National Library of Canada
Canadian Theses Division
Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada
Division des thèses canadiennes

49047

PERMISSION TO MICROFILM — AUTORISATION DE MICROFILMER

• Please print or type — Écrire en lettres moulées ou dactylographier

Full Name of Author — Nom complet de l'auteur

NAMS, VILIS OJARS

Date of Birth — Date de naissance	Country of Birth — Lieu de naissance
Sept 16 / 1955	Canada

Permanent Address — Résidence fixe

75 Elgar Ave, Scarborough, Ont
M1J 1M3

Title of Thesis — Titre de la thèse

Prey selection by the ermine (mustela erminea)

University — Université

UNIVERSITY OF ALBERTA

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M. Sc.

Year this degree conferred — Année d'obtention de ce grade	Name of Supervisor — Nom du directeur de thèse
1980	Dr. William A. Fuller

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

Date	Signature
Oct 17/80	Vilis Nams

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

THE UNIVERSITY OF ALBERTA

PREY SELECTION BY THE ERMINE (*MUSTELA ERMINEA*)

by

© VILIS OJARS NAMS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1980

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Prey selection by the ermine (Mustela erminea)" submitted by Vilis Ojars Nams in partial fulfilment of the requirements for the degree Master of Science.

.....
Supervisor

.....

.....

.....

Date. 16 Oct/80

ABSTRACT

I studied the selection mechanism of ermine (Mustela erminea) by tracking radio-tagged ermine and four prey (a male and female of each of Clethrionomys gapperi and Peromyscus maniculatus) in a 900-m^2 enclosure. An automatic radio scanner located the animals with a positional accuracy of ±0.75 m, and collected and stored the data at a maximum rate of once per second. Prey preference was tested by presenting ermine with two live prey simultaneously in a small arena.

The ermine showed overall prey selection. They approached C. gapperi more frequently than P. maniculatus, and once approached, male prey had a greater chance of being captured than did females. However, this was not because of a preference for males. Once prey were captured, female P. maniculatus were eaten less than the other prey. Selection at the approach step was independent of predator satiation, predator and prey activity, and temporal overlap of activity between predator and prey, but was a result of the ermine searching in those microhabitats that C. gapperi inhabited. Selection for male prey was independent of predator and prey activity, and of microhabitat type.

AKNOWLEDGEMENTS

I would like to thank my partner in this study, Laurie Davis, for designing and building the scanning system I used. Albert Huizinga made the radio transmitters - an unenviable job.

Steve Beare assisted me in the field, anaesthetized mice and weasels, kept the Station alive and running during the winter, and survived my guitar practising. Kevin Eberhart and Doug Powder also assisted in field work. I thank all the residents of Heart Lake for helping me now and then and for making the Station such a great place to work. These people include Lorne Duncan, Steve Mihok, Anne Mains, Greg Frank, Les Gyug, Doug May, Wendy Nixon, and Simon Pickering. I especially thank Magi Nietfeld for giving me moral support during the last summer of field work. I thank Cal and Alice for providing a home away from home during the winter of '79.

My supervisor, William A. Fuller, translated my writing into English, fought my stubborness, and provided much support throughout this study.

Ellie Prepas helped me to organize my thoughts and to put them douwn on paper. I benefitted immensly from many hours of discussion with Peter Everson about our respective studies. Miriam Diamond's cheery face every morning helped me to survive a summer of working in the office.

Last but not least, the study would have been impossible without the help (albeit not voluntary) of Oscar, Dainis, Tim, Sheila, Zeltite, Belinda, Laila, and White-face.

Financial assistance was provided by teaching and research assistantships from the Department of Zoology, by a Boreal Institute grant and by a Max and Marjorie Ward scholarship to myself; by National Science and Engineering Research Council of Canada grant No. A1410 to W. A. Fuller; and by support provided to the Heart Lake Biological Station from the University of Aberta.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

TABLE OF ABBREVIATIONS

CM	male *C. gapperi*
CF	female *C. gapperi*
PM	male *P. maniculatus*
PF	female *P. maniculatus*
P	probability
F	F statistic
X^2	chi-square statistic
d.f.	degrees of freedom
t	t statistic
r^2	coefficient of determination
O	observed value
E	expected value
Var	variance
Cov	covariance
N(E,Var)	Normal distribution
ANOVA	analysis of variance
ANCOVA	analysis of covariance
Σ	summation sign

Activities of animals during approaches (approach types):

	predator	prey
IM	inactive	moving
AM	active	moving
MM	moving	moving
MA	moving	active
MI	moving	inactive

1. INTRODUCTION

Most predators spend much of their time and energy searching for, capturing, and eating food. Often they eat prey in different proportions from those found in the environment (More 1978, Tinbergen 1960, Royama 1970, MacDonald 1977) - i.e. they select[1] their food. Optimal foraging theories suggest why it would be advantageous for an animal to select for prey (Pyke et al. 1977). Krebs and Cowie (1976) stated, in relation to foraging theories, that "In looking for generalizations, we are concerned with functional aspects of foraging behaviour, rather than details of mechanisms . . .". This statement suggests that it is not necessary to understand how prey selection occurs (i.e. the mechanism) for an understanding of why it occurs. However, selection could occur for various reasons - e.g. a preference for the selected prey, or a higher encounter rate with the selected prey. In fact, most foraging models do not analyse the whole predatory sequence, but consider individual steps. For example, the question of how an animal can maximize energy intake or minimize time spent foraging, has been studied by asking these questions: what patterns of movement will maximize rate of prey encounter (Royama 1970,

---

[1] For this paper "selection" is defined as any differential response by the predator to the prey (e.g. differences in capture probability or encounter frequency), and "preference" as an actual choice made by the animal.

MacArthur and Pianka 1966) and what is the optimal choice of prey (Emlen 1966, Schoener 1971, Rapport 1971, Pulliam 1974)? Therefore we must have an understanding of the mechanism of prey selection before we can ask why it occurs.

Overall prey selection is usually determined by comparing the proportions of prey items available to the predator to those found in its diet. However, the term "available" is often used ambiguously. For example, are prey available if they use space and time in such a way that the predator does not encounter them? I will consider prey to be available if they are present in the same general habitat type as the predator, and therefore I will regard prey encounter as part of the predation process.

1.1. Study animals

I studied ermine, or short-tailed weasels (Mustela erminea)[1]. They are large enough (60 to 120 g) to carry radio transmitters, and therefore could be followed as they

---

[1] Fitzgerald's (1977) nomenclature was used for common names of various weasel species. The New World varieties are: Mustela frenata: long-tailed weasel (the largest weasel), M. erminea: short-tailed weasel or ermine and M. nivalis: least weasel (the smallest weasel). The Old World varieties are: M. erminea: stoat and M. nivalis: European weasel. This distinction between Old and New World varieties is important because although M. erminea and M. nivalis are present in both the Old and New World, the Old World varieties are the size of, and are ecological equivalents of, M. frenata and M. erminea, respectively, in the New World. I will use "weasel" in a generic sense only.

hunted for prey in their natural habitat. They are also small enough (and therefore eat small prey) to allow manipulation of prey densities; ermine mostly hunt small mammals.

We must first know how the ermine searches for, detects, and captures prey, and what kind of prey it consumes, to be able to understand how it selects for prey. The ermine is a solitary predator which usually searches on the ground, although de Vos (1960) and Frith (1958) reported seeing weasels hunting in trees. There are conflicting reports about how prey are detected. Quick (1951) suggested, from subjective field observations, that weasels generally do not use smell to track prey over long distances. Long-tailed weasels were observed trailing rabbits in fresh snow, (Murie 1935, Addy 1939), but we cannot conclude whether they used smell or vision. Herman (1973) showed that least weasels can detect scent trails that are up to 10 min. old, and 1.5 m long, and that substrate-borne rather than air-borne cues are used. Observations by Smith (1978) on ermine in a small (1m x 2m) enclosure agreed with this. However, in another enclosure ($30m^2$) study, Erlinge et al. (1974) found that stoats used sound most often to locate prey, and that smell was quite unimportant. It seems that smell, if at all important, is only used for short-range prey detection.

Weasels spend much energy and time searching for prey relative to capturing prey (Erlinge 1974, 1977), and not all

prey that are detected are subsequently captured (Erlinge et al. 1974). Wustehube (1960) studied prey catching behaviour and noted that smell is not important for stoats and European weasels as a releasing stimulus. Once prey are killed, they may be cached (Polderboer et al. 1941) while the weasel returns to the hunt.

Even though there is disagreement over how weasels hunt for prey, most authors agree that voles are the main small mammal in weasel's diets (the larger stoats and long-tailed weasels often eat significant amounts of lagomorphs and other larger prey (King and Moors 1979)). Microtus is the major food item of ermine (Fitzgerald 1977, Aldous and Manweiler 1942) and European weasels (Tapper 1976). However, none of these authors estimated prey densities, so they could not demonstrate that the weasels were selecting Microtus over other available prey.

Authors who did estimate prey density reported conflicting results. Erlinge (1974, 1975) and Wobeser (1966) both concluded that weasels (European and long-tailed, respectively) eat prey species in the same proportions as captured in traps. Again, Microtus were eaten most frequently.

On the other hand, other authors report that weasels do select for prey. Day (1968) found that both stoats and European weasels ate more Microtus than Apodemus and Clethrionomys, even more than expected from trapping

results. He gave no reasons for this selection. Simms (1979) suggested that ermine catch fewer P. maniculatus than expected because of differential habitat use; male P. maniculatus were found in climax areas, while ermine in his study area used early successional areas. King (1980) thought that European weasels ate more Clethrionomys glareolus than Apodemus sylvaticus because of differences in the use of cover by prey, and in the reactions of prey to being hunted. Northcott (1972) studied ermine food habits near my study area, and found that they selected heavily for Zapus hudsonius. This result seems unlikely for three reasons: (1) Wooley (unpublished data from scat analysis, 1977) found that ermine at Heart Lake feed mainly on Microtus pennsylvanicus, Clethrionomys gapperi, and Peromyscus maniculatus, in that order, (2) Z. hudsonius are extremely rare in that area (Fuller 1969, Nams pers. observ.), and (3) C. gapperi and Z. hudsonius hairs are very similar and perhaps they were not identified properly (Wooley, pers. comm.). The authors that demonstrated selection also suggested reasons for it, but gave no concrete evidence.

I used C. gapperi and P. maniculatus as prey in the this study. Even though M. pennsylvanicus is usually the main food item, it is common only in grassy meadows (More 1978) and lowland habitats (Doyle 1979), whereas C. gapperi and P. maniculatus both commonly occur in the upland habitat type where the study was carried out. Therefore this study

only considered one habitat type.

1.2. Predatory sequence

We can use the aforementioned information about the ermine's hunting behaviour to list the steps in its predatory sequence (Fig. 1). This approach involves dissecting the act of predation into the separate steps which the animal goes through (it is analogous to the "feeding cycle" of de Ruiter (1967) and Holling's (1964) "component analysis"). Prey selection could occur at any step in the sequence.

1.2.1. Approach

During this first step, the ermine and the prey come close enough together for the ermine to be able to detect the prey. However, the ermine may not actually detect the prey, rather it may approach the prey and go by without detecting it. Some of the factors affecting selection at this step are differential microhabitat use (Royama 1970), and temporal overlap of activity patterns between predator and prey (Curio 1976).

1.2.2. Detection

After the approach, the predator may detect the prey, using vision, hearing, or smell. Detection may be affected by prey camouflage, prey activity, and place of encounter.

Tinbergen (1960) proposed that predators form a specific searching image for some prey types, in that they "learn to see" them. This concept can be extended to a composite of all the senses.

1.2.3. Choice

Once the predator has detected and identified a prey item, the ermine must choose whether or not to attack it. Selection at this step is, by definition, a preference.

1.2.4. Capture

Once the choice is made, it is assumed that the probability of capture is independent of any preference the predator may have (de Ruiter 1967) - i.e. the predator "tries" just as hard for all prey types. The capture probability depends on such things as defense reactions of the prey and place of encounter. Selection will occur if some prey types are more difficult to capture than others.

1.2.5. Consumption

If several prey items are killed before any are eaten, the predator may eat them preferentially.

The purposes of my study were two fold - first, to determine whether or not the ermine selects for certain prey

types (species and/or sex), and second, by quantifying certain steps in the predatory sequence, to find out at which step(s) selection occurs, and provide an empirical test of some predictions based on optimal foraging theory.

2. METHODS

I carried out the field work during fall of 1978, and spring and summer of 1979, at Heart Lake Biological Station, Northwest Territories (60°51'N, 116°38'W). The predation sequence was studied by tracking a weasel as it searched for and captured prey in an enclosed area of natural habitat, and I used a small arena to test for prey preference.

2.1. Justification

As noted in Section 1.1, there are conflicting results in studies of prey selection by weasels. This may, in part, reflect problems in technique. To study prey selection of free-roaming wild animals, one must measure relative numbers of available prey (= density) and relative numbers eaten by the predator, both of which are hard to do accurately.

Population density estimates not involving trapping are generally not practical for most small mammals (Smith et al. 1975), but trapping also has its problems. Traps do not sample different species (Martell 1979) nor different

segments of one population (Smith 1968, Tanton 1965) equally. In addition, these trapping biases may vary with season (Tanton 1965), habitat (Smith et al. 1975) and trap type (Boonstra and Krebs 1978, Martell 1979). Present methods generally are not adequate for accurately estimating prey densities (Smith et al. 1975).

Predator food habits are usually determined by scat and stomach content analyses (Day 1966), which are affected by different rates and extent of digestion (Marti 1972, Lockie 1959), even among different size classes of one food species (Floyd et al. 1978). It is almost impossible to collect all scats from a free-roaming animal, so scat collections may be biased. Therefore it is usually not possible to accurately estimate proportions of prey items in a predator's diet.

Prey density can be controlled and food input can be measured in an experimental laboratory situation. However, the two experimental weasel predation studies that have been done were limited by the difficulty of creating a realistic environment. The small enclosures used (1m x 2m: Jamison (1975); 30 m^2: Erlinge 1975, Erlinge et al. 1974) resulted in prey densities (5000 and 4000 individuals/ha, respectively) much higher than peak densities of most small mammals species observed in nature (several hundred individuals/ha (French et al. 1975)). Also, weasels were severely limited in their searching behaviour by the size of the enclosure. The small enclosures were required, because

the experimenters relied on visual observations, but this also meant that animals could not be observed in the dark. In addition, the enclosures did not contain natural weasel and prey habitat, and it is not known what specific (micro)habitat features affect weasel predation.

We need to know initial densities of prey eaten by the predator to be able to measure selection, and movements of predator and prey must be followed accurately to find out in which step or steps of the predatory sequence selection occurs. Ideally all this would be done in the animals' natural habitat, with little influence by man. I used a large natural enclosure and an automatic tracking system to accomplish most of these objectives.

2.2. Tracking system

The predation sequence was studied in a permanent enclosure used by Herman (1977) for an earlier study of *C. gapperi* activity patterns. The study area consisted of a 900-m^2 fenced-in area of natural jack pine (*Pinus banksiana*) forest, over which an orthogonal grid of antenna wires, spaced 1.5 m apart, was suspended 1 m above ground level. Signals coupled to each antenna wire were carried to a receiver by means of co-axial cables. This allowed radio-tagged animals to be located, with an accuracy of about 75 cm, by finding the intersection of the two orthogonal wires carrying the greatest signal strengths. The size of the pen

was limited by signal attenuation along the antenna wires and co-axial cables. Details of the enclosure are given in Chute et al. (1974).

In order to determine whether differential microhabitat use affected selection, microhabitats in the enclosure were described. I made a detailed map of the enclosure, and from it I measured the following structural features of microhabitat in a 2.25 m^2 area around each grid coordinate: total length of (1) large (>5cm) and (2) small (≤5cm) diameter logs; (3) number of logs; (4) area of rocks (on a scale of 0 to 3) added to the number of overturned stumps; and (5) number of trees. Although variable 3 was correlated with variables 1 and 2, (Spearman's r=0.55 and 0.48, respectively), log intersections may provide more, or a different type of, protection than logs, per se. All of the burrows that I found in the pen were either near rocks, upturned stumps, or at the bases of tree roots, and therefore I assumed that variables 4 and 5 represented availability of burrows and refuges for stationary animals.

A computer-controlled radio scanner (Davis 1978) automatically located the positions of up to 5 animals at once and stored the information on magnetic tape. Animals were located at a maximum scan rate of once per second, and the storage rate was set as a multiple of the scan rate - i.e. positions were determined every X seconds, and were stored every Y scans. However, data were stored only if an

animal's position had changed in the interim. Whenever one animal (the predator) moved to within a "critical distance" of any other (the prey), the storage frequency automatically increased to one per scan (i.e. Y=1), which ensured that information would not be lost during encounters. A marker was stored with the position coordinates if the signal strength of a test antenna outside the enclosure exceeded a threshold value. The marker indicated possible radio interference. The operator could pre-select storage and scan rates, critical distance, and interference threshold level, as part of the initialization procedure.

Transmitters (about 1 cm diameter) (Chute et al. 1974) were attached to the animals by means of collars that served as transmitting antennae. The total package (2.3 to 2.8 g weight) weighed from 2 to 4 % of the body weight of the weasels (male weasels weighed 110 to 130 g and females 55 to 85 g) and from 8 to 12 % of the body weight of the mice. The latter proportion is large, but I tried to use prey of similar weights, so that all prey would be affected equally by transmitters. I tested to see if prey types differed in weight relative to transmitter weight (Anderson and Lydic (1977) suggested the use of ANCOVA, since Atchley et al. (1976) showed that parametric tests using ratios of random variables are invalid) and found that C. gapperi weighed significantly more than P. maniculatus (24.3 and 21.0 g, respectively; Appendix 1). However the difference is small, with the transmitters weighing 10.1% of the body weight of

C. gapperi and 11.7% of the body weight of P. maniculatus. I therefore assumed that the prey species would be affected equally by the transmitters.

The radio-telemetry system gave some unexpected results. It was designed to give a positional accuracy of 75 cm (i.e. within one grid unit), but the actual position coordinates had a random component - i.e. there was some scatter. The amount of scatter was a function of position of animal, orientation of animal, transmitter signal strength, microhabitat, and radio-interference. Total randomness occurred in two experimental trials, perhaps because of a malfunction. These results were excluded from the analyses.

Random scatter also affected storage rate. With a 1 second scan rate and a 15 scan storage rate, it would be expected that data would be stored every second, every 15 seconds, or in multiples of 15 seconds (when an animal's position did not change). However, in reality, the storage rate varied from 1 per second to 1 per several hours, because an occasional erroneous position would cause a predator-prey distance of less than the "critical distance" and increase the storage rate for several seconds, or because the animal did not move for several hours. Sometimes when a prey animal was killed, the transmitter was inactivated, which resulted in completely random observed positions and a variable storage rate.

Radio interference also affected the results. Position

coordinates recorded when there was a significant amount of interference were effectively lost, because the data could not be trusted. Most interference occurred during winter and during the day, whereas all trials took place during spring, summer and fall, and most activity occurred at night.

Despite these problems, the whole system had many advantages over those used in the studies mentioned previously (Section 2.1). The large enclosure meant that relatively low prey densities (20/ha - equal to peak densities of C. gapperi and about twice the peak densities of P. maniculatus at Heart Lake (Mihok 1979)) could be used. Ermine could actually search for prey, rather that just choose and kill them. I could expect the animals to exhibit normal behaviour, because the area was natural habitat for both predator and prey. The tracking system allowed me to follow events remotely, and was particularly useful at night when the animals were most likely to be active. I knew exact prey densities, and by collecting prey carcasses, found which were eaten. This approach solved most of the problems mentioned before.

2.3. Protocol

All experimental animals were captured in live-traps in the vicinity of the research station. Mice used as prey were kept in cages under natural light and temperature regimes for up to 2 weeks before being used. Weasels, however, were

kept for the duration of the experiments. They were fed both live and dead (skinned carcasses) P. maniculatus and C. gapperi, but were starved for about 12 hours before each trial began.

Experimental animals were anaesthetized with ether (Lockie and Day 1964) and fitted with radio-transmitters the morning before they were introduced into the pen. I assumed that prey were accustomed to the transmitters by the time data collection began, but it should be noted that Hamley and Falls (1975) showed that although transmitter-carrying Microtus pennsylvanicus behaved normally as judged by casual observation and live-trapping, their activity on exercise wheels was reduced for several days. I did not outfit animals with transmitters earlier because the radios had a short life-span, and could not be turned off while on the animals. Also, if transmitters were left on for long periods of time, they often became entangled in terylene nest material and the mice died.

The original protocol was as follows. A male and female of each prey species was introduced into the pen at 2000 to 2100 hr, for a 24-hr familiarization period. Then they were tracked at 1 scan per 15 sec and data was stored every scan for a further 24 hr. The predator was introduced, the critical distance was set at 4.5 m (3 grid units), animals were tracked at 1 scan per second, and data was stored every 15 scans for 24 more hr. This protocol was modified later in

order to complete more runs. Herman (1977) showed that there were no significant differences in the activity and movements of female C. gapperi between a second and third consecutive 24-hr time period in the enclosure, so I omitted the familiarization period.

Live-traps were constantly in operation around the outside of the pen, and were set inside the pen whenever a trial was not in progress, to guard against the presence of unmarked mice in the pen.

At the end of each experimental trial, the ermine readily entered a live-trap, and I collected all working transmitters from the pen. Dead prey were separated into two groups - those that were at least 50% eaten, and those that were untouched, or with just the head eaten.

2.4. Analyses

I ranked the prey within each trial according to the order in which they were captured. If the capture time of any prey was unknown, the ranks were treated as ties and were divided up equally - e.g. if the order of capture of prey items A to D was either B,D,C,A or D,B,C,A, then prey B and D were each ranked 1.5, while C and A were ranked 3 and 4, respectively. Prey not captured were ranked 4, which represents the lowest capture probability.

Animal activity may affect selection, so activity

periods were determined. Changes in observed position coordinates were a result of actual movement by the animal, and/or a result of random variation. Short-term changes in the random effects could be caused by changes in orientation of the transmitter - i.e. when an animal was active. Therefore the amount of change in observed position coordinates per unit time (from now on called "scatter") can be used as an index of animal activity. If the scatter is low, then both real speed and animal activity must be low. I calculated the scatter (distance between observed coordinates per unit time) for each animal, in each 10 minute interval, in each trial. Position coordinates for several fixes were averaged, and "distance" travelled was calculated as the straight line distance between successive mean coordinates (Appendix 2).

Plots of scatter against time showed a series of cycles, which I used to determine periods of activity and inactivity for the animals. It was not feasible to use a single scatter value to differentiate activity states (i.e. active if above and inactive if below that value) because the whole cycle shifted up and down with changes in the other factors (besides transmitter orientation) that affect random variation (discussed in Section 2.1) An activity period occurred when the scatter values were in the crest of a cycle, and inactivity occurred during the trough. The division between crest and trough was set at 1/3 of the amplitude of the cycle, measured up from the trough. This

division was necessarily an arbitrary choice. For the first 10 hr of each run, I computed, for each prey type, the time spent active, and the overlap in time between the activity periods of the weasel and prey when either predator or prey were active. These overlap values were calculated using the prey data from the first 24-hour period of data collection - i.e. the period without the predator present - because most prey were killed when the weasel was introduced.

Numbers of approaches were counted. Whenever a weasel and a prey item were less than 3 m (2 grid units) apart, I considered it to be an "approach", and I counted multiple approaches within 30 min of each other as one.

Activity of predator and prey at each approach was noted. Three separate activity types for each animal can be considered: moving (M); stationary but awake, or active (A); and sleeping or inactive (I). An animal was considered to be moving (M) if the position at approach was different from its last known previous position - by "known", I mean those positions which were obviously not due to random scatter. If stationary, the animal could be awake or sleeping. When awake, the animal would change orientation of the transmitter relative to the antenna wires, which would result in a greater random variation in the position coordinates than when the animal was still. Factors that can affect random variation are transmitter orientation, position coordinate, microhabitat, signal strength of

transmitter, and radio interference. Only transmitter orientation will cause random variation to change in a short time span while the animal is stationary. After an animal stops moving, random variation, and therefore the scatter measurement, are high while the animal is active, then drop as the animal falls asleep, or becomes inactive. Therefore I considered an animal to be "active" (A) if it was stationary and if the approach occurred during an activity period - i.e. scatter was in the crest of a cycle. Appendix 3 gives some examples of approaches and scatter estimates.

Each type of approach will be symbolized by a pair of letters representing the activity states of first the predator, then the prey - e.g. MA means predator moving (M) and prey active (A). I grouped MA and MI as type 1 (predator moving), and IM and AM as type 2 (prey moving); MM approach types were rare (6% of the total), and therefore disregarded. Since almost all approaches took place between 2000 and 0600 hr, only those are considered here. Approaches were divided into two subsamples, those occurring before (time period 1) and after (time period 2) midnight. Numbers in these two groups were roughly equal.

Microhabitat use in the runs was calculated for each animal in each trial by:

sum of: (microhabitat variable) x
(time animal spends at that position) / (total time).

This was done for 2 activity states (active and inactive,

defined by speeds greater than and less than, respectively, 1/4 of the maximum speed of the animal in that trial), and for each time period mentioned above. Correlations of normality plots (Ryan et al. 1980) showed the resulting variables to be normally distributed.

I also determined the microhabitat at each approach. However, most of the variables were not normally distributed, as there were too many zeros. Therefore whenever a variable was zero I calculated a value between 0 and 1, which was an inverse function of the distance to the nearest feature of that variable (e.g. if there were no trees at the place of approach, then 1/(distance to nearest tree) was used). This value was transformed by a linear transformation (a different one for each variable) and the resulting variables were normally distributed. I considered it justifiable to transform these data, because exact values of the variables are not important, only the ordinal values are needed to test for differences in microhabitat use.

Tests of differences between microhabitats were done with the Hotelling T^2 statistic (Morrison 1976). Microhabitat use by prey was based on the first 24-hour period of data collection - i.e. the period without the predator present. This was done because most prey were killed when the predator was introduced, and because animals approached more often would have greater a priori

microhabitat correlations with the predator.

2.5. Preference experiment

A method was needed to test for prey preference independently of the probability of detecting, or of killing, a prey item. I used an 80 x 12.5 cm arena (Fig. 2) in which the weasel could simultaneously see, smell, and hear, two live prey but choose only one. The small (6 x 12 cm) prey chambers ensured that both prey would be visible at the same time, and that prey defense reactions would have little effect on the final choice. A red 25W light bulb illuminated the area. Prey types were distributed equally between the right and left chambers, to ensure independence between prey preference and a possible chamber preference.

The ermine was held for about 5 min in a covered plexiglas holding box, then released into the arena. I considered that the weasel had made a choice when it entered a prey chamber, and as soon as this happened, I locked the door to the other chamber. Time to choose a prey, and to kill a prey once chosen (which were measured with a key-board activated Esterline Angus event recorder), were used as more precise measures of preference than simply prey type chosen. Weasels presumably were satiated at the time of testing, because I took them straight from their cages where food was available.

2.6. Statistical analyses

I used the guidelines suggested by Cochran (1952, 1954) for determining minimum expected values in contingency tables: when $1 < d.f. < 30$, and less than 20% of the expected values were less than 5, I allowed a minimum expected value of 1, but when more than 20% of the expected values were less than 5, I allowed a minimum expected value of 2. A significance level of $P=0.05$ was used in all analyses.

The statistical computer packages used were MINITAB (Ryan et al. 1980) for normality tests and simulation, MIDAS (Fox and Guire 1976) for Hotelling T^2, SPSS (Nie et al. 1975) for discriminant functions analysis and BMDP (Dixon and Brown 1979) for analysis of covariance. Other computer programs were written by myself in PL/1.

3. RESULTS

Twenty-two useable trials were completed (9 with female and 13 with male ermine). During seven of these, new prey were introduced into the enclosure part way through the trials. Only data from the time period before the introduction of prey were used in the analyses. Appendix 5 summarizes the number of approaches and the fate of all prey. Note that the number of useable captures depends on the method of analysis - e.g. order of capture was known for

more prey than were actually retrieved after the trials (and used to study consumption).

3.1. Prey preference

The preference experiments simulated the behaviour of ermine after prey was detected. Ermine showed no preference for either sex ($X^2=1.13$, d.f.=1, $P>0.1$) or species ($X^2=0.53$, d.f.=1, $P>0.1$) of prey (see Appendix 13 for raw data). There was no significant difference between time taken to choose male or female prey (median test: $X^2=0.04$, d.f.=1, $P>0.5$), but once an ermine entered a compartment, female prey were killed faster than males (median test: $X^2=5.43$, d.f.=1, $P<.025$). Therefore if a preference existed, it was very weak, and was for females. In order to isolate the choice step from the detection and capture steps, a small artificial arena was used, which may have affected the natural behaviour of the ermine. The other steps, however, were studied in natural ermine habitat.

3.2. Field trials

3.2.1. Prey selection

I first tested the null hypothesis that the proportion of prey types eaten is the same as the proportion of prey types initially available to the predator (Fig. 1, T.1). The

null hypothesis was rejected for species, but not for sex (Table 1), with C. gapperi consumed significantly more frequently than P. maniculatus. Therefore I concluded that overall prey selection occurred in this study, and I proceeded to examine intermediate steps in the predatory sequence.

3.2.2. Selection mechanism

The predatory sequence can be divided into two segments - probability of capture (Fig. 1, T.3) and probability of consumption once captured (Fig. 1, T.2). The null hypothesis for the consumption step (Fig. 1, T.2) is that the proportions of each prey type eaten is independent of prey type. The hypothesis was rejected (Table 2.), but this result could have been brought about by a non-random order of capture of prey and subsequent consumption in the order of capture. Therefore I tested the null hypothesis that the proportion of prey eaten was independent of the order of capture. The null hypothesis was not rejected (Table 3.). Therefore, I conclude that there was selection at the consumption step - female P. maniculatus tended to be eaten least often.

Do capture probabilities differ between prey types (Fig. 1, T.3)? In many of the experimental runs all prey were eventually captured, so a comparison of the order in which prey were caught is a more precise test of the

question than a comparison of the number of prey caught. I modified the Friedman two-way analysis of variance, a nonparametric test, to include those runs with missing data (Appendix 4). This test measures the goodness-of-fit of the rank totals for each prey type to those expected under the null hypothesis of a random ordering (Marascuilo and McSweeney 1977). The order in which prey were captured was: male C. gapperi > (female C. gapperi, male P. maniculatus) > female P. maniculatus. C. gapperi were selected over P. maniculatus, and males over females (Table 4.). Therefore ermine in this study selected both species and sex of prey in the approach to capture steps, inclusive.

Probability of capture can be further divided into approach rate (Fig. 1, T.4) and probability of capture once approached (Fig. 1, T.5). I tested the null hypothesis for the former, that each prey type known to be alive at a given time has an equal expectation of being approached. Thus, at the beginning of a run, each of the four available prey types had an a priori probability of approach of 0.25. When one animal was approached, it was scored 1.0 in the "observed" column, and all four were scored 0.25 in the "expected" column. After one was captured, the survivors each had a probability of 0.33 of being approached, and if an approach occurred, then each animal was scored 0.33 in the expected column, and the one approached was scored 1.0 in the observed column, and so on until the end of the trial. Analysis of the resulting data showed that C. gapperi

were approached more often than expected (Table 5.), but there were no differences in approach frequency between prey sexes. Therefore interspecific selection occurred at the approach step.

Do capture probabilities differ between prey types once they are approached (Fig. 1, T.5)? If N is the number of approaches before eventual capture of a certain prey type, then 1/N is an estimate of the probability of capture once approached. The null hypothesis is that prey types are all approached an equal number of times before capture (i.e. they have equal N-values). There were not enough approaches to test for homogeneity between trials, but inspection of the data suggested that the pattern differed widely among trials (Appendix 10), which would render a chi-square test of the number of approaches invalid. Therefore I ranked the prey types in each trial, according to their N-values (a low rank means a high probability of capture once approached) and used the modified Friedman's 2-way ANOVA. The N-values were similar for C. gapperi and P. maniculatus, but males were selected over females (Table 6.). Therefore sexual selection occurred in the detection, choice, and capture steps.

Different capture probabilities once prey were approached may be a result of an actual preference for the selected prey (Fig. 1, T.6) - the ermine may not have tried to capture females. However, preference experiments showed

that male prey were not chosen over females (Section 3.1). Therefore selection for male prey in steps 2 to 4 was not a simple result of preference on the part of the weasel in step 3 (choice). I cannot distinguish between steps 2 and 4 with my data.

In summary, C. gapperi were selected over P. maniculatus at the approach step, males over females at the detection and/or capture step(s), and female P. maniculatus were selected against in the consumption step.

3.2.3. Sex of ermine

[redacted]ermine are nearly twice the size of females, so it [redacted] expected that they differ in behaviour. There were to[redacted] captures to test for overall differences in prey sel[redacted]ion between sexes and for selection at the consumption ste[redacted] However, male and female ermine differed in the order of [redacted]pture between C. gapperi sexes, in that males caught male C. gapperi first, and females caught female C. gapperi first (Appendix 7). Male ermine were used in more runs than females were (13 versus 9, respectively), so male selection affected the overall capture order more than did female selection. I adjusted the order of capture test (Fig. 1, T.3), for the different numbers of runs, and found the same result as before (Appendix 8). Therefore the overall pattern of capture order is not an artifact of unequal sample sizes betwee[redacted]rmine sexes, but the result of a stronger selection

by male ermine for male C. gapperi than by females for female C. gapperi.

I attempted, unsuccessfully, to discover at which step(s) the difference occurred. Male and female ermine did not approach prey in different proportions, (X^2=1.82, d.f.=3, P>0.1), nor did they capture prey in different proportions once approached (X^2=0.92, d.f.=3, P>0.1). Larger sample sizes are needed to clarify these results.

3.2.4. Factors affecting selection

Selection at the approach step could be affected or caused by: 1) whether the predator or prey are moving - i.e. approach type, 2) time of day, 3) whether predator and prey overlap with respect to their activity rhythms, and 4) whether predator and prey overlap with respect to the kinds of places they use.

It was possible to test for interacting effects of the first two variables on selection, so they were analyzed together. The null hypothesis for no effect on selection is that prey type is independent of approach type and time of day with respect to the approach frequency. A contingency table analysis of all 2- and 3- way interactions (prey type vs predator sex, approach type, and time of day) showed that only the prey x approach type term is significant (X^2= 19.1; d.f.=9, P<0.025) (see Appendix 9 for observed and expected values). However, Cramer's measure of association

(which is analogous to the r^2 of parametric correlation (Marascuilo and McSweeney 1977)) is only 0.04, so although the interaction is statistically significant, it is so weak that it can be ignored. Therefore prey selection at step 1 (different approach frequencies for different prey types) is independent of time of day, approach type and predator sex.

Clethrionomys gapperi may be approached more frequently than P. maniculatus because temporal overlap of activity patterns between the ermine and C. gapperi is greater than between the ermine and P. maniculatus. Approaches can occur only when at least one of the animals is moving. Overlap times for the two pairs were 5.5 and 6.2 hr, respectively; this would lead to selection for P. maniculatus, not C. gapperi. When the prey were moving, the species active for the longer period of time would be expected to approach the ermine most often, but C. gapperi were active for shorter periods of time than P. maniculatus (3.3 and 4.5 hr, respectively). Therefore temporal overlap does not appear to cause selection.

Clethrionomys gapperi may approach the ermine more frequently than P. maniculatus because of greater spatial overlap between C. gapperi and the ermine than between P. maniculatus and the ermine. However, the two prey species were active in similar kinds of microhabitats ($F(5,63)=0.91, P=0.50$), and they approached the ermine in similar microhabitats ($F(5,25)=1.97, P=0.12$). Therefore

spatial overlap does not explain selection for C. gapperi at the approach step when the prey are moving.

The ermine may approach C. gapperi more frequently than P. maniculatus because it searches in C. gapperi microhabitats rather than in P. maniculatus microhabitats. When the prey were inactive, the two species used different microhabitats during the trials ($F(5,24)=3.16, P=0.03$). The ermine spent time in different microhabitats from those used by P. maniculatus ($F(5,112)=4.32, P=0.002$), but not different from those used by C. gapperi ($F(5,106)=0.93, P=0.45$), and most importantly, the predator approached the two prey species in different microhabitats ($F(5,103)=2.46, P=0.04$). A discriminant functions analysis between prey microhabitats showed that C. gapperi occurred closer to logs than did P. maniculatus (Table 7.). I conclude that C. gapperi were approached more frequently than P. maniculatus because of spatial overlap between prey and predator when the predator was moving.

Selection for male prey at the detection and/or capture steps could be caused by differences between males and females in 1) activity or 2) microhabitats used.

Sex and activity of prey may interact with respect to probability of capture once approached. I tested the null hypothesis that the number of kills for each sex and activity type did not differ from that expected from the observed distribution of approaches (Appendix 12), by means

of a chi-square goodness-of-fit test. Sex of prey and activity type were independent ($X^2=0.25, d.f.=3, P>0.5$), and therefore activity affects the probability of detection and/or capture in the same way for both sexes.

Even though sex and activity of prey do not interact with respect to capture probability, capture probabilities may be dependent upon prey activity. I compared the number of kills for each type of prey activity to the values expected from the distribution of approaches, and found that more kills occurred than expected when the prey were inactive (the MI approach type) ($X^2=8.86, d.f.=2, P<0.01$). This would cause a greater capture probability for males only if a disproportionate number of males were approached at the MI approach type, but prey type is independent of approach type at the approach step (see p 29). Therefore selection at steps 2 and 4 appears to be independent of prey activity.

Female prey may use microhabitats that offer more protection from detection and/or capture than ones that males use. However, male and female approaches occurred in similar microhabitats ($F(5,103)=1.14$, $P=0.33$). Even though prey sexes use similar types of places, females may use certain microhabitats for defense more efficiently than males. If so, then males and females would be captured in different kinds of places, but they were captured in similar microhabitats ($F(5,9)=0.85, P=0.55$). Therefore microhabitat

does not appear to be involved in prey selection in steps 2 and 4.

4. DISCUSSION

Part of the validity of the analysis of approaches hinges on choice of approach distance. As discussed previously (Section 1.1), researchers do not even agree on what senses are used for prey detection (although smell seems to be least important), let alone at what distance prey can be detected. If ermine consistently used smell to track prey in this study, then approach probability would be inversely related to the time since the prey last moved; fresh scent trails are easier to follow than old ones. However, my data show no difference in the number of approaches between inactive and active prey ($P=0.54$, $N=103$, Binomial one-tailed probability). Therefore I assumed that ermine do not use smell to detect prey at long distances, and that the 3-m approach distance I used is not unreasonably short.

Instead of a constant selection for *C. gapperi* over *P. maniculatus* during the whole trial, the observed order of capture of prey may have occurred because ermine selected *C. gapperi* at first, and later switched to *P. maniculatus*, because experimental runs were all started at approximately the same time of day. However, independence between time of day and selection shows that the overall selection pattern

did not change with time. Such a switch would be expected if temporal overlap caused selection, and if the overlap with P. maniculatus was greater in the second half of each trial than in the first half.

Satiation may have affected prey selection, because ermine in the enclosures probably became satiated with time - they require one to two prey per day (Short 1961). It has been shown that vertebrates decrease searching activity with decreasing hunger (de Ruiter 1967), but ermine prey selection in this study was independent of time, and therefore, presumably, of satiation.

My data show that ermine approach C. gapperi more frequently than P. maniculatus because of differential microhabitat use. Royama (1970) hypothesized that the Great Tit (Parus major) optimized its diet by selectively searching in specific microhabitats, rather than by selectively choosing prey items. He argued that the greater the profitability differences between microhabitats (that is if prey are found in different kinds of places), the more time would be spent by the predator in the most profitable microhabitats. Prey species did use different microhabitats in my experiments, and there would probably be relatively large profitability differences between these microhabitats, because of the following reasons. Within a microhabitat, at high prey densities, rate of prey capture would be limited by handling time, which would result in an asymptotic

relationship between prey density and microhabitat profitability. Therefore profitability differences between microhabitats would be greater at low, rather than at high prey densities. The ermine has a short handling time relative to searching time, which suggests that the animal hunts in areas of relatively low prey densities. Therefore any differences in prey densities would result in relatively large profitability differences between microhabitats. Royama predicts that in this situation the predator should select prey by searching in specific microhabitats, and my results support this prediction.

Microhabitat selection implies that ermine 'know' which microhabitats are more profitable. The study animals were captured as adults (and were therefore experienced), they were familiarized to the enclosure before the experiments, and the enclosed area was natural ermine habitat. Therefore I assumed that they treated the pen as they would a part of their natural home range. This assumption would hold even if knowledge of the most profitable microhabitat(s) must be learned - i.e. if it is not a hereditary trait.

My data show that prey selection is independent of temporal overlap of activity, but other studies have shown that activity patterns of predators overlap those of their main prey - e.g. pigmy owl (Glaucidium passerinum) and bank vole (Clethrionomys glareolus) (Mikkola 1970); pine marten (Martes americana) and C. gapperi (More 1978). Because

neither of these predators can enter small mammal burrows, they are restricted to capturing prey active outside burrows, so activity overlap would be important. Ermine, however, readily enter burrows, (Simms 1979) so their prey need not be active above ground in order for the predator to be able to encounter and catch them.

When the prey was moving and the predator was stationary, C. gapperi approached the weasel more frequently than did P. maniculatus, but neither temporal nor spatial overlap provided an explanation. Stoddart (1976) showed that Microtus agrestis avoided live-traps smeared with least weasel anal gland secretion, but Apodemus sylvaticus were not affected. Perhaps P. maniculatus and C. gapperi respond differently to weasel scent, but it is not known at what distance they can detect a weasel.

The only study of weasel predation in which prey were sexed was that of MacLean et al. (1974), who examined the remains of lemming (Lemmus trimucronatus and Dicrostonyx groenlandicus) winter nests in spring, and found that least weasels had preyed more heavily on breeding females than on males. No reasons were given for this result. In several cases avian predators have been shown to prey selectively upon male microtines (Beacham 1979, Pitelka 1957), which may be a result of greater mobility, and therefore exposure, on the part of the males (Thompson 1955, cited by Beacham 1979). However, this would explain neither sexual selection

by ermine in my study, nor by least weasels in the aforementioned study, since weasels can enter burrows and subterranean tunnels (Simms 1979).

My study showed that probability of capture is independent of microhabitat type. However, Erlinge et al. (1974) noted that once seen by a weasel, prey had the highest chance of escape if they ran into holes or tunnels, and that different prey species used different escape tactics. This discrepancy might be a result of the large number of artificial runways and dens in Erlinge's enclosure, which would give prey a wider choice of microhabitats. Also, the stoats he used are about twice as large as ermine, so would be less able to enter prey tunnels and burrows.

Preference tests were done in an artificial arena, but the results were probably valid. Predators show the greatest prey preference when they are satiated (Zach and Falls 1978, Ivlev 1961), as were the ermine used in the preference experiments. It would be easier for weasels to choose more profitable prey when the prey are encountered simultaneously, as in the experiments, rather than when they are encountered sequentially, as in the wild. These two points imply that ermine in the experiments would be expected to exhibit a maximum preference. Therefore the lack of preference for C. gapperi over P. maniculatus or males over females in the experiments probably holds in the wild

as well.

Most optimal foraging theories predict that once encountered, prey should be either ignored or captured - i.e. if a prey type is to be included at all in the diet, it should always be captured (Pulliam 1974, MacArthur and Pianka 1966, Schoener 1971, Emlen 1966). Some experimental tests have not supported this prediction (Zach and Falls 1978, Krebs et al. 1977). A graduated rather than an all-or-none preference would be predicted if the animals occasionally sampled all prey to estimate profitability of different prey types (Krebs et al. 1977), if there were certain nutritional constraints on the diet (Pulliam 1975), or if they made "mistakes" (Emlen and Emlen 1975). Perhaps we would see a graduated response in the ermine if a wider range of prey items had been tested, but the lack of preference is not surprising. At the relatively low prey densities in the wild, a weasel that rejected less profitable but acceptable prey would face another long search that would probably outweigh any advantages gained by choosing only the most profitable prey (MacArthur and Pianka 1966).

Weasels ate prey preferentially in this study. Prey density in the pens at the beginning of a trial was 22 animals/ha for each prey species - approximately the maximum density for C. gapperi in the area and about twice the maximum density for P. maniculatus (Mihok 1979). However, it

is not unreasonable to expect ermine to be exposed to even higher densities of P. maniculatus elsewhere in their range, because small mammal densities at Heart Lake are much lower than in other areas (French et al. 1975). Therefore the high capture rate of four prey per night (high relative to the one or two required) is to be expected, as evidenced by reports of weasels caching, or storing, prey in the wild (Polderboer et al. 1941, Parovshchikov 1963).

Caching behaviour has also been observed in red foxes (Vulpes vulpes)(MacDonald 1976) and American kestrels (Falco sparverius)(Mueller 1974). Polsky (1975) suggested that the acts of killing and feeding on prey by experienced predators, especially the Carnivora, are not linked, and Kruuk (1972) argued that satiation does not inhibit further catching and killing of prey. Once several prey are cached, it is advantageous for a predator to rank them, and eat the most profitable ones first, because another preferred item may be captured before all cached prey are eaten.

Other prey selection studies mentioned here so far do not consider the whole predatory sequence. However, Elliot et al. (1977) studied prey capture by the African lion, and separated the components into "search", "stalk", "attack", and "subdue". They showed that capture success is primarily dependent upon the failure of the prey to see the approaching lion until it is within its effective distance, but also that overall stalk success did not differ among

prey types. Mech (1970) followed 131 wolf-moose interactions, 6 of which went to completion (capture). Hunting success here was directly related to prey behaviour - if prey followed a series of behaviours while being chased, then they were captured. Selection occurred when some prey types acted differently. For example, animals that stood at bay when the wolves caught up to them were not captured. Most selection occurred during capture attempts - i.e. the capture step. However, ermine do not have such long capture times as do lions and wolves. Instead, the approach step is most important for ermine; this is where selection for C. gapperi occurs.

My study showed that ermine selected C. gapperi over P. maniculatus because of different frequencies of approach, which may, in turn, be related to differential microhabitat use. Once prey were approached, males had a greater chance of being captured than did females, but this was not a result of a preference for males. Female P. maniculatus tended to be eaten after the other prey types, if eaten at all. This selection mechanism can be related to the ermine's habits, in that it is a predator that spends much energy searching, and little in the final attack and capture. Therefore it would be advantageous for it to select by hunting in those microhabitats in which the more profitable prey are found, rather than to attack only these prey once they are encountered. If captured prey are stored temporarily before they are eaten, the ermine should eat

more profitable items first, because there is always a chance that it can capture another more profitable item before it has to eat the less profitable ones.

5. LITERATURE CITED

Ad[illegible],E. [illegible] weasel trails a rabbit. J. Mammal. 20:372-373.

Al[illegible]s,S. [illegible] and J.Manweiler. 1942. The winter food habits of the [illegible]hort-tailed weasel in Northern Minnesota. J. Mam[illegible]l. 23:250-255.

Ande[illegible]D.E. and R.Lydic. 1977. On the effects of using [illegible]os in the analysis of variance. Biobehav. Rev. [illegible]25-229.

Atchl[illegible]W.R., C.T.Gaskins and D.Anderson. 1976. Statistical p[illegible]perties of ratios. I. Empirical results. System. Z[illegible]l. 25:137-148.

Beacham,D. 1979. Selectivity of avian predation in de[illegible]ining populations of the vole Microtus townsendii. Can. J. Zool. 57:1767-1772.

Boonstra,R. and C.J.Krebs. 1978. Pitfall trapping of Micr[illegible]us townsendii. J. Mammal. 59:136-148.

Chute,F.[illegible]W.A.Fuller, P.R.Harding and T.B.Herman. 1974. Rad[illegible]tracking of small mammals using a grid of overhead wire antennas. Can. J. Zool. 52:1481-1488.

Cochran,W.G. 1952. The chi-square test of goodness of fit. Annals Math. Stat. 23:315-345.

Cochran,W.G. 1954. Some methods for strengthening the common chi-square tests. Biometrics 10:417-451.

Curio,E. 1976. The ethology of predation. Springer-Verlag, New York. x+250 pp.

Davis,L. 1978. Data acquisition system for biotelemetry. M.Sc. thesis, University of Alberta.

Day,M.G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. J. Zool., Lond. 148:201-217.

Day,M.G. 1968. Food habits of British stoats (Mustela erminea) and weasels (Mustela nivalis). J. Zool., Lond. 155:485-497.

de Ruiter,L. 1967. Feeding behavior of vertebrates in their natural environment. chapter 7 in: Handbook of physiology, Sect. 6: Alimentary canal, Vol 1: Food and water intake. Am. Physiol. Soc., Wash. D.C.

de Vos,A. 1960. Long-tailed weasel climbing trees. J.

Mammal. 41:520.

Dixon,W.J. and M.B.Brown (eds). 1979. Biomedical computer programs P-series. University of California Press, Berkeley. xiii+880 pp.

Doyle,D. 1979. Population dynamics and ecology of subarctic shrews. M.Sc. thesis, University of Alberta.

Elliot,J.P., I.M.Cowan and C.S.Holling. 1977. Prey capture by the African lion. Can. J. Zool. 55:1811-1828.

Emlen,J.M. 1966. The role of time and energy in food preference. Amer. Nat. 100:611-617.

Emlen,J.M. and M.G.R.Emlen. 1975. Optimal choice in diet: test of a hypothesis. Am. Nat. 109:427-435.

Erlinge,S. 1974. Distribution, territoriality and numbers of the weasel Mustela nivalis in relation to prey abundance. Oikos 25:308-314.

Erlinge,S. 1975. Feeding habits of the weasel Mustela nivalis in relation to prey abundance. Oikos 26:378-384.

Erlinge,S. 1977. Home range utilization and movements of the stoat, Mustela erminea. Int. Congr. Game Biol. 13:31-42.

Erlinge,S., B.Bergsten and H.Kristiansson. 1974. Hermelinen och dess byte - jaktbeteende och flyktreaktioner. Fauna och Flora 69: 203-211. (English translation)

Fitzgerald,B.M. 1977. Weasel predation on a cyclic population of the montane vole (Microtus montanus) in California. J. Anim. Ecol. 46:367-399.

Floyd,T.J., L.D.Mech and P.A.Jordan. 1978. Relating wolf scat content to prey consumed. J. Wildl. Mgmt. 42:528-532.

Fox,D.J. and K.E.Guire. 1976. Documentation for Michigan Interactive Data Analysis System (3 ed) Statistical Research Lab., University of Michigan. ix+203pp

French,N.R., D.M.Stoddart and B.Bobek. 1975. Patterns of demography in small mammal populations. chpt. 4 in: Small mammals: their productivity and population dynamics (F.B.Golley, K.Petrusewicz and L.Ryszkowski eds). Cambridge University Press, Cambridge. xxv+451pp.

Frith,R. 1958. Observation of a short-tailed weasel capturing a chipmunk. Can. Field-Nat. 72:144-145.

Fuller,W.A. 1969. Changes in numbers of three species of small rodents near Great Slave Lake, N.W.T., Canada, 1964-1967 and their significance for general population theory. Annales Zoologica Fennici 6:113-144.

Hamley,J.M. and J.B.Falls. 1975. Reduced activity in transmitter-carrying voles. Can. J. Zool. 53:1476-1478.

Herman,D.G. 1973. Olfaction as a possible mechanism for prey selection in the least weasel, Mustela nivalis. M.S. thesis, Michigan State University.

Herman,T.B. 1977. Activity patterns and movements of subarctic voles. Oikos 29:434-444.

Holling,C.S. 1964. The analysis of complex population processes. Can. Ent. 96:335-347.

Ivlev,V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven.

Jamison, Van C. 1975. Relative susceptibility of resident and transient Peromyscus subjected to weasel predation. M.A. thesis, University of Wisconsin-Madison.

King,C.M. 1980. The weasel Mustela nivalis and its prey in an English woodland. J. Anim. Ecol. 49:127-159.

King,C.M. and P.J.Moors. 1979. On co-existence, foraging strategy and the biogeography of weasels and stoats (Mustela nivalis and M. erminea) in Britain. Oecologia 39:129-150.

Krebs,J.R. and R.J.Cowie. 1976. Foraging strategies in birds. Ardea 64:98-116.

Krebs,J.R., J.T.Erichsen, M.I.Webber and E.L.Charnov. 1977. Optimal prey selection in the great tit (Parus major). Anim. Behav. 25:30-38.

Kruuk,H. 1972. Surplus killing by carnivores. J. Zool., Lond. 166:233-244.

Lockie,J.D. 1959. The estimation of the food of foxes. J. Wildl. Mgmt. 23:224-227.

Lockie,J.D. and M.G.Day. 1964. The use of anaesthesia in the handling of stoats and weasels. in: Symposium on small mammal anaesthesia. (O. Graham Jones, ed). pp 187-189, Pergamon Press, Oxford.

MacArthur,R.H. and E.R.Pianka. 1966. On optimal use of a patchy environment. Amer. Nat. 100:603-609.

MacDonald,D.W. 1976. Food caching by red foxes and some other carnivores. Z. Tierpsychol. 42:170-185.

MacDonald,D.W. 1977. On food preference in the red fox. Mammal Rev. 7:7-23.

MacLean,S.F.Jr, B.M.Fitzgerald and F.A.Pitelka. 1974. Population cycles in arctic lemmings: winter reprodution and predation by weasels. Arctic Alpine Res. 6:1-12.

Marascuilo,L.A. and M.McSweeney. 1977. Nonparametric and distribution-free methods for the Social Sciences. Brooks/Cole, Montery, Calif. xvii+556 pp.

Martell,A.M. 1979. Relative efficiencies of Museum Special, Victor, and Holdfast traps for sampling small mammal populations. Can. Field-Nat. 93:313-315.

Marti,C.D. 1972. Food consumption and pellet formation rates in four owl species. Wilson Bull. 85:178-181.

Mech,D.L. 1970. The wolf. Am. Mus. Nat. Hist., New York. xx+384 pp.

Mihok,S. 1979. Demography, behavior, and protein polymorphism in subarctic Clethrionomys gapperi. Ph.D. thesis, University of Alberta.

Mikkola,H. 1970. On the activity and food of the pygmy owl Glaucidium passerinum during breeding. Ornis. Fenn. 47:10-14. (English summary)

More,G. 1978. Ecological aspects of food selection in pine marten (Martes americana). M.Sc. thesis, University of Alberta.

Morrison,D.F. 1976. Multivariate statistical methods. McGraw-Hill, New York. xv+415 pp.

Mueller,H.C. 1974. Food caching behaviour in the American kestrel (Falco sparverius). Z. Tierpsychol. 34:105-114.

Murie,A. 1935. A weasel goes hungry. J. Mammal. 16:321-322.

Nie,N.H., C.H.Hull, J.G.Jenkins, K.Steinbrenner and D.H.Bent. 1975. Statistical Package for the Social Sciences (SPSS). (2 ed) McGraw-Hill Inc. xxiv+675 pp.

Northcott,T.H. 1972. Winter predation of Mustela erminea in Northern Canada. Arctic 24:141-143.

Parovshchikov,V.Y. 1963. A contribution to the ecology of Mustela nivalis Linnaeus 1766, of the Arkhangel'sk

North. Vestnik Ceskoslovenske Spolecnosti Zoologicke. 27:335-344. English translation in: Biology of Mustelids. Some Soviet research. (C.M.King ed.). British Library Lending Division, U.K.

Pitelka,F.A. 1957. Some aspects of population structure in the short-term cycle of the brown lemming in northern Alaska. Cold Springs Harb. Symp. Quant. Biol. 22:237-251.

Polderboer,E.B., L.W.Kuhn and G.O.Hendrickson. 1941. Winter and spring habits of weasels in central Iowa. J. Wildl. Mgmt. 5:115-119.

Polsky,R.H. 1975. Hunger, prey feeding, and predatory aggression. Behav. Biol. 13:81-93.

Pulliam,H.R. 1974. On the theory of optimal diets. Am. Nat. 108:59-74.

Pulliam,H.R. 1975. Diet optimization with nutrient constraints. Am. Nat. 109:765-768.

Pyke,G.H., H.R.Pulliam and E.L.Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52:137-154.

Quick,H.F. 1951. Notes on the ecology of weasels in Gunnison County, Colorado. J. Mammal. 32:281-290.

Rapport,D.J. 1971. An optimization model of food selection. Am. Nat. 105:575-587.

Royama,T. 1970. Factors governing the hunting behaviour and selection of food by the great tit (Parus major L.). J. Anim. Ecol. 39:619-668.

Ryan,T.A.Jr., B.L.Joiner and B.F.Ryan. 1980. Minitab reference manual. Statistics Department, Pennsylvania State University, Pennsylvania.

Schoener,T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2:369-404.

Short,H.L. 1961. Food habits of a captive least weasel. J.Mammal. 42:273-274.

Simms,D.A. 1979. North American weasels: resource utilization and distribution. Can. J. Zool. 57:504-520.

Smith,D.H. 1978. Vulnerability of bot fly (Cuterebra) infected Peromyscus maniculatus to shorttail weasel predation in the laboratory. J. Wild. Dis. 14:40-51.

Smith,M.H. 1968. A comparison of different methods of capturing and estimating numbers of mice. J. Mammal. 49:455-462.

Smith,M.H., R.H.Gardner, J.B.Gentry, D.W.Kaufman and M.H.O'Farrel. 1975. Density estimations of small mammal populations. chpt. 2 in: Small mammals: their productivity and population dynamics (F.B.Golley, K.Petrusewicz and L.Ryszkowski eds). Cambridge University Press, Cambridge. xxv+451pp.

Stoddart,D.M. 1976. Effect of the odour of weasels (Mustela nivalis L.) on trapped samples of their prey. Oecologia 22:439-441.

Tanton,M.T. 1965. Problems of live-trapping and population estimation for the wood mouse, Apodemus sylvaticus (L.). J. Anim. Ecol. 34:1-22.

Tapper,S.C. 1976. The diet of weasels (Mustela nivalis) and stoats (Mustela erminea) during early summer, in relation to predaton on gamebirds. J. Zool., Lond. 179:219-224.

Thompson,D.Q. 1955. Ecology of the lemmings. Arct. Inst. North Am., Final Rep. Proj. ONR-133. (cited by Beacham 1979)

Tinbergen,L. 1960. The natural control of insects in pinewoods 1. Factors influencing the intensity of predation by songbirds. Archs. Neerl. Zool. 13:265-336.

Wobeser,G.A. 1966. Ecology of the long-tailed weasel (Mustela frenata novaboracensis (Emmons)) in Rondeau Park, Ontario. M.Sc. thesis, University of Guelph.

Wustehube,C. 1960. Beitrage zur Kenntnis besonders des Spiel- und Beuteverhaltens einheimischer Musteliden. Z. Tierpsychol. 17:579-613. (English summary)

Zach,R. and J.B.Falls. 1978. Prey selection by captive ovenbirds (Aves: Parulidae). J. Anim. Ecol. 47:929-943.

Table 1. Overall prey selection: number of prey consumed and not consumed, in all experimental runs.

Species	Sex	Consumed	Not Consumed
C. gapperi	M	10	3
C. gapperi	F	10	3
P. maniculatus	M	6	6
P. maniculatus	F	2	12

$X^2 = 14.5$, d.f.=3, $P<0.005$

Partitioning of X^2	d.f.	X^2	P
Species x Eat	1	11.2	<0.01
Sex x Eat	1	2.0	>0.10
Species x Sex x Eat	1	1.3	>0.10

Table 2. Number of captured prey recovered: consumed and not consumed.

Species	Sex	Consumed	Captured But Not Eaten
C. gapperi	M	10	3
C. gapperi	F	10	2
P. maniculatus	M	6	1
P. maniculatus	F	2	7

$X^2 = 11.5$, d.f.=3 $P<0.025$

Partitioning of X^2	d.f.	X^2	P
Species x Eat	1	4.1	<0.05
Sex x Eat	1	1.8	>0.10
Species x Sex x Eat	1	5.7	<0.025

Table 3. Number of prey eaten, and order in which they were captured, from all experimental runs.

	Rank order captured			
	1	2	3	4
Eaten	10.0	7.6	7.2	3.2
Not Eaten	1.3	3.9	2.9	4.9

$X^2=5.29$, d.f.=3, $P>0.10$

Note: Fractions are caused by ties and some unknown ranks.

Table 4. Modified Friedman 2-way ANOVA: Capture order between all prey types.

	Prey Type			
	CM	CF	PM	PF
Rank Total	28.5	34.0	39.0	61.5
Expected Total	34.0	38.5	40.5	45.0

Variance-covariance matrix

CM	CF	PM	PF	
15.88	-4.72	-5.13	-6.04	CM
	15.13	-4.88	-5.54	CF
		15.96	-5.97	PM
			17.54	PF

$X^2 = 17.54$ d.f.=3 $P<0.005$

Planned Comparisons			O-E	Var		Cov	X^2	P
	1	2		1	2			
Species	CM+CF	PM+PF	±15	21.59	21.58	-21.60	10.42	<0.005
Sex	CM+PM	CF+PF	±12	21.58	21.58	-21.59	6.62	<0.01
Sex x Species	CM+PF	CF+PM	±6	21.33	21.33	-21.33	1.69	>0.10

Note: see Appendix 4 for rank data.

Table 5. Numbers of approaches: expected numbers were calculated for all prey present at times of approaches.

Species	Sex	Observed	Expected
C. gapperi	male	27	22.2
C. gapperi	female	42	33.0
P. maniculatus	male	35	42.5
P. maniculatus	female	70	76.5

Among all prey: $X^2=5.47$, d.f.=3, $P>0.10$

Prey species: P=0.03 *

Prey sex: P=0.76 *

Sex x Species: P=0.76 *

* Binomial exact probability test

Table 6. Modified Friedman 2-way ANOVA: Number of approaches before capture among all prey types.

	Prey Type			
	CM	CF	PM	PF
Rank Total	25.0	30.5	26.0	44.5
Expected Total	28.5	30.0	32.0	35.5

Variance-covariance matrix

CM	CF	PM	PF	
10.00	-3.25	-3.58	-3.83	CM
	10.25	-3.58	-4.08	CF
		10.92	-4.42	PM
			11.33	PF

$X^2 = 8.41$ d.f=3 $P<0.05$

Planned Comparisons			O-E	Var		Cov	X^2	P
	1	2		1	2			
Species	CM+CF	PM+PF	±3.0	13.75	13.41	-15.07	0.66	>0.10
Sex	CM+PM	CF+PF	±9.5	13.76	13.42	-15.08	6.64	<0.01
Sex x Species	CM+PF	CF+PM	±5.5	13.67	14.01	-15.33	2.19	>0.10

Table 7. Discriminant functions analysis of microhabitats used by C. gapperi and P. maniculatus in the experimental trials.

Microhabitat variable	Standardized coefficient
logs > 5 cm diameter	-0.77
logs ± 5 cm diameter	-0.59
stumps and rocks	-0.34
trees	-0.11
log intersections	0.34

Group centroids C. gapperi: -0.31

P. maniculatus: 0.24

Difference between groups:

F=2.46, d.f.=5,103, P=0.04

Fig. 1. Idealized predatory sequence of ermine. The T's refer to tests which are presented in the results.

Step 1: APPROACH

Do weasel and prey come close?

No ←

| Yes

V

T.4

Step 2: DETECTION

Can the weasel detect and identify the prey?

No ←

| Yes

V

T.3

Step 3: CHOICE

Does the weasel decide to attack the prey?

No ←

| Yes

V

T.6

T.5

T.1

Step 4: CAPTURE

Can the weasel capture the prey?

No ←

| Yes

V

Does the weasel eat the prey?

No ←

| Yes

V

T.2

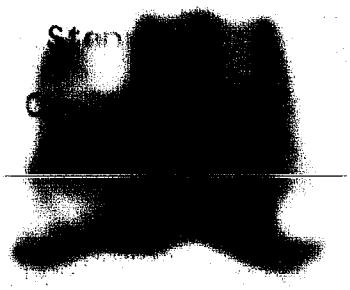


Fig. 2. Arena used to test for prey preference.

A. Top view of whole arena.

1 - Prey chamber.

2 - Plexiglas holding box for weasel.

B. Side view of one prey chamber.

3 - Screen top to arena.

4 - Screen barrier part way down front entrance to chamber.

5 - Screen door; hinged at top.

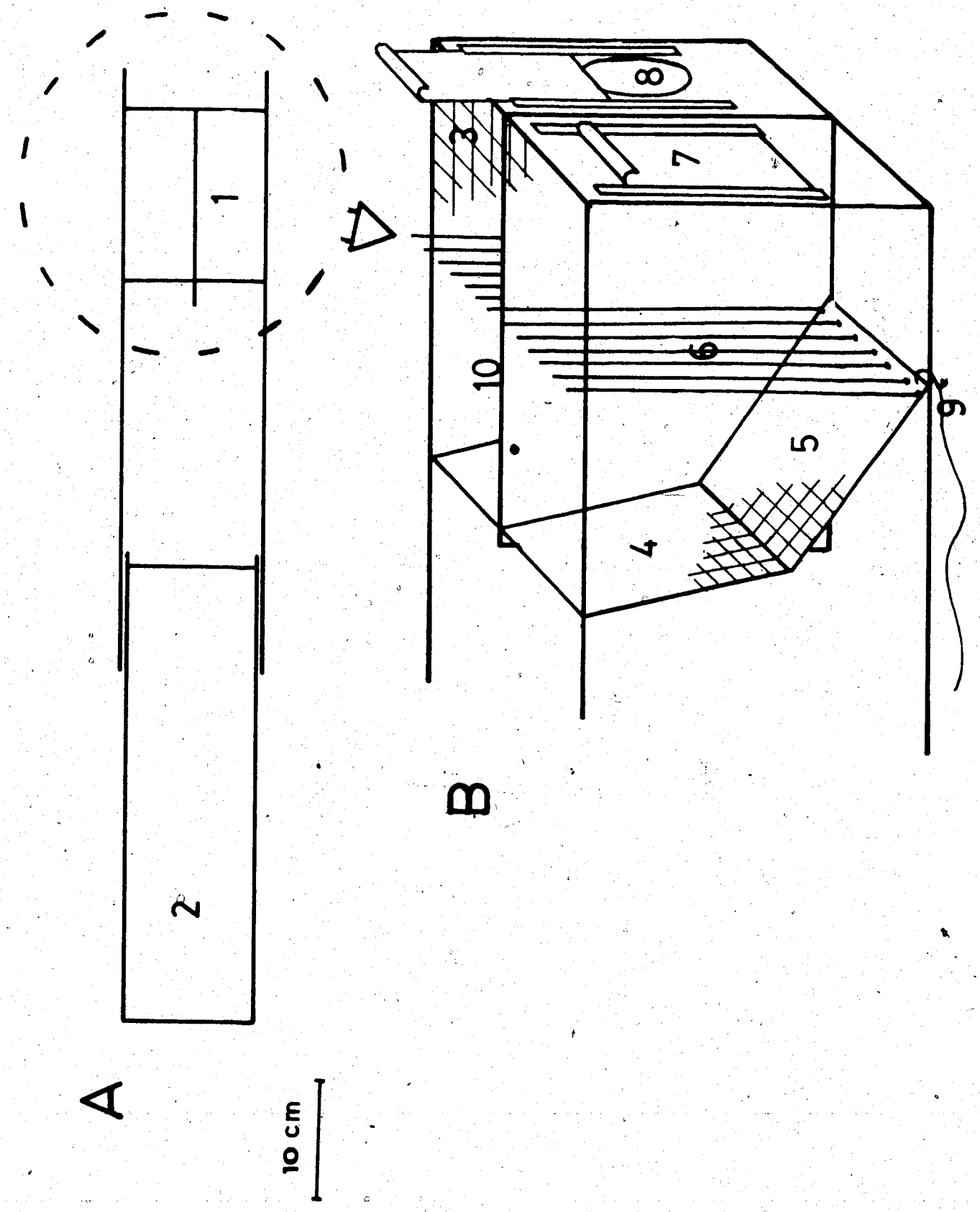
6 - Bars which are hinged at door (#5); they slide up when door opens, to keep prey from climbing onto top of door.

7 - Sliding door to back of chamber for introduction of prey.

8 - Opening behind sliding door (#7).

9 - Door lock; is locked by pulling string.

10 - Partition between prey compartments.


1
2
3
4
5
6
7
8
9
10
A
B
10 cm

Appendix 1. Analysis of covariance among weights of different prey, with transmitter weight as the covariate.

Source of Variance	d.f.	Sum of Squares	Mean Square	F-value	P
Equality of adjusted prey weight means	3	229.39	76.46	7.18	.000
Zero slope	1	3.91	3.91	0.37	.546
Error	79	840.79	10.64		
Equality of slopes	3	35.96	11.99	1.13	.342
Error	76	804.82	10.60		
Total	83	1074.08	12.94		

Contrasts		T-value	P
Species	CM+CF-PM-PF	4.584	.000
Sex	CM-CF+PM-PF	0.710	.480
Species x Sex	CM-CF-PM+PF	0.186	.853

Group Means:

Species	Prey weight (g)	Radio weight (g)	% Body weight
C. gapperi	24.31	2.46	10.1
P. maniculatus	21.07	2.47	11.7

Appendix 2: Scatter algorithm

Scatter was calculated as distance between successive observed coordinates per unit time. The random variation in the position coordinates was high relative to the actual distance travelled. To decrease this random variation (from now on called "bias"), position coordinates were averaged over several fixes, and the distance was measured between successive averages. The problem is to determine over what time interval or number of position coordinates to average the fixes.

Let

M = number of points to average

T = time between scans (seconds).

L = MT = length of time to average.

N = number of intervals in 10 minutes

(Xij,Yij) = position coordinate number i in interval number j; i = 1 to M, j = 1 to N.

M and L could not both be held constant, because the store frequency was not constant in the runs with the predator; T varied from one sec to several hours.

Let us assume the position at any one time is an unbiased estimate of the true position, and let

$$(\hat{X}ij,\hat{Y}ij) = (Xij,Yij)+(Aij,Bij)$$

be measured position coordinate number i, in interval number j, where Aij and Bij are random variables which are

distributed as $N(0,V)$; $V = Var(Aij) = Var(Bij)$. Therefore the estimated mean position for interval j is

$$(\hat{\bar{X}}j, \hat{\bar{Y}}j) = \left(\sum_{i=1}^{M} \hat{X}ij/M, \sum_{i=1}^{M} \hat{Y}ij/M\right) = (\bar{X}j, \bar{Y}j)+(\bar{A}j, \bar{B}j)$$

$$= \left(\sum_{i=1}^{M} Xij/M, \sum_{i=1}^{M} Yij/M\right)+\left(\sum_{i=1}^{M} Aij/M, \sum_{i=1}^{M} Bij/M\right)$$

and the estimated distance travelled from interval j to j+1 is:

$$\hat{D}j = ((\hat{\bar{X}}j_{+1}-\hat{\bar{X}}j)**2+(\hat{\bar{Y}}j_{+1}-\hat{\bar{Y}}j)**2)**1/2$$

$$= ((\bar{X}j_{+1}-\bar{X}j+\bar{A}j_{+1}-\bar{A}j)**2+(\bar{Y}j_{+1}-\bar{Y}j+\bar{B}j_{+1}-\bar{B}j)**2)**1/2$$

$$= ((dXj+dAj)**2+(dYj+dBj)**2)**1/2$$

$$= (dXj**2+2dXjdAj+dAj**2+dYj**2+2dYjdBj+dBj**2)**1/2$$

where

$$dXj = \bar{X}j_{+1}-\bar{X}j \text{ and } dAj = \bar{A}j_{+1}-\bar{A}j, \text{ etc.}$$

If Dj is the true distance travelled, then

$$Dj = (dXj**2+dYj**2)**1/2.$$

Let

$$bDj = \hat{D}j-Dj = \text{the bias in the distance estimate}$$

$$Lj = \text{length of interval number j (in seconds).}$$

Therefore the estimated speed throughout the N intervals (10 minutes) is:

$$\hat{S} = (\text{total distance})/(\text{total time})$$

$$= \left(\sum_{j=1}^{N} \hat{D}j\right)/\left(\sum_{j=1}^{N} Lj\right)$$

$$= \left(\sum_{j=1}^{N} Dj\right)/\left(\sum_{j=1}^{N} Lj\right)+\left(\sum_{j=1}^{N} bDj\right)/\left(\sum_{j=1}^{N} Lj\right) = S+bS \qquad (1)$$

where

S = real speed

bS = bias in scatter.

We want to know how changes in T, M and L will affect bS, and how to choose M and L, such that: 1) the bias (bS) is constant with respect to the scan frequency and 2) M does not become very large. Eq. 1 does not simplify, so I simulated the behaviour of bD and bS by using a random number generator for dAj and dBj.

$$E(dAj) = E(\bar{A}j_{+1}) - E(\bar{A}j) = \sum_{i=1}^{M} E(Aij_{+1})/M - \sum_{i=1}^{M} E(Aij)/M = 0$$

$$Var(dAj) \doteq Var(\bar{A}j_{+1} - \bar{A}j) = Var(\bar{A}j_{+1}) + Var(\bar{A}j)$$

$$Var(\bar{A}j_{+1}) = Var(\bar{A}j) = Var\left(\sum_{i=1}^{M} Aij/M\right) = \sum_{i=1}^{M} Var(Aij)/M^2 = V/M$$

I assumed that Aij and Bij for successive coordinate points are all independent. Therefore

$$Var(dAj) = 2V/M$$

and dAj and dBj are distributed as N(0,2V/M).

For the simulation, I used V=1.5, which gives ±2.4 grid units as 95% confidence intervals for each coordinate point.

The maximum mean speed any animal travelled, over 10 minutes, was about .12 grid units per sec, which corresponds to a distance of 7.2 units during time intervals of 60 sec length. Fig A shows a graph of bD against Dj. Note that the bias is greatest at zero speeds, and quickly drops. Therefore I used Dj = 0 to simulate the action of dS. I tested several tactics for determing M and L.

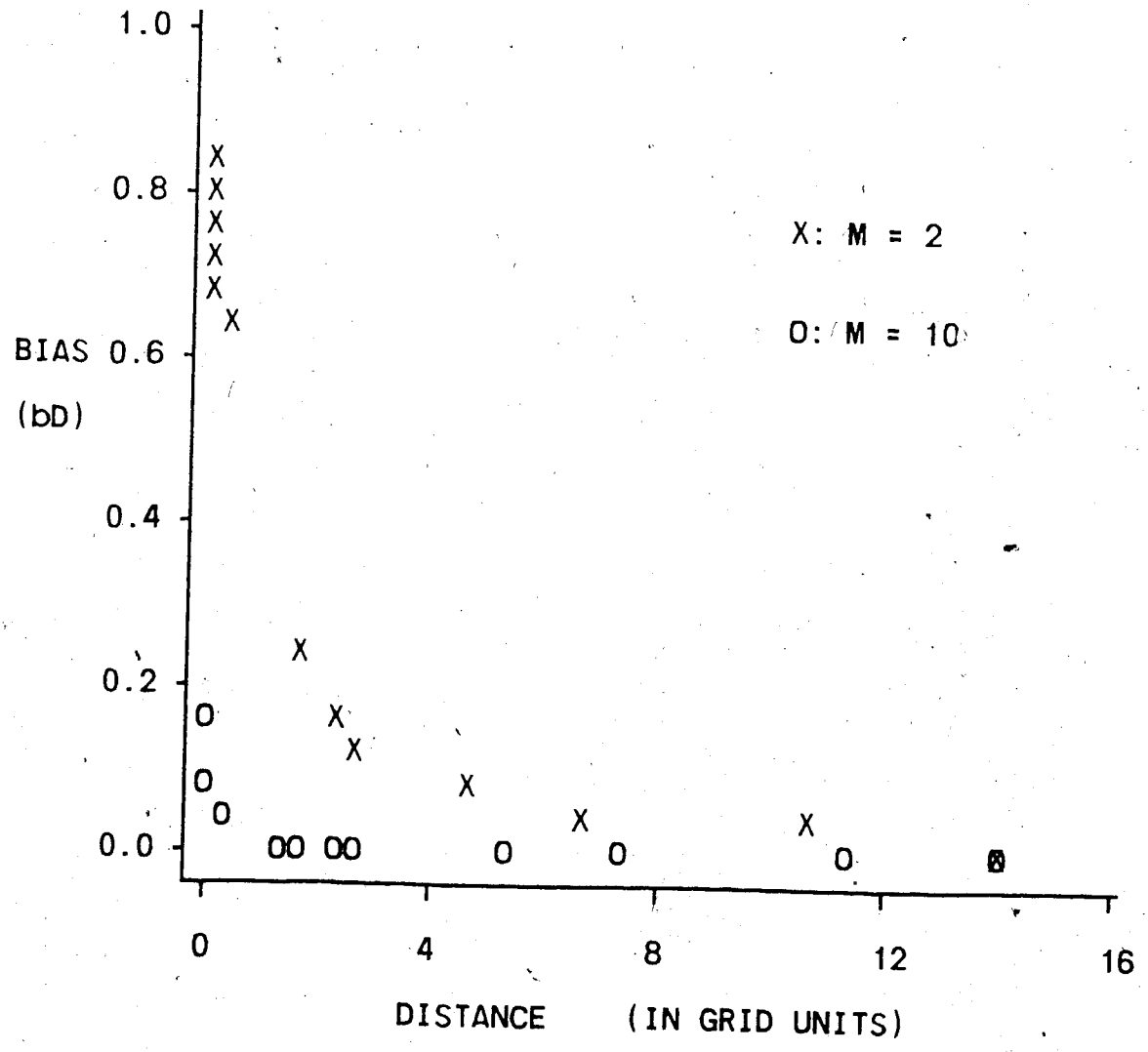


Fig. A. Simulation of bias component of distance estimate.

T (sec)	M	L (sec)	bS (grid units per sec)
Tactic 1			
1	5	5	.050
20	5	100	.00013
Tactic 2			
1	60	60	.00011
20	3	60	.00042
Tactic 3			
1	25	25	.0011
20	3.3	66	.00035

Tactic 1. Keep M constant, and let L vary with T. bS is large for T = 1, and changes by a factor of 300 between T = 1 and T = 20.

Tactic 2. Keep L constant and let M vary with T. bS is small, and changes by a factor of 4 between T = 1 and T = 20, but at T = 1, M = 60.

Tactic 3. It appears that the bias is strongly inversely related to L, so we want a way of keeping L from varying a lot, but also not letting M get very large. I chose L(M**1/2) = K; where K is a constant. I used K = 120. The bias is small, varies by a factor of 3 (which is less than either Tactic 1 or 2) between T = 1 and T = 20, and an M of 25 is smaller than the 60 which tactic 1 resulted in. I used this function to calculate the scatter.

The L's for each interval were calculated from the M and T of the previous interval, and eq. 1 was used to find the scatter.

Appendix 3. Position coordinates for MM and MI approaches occurring on August 24, 1979, between male ermine and female P. maniculatus and between ermine and male P. maniculatus, respectively. Approaches are underlined. Blank spaces mean the position has not changed since the last one recorded.

Time	Ermine	Prey			
	Male	CM	PF	PM	CF (dead)
031104			8 8		20 19
031119	13 11		4 9		20 19
031134	13 11		4 9		19 6
031149	13 11		4 8		19 3
031204			4 7		14 19
031219			5 6		19 19
031234	13 15		4 7		11 3
031249	13 11		5 8		20 17
031304	13 11		5 9	8 16	20 19
031319	13 11		4 9	8 15	19 3
031334	13 11		5 10	8 15	20 19
031349	13 11		4 10		20 3
031404	13 11		2 10		11 3
031419	13 11		2 11		20 6
031434	13 11		2 11		7 19
031439	13 11		3 11		12 11
031440	13 11				12 19
031452	12 11	8 3			11 11
031453	13 11	8 2	3 14		10 6
031408	12 11	8 2	13 11		11 6
031509	12 10		3 11		12 11
031510			2 11	8 16	12 6
031525	13 10		1 11	8 15	19 3
031527			3 11	8 16	12 11
031528			2 11	8 15	11 3
031543	12 10		4 11	8 15	12 3
031548	12 10				13 11
031549	13 11				13 3

Time	Ermine	Prey			
	Male	CM	PF	PM	CF (dead)
031504	10 11		5 11		19 11
031605		8 3	5 11		12 11
031606		8 2	4 11		12 11
031607	10 10	8 11	5 11	8 16	20 11
031608	12 11	8 3	4 11		12 11
031609	10 10	8 2	3 11		12 11
031610	13 10		4 11		13 13
031611	10 11	8 3			11 11
031612	8 10	8 2	4 11	8 15	12 11
031613	10 11	8 3	4 13	8 16	10 11
031614			4 13	8 15	19 3
031629	8 13	8 2	4 12	8 15	20 19
031630	8 12	8 3	6 12		20 18
031631		8 2	6 12		13 19
031632		8 3	6 13		11 19
031633	7 14		7 12		
031634					19 19
031636	6 14				12 19
031641	7 15	8 6			20 6
031642	6 15	8 2	6 12	8 16	18 19
031643		7 2	6 13		8 3
031658	2 17	8 2	9 13	8 15	11 19
031711	12 19	8 2	8 10	8 15	11 19
031712		8 2	10 9		19 19
031727	1 19	8 2	10 7		13 20
031742	0 19	8 2	9 6		10 6
031757	9 19	7 2	9 6	8 16	9 8
031812	0 19	8 3	9 19	8 15	9 6
031814	12 19	10 3	9 7		11 19

Position coordinates for MA approach occurring on August 26, 1979, between male ermine and female *C. gapperi* Data are for period when prey moving, then for when it stops, to show how random scatter decreases.

Time	Ermine	Prey							
	Male	CF		PF (dead)		CM (dead)		PM (dead)	
215543	5 8	3	7						
215544		3	15			13	2	5	9
215545		19	13	12	6	1	1	4	9
215546		12	13	13	5	12	1	4	9
215547		3	11	13	6	2	1	5	9
215550		3	15	13	5	1	2	4	9
215559		20	11	12	7	1	2	4	9
215600		2	11	12	5			4	8
215605		20	11	11	5			5	9
215608		2	11	12	4				
215623		1	11	10	6			5	2
215638		0	11	11	7	0	1	6	1
215653		19	10	10	7	1	1	1	1
215708		13	8	10	7	1	1	102	
215723		0	7			1	2	12	2
215738		1	7			1	2	15	2
215753		1	6					1	2
215808		2	6	11	6	0	2	20	2
215823		2	6	13	6	1	2	1	2
215838		2	5	15	5	1	2	1	2
215839		3	6						
215841				16	4				
215849		4	5					19	2
215852				16	5			1	2
215853				16	4				
215854		4	5						
215857								1	2
215858				16	4				
215859								19	13
215900								19	2
215901								1	2
215902		5	5	17	7			18	2
215905				16	4			1	2
215920		5	3	17	3			1	2
215935		6	3	18	3				
215950		8	2	19	2			19	2

Female C. gapperi now stationary. Random scatter is quite high, indicating that animal is active.

Time	Ermine	Prey									
	Male	CF		PF (dead)		CM (dead)		PM (dead)			
220629		7	3	14	15			1	16		
220630		20	3								
220631				14	14						
220632		19	3	15	14						
220633	0 2	7	3	14	14						
220634		13	2	15	14						
220635	1 2	13	3					1	15		
220636		13	3	15	15			1	16		
220637	2 3	12	3	15	14			1	16		
220638		20	3	14	14						
220639	2 4	12	3								
220633	1 3	2	3	15	14			1	1		
220644		20	3					1	16		
220645		7	3								
220646	2 4	20	3								
220647								1	3		
220651	2 3	11	3	15	14			1	1		
220652	2 4	19	3					1	15		
220707	3 4	20	3	14	14	1	0	1	16		
220713	5 2	7	3	15	15	1	1	1	16		
220717	12 1	12	3	14	14						
220722	5 2	7	3	14	15	1	1				
220732	6 2	7	3	15	14						
220734	6 1			14	14	1	0				
220736	7 2	8	3	14	14	1	1	1	16		
220740	7 1	7	3					1	1		
220749	11 1	12	3	15	15	1	1	1	1		
220754	13 1	12	3	15	14			1	16		
220803	16 2	17	3	16	14			1	14		
220806	18 1	20	2	15	14						
220807	19 1	19	3	16	14						
220810		19	2					8	14		

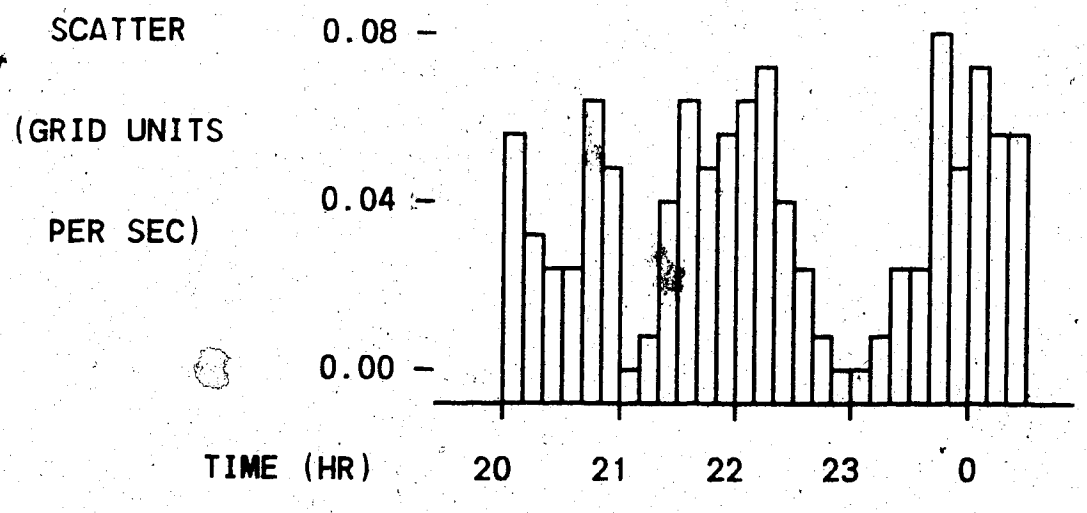
MA approach occurs at underlined time. Random scatter lower than at previous time.

Time	Ermine	Prey							
	Male	CF		PF (dead)		CM (dead)		PM (dead)	
221836	17	15	7	3	17	15			
221837					17	15		1	1
221838					17	14		1	13
221839	17	14			17	15		1	14
221840	17	15							
221841	17	13	7	3				1	13
221842			19	3	17	14		1	1
221843			20	3					
221844	17	15	7	3	17	14		1	14
221845	17	13			17	14		1	12
221853	17	13	7	3	17	14			
221854					17	15			
221857	18	13			17	14		1	15
221900	19	11			17	11			
221910	18	10			17	11		1	15
221911	18	10	20	3				1	15
221912	18	11	19	3				1	16
221913			20	3				1	16
221915	18	10						1	16
221919	17	13	7	3	17	11		5	16
221921	18	10	20	3				1	16
221923	18	11			17	11			
221926			7	3				1	17
221928	18	6			17	8			
221930	18	8	7	3	17	8			
221942	18	6						1	17
221943	20	5	20	3	17	15			
221958	11	4	20	3	17	14		1	18
222008	8	1	7	3	17	15		1	18
222009					17	1		1	18
222010	7	1			17	14			
222011					17	15			
222016	3	1	7	3	17	8			
222017					17	14	1 0		
222018	2	4			17	15	1 1		
222019	2	1					1 0		
222020	1	1			17	14	1 1	3	18
222022								1	1
222023					17	15			

Very low random scatter, indicating that female C. gapperi is inactive.

Time	Ermine	Prey			
	Male	CF	PF (dead)	CM (dead)	PM (dead)
222358	6 8	7 3			
222359	7 9	20 2	17 14		
222401	6 8	19 3	17 15		6 7
222402		7 3			5 7
222403			17 8		
222404					5 7
222405					6 7
222406	6 8				5 7
222407	6 8	7 3	17 14		
222408			17 14		6 7
222409			17 8		5 7
222410	6 7		17 14		6 7
222411	7 8		17 15		5 7
222412			17 14		6 7
222413			17 8		5 7
222415	8 8				
222416	7 8		17 14		6 7
222417					5 7
222418			17 15		
222419	7 9		17 14		4 7
222420	7 8		17 17		5 7
222421	6 8		17 15		
222422			17 14		
222423	7 8		17 8		
222424	6 8				
222425	7 8				6 7
222426					
222428	6 8		17 8		7 7
222429	6 6				6 7
222430	5 7	20 3			5 7
222431		7 3	17 14		
222432			17 7		
222433			17 15		
222435	6 7		17 15		5 7
222436	5 7	7 3	17 7		
222440	6 6		17 8		

Estimated scatter for same time period as previous position data.



Appendix 4. Friedman 2-way ANOVA, adjusted for missing data

The Freidman 2-way ANOVA tests the null hypothesis that the order of K objects, replicated N times, is random. However, this test is not valid with missing data. The derivation for the Friedman test[1] will be given first, then the calculations for missing data.

Let

Rij = rank of object j in replicate i.

$R.j = \sum_{j=1}^{K} Rij$ = rank total of object j, over all K replicates.

C = correlation between any pair of rank totals.

R.j are distributed as N(E(R.j),Var(R.j)). Under the null hypothesis,

$$E(R.j) = \left(\sum_{j=1}^{K} R.j \right)/K$$

and

$$(1/(1-C))\left(\sum_{j=1}^{K} (R.j-E(R.j))^2/Var(R.j) \right) \qquad (1)$$

is distributed as chi-square with K-1 degrees of freedom. This equation can be reduced to the Friedman equation. However, with missing and tied data, the variances, expected

---

[1] The derivation for the Friedman 2-way ANOVA is from Marascuilo and McSweeney, 1977.

values, and covariances, have to be calculated separately. Let

Ki = number of objects to be ranked in replicate i

Mi = (Ki+1)/2 = mean rank in replicate i.

Nj = number of replicates which have objects j present.

NjK = number of replicates which have both objects j and k present.

Then

$$E(R.j) = E\left(\sum_{i=1}^{Nj} Rij\right) = \sum_{i=1}^{Nj} E(Rij) = \sum_{i=1}^{Nj} (Ki+1)/2$$

$$Var(R.j) = Var\left(\sum_{i=1}^{Nj} Rij\right) = \sum_{i=1}^{Nj} Var(Rij)$$

$$= \sum_{i=1}^{Nj} \left(\sum_{j=1}^{Ki} (Rij-E(Rij))^2/Ki \right) \qquad (2)$$

(from variance of discrete random variable)

$$Cov(R.j,R.k) = \sum_{i=1}^{NjK} Cov(Rij,Rik)$$

$$= \sum_{i=1}^{NjK} \left(\sum_{\substack{n=1 \\ n\neq m}}^{Kj} \sum_{m=1}^{Kj} (Rin-Mi)(Rim-Mi) \right)/(Kj|2)$$

$$= \sum_{i=1}^{Nij} \left(\sum_{\substack{n=1 \\ n\neq m}}^{Kj} \sum_{m=1}^{Kj} (RinRim)-(Kj|2)Mi^2 \right)/(Kj|2) \qquad (3)$$

(where (Kj|2) = Kj choose 2 = number of pairs of Rin,Rim with n = m)

These values are calculated, and under the null hypothesis, the variables (R.j-E(R.j)) are multinormally

distributed with zero means and unequal correlations. If the correlations were equal, equation 1 could be used. The K x K variance-covariance matrix (S) will have a rank of K-1. Therefore, a transformation of these variables to the principle component space will result in K-1 independently distributed variates, Xj, where Xj are distributed as N(0,Vj); Vj = eigen value number j of S. If Q is the matrix of the K-1 eigen vectors of S, and (R-E) is the vector of Rj-E(Rj), then

$$Q'(R-E) = X$$

where X is the K-1 vector of the Xj's. Therefore

$$\sum_{j=1}^{K-1} Xj^2/Vj \qquad (4)$$

is distributed as chi-square with K-1 degrees of freedom.

Suppose that we want to test for differences between linear combinations of Rj's - e.g. a nonrandom order between prey species. Then we need to find the variances and covariances of the linear combinations. For example, let (R1+R2) = T1 & (R3+R4)=T2 be two such linear combinations. Therefore

$$E(T1) = E(R1+R2) = E(R1)+E(R2)$$

$$Var(T1) = Var(R1+R2) = Var(R1)+Var(R2)+2Covar(R1,R2)$$

$$Cov(T1,T2) = Cov(R1+R2,R3+R4)$$

$$= Cov(R1,R3)+Cov(R1,R4)+Cov(R2,R3)+Cov(R2,R4)$$

$$C = Cov(T1,T2)/((Var(T1)Var(T2))**1/2$$

and

$$(1/(1-C))((T1-E(T1))^2/Var(T1)+(T2-E(T2))^2/Var(T2))$$

is distributed as chi-square with 1 degree of freedom.

For an overall significance level of P, use a level of P/M; M = number of planned comparisons (the Bonferroni inequality).

If the initial null hypothesis is rejected, then suppose we want to see if the non-random order is different for two blocks of replicates - e.g. whether the two weasel sexes select differently.

Let

Nj1 = number of replicates in group 1

Rj1 = Rj1/Nj1 = rank mean for object i, for replicates of group 1.

E(Rj1) = E(Rj1)/Nj1 = estimated expected value of Rj1 under the initial null hypothesis of an overall random order.

Dj1 = Rj1-E(Rj1) = deviation of object j in group 1 from the expected value under the randomness null hypothesis.

Use similar definitions for group 2.

Therefore the null hypothesis is that Dj1 = Dj2 for all j = 1 to K. (Dj1-Dj2) is distributed as N(0,Var(Dj1-Dj2)) where

$$Var(Dj1-Dj2) = Var(Dj1)+Var(Dj2)$$

$$Var(Dj1) = Var(Rj1) = Var(Rj1)/Nj1^2$$

which is estimated as in eq. 2.

$$Cov(Dj1-Dj2,Dk1-Dk2) = Cov(Dj1,Dk1)+Cov(Dj2+Dk2)$$

$$Cov(Dj1,DK1) = Cov(Rj1,Rk1) = Cov(Rj1,Rk1)/(Nj1Nk1)$$

and the covariance of the rank totals is calculated as in eq. 3. The (Dj1-Dj2) are distributed multinormally, and to test for the null hypothesis, that E(Dj1-Dj2) = 0 for all j, transform these variables, as explained above, and use eq. 4.

Appendix 5. Breakdown of numbers of approaches and fate of prey in enclosure trials. Type A trials were run with 4 original prey only, whereas Type B trials had new prey introduced when animals were captured. Only original prey are counted for Type B trials..

	Type A	Type B	Total
Number of Trials	17	5	22
Number of Approaches	163	11	174
Number Lost	9	5	14
Total Number Captures	48	15	63
Number Useable Captures (time or approach type known)	46	6	52
Number Prey Recovered (# consumed:# not consumed)	36 (26:10)	5 (2:3)	41 (28:13)
Number Prey Not Captured	11	0	11
Total Number Prey Used	68	20	88

Appendix 6. Order in which prey were captured.

Male Ermine

Trial #	Prey Types				Var	Covar
	CM	CF	PM	PF		
16	1	3	2	4	1.25	-0.417
18	1	3	2	4	1.25	-0.417
20	1	3	2	4	1.25	-0.417
28	2	1	3.5	3.5	1.125	-0.375
29	1.5	4	1.5	3	1.125	-0.375
10	1	3	3	3	0.75	-0.250
26	1	-	3	2	0.667	-0.333
8	2	-	1	3	0.667	-0.333
22	1	-	2	3	0.667	-0.333
23	1	2.5	-	2.5	0.500	-0.250
24	-	2.5	1	2.5	0.500	-0.250
13	-	2	1	-	0.250	-0.250
Rank Total	12.5	24.0	22.0	34.5		
Expected Total	23.0	20.5	24.5	25.0		

Variance-covariance matrix

CM	CF	PM	PF	
9.20	-2.510	-3.251	-3.510	CM
	8.000	-2.751	-2.751	CF
		9.500	-3.510	PM
			9.750	PF

Female Ermine

Trial #	Prey Types				Var	Covar
	CM	CF	PM	PF		
7	4	2	1	3	1.250	-0.417
25	2	1	3.5	3.5	1.125	-0.375
27	2	1	3.5	3.5	1.125	-0.375
12	2	1	3.5	3.5	1.125	-0.375
11	-	2	1	3	0.667	-0.333
17	2	1	-	3	0.667	-0.333
9	1	-	2	3	0.667	-0.333
15	3	1	-	2	0.667	-0.333
21	-	1	2.5	2.5	0.500	-0.250
Rank Totals	16	10	17	27		
Expected Totals	16	18	16	20		

Variance-covariance matrix

CM	CF	PM	PF	
6.630	-2.209	-1.875	-2.542	CM
	7.130	-2.125	-2.792	CF
		6.460	-2.459	PM
			7.790	PF

Appendix 7. Modified Friedman 2-way ANOVA: Male versus female predator - order of capture of prey types.

	Prey Type			
	CM	CF	PM	PF
Djm-Djf	-1.050	1.389	-0.261	0.086

Variance-covariance matrix

CM	CF	PM	PF	
.228	-.0673	-.0678	-.0723	CM
	.210	-.0657	-.0666	CF
		.210	-.0680	PM
			.177	PF

$X^2 = 10.99$ d.f.=3 $P<0.025$

Appendix 8. Modified Friedman 2-way ANOVA: Capture order between all prey types - adjusted for unequal number of male and female predator replicates.

	Prey Type			
	CM	CF	PM	PF
Adjusted Mean Observed - Expected (=Djm+Djf)(see App. 4)	-1.050	-0.611	0.006	1.641

The variance-covariance matrix is the same as for Djm-Djf (Appendix 6)

$X^2 = 15.66$ d.f.=3 $P<0.005$

Planned Comparisons			O-E		Var		Cov	X^2	P
	1	2	1	2	1	2			
Species	CM+CF	PM+PF	-1.66	1.65	.303	.251	-.272	10.02	<0.005
Sex	CM+PM	CF+PF	-1.04	1.03	.303	.254	-.273	3.93	<0.05
Sex x Species	CF+PM	CM+PF	-0.61	0.59	.289	.260	-.270	1.41	>0.10

Appendix 9. Number of approaches, for all approach types, prey types, and predator sexes. Expected values were calculated (see Section 3.2.2) among all prey types for each combination of approach type and predator sex.

Prey Species	Prey Sex	Predator Sex	Approach Type										Subtotal		Total	
			IM		AM		MM		MA		MI					
			O	E	O	E	O	E	O	E	O	E	O	E	O	E
C. gapperi	male	male	1	1.08	5	4.42	1	0.83	3	2.67	7	3.33	17	12.33	27	22.0
		female	0	1.00	1	0.75	0	0.00	5	4.34	4	3.58	10	9.67		
C. gapperi	female	male	6	5.08	7	3.08	2	2.00	8	7.83	7	7.34	30	25.33	42	33.0
		female	0	0.00	4	1.92	0	0.00	2	2.83	6	2.92	12	7.67		
P. maniculatus	male	male	8	7.42	0	5.75	2	3.34	5	3.83	7	9.00	22	29.34	35	42.5
		female	4	3.00	0	0.91	0	0.00	5	6.00	4	3.25	13	13.16		
P. maniculatus	female	male	8	9.42	9	7.75	5	3.83	9	10.67	14	15.33	45	47.00	70	76.5
		female	4	4.00	4	5.42	0	0.00	12	10.83	5	9.25	25	29.50		
Subtotal		male	23		21		10		25		35		114		174	
		female	8		9		0		24		19		60			
Total			31		30		10		49		53		174			

Appendix 10. Number of approaches before capture, for all prey types.

Trial #	Prey Types				Total
	CM	CF	PM	PF	
Male Predator					
1	-	-	1	1	2
10	3	9	2	5	19
16	3	1	1	1	6
18	1	3	4	8	16
20	1	3	1	1	6
22	1	-	1	6	8
24	-	-	1	6	7
26	1	-	6	8	15
28	5	1	1	7	14
29	1	11	2	2	16
Female Predator					
7	-	1	1	2	4
11	-	3	1	5	9
17	1	1	-	3	5
21	-	1	-	3	4
23	1	3	1	1	6
25	2	1	1	1	5
27	3	1	8	9	21

- no data

Appendix 11. Modified Friedman 2-way ANOVA: Male versus female predator - number of approaches before capture among all prey types (see App. 10)

	Prey Type			
	CM	CF	PM	PF
Djm-Djf	-0.438	-0.569	-0.044	-0.016

Variance-covariance matrix

CM	CF	PM	PF	
.2930	-.0851	-.0829	-.0787	CM
	.2552	-.0814	-.0794	CF
		.2339	-.0789	PM
			.1722	PF

$X^2 = 0.92$ d.f.=3 P>0.50

Appendix 12. Number of captures for each approach type and prey type.

Species	Sex	Approach types					Total
		IM	AM	MM	MA	MI	
C. gapperi	male	0	2	0	5	9	16
C. gapperi	female	0	4	0	3	6	13
P. maniculatus	male	4	0	0	1	7	12
P. maniculatus	female	0	2	1	3	5	11
Total		4	8	1	12	27	52

Appendix 13. Results from preference experiment. The times are in units of distance on the recorder chart.

Weasel	Trial #	Prey Type				Time to Choose	Time to Kill Once Chosen
		CM	CF	PM	PF		
Laila	1	-	C	N	-	-	-
	4	-	N	-	C	16.2	1.0
	8	-	N	C	-	9.3	0.5
	11	X	-	X	-	-	-
	14	-	C	N	-	19.4	0.2
	18	N	-	C	-	5.2	1.4
	22	-	C	N	-	14.0	1.1
	24	-	C	N	-	11.6	0.0
	28	C	-	N	-	15.4	1.2
	32	N	-	C	-	8.5	0.5
	36	-	C	-	N	17.9	0.8
	38	-	C	N	-	45.6	1.1
Zeltite	5	-	N	C	-	-	-
	13	-	X	X	-	-	-
	16	-	N	C	-	9.9	5.6
	20	N	-	C	-	22.3	2.5
	23	-	N	C	-	11.4	0.0
	25	C	-	N	-	8.5	0.9
	29	N	-	-	C	8.3	0.0
	33	X	-	X	-	-	-
	35	-	X	-	X	-	-
Dainis	2	-	N	C	-	-	-
	6	-	C	-	N	5.5	0.0
	9	-	C	-	N	5.6	0.0
	12	N	-	C	-	-	0.4
	15	-	C	N	-	1.0	0.2
	19	C	-	N	-	1.9	0.2
	21	C	-	N	-	1.9	0.5
Oscar	3	N	-	C	-	-	-
	7	-	N	C	-	14.0	0.7
	10	N	-	C	-	17.1	1.0
	17	-	C	-	N	12.3	4.1
	26	-	C	N	-	14.3	0.0
	27	N	-	-	C	5.0	0.0
	30	N	-	C	-	9.7	1.9
	31	N	-	C	-	19.9	0.0
	34	-	N	-	C	23.3	0.1
	37	-	N	-	C	15.6	0.0

C = Prey type chosen; N = Not chosen; X = No choice made