u>. <u>erminea</u> <u>richardsoni</u>,

the short-tailed weasel, in southern Manitoba

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ABSTRACT

Gut (n = 203) and scat (n = 95) analyses, field obser-
vations and laboratory feeding trials revealed that <u>Mustela
frenata longicauda</u> are generalists and <u>M. erminea richard-
soni</u> are specialists. Weasel hunting sets partition resources
by means of the proportion of prey species consumed. Diet in
weasels is a function of the frequency of occurrence and bio-
mass of prey species. The average prey size of <u>M. frenata</u>
females was smaller than that of males. Similarly, <u>M. frenata</u>
consumed, on average, larger prey than <u>M. erminea</u>. Prey
selection in weasels is a function of size and sexual prefer-
ence in foraging strategies. Bird species comprise a substan-
tial part of a weasel's diet. Egg depredation by weasels is
learned. Soricids are distasteful to weasels but are eaten
in times of food stress. The occurrence of muskrat in the
diet of male <u>M. frenata</u> and frequency of captures within
muskrat houses suggest <u>M. frenata</u> males may actively prey on
this species. <u>M. frenata</u> will kill and eat <u>M. erminea</u> and
<u>M. rixosa</u> in sympatry but predation of other <u>Mustela</u> spp. by
<u>M. frenata</u> is not a coexistence stabilizing factor.

INTRODUCTION

Mustela spp. exhibit a high degree of dietary overlap (Glover 1942; Hall 1951; Wobeser 1966; Day 1968; Erlinge 1975 and 1977; Simms 1979) and often coexist in hunting sets (Rosenzweig 1966). Population biologists, however, have reasoned that coexisting species must differ in their ecological requirements to avoid competitive exclusion (Hardin 1960; Pianka 1974). Rosenzweig (1966) has suggested that within weasel hunting sets each species has specialized on some interval of the resource axis.

The purpose of this study was to quantify resource use in two closely related sympatric carnivores. Community structure is, in part, the result of resource partitioning. Dimensions along which species partition resources are: diet, habitat and activity (Schoener, 1974). This paper will confine its scope to discussing the diet of two weasel species: _Mustela_ _frenata_ _longicauda_ Bonaparte and _M._ _erminea_ _richardsoni_ Bonaparte.

METHODS

Food habits were determined from scat and stomach
analyses. Scats were collected from traps, dens and scent
posts at Delta, Manitoba ($50^{\circ}10'$N $98^{\circ}22'$W). Only those
scats clearly identified to species by tracking data and/or
odour and/or captures were used, as scat sizes attributable
to known Mustela spp. were found to overlap. The size of
a weasel's scat varies with the quantity and quality of prey
consumed. Scat size as proposed by Simms (1979) was not
considered to be a reliable indicator of a species. Ninety-
five scats were examined of which 45 were from M. frenata
and 50 were from M. erminea.

One hundred and eighty-six frozen carcasses of M.
frenata were purchased from commercial trappers throughout
the range of long-tailed weasels in southern Manitoba from
November 15, 1977 to February 28, 1978. Seventeen M. erminea
carcasses were provided as incidental purchases. Information
was provided on location, bait, habitat, type of set and
date of capture. Collection was coordinated by the Manitoba
Department of Mines, Natural Resources and Environment who
posted notices in licensing vendors, post offices and with
trapping associations.

Scats and stomach were examined for items such as teeth and some soft body parts (e.g. footpads) which were diagnostic and provided reliable identifications. Hair analysis (Day 1966; Adorjan and Kolenosky 1969; Korschgen and Stuart 1972), though subjected to criticism (Homan and Genoways 1978), furnished positive prey species identification when augmented by other data including bone fragments, claws, and soft body parts (e.g. toes, pads). Guard hair was identified using gross examination (texture, color, size) and negative impressions (Williamson 1951). No attempt was made to categorize bird, insect or plant material. All scat and stomach contents were considered to represent one food item, unless proven otherwise. Food habits are expressed in terms of frequency of occurrence and biomass (Pils and Martin 1978). Per cent frequency of occurrence was found by dividing the total occurrences of a particular food item by the total occurrences of all food items. Per cent biomass was calculated by multiplying the mean food item weights (taken from specimens at the Manitoba Museum of Man and Nature and field data from trapped animals) times total occurrences. This product was then divided by the total biomass of all food items.

Occasionally direct observations were made on weasels securing and/or transporting prey. Lab feeding trials were conducted using garter snakes (Thomnophis sirtalis), shrews (Sorex spp. and Blarina brevicauda) and eggs: sora rail (Porzana carolina), coot (Fulica americana) and domestic chicken.

RESULTS

Forty-two per cent of the stomachs of M. frenata

and 41% of the stomachs of M. erminea were empty.

Twenty-one and 24% of the stomachs of M. frenata and M.

erminea contained unidentifiable animal tissue. Samples

containing bait were treated separately.

Table 1 provides the distribution of prey items found

in the diet of M. frenata. The sample was sufficiently

large to allow division by sex and into snowfree (April 10

to November 5 (Atomspheric Environment Service)) and snow

cover periods in Manitoba. The mean weights of prey species

are given, which were used in formulation of biomass. Figure

1 compares frequency of mammalian prey items found in the

diet of M. frenata with that of biomass. Using biomass,

emphasis shifts from the cricetids to the leporids. Ondatra,

muskrat, increases slightly in significance.

Table 2 provides the distribution of food items found

in the diet of M. erminea. Sample size precluded further

division.

M. erminea consume voles primarily, in contrast to

M. frenata which rely heavily on mid-size prey. Statistical

analyses of dietary overlap (χ^2), in terms of frequency,

provided conclusive evidence that the proportion of prey

items selected by each species is significantly different at

levels less than α = .005. M. frenata further exhibited a

dietary shift from summer (snow free) to winter (snow cover) ($\alpha \leq .005$). Females consume a larger proportion of small prey items than males ($\chi^2 = 13.3$, 5 d.f. $\alpha \leq .025$).

Feeding trails provided evidence that M. frenata would consume soricids. Soricids did not appear in either stomach contents or scats from my sample. A male long-tailed weasel was observed caching Blarina. Two short-tailed weasel stomachs contained soricid remains; both were trapped in the winter. Soricids did not appear in the diet of M. erminea in the summer.

M. erminea and M. frenata would stalk and kill garter snakes by biting through the base of the skull but they would consume the carcass from either end unlike other vertebrate prey. Often only part of the snake was eaten. Snake remains were found at the entrance to a long-tailed weasel den which I feel were the result of weasel predation.

A weasel's response to a bird egg is highly variable. Some individuals break eggs and lap the contents while others ignored eggs as a source of food. Short-tailed weasels would break eggs at one end and lap the contents. Long-tailed weasels, in contrast, broke sora and coot eggs entirely but would follow the procedure of short-tailed weasels on chicken eggs. Weasels learn to recognize eggs as a food resource. Individuals, unresponsive to eggs intact, once shown how to get at the contents through breakage, would eat them in subsequent trials

I observed two instances in which ermine preyed upon
teal eggs, <u>Querquedula</u> <u>discors</u>. The eggs were carried
several meters from the nest and eaten. On both occasions,
the weasel did not destroy the entire clutch but selectively
removed 2 or 3 eggs. Eggs apparently supplemented a weasel's
diet.

Weasels were observed preying on and consuming
red-winged blackbirds (<u>Agelaius</u> <u>phoeniceus</u>), robins
(<u>Turdus</u> <u>migratorius</u>) and Baltimore orioles (<u>Icterus</u>
<u>galbula</u>). A tetraonid (grouse) was present in the stomach
of one long-tailed weasel. Ground dwelling birds would
appear to be important items in a weasel's diet. Birds
contributed 6% of a weasel's diet in the summer and 22% in
the winter.

DISCUSSION

The diet of most carnivores is given as the frequency of occurrence. Few researchers compare the frequency of occurrence of prey items in the diet in relation to prey biomass. Neither method is totally satisfactory but together they provide a means of weighting prey consumption in accordance with the metabolic demands of the carnivore. Weighting prey consumption in this manner is of particular importance to the smaller carnivores which consume prey species much larger than themselves.

It is frequently assumed that prey items are equally identifiable in the diets of sympatric carnivores of similar morphology and hunting abilities (i.e. weasel hunting sets). A carnivore which preys on animals much larger than itself will consume these prey species in part, whereas prey species smaller than the carnivore are often eaten intact. Animals eaten entirely are more often identifiable. Frequency tables prepared from these identifications would contain disproportionately more small prey items in relation to predator size. In both _Mustela_ _frenata_ and _M_. _erminea_ a large portion of stomach contents were unidentifiable animal tissue probably from large prey types and/or scavenged carcasses. This material, if included within the mid-sized prey category, would reduce the frequency values given in the small mammal category.

Dietary tables depicting biomass assume consumption
of all prey types and are based on mean prey weights.
Weasels store surplus food but do not necessarily consume
these cached items (Hall 1974). A conservative estimate based
on the data of other researchers,gives a figure of 25%
of the body weight as the daily food requirement for
Mustela spp. (Hamilton 1933; Glover 1942; Moore 1944;
Moors 1977). My estimates agree with this figure. Prey
items much larger than 25% of a weasel's body weight
would be partially eaten and probably the remainder stored.
Items less than this value would probably not satiate the
predator which would continue hunting. Therefore, smaller
prey species could be taken more frequently than large
ones and still not be as important in meeting a weasel's
food requirements as are larger species. During conditions
of equal availability,larger Mustela spp. and males within
species should select larger prey types. The ecological
significance to a carnivore of prey types that meet its
bioenergetic requirements in one feeding, perhaps, are
underestimated.

Erlinge (1979) similarly found that the average prey
size of M. erminea females was smaller than that of males.
Body size influenced prey selection but was not the only
factor involved since the largest microtine species in his
study were equally frequent in the diets of both sexes. I
found female M. erminea and M. frenata to be more subnivean

than males of both species though male short-tailed weasels

are smaller. Female, which are active primarily in subnivean

runways, unlike male M. frenata in this study, consumed pocket

gophers and chipmunks in the winter. It would seem that

there is a sexual preference involved in habitat selection

which in turn affects prey selection. Erlinge (1979),

too, found that female M. erminea spent more time hunting

in tunnels than males. Day (1968) found, in areas in which

stoats and weasels (=M. nivalis) were sympatric, that these

carnivores occupy different ecological niches and that

differences in the size of stoat and weasel home ranges or

areas of activity reflect the differences in their diets.

Andersson and Erlinge (1977) suggest several functional

types of predators may be distinguished, depending on their

degree of specialization and mobility. Long-tailed weasels

and short-tailed weasels are resident generalists and

resident specialists respectively (Rosenzweig 1966; Simms

1979; Gamble). M. erminea is well adapted for hunting and

killing rodents and their abundance is closely related to

the rodent density (Lockie 1955; Tapper 1979). Resident

generalists exploit a wide range of food items and are not

affected directly by cyclic prey species as are resident

specialists. I found long-tailed weasel populations

are relatively stable. Andersson and Erlinge (1977) suggested

that generalist populations ought to be more stable. This

species adjusts hunting pressure in accordance with prey

abundance and suitability. Dietary shifts are evident from summer to winter. Tapper (1979) found similar adjustments were made by M. nivalis but were insufficient in delaying population declines. M. nivalis females fail to breed in low vole years. Dietary shifts by M. erminea have also been observed (Hall 1951; Day 1968; Erlinge 1975; Gamble) but are believed to be a temporary measure. Generalists can rear young on non-rodent prey (Andersson and Erlinge 1977). Male parental care in M. frenata may contribute to the success of female long-tailed weasels rearing offspring (Chapter III) since males have a broader feeding spectrum. In contrast, however, long-tailed weasel distribution appears restricted by the diversity of species within a community. The Boreal Forest or Taiga is impenetrable to this species due to the low diversity of species, cyclic nature of the prey, and occupation of available trophic niches by other more suited carnivores (p. 118).

Long-tailed weasles will prey upon one species of animal if that species is continually available (Hall 1974). Hall (1951; 1974) did not believe, however, that birds could be a principle component in a weasel's diet. I found birds were consumed more often in the winter diet of M. frenata than in summer when species diversity and density of birds are greatest. Tapper (1979) similarly found that when vole numbers were low, birds were the main alternate food in M. nivalis. Day (1968) found that birds were an important part of the diet

of both M. erminea and M. nivalis and comprised species from
the orders Galliformes, Passeriformes, and Columbiformes. My
results also suggest that most bird species consumed are
ground nesters or feeders. Dearborn (1932), Glover (1942),
Wobeser (1966) and Simms (1979) also found bird species com-
prise a substantial part of a weasel's diet. Weasels are
opportunists and would not ignore such a valuable resource
particularly when mammalian prey types are scarce. The low
body line of a weasel and felid-like agility would certainly
provide weasels with a stalking ability very likely unsur-
passed in the animal kingdom. M. erminea (Seton 1929;
McCamey 1941; Barger 1950), M. frenata (Bryant 1940; Moore
1944; de Vos 1960; Jeanne 1965; Pettingill 1976) and M. nivalis
(Fern 1974) are as agile in an arboreal environment as a ter-
restrial one.

Weasels may at times supplement their diet with eggs
(Shufeldt 1920; Amundson 1950; Teer 1964; Wobeser 1966;
Gamble). Teer (1964) observed depredation of teal nest and
noted that the entire clutch was not consumed by weasels.
In two of three instances reported, weasels consumed the con-
tents of the eggs in the nest. Where eggs had been incubated
for an extended period and embryos were present, the liquid
content was ignored. Teer (1964), however, did not report
that egg depredation was a learned behaviour in weasels.

Soricids, on occasion, are preyed on by weasels but are rarely consumed. Lockie (1960) and Erlinge (1975) believe shrew are distasteful to weasels. I concur with this belief but feel during times of food stress that soricids may be a valuable resource. Dearborn (1932), Hamilton (1933), Polderboer et al. (1941), Glover (1942), Wobeser (1966) and Simms (1979) all reported a high frequency of soricids in the diet of long-tailed weasels. All of the subspecies reviewed by these authors are considerably smaller than M. f. longicauda and live in a more restrictive (in terms of prey types available) environment. Bioenergetically, the contribution of a shrew to the diet in these areas would be greater. For example, the mean weight of a male M. f. noveboracensis is 225g. It is not unusual to capture male M. e. richardsoni as large as 210g. Female M. f. longicauda, though their mean weight is given as 212 may get as large as 398g (Soper 1964). It would seem that M. f. noveboracensis trophically would occupy a niche not much different from M. e. richardsoni which consume soricids primarily in the winter.

Snakes rarely are reported in the diet of weasels, yet, many parasites which require them as auxiliary transport hosts (Hobmaier 1941; Johnson 1968; Gamble), are prevalent in these carnivores. Some evidence of snake predation was found in this study. Hamilton (1933), Hall (1951) and Wobeser (1966) likewise, report snake consumption by weasels.

I found muskrat in the winter diet of M. f. longicauda.
Hamilton (1933) and Wobeser (1966) similarly provided dietary
records of muskrat occurring in the diet of long-tailed
weasel. Male M. frenata were captured by commercial trappers
5% of the time in muskrat houses. The frequency of captures
of M. frenata in muskrat houses and dietary records suggest
that male long-tailed weasels may prey on this species.

On two occasions in the winter I noted that M. frenata
preyed on M. erminea and/or M. rixosa. Polderboer et al.
(1941) similarly found M. rixosa in his sample. It has been
suggested that coexistence of Mustela spp. in sympatry may
persist if the larger "poorer competitors" preyed on the
smaller "better ones" (Rosenzweig 1966). Although dietary
records appear to concur with this hypothesis, I believe that
diets are significantly different and interspecific competi-
tion is not necessary for coexistence to occur in areas of
sympatry. Hunting strategies of M. erminea and M. frenata
in the winter are different (Gamble). Further, Erlinge
(1977), Powell (1979) and Gamble have found a dominant -
subordinate hierarchy exists between weasel species. A pre-
dator attacking and killing another carnivore runs the risk
of injury to itself. I suggest that larger Mustela spp.
would only risk injury in times of food stress and that under
normal circumstances interference interactions would normally
suffice to partition resources.

CONCLUSION

Weasels are opportunistic predators. Inter-and
intraspecific dietary analysis suggest weasel species
partition food resources by the proportion of prey species
consumed. There is a clear trend towards an increase in
food size with body size. Mustela frenata and M. erminea
occupy different trophic niches. M. erminea is primarily
a vole specialist (Rosenzweig 1966; Simms 1979; Gamble)
while long-tailed weasels are generalists. Male M. frenata
consume mostly mid-sized prey while females consume both
voles and sciurids. Selection favours dietary segregation
both between and within Mustela spp. Prey selection varies
seasonally, according to availability, accessibility and
capability of the predator. Females of both species are
more subnivean than males as shown in their diets as well
as distribution (Gamble). The larger Mustela spp. though
capable of obtaining smaller prey under certain conditions
must also meet their bioenergetic demands. The net
expenditure of energy and input acts as a feedback mechanism
in dictating what proportion of prey of a given size are
consumed. In weasel hunting sets resources are divided along
a continuum which in turn is a product of the environment.
Community structure is, in part, the result of resource
partitioning.

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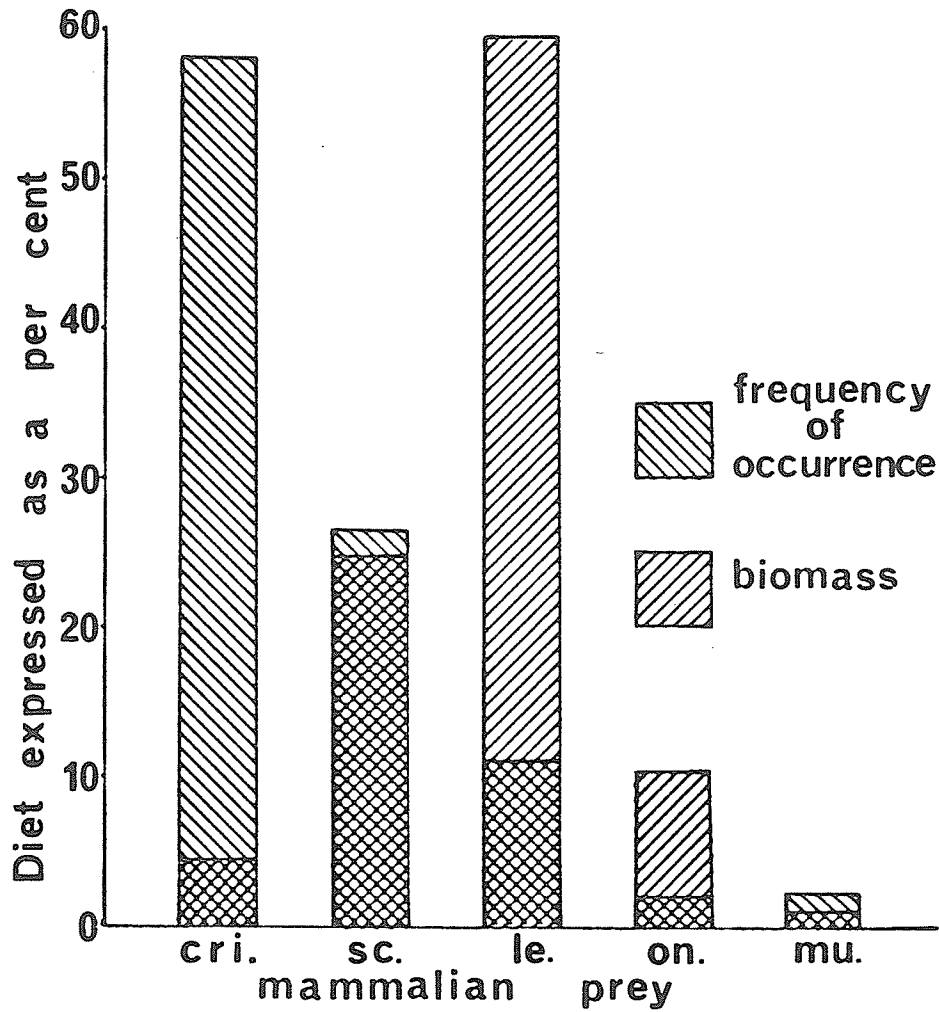
Figure 1. Mammalian prey-types consumed by
M. frenata longicauda (cri. =
cricetids, sc. = sciurids, le. =
leporids, on = Ondatra and mu. = mustelids).

Table 1. Combined dietary items found in 186 stomachs and 45 scats of Mustela frenata longicauda.

Prey items in 186 stomachs and 45 scats		Snow Free				Snow cover			⚥♀	⚥♂	Mean live food item weight (g)
		♀	♂	?	⚥	♀	♂	⚥			
Microtus spp.	15	1	1	2	4	5	6	11	6	7	37.2
Cleithrionomys gapperi	32	5	3	9	17	4	11	15	9	14	13.6
Peromyscus spp.	3		1		1	1	1	2	1	2	21.0
Mus musculus	4	1	2	1	4				1	2	15.5
Microtinae (unident.)	3	1	2		3				1	2	18.0
Tamiasciurus hudsonius	3						3	3		3	190.0
Glaucomys sabrinus	1						1	1		1	112.0
Thomomys talpoides	11		3	6	9	2		2	2	3	139.0
Sciurus carolinensis	4						4	4		4	523.0
Spermophilus franklini	3		1	2	3					1	450.0
chipmunk (Eutamias or Tamias)	2		1		1	1		1	1	1	70.0
Sciurid (unident.)	2	1	1		2				1	1	250.0
Lepus americanus	7					1	6	7	1	6	1490.0
Sylvilagus floridanus	2						2	2		2	1200.0
Leporidae probably L. townsendi	2						2	2		2	1300.0
Ondatra	2						2	2		2	1360.0
Mustela spp.	2						2	2		2	115.0
Aves	18		3		3	2	13	15	2	16	
Total number of food items	116	9	18	20	47	16	53	69	25	71	

Table 2. Prey types consumed by $\underline{M}$. $\underline{erminea}$ in both summer
          and winter.

Prey species in 50 scats and 17 stomachs	Frequency of occurrence
$\underline{Microtus}$ spp.	35
$\underline{Cleithrionomys}$ $\underline{gapperi}$	19
$\underline{Zapus}$ $\underline{hudsonius}$	1
Soricidae	2
Aves	2
unidentifiable animal tissue	4
vegetation	2

CHAPTER III

A review and some new data on

social behaviour in <u>Mustela</u> <u>frenata</u>,

·the long-tailed weasel

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ABSTRACT

Spacing of <u>Mustela</u> <u>frenata</u> <u>longicauda</u> was ascertained by live trapping studies (24,583 trap nights) and radio telemetry. <u>M</u>. <u>frenata</u> forms aggregations in optimal habitat and is social. Home ranges are shared and individuals contribute to a common gene pool. These demes appear to be patriarchies in that males are related. Male long-tailed weasels participate in parental care and may remain paired with the same female. Pairing apparently does not prevent promiscuity. Suitable whelping dens are reoccupied. Sexual dimorphism appears to favour male dominance. Young disperse from whelping dens in August but normally remain in the occupied area. Sociability may be one means <u>Mustela</u> spp. partition resources. A dominant-subordinate hierarchy exists within weasel hunting sets.

INTRODUCTION

Social behaviour of carnivores is not well understood and has led to many complex phenomena being interpreted simplistically (Ewer 1973). Infrequent field observations and a lack of detailed study led to the belief that most mustelids were solitary, socially intolerant and highly territorial (Wright 1963). Mustela frenata, the long-tailed weasel, does not fit this hypothesis. My results suggest that long-tailed weasels are social rather than solitary in optimal habitat. As Mustela spp. are often sympatric, sociability could conceivably be one means by which they partition resources in a seemingly competitive ecosystem. Most animal characteristics are the product of an interaction between inherited predispositions and the environment (Bekoff and Wells 1980).

METHODS

Live trapping studies were conducted at Delta, Manitoba (50°10'N 98°22'W) (Fig. 1) from July 1977 to December 1978. Movements of three adult males and eleven juveniles (7 females and four males) so trapped were monitored by radio telemetry from August to November 1978. A "contact" between individuals occurred whenever two or more individuals were recorded at the same time within 30 m of one another. Parent-young associations at the den site were treated separately from the "contacts" as defined above.

RESULTS

Four long-tailed weasels were taken at Oxbow in 1977
while   18 were taken in 1978. I concluded from the data
obtained in 1978 that the 1977 trap sites were situated
on the southern and eastern margins of the area frequented
by this species. All long-tailed weasel captures were
made at 9 of 84 possible trap sites in 1978 (Fig. 2) and
4 of 42 trap sites in 1977 (Fig. 3). Thirty-one short-
tailed weasels were captured 40 times at 29 trap sites in
1977-78. Few short-tailed weasels could be described as
residents. Resident status was conferred on individuals
which remained in the area for more than 30 days. (Simms
1979).

Figure 4 depicts the distribution of M. frenata as
indicated by radio telemetry, captures and scat deposition.
Long-tailed weasel movements were confined to an area
consisting of approximately 111 hectares of the 400 hectare
study site. Sixty-nine per cent. of long-tailed weasel
activity was confined to within 100 meters of Blind Channel
with the remainder along ecotonal margins. Similar habitat
to that occupied was available in the immediate vicinity but
did not appear to be used. Long-tailed weasels appeared
to share a common home range. Females were less mobile than
males and occupied a minimum area of 7 hectares and a maximum
of 62 hectares while males occupied from 8 to 111 hectares.

Distances between individuals; namely male-female, male-male and female-female were measured on given days (Fig. 5). The mean distance in m for male-female, male-male and female-female were 750 m ± 76 S.E., 614 m ± 66 and 919 m ± 90 respectively. Male-male and male-female spacing is similar. Female-female spacing shows a marked peak at interval 1000 -1500 m. A finer resolution frequency graph (200 m intervals) accentuates the peak between 1000 -1200 m.

Seventeen contacts were recorded, of which 11 were male-female, 4 were male-male and 2 were female-female. Forty-six per cent of the male-female contacts were between adult males and juvenile females.

One mature adult male (Chapter IV), N, was present at one den site in both 1977 and 1978. M, an adolescent male, was present within the study site in 1978 and was raised at the above den in 1977. In 1978 five young (four females and one male) were caught at this den; the male and one runt female died soon after. A second mature male, Z, was located at this den in May 1978.

DISCUSSION

Spacing patterns indicate social relationships and are of
particular importance in studying the smaller, less visible
carnivores. Spacing patterns are easier now to delineate
with radio telemetry which permits location in both time
and space.

Species, which, as individuals, are territorial (an
area from which conspecifics are actively excluded)
usually restrict contact with conspecifics (Ewer 1973).
Social or gregarious species rank members within dominant-
subordinate hierarchies to prevent antagonistic interactions
(Ricklefs 1974). The establishment of social groups and/
or a more flexible degree of social contact is fashioned
to a great extent by prevailing conditions. Kruuk (1976)
concluded that for many carnivores, which typically have
few predators, food is an important factor influencing
social behaviour.

Field data strongly suggest that $\underline{M}$. $\underline{frenata}$ form
aggregations in optimal habitat. These animals occupy
common home ranges (an area covered by an animal in its
normal day to day activity) and share a common gene pool.
The high frequency of catches in four and nine traps in
1977 and 1978 respectively and no catches at the remaining
trap sites showed a general funnelling of foraging
animals through a particular part of the area (Fig. 2 & 3).

The spacing relationship between males is similar
to male-female spacing (Fig. 5) suggesting males move
freely within their shared range irrespective of other
males. Females, being relatively localized in their
distribution, are, at any given time, more evenly spaced in
relation to other females (Fig. 5).

Quick (1944), Musgrove (1951) and Wobeser (1966),
likewise reported considerable home range overlap between
M. frenata males. Musgrove (1951) also found that weasel
movements were channelled through relatively defined areas
and coined the term "funnelling" for this effect. Faeces,
urine and scent markings are left within these defined
areas, providing evidence of social communication.
Trapping records from Wobeser (1966) and this study
indicated that two or more individuals can be trapped at
any one of these sites on a given day. These "funnelling"
sites account for the majority of the trapping records.
Crepuscular activity (Wobeser 1966, Kavanau and Ramos 1975,
and Gamble) by both sexes precludes temporal spacing
though when confronted with unfavourable circumstances,
activity may shift (Hall 1951; Kavanau and Ramos 1975).

Wright (1931) defined a local population of potentially
interbreeding individuals as a "deme". Mating can be random,
but physical barrier or behavioural segregating mechanisms
tend to isolate a deme within the greater population
Anderson (1964;1967), Reimer and Petras (1968) and

Sealander (1970) suggested that a deme may be composed
of as few as ten individuals. Territorial and home
range maintainence behaviours may be responsible for the
long term division of a population into demetic units.
Demes often occur in areas of sharply defined, patchy
habitat discontinuities. Schultz and Tapp (1973)
argued that preferences for the odors of some group
members may facilitate group cohesion.

Dispersal

Young disperse from the den site in August with
juvenile females sometimes moving outside the group range.
This would seem to be the mechanism of gene flow between
demes though supernumeraries of either sex may be
evicted when resources (food and/or space) become
limiting (Wobeser 1966, Smith 1974, and Powell 1979).
Sexual dimorphism can influence expulsion because females
are considerably smaller ($\bar{x}$=212 g) and would be disadvantaged
in an aggressive encounter with a male ($\bar{x}$=394 g). Within
populations smaller animals tend to be subordinate (Turner
and Iverson 1973; Erlinge 1979).

Relationships between males and females

The majority of contacts observed were between males
and females and suggest a close association between the
sexes. Adult males were in contact with females more

frequently than subadult males. Hall (1951) and Wright
(1963) contend that M. frenata males mate with mature
adult females after parturition and with juveniles
(3 - 7.5 months) in the summer. I found that breeding
is protracted in Manitoba and may extend from April
through September with juveniles being serviced in the fol-
lowing spring rather than the summer of the previous year.
Male-juvenile female contacts would seem to function for
purposes of enhancing social ties. Female activity being
relatively localized would increase the likelihood of
male-female contact.

Hamilton (1939) believed long-tailed weasels remained
paired for long periods, perhaps for life. Pair formation,
as demonstrated in commercial mink, M. vison (Enders 1955)
may promote success in breeding. I found suitable welping
dens are reoccupied, possibly by the same pair. Harper
(1927) suggested that females will occupy suitable dens for
several years. Mature resident females rearing offspring are
likely to have a higher social position within the hierarchy.
I found 77% of subadult females (7.5 - 11 months) were
barren in their first summer whereas better than 94%
of mature females were pregnant. Erlinge (1977a and
1977b) found that adult male M. erminea were dominant
over resident members of all other sex-age classes except
pregnant or oestrous females. Hamilton (1933) and Quick
(1944) stated that male and female long-tailed weasels were

found together or were seen travelling together even in
non-breeding seasons. Wobeser (1966) twice observed
what he believed to be a female in the immediate vicinity
of a trap containing an adult male.

Male-male contact

Male-male contact was less frequent than male-female
contact. Sexes were in contact at random (Fig. 5). Females
require a degree of familiarity with males in order for
breeding to be successful (Enders 1955). Females,
being relatively localized, would certainly have the
opportunity to obtain such contact.

Wobeser (1966) suggested males may partition home
ranges on a temporal rather than a spatial basis using
scent markers. Temporal spacing, he suggested, is a means
of avoiding overt aggression. Olfaction can be used as
an interdeme isolating mechanism (Cox 1978). Eisenberg
(1963) found that several animals living in proximity can
communicate their individuality and reproductive condition
without ever coming into physical contact yet maintain
the autonomy of the group. Foreign olfactory stimuli
from conspecifics not part of the group would either be
received as neutral or aversive. Familiarity with the
scent of other male long-tailed weasels within the deme
would, perhaps, suffice to maintain group cohesion. Some

canids have a similar mechanism for maintaining group
cohesion (Mech 1970; Bekoff and Wells 1980).

The extent of the group range in M. frenata may
determine the frequency of contact. Males range farther
than females in response to this species reproductive and
foraging strategies. Females have more restricted ranges
due in part to the trophic niche they occupy. Females
consume a higher proportion of microtines in their diet
than males which rely to a greater extent on larger prey
items, e.g. scuirids and leporids. The degree of segregation
in the diet is biologically significant (p. 51). Sexual
dimorphism would enhance partitioning of resources by
defining the prey size range each is capable of procuring
or that meets their bioenergetic requirements. Further,
where snow occurs in winter, females would have greater
access to the subnivean environment (Simms 1979 and p. 21)
and in turn greater accessibility to microtines.
Undoubtedly males, due to the nature of their prey, would
be wide-ranging as shown by home range data (Chapter I).

Hansen (1952) observed two adult males playing and
travelling together in July during the breeding season.
One might expect antagnostic behaviour between sexually
mature males. Certainly, breeding does not prohibit
contact nor do male long-tailed weasels appear territorial
at this time.

Dempsey (in Enders 1955) suggested that contrary
to popular belief, animals are not born knowing how
to copulate and apparently must learn. I found that,
though male long-tailed weasels' testes develop in their
second summer, the baculum does not reach maturity until
they are 23 months of age in much the same manner as that
of mink. A high percentage of male mink will not breed
in their first reproductive season (Enders 1955). Perhaps
this reproductive season is a period of learning how to
copulate, a situation which would require close contact with
mature adult males.

Female-female contact

Female-female contact was infrequent in relation to
other contact types due primarily to spacing. Powell (1979)
suggested that within mustelinae, territories are defended
intrasexually. During whelping one would expect territorial
maintenance for females to be critical. Yet Hall (1974)
observed two female long-tailed weasels with dens 183m apart
containing young. An adult male occupied a den 46 m
south of the two females. All three were in a single
hectare which contained a minimum of seven weasels. One
could argue that resources were not limiting, but Hall
(1974) commented that "they probably would have cleaned
out the entire population of pocket gophers in this small
meadow before moving on" suggesting spacing in females is

a function of the availability of prey not aggressive

interactions. Hall's account also suggests under certain

circumstances nomadic populations occur. As in coyotes

Canis latrans (Bekoff and Wells 1980), long-tailed weasel

populations seem to consist of solitary to gregarious and

transient to stable groups.

Parental Investment

Courtship and mating in animals results in production

of young and behaviour then becomes oriented towards their

care and protection (Smith 1974). In weasels it generally

was believed to be the responsibility of the female to

rear the young (Hall 1951). My data suggest male long-

tailed weasels actively participate in parental care.

Adult males are frequently reported at dens containing

young (Hamilton 1933, Green 1936, Bradt, 1947, Amundson

1950, Hall 1951, Wobeser 1966, and Gamble). Males

contribute to feeding by securing prey (Hamilton 1933;

Bradt 1947) and cooperate with the female in defence of

the offspring (Green, 1936; Amundson 1950). Hall (1951)

proposed that males might simply help until weasel pups are

half grown. Field observations in the current study

provided evidence that males frequent the den until departure

of the young. Multiple capture data obtained by Wobeser

(1966) suggested that juveniles move in close contact with

the adults for more than a month after desertion of the den. Juveniles in the current study simply remained in a shared home range and were in frequent contact with adults.

Dens are not always exclusive to the attending male. Wobeser (1966) similarly observed a second male at an occupied den. It would seem other adult males are tolerant of young not necessarily their own. Tolerance perhaps evolved as a function of weasel reproductive strategy.

Parents should only invest time and energy in young if it increases the genetic fitness of both the parent and young (Trivers 1974). Basically, all adaptations for increased or specialized parental care tend to increase the survival of the young and make the young more dependent on the parents (Brown 1975). Weasels are promiscuous (Skinner 1927; Hall 1951; Erlinge 1979); often copulating with several individuals. Males attending young are not necessarily rearing their own offspring. Male parental investment would then seem counter-productive in terms of time and energy. Within demes males contribute to a common gene pool. The combined reproductive success of the group would be a measure of a male's inclusive fitness (based on gene frequency rather than on the number of offspring sired). A deme should select for a degree of genetic homogeneity (Brown 1975). Males may be tolerant of offspring within the deme due to selective advantage.

Tail flagging (tail extended perpendicular to the body) was observed in six adult male long-tailed weasels. This behaviour is so exaggerated it is unlikely to function in locomotion (Kiley-Worthington 1976). It can be viewed instead as a display. Kiley-Worthington (1976) found in ungulates, canids and felids that tail elevation could be used in sexual, aggressive, greeting or puzzled contexts. The threshold for elicitation is species, age and sex dependent. Neither M. rixosa, the least weasel, nor M. erminea were seen to elevate their tails in this manner.

The underlying cause of variation, both seasonally and geographically, in coloration in weasels seems to be protective in nature (Hall 1951; Hammel 1956). The black tail tip is believed to function as distraction coloration to encourage aerial predators to strike at a non-vital area. Flagging the tail appears to make males more vulnerable to aerial predation (rearward attacks) and also advertises the animal's position. Perhaps the disadvantages are outweighed by social advantages.

There are those who believe that the weasel's black tail tip in the summer may aid young in following their mother as she moves through dense undergrowth (Shufeldt 1920). Perhaps, on occasion, the male takes the lead in mobile family units and by elevating the tail provides a better directional point. The male's size and, hence, increased physical capabilities may provide a more secure

defence system.

The presence of a runt female may suggest unequal distribution of food resources which might stem from an early establishment of a social hierarchy. Unequal distribution might arise by preferential treatment by the parents or establishment of a peck order within the litter.

Resource partitioning is a major determinant of the diversity of coexisting species within a community. Mustela spp. frequently occur in hunting sets (Rosenzweig 1966) which structurally appear similar. Generally, it is believed that no two species can coexist unless they exploit their environment differently (Hardin 1960). Vance (1978) suggested coexistence of two species in one niche is possible where regulation of one species through selective predation permits another to coexist. Within weasel hunting sets this is believed to be the case (Rosenzweig 1966) with the larger species, M. frenata preying on smaller members: M. erminea and/or M. rixosa. Competition is not a necessary consequence of coexistence, rather competition seems to be the exception rather than the rule (Kropotkin 1902).

The ordering of dominance is of the utmost value to carnivorous species who live in closed societies, for such animals must establish ways to promote harmony among themselves (Ryden 1979). Interspecifically (Powell 1979), a dominance-subordinance relationship exists between M.

frenata and M. erminea in favour of the former. It would
seem long-tailed weasels repress ermine through interference
interactions (p. 18). In the Oxbow community M. frenata
did not exclude M. erminea and M. rixosa, rather the numbers
of M. erminea and M. rixosa were maintained at lower levels
than within areas where M. frenata was absent or solitary.
M. frenata was dominant to M. erminea and M. rixosa in terms
of numbers. Errington (1967) suggested that predators do
not randomly prey on individuals from a population but re-
move those individuals whose social position renders them
more vulnerable. Perhaps, within weasel hunting sets social
relationships are equally if not more important than preda-
tion upon the smaller species. Certainly the smaller
weasel species, M. erminea and M. rixosa, are capable of
inflicting an injury on the larger species, M. frenata,
which could have severe ecological repercussions. Animals,
above all, are "pragmatists", taking the path of least
effort for the greatest reward (Leakey and Lewin 1978).

A hierarchy is not a system by means of which a supe-
rior can enslave the inferior. In a well-ordered hierarchy,
individual members learn to know their respective places
and thereby avoid conflict (Ryden 1979). Intraspecifically,
M. frenata lives in closed societies (demes) in optimal
habitat. Behavioural mechanisms should dictate a prefer-
ence for intra-population matings and is often referred to
as "ethological" or "behavioural" isolation (Cox 1978).

Territorial behaviour is generally considered to be the behavioural mechanism which isolates individual population units and may be responsible for the long-term division of a population. Evolution takes place within species (Wilcock 1972) and thus reproductive isolation might be expected to occur below the species level (Wright 1931). Long-tailed weasel populations seem to consist of solitary to gregarious and transient to stable groups. Whether selection acts to favour a single individual or a promiscuous reproductive unit, the critical factor is the effect of exploitation and habitat suitability (Baker 1978).

Evolution of a social system may not be unique to this *Mustela* species. Kropotkin (1902) stated that during the last century in Scotland and the Unterwalden canton of Switzerland the common weasel, M. *erminea*, was more sociable than it is now and was seen in larger groups. Van den Brink (1977) reported that the British stoat, M.e. *stabilis* often hunts in packs. Seton (1929), Hamilton (1933), Grigoriev (1938) and I have observed male M. *erminea* in attendance at dens containing young and on occasion providing food.

CONCLUSION

Distribution of M. frenata in optimal habitat seems to
be the result of both mutual attraction and availability of
prey. M. frenata occupy common home ranges in optimal
habitat and share in a common gene pool or "deme". Demetic
units are likely patrilineal groupings. Male long-tailed
weasels participate in parental care and may remain paired
with the same female over a number of years although cuckol-
dry may still occur. Suitable whelping dens are reoccupied.
Young disperse from whelping dens in August but normally
remain in the occupied area. Sexual dimorphism appears to
favour male dominance in M. frenata. Sociability may be one
means Mustela spp. partition resources.

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Figure 1   Oxbow community

Woodlands (deciduous)   Old field succession

Marsh   Farmland (hay)

Wet meadows   Farmland (under tillage)

Prairie   Phragmites (seasonally dry)

Figure 2 - Capture and trap sites for <u>M</u>. <u>frenata</u>
at Oxbow in 1978.
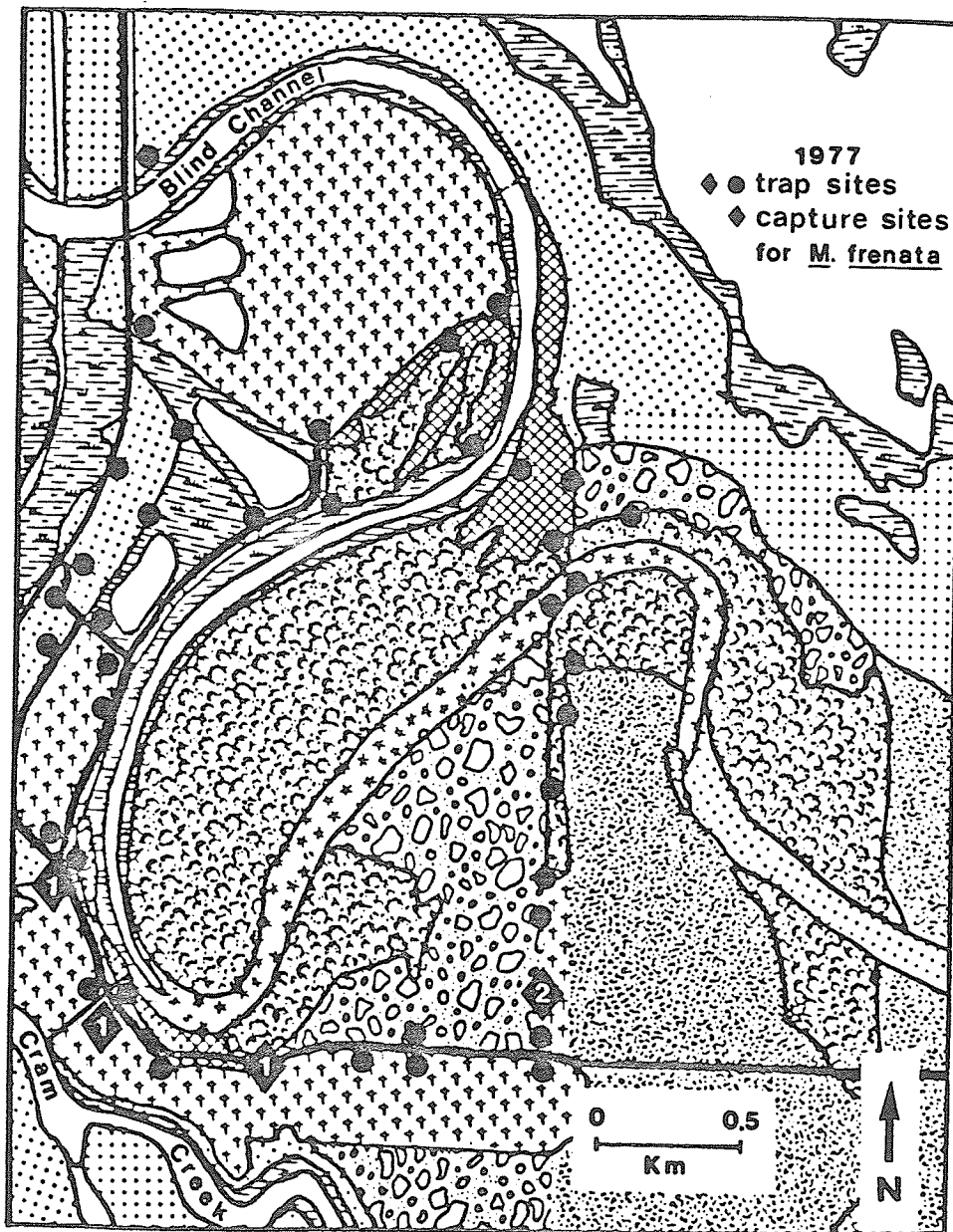
Figure 3 - Capture and trap sites for M. frenata
at Oxbow in 1977.
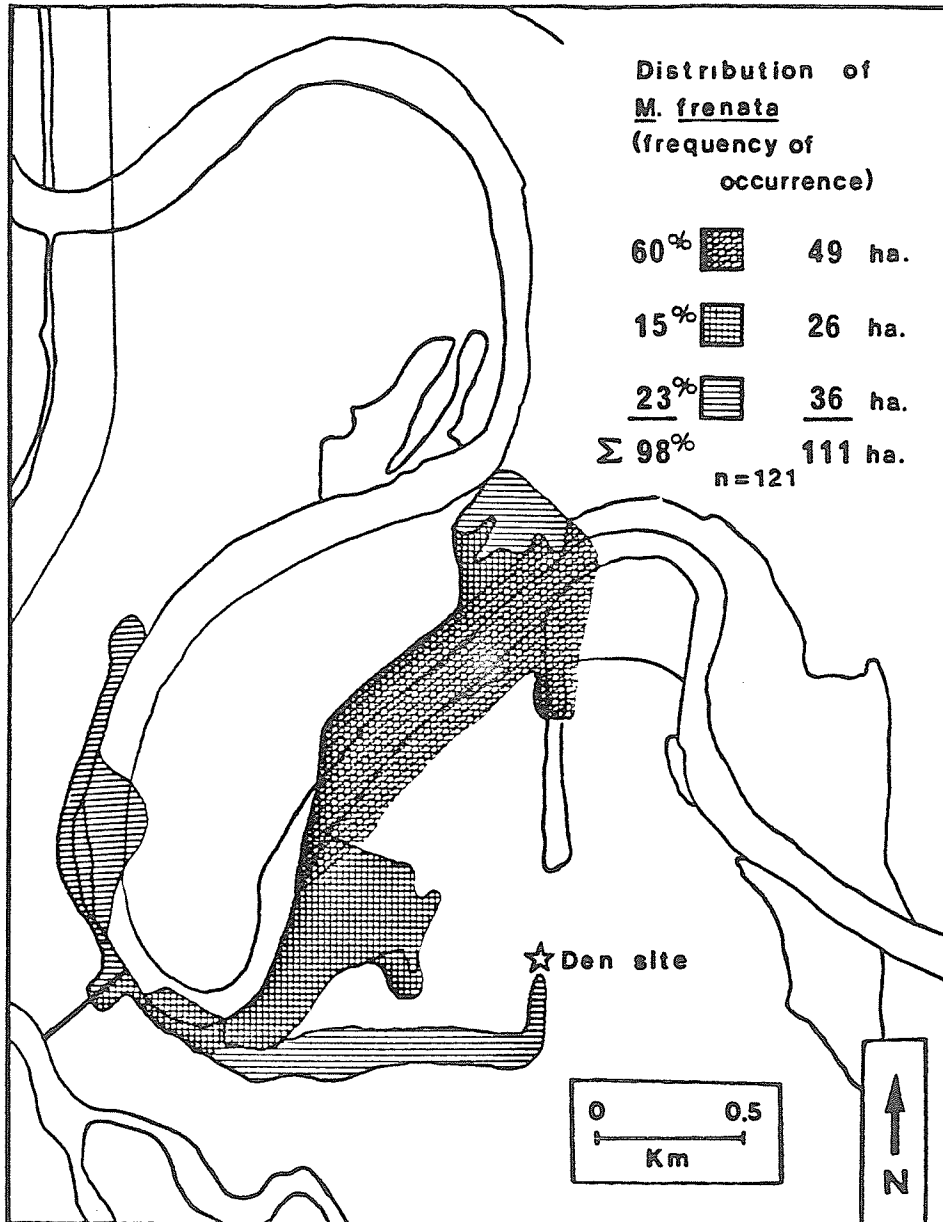
Figure 4 - Site tenacity of M. frenata within the
Oxbow community. Heavy shaded areas
are those areas most intensively used.
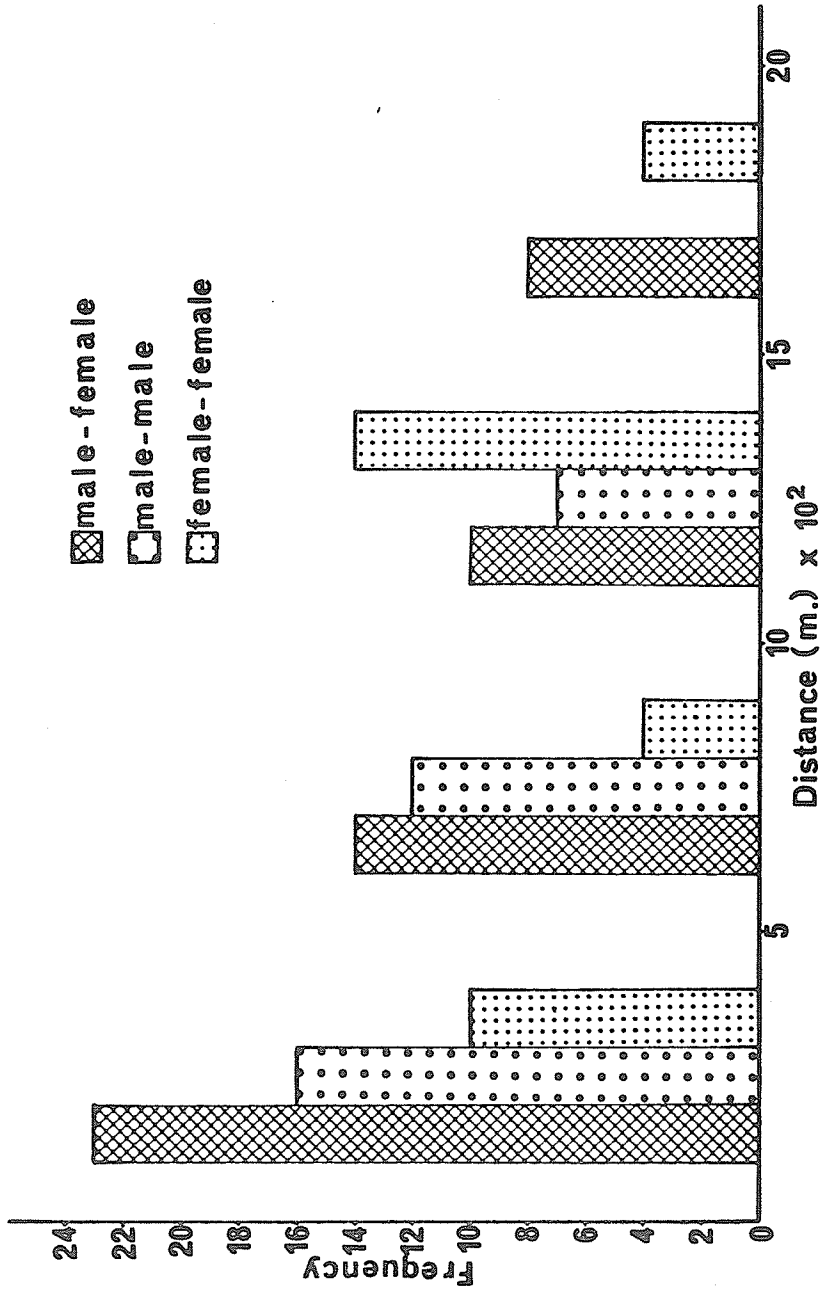
Figure 5 - Spacing of <u>M</u>. <u>frenata</u> relative to other individuals.

CHAPTER IV

Reproduction and Development in <u>Mustela</u>

<u>frenata</u> Lichtenstein, the long-tailed weasel

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ABSTRACT

Data were obtained on reproduction and development in
M. frenata from 90 bacula and 39 uteri. Males do not obtain
sexual maturity until they are two years old at which time
bacula are fully developed. Bacula morphology and weight
are reliable criteria for ageing M. frenata males. Most
adult females exhibited suppressed embryonic development
or delayed implantation. Subadult females, however, appear
not to breed in their first summer. Conception in subadults
may occur in the spring. Not all individuals react in the
same fashion to external stimuli.

INTRODUCTION

Wright (1942, 1947, 1948, 1951 and 1963) described the breeding of captive long-tailed weasels, _Mustela frenata_. He suggested that breeding normally occurs in young (3-4 months) and adult females in July and August with partuition occurring in April or May the following year. Embryonic development of the blastula is suppressed until spring (delayed implantation). Adult testicular development is reached at eleven months of age (Wright 1947). Nidation (time of implantation of the blastula) and testicular development coincide with the onset of the spring molt from white to brown (Wright 1947).

I tested Wright's hypothesis on _M. f. longicauda_ in Southern Manitoba. Field evidence did not always agree with Wright's data indicating that a refinement of his hypothesis is necessary.

METHODS

Live trapping studies were conducted at Delta,
Manitoba (50^0 10' N 98^0 22' W) from July 1977 to
December 1978 (Gamble).   Trappers provided 181 carcasses
of M. f. longicauda of which 128 were males and 53 were
females.   Information on locale, date of capture, habitat,
bait and type of set was provided.   Weasels were aged by
examination of dental cementum annulae, baculum weights
and skull osteology.   Shrinkage of the size of the pulp
cavity in the canines with increasing age was a reliable
cross reference.   Bacula were scraped with forceps and air
dried before weighing.   Gross morphology of the baculum
was noted.   The entire reproductive tract of females was
removed.   Gross histological examinations were conducted
to reveal blastulae present in the uteri.   Oviducts and
uteri were flushed with water to free the blastulae.   In
the field, testes size was determined by palpating the
scrotal region (Wright 1942).   Females were examined for
swollen vulva.

RESULTS

Figure 1 compares the relationship of baculum weight (log Y) with age (X). The regression line has been extended to the point at which mean adult weight is attained (.0802 g ± .0054 S.E.), 23 months of age. Figure 2 depicts the progressive changes observed in baculum morphology. Bacula go through characteristic stages of growth and development. At maturity, bacula are fully ossified and rigid. Prior to attaining maturity bacula are flexible due to the proportion of cartilage present. Maximum baculum length apparently is reached early in development between $7\frac{1}{2}$ - 10 months of age. The proximal end changes both in size and shape by addition of spongy bone. The distal end appears to reach its characteristic shape at 21 months of age. The shaft increases in diameter until fully ossified.

A comparison of pregnancy as indicated by blastula presence is made between subadult (7.5 - 10 months) and adult females (Table 1). Most subadult females were not pregnant in contrast to adult females. No noticable vulval swellings were evident in females trapped from August - October.

Males showed a marked increase in testicular size
in March that remained until November. Testicular development
seems to correspond to pelage changes. The spring molt
from the white winter pelage to the brown summer pelage
generally occurs in March or April, though brown hair
first appears in February. The autumn molt (brown to white)
ranges from October through November. The trapping season
for weasels in Manitoba is November 15 through the last
day of February. Mixed white and brown haired individuals
taken in late November in Manitoba are not uncommon as
revealed by trapper's catches.

DISCUSSION

Bacula develop in the two year period required
for M. frenata to attain maturity. Baculum morphology
and weights suggest two subadult classes exist; namely,
(1) subadult 1 defined here as individuals less than
11 months of age and (2) subadult 2 or adolescent
males between 11-23 months of age. Adolescent male
baculum weights between 20-23 months of age overlap with
adult males but baculum morphology, particularly at the
basal (proximal) end, often permits discrimination.
Heidt (1970) found the basilar breadth of the baculum
in M. rixosa also showed the highest correlation with
age.

Elder (1951) found that bacula in mink, M. vison,
as in M. frenata, do not attain full size in their first
year of testicular development. Statistical analysis
of mink bacula showed a high correlation between weight
and age (r = .849), but a poor correlation between length
and age. Elder (1951) found that the transition to
adult-type baculum occurred at 18 months of age. Breeding
begins in February in mink while in long-tailed weasel
active spermatogenesis starts in March (Wright 1947).
Testosterone levels are responsible for baculum development

(Wright 1951) in mustelids and perhaps account for the lag observed in long-tailed weasels in reaching the transition to adult-type baculum.

Spermatogenic activity is reached at one year and usually indicates sexual maturity (Wright 1947). Mechanical and perhaps, ethological isolating mechanisms (Chapter III), would prevent or decrease adolescent male fertility. The use of testicular development as a measure of maturity is unwise.

Elder (1951), Long (1969) and Heidt (1970) found that the size of the baculum in Mustela spp. depends on age and thus sexual maturity. The complexity of the bacular base and tip and of the pattern and structure of the blood vessels and erectile tissue increases with the length or mass of the penis or baculum (Long 1969). In mustelids a direct relation apparently exists between function and form.

Observations on male mink demonstrated that a high percentage would not breed during their first reproductive season (Enders 1955). Dempsey (in Enders 1955) suggested that most animals are not born knowing how to copulate but are taught. Wright (1948) similarly found that most "adult" male long-tailed weasels showed no interest in mating, but once a male had breeding experience breeding always ensued.

The majority of subadult female M. f. longicauda
did not breed in their first summer. Most adult females
showed signs of delayed implantation. Wright (1942)
found in M. f. oribasus that all females taken during
the autumn and winter months ultimately proved to be
pregnant. My data suggest that either a delay in breeding
occurs in most subadult females or the existence of
spring breeding. Deanesly (1935), Watzka (1940),
Ender (1955) and Tumanov (1977) suggested that in M.
erminea some animals breed in the summer and have a long
gestation period, but others come into heat in March.
Hamilton (1933) considered that the short-tailed weasel
has the same type of sexual cycle as the long-tailed
weasel. Wright (1942) found, in two captive females
which were not bred during the summer, that in the following
spring both showed the enlarged vulva of animals in heat.
Loss in the blastscyst stage or in the earlier
stages of fetal development may have a similar effect
(Enders 1955, Tumanov 1977).

Wright (1948) provided data on mating in captivity
resulting in birth of young. Females 89% of the time
were 2 years or older at partuition. One female, when
exposed to modified light conditions prior to breeding,
produced young after 103 days at 1 year old. Enders
(1955) found other factors; namely auditory, visual and
olfactory cues and activity are responsible for development

of breeding condition. Extrinsic factors would appear
to influence gestation.

Individuals of M. frenata and M. erminea did not
molt at the same time at Delta; instead a broad range
was evident in the autumn and spring. Bissonnette (1943)
also found that not all animals of the same species react
alike even if secured from the same locality.

The pituitary gland regulates pelage cycles and
sexual development (Rust and Meyer, 1969) but the capacity
to acquire a white coat or a brown coat in winter is a
hereditary matter (Hall 1951). Photoperiod (Rust and
Meyer 1968), temperature (Rust 1962), snow (Gaiduk 1977),
metabolism (Flintoff 1933), activity (Baumler 1973),
nutrition and latitude (Hall 1951) and altitude influence
the seasonal molt in weasels. Certainly selection
would favour independence of some of these variables in
relation to breeding.

CONCLUSION

Testicular development is not an indicator of
sexual maturity in M. f. longicauda. Baculum development
is a better indicator of maturity. Baculum morphology
and weight are reliable criteria for ageing M. frenata
males for management purposes.

Most females do not breed in their first summer.
Conception in subadults may occur in the spring.
Spermatogenesis in males and observations of females in
heat at this time provide support for this contention.

M. frenata males resemble mink in bacular morphology
and development. Adult females exhibit a latent period of
the ermine type, prolonged up to 10 months (Kuris and Bakeev
1974) but in subadult females or barren females (Wright 1948)
the period of sexual activity may be reduced to a two month
season (spring breeding). A life history strategy of this
nature would permit long-tailed weasels to maximize their
reproductive potential under highly variable environmental
conditions.

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Fig. I. Baculum weight in relation to age (▲ mean adult weight).
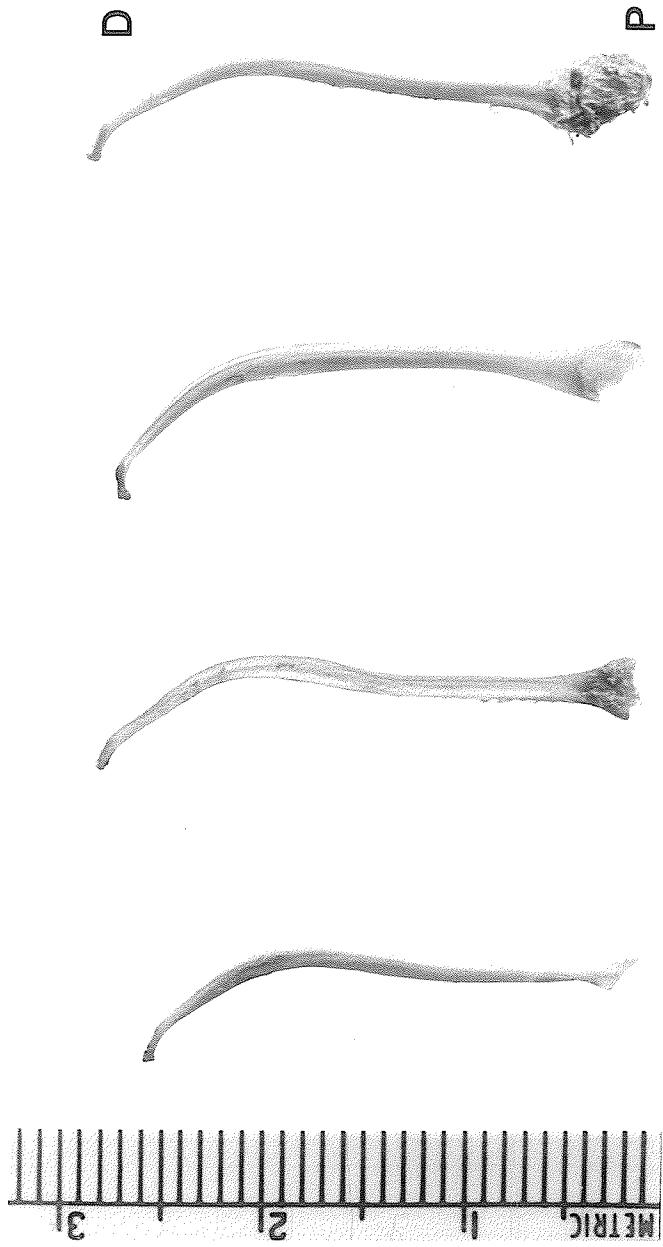
Figure 2. Progressive changes in baculum morphology with age
(D = distal, P = proximal).

Table I. Proportion of females with blastula present or absent
in relation to age. Techniques for ageing females are
taken from Hall (1951).

	N	Blastula Present (Pregnant)	Blastula Absent (Barren)
Subadult females	22 (56.4%)	5 (22.7%)	17 (77.3%)
Adult females	17 (43.6%)	16 (94.4%)	1 (5.6%)
Total	39	21 (53.8%)	18 (46.2%)

CHAPTER V

Distribution in Manitoba of

Mustela frenata longicauda Bonaparte,

the long-tailed weasel, and the interrelation

of distribution and habitat selection in

Manitoba, Saskatchewan, and Alberta

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ABSTRACT

The distribution of <u>Mustela</u> <u>frenata</u> <u>longicauda</u> was ascertained for Manitoba, Saskatchewan and Alberta by examination of 91 labelled museum specimens and 186 carcasses provided by trappers from Manitoba. Collection records on site selection and distribution reaffirm the author's contention that <u>M</u>. <u>frenata</u> prefers late seral stages or ecotones in close proximity to free standing water. The transition between Aspen Parkland and the Boreal Forest or Taiga is the northern-most distribution of this species in the Canadian Prairies.

INTRODUCTION

Banfield (1974) is often cited as the major source for distribution of mammals in Canada. Distribution data are normally procured from labelled museum specimens. Museum holdings of <u>Mustela</u> <u>frenata</u> <u>longicauda</u> are few and thinly scattered geographically. Records are principally confined to the southern and more populated regions.

Few studies have reviewed the ecology and distribution of <u>M</u>. <u>frenata</u>. This paper will elucidate the bionomics of <u>M</u>. <u>f</u>. <u>longicauda</u> and provide data on its distribution in Manitoba. Soper (1964) provided a thorough review of the occurrence of this species in Alberta. From what is known of its distribution and habitat preferences in Manitoba and its distribution in Alberta one can extrapolate for Saskatchewan.

METHODS

Specimens of M. f. longicauda were borrowed from the
Manitoba Museum of Man and Nature, National Museum of Canada,
Provincial Museum of Alberta, Royal Ontario Museum and
the Saskatchewan Museum of Natural History. Trappers
provided 186 carcasses of M. frenata taken in the range of
this species during the winter of 1977-78 in Manitoba.
Data on locality, habitat, date of capture and bait were
included. Skeletal materials were prepared by means of
enzymes and were deposited at the Manitoba Museum of Man
and Nature. A total of 216 specimens were examined from
Manitoba, 39 from Alberta and 22 from Saskatchewan.

Verbal reports of captures of M. frenata within the
Interlake region, between Lake Manitoba and Lake Winnipeg,
were received but no specimens have been obtained to date.

RESULTS

Figure 1 shows the distribution of <u>M</u>. <u>frenata</u> in

Manitoba according to the number of specimens recorded from

a given area (frequency). Holland, Delta, Swan River,

Dauphin and Steinbach are areas in which agriculture occupies

a small proportion of the total area. A mosaic of land

under tillage, grazed and undisturbed is present. Capture

records are usually associated with waterways not suitable

for cultivation.

Figure 2 portrays the distribution of <u>M</u>. <u>f</u>. <u>longicauda</u>

throughout the prairie provinces. Community structure in the

more northerly areas changes in per cent cover from aspen

in the south to primarily conifers in the north until

community structure is such that it can be defined as the

Boreal Forest proper or Taiga (Nat. Atlas Can., 1974).

Frequency of captures and sightings of <u>M</u>. <u>frenata</u> decrease

as one approaches this line. Extralimital records are found

in isolated stands of Aspen Parkland (The Pas, $53^\circ 90'N$ 103°

$20'W$; Fort McMurray, $56^\circ 44'N$ $111^\circ 22'W$; Athabasca, $54^\circ 34'N$

$113^\circ W$; Grand Prairie, $55^\circ N$ $119^\circ W$). <u>Taxidea</u> <u>taxus</u>, the

American badger, shows a similar distribution and was

reported from Fort Vermilion ($58^\circ 23'N$ $116^\circ W$) as well as

Fort McMurray, Athabasca and Grande Prairie. Soper (1964

provided a list of typical transition species (Aspen Parkland)

which includes: <u>Spermophilus</u> <u>richardsoni</u>, <u>S</u>. <u>franklini</u> and <u>Thomomys</u> <u>talpoides</u>. These mammals are major items in the diet of <u>M</u>. <u>frenata</u> and <u>T</u>. <u>taxus</u>.

DISCUSSION

In Manitoba, I found M. f. longicauda preferred late
seral stages or ecotones where prey species diversity was
greatest. Soper (1964), Wobeser (1966) and Simms (1979)
reported a similar preference. This preference in habitat
selection was indicated in the diet of M. f. longicauda.
Long-tailed weasels are generalist predators preying upon
a variety of cricetids, sciurids, leporids and bird species.
(Dearborn 1932; Hamilton 1933; Polderboer et al. 1941;
Glover 1942; Quick 1951; Wobeser 1966; Simms 1979; Gamble).
Populations of long-tailed weasels are relatively stable
(Hall 1951; Gamble) in contrast to M. erminea, M. rixosa and
M. nivalis which exhibit periodic fluctuations (Osgood 1935;
Jeffries and Pendlebury 1968; Bakeev 1971; Lakemoen and
Higgins 1972). Breeding in M. erminea is a function of
the availability of microtines (Andersson and Erlinge 1977)
whereas generalists are capable of rearing young on alternate
prey species(Andersson and Erlinge 1977; Gamble). An
important component of a long-tailed weasel's life history
strategy is this ability to switch to alternate prey. Prey
species diversity would seem to be the principal factor governing
whether a particular environment is suited to this species
existence.

The most northerly distribution of M. frenata in
western Canada follows the southern margin of the Boreal
Forest. Distribution of long-tailed weasels in western Canada

is a product of diet and metabolic requirements (i.e. proximity to water). Extralimital records are confined to isolated stands of Aspen Parkland which contain the mammalian species normally associated with this vegetation type. The Boreal Forest does not contain the diversity of species found to the south (Simpson 1964). I found at Delta ($50^{o}10'$N $98^{o}22'$W) alone a minimum of 27 mammalian prey species were present. Further, the niches available to carnivores in the Boreal Forest are occupied by M. erminea (principally a vole predator), Martes americana (hares, tree squirrels and mice) and Martes pennanti (hares, squirrels, mice and porcupine). Niche breadth would seem too narrow to permit the intrusion of another carnivore.

Simms (1979) suggested that long-tailed weasels are limited in their northern distribution by snow cover which restricts the size of foraging spaces, thereby conferring an advantage to the smaller weasels. Simms used Banfield (1974) in determining the distribution of M. frenata in relation to snow cover. The area of distribution in Manitoba is almost twice that presented by Banfield (1974). Extralimital records from Alberta and Manitoba are north of the snow isopleth given by Simms (1979). Further, female long-tailed weasels are more subnivean than male short-tailed weasels though female M. frenata ($\bar{x}$ = 212 g) are larger than M. erminea males ($\bar{x}$ = 162 g).

Wobeser (1966) and Fitzgerald (1977) reported that long-tailed weasels are better tunnellers in snow cover than M. erminea. Snow cover would seem not to be a barrier to M. frenata.

M. frenata appears partially restricted to the vicinity of free standing water (Hall 1951; Gamble). M. frenata also uses waterways in daily activity and perhaps these are avenues for dispersal. Extralimital records are found along the Peace River system, the Athabaska River system, and the North Saskatchewan. All systems run from south to north. In southern Manitoba, trapping records of M. frenata were most often associated with waterways. Unlike most other areas of southern Manitoba, the southern Interlake region is nearly devoid of surface waterways. There are no documented records of M. frenata from this region. The northern drainage system of the Interlake does not extend far enough south to provide an access corridor to the northern Interlake though it is Parkland. Aspen Parkland within the Interlake is inferior (in terms of prey species diversity) to that found elsewhere in southern Manitoba.

Similarly, historical reports of T. taxus in the interlake are absent though recent records suggest that colonization is underway. Roads into this area have provided hibernacula for ground squirrels which now occupy this region

but were absent or rare before road construction. It would
seem that the Interlake is unsuitable for long-tailed weasels
in not having sufficient waterways for dispersal or an
adequate diversity of prey species.

CONCLUSION

The northern limits of long-tailed weasel distribution in the Canadian prairies is the Boreal Forest. The long-tailed weasel is correctly defined as a transition species within the Prairies. Transition areas provide a wide variety of prey species suited to the life history strategy of this species. Waterways provide access corridors to suitable habitat and are a means of dispersal.

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Figure 1. Records of long-tailed weasels in southern
Manitoba from museum specimens and commercial
trapping records.

The Pas

Lake

Winnipeg

1-3 captures
4-6
7-9
10 +

53°

52°

Swan
River

Dauphin

Lake

51°

Manitoba

Delta

50°

Virden

Winnipeg

Holland

Steinbach

49°

101°   100°   99°   98°   97°   96°
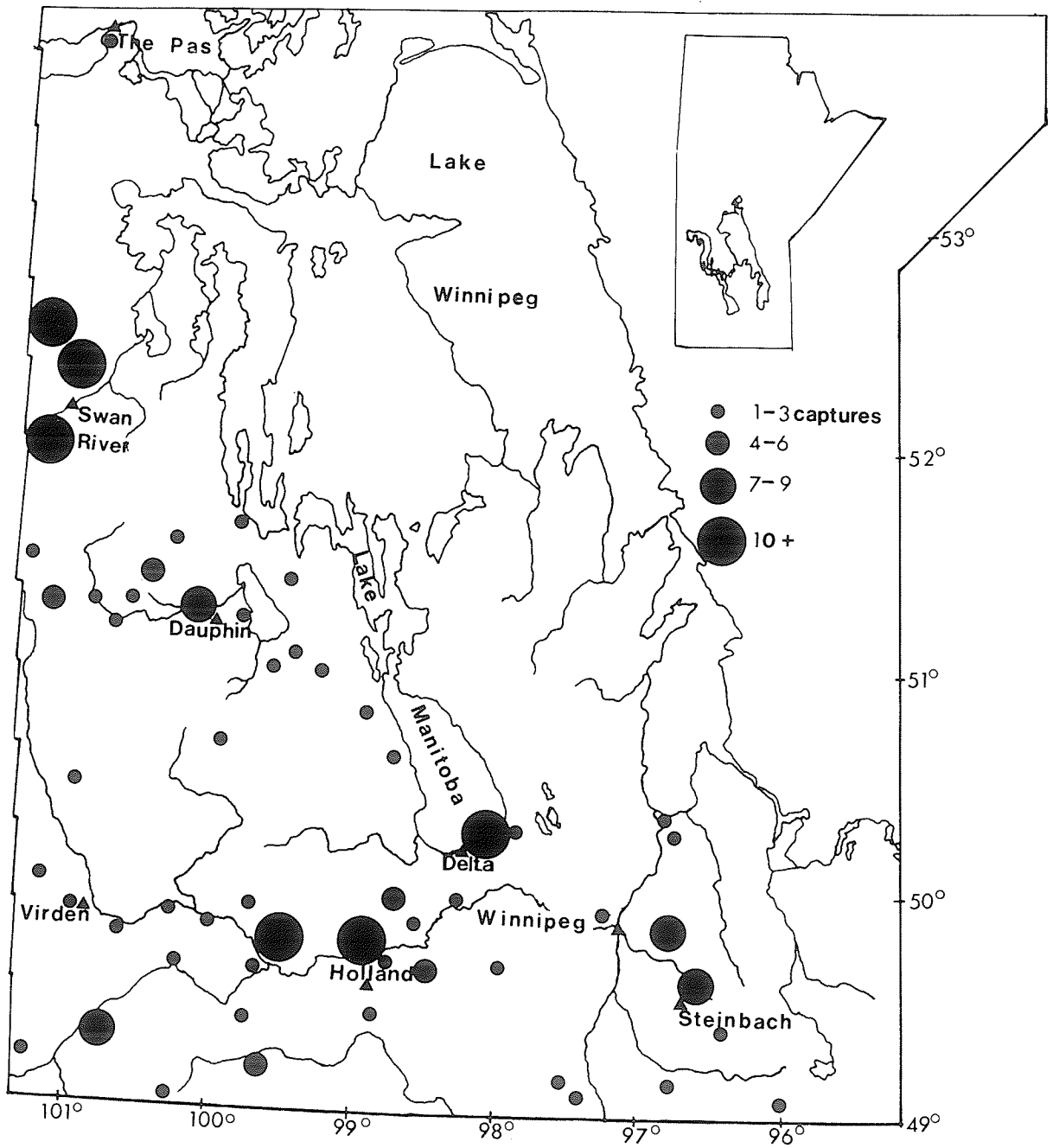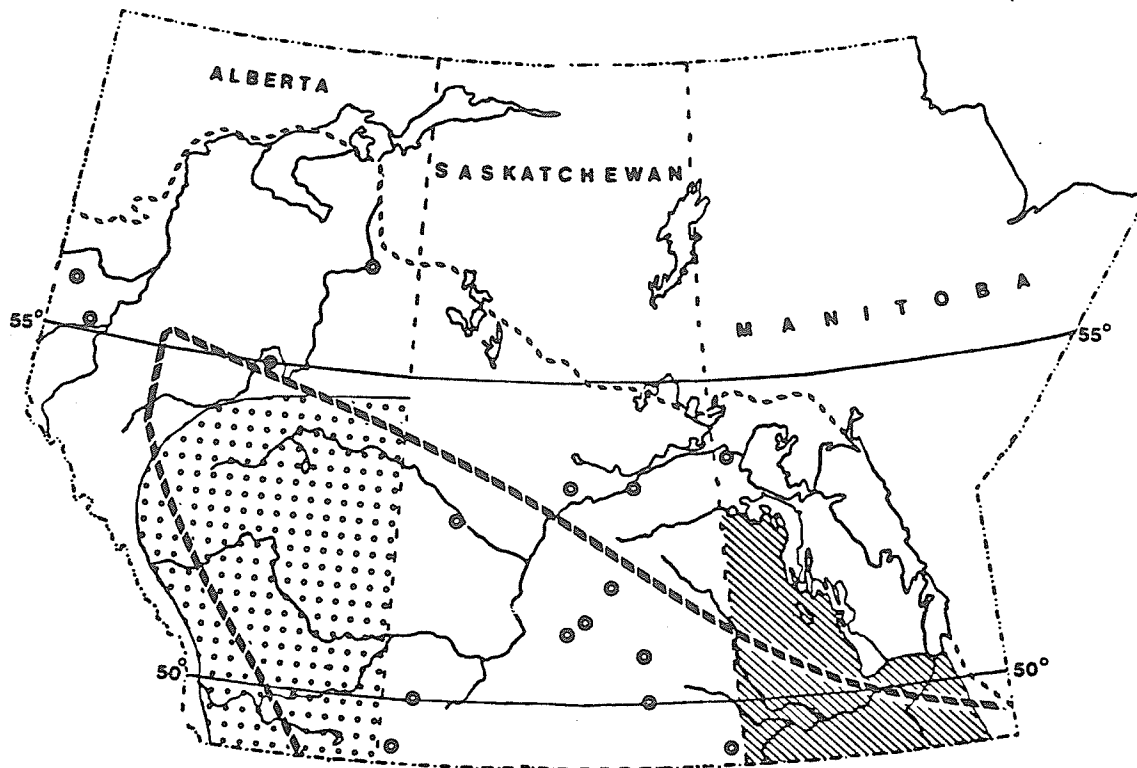
Figure 2.   Comparison of distribution of _Mustela frenata longicauda_
            according to various sources.

⊡	Soper (1964)
▨	after figure 1
⌇⌇⌇	Banfield (1974)
⊚	Museum records, Soper (1964) and Gamble
⌇⌇⌇	Southern border of Boreal forest proper or Taiga

CHAPTER VI

Infestations of the nematode <u>Skrjabingylus</u>
<u>nasicola</u> (Leukart 1842) in <u>Mustela</u> <u>frenata</u>
(Lichtenstein), the long-tailed weasel, and some
evidence of a paratenic host in the life
cycle of this nematode.

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ABSTRACT

Mustela frenata and M. erminea from southern Manitoba
had cranial lesions attributable to Skrjabingylus nasicola.
The frequency of infection of subadult and adult weasels was
100%. The extent of damage varied inter-and intraspecifically.
The frequency of infestation and damage is a function of diet
and climate in weasels. Dietary analyses provide evidence of
a paratenic host in transmission of S. nasicola. Results
suggest repeated invasions of the definitive host independent
of a possible immune response to the parasite. Hormones may
affect establishment of the nematode. Skryabingyliasis does not
appear to affect the size of the definitive host. Damage
sometimes renders certain taxonomic measures unreliable.
Bilateral asymmetry of damage is frequently observed. Despite
severe damage, Mustela spp. show a high degree of tolerance.
It is unlikely that heavy infections play a part in differential
mortality.

INTRODUCTION

Skrjabingylus nasicola (Leukart 1842) has long
been recognized as a parasitic nematode of the nasal
sinus of mustelids in which it often causes massive
lesions of the skull. Skrjabingylus spp. have a
restricted host-specificity for mustelids (Dougherty
and Hall 1955; Lankester and Anderson 1966). External
inspection of skulls and comparison to a standardized
scale of damage (King 1977) is an indirect but reliable
means of measuring the occurrence and degree of damage
of skrjabingyliasis. Lewis (1978) confirmed the
validity of such a scale in estimating the intensity of
infestation. Assessment of damage without dissection
of the skull permits the skull to be used for taxonomic,
ecological and distributional purposes.

Life cycle of S. nasicola

First stage juveniles of S. nasicola are borne
ovoviviparously and pass out of the host with the faeces
(Hobmaier 1941; Dougherty and Hall 1955). Juvenile nematodes
are eaten with food by terrestrial snails and slugs (Order:
Pulmonata) in which the juveniles develop to their third
(invasive) stage (Hobmaier 1941, Lankester and Anderson 1971;
Duncan 1976). Gastropods are the only obligate intermediate
host (Hobmaier 1941). Adaptations of the parasite's life
cycle increases the likelihood of its consumption by the next

host in the cycle (Duncan 1976). Weasels rarely eat snails

therefore it is necessary to postulate transmission by a

paratenic (auxiliary transport) host to the definitive host

(Dougherty and Hall 1955). Proof of a link between gastropod

and mustelid hosts would require a detailed study. Ecological

relationships of parasite and host provide an insight into

the mechanism of transmission and infection.

MATERIALS AND METHODS

Trappers provided 178 carcasses of M. frenata and 20 of M. erminea taken in the range of M. frenata in Manitoba during the winter of 1977-78. The most northerly known extension of the long-tailed weasel's range is The Pas (54^0) in the north-west. The range falls south of a line extending from The Pas to the south-east corner of the province (49^0). Data on locality, habitat, and bait were included. Skeletal material was prepared by means of enzymes.

Nineteen cranial measurements, as defined by Hall (1951), were taken. The following measurements are considered herein; namely, the condylobasal length (defined as the least distance from a line connecting the most posterior part of the exoccipital condyles to a line connecting the most anterior projections of the premaxillary bones), and the interobital breadth (least distance across the top of the skull between orbits). Broken skulls could not be measured and/or scaled and reduced the sample of M. frenata to 153 and M. erminea to 16.

Skulls were scaled by an adaptation of the system of King (1977) (Fig. 1). Indices are as follows:

0. undamaged

1. damage slight: small swelling or dark shadow, no perforations visible externally.

2.   damage moderate: not extending beyond the interorbital constriction, medium sized swelling and/or dark shadow.

3.   damage moderate, but more extensive: medium size swelling often progressing past the interorbital constriction and/or small perforations.

4.   damage severe: large swelling vaulted dorsally and dark shadow, and/or small but not large perforations.

5.   damage massive: large swelling and dark shadow, vaulted with large perforations.

Definition of terms

Intensity - The number of S. nasicola found in a given number of hosts, expressed as a mean value.

Damage - Visible lesions seen on the external surface of the skull including discoloration, and quantified on an arbitrary scale of 0-5 for each side of the skull and having a maximum score of 10.

Frequency - The number of skulls showing external signs of damage expressed as a percentage of the total number examined in a given sample.

Ageing

Weasel skulls were separated into young (3 - 7.5 months), subadults (7.5 - 10 months) and adults (10^+ months) according to their morphology (Hall 1951). Baculum weights were used to confirm age determination in males (Wright 1947).

The dental cementum annulae of adults were also used to

check age determinations.

Diet

Food consumed by the long-tailed weasel is shown

in Table 1. Food items were identified from analyses

of weasel scats and intestinal and stomach contents.

Frequently, more than one item was found in a given

sample. Digestive tracts were sometimes empty or

contained unidentifiable animal tissue. Results may

be biased because weasels sometimes consume larger prey

or carrion in part. Smaller prey species are more likely

to be consumed in total making   identification   easier.

Statistical treatment

The chi-square test was used to determine if the

frequency of infestation and degree of damage were

related. A biologically "significant" level was taken to

be $p \leq$ .05. Highly significant values had to be $p \leq$ .01.

A modified t-test was used twice. This involved

Bartlett's test and the Behrens-Fisher problem (Steel

and Torrie 1960; Wilks 1962).

Weasel taxonomy

Four species of weasels are discussed; namely,

M. erminea, the short-tailed weasel or stoat, M. frenata,

the long-tailed weasel, M. rixosa, the least weasel, and

M. nivalis, the ermine. M. rixosa and M. nivalis are ecological analogues (Fiechstein 1957), and perhaps taxonomic designation as separate species is unjustified. Two subspecies of M. erminea; namely, M. e. richardsoni and M. e. bangsi occur in Manitoba. Characteristics of both show a regular progression or are clinal in nature. I consider that M. e. richardsoni is the dominant subspecies in this study.

RESULTS

Frequency of infestation for M. f. longicauda
(n = 153) and M. e. richardsoni (n = 16) was 100 per
cent.in subadults and adults. Damage ranged from 0 - 3
in five young (3 - 7.5 months). Mean damage scores and
standard error for subadults and adult long-tailed
weasel skulls are given in Table 2. The mean damage score
for short-tailed weasel skulls was 6.4 ± .5, but for
comparative purposes only the results for males were
used ($\bar{x}$ = 6.6 ± .5, n = 14). Male short-tailed weasels
showed a significantly higher degree of damage than
male long-tailed weasels (t'= 2.98, 13d.f.,d = .01).

Pooled mean damage for male M. frenata was 4.9 and
for females 4.7 and was not significantly different when
compared. When separated into age classes by sex, adult
males had more damage than adult females (t' = 2.204,
11d.f., α= .025). This difference was not significant
in subadult males and females. Cranial damage was more
severe in adults than subadults (χ^2 = 26.0, 5d.f., α=
.005). Intrasexually, adult males and females had a
greater degree of damage than subadults (χ^2 = 26.14,
4d.f. α= .005 and χ^2 = 9.375, 1d.f. α= .005 respectively.

Sixty one per cent of the skulls were damaged equally
on the right and left sides; where damage was unequal it was

frequently more severe on the right (χ^2 = 4.27, ld.f. α =

.05. Damage was unrelated to geographical distribution

in Manitoba.

Mean condylobasal lengths and interorbital breadths

are given in Table 3. Differences between subadults and

adults were not significant.

DISCUSSION

Frequency of infestation

M. e. richardsoni and M. f. longicauda had a frequency of infestation by S. nasicola of 100% in subadults and adults. My results agree with the findings of Dougherty and Hall (1955) for M. e. richardsoni and M. e. bangsi, but are markedly different for M. f. longicauda in which they found a frequency of 8%. This is likely a function of climate as Dougherty and Hall (1955) acquired specimens of M. f. longicauda from southern Alberta and Saskatchewan (predominately short grass prairie) while the current study dealt with Manitoba (predominately Aspen Parkland) which has a higher mean annual percipitation. Dougherty and Hall (1955) found a close correlation between climate and the frequency of infestation in weasels throughout North America. S. nasicola is generally in the more northerly and wetter parts of Europe, the U.S.S.R. and North America (Hansson 1970; Duncan 1976). Hansson (1974) demonstrated that low humdities and high temperatures reduced larval nematode survival in scats. King (1977) found a tendency for S. nasicola to increase in weasels with increasing number of wet days.

Interspecific damage

Damage was greater in M. erminea than M. frenata

in Manitoba though specimens were collected in areas

of sympatry. Similarly, Dougherty and Hall (1955) found

the frequency of skrjabingyliasis higher in M. erminea

than in M. frenata. Hansson (1970) suggested that a

correlation may exist between the size of the species and

the frequency and extent of damage within each geographical

region. Hansson (1967 and 1970) found damage was most

frequent and often more severe in the smaller mustelids;

M. nivalis and M. erminea. This may simply be a function

of diet as indicated by M. e. richardsoni and M. f.

longicauda. Van Soest et al. (1972) reported similar findings

for M. erminea and M. nivalis.

The size of a weasel species determines the diet (Gamble)

which in turn is a direct function of bioenergetics in

the species (Brown and Lasiewski 1972, Iverson 1972; Moors

1977). M. erminea and M. frenata consume different proportions

of prey species with the former securing proportionately

more smaller prey, particularly soricids (Chapter II). Other

components in the diet of M. f. longicauda and M. e.

richardsoni did not change appreciably after being adjusted to

a basis of total prey consumed annually (Gamble). Hansson (1967)

found that soricids are a paratenic host of S. nasicola.

Distributional records of soricids and infected M. erminea in

north-eastern Canada and Greenland support this contention of

Hansson (1970). Van Soest et al. (1972) found at least

partial correlation of shrews as transmitting agents in
M. erminea and M. nivalis from the Netherlands.

My data indicate that soricids contribute to damage,
but cannot account for the frequency of infestation.
Soricids occur as trace components in the diet of M. f.
longicauda, yet subadults and adults are 100% infected.
One would expect to find, if soricids were the only major
paratenic host, a higher frequency of infestation in those
subspecies of M. frenata which consume soricids in higher
proportions (Table 1). Dougherty and Hall (1955) found
that M. f. noveboracensis and M. f. primulina had a 96.5%
and 32.0% frequency of infestation respectively. Both consume
relatively equal proportions of soricids but show different
frequency of infestation. King (1977) found that M. e.
stabilis had a frequency of infestation from 69-100% yet
rarely consumed soricids. King (1974) earlier reported that
in Newfoundland prior to the introduction of shrews, M.
erminea showed typical cranial lesions in 10% (n = 40) of
the skulls, and that in New Zealand despite the absence of
shrews, S. nasicola persists with its definitive host since
introduction of M. erminea in 1867.

Hobmaier (1941) postulated that poikilotherms are
intermediate hosts. Hansson (1974) and Lewis (1978) found
frogs and snakes were paratenic hosts of Skrjabingylus. I
found that amphibians and reptiles were trace components in
the diet of M. frenata and were also found in M. erminea

(Hall 1951; Sturges 1955; Asahi 1975). A parallel situation may exist with mustelids infected with Alaria. Weasels in Manitoba had heavy infections of Alaria spp. (often > 40%) which agrees with Johnson (1979). Amphibians and reptiles are the principal intermediate hosts of Alaria (Johnson 1979) which may suggest consumption of these poikilotherms is greater than observed. Amphibians and reptiles may account for the frequencies of infestation observed in weasels.

Other mammals contribute the greatest bulk to weasels' diet, but vary in their frequency of occurrence geographically both within and between species of Mustela. Most rodents are omnivorous in varying degrees, consuming slugs, snails, frogs, salamanders and snakes. Lankester and Anderson (1966) found that such small mammals as: Sorex fumeus (4.0%), Peromyscus maniculatus (3.7%), Tamia striatus (5.9%) and Blarina brevicauda (12.3%) serve as paratenic hosts for lungworm, Filaroides martis and Aelurostrongylus pridhami (Metastrongyloidea). Because lungworms share the same molluscan intermediates as S. nasicola one might expect similar infestation levels in these mammalian paratenic host. Hobmaier (1941) infected mice and rats with S. nasicola by feeding of third stage larvae. These were recovered in the stomach walls and mesenteries for two weeks after initial ingestion and then disappeared. Lankester (in Hansson 1974) later found that the larvae were in the musculature rather than the liver.

Cricetids constitute 49% of the prey items taken by
M. f. longicauda in Manitoba. Weasels consume approximately
25% of their body weight in prey per day or about two cri-
cetids per day in M. frenata. An average M. frenata consider-
ing both sexes, weighs 303 g and the cricetids 18 g).
Annually, 730 cricetids would be consumed. A low infection
rate in cricetids would be sufficient to transmit S. nasi-
cola, yet account for a high frequency.

Sciurids constitute 22% of a long-tailed weasel's diet
and metastrongloids are known to occur in at least one,
sciurids, T. striatus. Seven sciurid species are found
within the range of M. frenata in Manitoba and most sciurids
are omnivorous.

Transmission of S. nasicola to the definitive host may
not require ingestion of a large number of suitable para-
tenic hosts (Hansson 1967), but must be a regular component
of a weasel's diet. Neither soricids nor amphibians and
reptiles qualify because they cannot account for the 100%
frequency of infestation.

Age

This study showed a highly significant increase
in the severity rather than the frequency in subadults
and adults; this suggests several invasions. Juveniles
(3 - 7.5 months) vary both in intensity and frequency.
Lewis (1978) showed that the intensity of infestation is
directly related to increasing severity of skull damage
which increases as the weasel ages. Lewis (1978) observed
no apparent immunity to develop with age but the walling off
of the parasite through secondary shelving of bone observed
in my study might act to localize and confine damage.
Whether confining the parasite is an immune response or
a product of the damage incurred has yet to be established.
Indexing skull damage counts all infestations both past
and present and might artificially increase its correlation
with age (King 1977).

Sex

Damage was more severe in adult males than adult
females. King (1977) also found a similar relationship.
Hansson (1967), Duncan (1976) and King (1977) expected
smaller females to show a significant difference in
frequency or a greater degree of damage to that of males.
Female weasels may have a lower damage index than males due
to a lower threshold for crowding of the parasite (Lewis 1978).
Hansson (1970) suggested, oestrogen may inhibit development
and establishment of larvae. Subadult males and females
showed no significant difference in degree of infestation

in the present study. Females take a higher proportion of smaller prey items, which include most of the possible paratenic hosts, so one would expect exposure to be greater or equal to that of males. It appears that damage depends on the sex of the host but is not a function of maturity. Subadult females are sexually mature (Wright 1948).

Hansson (1974) in Scandanavia found that the most favourable seasons for larval survival were autumn and spring, indicated by the presence of two overlapping nematode generations. New invasions of Mustela spp. were found in the cold months of the year with mean number per host higher in winter and spring. The spring invasion coincides with parturition in adult females, so perhaps it is the elevated levels of reproductive hormones that affect establishment of Skrjabingylus larvae.

Size

No correlation was evident between the condylobasal length of the skull of M. frenata and frequency of damage. King (1977) found a similar relationship in the British stoat. In contrast, Van Soest et al. (1972) and Hansson (1970) found a positive correlation existed between condylobasal length of the skull and frequency in weasels.

In M. frenata full body size is achieved at
3 - 4 months of age (Wright 1951). One would expect
most individuals to attain maximum size before being
infected considering that long-tailed weasel pups do
not consume solid food until they are at least 3½ weeks
of age and it usually takes several months for damage
to occur (Dougherty and Hall 1955).

No significant difference was observed between
subadults and adults in the size of the post-orbital
constriction in M. frenata. Swelling or distortion
of the skull in this region by S. nasicola would mask
any appreciable change in size with age. Use of this
measurement for ageing (King 1977) or taxonomy in areas
of heavy infestation or pronounced damage would be
unwise. Hansson (1972) found a similar relationship
between damage and interorbital breadth.

Differential mortality

M. frenata appears not to cycle in the characteristic
manner of other weasel species (Osgood 1935, Jeffries
and Pendlebury 1968; Bakeev 1971; Erlinge 1974) but
maintains a rather stable population (Chapter I). No
correlation was evident between the frequency of damage
and population density in M. frenata nor does it seem likely
that such a correlation exists for M. erminea, M. rixosa
and M. nivalis which cycle in accordance with their prey
(Erlinge 1974). Possibly a change in diet to a less

desirable species (e.g. soricid) may sustain weasels temporarily and account for corresponding changes in damage and frequency.

Trappability generally increases in proportion to a decrease in prey, thus further reducing weasel populations. Recovery generally would not be accomplished by the following season. This would correspond to the lag period often recognized between declines of prey populations and corresponding predator decline. In contrast, when prey populations increase, trappability often declines because weasels become more selective in prey preference.

Popov (1943) and Lavrov (1944) observed that infected short-tailed weasels weighed less than uninfected individuals and suggested S. nasicola may affect the physical stature of its host. Both authors recognized that where skrjabingyliasis was prevalent (i.e. heavy infestations) one year, populations were lower the following year. Over a twelve year period Popov (1943) recognized an inverse correlation between frequency of damage and population density based on winter trapping. I suggest that changes in frequency and damage are a direct result of the availability of prey and that the observed inverse correlation recognized by Popov (1943) is a function of trappability not mortality attributable to S. nasicola.

It is difficult to judge how a parasite affects the host. Skrjabingyliasis has some biological impact on its

host as suggested by damage to the alveolus of the canines, perforated skulls often having a second shelf of bone associated with the larvae, reports of herniation of part of the brain associated with larvae (von Linstow in Dougherty and Hall 1955), and anecdotal evidence of abnormal behaviour not unlike the symptoms of epilepsy (Goble 1942; Lewis 1967). Despite the severe damage which heavy infestations can cause, tolerance must exist (Duncan 1976 and Gamble). Weasels are a highly successful predator and their populations are capable of carrying a relatively high incidence of S. nasicola.

Bilateral asymmetry of damage is frequently observed in skulls of Mustela spp., but no pattern is evident. In the Manitoban material, cranial damage in M. frenata was chiefly symmetrical (61%), but when unequal it was more severe on the right. Hansson (1967) found no difference in degree of damage on either the right or left in M. nivalis and M. erminea whereas Petrov (1927) and King (1977) found that in M. nivalis and M. erminea damage was greater on the left. Hansson (1968) recovered significantly more worms from the right side of M. nivalis than the left side of M. erminea.

CONCLUSIONS

A wide variety of paratenic hosts may transmit
S. nasicola to its definitive host. It seems most likely
that snail-eating cricetids are probably the major
paratenic host under normal circumstances. Soricids,
amphibians and reptiles as paratenic hosts contribute
significantly to the frequency and damage observed in
the definitive host. Soricids, amphibians and
reptiles fluctuate in degree of importance both
seasonally and annually in relation to prey abundance.

A close correlation exists between the frequency
of infestation of S. nasicola and climate. Frequency
of infestation is directly related to the temperature and
humidity of the microenvironment (Hansson 1974).

The frequency of infestation and damage by
S. nasicola increases with age in weasels, suggesting
several invasions of the host. Immune reactions may occur.
Hormonal levels during parturition may inhibit development
and establishment of larvae in females. An apparent
correlation between body size and frequency and/or
damage may be a function of diet. Despite severe damage,
Mustela spp. show a high degree of tolerance.

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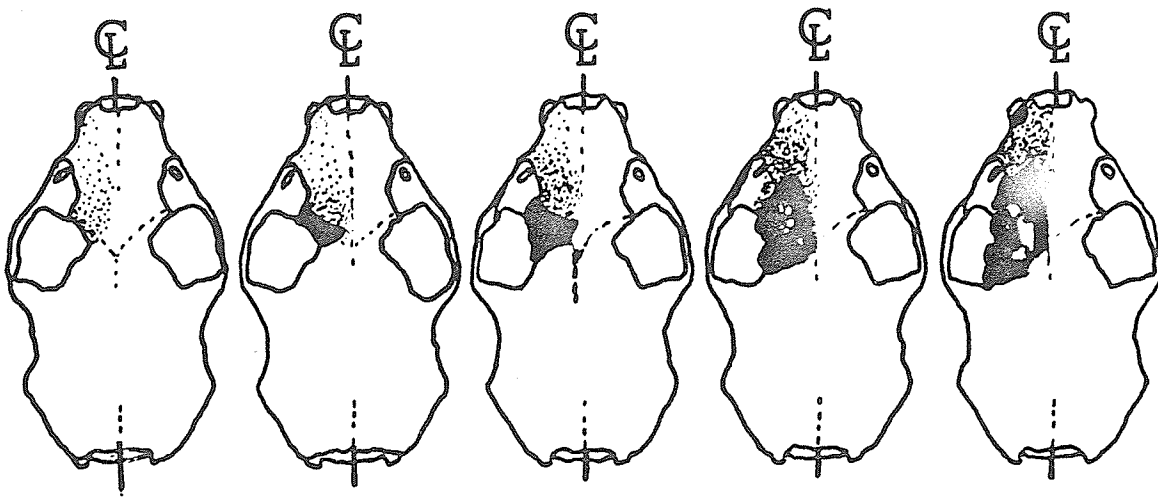Biol. 75: 820-822.

Fig. 1.   Weasel skulls depicting indices of damage from left to right on a scale of 1-5.

Table I. Frequency of occurrence of prey items in the diet of _M. frenata_ subspp.

Mustela frenata subspp. Locale Authority	Weights g	?	Crustacea	Insecta	Amphibia	Reptilia	Aves	Soricidae	Talpidae	Lagomorpha	Geomyidae Sciuridae	Cricetids (excludes Ondatra)	Ondatra	Mustelidae	Sample Size
noveboracensis Michigan Dearborn 1932	170–247 x̄ = 208	85–100 x̄ = 92		7			10	12	2	14		55			37
noveboracensis New York Hamilton 1933	196–267 x̄ = 225	72–126 x̄ = 102		.6			1.2	5.9	.8	17.3	3.7	71.1	.8		163
primulina Iowa Polderboer et al. 1941	293	–						5.4		8.4	.6	76.5		5.4	135
noveboracensis Pennsylvania Glover 1942	119–256 x̄ = 172	74–90 x̄ = 82		7.9			13.2	12.3		10.5	2.6	51.8			86
nevadensis Colorado Quick 1951	226–345 x̄ = 267	115–148 x̄ = 129		11.7			3.2			3.2	22.3	59.6			77
noveboracensis Ontario Wobeser 1966	196–267 x̄ = 225	72–126 x̄ = 102	.5	5.8	.5	.2	15.7	3.6		0.5		60.1	.4		458
noveboracensis Ontario Simms 1979	196–267 x̄ = 225	72–126 x̄ = 102					18.2	15.2		12.1	1.5	51.5			66
longicauda Manitoba Gamble	368–420 x̄ = 394	164–398 x̄ = 212		T	T	T	15.5	T		9.5	22.4	49.1	1.7	1.7	223

Food items (Frequency of occurrence in Per cent.)

Table 2. Distribution of skull damage by age classes in
          M. frenata

Mean damage score $\pm$ S.E.

subadult	adult	total
males n = 84 $\bar{x} = 4.6 \pm .1$	males n = 24 $\bar{x} = 6.3 \pm .3$	males n = 108 $\bar{x} = 4.9 \pm .1$
females n = 33 $\bar{x} = 4.5 \pm .2$	females n = 12 $\bar{x} = 5.3 \pm .3$	females n = 45 $\bar{x} = 4.7 \pm .2$
total n = 117 $\bar{x} = 4.5 \pm .1$	total n = 36 $\bar{x} = 5.9 \pm .3$	sample n = 153 $\bar{x} = 4.7 \pm .1$

Table 3. Mean condylobasal length and interorbital breadth grouped by sex and age class

Measurement	Subadult Females	Adult Females	Total Females	Subadult Males	Adult Males	Total Males
Condylobasal length ± S.E.	46.2 ± .3	47.1 ± .4	46.5 ± .2	51.2 ± .2	51.2 ± .4	51.2 ± .2
sample size	n = 33	n = 14	n = 47	n = 86	n = 24	n = 110
Interorbital breadth ± S.E.	9.8 ± .1	10.1 ± .2	9.9 ± .1	11.3 ± .1	11.6 ± .2	11.4 ± .1
sample size	n = 34	n = 12	n = 46	n = 88	n = 24	n = 112

CONCLUSION

M. f. longicauda selects late seral stages or
ecotones in close proximity to water and are resident
generalists. Distribution is a function of the availability
of prey in weasels but factors such as sociability, species
diversity and sexual preference may influence distribution.
Long-tailed weasels are site tenacious and populations are
relatively stable. Male long-tailed weasels are not
capable of breeding in their first year as suggested by
testicular development. Bacula are not functional until
2 years of age. Young are generally not produced by
female M. frenata until 2 years of age. Females which
produce litters at one year old are probably bred in the
spring. Males provide parental care.

M. e. richardsoni prefers early successional
communities and are resident specialists. Populations fluctuate
in accordance with prey abundance. Home ranges are commonly
maintained in low vole years. The reproductive capabilities
of this species are adjusted accordingly.

Within weasel hunting sets M. frenata is dominant to
M. erminea and M. rixosa. Interference interactions and
resources determine community composition.

Activity patterns of _Mustela_ spp. in the winter suggest snow cover is another dimension along which resources are partitioned. _M_. _erminea_ and _M_. _frenata_ females are more subnivean than males.