Ecologie de *Mustela erminea* L.:

dynamique des composantes structurales, trophiques et parasitaires de deux populations.

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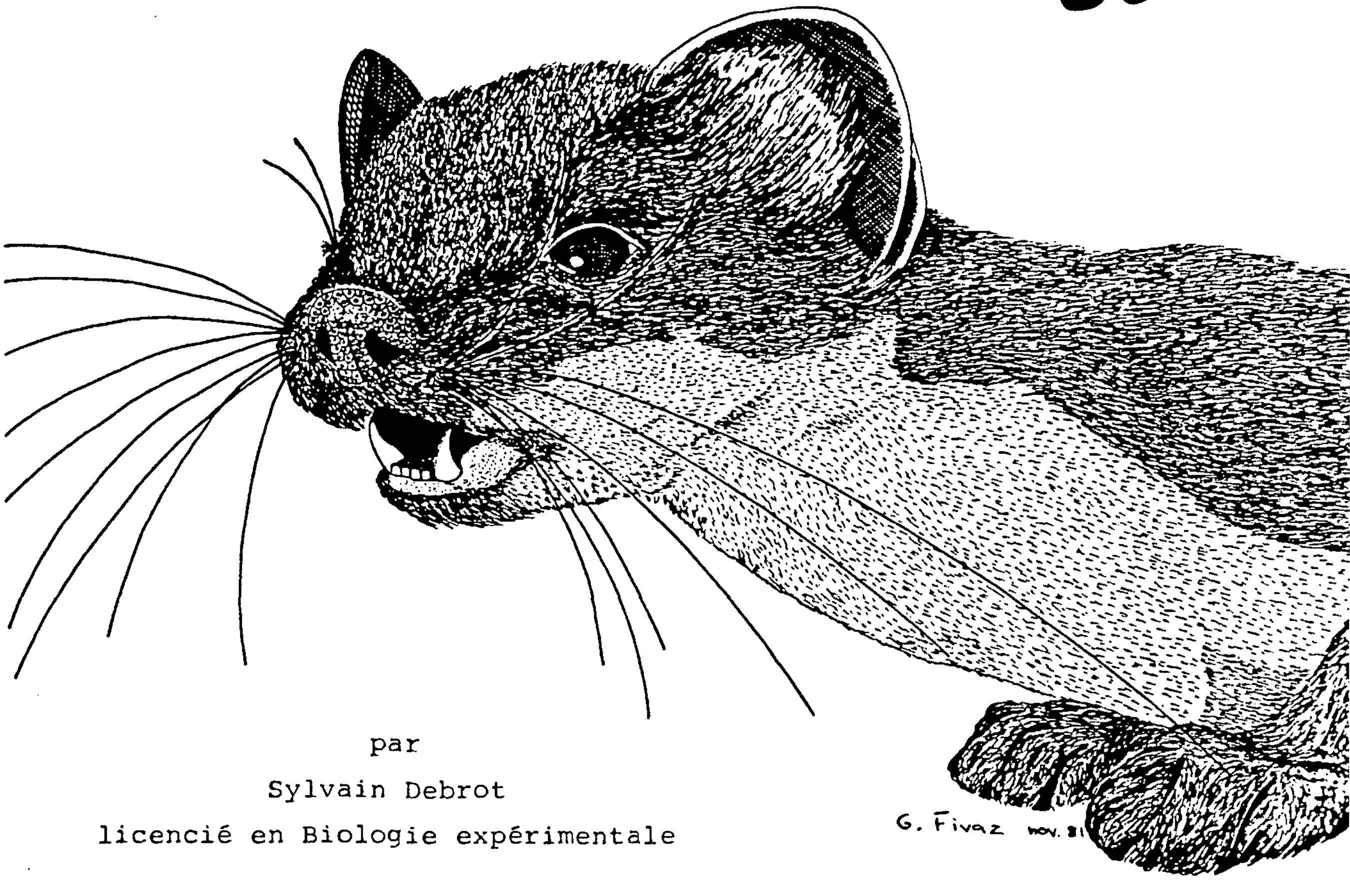

par
Sylvain Debrot
licencié en Biologie expérimentale

Thèse présentée à la Faculté des Sciences de l'Université de Neuchâtel pour obtenir le grade de docteur ès sciences.

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Ecologie de Mustela erminea L.: dynamique des composantes structurales, trophiques et parasitaires de deux populations

de M*onsieur Sylvain Debrot*

UNIVERSITÉ DE NEUCHATEL

FACULTÉ DES SCIENCES

La Faculté des sciences de l'Université de Neuchâtel, sur le rapport des membres du jury,

Messieurs C. Mermod, A. Aeschlimann, U. Rahm (Bâle) et S. Erlinge (Lund)

autorise l'impression de la présente thèse.

Neuchâtel, le *27 septembre 1985*

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Liste des publications de thèse

Note : le texte complet peut être consulté à la bibliothèque de l'Institut de Zoologie de l'Université , Le Mail, 2000 Neuchâtel.

Debrot, S. & C. Mermod. Morphométrie crânienne par radiographie. II: Application à une population d'hermines (*Mustela erminea* L.). Rev. suisse Zool. 85(4):738-744.

Debrot, S. 1981. Trophic relations between the stoat (*Mustela erminea*) and its prey, mainly the water vole (*Arvicola terrestris scherman*). Worldwide Furbearer Conference Proceedings, 3-11 août 1980, Frostburg, Maryland (J.A. Chapman & D. Pursley, eds), volume II: 1259-1289. R.R. Donnelley and Sons Co, Falls Church, Virginia.

Debrot, S. & C. Mermod. 1981. Cranial helminth parasites of the stoat and other mustelids in Switzerland. Worldwide Furbearer Conference Proceedings, 3-11 août 1980, Frostburg, Maryland (J.A. Chapman & D. Pursley, eds), volume II: 690-705. R. R. Donnelley and Sons Co, Falls Church, Virginia.

Debrot, S. & C. Mermod. 1982. Quelques Siphonaptères de Mustélidés, dont Rhadinopsylla pentacantha (Rothschild, 1897), nouvelle espèce pour la Suisse. Rev. suisse Zool. 89(1): 27-32.

Debrot, S. & C. Mermod. 1983. The spatial and temporal distribution pattern of the stoat (*Mustela erminea* L.). Oecologia 59: 69-73.

Debrot, S. 1983. Fluctuations de populations chez l'hermine (*Mustela erminea* L.). Mammalia 47(3) : 323-332.

Debrot, S.,J.-M. Weber, P. Marchesi & C. Mermod. In press. The day and night activity pattern of the stoat (*Mustela erminea* L.). Mammalia 49(1) : 14-17.

Debrot, S. Dynamique du renouvellement et structure d'âge d'une population d'hermines (*Mustela erminea*).Rev. Ecol. Terre Vie, vol. 39 : 78-88.

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DE GENÈVE

S. DEBROT et C. MERMOD

Morphométrie crânienne par radiographie. II: Application à une population d'hermines (Mustela erminea L.)

GENÈVE
IMPRIMERIE KUNDIG
DÉCEMBRE 1978

Revue suisse Zool.	Tome 85	Fasc. 4	p. 738-744	Genève, décembre 1978

S. Debrot et C. Mermod. — Morphométrie crânienne par radiographie. II: Application à une population d'hermines (*Mustela erminea* L.)[1].

Institut de Zoologie, Université de Neuchâtel.

ABSTRACT

Craniometry by radiography. II: Application to a stoat population (*Mustela erminea* L.). — As an application of a method of radiographical craniometry, 73 X-ray photographs of live stoats are measured. A statistical analysis permits the comparison of adults and juveniles of both sexes.

The difficulties in comparing a museum collection with live animals are discussed.

INTRODUCTION

Dans la première partie de cette étude (MERMOD & DEBROT 1978), nous avons examiné les avantages et les limites de l'utilisation de la radiographie en morphométrie. Nous nous proposons ici d'appliquer cette méthode à l'étude d'une population d'her-

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[1] Ce travail fait partie d'une thèse présentée par S. Debrot sous la direction du professeur C. Mermod. Il a été réalisé grâce à un subside du Fonds national suisse de la recherche scientifique (requête n° 3.685-076).

mines, cette approche devant nous permettre d'en comparer les caractéristiques avec celles décrites dans la littérature (VAN SOEST & VAN BREE 1970; PETROV 1956; REICHSTEIN 1956).

MATÉRIEL ET MÉTHODE

De décembre 1976 à octobre 1977, 73 hermines différentes ont été capturées dans la vallée de la Brévine (Jura neuchâtelois, Suisse). Chaque individu a été anesthésié par une injection intramusculaire, après une pré-narcose à l'éther, de 20 à 25 mg de Nembutal par kilogramme de poids corporel, puis radiographié en incidence dorso-ventrale. (Appareil Siemens NANODOR 1, temps de pose: 0,5 seconde à 18 mA et 60 kV).

L'âge est déterminé sur la base des radiographies, par la largeur relative de la cavité pulpaire des canines inférieures (ERLINGE 1977). Ce critère nous permet de séparer les individus nés au printemps (juvéniles) de ceux ayant plus d'un an d'âge (adultes). La planche I présente une radiographie de chaque classe d'âge pour les deux sexes.

La catégorie des juvéniles comprend des individus d'un âge allant jusqu'à 3 à 4 mois. Nous nous proposons ultérieurement d'examiner l'évolution des mensurations crâniennes chez les sub-adultes.

PROBLÈMES TECHNIQUES

Nous avons étudié précédemment (MERMOD & DEBROT 1978) l'influence des facteurs inhérents aux techniques radiologiques, sur les dimensions crâniennes apparentes. Lors de l'examen de matériel vivant, quelques facteurs supplémentaires doivent être pris en considération:

1) La distance film-crâne est légèrement augmentée par la présence de tissus mous (peau, muscles...). Mais la différence n'influence pas de manière sensible le facteur de correction *a'*, calculé pour les radiographies de crânes secs.
2) La disposition de l'animal sur le film est très importante pour l'horizontalité des plans de mesure. La narcose doit être suffisante pour assurer une parfaite décontraction de la musculature.
3) Le flou cinétique n'est pas négligeable non plus: même en anesthésie profonde, la respiration et les battements cardiaques peuvent diminuer la netteté de l'image. L'impact du flou cinétique sur les mensurations n'est malheureusement ni estimable par une méthode directe, ni prévisible par le calcul.

Les mensurations crâniennes, relevées sur les radiographies, ont été multipliées par les coefficients *a'* (MERMOD & DEBROT 1978).

RÉSULTATS

Les valeurs corrigées ont été analysées par âge et par sexe et résumées dans le tableau 1. Les différences entre les deux sexes sont toutes hautement significatives, tant pour les jeunes que pour les adultes.

Les différences entre adultes et juvéniles, pour chaque sexe, sont données dans le tableau, avec leur limite de signification.

TABLEAU 1

*Nombre (N), moyenne ($\bar{x}$), écart-type (s) et cœfficient de variation (CV) des paramètres mesurés. CB = longueur condylo-basale ; BZ = largeur bi-zygomatique ; Bc = largeur de la boîte crânienne ; Ma = largeur mastoïdienne ; Ro = largeur du rostre. Test-t de Student-Fisher : NS = non significatif ; * = différence significative pour α = 0,05 ; ** = idem pour α = 0,01 ; *** = idem pour α = 0,001*

Paramètre	sexe	âge	N	$\bar{X}$	s	CV
CB	♂♂	ad.	31	48,93	1,31	2,7
				**		
		juv.	12	47,69	0,88	1,8
	♀♀	ad.	21	44,09	1,12	2,5
				NS		
		juv.	9	43,66	0,86	2,0
BZ	♂♂	ad.	31	27,87	0,88	3,2
				***		
		juv.	12	26,54	0,86	3,2
	♀♀	ad.	21	24,29	0,67	2,8
				*		
		juv.	9	23,65	0,74	3,1
Bc	♂♂	ad.	31	21,91	0,69	3,1
				***		
		juv.	12	23,46	0,52	2,2
	♀♀	ad.	21	19,95	0,61	3,1
				***		
		juv.	9	21,80	0,58	2,7
Ma	♂♂	ad.	31	23,29	0,76	3,3
				***		
		juv.	12	22,16	0,74	3,3
	♀♀	ad.	21	20,78	0,77	3,7
				*		
		juv.	9	20,15	0,52	5,6
Ro	♂♂	ad.	31	9,70	0,44	4,5
				**		
		juv.	12	9,24	0,33	3,6
	♀♀	ad.	21	8,36	0,29	3,5
				NS		
		juv.	9	8,23	0,25	3,0

On remarquera que les dimensions moyennes des juvéniles sont toujours inférieures à celles des adultes, à l'exception de la largeur de la boîte crânienne. Cette particularité traduit l'allure piriforme des crânes des jeunes (planche 1). Nous l'illustrons par les histogrammes des figures 1 et 2.

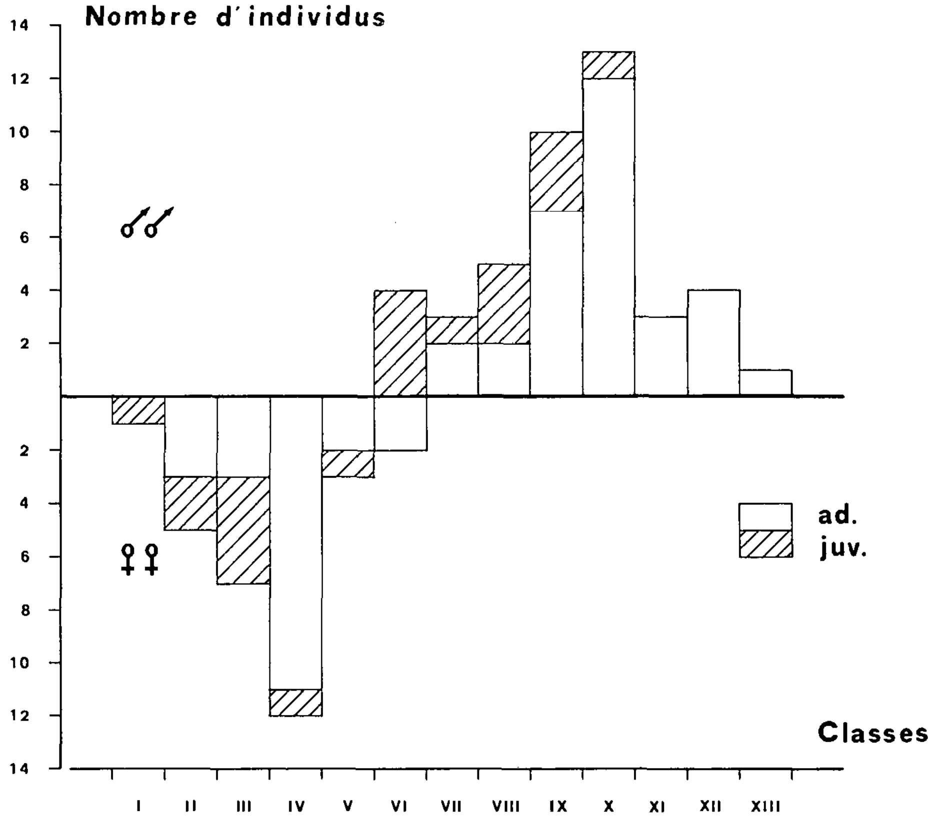


FIG. 1.

Histogramme de la répartition en classes de la largeur bi-zygomatique.
Classe I: 22,3-22,8 mm... classe XIII: 29,5-30,0 mm.

DISCUSSION

L'appréciation quantitative de la forme globuleuse des crânes de juvéniles est un des points intéressants qui ressort de l'analyse statistique des mensurations crâniennes. Ce caractère a déjà été observé et étudié par BUCHALCZYK & RUPRECHT (1977): la capacité de la boîte crânienne chez le Putois diminue aussi avec l'âge. Le rapport de la largeur de la boîte crânienne avec un autre des paramètres étudiés permet de distinguer efficacement les jeunes individus (DEBROT, non publié). L'examen des sub-adultes nous montrera s'il existe une relation directe entre Bc et l'âge.

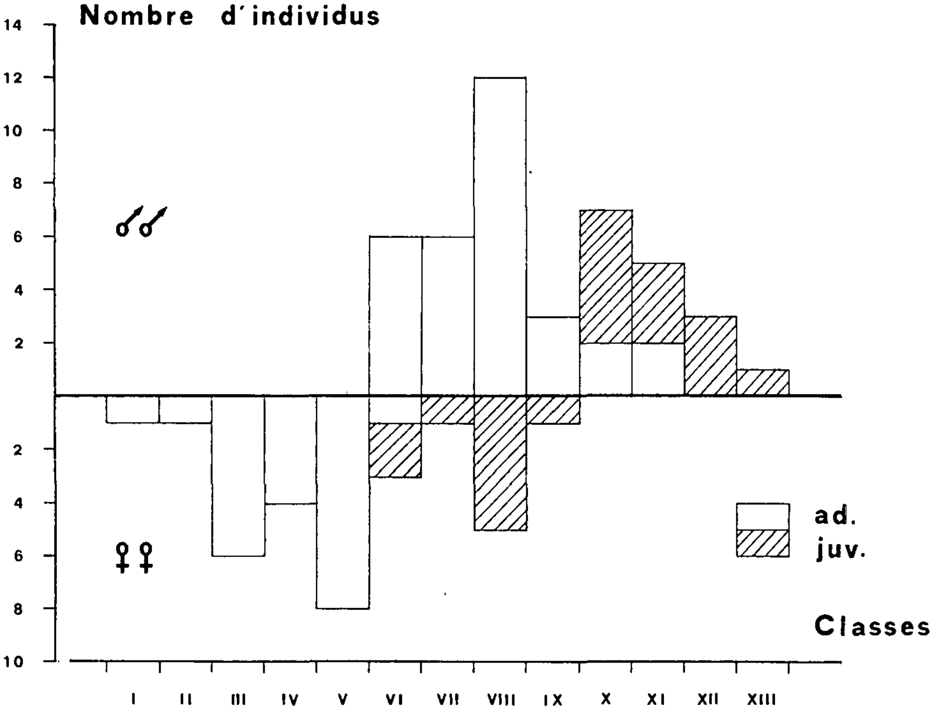


FIG. 2.

Histogramme de la répartition en classes de la largeur de la boîte crânienne. Classe I: 18,3-18,7 mm... classe XIII: 24,3-24,7 mm.

TABLEAU 2

Largeur bi-zygomatique illustrant la contraction de l'ossature sur les crânes secs

sexe	âge	Mesures sur crâne sec a: directe	 b: radiog.	Mesure sur cadavre c: radiographie	différence c-b
			(valeurs corrigées)		
♀	juv.	22,0	22,0	22,9	0,9
♀	juv.	22,0	22,1	23,1	1,0
♂	juv.	24,5	24,6	25,4	0,8
♂	juv.	26,9	27,0	27,8	0,8
♀	ad.	23,1	23,0	23,7	0,7
♀	ad.	23,9	23,8	24,6	0,8
♂	ad.	27,2	27,1	27,9	0,8
♂	ad.	27,2	27,2	27,9	0,7

La comparaison des mensurations crâniennes caractérisant une population d'animaux vivants avec une collection de musée peut être enrichissante à plus d'un titre (homogénéité de la population, variations locales et saisonnières de taille, races, sous-espèces, etc.). Mais elle doit être faite avec précaution: nous avons en effet remarqué, sur quelques individus morts dont le cadavre a été radiographié et dont nous avons ensuite préparé le crâne, que le séchage s'accompagne d'une contraction de l'ossature. Dans le tableau 2, nous présentons quelques exemples de la largeur BZ, qui est sujette à la plus forte réduction. La variation des dimensions n'étant pas identique pour chaque paramètre, nous n'avons pas une réduction homothétique du crâne. Ainsi il y aura lieu de calculer un facteur de contraction pour chaque mensuration.

CONCLUSIONS

La méthode que nous avons appliquée dans ce travail permet l'étude crâniométrique d'animaux rares ou protégés, comme le Putois, par exemple, dans notre canton, et de populations à faible densité (cas général des Carnivores). Elle se justifie également pour suivre l'évolution de la structure et de la forme du crâne en fonction de l'âge, sur un même individu.

Une radiographie présente aussi l'avantage de fournir plusieurs renseignements tels que: dimensions crâniennes, critères d'âge, lésions parasitaires, malformations éventuelles, etc.

La principale difficulté consiste à tenir compte de tous les facteurs, dépendants de la technique ou du matériel, pouvant modifier d'une manière significative les dimensions crâniennes sur une radiographie.

REMERCIEMENTS

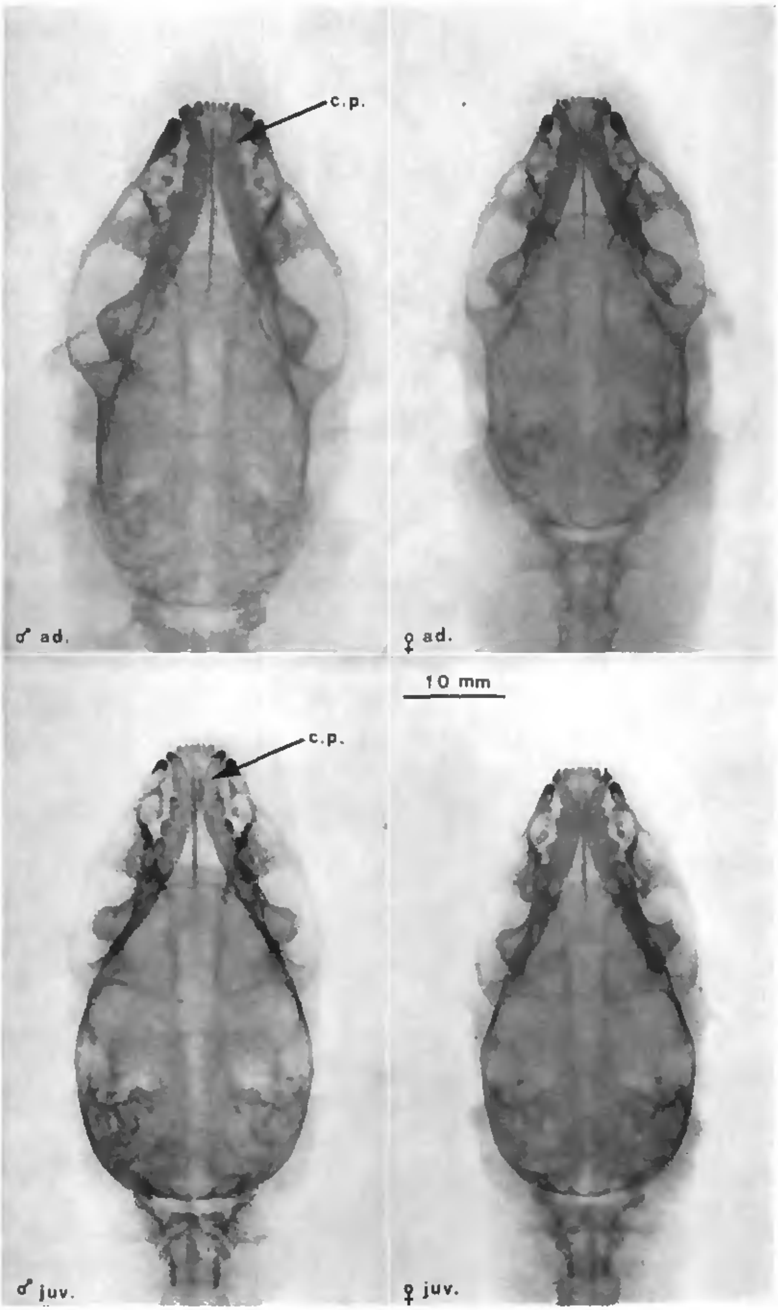
Nous adressons tous nos remerciements à notre assistant technique, Monsieur G. Fivaz, pour la composition des figures.

RÉSUMÉ

En application d'une méthode de crâniométrie sur matériel vivant, 73 radiographies d'hermines sont mesurées. Une analyse statistique permet de comparer les adultes et les juvéniles, pour les deux sexes. Les problèmes posés par la comparaison des crânes de collection et des radiographies d'animaux vivants sont discutés.

ZUSAMMENFASSUNG

Mit Hilfe einer Schädel-Messmethode an lebenden Tieren wurden 73 Röntgenaufnahmen von Hermelinen ausgemessen. Eine statistische Analyse erlaubt es, bei beiden Geschlechtern die Erwachsenen mit den Jungen zu vergleichen. Die Probleme des Vergleichs zwischen präparierten Schädeln und Röntgenaufnahmen lebender Tiere werden besprochen.



Radiographies de crânes d'hermines montrant la largeur de la cavité pulpaire (c.p.) et la forme de la boîte crânienne des adultes et des juvéniles.

BIBLIOGRAPHIE

BUCHALCZYK, T. and A. L. RUPRECHT. 1977. Skull variability of *Mustela putorius* Linnaeus, 1758. *Acta theriol.* 22: 87-120.

ERLINGE, S. 1977. Spacing strategy in stoat *Mustela erminea. Oikos* 28: 32-42.

MERMOD, C. et S. DEBROT. 1978. Morphométrie crânienne par radiographie. I: Problèmes techniques. *Revue suisse Zool.* 85: 730-738.

PETROV, O. V. 1956. Sexual dimorphism in the skull of *Mustela erminea.* L. *Vest. leningr. gos. Univ.* 1956 (15): *(Serie biol.)* (3): 41-46.
Traduction: KING, C. M. *1975. Biology of Mustelids, some Soviet research:* 55-78.

REICHSTEIN, H. 1956. Schädelvariabilität europäischer Mauswiesel *(Mustela nivalis* L.*)* und Hermeline *(Mustela erminea* L.*)* in Beziehung zu Verbreitung und Geschlecht. *Z. Säugetierk.* 22: 151-182.

VAN SOEST, R. W. M. and P. J. H. VAN BREE. 1970. Sex and age composition of a Stoat popullation *(Mustela erminea* Linnaeus, 1758*)* from a coastal dune region of the Netherlands. *Beaufortia* 17: 51-77.

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CRANIAL HELMINTH PARASITES OF THE STOAT AND OTHER MUSTELIDS IN SWITZERLAND[1]

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ABSTRACT: Mustelid populations, mainly stoats (Mustela erminea), were studied by mark-recapture in 2 areas of the Swiss Jura Mountains from the spring of 1977 to the spring of 1980. In the 1st area, the population had decreased since the summer of 1977, following a "crash" of the water vole (Arvicola terrestris scherman), their main food source. After the summer of 1977, their food habits diversified. The percentage prevalence of infection by Skrjabingylus nasicola increased from 4 - 50 percent. In the 2nd area, no rodent pullulation occurred, the stoat population remained stable, the diet was diversified and the prevalence of infection was 37 percent. S. nasicola has 1 intermediate host, a gastropod, and probably a paratenic host which must be a mollusc-eater. Arvicola, being exclusively herbivorous, cannot be the carrier. This explains the low prevalence of infection when stoats fed mainly on this species. The possible paratenic hosts found through analysis of the diet are other small rodents and birds. Shrews, found only 3 times in the scats, probably are not involved in transmission of the parasite. Troglotrema acutum eggs were found only in scats of polecats. Mixed infection of T. acutum and S. nasicola occurred in 3 of 4 captured polecats.

In western Europe, 2 helminths frequently infect the frontal sinuses of mustelids: Skrjabingylus nasicola (Nematoda: Metastrongyloidea, Skrjabingylidae) and Troglotrema acutum (Trematoda: Troglotrema, Troglotrematidae). The nematode has been reported as a parasite of several

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[1] This study is part of a Ph.D. thesis prepared by S. Debrot under the supervision of Prof. C. Mermod. Financial support was provided by the Swiss National Science Foundation, grant no. 3.685.76.

species of mustelids (Swales 1938, Dubnitskii 1956, Hansson 1968, Machida and Mikuriya 1968), and its distribution is cosmopolitan. The trematode probably has a distribution restricted to central Europe (van Soest et al. 1972), and has been less studied than S. nasicola. Other species of the genus Skrjabingylus have been described and studied (Duncan 1976); however, they do not have such a widespread distribution as nasicola.

Literature on this subject can be roughly separated into 3 categories. First, there are those in which the authors studied preserved or fresh skulls in order to describe the extent of infection and the damage caused by the parasite. Prevalences of infection are often compared in different species of mustelids, or in different areas or countries (Lavrov 1944, Dougherty and Hall 1955, Lewis 1967 and 1968, Hansson 1968 and 1970, van Soest et al. 1972, King 1977). The 2nd category includes research on the cycle and transmission of the parasites (Duncan 1976, Vogel and Voelker 1978). The 3rd group of papers includes research on the systematics and taxonomy of these helminths (Petrov 1928, Baer 1931, Hill 1939, Goble and Cook 1942, Sprehn 1955, Webster 1965, Marconcini and Tasselli 1969, van Soest et al. 1972). In the present research, the epizootiology of S. nasicola was studied in 2 populations of living mustelids (mainly stoats, Mustela erminea) and considered in relation with the population dynamics and the food pattern (Debrot 1981) of this host.

STUDY AREAS

There were 2 study areas in the Jura Mountains, Switzerland.

Brévine Area

The Brévine Valley, trapped since the spring of 1977, is situated at an altitude varying between 1,040 and 1,200 m. The trapping area (1,875 ha) includes pastures, wooded pastures and red spruce forests. Some remaining peat-bogs in the bottom of the valley and numerous stonewalls offer shelter to stoats (Figure 1a). The climate is rather severe for this latitude (47° N).

Val de Ruz Area

The Val de Ruz, trapped since the spring of 1978, is situated at the same latitude but the altitude is 670 - 740 m. This area (616 ha) includes cultivated fields, a brook and several little tributaries bordered with trees and bushes, and little mixed woodlands (Figure 1b). The climate is more temperate than in the Brévine Valley.

MATERIALS AND METHODS

Trapping

Mustelids were caught in wooden live-traps baited with white mice. Sixty traps were set during 4 day trapping sessions in an average density of 1 trap per 10 ha, and checked twice a day. The trapping effort was 6,693 trap-units (1 trap-unit means 1 trap set during 24 hr) in the Brévine area (from March 1977 - March 1980) and 4,952 trap-units in the Val de Ruz area (from April 1978 - May 1980).

Trapped mustelids were transferred to the laboratory where sex, external measurements and weight were recorded; animals were anesthetized (sodium pentobarbital, 20 - 25 mg/kg, intramuscular), and marked by ear-clipping (Twigg 1978). An X-ray of the skull was made in order to recognize 2 age classes (Mermod and Debrot 1978, Debrot and Mermod 1978): "juveniles" (born in the current year) and adults. After recovery, mustelids were released at the exact place of the capture; as a rule 24 hr later. When a marked animal was recaptured, it was examined, weighed and released immediately.

Parasites

Infection in trapped animals was determined by examination of fresh scats for 1st stage larvae of S. nasicola. However, because some stoats may have been infected with only 1 sex of S. nasicola (Hansson 1968) and, hence, not passing larvae, prevalence figures were minimal. Telemann's method (Golvan and Drouhet 1972) was used to search for eggs of other helminths, particularly T. acutum.

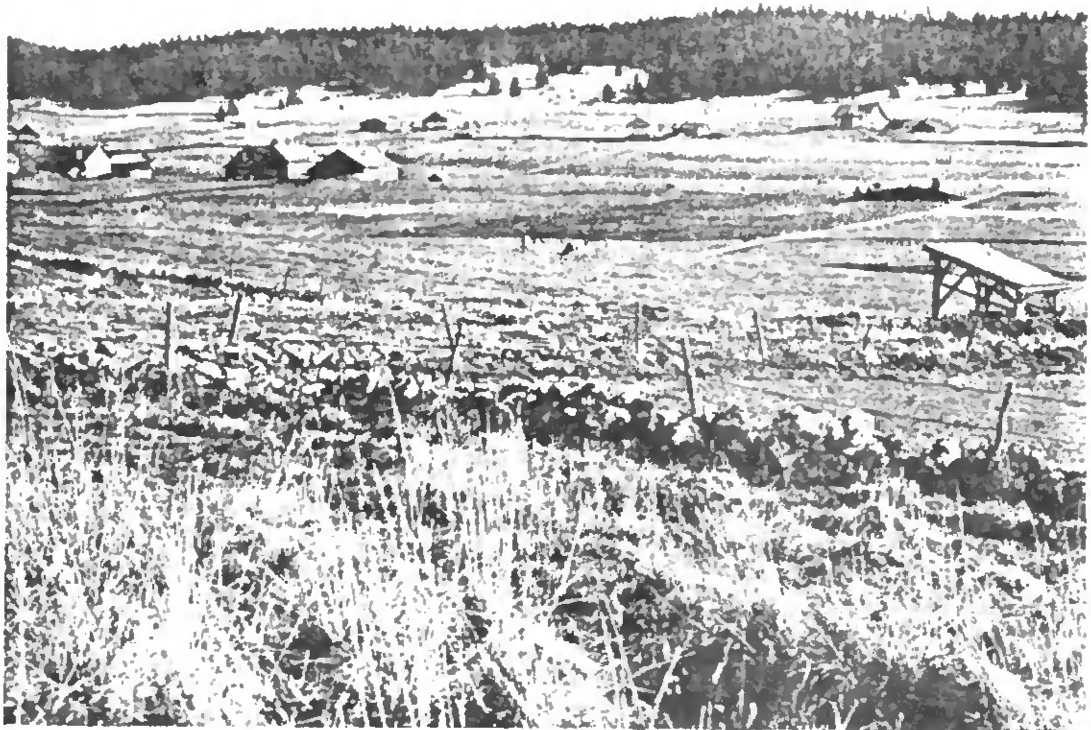

Figure 1a. (Top) Partial view of the Brévine study area. Figure 1b. (Bottom) Partial view of the Val de Ruz study area.

Analysis of the Data

Results are given by meterological seasons: spring (March - May), summer (June - August), fall (September - November) and winter (December - February). Following the example given in Table 1, a calendar of catches was established, based on all the captures and recaptures. It permits an estimation of the population present in the area even when no trapping sessions have been made. For instance, from the data in Table 1, it can be seen that 7 stoats, at least, were in the area in November 1979. So, the calendar of catches gives a good idea of the population fluctuations (Figure 2), however, it must be considered only as an index of abundance.

Statistical tests used to compare frequencies were the Fisher exact-probability-test (Siegel 1956) or, with large samples, the χ^2-test.

RESULTS

Captures and Prevalence of Infection

Brévine Area. In spring 1977, a trapping was made on a small area. Four stoats were caught. At the end of June 1977, the 1st main trapping session began. Numerous stoats were caught during the summer (Figure 2). In the fall, the number of catches diminished drastically, and remained very low until the spring of 1980.

Only 3 of 41 stoats had larvae of S. nasicola in the summer of 1977. The prevalences of infection, computed from the calendar of catches were found to be significantly different between the following seasons:

Summer 1977 - Fall 1977 ($p = 0.014$)
Summer 1977 - Summer 1978 ($p = 0.001$)
Summer 1977 - Fall 1978 ($p = 0.0002$)
Fall 1977 - Fall 1978 ($p = 0.0035$)
Winter 1977 - 1978 - Fall 1978 ($p = 0.048$)

The decrease of the population was corroborated by the scarcity of scats or snow tracks found in the area since the fall of 1977. A notable

Table 1. Partial example of the calendar of catches (Val de Ruz area).

Animal	Age	Weight (at 1st capture) (g)	1979									1980			
			Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
E38	ad	278	2I[a]												
E39	ad	271	1U[b]												
E40	ad	242	1U	---	---	---	---	---	---	---	---	---	---	---	1I[c]
E41	ad	205			1U										
E42	ad	153			1I	1I	---	---	---	---	1I	1I			
E43	juv	248				1U									
E44	juv	255					3U	---	1U	---	---	1U	---	---	1U
E45	juv	265					5U								
E46	juv	165					1U								
E47	juv	234					2U	1U	1U	---	---	1U	---	---	1U
E48	juv	175					1U	1U	---	---	---	---	---	---	1U
E49	juv	169					1U								
E50	juv	131					1U								
E51	ad	193					2I	2I	1I						
E52	juv	165					1U	1U							
E57	juv	158						3U	---	---	---	---	1U	1U	
E58	juv	223						1U	---	---	1I	---	1I[d]		
E59	juv	257						1I							

[a] Two captures as infected (I)

[b] One capture as uninfected (U)

[c] Capture outside the area

[d] Found killed by car

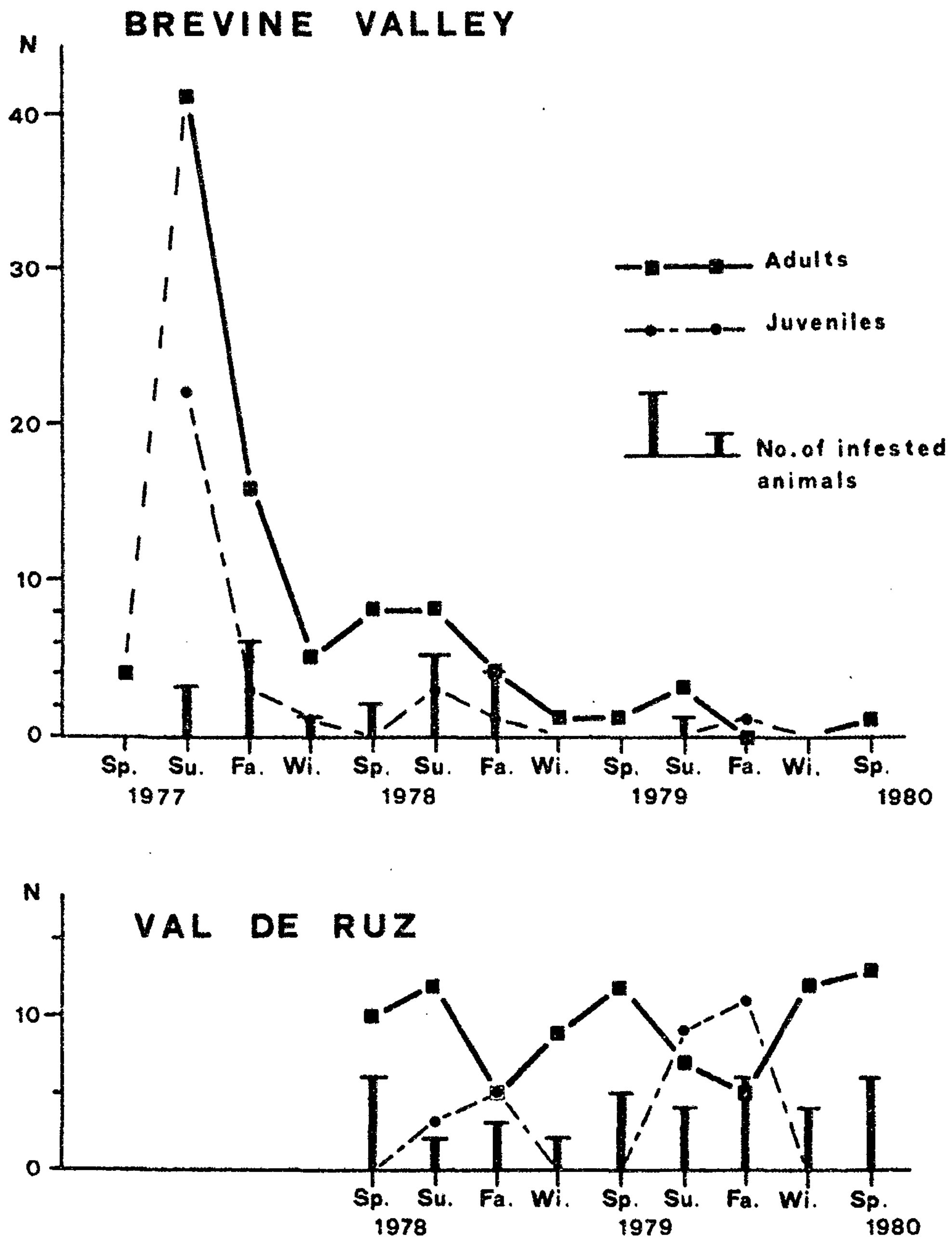

Figure 2. Summary of the changes in stoats numbers in the study areas, based on the "calendar of catches", and numbers of individuals infected by S. nasicola.

shift in the food habits of the stoats had been observed by Debrot (1980): until the spring of 1977, their diet was comprised almost entirely of the water vole (Arvicola terrestris scherman). From the summer of 1977 to the spring of 1978, this species decreased and the diet was more diversified (transition period, Table 2). Later on, the stoats fed mainly on "grey voles" of the genus *Microtus*, bank voles (*Clethrionomys glareolus*), woodmice (*Apodemus* sp.) and birds.

Table 2. Temporal relationships among food pattern, density of the stoat population and prevalence of infection by *S. nasicola*.

Seasons	Food Pattern[a]	Stoat Population	Prevalence of Infection
Fall 1976	*Arvicola*-dominated period	high density[b]	
Winter 1976 - 1977			
Spring 1977			low
Summer 1977	transition period	high density	
Fall 1977			increasing
Winter 1977 - 1978	*Microtus*-dominated period	decreasing phase	high
Spring 1978	transition period		
Summer 1978	*Microtus*-dominated period		
Fall 1978			
Winter 1978 - 1979			
Spring 1979		low density	
Summer 1979			
Fall 1979			
Winter 1979 - 1980			
Spring 1980			

[a] Data from Debrot (1981)

[b] As revealed by snow tracking and scats collecting

Val de Ruz Area. Seasonal captures were more evenly distributed in this area (Figure 2). The rate of adult infection was lowest in the summer of 1978 (17 percent) and highest in the fall of 1979 (80 percent). However, the only significant seasonal variation occurred during the summer of 1978 vs fall of 1979 samples ($p = 0.028$).

Five of 17 juveniles were infected: 1 female, caught for the 1st time on 24 October 1978; 1 male on 25 October 1978; and 2 males, 1 caught for the 1st time on 19 September 1979 and the other 7 days later, and 1 young male, uninfected at the 1st capture (25 September 1979) was infected at recapture on 5 December 1979.

Other mustelids were also captured in this area: 5 weasels (*Mustela nivalis*), 4 polecats (*Mustela putorius*), 1 pine marten (*Martes martes*) and 1 stone marten (*Martes foina*). One weasel, the pine marten and all 4 polecats were infected by *Skrjabingylus* sp.. *Troglotrema acutum* eggs were also detected in the scats of 3 polecats. To our knowledge, this is the 1st record of a mixed infection with these species in mustelids.

Analyses of the scats from the Val de Ruz area showed that the stoat diet was fairly diversified, and included more mice (*Apodemus* sp.) and birds than in the Brévine area. No *Arvicola* pullulation has occurred in this area for at least the past 10 yr.

Comparison Between Sexes and Ages

There was no significant difference in prevalence of infection between males and females or between adults and juveniles.

Comparison With Other Countries

Data from some countries were gathered from Vik (1955), Hansson (1970) and van Soest et al. (1972) and compared with the results of this study (Table 3). The prevalence of infection in the Brévine Valley during the spring and summer of 1977 was significantly lower ($p < 0.01$) than all other combinations.

Table 3. Summary of published prevalences of S. nasicola in stoats of some European countries.

Countries	Data	Data Source
Denmark	61/221 (28)[a]	Hansson 1970
England	14/ 46 (30)	van Soest et al. 1972
Finland	41/ 82 (50)	Hansson 1970
Netherlands	139/345 (40)	van Soest et al. 1972
Norway	26/ 88 (30)	Vik 1955
Sweden	159/386 (41)	Hansson 1970
Switzerland		
Brévine area[b]	2/ 55 (4)	
Brévine area[c]	18/ 36 (50)	
Val de Ruz area	24/ 65 (37)	
Σ Switzerland	44/156 (28)	

[a] Number infected/Number examined (percent infected)

[b] Period from the spring of 1977 to the summer of 1977

[c] Period from the fall of 1977 to the spring of 1980

Period of Infection

Eleven stoats, uninfected at 1st capture, were infected at recapture (Figure 3). Nine were adults when caught for the 1st time. According to Dubnitskii (1956) with Mustela vison and Hansson (1967) with M. nivalis and M. erminea, 1st stage larvae appear in the scats 18 - 25 days post-exposure. Using 25 days as a prepatent period, we estimate that the most favorable period for stoats to be invaded ranges from mid-June to mid-November.

Effects of the Parasites

Cranial X-rays made on anesthetized animals did not show obvious skull deformations. In about 1/2 of the cases, a light cranial asymmetry was found in the skull of 1st stage larvae distributors (i.e., animals with 1st stag larvae in scats). Some non-distributors also showed light asymmetries of their skull; it is possible that they were infected (either by only 1 sex or both sexes isolated from each other). Weight,

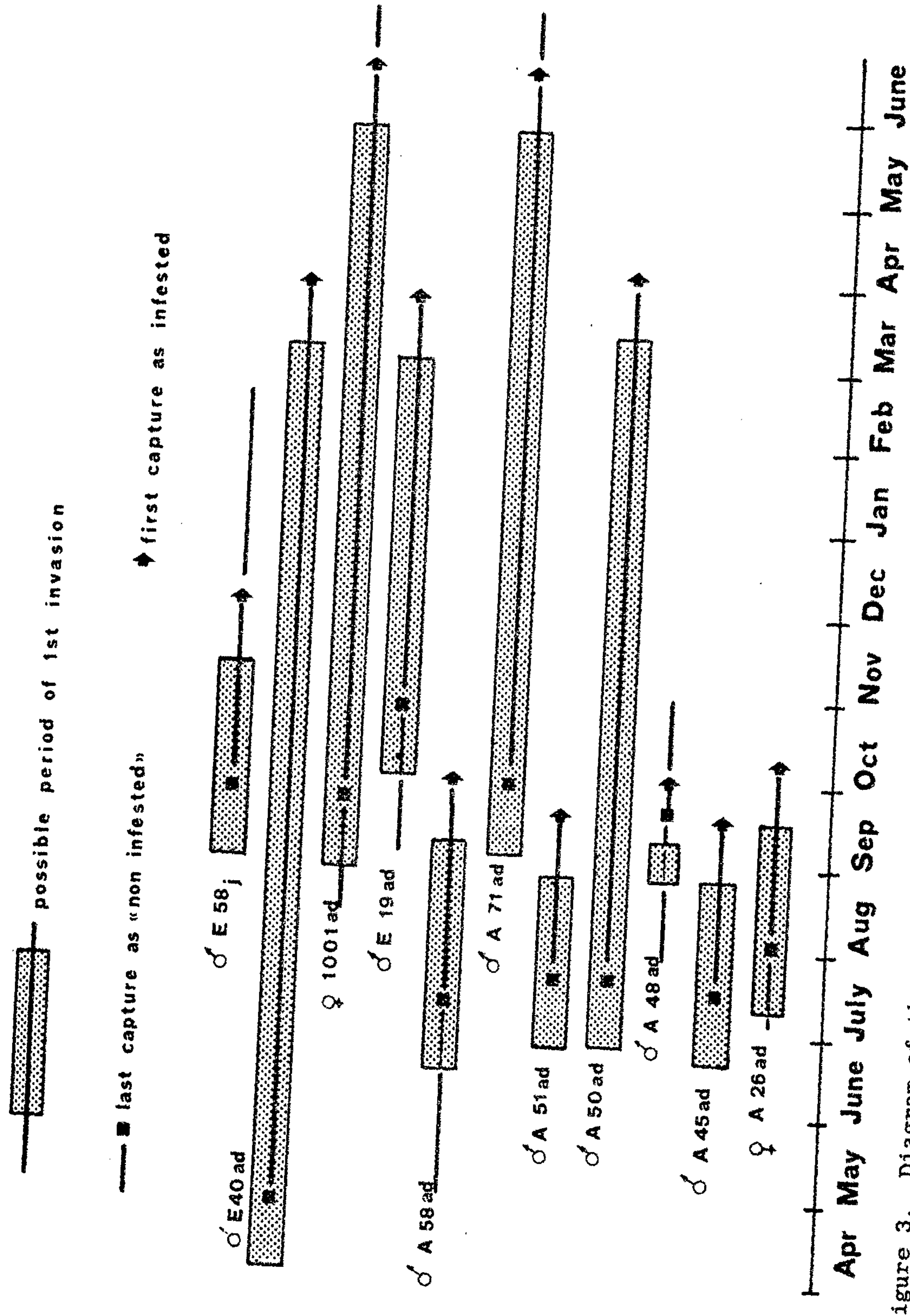

Figure 3. Diagram of the possible periods of transmission of S. nasicola to 11 stoats. (ad = adults, j = juveniles)

cranial and external measurements of adults of both sexes were compared by the Student-Fisher t-test, between distributors and non-distributors. Although infected stoats had greater values, there were no significant differences. Behavior seemed unaltered although 1 infected stoat presented epileptoid-like crisis, in captivity.

DISCUSSION

Transmission of S. nasicola to the Mustelids

According to several authorities (Hobmaier 1941, Dubnitskii 1956, Lankester and Anderson 1971, Théron 1975), the 1st intermediate host of S. nasicola is a pulmonate gastropod. In the Val de Ruz area, 3rd stage larvae (=infective stage) were found in 5 of 61 snails (Arianta arbustorum) (Weber, pers. comm.). The question of whether or not a carrier or paratenic host is involved, is still unsolved. Van Soest et al. (1972) thought that a Soricinae could be that host, and Hansson (1967) infected mustelids by feeding them with Sorex araneus. However, King (1974) found S. nasicola in New Zealand where there are no shrews. Hansson (1967) could not infect mustelids, using bank voles (Clethrionomys glareolus) (125 specimens) or mice (Apodemus sp.) (137 specimens). Indeed, these species, together with Microtus sp. eat snails and slugs (Duncan 1976), although this author stated that "it does not seem likely that these (i.e. molluscs) form a significant part of the rodent's diet." Yet, we found numerous broken snail shells, in winter, next to microtines holes, and observed Apodemus in captivity eating slugs. Hobmaier (1941) and Dubnitskii (1956) thought that no paratenic host is obligatory; but, according to Hansson (1967), "molluscs are not normally taken by species of Mustela." Debrot's (1981) detailed food analysis for stoats showed that remains of Soricinae (Sorex sp. and Neomys fodiens) occur in limited number in the scats. One scat sample from the Val de Ruz contained remains of tissue and snail shell. Microtus sp., C. glareolus and Apodemus sp. were eaten by stoats when A. terrestris was scarce. Weasels (M. nivalis) also fed on this prey (King 1980). If there is little doubt that a molluscan intermediate host is involved (Hobmaier 1941, Dubnitskii 1956, Hansson 1967, Lankester and Anderson 1971, Théron 1975, Duncan 1976, King 1977), our results suggest that transmission of S. nasicola to stoats occurs via a paratenic host that may be a rodent. Birds are also possible paratenic hosts (King 1977).

Prevalence of Infection by S. nasicola

Lavrov (1944) found an inverse relationship between pelt returns by stoat trappers and the degree of infection in stoats the previous year. He concluded that the decline in the stoat must be attributed to the high prevalence of infection by S. nasicola. Moreover, he stated that food supply is another important regulating factor; however, in his opinion, the degree of infection by S. nasicola and the availability of prey are not connected. Our results suggest such a relationship: both the decrease of the stoat population and the increase in the prevalence of infection by S. nasicola seem to be the consequences of the change in the prey species available (Table 2).

The large numbers of A. terrestris in 1975 - 1976 in the Brévine Valley (Debrot 1981) provided an abundant food source for the stoats and allowed an increase in their population. The water vole does not eat molluscs, hence, it cannot be a paratenic host for S. nasicola. This may be the reason why prevalence of S. nasicola was low when stoats fed mainly on this prey. After summer of 1977, the water vole population decreased and the stoat shifted its food habits towards less available prey, including mollusc-eaters. Prevalence of S. nasicola increased, taking into account a time-lag with the beginning of the shift in diet (Table 2). An alternative hypothesis is that the stoat is under stress by the shift in the diet. This stress may reduce the resistance of mustelids to invasion by S. nasicola (Hansson 1968), and could also explain the particularly high prevalence of infection found in the Brevine area since the fall of 1977. In the Val de Ruz area, where water vole pullulations do not occur, the diet of the stoats has always been diversified (Debrot, in prep.) and the prevalence of infection remained moderately high. We are proposing that these phenomena (food habits and prevalence of infection) are more than randomly connected.

Period of infection

Hansson (1974) found that stoats were infected mainly during the cold months of the year. Hansson (1968) suggested that infection occurs "when soricids probably form an increasing proportion of their diet because of the diminishing population of small rodents." Results of our study differ from this in that the most favorable period of infection was mid-June to mid-November, and no remains of Soricinae were found in scats collected in winter (Debrot 1981).

CONCLUSIONS

Two stoat populations have been studied: one, in the Brévine Valley, which was in a decreasing phase during the study and another, in the Val de Ruz, which was fairly stable. The very low rate of infection by S. nasicola found in the summer of 1977 in the Brévine area was a consequence of the particular relationship between the predator and its prey. When the diet was more diversified, as was the case later on in the Brévine area, or in the Val de Ruz, the rate of infection was close to the rate found elsewhere in Europe.

Our results on the prevalence of infection in relation to the food pattern support the hypothesis of a paratenic host for the 3rd stage larvae of S. nasicola. The proportion of the different prey items identified in the scats suggests that a rodent such as Microtus sp., Clethrionomys glareolus or Apodemus sp., or a bird, could be that paratenic host. The number of shrews found in the scats seems too low to be a reliable way of transmission for the parasite. However, it is possible that several species of mollusc-eaters are paratenic hosts for S. nasicola.

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LITERATURE CITED

BAER, J.G. 1931. Quelques helminthes rares ou peu connus du Putois. Rev. suisse Zool. 38:313-334.

DEBROT, S. 1981. Trophic relations between the stoat (*Mustela erminea*) and its prey, mainly the water vole (*Arvicola terrestris sherman*). IN: Worldwide Furbearer Conference Proceedings. J.A. Chapman and D. Pursley (eds.). R.R. Donnelley and Sons Co. Falls Church, Virginia. Vol. II:1259-1289.

———, and C. MERMOD. 1978. Morphométrie crânienne par radiographie. II: Application à une population d'hermines (*Mustela erminea* L.). Rev. suisse Zool. 85:738-744.

DOUGHERTY, E.C., and E.R. HALL. 1955. The biological relationships between American weasels (genus *Mustela*) and nematodes of the genus *Skrjabingylus* Petrov, 1927 (Nematoda: Metastrongylidae), the causative organisms of certain lesions in weasel skulls. Revista ibér. Parasit. Tomo Extraordinario:531-576.

DUBNITSKII, A.A. 1956. (A study of the development of the nematode *Skrjabingylus nasicola*, a parasite of the frontal sinuses of mustelids). Karakul. Zverovod. 1:59-61. Translation in: King, C.M., ed. 1975. Biology of mustelids: some Soviet research. British Lib. Lend. Div., Spa, Yorkshire. 266 pp.

DUNCAN, N. 1976. Theoretical aspects concerning transmission of the parasite *Skrjabingylus nasicola* (Leuckart 1842) to stoats and weasels, with a review of the literature. Mammal. Rev. 6:63-74.

GOBLE, F.C., and A.H. COOK. 1942. Notes on nematodes from the lungs and frontal sinuses of New York furbearers. J. Parasitol. 28:451-455.

GOLVAN, Y.J., and E. DROUHET. 1972. Techniques en parasitologie et en mycologie. Flammarion Médecine-Sciences, Paris, France. 470 pp.

HANSSON, I. 1967. Transmission of the parasitic nematode *Skrjabingylus nasicola* (Leuckart 1842) to species of *Mustela* (Mammalia). Oikos 18:247-252.

———. 1968. Cranial helminth parasites in species of Mustelidae. I. Frequency and damage in fresh mustelids from Sweden. Oikos 19:217-233.

———. 1970. Cranial helminth parasites in species of Mustelidae. II. Regional frequencies of damage in preserved crania from Denmark, Finland, Sweden, Greenland and the northeast of Canada compared with the helminth invasion in fresh mustelid skulls from Sweden. Arkiv. Zool. 22:571-594.

———. 1974. Seasonal and environmental conditions affecting the invasion of mustelids by larvae of the nematode *Skrjabingylus nasicola*. Oikos 25:61-70.

HILL, W.C. 1939. The nematode *Skrjabingylus chitwoodorum* n. sp. from the skunk. J. Parasitol. 25:475-478.

HOBMAIER, M. 1941. Extramammalian phase of *Skrjabingylus chitwoodorum* (Nematoda). J. Parasitol. 27:237-239.

KING, C.M. 1974. The nematode *Skrjabingylus nasicola* (Metastrongyloidea) in mustelids: a new record for New Zealand. New Zealand J. Zool. 1:501-502.

———. 1977. The effects of the nematode parasite *Skrjabingylus nasicola* on British weasels (*Mustela nivalis*). J. Zool., London. 182:225-249.

————. 1980. The weasel *Mustela nivalis* and its prey in an English woodland. J. Anim. Ecol. 49:127-159.

LANKESTER, M.W., and R.C. ANDERSON. 1971. The route of migration and pathogenesis of *Skrjabingylus* spp. (Nematoda: Metastrongyloidea) in mustelids. Can. J. Zool. 49:1283-1293.

LAVROV, N.P. 1944. (Effect of helminth invasions and infectious diseases on variations in numbers of the ermine, *Mustela erminea* L.). Trudy tsentral. Lab. Biol. Okhotn. 6:151-163. Translation in: King, C.M., ed. 1975. Biology of mustelids: some Soviet research. British Lib. Lend. Div., Spa, Yorkshire, England. 266 pp.

LEWIS, J.W. 1967. Observations on the skull of Mustelidae infected with the nematode *Skrjabingylus nasicola*. J. Zool., London. 153:561-564.

————. 1978. A population study of the metastrongylid nematode *Skrjabingylus nasicola* in the weasel *Mustela nivalis*. J. Zool., London 184:225-229.

MACHIDA, M., and M. MIKURIYA. 1968. Studies on Skrjabingyliasis in Japan. Bull. Nat. Sci. Mus. Tokyo. 11:153-157.

MARCONCINI, A., and E. TASSELLI. 1969. Trematodi e nematodi reperiti nella puzzola (*Putorius putorius*) in Toscana. Annali. Fac. Med. Vet. Pisa. 22:203-216.

MERMOD, C., and S. DEBROT. 1978. Morphométrie crânienne par radiographie. I: Problèmes techniques. Rev. suisse Zool. 85:730-738.

PETROV, A.M. 1928. Addition to the explanation of systematics of Nematodes parasitic in the frontal sinus and lungs of Mustelidae. Annals Trop. Med. Parasitol., Liverpool. 22:259-264.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Kogakusha, Tokyo, Japan. 312 pp.

SPREHN, C. 1955. Trematoden in deutschen Farmnerzen (*Lutreola vison* Schreb.) mit einem Bestimmungsschlüssel der Parasiten. Z. Angew. Zool. 42:411-422.

SWALES, W.E. 1938. *Skrjabingylus nasicola* (Leuckart 1842) Petrov, 1927, a nematode parasitic in the frontal sinuses of American Mustelidae. Libro Jub. Prof. L. Travassos, Rio de Janeiro. 455-458.

THERON, A. 1975. Recherches expérimentales sur l'évolution larvaire de de *Skrjabingylus nasicola* (Nematoda: Metastrongyloidea) chez deux Mollusques terrestres. Vie et Milieu 25, Sér. C:49-54.

TWIGG, G.I. 1978. Marking mammals by tissue removal. Pp. 109-118. In: Animal marking. Recognition Marking of Animals in Research (B. Stonehouse, ed.). Macmillan Co., London, England. 257 pp.

VAN SOEST, R.W.M., J. van der LAND, and P.J.H. van BREE. 1972. *Skrjabingylus nasicola* (Nematoda) in skulls of *Mustela erminea* and *Mustela nivalis* (Mammalia) from the Netherlands. Beaufortia 20:85-97.

VIK, R. 1955. Invasion of *Skrjabingylus* (Nematoda) in Norwegian Mustelidae. Nytt Mag. Zool. 3:70-78.

VOGEL, H., and J. VOELKER. 1978. Über den Lebenszyklus von *Troglotrema acutum*. Tropenmed. Parasit. 29:385-405.

WEBSTER, W.A. 1965. *Skrjabingylus magnus* n. sp. (Nematoda: Trichostrongylidae) from the skunk, *Mephitis mephitis*. Can. J. Zool. 43:229-231.

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TROPHIC RELATIONS BETWEEN THE STOAT (MUSTELA ERMINEA) AND ITS PREY, MAINLY THE WATER VOLE (ARVICOLA TERRESTRIS SHERMAN)[1]

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ABSTRACT: A live-trapping program was conducted to study a stoat population in a 1,875-ha study area. The animals were abundant in summer 1977, after which the population gradually decreased until spring 1980. This decrease coincided with a decline in the water vole population. Scats (657) were collected from live-trapped stoats and in the field. The 690 prey items identified were grouped according to the seasons. The change in food habits with time and food niche width was analyzed. Water voles were the dominant prey from fall 1976 - spring 1977. Since summer 1977, its contribution to the diet decreased and was replaced partly by small microtines together with other less common prey. Reciprocal averaging showed groups of seasons associated with specific prey classes and indicated a tendency toward a seasonal variation during the *Microtus*-dominated period. The niche width varied in relation to the availability of the main prey species.

Numerous studies have been carried out in Europe and North America on the population (Nyholm 1959, Lockie 1966, Erlinge 1977a,b) and food habits of *Mustela erminea* (Hamilton 1933, Klimov 1940, Lavrov 1956, Day 1968, Müller 1970, Hewson and Healing 1971, Northcott 1971, Potts and Vickerman 1974, Tapper 1976, Brugge 1977, Howes 1977, Fitzgerald 1977, Simms 1978, 1979, Erlinge 1979). However, most of the data on the food patterns was obtained with material collected over a large area and/or during a long time period (Table 1). Moreover, the densities of the stoat and the prey populations were unknown or not specified.

There is little information on prey-predator relationships and their dynamics within a limited stoat population, although food habits of

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Table 1. Summary of information on the main prey species exploited by stoats and ermines.

Reference	Locality	Duration of Collecting	Material Analyzed[a] (Number Vertebrate Prey Identified)
Debrot (present study)	1st period	Fall 1976 - Spring 1977	S (105)
	3rd period	Winter 1978 + Summer 1978 - Fall 1980	S (367)
Brugge (1977)	Holland	7 yr	GC (61)
Day (1968)	Britain	4 yr	GC (149)
Potts and Vickerman (1974)	Britain	2 yr	GC (31)
Tapper (1976)	Britain	4 summers	GC (59)
Lavrov (1956)	North Kazakhstan	3 yr	GC + S (409)[d]
	Achinsk district	4 yr	GC (101)
Klimov (1940)	Novosibirsk district	2 winters	GC (351)
Simms (1979)	Southern Ontario	3 yr	S (350)
Northcott (1971)	Fort Providence Grande Prairie[e]	1 winter	GC (97)
Aldous and Manweiler (1942)	Minnesota	3 winters	GC (80)

Reference	Main Prey (Percentage Occurrence[b])	Secondary Prey[c] (Percentage Occurrence[b])
Debrot (present study)	*Arvicola* (91.4) Grey voles (64.6)	none *Arvicola* (13.4)
Brugge (1977)	*Microtus* and *Clethrionomys* (49)	Lagomorphs (23) Birds (21)
Day (1968)	Birds (37.6)	Lagomorphs (31.5) *Microtus* (10.7)

Table 1. (Cont'd.).

Reference	Main Prey (Percentage Occurrence[b])	Secondary Prey[c] (Percentage Occurrence[b])
Potts and Vickerman (1974)	Lagomorphs (38.7)	Birds (22.4) Microtus (19.3) *Muridae* (12.8)
Tapper (1976)	Lagomorphs (55.9)	Birds (35.6)
Lavrov (1956)	*Microtus* (53.3) *Arvicola* (41.1)	Arvicola (12.0) *Microtus* (36.6)
Klimov (1940)	*Arvicola* (67.0)	"Small mouse-like rodents" (31.0)
Simms (1979)	*Microtus* (88.9)	none
Northcott (1971)	*Zapus* (27.8)	Peromyscus (21.6) *Fishes* (12.4) *Microtus* (10.3)
Aldous and Manweiler (1942)	Microtines[f]	-

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[a] S = scats; GC = gut contents.

[b] Percentage of prey items identified when available, otherwise percentage of samples analyzed.

[c] Prey class over 10 percent was considered as secondary prey.

[d] Only the prey items identified to the genus were taken into account.

[e] Both areas were summarized, differences being insignificant ($\chi^2 = 8.15$; $p > 0.05$).

[f] Incomplete data.

other Mustelids have been examined in relation to the availability of the prey. King (1980) and Erlinge (1975) studied Mustela nivalis in Britain and Sweden, respectively; Gerell (1967, 1968) studied M. vison in Sweden; Simms (1979) studied American weasels; and Cowan and Mackay (1950), Quick (1955), Jonkel (1959), Weckwerth and Hawley (1962) studied Martes americana.

In this study, the above parameters were investigated in a natural stoat population in a given area of Switzerland. Results from the 1st trapping period enabled us to study the population dynamics, especially during the decrease phase. Thus, 3 sources of data form the basis of this paper: the dynamics of the population of stoats simultaneously with their diet, and the fluctuations of the water vole population.

MATERIALS AND METHODS

Study Area

The study, mainly based on trapping, was initiated in fall 1976 in the Brévine Valley (Swiss Jura Mountains). The study area (1,875 ha, 1,000 - 1,200 m) consists of pastures (50 percent), wooded pastures (20 percent), forest and small peat bogs (30 percent). Pastures are partly used for grazing and partly for hay harvest. Barley fields occupy a very small area. A high density of stone walls (86 km) and peat bogs are the primary habitat of the stoats. This farming country was selected for its abundance of stoats reported by local farmers.

Live Trapping

Mark-and-recapture technique was used in this study. Stoats were captured in live traps baited with laboratory white mice, whose remains in scats are easily distinguished from those of wild mammals.

Number and distribution of the traps, and trapping effort were chosen to allow a comparison of population densities between the succesaive trapping sessions. A restricted area, including peat bogs inside the main study area, had been trapped more often. The trapping results from this restricted area are correlated with those from the entire area ($r = 0.992$; $p < 0.01$). Thus, a more detailed pattern of the dynamics of the stoat population is available from the restricted area.

Water Vole Population

At the beginning of the food analysis, water voles were found frequently. Thus, data on the density of their populations were of great interest.

In Switzerland, the fossorial form of the water vole (Arvicola terrestris scherman) is well known for its large fluctuations (Meylan 1977). Its general biology (e.g., habitat, food habits, population structure) distinguishes it from the form A. t. amphibius in Great Britain, A. t. terrestris in northern and eastern Europe, and the species A. sapidus in Spain and in southern and western France. Arvicola t. scherman is associated only slightly with water and digs extensive systems of tunnels, very like those of a mole (Talpa europaea) (Corbet 1966). It is widely distributed, except in woodlands, and mainly colonizes open fields.

Because of its effects upon agriculture, it is considered a pest; the village authorities give rewards for each capture made by the farmers. A survey allowed the determination of the yearly captures in 6 regions chosen around the study area.

This sampling method is subject to criticism in many aspects, mainly: 1) variable trapping efforts (probably increasing during the peak phase); 2) local and temporary use of rodenticides; 3) confusion with the mole (2 village authorities have separate accounts for the water vole and the mole; thus, it was noticed that the population of the latter is relatively constant and would not alter the periodicity of the water vole population). Therefore, the curve obtained (Figure 1) should be taken as an index and not as an exact estimation of the yearly densities.

Food Habits

The 657 scats analyzed in this study were collected from live-trapped

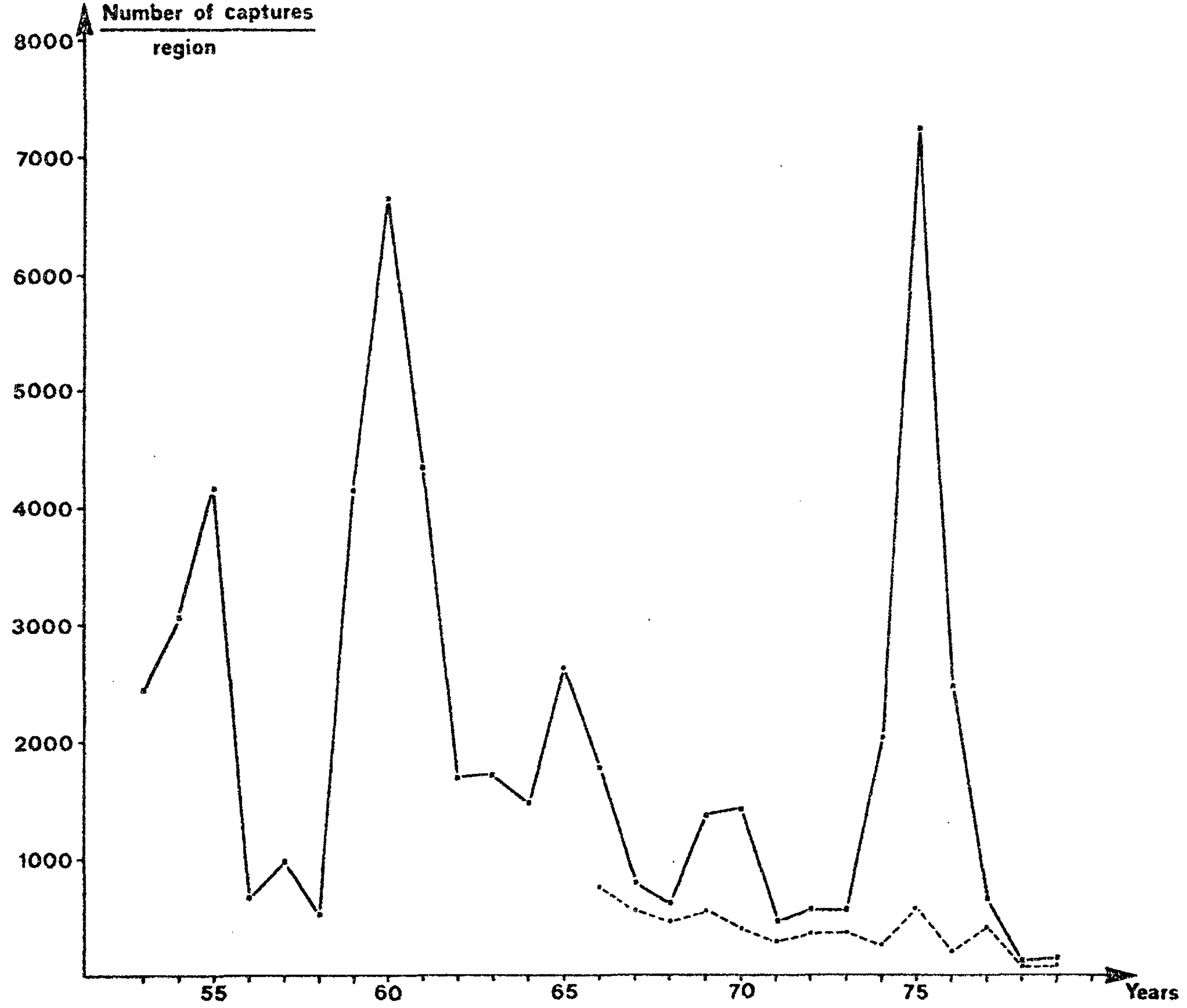

Figure 1. Statistics of the captures (both *Arvicola* and *Talpa*) recorded around the study area; average amount per region (unbroken line) and estimated proportion of moles (broken line).

stoats, from dens, along stone walls, and wherever they could be found. The origin and size of the samples are given in Table 2: scats were grouped according to the seasons (winter *n* = December n-1 + January n + February n). All the scats collected during 1 season form 1 sample. According to Erlinge (pers. comm.), scats do not remain longer than 1 mo in the field. In the spring samples, the scats found just after the snow melted may have kept longer in the snow. Therefore, a bias in the data is possible in some of the samples. The winter 1978 sample is another case: the 187 scats recorded all were collected in a "winter den" - probably used by an adult male (A80). In fall 1979 and winter 1980, only 1 juvenile (i.e., born in 1979) female (A89) was known to be in the restricted area. It disappeared during the winter and an adult female (A90) took its place in spring. Thus, the 3 last samples (fall 1979, winter 1980, and spring 1980) are mainly from 2 female stoats. This disadvantage of samples constituted by scats from few individuals

Table 2. Seasonal repartition of the scats analyzed and number of prey items identified (plant material and insects included).

	Number Scats Collected		Number Prey Identified	
Seasons	Field	Traps	Field	Traps
Fall 1976	5	0	5	0
Winter 1977	9	0	9	0
Spring 1977	89	2	91	2
Summer 1977	60	56	76	65
Fall 1977	12	15	16	16
Winter 1978	187	0	206	0
Spring 1978	24	1	31	1
Summer 1978	46	13	57	16
Fall 1978	2	3	2	3
Winter 1979	0	0	0	0
Spring 1979	11	0	11	0
Summer 1979	12	5	13	5
Fall 1979	42	0	45	0
Winter 1980	1	0	1	0
Spring 1980	18	1	18	1

is unavoidable when studying a carnivorous population in the phase of low numbers.

Prey items were identified from the remains found in the fecal matter. Some prey classes could have been missed (e.g., molluscs, earthworms, eggs when the shell was not ingested). Insects and plant material were taken into account when they formed more than 50 percent of the volume of the scat (Table 3). Mammalian items were identified according to the method of Day (1966). However, an extended reference collection was necessary to compare all potential prey species available in the study area (Debrot in prep.). Medulla and cross-sections were observed under the microscope and scale patterns identified using a scanning electron microscope. Twenty-five percent of the rodents were partly or fully recognized from the teeth found.

Each prey item was considered as 1 prey killed and ingested, even if only a trace of hair was detected. Data were assessed as frequency of occurrence, calculated as relative occurrence of the total number of prey items determined in the sample, and not in percentage of the scats containing wild prey. In this study, we were interested in the prey species eaten by the stoats, not in the average composition of a meal. Moreover, the time of transit of a food item is not necessarily constant from 1 prey to the other (Brugge 1977). The known disadvantage of this recording method is to underestimate large prey and overestimate small prey. But, no conversion to ingested weights is believed adequate; the majority of the prey is of 1 size class and age is unknown. Moreover, large prey species probably are exploited as young ones (Lepus capensis occurred only in summer) or as carrions (e.g., Capreolus capreolus and Mustela sp.).

When a scat contained more than 1 prey item (Table 4), each prey identified was recorded; but, if a scat contained the remains of 2 individuals of the same species or of 2 indistinguishable species, they were recorded as 1. The potential error committed, although low (only 9.6 percent of the scats were found with more than 1 vertebrate item), will underestimate abundantly exploited prey species.

Table 3. Seasonal repartition of the prey items identified.

	Fall 1976	Winter 1977	Spring 1977	Summer 1977	Fall 1977	Winter 1978	Spring 1978	Summer 1978	Fall 1978	Winter 1979	Spring 1979	Summer 1979	Fall 1979	Winter 1980	Spring 1980	TOTAL
Number Scats	5	9	91	116	27	187	25	59	5	-	11	17	42	1	19	614
Number Prey	5	9	93	141	32	206	32	73	5	-	11	18	45	1	19	690
Arvicola	5	8	83	64	11	34	11	9	-	-	2	1	2	-	1	231
Microtus or *Pitymys*	-	1	4	15	5	135	10	29	4	-	9	6	38	1	15	272
Clethrionomys	-	-	-	2	1	8	-	-	1	-	-	2	1	-	-	15
Apodemus	-	-	-	2	1	28	-	1	-	-	-	-	2	-	-	34
Mus	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
Eliomys	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	3
Muscardinus	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Sciurus	-	-	-	1	1	-	4	2	-	-	-	-	-	-	1	9
Unidentified Rodents	-	-	-	2	1	-	2	-	-	-	-	-	-	-	-	5
Talpa	-	-	-	-	2	-	1	1	-	-	-	1	-	-	-	5
Soricinae	-	-	-	1	-	-	-	2	-	-	-	-	-	-	-	3
Lepus	-	-	-	3	-	-	-	9	-	-	-	1	-	-	-	13
Mustela	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	3

Table 3. (Cont'd.).

	Fall 1976	Winter 1977	Spring 1977	Summer 1977	Fall 1977	Winter 1978	Spring 1978	Summer 1978	Fall 1978	Winter 1979	Spring 1979	Summer 1979	Fall 1979	Winter 1980	Spring 1980	TOTAL
Number Scats	5	9	91	116	27	187	25	59	5	-	11	17	42	1	19	614
Number Prey	5	9	93	141	32	206	32	73	5	-	11	18	45	1	19	690
Capreolus	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Reptiles	-	-	-	13	-	-	1	3	-	-	-	-	2	-	-	19
Birds	-	-	2	20	4	-	3	7	-	-	-	7	-	-	2	45
Eggs	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	3
Insects	-	-	1	6	4	-	-	9	-	-	-	-	-	-	-	20
Plant Material	-	-	1	3	1	1	-	1	-	-	-	-	-	-	-	7

Table 4. Composition of the scats.

Number	Origin		
	Field	Traps	Total
Scats analyzed	522	135	657
Scats with wild prey	518	96	614
Scats with bait only	4	39	43
Scats with 1 prey	463	85	548
Scats with 2 prey	48	9	57
Scats with 3 prey	6	2	8
Scats with 4 prey	1	0	1
Scats with 1 vertebrate prey	458	87	545
Scats with 2 vertebrate prey	44	7	51
Scats with 3 vertebrate prey	3	1	4
Scats with 4 vertebrate prey	1	0	1
Prey identified	581	109	690
Vertebrate prey identified	559	104	663

Statistical Tests

When not specified, the statistical tests used are the chi-square test and, when possible (2-sample case, if figures are not too high for the capacity of the computer) Fisher exact probability test (Siegel 1956).

Reciprocal averaging was used to compare prey classes and seasons. Reciprocal averaging (Analyse factorielle des correspondances) is an efficient method which analyses data from an incidence matrix where rows represent observations (prey classes in this case) and columns represent variables (seasons). The analysis consists of building a multidimensional space in which both observations and variables are dispersed relative to their distances (the distance used is χ^2). The space (9 dimensions in this case) is projected on axes chosen successively to give as much information as possible. The "quantity of information" associated with an axis i is defined as the proportion of variability (PV_i)

absorbed by the factor corresponding to this axis. The same is true in maps constituted by 2 axes. For example, map_I (1,2) is defined by axis 1 and axis 2 and $PV_I = PV_1 + PV_2$.

The reciprocal averaging given in this paper has the following PV for the 1st 5 axes:

$$\left.\begin{array}{l}\text{Factor 1 : } PV_1 = 0.52 \\ \text{Factor 2 : } PV_2 = 0.24\end{array}\right\} \text{Map (1,2) : } PV_I = 0.76$$

Factor 3 : $PV_3 = 0.08$
Factor 4 : $PV_4 = 0.07$
Factor 5 : $PV_5 = 0.04$

A map having $PV > 0.6$ is usually considered as a good representation the multidimensional space. Thus, the 3rd axis was useful only for group 4.

Calculation and plotting were performed on the WAX 11/780 computer, using a program developed by the "Groupe de recherche en methodes quantitatives, Universite de Neuchâtel (Suisse)." For more detailed information on reciprocal averaging, see Hill (1973).

RESULTS

Stoat Population

During the 1st trapping session (June - July) stoats were abundant with 50 individuals being recorded in the main area. Three months later, only 14 individuals were captured. This strong decrease of the population continued in 1978 and 1979 (Figure 2). The trapping data in spring 1980 indicated a probable stabilization of the population (phase of scarcity).

Computed in the main area, the rate of capture (each individual being recorded only once) in summer 1977 was significantly higher ($\chi^2 = 15.45$; $p < 0.001$) than in fall 1977. The rate of capture in fall 1977 was not significantly different from that of summer 1978 ($\chi^2 = 2.10$;

$0.2 > p > 0.1$); however, the rate of capture in fall 1977 was higher than in fall 1978 ($\chi^2 = 3.97$; $p < 0.05$) and in summer 1979 ($\chi^2 = 6.75$; $p < 0.01$).

Water Vole Population

The survey concerned an area of 8,337 ha of fields and pastures, and involved 177,268 individuals (water vole and mole). The population curve (Figure 1) showed 5 peaks spaced 5 yr apart. Two higher peaks occurred with an interval of 15 yr. The current study began at the time of the decline phase of the 2nd main peak. Both Arvicola and Talpa were recorded and summarized. From the data available on both species in the 2 regions, it was estimated that the moles represent 60 - 70 percent of the trapped population during the low number phases, 30 - 40 percent during the little peak phases and less than 1 percent during the last peak phase. The estimation of the yearly number of moles given in Figure 1 was calculated from the number found in these 2 regions.

Other Prey

Local qualitative sampling by means of trapping small mammals was performed at different seasons and in different habitats. Microtus arvalis, Microtus agrestis and Talpa europaea were caught mainly in meadows. Apodemus sylvaticus, Apodemus flavicollis, Pitymys subterraneus, Clethrionomys glareolus, Eliomys quercinus, Sciurus vulgaris, and Sorex sp. were recorded in forests, wooded pastures, and wooded parts of the peat bogs. No quantitative study was conducted to estimate Microtus densities. However, field observations and limited trapping indicated an increase during 1979 and the 1st half of 1980. Birds were abundant all over the area (more than 60 nesting species).

Food Habits

Prey Classes. Occurrence of prey items is given in Table 3. Microtines constituted the bulk of the food for stoats, with 76.1 percent of the prey items identified. Their occurrence varied between 50 and 100 percent during the different seasons. Other prey classes generally were found in low numbers. Invertebrates and plant material constituted a

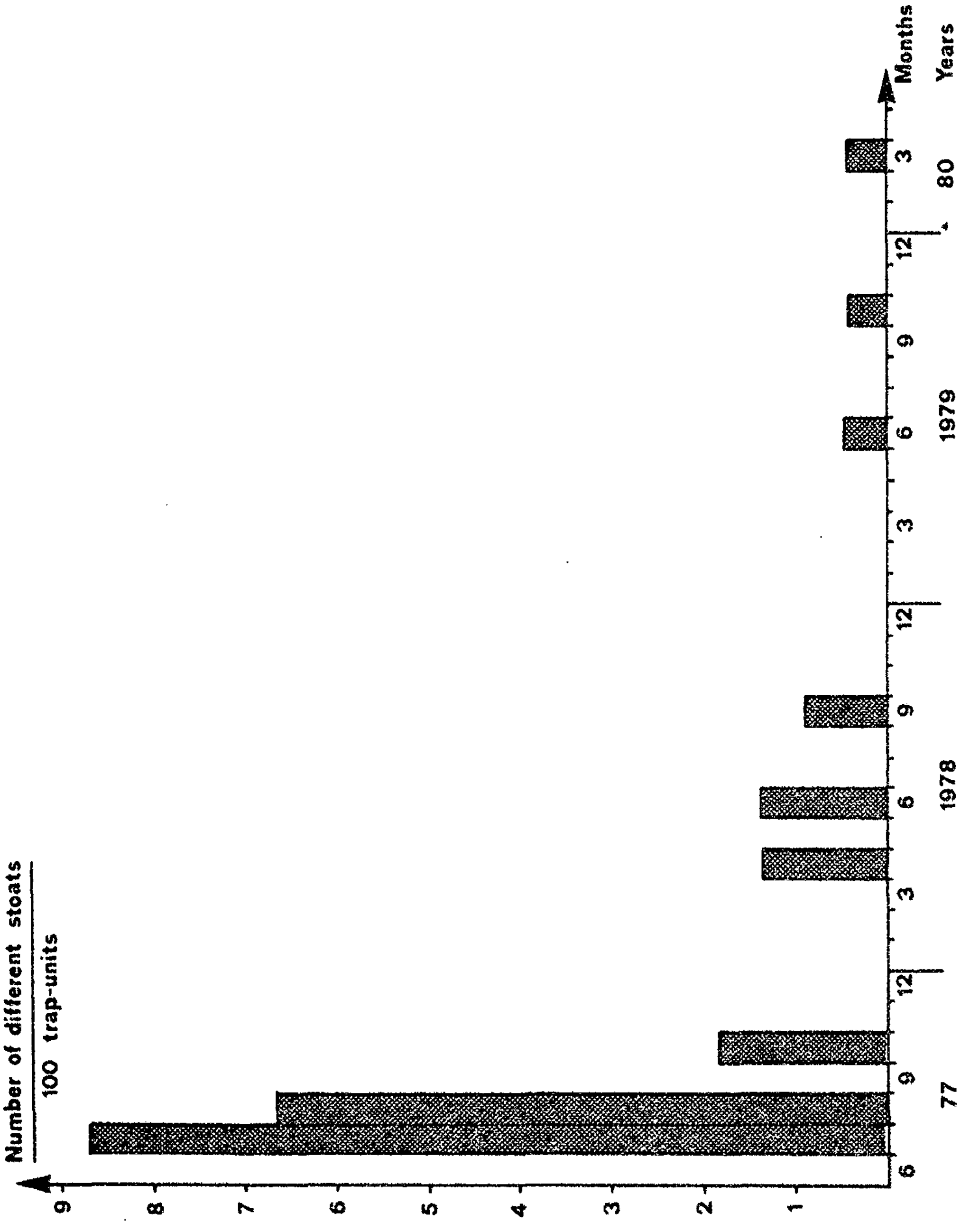

Figure 2. Dynamics of the captured stoat population in the Brévine Valley.

negligible amount, in quantity and/or in quality and were not considered in the analysis of these results.

Arvicola was intensively exploited by stoats (Figure 3) at the beginning of the study period. Then, their proportion in the diet decreased progressively. Since 1979, water voles were a scarce prey item.

Four species of small microtines are known to live in the study area: 1) *Clethrionomys glareolus*; 2) *Microtus agrestis*; 3) *Microtus arvalis*; and 4) *Pitymys subterraneus*. Of these, *C. glareolus* constituted 2.3 percent of the diet. It was not possible to distinguish the respective contribution of the remaining microtines from hair analysis. However, in nearly 10 percent of the occurrences the 1st inferior molar found in the scats allowed the determination of genus: only *Microtus* were recorded (among the 249 grey voles found, the maximum theoretical number of *Pitymys* is 37; for $p = 0.05$). The exploitation of the grey voles populations increased in 1978 and constituted the main substitution food (Figure 3).

Other rodents (Muridae, Gliridae, Sciuridae and unidentified rodents) occurred occasionally (Figure 3). They represent 8.0 percent of the total number of prey items identified. *Apodemus* (both species *A. sylvaticus* and *A. flavicollis* could not be distinguished) was the most frequent genus recorded in these prey classes.

The 13 occurrences of *Lepus europaeus* (2.0 percent) were recorded in summer (Figure 3). Eight insectivores were identified (1.2 percent): 5 *Talpa europaea*, 1 *Sorex minutus*, 1 *Neomys fodiens*, and 1 Soricinae (Figure 3). The 4 items classified in "other mammals" (Figure 3) were 1 roe deer (*Capreolus capreolus*) and 3 *Mustela* sp. They were probably carrion. The 3 *Mustela* were recorded in summer 1977, during the drastic decrease of the stoat population. Reptiles (2.9 percent) were probably of the species *Lacerta vivipara* (Figure 3). Birds were the 3rd most important prey class (7.2 percent), after the 2 classes of microtines. No attempt was made to determine orders. This food supply was exploited mainly in summer (Figure 3).

Food Niche Width. Simpson index [B = niche width = $(\Sigma p_i^2)^{-1}$, where,

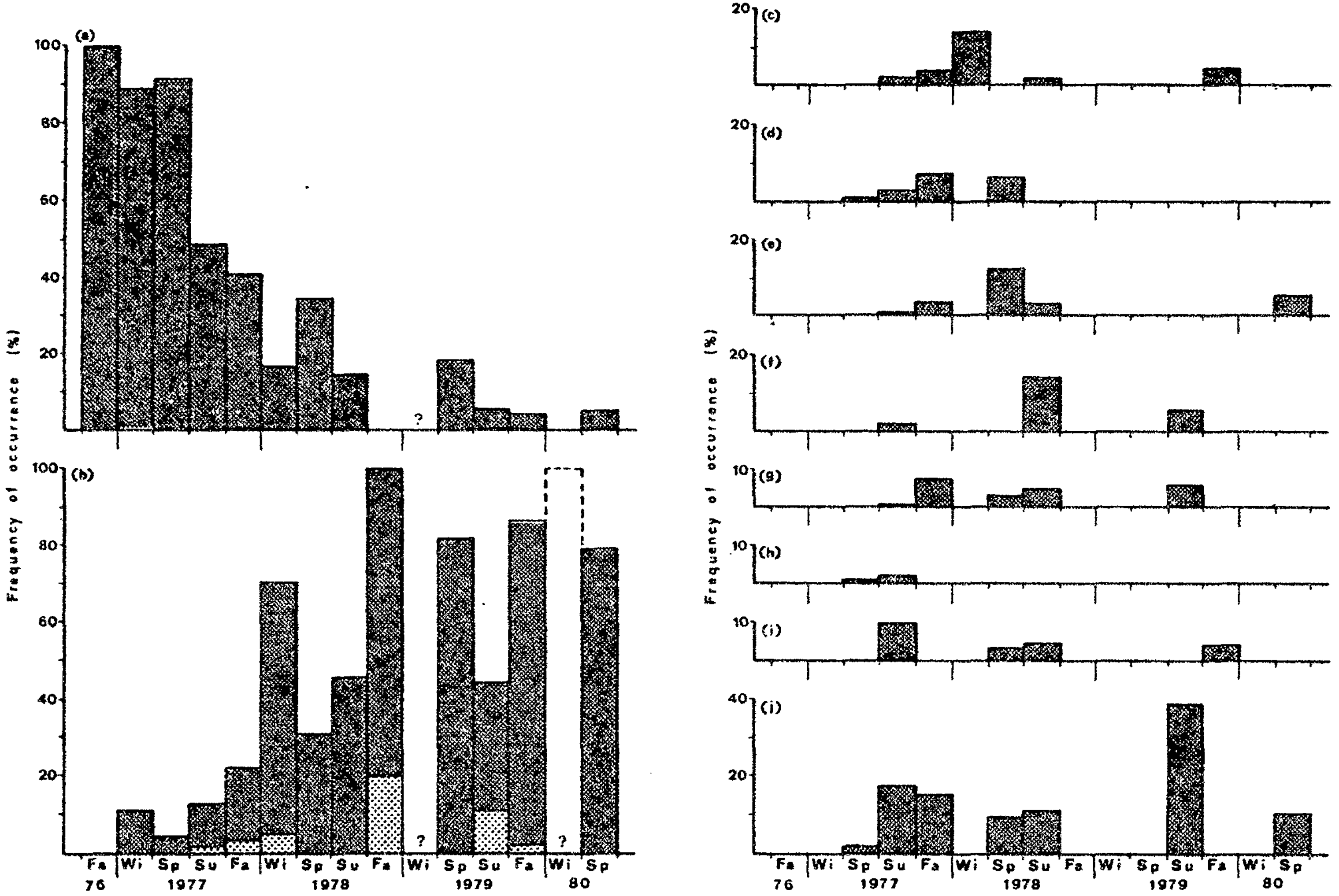

Figure 3. Evolution with time of the prey items eaten by stoats in the Brévine Valley. [(a) = Arvicola, (b) = Clethrionomys (stippled) and grey voles, (c) = Murinae, (d) = Gliridae and unidentified rodents, (e) = Sciurus, (f) = Lepus, (g) = Insectivores, (h) = Other mammals, (i) = Reptiles, (j) = Birds.]

p_i = proportion of the i^{th} prey class] is unsuitable for comparing data when the number, n, of prey classes is not equal. The standardized niche width [$B_s = (B-1)(n-1)^{-1}$], developed by Hespenheide (1975) is better adapted to the current study. Prey classes were chosen taking into account both size and availability as follows:

1. Arvicola
2. Grey voles and Clethrionomys
3. Murinae
4. Gliridae and unidentified rodents
5. Sciurus
6. Insectivores
7. Lepus
8. Other mammals
9. Reptiles
10. Birds and eggs.

The standardized niche width showed changes between fall 1976 and spring 1980 (Figure 4). It shows large variations, ranging between low values (narrow niche) and relatively high values (wide niche).

Reciprocal Averaging. Results of the reciprocal averaging (Figure 5) show 5 groups of seasons associated with specific prey classes (same classes as defined in food niche width):

Group 1. Fall 1976, winter 1977 and spring 1977 are closely related with Arvicola.

Group 2. Summer 1977 is characterized by reptiles (and other mammals).

Group 3. Summer 1978 and summer 1979 are characterized by insectivores and Lepus.

Group 4. Fall 1977 and spring 1978 are characterized by Sciurus and other rodents. Factor 3 was used to separate this group from Groups 2 and 3.

Group 5. Winter 1978, fall 1978, spring 1979 and fall 1979 are closely associated with the small microtines class and the Murinae.

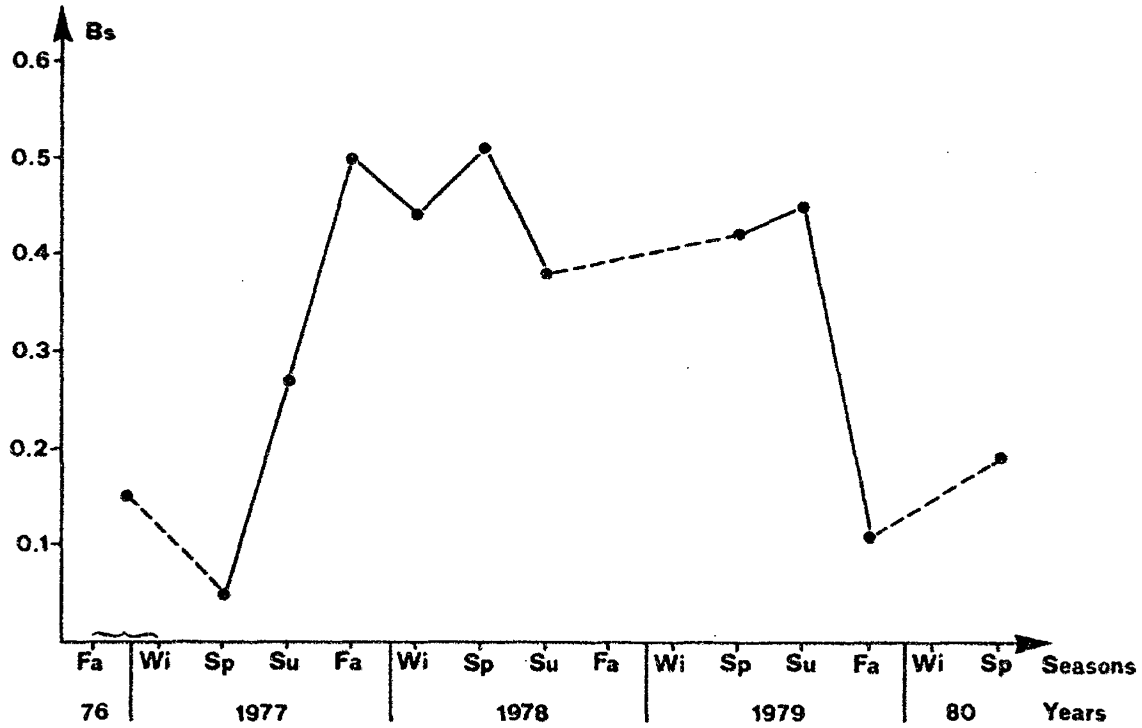

Figure 4. Evolution with time of the standardized food niche width (B_s) of the stoats in the Brevine Valley (when insufficient data, broken lines were used).

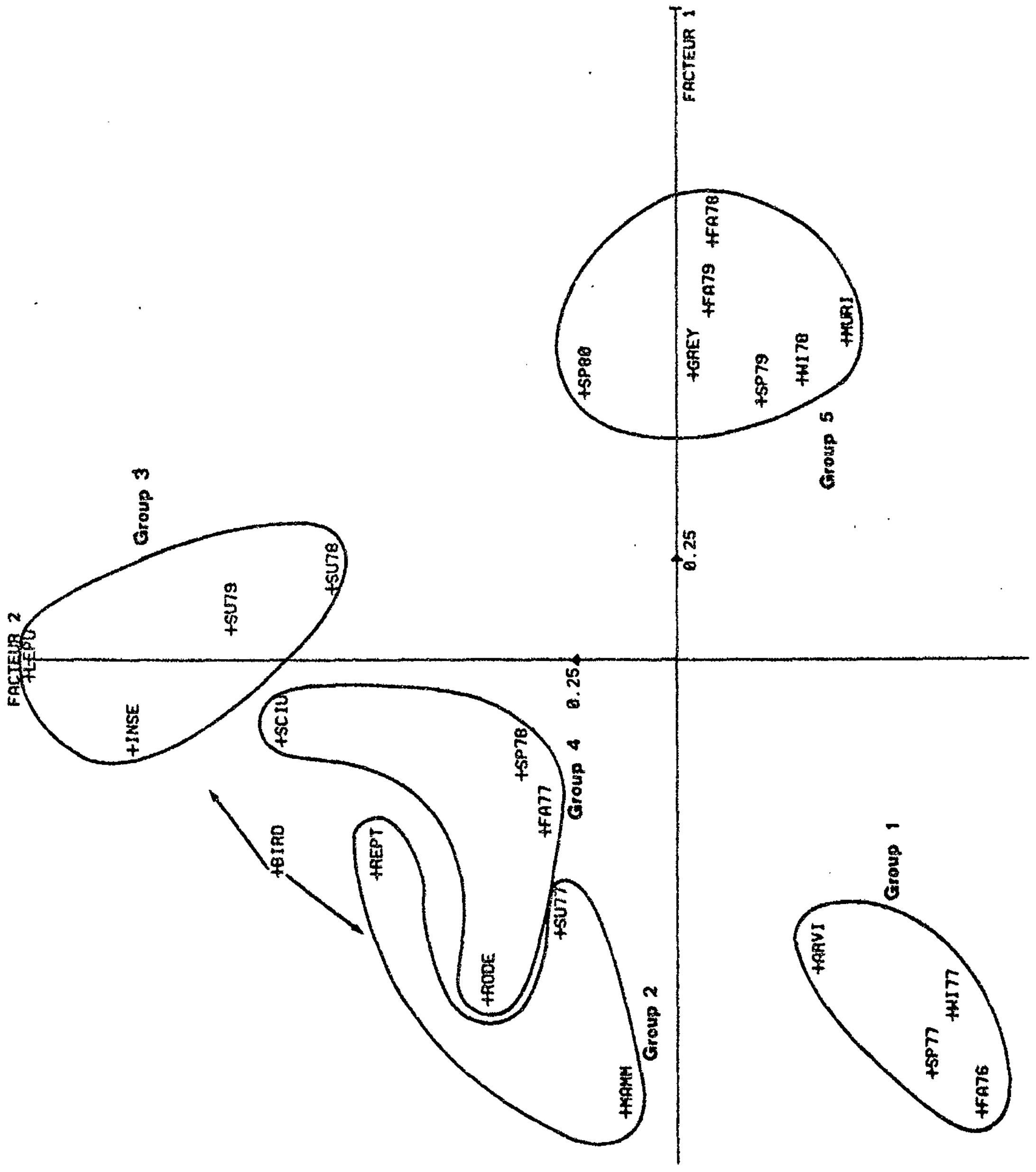

Figure 5. Reciprocal averaging ordination of both seasons and prey classes. (See explanation in text.)

Birds are found in an intermediate position between Groups 2 and 3.

When the contributions of the observations to the factors are examined, factor 1 is aligned with the shift of the food habits after fall 1977:

axis 1
Food pattern 1976 - 1977 ←——→ Food pattern 1978 - 1980.

Factor 2 appears to be an expression of the seasonal variations:

Summer food pattern
↑
| axis 2
|
Winter food pattern

DISCUSSION

To avoid confusion, in the following part of this paper, stoat refers to *Mustela erminea* and weasel to *M. nivalis* in Europe, and ermine to *M. erminea* in North America. In addition, comparisons between stoats and ermine have to be considered carefully; it appears that both have morphological and ecological differences, although they are classified under the same specific name.

Stoat Population

Changes in numbers of stoats are noted in the literature, and different explanations have been presented. Lavrov (1944) relates the decrease in the number of trapped stoats to the increase in the rate of invasion by the parasite of the frontal sinusis: "when there is widespread invasion by *Skrjabingylus nasicola*, the number of stoats may go down." This is discussed in Debrot and Mermod (1981). Aspisov and Popov (1940) assumed that the number of the water vole pelts in the 2nd quarter of the current year can be used to forecast the stoat harvest in the next year. Later, Lavrov (1956) noted, in agreement with other Russian authors, the importance of the density of the prey populations for the stoat. However, in his opinion, the prolonged depression of stoat numbers (in the years 1940 to the early 1950s) were due to a complex combination of diverse causes (e.g., unfavorable conditions, intensified trapping in the years of slight increase in stoat numbers).

More recently, Rosswall et al. (1975), Bunnel et al. (1975), and Kallio (1975) described the stoat population as being cyclic and associated with rodents cycles. These assumptions appear to be based on field observations.

King and Moors (1979) noted the dependency of the stoat on lagomorphs, as revealed during the advent of myxomatosis in Britain. This trophic relation is confirmed by Potts' and Vickerman's (1974) study. Furthermore, these authors assumed that the recovery of the rabbit is partly responsible for the recent increase in number of stoats. However, none of these studies provided data on the dynamics of both prey and predator populations, together with the food habits, especially during the decrease phase.

In the Brévine Valley, the trapped population on the main area decreased from 50 (summer 1977) to 3 (summer 1979). The data during the low number phase may have decreased significance; at low densities, the portion of transients (Lockie 1966) in the residual population increases, especially by males (Debrot in prep.). Yet, direct observation, scat collecting and snow tracking confirmed the trapping results. This drastic decrease is assumed to have been more pronounced, considering that the peak was in 1976. This suggests that the difference recorded between the highest and the lowest values (Figure 2) represents the minimum value of the decline.

Water Vole Population

The cyclic periodicity of microtines has been noted for a long time. The most common periods are 3 and 4 yr, but cycles of 5 yr also have been observed (Krebs and Myers 1974).

As far as is known, the periodicity of the fossorial form of <u>Arvicola</u> never has been demonstrated clearly. Habert (1975) indicated a periodicity of 4 - 6 yr. The present results show a periodicity of 5 yr during 5 cycles around the study area. It would be interesting to determine if the same cycles occur in other areas (Meylan and Debrot in prep.). Cycles are difficult to estimate by trapping because of the weak amplitude of the smallest peaks and the clumped pattern of distribution during the low numbers phase. The method used here, although subject to criticism (mainly variable sampling technique and possible confusion with the mole) has the advantage of the high numbers and large sampling area. Figure 1 shows 2 high peaks; unfortunately, the period investigated is too short to state whether these peaks were cyclic. Meylan (1977) suggested that abiotic factors are partly responsible for outbreaks, e.g., winter climatic conditions favorable to winter reproduction (Meylan and Airoldi 1975).

In high peak phases, densities may reach or exceed 1,000 voles.ha^{-1} (Morel and Meylan 1970). The outbreak of 1975 was especially disastrous. In the Brévine Valley, injury to plant cover in meadows by consumption and burrowing activity were estimated at nearly 50 percent. The present results indicate that the very high density of water voles during this peak was responsible for the high number of stoats found in summer 1977.

Some other carnivores and birds of prey are known to be favored by outbreaks of the water vole. Tikhvinskaya and Gorshkov (1971) found it in relation to fur harvest of the foxes. In 1976 and 1977 we observed a higher number of domestic cats (*Felis catus*), and raptors like black kites (*Milvus migrans*), buzzards (*Buteo buteo*), and long-eared owls (*Asio otus*).

Food Habits

In Table 1 the primary and secondary (more than 10 percent, arbitrary choice) food classes found in the diet of the stoats and ermines in different countries are listed. There is considerable variation in the main prey exploited. This suggests the ability of *M. erminea* to feed on different prey classes, according to the availability of species in the area. In comparison weasels fed more specifically on little microtines as revealed by Day (1968), Potts and Vickerman (1974), Moors (1975), Tapper (1976), King (1980) in Britain; Erlinge (1975) in Sweden, and

Brugge (1977) in Holland. Nevertheless, the secondary prey class varies to a large extent. For example, birds were found in the British studies, Muridae by Day (1968), Potts and Vickerman (1974), Moors (1975), Erlinge (1975), Brugge (1977), King (1980); and lagomorphs by Day (1968), Potts and Vickerman (1974) and Erlinge (1975). In 1 case insectivores were found as secondary prey (Brugge 1977).

Water Voles. Some studies have indicated that the water vole is an important constituent in the diet of the stoat (Table 1, Klimov 1940). Moreover, Erlinge (1979) revealed a sexual and seasonal variation in the exploitation of Arvicola as prey. In Lavrov's (1956) data the water vole represented 13.0 percent of the prey items when 2 areas are considered together. The proportion ranges from 4.1 percent (winter 1939 - 1940; North Kazakhstan province) to 40.5 percent (same season; Achinsk district). In Holland Arvicola was eaten occasionally (Brugge 1977) and in Britain it was neglected (Day 1968, Potts and Vickerman 1974, Tapper 1976). Of course, the comparison of the data from the literature with those from the Brévine Valley has to be considered carefully. Indeed, it concerns different subspecies.

In the Brévine Valley, Arvicola was almost an exclusive prey at the beginning of the study and became an exceptional prey in 1979 and early 1980. Table 5 shows a compared analysis of the proportion of Arvicola from season to season. Three periods are distinguishable:

1. The Arvicola-dominated period, from fall 1976 - spring 1977, is significantly different from the following seasons.
2. Summer 1977 - spring 1978 was a transition period during which Arvicola was consumed in the proportion of a secondary prey. It is assumed that stoats exploited intensively the residual population islets. Winter 1978 is statistically closer to the 3rd period. The particular origin of this sample may explain it; the stoat from which all the scats came probably had a few water voles left in its home range and fed on other prey species, mainly Microtus (Table 3). Later, this season will be included in the 3rd period.
3. From summer 1978 Arvicola were scarce. It is difficult to determine if its contribution to the food habits of the stoats was constant because of the low number of scats analyzed and the fact that it occurred erratically. This period was called the grey voles-dominated period.

Table 5. Comparison of the seasonal proportion of *Arvicola* in the diet of stoats. (Double lines indicate the transition period)

	Winter 1977	Spring 1977	Summer 1977	Fall 1977	Winter 1978	Spring 1978	Summer 1978	Fall 1978	Spring 1979	Summer 1979	Fall 1979	Spring 1980
Fall 1976	-[a]	-	-	+[b]	++[c]	+	++	++	++	++	++	++
Winter 1977		-	+	+	++	++	++	++	++	++	++	++
Spring 1977			++	++	++	++	++	++	++	++	++	++
Summer 1977				-	++	-	++	-	-	++	++	++
Fall 1977					++	-	+	-	-	+	+	+
Winter 1978						+	-	-	-	-	-	-
Spring 1978							+	-	-	-	++	+
Summer 1978								-	-	-	-	-
Fall 1978									-	-	-	-
Spring 1979										-	-	-
Summer 1979											-	-
Fall 1979												-

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[a] - = insignificantly different ($p > 0.05$).

[b] + = significantly different ($0.05 > p > 0.01$).

[c] ++ = significantly different ($p < 0.01$).

Grey Voles. Little microtines, especially Microtus, are a common prey for stoats and ermines (Table 1). They were the dominant prey in "W meadows" of the Revinge area (Erlinge 1979). Grey voles are an important food supply for other Mustelids also; for instance, Mustela nivalis (see above), M. frenata and M. erminea (Fitzgerald 1977), Martes martes (Lockie 1961), Martes americana (Cowan and Mackay 1950, Weckwerth and Hawley 1962), Mustela vison (Gerell 1967), Genetta genetta (Cugnasse and Riols 1979).

Proportion of grey voles was analyzed comparing the 3 main periods as revealed by the analysis of the frequency of Arvicola:

1st period - 2nd period : $\chi^2 = 6.77; p < 0.01$

1st period - 3rd period : $\chi^2 = 114.5; p << 0.001$

2nd period - 3rd period : $\chi^2 = 118.3; p << 0.001$

Grey voles were scarce until fall 1977. Later they increased in number, both in the area and in the scats; but stoats never exploited them to the same extent as the water vole during the 1st period. This difference may be discussed regarding both the accessibility and the "profitability" of the voles. It is suggested that water voles together are easily accessible [stoats enter the tunnels as revealed by radio tracking (Erlinge 1979) and by personal observations] and energetically favorable (weights ranging from 60 - 120 g) and, therefore, can constitute the main diet of the stoat. On the other hand, Microtus are less accessible (smaller tunnel diameter) and less profitable (weights ranging from 15 - 50 g). Thus, during the transition period and the grey voles-dominated period other food supplies became more attractive and were more intensively exploited by stoats. This was especially relevant in summer, when birds are nesting, hares have young, and reptiles are active (Figure 5).

Other Prey. Other rodents (Apodemus, Mus, Eliomys, Muscardinus and Sciurus) were found in low numbers in the scats. They probably are eaten in the same order of frequency as they occurred in the area. Furthermore, these species are more or less forest rodents and stoats rarely were found to enter into this habitat (Debrot in prep.).

Lepus capensis were uncommon in scats and occurred only in summer. This suggests that mainly young are eaten. It is known that lagomorphs are an important prey for stoats when both rabbits and hares are present (Day 1968, Potts and Vickerman 1974, Tapper 1976, Brugge 1977, Erlinge 1979). As it is difficult to distinguish them by means of their hair remains (Day 1966, Brunner and Coman 1974), researchers could not specify their respective proportion in the diet. Day (1968) and Erlinge (1979) suggested that rabbit is rather dominant in food habits. This was confirmed in our results by the low number of hares, with rabbits being absent from this region.

Birds constitute the main prey class after the microtines. The structure of their remains in the scats (shells and feathers) suggested that stoats hunted birds mainly in nests. When sexual differences in the food pattern were examined (81 prey items for males and 23 for females) only the frequency of birds was significantly higher in males' food ($p = 0.038$). Such a sexual difference in the consumption of birds had never been found (Moors 1980).

Lizards are an uncommon prey for mustelids. Reptiles have been found twice in Mustela nivalis (Erlinge 1975), once in Mustela frenata (Simms 1979), in 4 occurrences in Genetta genetta (Cugnasse and Riols 1979), and in 8 scats from Martes foina (Delibes 1978). The large number of stone walls favorable to Lacerta vivipara and intensively used by stoats may be correlated with the occurrence of reptiles in the food.

As expected, insectivores were scarce in the food habits, although common in the field. Except in some cases, [e.g., Aldous and Manweiler 1942, Simms 1979 (for M. frenata only), Brugge 1977], mustelids avoid them and stoats neglected Sorex araneus in feeding tests (Erlinge 1979). Shrews may be attractive for some particular individuals (Erlinge, pers. comm.) and this could explain why they are found in scats and gut contents.

Reciprocal Averaging. The reciprocal averaging confirms the other analysis of the food habits and shows a general picture of the food pattern

(Figure 5). Furthermore it reveals some other aspects, particularly the seasonal variations. Although figures are often low, this method indicates a trend towards the diversification of the prey items eaten in summer and a food pattern closely related to Microtinae and Murinae in winter; fall and spring having an intermediate position. The exploitation of the prey of 3rd order is well illustrated during the 2 summers of the grey voles-dominated period (Figure 5, Group 3). Unfortunately, no summer period was included in the 1st period. However, it is reasonable to assume that Arvicola will be exploited intensively in the summer, if abundant.

From the analysis of the frequency of occurrence of the water vole (Table 5), it has been concluded that winter 1978 was closer to the 3rd period than to the transition period. The position of winter 1978 in Figure 5 confirms this assumption, even when all prey classes are taken into account. This particular case suggests that stoats did not modify simultaneously their food habits during the transition period,

Food Niche Width. The niche width given in Figure 4 was not constant during the time of the study. From fall 1976 - spring 1977 the small value of B_s indicates that the water vole population was rather intensively exploited. During this period stoats may be considered as stenophagous. When the population of Arvicola decreased B_s increased (summer 1977) to reach a relatively high value between 0.4 and 0.5 (spring 1977 - summer 1979). In comparison with the 1st period, the niche was that of a generalist (King and Moors 1979). From fall 1979, B_s decreased again because of the more intensive exploitation of the grey voles and the decline of the water voles.

CONCLUSIONS

The data reported in this paper indicate that the stoat populations are highly dependent on the fluctuations of its main prey (Figure 6). When no favorable prey species are available the stoat populations remain at low density exploiting a wide prey spectrum. However, if a profitable prey (Arvicola terrestris sherman in the Brévine Valley) is abundant stoats exploit it intensively, excluding other food supplies, and increase to a population of high density.

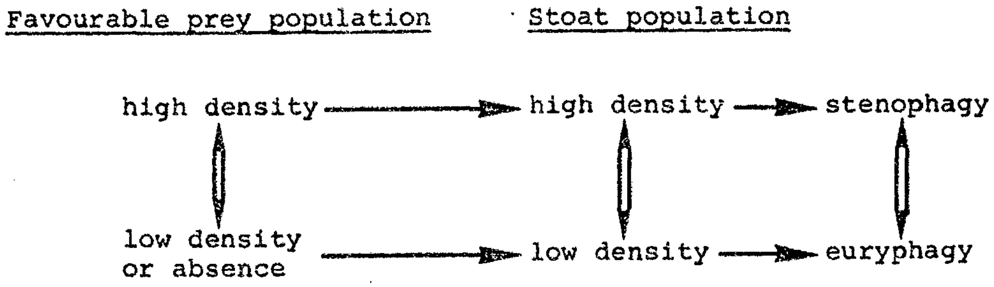

Figure 6. Causal sequences (single lines) in the prey-predator relations. (Double lines denote synchronized variations.)

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LITERATURE CITED

ALDOUS, S.E., and J. MANWEILER. 1942. The winter food habits of the short-tailed weasel in northern Minnesota. J. Mammal. 23:250-255.
ASPISOV, D.I., and V.A. POPOV. 1940. Factors influencing variations in the stoat population. Trud. Obshch. Estestvoispyt. pri. Kazan Univ. 56:3-4. (In Russian).
BRUGGE, T. 1977. Prey selection of weasel, stoat and polecat in relation to sex and size. Lutra 19:39-49. (In Dutch).
BRUNNER, H., and B. COMAN. 1974. The identification of mammalian hair. Inkata Press, Melbourne, Australia. 176 pp.
BUNNEL, F.L., S.F. MACLEAN, and J. BROWN. 1975. Barrow, Alaska, U.S.A. Pp. 73-124. In: Structure and function of tundra ecosystems (T. Rosswall and O.W. Heal, eds.). Ecol. Bull. No. 20.
CORBET, G.B. 1966. The terrestrial mammals of Western Europe. Foulis and Co., London, England. 264 pp.
COWAN, I.McT., and R.H. MACKAY. 1950. Food habits of marten (*Martes americana*) in the Rocky Mountain region of Canada. Can. Field. Nat. 64:100-104.
CUGNASSE, J.M., and C. RIOLS. 1979. Contribution à la connaissance du régime alimentaire hivernal de la genette, *Genetta genetta* L. O.N.C. Faune sauvage. Pp. 9-11.
DAY, M.G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. J. Zool., London 148:201-217.
———. 1968. Food habits of British stoats (*Mustela erminea*) and weasels (*Mustela nivalis*). J. Zool., London 155:485-497.

DELIBES, M. 1978. Feeding habits of the stone marten (Martes foina) (Erxleben 1777), in northern Burgos, Spain. Z. für Säugetierk. 43:282-288.

DEBROT, S., and C. MERMOD. 1981. Cranial helminth parasites of the stoat and other mustelids in Switzerland. Pp. In: Worldwide Furbearer Conference Proceedings (J.A. Chapman and D. Pursley, eds.). R.R. Donnelley and Sons Co., Falls Church, Virginia.

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

———. 1977a. Spacing strategy in stoat Mustela erminea. Oikos 28:32-42.

———. 1977b. Home range utilization and movements of the stoat, Mustela erminea. XIII Int'l. Congr. Game Biol. Pp. 31-42.

———. 1979. Adaptive significance of sexual dimorphism in weasels. Oikos 33:233-245.

FITZGERALD, B.M. 1977. Weasel predation on a cyclic population of the montane vole (Microtus montanus) in California. J. Anim. Ecol. 46:367-397.

GERELL, R. 1967. Food selection in relation to habitat in mink (Mustela vison Schreber) in Sweden. Oikos 18:233-246.

———. 1968. Food habits of the mink, Mustela vison Schreb., in Sweden. Viltrevy 5:119-211.

HABERT, M. 1975. Quinze années de lutte contre le campagnol terrestre dans le Jura et le Haut-Doubs. Phytoma 273:11-14.

HAMILTON, W.J. 1933. The weasels of New York. Am. Midl. Nat. 14:289-344.

HESPENHEIDE, H.A. 1975. Prey characteristics and predator niche width. Pp. 158-180. In: Ecology and evolution of communities (M.L. Cody and J.M. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts.

HEWSON, R., and T.D. HEALING. 1971. The stoat Mustela erminea and its prey. J. Zool., London 164:239-244.

HILL, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61:237-249.

HOWES, C.A. 1977. A survey of the food habits of stoats (Mustela erminea) and weasels (Mustela nivalis) in Yorkshire. Naturalist 102:117-121.

JONKEL, C.J. 1959. An ecological and physiological study of pine marten. M.S. Thesis. Montana St. Univ., Bozeman, Montana. 81 pp.

KALLIO, P. 1975. Kevo, Finland. Pp. 193-223. In: Structure and function of tundra ecosystems (T. Rosswall and O.W. Heal, eds.). Ecol. Bull. No. 20.

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

———, 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.

KLIMOV, Y.N. 1940. Data on the biology of the ermine. Trudy Biologicheskogo Instituta 7:80-88. (In Russian). Translated In: King, C.M. (ed.) 1975. Biology of mustelids: some Soviet research. British Lib. Lend. Div. Spa, Yorkshire, England. 266 pp.

KREBS, C.J., and J.H. MYERS. 1974. Population cycles in small mammals. Adv. Ecol. Res. 8:267-399.

LAVROV, N.P. 1944. Effect of helminth invasions and infectious diseases on variations in numbers of the ermine. Trudy tsentral'noi Laboratorii Biologii i Okhotnichego Prom. Nark. SSSR 6:151-163. (In Russian). (Transl. in King 1975).

———. 1956. Characteristics and causes of the prolonged depression in number of the ermine in forest-steppe and steppe zones of USSR. Trudy Vses. n-i-Inst. Okhotnichego Prom. 16:89-107. (In Russian). (Transl. in King 1975).

LOCKIE, J.D. 1961. The food of the pine marten, *Martes martes* in West Ross-shire, Scotland. Proc. Zool. Soc., London 136:187-195.

———. 1966. Territory in small carnivores. Symp. Zool. Soc., London 18:143-165.

MEYLAN, A. 1977. Fossorial forms of the water vole, *Arvicola terrestris* (L.), in Europe. EPPO Bull. 7:209-221.

———, and J.P. AIROLDI. 1975. Reproduction hivernale chez *Arvicola terrestris sherman* Shaw (Mammalia: Rodentia). Rev. Suisse Zool. 82:689-694.

MOORS, P.J. 1975. The food of weasels (*Mustela nivalis*) on farmland in northeast Scotland. J. Zool., London 177:455-461.

———. 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. Oikos 34:147-158.

MOREL, J., and A. MEYLAN. 1970. Une pullulation de campagnols terrestres (*Arvicola terrestris* L.) (Mammalia: Rodentia). Rev. Suisse Zool. 77:705-712.

MÜLLER, H. 1970. Beiträge zur Biologie des Hermelins (*Mustela erminea* L.). Säugetierk. Mitt. 18:293-380.

NORTHCOTT, T.H. 1971. Winter predation of *Mustela erminea* in northern Canada. Arctic 24:141-143.

NYHOLM, E.S. 1959. Stoats and weasels in their winter habitat. Suomen Riista 13:106-116. (In Finnish). (Transl. in King 1975).

POTTS, G.R., and G.P. VICKERMAN. 1974. Studies on the cereal ecosystem. Adv. Ecol. Res. 8:107-197.

QUICK, H.F. 1955. Food habits of marten (*Martes americana*) in northern British Columbia. Can. Field. Nat. 69:144-147.

ROSSWALL, T., J.G.K. FLOWER-ELLIS, L.G. JOHANSSON, S. JONSSON, B.E. RYDEN, and M. SONESSON. 1975. Stordalen (Abisko), Sweden. Pp. 265-294. *In*: Structure and function of tundra ecosystems (T. Rosswall and O.W. Heal, eds.). Ecol. Bull. No. 20.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Co., Kogakusha, Tokyo, Japan. 312 pp.

SIMMS, D.A. 1978. Spring and summer food habits of an ermine (*Mustela erminea*) in the central Arctic. Can. Field. Nat. 92:192-193.

———. 1979. North American weasels: resource utilization and distribution. Can. J. Zool. 57:504-520.

TAPPER, S.C. 1976. The diet of weasels, *Mustela nivalis* and stoats, *Mustela erminea* during early summer in relation to predation on gamebirds. J. Zool., London 179:219-224.

TIKHVINSKAYA, M.V., and P.K. GORSHKOV. 1971. The trophic relations of foxes and *Arvicola terrestris* L. in different landscape regions of the Tatar SSSR. Bull. Mosk. Obshch Isp. Prir. Otd. Biol. SSSR 76: 33-43. (In Russian).

WECKWERTH, R.P., and V.D. HAWLEY. 1962. Marten food habits and population fluctuations in Montana. J. Wildl. Manage. 26:55-74.

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Sylvain DEBROT et Claude MERMOD

Quelques Siphonaptères de Mustélidés, dont Rhadinopsylla pentacantha (Rothschild, 1897), nouvelle espèce pour la Suisse

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Quelques Siphonaptères de Mustélidés, dont *Rhadinopsylla pentacantha* (Rothschild, 1897), nouvelle espèce pour la Suisse[1]

par

Sylvain DEBROT et Claude MERMOD *

ABSTRACT

On some fleas (Siphonaptera) from Mustelidae, including the first record of Rhadinopsylla pentacantha **(Rothschild, 1897) from Switzerland.**—Fleas were collected from 397 Mustelids livetrapped and anaesthetized *(Mustela erminea, M. nivalis, M. putorius* and *Martes martes)*, over a period of 4 years, mainly in the Jura mountains. The 105 fleas belong to 14 species and subspecies from which 12 were recorded on stoat. One *Rhadinopsylla pentacantha* collected on a stoat is a new species from Switzerland. The species distribution of the fleas on stoats presented in this study is compared with those described in neighbouring countries. The record of fleas normally occurring on moles (*Ctenophthalmus b. bisoctodentatus, B. b. heselhausi* and *Palaeopsylla minor*), birds *(Dasypsyllus g. gallinulae)* or rats *(Nosopsyllus fasciatus)* suggests that the stoats were infested during their displacements rather than by contact with their prey.

INTRODUCTION

De l'automne 1976 à l'automne 1980, 2 populations d'hermines *(Mustela erminea* L.*)* ont été étudiées par capture-recapture. Quelques puces ont été récoltées au cours de la manipulation des animaux.

Les données sur les Siphonaptères de Mustélidés en Suisse sont rares et fragmentaires: Smit (1966) ne signale que 2 espèces *(Ctenocephalides f. felis* et *Ctenophthalmus*

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[1] Ce travail fait partie d'une thèse de doctorat présentée par S. Debrot sous la direction du Professeur C. Mermod. Il a été réalisé grâce à un subside du Fonds national suisse de la recherche scientifique (requête n° 3.685-76).

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agyrtes impavidus). Il nous a paru intéressant de signaler les espèces récoltées et de comparer nos résultats avec quelques travaux réalisés dans les pays voisins.

Bien que l'étude concerne principalement l'hermine, nous y avons associé les quelques données obtenues sur d'autres Mustélidés capturés.

MATÉRIEL ET MÉTHODES

Les animaux capturés ont été examinés en laboratoire sous narcose (DEBROT & MERMOD 1981) avant d'être relâchés. Les puces ont été récoltées régulièrement, bien qu'elles n'aient pas fait l'objet d'une recherche intensive. Il ne s'agit donc pas d'une récolte exhaustive, qu'il serait difficile de réaliser sur des animaux vivants, mais d'un échantillonnage. Le matériel présenté dans ce travail provient de 3 lieux différents (Tableau 1).

TABLEAU 1.

Nombre de Mustélidés capturés et examinés
(Nombre d'individus trouvés infestés par des puces) et provenance.

	Thun (BE)	Vallée de la Brévine (NE)	Val de Ruz (NE)
Mustela erminea	—	201 (10)	179 (36)
Mustela nivalis	2 (1)	—	7 (1)
Mustela putorius	—	—	6 (1)
Martes martes	—	—	1 (1)
Martes foina	—	—	1 (0)

RÉSULTATS

Les 105 puces déterminées appartiennent à 14 espèces et sous-espèces (Tableau 2): 12 ont été trouvées sur *M. erminea,* 3 sur *Mustela nivalis,* et *Monospyllus s. sciurorum* sur *Mustela putorius* et *Martes martes.*

Rhadinopsylla pentacantha est une nouvelle espèce pour la Suisse. De plus, à l'exception de *Megabothris walkeri* sur *M. nivalis, C. a. impavidus* sur *M. nivalis* et *M. erminea* et de *M. s. sciurorum* sur *M. martes,* toutes les autres espèces étaient inconnues en Suisse, sur les hôtes que nous avons examinés.

Aucune infestation massive n'a été observée à l'examen des 397 Mustélidés: les infestations les plus importantes ne dépassaient pas 10 puces, tant sur *M. erminea* que sur *M. nivalis.*

C. a. impavidus et *Ctenophthalmus b. bisoctodentatus* sont les deux espèces dominantes sur *M. erminea,* et représentent respectivement 27,2% et 51,1% des puces récoltées.

DISCUSSION ET CONCLUSION

R. pentacantha est une puce qui a été signalée relativement fréquemment sur les Mustélidés du genre *Mustela*: BEAUCOURNU (1973), ARTZ (1975), KING (1976) et MARDON & MOORS (1977) l'ont trouvée sur *M. nivalis*; MARDON & MOORS (1977) l'ont également

TABLEAU 2.

Siphonaptères récoltés sur Mustélidés dans le Jura neuchâtelois et la région de Thun, de 1976 à 1980.

	M. erminea			*M. nivalis*			*M. putorius*			*M. martes*		
	nb. de ♂	nb. de ♀	nb. d'hôtes infestés	nb. de ♂	nb. de ♀	nb. d'bôtes infestés	nb. de ♂	nb. de ♀	nb. d'hôtes infestés	nb. de ♂	nb. de ♀	nb. d'hôtes infestés
Ctenophthalmus agyrtes impavidus Jordan, 1928	6	19	15		1	1						
Ctenophthalmus b. bisoctodentatus Kolenati, 1863	15	32	20		1	1						
Ctenophthalmus bisoctodentatus heselhausi (Oudemans, 1914)	1	2	3									
Ctenophthalmus s. solutus Jordan & Rothschild, 1920		1	1									
Dasypsyllus g. gallinulae (Dale, 1878)	1		1									
Hystrichopsylla talpae ssp.		2	2									
Hystrichopsylla t. talpae (Curtis, 1826)	1		1									
Megabothris turbidus (Rothschild, 1909)	1		1									
Megabothris walkeri (Rothschild, 1902)				6	3	1						
Monopsyllus s. sciurorum (Schrank, 1803)	1	5	4					1	1		1	1
Nosopsyllus fasciatus (Bosc, 1800)		1	1									
Palaeopsylla minor (Dale, 1878)	1	1	2									
Peromyscopsylla bidentata (Kolenati, 1863)	1		1									
Rhadinopsylla pentacantha (Rothschild, 1897)		1	1									

TABLEAU 3.

Puces identifiées sur Mustela erminea *dans quelques pays européens.*

	présent travail	Artz (1975)	Beaucournu (1973)	Biocca *et al.* (1975)	George (1977)	Mardon & Moors (1977)	Smit (1966)
Amphipsylla sp.				×			
Callopsylla saxatilis				×			
Ceratophyllus garei		×					
Ceratophyllus lunatus			×				
Chaetopsylla homoea			×	×			
Ctenocephalides felis							×
Ctenophthalmus agyrtes	×	×					×
Ctenophthalmus assimilis		×					
Ctenophthalmus bisoctodentatus	×	×	×				
Ctenophthalmus nivalis			×				
Ctenophthalmus solutus	×						
Ctenophthalmus sp.			×				
Ctenophthalmus uncinatus		×					
Dasypsyllus gallinulae	×	×					
Hystrichopsylla talpae	×	×			×		
Malareus penicilliger			×	×			
Megabothris rectangulatus						×	
Megabothris turbidus	×	×					
Megabothris walkeri		×					
Monopsyllus sciurorum	×		×				
Nosopsyllus fasciatus	×	×					
Palaeopsylla minor	×	×					
Peromyscopsylla bidentata	×						
Peromyscopsylla spectabilis			×				
Rhadinopsylla mesa			×				
Rhadinopsylla pentacantha	×					×	

NB. Dans ce tableau, il n'a pas été tenu compte des sous-espèces.

signalée sur *M. erminea*; Smit (1957) et Walton & Page (1970) l'ont récoltée sur *M. putorius*. L'exemplaire que nous avons identifié est une ♀ récoltée sur l'hermine ♂ (A50), capturée en avril 1978 dans les tourbières du Cachot (Vallée de la Brévine). Cependant, *R. pentacantha* est connue comme une puce de nid qui n'est que rarement transportée par l'hôte qu'elle parasite. Artz (1975) en a récolté 6 exemplaires sur 691 rongeurs, alors que l'examen de 83 nids de *Microtus arvalis* lui a permis d'en dénombrer 117. Nous pensons que c'est par cette caractéristique de son écologie que sa présence a, jusqu'à aujourd'hui, échappé aux zoologistes suisses.

On l'a trouvée en effet dans les pays voisins de la Suisse: la France, l'Allemagne, l'Autriche et l'Italie. Elle est signalée d'autre part des pays suivants: Belgique, Danemark, Espagne, Grande-Bretagne, Hongrie, Irlande, Pays-Bas, Pologne, Roumanie, Suède (Sud), Tchécoslovaquie, Yougoslavie.

Nos résultats confirment ceux de BEAUCOURNU (1973) qui n'a pas trouvé de puce spécifique à l'hermine en dehors des Alpes. En effet, les espèces que nous avons identifiées ont pour hôte principal des oiseaux *(Dasypsyllus g. gallinulae)*, la taupe *(C. b. bisoctodentatus, C. b. heselhausi* et *Palaeopsylla minor)*, les rats *(Nosopsyllus fasciatus)*, ou différentes espèces de rongeurs, selon un degré de spécificité variable.

Nous n'avons trouvé qu'une seule des deux espèces de puce que SMIT (1966) connaissait sur l'hermine en Suisse, par contre, nous avons rencontré une diversité d'espèces comparable à ce que signalent d'autres auteurs dans les pays voisins (Tableau 3).

Notre spectre d'espèces se rapproche plus de celui décrit par ARTZ (1975) pour l'Allemagne du Nord que de ceux observés en France (BEAUCOURNU 1973) ou dans le Parc National du Gran Paradiso en Italie (BIOCCA, BALBO & COSTANTINI 1975).

La distribution des espèces sur *M. erminea* suggère qu'elles acquièrent leurs puces plus au cours des déplacements (exploration des galeries et des nids de micromammifères) et sur les sites de repos, que par contact direct avec leurs proies. Nous avons par exemple déterminé 3 espèces de parasites inféodés à *Talpa europaea (C. b. bisoctodentatus, C. b. heselhausi* et *P. minor)* alors que la taupe est une proie accidentelle: 5 cas sur 690 proies identifiées (DEBROT 1981). Ces résultats confirment ceux de KING (1976) obtenus sur *M. nivalis* en Grande Bretagne et sur *M. erminea* en Nouvelle Zélande.

RÉSUMÉ

Des puces ont été récoltées principalement dans le Jura neuchâtelois sur 397 Mustélidés capturés et endormis *(Mustela erminea, M. nivalis, M. putorius* et *Martes martes)*, pendant une période de 4 ans. Les 105 Siphonaptères récoltés appartiennent à 14 espèces et sous-espèces, dont 12 ont été identifiées sur l'hermine. Un exemplaire de *Rhadinopsylla pentacantha* trouvé sur une hermine représente une nouvelle espèce pour la Suisse. Le spectre des espèces déterminées dans ce travail est comparé à ceux des pays voisins. Il est probable que la présence de puces de taupes *(Ctenophthalmus b. bisoctodentatus, C. b. heselhausi* et *Palaeopsylla minor)*, d'oiseaux *(Dasypsyllus g. gallinulae)* ou de rats *(Nosopsyllus fasciatus)* est due à des infestations de l'hôte au cours de ses déplacements et non par contact avec ses proies.

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BIBLIOGRAPHIE

ARTZ, V. 1975. Zur Synökologie der Ektoparasiten von Kleinsäugern in Norddeutschland (Siphonaptera, Phthiraptera, Acarina, Coleoptera: Leptinidae). *Entomol. ger.* 1: 105-143.

BEAUCOURNU, J.-C. 1973. Notes sur les Siphonaptères parasites de Carnivores en France. *Annls Parasit. hum. comp.* 48: 497-516.

BIOCCA, E., T. BALBO & R. COSTANTINI. 1975. Osservazioni sulle pulci dei micromammiferi del Parco Nazionale del Gran Parasidio (Alpi Occidentali Italiane). *Parassitologia, Roma* 17: 103-120.

DEBROT, S. 1981. Trophic relations between the stoat *(Mustela erminea)* and its prey, mainly the water vole *(Arvicola terrestris scherman). Worldwide Furbearer Conf. Proc., Frostburg, Maryland (J. A. Chapman & D. Pursley, eds), volume II:* 1259-1289. *R. R. Donnelley and Sons Co. Falls Church, Virginia.*

DEBROT, S. & C. MERMOD. 1981. Cranial helminth parasites of the stoat and other Mustelids in Switzerland. *Worldwide Furbearer Conf. Proc., Frostburg, Maryland (J. A. Chapman & D. Pursley, eds), volume II:* 690-705. *R. R. Donnelley and Sons Co. Falls Church, Virginia.*

GEORGE, R. S. 1977. Some fleas (Siphonaptera) of interest in the Bolton Museum. *Entomologist's Gaz.* 28: 275-276.

KING, C. M. 1976. The fleas of a population of weasels in Wytham Woods, Oxford. *J. Zool., Lond.* 180: 525-535.

MARDON, D. K. & P. J. MOORS. 1977. Records of fleas collected from weasels (*Mustela nivalis* L.) in north-east Scotland (Siphonaptera: Hystrichopsyllidae and Ceratophyllidae). *Entomologist's Gaz.* 28: 277-280.

SMIT, F. G. A. M. 1957. The recorded distribution and hosts of Siphonaptera in Britain. *Entomologist's Gaz.* 8: 45-75.

— 1966. Insecta helvetica. I: Siphonaptera. *Imprimerie de la Concorde, Lausanne.* 107 pp.

WALTON, K. C. & R. J. C. PAGE. 1970. Some ectoparasites found on polecats in Britain. *Nature Wales* 12: 32-34.

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Oecologia

The spatial and temporal distribution pattern of the stoat (*Mustela erminea* L.)*

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Summary. The distribution and movements of two stoat populations were studied by capture-recapture and tracking in the Swiss Jura Mountains. On the Brévine area in summer 1977 the population was at a high density phase and evenly distributed. A well established intrasexual territorial system was observed, with a high degree of sedentarity in adults. During the decline and the following phase of scarcity, the stoats were progressively restricted to a peat-bog area and the territorial system broke down. The adult males became transient and a high degree of dispersal was recorded among the juveniles. On the Val de Ruz area, the population was fairly stable and the stoats had home ranges and movements adapted to habitat characteristics. Adult males in March–April and juveniles moved around considerably. These aspects of the spatio-temporal distribution pattern of *Mustela erminea* are discussed in relation to the main factors affecting it, such as population density, habitat, sex and age, activity, and seasons.

Introduction

In his review of territoriality in small carnivores, Lockie (1966) stated that the task was "fairly easy since the literature is meagre". During the 1970s our knowledge of this subject was increased by several studies of which Powell (1979) made an extensive review: the Mustelids of the genus *Mustela* and *Martes* have developed a system of intra- and intersexual relationships, setting up well-defined patterns of spatial distribution. Although most studies described populations in a fairly stable state, Erlinge (1974) and Moors (1974) found that ecological factors such as food availability and habitat (King 1975) affect the territorial pattern of weasels, and Powell (1979) concluded that territoriality may break down under certain conditions.

Our investigations on two stoat populations were mainly concerned with some factors affecting them, such as food supply and feeding habits (Debrot 1981), parasitism (Debrot and Mermod 1981, 1982), and population fluctuations (Debrot in press). In this paper, we present some results showing the connection of the spacing pattern in the stoat with population parameters, and changes in these over time.

Space utilization by the stoat has been mainly studied by investigations on small numbers of animals (Nyholm 1959; Lockie 1966; Vaisfeld 1972; Erlinge 1977a, c, 1979a; Simms 1979). The results presented here deal with the distribution and mobility of larger groups of stoats, designated here as populations for convenience.

Study areas and methods

Stoat populations were investigated in two valleys of the Jura Mountains, Switzerland.

1. Brévine area

This 1,875-ha trapping area (47°01′N, 6°40′E; alt. 1,000–1,200 m) consists of 47% open fields mowed or grazed by cattle, 19% wooded pastures and 31% forests. A very restricted part of the area is cultivated. Small peat-bogs in the bottom of the valley and 86 km of stone walls offer good shelter to stoats. Live-trapping was conducted from March 1977 to September 1980, with two or three sessions each year. A more intensive trapping effort was achieved in a restricted area, including peat-bogs.

2. Val de Ruz area

The Val de Ruz is dominated by agricultural activities, covering 77% of the study area (47°02′N, 6°55′E; alt. 670–740 m). The traps were mainly set along a brook and its several tributaries bordered with trees and bushes, and around small mixed woodlands. This 616-ha study area was investigated during most months between April 1978 and April 1981.

3. Trapping and handling

The stoat populations were investigated by live-trapping, using large wooden treadle-traps (85 × 16 × 24 cm) baited with dead or live laboratory mice. Sixty traps were usually set during 5-day sessions in order to obtain 4 trap-units (*t-u*) per trap. One session was sufficient for the Val de Ruz area, while the Brévine area was investigated in four successive sessions. The traps were examined twice a day, early in the morning and late in the afternoon. Captured

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** Present address and offprint requests to: S. Debrot, Institut of Zoology, University of Fribourg, Switzerland animals were transferred to the laboratory, anaesthetized and marked (Debrot and Mermod 1981). Recaptured stoats were examined, weighed, and released immediately at the capture site.

Age and sex were determined by examination and X-ray photographs (Erlinge 1977a; Mermod and Debrot 1978). The stoats were considered "juveniles" if born in the current year and independent.

Complementary information was gathered from snow tracking on the two areas during the cold season and from collecting scats throughout the year.

Results

In the Brévine area, 36 trapping sessions gave 194 captures of 87 stoats, with 7,791 *t-u*. In the Val de Ruz 7,276 *t-u* gave 178 captures of 95 individuals, over 39 sessions. Part of this trapping effort (1,552 *t-u*) was beyond the study area, in order to collect data on longer distance movements.

1. Population density

In the Brévine area, a high density of stoats was observed in summer 1977 when the rate of capture was 6.8 captures/100 *t-u*. Since autumn 1977 the population has decreased drastically, and the rate of capture was 3.5 in autumn 1977, 1.6 in summer 1978, 0.8 in autumn 1978, 0.7 in summer 1979 and 0.4 in autumn 1980. In the other area, the population was fairly stable from spring 1978 to spring 1981, with a mean rate of capture of 2.6 captures/100 *t-u*.

2. Space occupation

Brévine area. During the high density phase, stoats were captured almost all over the area, in all habitats except forest, and an intrasexual territorial system was observed (Fig. 1). Three separated home ranges of resident males and three of resident females were identified in the peat-bog region, with large portions of overlap between the sexes. Movements of juvenile males between the male home ranges are indicated.

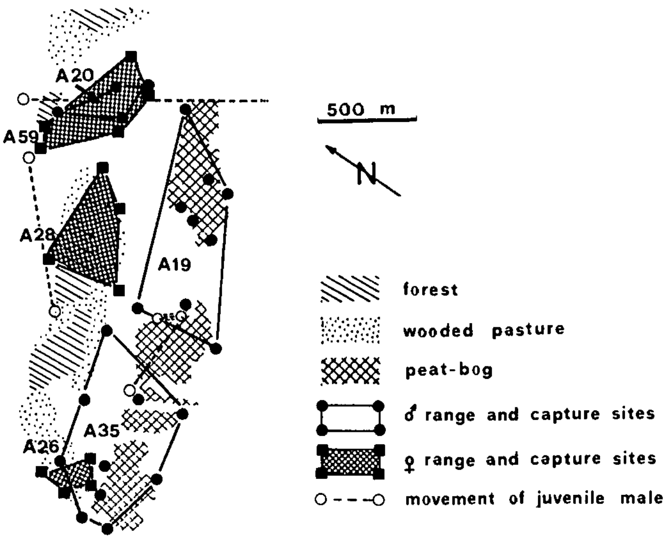

Fig. 1. Estimated home ranges of stoats in the Brévine area, summer and autumn 1977. Numbers refer to individuals

During the population decrease, the stoats were progressively restricted to the vicinity of the peat-bog habitat. The adult male A35 was identified as resident in summer 1978, and the adult female A85 was captured four times in the peat-bog area in 1978. Apart from these cases, no animal of resident status was identified among the captured stoats from 1978 to 1980.

Val de Ruz area. The home ranges generally had linear shapes along the brooks and hedgerows, and the stoats travelled mainly along them. Trapping results and snow tracking indicate that they also exploited the surrounding fields and tillages as hunting areas.

3. Movements and dispersal

Distances between the first site of capture and subsequent ones were measured and related to the interval of time between these two events. The proportion of the stoats recaptured at less than 1,000 m around their first capture site gives an estimate of the degree of sedentarity of the population. This proportion was 68.3% ($N = 205$) when computed for the two areas (69.7% for adult males, 94.3% for adult females, 39.5% for juvenile males and 69.6% for juvenile females). Significant differences were found between adults and juveniles ($P < 0.001$, χ^2test with Yate correction), males and females ($P < 0.005$, χ^2test with Yate correction), adult males and adult females ($P = 0.0027$, Fisher exact probability test) and between juvenile males and juvenile females ($P = 0.034$, Fisher exact probability test). Similar degrees of sedentarity were observed ($P > 0.3$, χ^2test with Yate correction) when short-term movements (during the first month of capture) and longer ones were compared.

a) Sedentarity. A few home ranges were identified by capture-recapture (Fig. 1) and, although they are probably under-estimated in extent (few recaptures, few cases, and conservative method), they provide an estimate of the maximum linear distances travelled by resident stoats (Table 1).

b) Particular movements. Male stoats exhibited intensive locomotor activity in spring, mainly in March and April. The adult male E33 was captured in January, February, and September 1979 near a pool in the Val de Ruz and snow tracking confirmed his resident status in winter. On March 1980, he was recaptured in the main study area, 3 km from his last capture site. The adult male A35 provides another exemple. He was captured 24 times in the same area (Table 1) in July, August, and October 1977 and in June and July 1978. His resident status was obvious during these two periods. However trapping occurred in April 1978 without capturing him. Snow tracking and scat collecting confirmed the absence of stoats in March–April in his area.

The movements of male stoats during March–April in the Val de Ruz in 1979 and 1980 are illustrated in Fig. 2. The distances travelled by males from their first capture site in March–April are indicated in Fig. 3C.

We found great mobility in juvenile stoats too (Fig. 3A, B, C). Large movements were observed and a high degree of dispersal. Only 15% of the juveniles captured in the study area were trapped there the next year (Table 2) and even fewer were recaptured during the following breeding season (May onwards).

c) Movements related to population density. During the high density phase in the Brévine area in 1977, the stoats were

Table 1. Estimated home ranges of stoats, identified by capture-recapture in the Brévine Valley

Stoat No.	Season		No. of captures	Home range estimates[a] (ha)	Maximum diameter (m)	Habitat caracteristics
A. Males						
A 19	July–August	1977	11	16.5	950	mainly peat-bogs.
A 35	July–August	1977	6	14.8	900	peat-bogs and pastures.
A 35	October	1977	6	8.8	650	peat-bogs and partly wooded pastures.
A 35	June–July	1978	12	9.7	650	peat-bogs and partly wooded pastures.
A 43	July–September	1977	9	39.6	1,050	partly wooded pastures and forest (22.3 ha)
A 48	July–October	1977	4	36.6	1,350	partly wooded pastures and forest (24.3 ha)
B. Females						
A 26	July–October	1977	4	1.6	375	partly wooded pastures.
A 28	July–October	1977	4	7.4	550	wooded pastures and forest (2.7 ha)
A 59	August–October	1977	5	6.4	625	pastures.

[a] Minimum area method

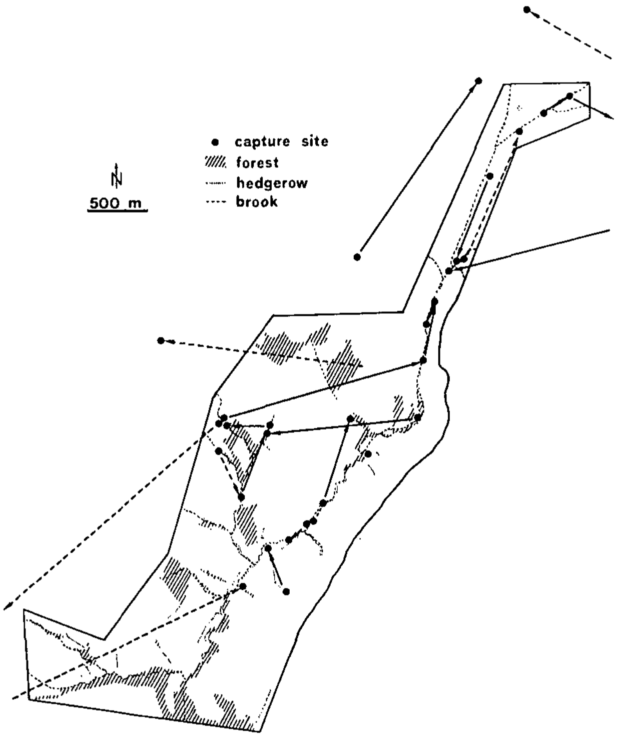

Fig. 2. Movements of adult male stoats (unbroken arrows) in March–April 1979 and 1980 on and around the Val de Ruz area. Broken arrows indicate movements from the previous or to the next capture site

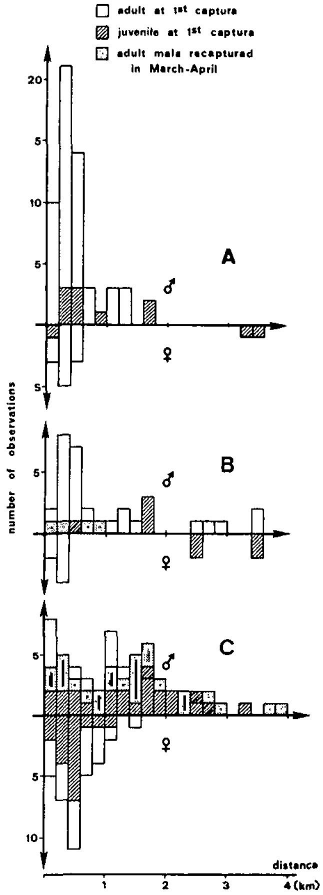

Fig. 3A–C. Diagram of dispersal of the stoats. Distances are calculated linearly from first capture to recapture sites, and related to the age of the individual at first capture. A Brévine area, 1977 (phase of high density); B Brévine area, 1978–1980 (phase of scarcity); C Val de Ruz area, 1978–1981

mostly recaptured in the close vicinity of their first capture site (Fig. 3A). At this time, the greatest recorded movements were for adult males and adult females, 1,350 m and 500 m respectively. The juvenile female A32, marked and released in July, was recaptured twice in October more than 3 km from her first capture site.

During the phase of scarcity, since 1978, the diagram of dispersal (Fig. 3B) was significantly different for the adult males ($P<0.025$, χ^2 test) but not for the adult females ($P>0.9$, χ^2 test). The juvenile females also exhibited a high degree of dispersal.

In the Val de Ruz area, we recorded large movements by juvenile males and by adult males during March and April (Fig. 3C). On the other hand, adult and juvenile females and adult males outside the spring period show a high degree of sedentarity. However, in this valley, the movements made by adult females are greater than in the Brévine area ($P<0.025$, χ^2 test).

Table 2. Dispersal of the juvenile stoats captured on the two study areas

Study area	Sex	No. of juvenile stoats captured	No. of individuals recaptured as adults	No. of individuals recaptured the next breeding season
Val de Ruz	♂	22	3	0
Val de Ruz	♀	15	5	2
Brévine	♂	12	1	1
Brévine	♀	16	1	1
Total		65	10	4

Discussion

The spatio-temporal distribution of stoats appears to be governed by several factors such as population density, age and sex, habitat, and season.

1. Population density

High density. The study of the feeding habits of the stoat population during the high density phase, the following decrease, and the phase of scarcity in the Brévine area (Debrot 1981) revealed its close relation to the water vole *Arvicola terrestris scherman.* Parallel but out of phase prey and predator oscillations have been observed in this region over more than 25 years (Debrot, in press).

During the high density phase, the stoat population appears to display a typical intrasexual territorial system (the term territory is used here in its ethological sense, since defence has been clearly demonstrated (Lockie 1966; Erlinge 1977b) with agonistic behaviour, scent marking and/or social contact). This implies territoriality of males against males and of females against females, and territorial overlap between the sexes (Lockie 1966). Moreover, the juvenile males appear to be forced by adult resident males to peripheral areas, which are probably less favourable, with lower food supplies and/or less shelter (Erlinge 1977a and Fig. 1). This typical spacing pattern has been observed in several species of Mustelinae (Powell 1979). However, such a territorial system tolerates partial intrasexual overlaps, which may sometimes be important (Simms 1979): exclusive territoriality might be too costly in energy (King 1975), especially for small carnivores such as *M. erminea* and *M. nivalis.*

The estimated sizes of home ranges (Table 1) are comparable with those described by Nyholm (1959) with 34.2 ha for males and 7.4 ha for females, Erlinge (1977a) with 4.5 and 7 ha for females, and Simms (1979) with 21.3 ha for males and 8.3 ha for females, in spite of the different methods used. Vaisfeld (1972) however reports larger home ranges, up to 160 ha for males and up to 124 ha for females.

The maximum estimated diameters (Table 1) are similar to the maximum distances of dispersal recorded in 1977 (Fig. 3A). These results suggest that most adults are resident during high density phases.

In populations of high or medium density (i.e. Val de Ruz), the juvenile females did not show long distance dispersal (Fig. 3C). This confirms the prediction of Erlinge (1977a): a juvenile female would probably settle in the nearest area providing food *and* shelter.

Low density. Few data are available on low density populations in Mustelids. Powell (1979) supposes a minimum supply of food to be necessary for territoriality to exist. In fact, poor food conditions lead to low predator density (Lockie 1966; Erlinge 1974; Debrot 1981) and low predator density implies few or no social contacts, suppressing the active defence of the home range. Erlinge (1977c) reports that female stoats use larger areas when small rodents are scarce.

Our results imply that in a low density phase due to very low density of the water vole, when the stoats feed mainly on *Microtus* sp. (Debrot 1981), the territorial system breaks down and male stoats behave essentially as transients (Fig. 3B). The females remain in limited areas (Fig. 3B), exploiting the most favourable habitat, such as the peat-bog area in the Brévine valley.

Erlinge (1977a) reports that juvenile females tend to remain close to their birth-place (see above). Ten juvenile females were captured in summer 1977 and only one (A32) was recaptured later: she had moved more than 3 km from her first capture site (Fig. 3A). The other movements of juvenile females in the Brévine area were fairly large too (Fig. 3B). It is possible that the conditions necessary to induce sedentarity (i.e. sufficient food, shelter) by juvenile females have not been fulfilled since autumn 1977.

2. Habitat

Lockie (1966) noted that the extent of home ranges was not reduced when the number of voles increased from 45 to 220 individuals/ha. Nyholm (1959), Vaisfeld (1972) and Erlinge (1977c) report however that home ranges were larger when voles became scarce.

We found habitat characteristics to be another factor affecting home range sizes. Two large home ranges were identified among the males (Table 1), both covering a large amount of spruce forest. The wood-free portion (17.3 ha for A43 and 12.3 ha for A48) was of the same order of size as the other home ranges observed in open areas. In high density populations, when most favourable habitats are occupied, stoats may establish residence in remaining areas and compensate for unfavourable conditions by increasing home ranges.

The shape of the home ranges appears to vary from place to place. They were more linear in the Val de Ruz than in the Brévine area. Erlinge (1977a) estimates their size in distances of stone walls in a farmland area, and Simms (1979) reports that "resident ermines" established themselves in "early successional communities" and avoided more mature ones. This may explain the significantly larger movements observed for females in the Val de Ruz area (Fig. 3C).

3. Sexual activity

The increasing activity of male Mustelinae in spring and summer has been reported by several authors (Lockie 1966; Gerell 1970; Moors 1974; Erlinge 1974, 1977a, 1979a). Similar observations were made in the two study areas, especially in the Val de Ruz where intensive trapping occurred in spring (Fig. 2). Dispersal movements up to 4 km were recorded by males (Fig. 3C), and they may cover larger distances; the size of the study area was the main limiting factor for our observations. This particular activity pattern of males in March-April is related to a change of the day-night activity rhythm (Debrot et al., in prep.). At this time, males are more active during the day than females.

In March–April, male stoats are not able to reproduce (Danilov and Tumanov 1972; Gulamhusein 1972; Gulamhusein and Tam 1974) since spermatozoa are not found in the *corda epididymidis* until May, and the mating period extends in Switzerland from June to August (Müller 1970). Thus, the intensive locomotor activity of the males in spring is probably related to a restructuring of the spatial distribution of the stoats. This may be due to the effect of the newly arrived cohort – the "one-year-old males" (Erlinge 1977a) – on the reproductive system of the population. This redistribution of the males appears to be of selective advantage to the more dominant males: they establish themselves in ranges including more females for the future mating period (Erlinge 1979b).

4. Age and sex

Different spatio-temporal strategies depend on sex and age classes. This is clearly illustrated in Fig. 3 and by the significant differences revealed by the pattern of dispersal. The high degree of mobility of the juveniles, the differential rate of mortality, and the renewal of the population will be developed elsewhere (Debrot, in prep.).

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References

Danilov PI, Tumanov IL (1972) Male reproductive cycles in the Mustelidae, In: King CM (ed) Biology of Mustelids, some Soviet research: vol 2 (1980), Sciences Information Division, Dpt Scientific and Industrial Research, Wellington, New Zealand, pp 70–80

Debrot S (1981) Trophic relations between the stoat (*Mustela erminea*) and its prey, mainly the water vole (*Arvicola terrestris scherman*). In: Chapman JA, Pursley D (eds) Worldwide Furbearer Conf Proc, Vol II, pp 1259–1289

Debrot S (in press) Fluctuations de populations chez l'hermine (*Mustela erminea* L.). Mammalia 47

Debrot S, Mermod C (1981) Cranial helminth parasites of the stoats and other mustelids in Switzerland. In: Chapman JA, Pursley D (eds) Worldwide Furbearer Conf Proc, Vol II, pp 690–705

Debrot S, Mermod C (1982) Quelques Siphonaptères de Mustélidés, dont *Rhadinopsylla pentacantha* (Rothschild 1897), nouvelle espèce pour la Suisse. Rev suisse Zool 89:27–32

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

Erlinge S (1977a) Spacing strategy in stoat *Mustela erminea.* Oikos 28:32–42

Erlinge S (1977b) Agonistic behaviour and dominance in stoats (*Mustela erminea* L). Z Tierpsychol 44:375–388

Erlinge S (1977c) Home range utilization and movements of the stoat, *Mustela erminea.* Wildl Biology and Ethology, XIIIth Congress of Game Biologists, pp 31–42

Erlinge S (1979a) Movements and daily activity pattern of radio tracked male stoats, *Mustela erminea.* In: Amlaner CJ Jr, MacDonald DW (eds) A handbook on biotelemetry and radio tracking, Pergamon Press, Oxford and New York, pp 703–710

Erlinge S (1979b) Adaptative significance of sexual dimorphism in weasels. Oikos 33:233–245

Gerell R (1970) Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. Oikos 21:160–173

Gulamhusein AP (1972) Reproductive studies in the stoat. J Zool 166:574–576

Gulamhusein AP, Tam WH (1974) Reproduction in the male stoat *Mustela erminea.* J Reprod Fert 41:303–312

King CM (1975) The home range of the weasel *Mustela nivalis* in an English woodland. J Anim Ecol 44:639–669

Lockie JD (1966) Territory in small carnivores. Symp zool Soc Lond 18:143–165

Mermod C, Debrot S (1978) Morphométrie crânienne par radiographie. I: Problèmes techniques. Rev suisse Zool 85:730–738

Moors PJ (1974) The annual energy budget of a weasel (*Mustela nivalis* L.) population in farmland. Unpubl Ph D Thesis, Univ Aberdeen, Scotland

Müller H (1970) Beiträge zur Biologie des Hermelins (*Mustela erminea* L.). Säugetierk Mitt 18:293–380

Nyholm ES (1959) Stoats and weasels and their winter habitats. In: King CM (ed) Biology of mustelids: some Soviet research, British Library Lending Division, Boston Spa Yorks (1975) pp 18–31

Powell RA (1979) Mustelids spacing pattern: variations on a theme by *Mustela.* Z Tierpsychol 50:153–165

Simms DA (1979) Studies of an ermine population in southern Ontario. Can J Zool 57:824–832

Vaisfeld MA (1972) Ecology of the ermine in the cold season in the European North. In: King CM (ed) Biology of Mustelids, some Soviet research: vol 2 (1980), Sciences Information Division, Dpt Scientific and Industrial Research, Wellington, New Zealand, pp 1–10

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Experimental field evidence of interspecific aggression between two species of kangaroo rat (*Dipodomys*)

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Summary. The competitive coexistence of heteromyid rodents has been primarily ascribed to differential utilization of resources such as microhabitats and seeds. An examination of the use of space by the kangaroo rat *Dipodomys merriami* indicates this species is aggressively subordinate to a larger species, *Dipodomys spectabilis* and is excluded from the larger species home range during the critical fall harvesting season. These experiments suggest that interspecific aggression may be involved in the coexistence of these species. Additional evidence is presented that small scale spatial variations in resource productivity may promote the coexistence of these two species.

Introduction

During the past twelve years ecologists have focused considerable attention on elucidating the structure of Heteromyid rodent communities (see Brown, 1979 and Rosenzweig, 1977 for reviews). Three major hypotheses regarding the mechanisms of competitive coexistence have emerged from these efforts: differential microhabitat selection (Rosenzweig and Winakur 1969; Brown 1973; Brown and Lieberman 1973; Rosenzweig 1973; Brown 1975; Schroder and Rosenzweig 1975; Lemen and Rosenzweig 1974; Whitford 1978), seed size selection (Rosenzweig and Sterner 1970; Brown and Lieberman 1973; Smigel and Rosenzweig 1974; Mares and Williams 1977; Hutto 1978; Lemen 1978), and seed distribution (clump size) selection (Wondolleck 1975; Reichman and Oberstein 1977; Hutto 1978; Price 1978; Frye and Rosenzweig 1980). These hypotheses implicitly assume that the fundamental nature of the competitive process is exploitative. My own initial research (Frye and Rosenzweig 1980) was also based on this assumption. The inadequacy of my research to explain the competitive coexistence of *Dipodomys spectabilis* (120 gm.) and *D. merriami* (40 gm.) led me to reevaluate this assumption and I subsequently hypothesized that direct interference competition may play a role.

The aggressive nature of Heteromyid rodents under laboratory conditions has been documented for the last thrity years (Bartholemew and Caswell 1951; MacMillen 1964; Bateman 1967; Christopher 1973; Congdon 1974; Blaustein and Risser 1976; Ambrose and Meehan 1977) and is well known to all who have kept these species in the laboratory.

Evidence of aggression between Heteromyids under field conditions has also not been lacking, although these data are of an inferential or anecdotal nature. Grinnell (1932) noted that *Dipodomys ingens*, the largest of the kangaroo rats, was found only in exclusive areas devoid of any other nocturnal granivorous rodent species even though *D. nitratoides* and *D. heermani* (Tappe 1941; Hawbecker 1944) could be found immediately adjacent to these exclusive areas. Further, Shaw (1934) observed *D. ingens* attack and drive off an individual of the genus *Peromyscus*. Such chases have also been noted between *D. merriami* and *D. microps* (Kenagy 1976) and *D. merriami* and *Perognathus amplus* (Wondolleck 1975). Observing a baited area, Congdon (1974) found that *D. deserti* chased the smaller *D. merriami* and both kangaroo rats would drive off the confamiliar *Perognathus longimembris*.

Stronger evidence of interspecific aggression was gathered by Wondolleck (1978) during a foregoing microhabitat study. He found when he removed *D. merriami, Perognathus amplus* – which in the presence of *D. merriami* avoided open habitats – altered its response: it used the open microhabitat to an extent equal to the other microhabitats recognized in his study. Recently, Cliff Lemen and Patricia Freeman (pers. comm.), using removal experiments, have found that when *D. merriami* and *D. ordii* were removed from an area, *Perognathus* species invaded within two weeks.

Strong evidence does exist for the occurence of intraspecific aggression within populations of *D. spectabilis*. Schroder and Geluso (1973) found that active *D. spectabilis* mounds were uniformly distributed. Using radiotracking techniques, Schroder (1979) then demonstrated that individual *D. spectabilis* occupy intraspecifically exclusive territories.

This evidence led me to conduct preliminary live trapping experiments. The results, though not statistically significant, reinforced my suspicions and I designed the following experiments. Here, will present evidence that the competitive interaction between these two species of *Dipodomys* is primarily by direct interference and is seasonal in occurence.

Methods

Research site and general field procedures

Experiments were performed in the San Simon Valley, Cochise Co., Arizona; approximately 7 km. ESE of Portal, Arizona. Located at an elevation of 1,350 m, this desert grassland receives an average of 850 nm precipitation an-

EXTRAIT DE

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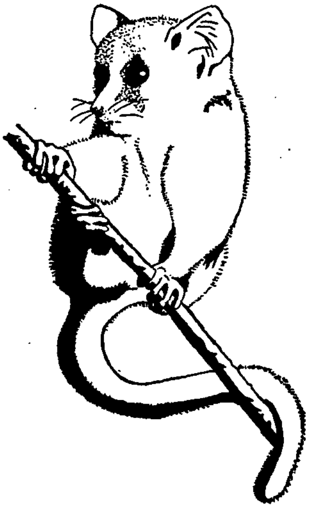

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Fluctuations de populations chez l'hermine (*Mustela erminea* L.) *

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L'étude, réalisée en Suisse, de deux populations d'hermines par capture-recapture, accompagnée de l'analyse de leur régime alimentaire, a montré l'étroite dépendance de ce petit carnivore vis-à-vis du campagnol terrestre *Arvicola terrestris scherman*. Cette relation proie-prédateur est confirmée par la mise en évidence de fluctuations cycliques parallèles, à une échelle locale, pendant plus de 25 ans. L'examen des variations de populations, par l'intermédiaire des statistiques de chasse, sur des superficies plus étendues, a révélé des fluctuations apériodiques dont les causes possibles sont discutées.

INTRODUCTION

Les changements de densité des populations font partie intégrante de l'évolution naturelle des écosystèmes qui les abritent. La « marche suicidaire » des lemmings, les allusions bibliques aux envahissements par les rongeurs, ou les fréquents dégâts occasionnés aux cultures par les campagnols ne sont que les aspects les plus spectaculaires de ces pullulations. En fait, les écologistes s'accordent à penser que toute population est fondamentalement fluctuante, et que seules des conditions particulières peuvent entraîner une relative stabilité ou, au contraire, l'apparition de fluctuations plus ou moins marquées et régulières. Il s'agit donc de clairement distinguer les variations apériodiques de celles qui émanent d'oscillations régulières.

Notre propos est d'illustrer, par l'examen successif de populations de taille croissante, étudiées sur des surfaces concentriques (niveaux terrain d'étude, district, canton, pays), l'ambivalence existant entre ces deux types de fluctuations. Dans ce but, nous suggérons l'hypothèse suivante : le mode de fluctuation mis en évidence est fonction de la surface d'investigation et de sa diversité en milieux. Lorsque l'étude concerne une population homogène à évolution cyclique, sa périodicité et l'amplitude de ses variations pourront être mises en évidence. Par contre, si les données sont récoltées sur une surface où évoluent plusieurs populations

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fluctuant indépendamment, la périodicité sera absorbée par la superposition des cycles et la courbe résultante pourra éventuellement révéler des variations apériodiques.

METHODES

Nous ferons appel, dans ce travail, à des données officielles (Statistiques de chasse et lutte contre les campagnols) et à des données personnelles (Debrot, 1982), récoltées dans le cadre de l'étude de deux populations d'hermines (*Mustela erminea* L.).

a) *Statistiques de chasse.*

En Suisse, la chasse est placée sous la juridiction des cantons, dont les autorités, dans la majorité des cas, délivrent aux particuliers des permis de chasse, valables pour la saison sur l'ensemble du territoire cantonal. Dans un rapport annuel, ces mêmes autorités publient des statistiques de chasse indiquant le nombre de permis délivrés, le nombre d'animaux tirés par espèce et par district, les efforts de protection ou de réintroduction effectués, etc. L'Office fédéral des forêts reprend ces statistiques cantonales, pour une publication de synthèse couvrant l'ensemble du territoire helvétique.

Nous avons établi des courbes de population basées sur le nombre d'animaux tirés annuellement, pour trois niveaux successifs : les districts du Locle et du Val de Ruz, le canton de Neuchâtel, et la Confédération (fig. 1). Dans ce dernier cas, il n'a pas été tenu compte des cantons à chasse affermée, sur lesquels la pression de chasse n'est pas comparable avec celle des cantons à chasse par permis.

b) *Estimation des populations proie.*

La dynamique de population de la proie principale (*Arvicola terrestris scherman* Shaw) a été établie d'après les résultats d'une enquête menée auprès des communes de la région de la Brévine et basée sur les primes à la destruction allouées aux agriculteurs pour chaque animal capturé (Debrot, 1981).

c) *Piégeage et régime alimentaire.*

Deux populations d'hermines ont été étudiées par capture-recapture de 1976 à 1981, la première sur une surface de 1875 ha dans la vallée de la Brévine, la seconde sur une station d'étude de 616 ha au Val de Ruz (fig. 1). Les dynamiques respectives des populations ont été analysées selon des calendriers de captures (Debrot et Mermod, 1981).

Le régime alimentaire des hermines des deux stations a été déterminé par l'identification des proies dont les restes sont retrouvés dans les fèces (Debrot *et al.*, 1982).

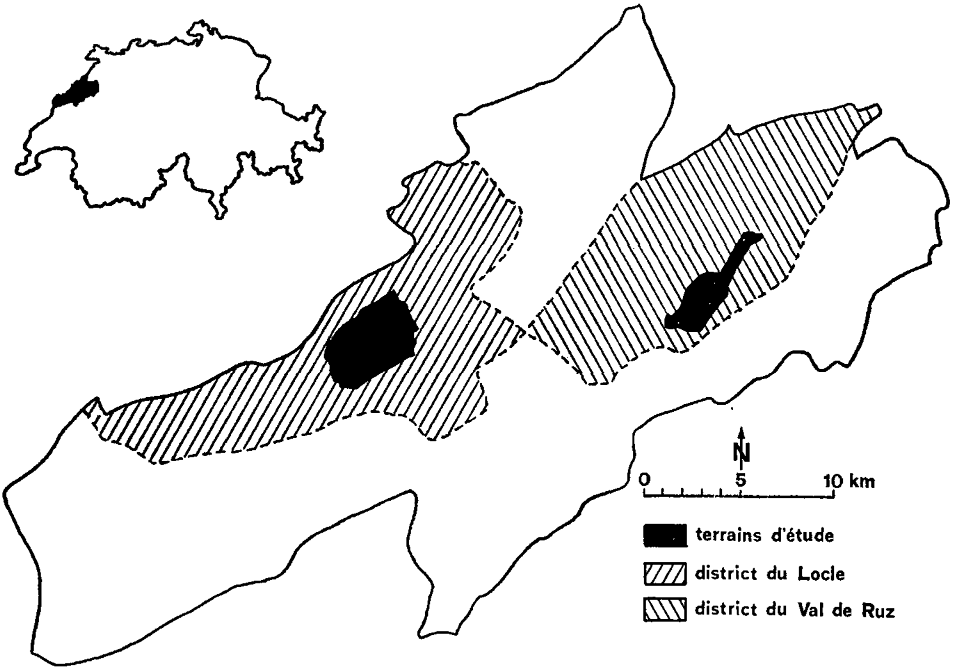

Fig. 1. — Le canton de Neuchâtel : régions d'étude et situation en Suisse.

RESULTATS

a) *Relations trophiques et périodicité.*

Dans un travail précédent (Debrot, 1981), nous avons décrit les phases de déclin et de faible densité de la population d'hermines, sur la station de la Brévine, de 1976 à 1980. L'étude parallèle du régime alimentaire saisonnier a clairement montré qu'elles se nourrissaient presque exclusivement de campagnols terrestres lorsque ceux-ci étaient abondants. Leur chute de population suivit la disparition presque totale de leur proie favorite et a coïncidé avec un changement radical de leur régime alimentaire. Il a été également établi que, dans cette région, les campagnols terrestres présentaient des variations cycliques de population et que les périodes avaient été régulièrement de 5 ans au cours des 25 dernières années (fig. 2).

Il restait à démontrer que cette étroite dépendance de l'hermine envers le campagnol terrestre n'avait pas seulement existé pendant la période étudiée, mais qu'elle correspondait à un lien proie-prédateur stable. Nous avons alors comparé la statistique de chasse des hermines dans le district du Locle avec celle des captures subventionnées d'*A. t. scherman* (Debrot, 1981) : chaque maximum de la population estimée de campagnols précède d'une année un maximum de la population estimée d'hermines (fig. 2).

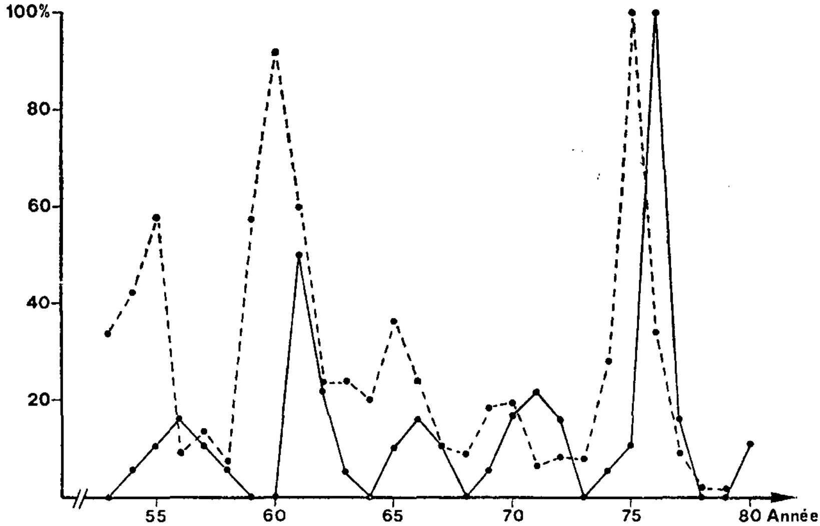

Fig. 2. — Fluctuations périodiques de la population de campagnols terrestres *Arvicola terrestris scherman* (en trait interrompu) dans la région de la Brévine (selon les captures indemnisées par les communes) et de la population d'hermines *Mustela erminea* (en trait continu) dans le district du Locle (selon les statistiques de chasse), exprimées en pour-cent de la valeur maximale observée.

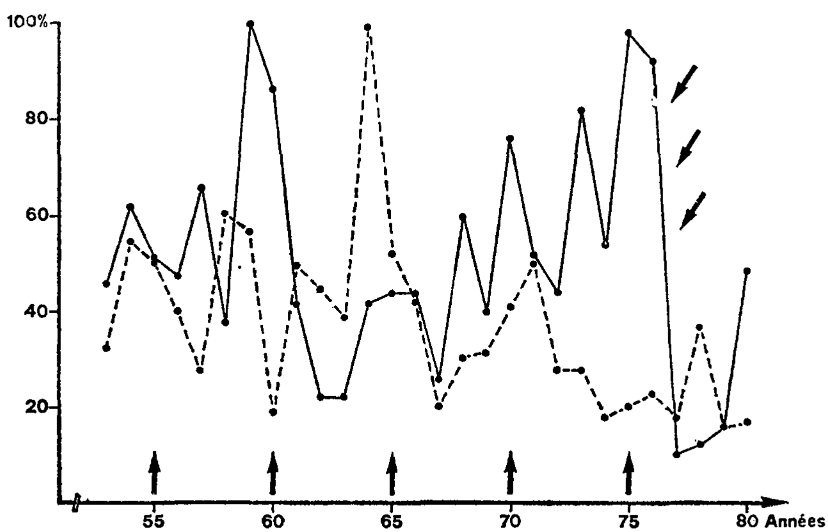

Fig. 3. — Fluctuations des populations de chat domestique *Felis catus* (en trait interrompu) et de renard *Vulpes vulpes* (en trait continu) dans le district du Locle, d'après les statistiques de chasse, exprimées en pour-cent de la valeur maximale observée. Les flèches verticales indiquent les années de pullulation du campagnol terrestre *Arvicola terrestris scherman*, les flèches obliques l'épizootie de rage.

Afin de déterminer si les autres carnivores communs dans cette région dépendaient de la même manière d'*A. t. scherman*, nous avons également établi les courbes de dynamique de population (fig. 3), extraites des mêmes statistiques, pour le renard (*Vulpes vulpes*) et le chat domestique (*Felis catus*).

b) *Cas intermédiaire.*

La comparaison des statistiques de chasse pour les districts voisins du Locle et du Val de Ruz montre que les maxima des populations estimées ne correspondent pas entre ces deux régions (fig. 4). Le coefficient de corrélation $|r| = 0{,}022$ traduit l'indépendance de ces deux courbes. Dans le premier district, qui s'étend sur une région du Haut Jura (1 000 à 1 300 m), les intervalles entre chaque maximum sont régulièrement de 5 ans, alors qu'ils varient de 3 à 7 ans dans le second district, qui comprend une vallée (700 à 800 m) entourée de montagnes (1 000 à 1 400 m). L'étude par capture-recapture des hermines de cette vallée a révélé que leur population était restée remarquablement stable de 1978 à 1981 (Debrot, 1982).
La courbe de population (fig. 4) établie sur la base des statistiques de chasse

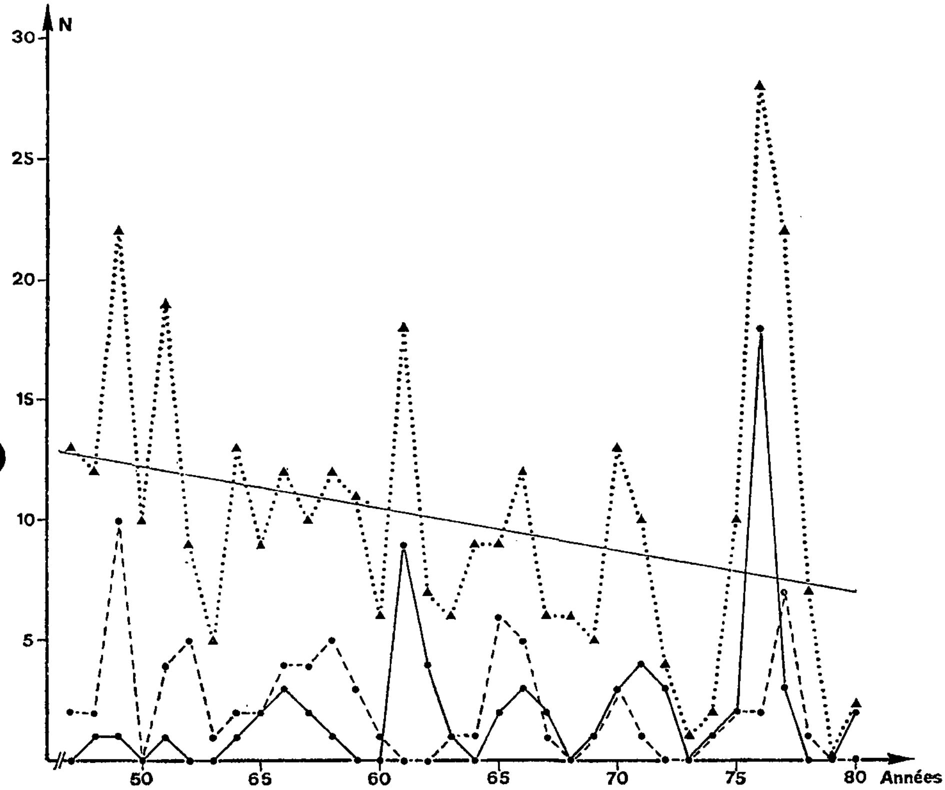

Fig. 4. — Statistiques de chasse de l'hermine *Mustela erminea*: district du Locle (trait continu), district du Val-de-Ruz (trait interrompu) et canton de Neuchâtel (en pointillé) La droite indique la tendance (droite des moindres carrés) au niveau cantonal de 1947 à 1980.

pour le canton de Neuchâtel présente des fluctuations en « dents de scie », avec un maximum important en 1976-1977. D'autre part il apparaît, au travers de cette courbe, une tendance générale à la diminution : tendance (pente de la droite des moindres carrés) = — 0,17 hermines/an, entre 1947 et 1980.

c) *Variations acycliques.*

La figure 5, établie à partir des statistiques fédérales de chasse, donne le nombre de petits Mustélinés (hermines et belettes ne sont pas distinguées) tirés chaque année dans les cantons à chasse par permis. Aucune périodicité de courte durée ne ressort de cette courbe. Par contre, on observe une période d'augmentation, de 1962 à 1968, comprenant un pic en 1964 qui est uniquement dû à la valeur enregistrée dans un canton (Tessin), puis une diminution marquée, dès 1970, malgré une courte phase d'augmentation de 1975 à 1977. La tendance générale au niveau fédéral est de — 13,2 individus/an, entre 1962 et 1980.

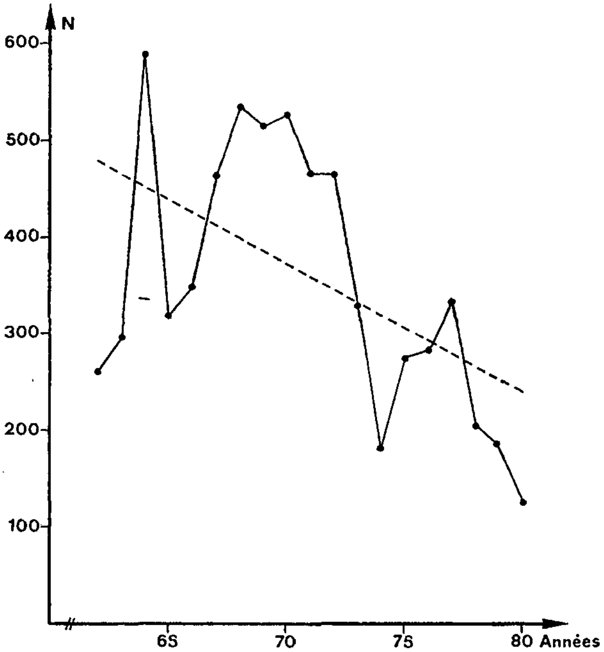

Fig. 5. — Statistiques de chasse des petits Mustélinés (*Mustela nivalis* et *M. erminea*) en Suisse. La droite indique la tendance (droite des moindres carrés) de 1962 à 1980.

DISCUSSION

a) *Fluctuations périodiques.*

Quelques auteurs ont remarqué, par des observations directes sur le terrain ou par des relevés de traces, que les populations d'hermines pouvaient présenter des fluctuations de nature cycliques (Kallio, 1975 ; Ostbye *et al.*, 1975). Ces variations ont en général été attribuées à des facteurs dépendant de la densité, essentiellement aux fluctuations de la nourriture disponible (Vershinin, 1972). Fitzgerald (1977) a montré qu'en hiver, *Mustela frenata* et *M. erminea* consommaient intensivement *Microtus montanus*, un campagnol à populations cycliques. La durée de son étude et les méthodes utilisées ne lui ont toutefois pas permis d'observer si les populations des prédateurs fluctuaient parallèlement à leur proie. Une telle relation ressort clairement de la comparaison des dynamiques de population d'*A. t. scherman* et de *M. erminea* (fig. 2) dans le district du Locle. Elle confirme la conclusion que nous avions tirée de l'étude du régime alimentaire pendant la phase de forte population et de son évolution au cours des phases de déclin et de faible densité, conclusion qui soulignait les relations causales étroites existant entre la proie et le prédateur (Debrot, 1981).

Il est bien connu que les rapaces se dispersent lorsque la nourriture fait défaut dans une région (Remmert, 1980). Cependant, des déplacements d'une telle amplitude ne sont pas possibles pour les mammifères carnivores. Ainsi, lors de la disparition de la proie favorable, il ne leur reste qu'une alternative : la réduction de la population ou le changement de régime alimentaire. Dans le premier cas, l'espèce peut survivre jusqu'à la prochaine pullulation de la proie dominante par la répartition entre quelques individus seulement des ressources alimentaires encore disponibles. Cette stratégie, qui est essentiellement suivie par les sténophages à haut degré de spécialisation, semble être rendue encore plus efficace chez *M. erminea* par la dissolution des structures territoriales, permettant sans doute l'économie des dépenses de maintenance du territoire (Debrot, non publié). Au contraire, d'autres carnivores réduisent leur dépendance vis-à-vis d'*A. t. scherman* en exploitant efficacement d'autres ressources de nourriture. Cette stratégie, qui est plutôt l'apanage des « généralistes » euryphages, semblent avoir été adoptée par le renard et le chat domestique dans le district du Locle. Ceci se traduit par l'absence de corrélation existant entre les maxima de population du campagnol terrestre et les fluctuations des populations estimées des deux carnivores (fig. 3). Une telle relation de dépendance proie-prédateur a cependant déjà été observée en URSS par Tikhvinskaya et Gorshkov (1971), qui ont mis en relation les oscillations d'*A. terrestris* avec les fluctuations du nombre de fourrures de renard commercialisées.

b) *Variations apériodiques.*

Les courbes d'estimation des populations d'hermines sur les districts du Locle et du Val de Ruz (fig. 4) révèlent l'absence de synchronisation entre leurs fluctuations. Ainsi, la dynamique très irrégulière des hermines sur l'ensemble du canton de Neuchâtel peut être considérée comme l'illustration de la combinaison de plusieurs populations fluctuant indépendamment : chaque pic est l'expression du maximum atteint par l'une d'elles dans une région du canton. Si on extrapole cette interprétation sur une plus large échelle, l'intégration d'un plus grand nombre de populations indépendantes devrait absorber toutes les fluctuations à court terme. C'est en effet ce qui se passe (à l'exception du pic dû aux données du Tessin en 1964) sur le territoire helvétique. Les variations qui y sont observées ne sont pas, jusqu'à preuve du contraire, de nature cyclique, bien qu'il ne soit pas exclu que des études à long terme puissent révéler des cycles à grande période, tels que ceux observés par Bakeev (1971) chez *Mustela sibirica*. Celui-ci décrit en effet des cycles de 10 à 20 ans sur une période de 80 ans.

Des variations non cycliques de populations d'hermines ont été mentionnées de longue date, partout où elles ont été recherchées pour leur fourrure. En effet, la discrétion de ces petites carnivores et la faible densité de leurs populations en ont fait une espèce difficile à observer et surtout à étudier quantitativement. Ainsi, la grande majorité des renseignements à disposition des chercheurs provenait de l'exploitation commerciale de la fourrure hivernale. De plus, les fluctuations importantes ont été particulièrement remarquées dans la mesure où elles revêtaient une importance économique. Aspisov et Popov (1940), Lavrov (1944 et 1956), Kopein (1970) ont fait état de très brusques diminutions de population, sur la base du nombre de fourrures récoltées sur de larges superficies. Les causes de ces fluctuations sont recherchées essentiellement dans des facteurs indépendants de la densité : variations climatiques, impact de la chasse ou des activités de piégeage, modifications de l'environnement, parasitisme ou biais dû à la méthode d'échantillonnage. Les fluctuations révélées par les statistiques fédérales de chasse sont de même nature. Il est difficile d'établir la raison de ces variations, et surtout des diminutions générales observées tant au niveau du territoire helvétique que de celui du canton de Neuchâtel. Il est toutefois raisonnable de penser qu'elles sont bien réelles et non imputables à des erreurs d'échantillonnage. Les mêmes statistiques ont en effet montré que d'autres Mustélidés tels que la fouine *Martes foina* sont en nette augmentation (+ 56,6 individus/an sur une moyenne de près de 900 animaux tirés chaque année).

Lavrov (1944) a noté qu'il y avait une relation inverse entre la densité des populations d'hermines (nombre de fourrures récoltées par les trappeurs) et le taux d'infection par le Nématode parasite des sinus frontaux *Skrjabingylus nasicola.* Il en conclu que le parasitisme doit être considéré comme un facteur de contrôle des populations. Un examen plus détaillé de la dynamique du taux d'infection par *S. nasicola,* en relation avec le régime alimentaire et la densité de population, nous a conduit à développer une hypothèse alternative (Debrot et Mermod, 1981) selon laquelle la fréquence d'infection *et* la densité de population sont les conséquences du changement de régime alimentaire.

Si les fluctuations apériodiques ne semblent pas être imputables au parasitisme, *ni* aux méthodes d'échantillonnage seules, leurs causes peuvent cependant être variées et multiples. L'arrivée d'une substance toxique nouvelle dans l'environnement peut, par exemple, perturber fondamentalement l'équilibre d'une espèce : le déclin de population observé chez *Lutra lutra* à la fin des années 50 en Grande-Bretagne semble avoir été provoqué par la dieldrine, une substance utilisée en agriculture, qui a également été tristement responsable de la mort de renards et de blaireaux (*Meles meles*) et de la perturbation de la population de ce dernier (Wood, 1979). De même, une épizootie de rage a des conséquences spectaculaires sur les populations de renard (fig. 3).

On peut trouver un autre exemple de brusque chute de population due à une perturbation du système hermine-proie en considérant l'apparition de la myxomatose en Grande-Bretagne en 1953 : Day (1968) a mis en évidence l'importance des lagomorphes dans l'alimentation des hermines anglaises ; or cette dépendance est étroite ainsi que le soulignent King et Moors (1979), puisque le nombre d'hermines observées est significativement plus élevé avant qu'après l'épidémie (Hewson, 1972). Il est intéressant de noter à ce propos que *Mustela nivalis* n'a pas montré la même évolution puisqu'elle a été plus abondante après l'arrivée de la myxomatose (Hewson, 1972 ; King, 1980).

CONCLUSION

L'examen de populations d'hermines sur des surfaces de taille croissante a permis de mettre en évidence des fluctuations de nature différente. A un niveau local, dans un milieu relativement homogène, et en présence d'un système proie-prédateur particulier, il a été possible d'observer des fluctuations cycliques régulières. Au fur et à mesure que la surface d'investigation s'agrandit et par conséquent se diversifie, les oscillations périodiques s'estompent et il apparaît des fluctuations acycliques imputables à des causes complexes, difficiles à élucider.

REMERCIEMENTS

Il m'est particulièrement agréable de remercier le Prof. C. Mermod, qui a suivi et guidé ce travail avec beaucoup de compétence et d'intérêt. Je remercie également l'Office fédéral des forêts, section forêts et chasse, ainsi que l'Inspectorat cantonal de la chasse et de la pêche pour la mise à disposition des statistiques de chasse.

SUMMARY

This capture-recapture study of two stoat populations in Switzerland, together with analyses of food habits, has shown the close dependence existing between this carnivore and the water vole *Arvicola terrestris scherman*. These prey-predator relationships are confirmed by cyclic fluctuations observed over 25 years, in a local area. Aperiodic fluctuations were revealed by the examination of hunting statistics covering a larger region. The causes of these variations of populations are discussed in connection with the literature.

BIBLIOGRAPHIE

ASPISOV, D.I., et V.A. POPOV, 1940. — Factors determining fluctuations in the numbers of ermines. *In* C.M. KING (Ed.), 1980: cf. *infra*.

BAKEEV, Y.N., 1971. — The distribution and population dynamics of the Siberian kolinsky in the western part of its range in the USSR. *In* C.M. KING (Ed.), 1980: cf. *infra*.

DAY, M.G., 1968. — Foods habits of British stoats (*Mustela erminea*) and weasels (*Mustela nivalis*). *J. Zool.*, 155: 485-497.

DEBROT, S., 1981. — *Trophic relations between the stoat* (Mustela erminea) *and its prey, mainly the water vole* (Arvicola terrestris scherman). Worldwide Furbearer Conf. Proc., Frostburg, Maryland, August 1980. Vol. II: 1259-1289.

DEBROT, S., 1982. — *Ecologie de* Mustela erminea *L.: dynamique des composantes structurales, trophiques et parasitaires de deux populations.* Thèse de doctorat, non publiée, Université de Neuchâtel, Suisse. 279 p.

DEBROT, S., G. FIVAZ, C. MERMOD et J.-M. WEBER, 1982. — *Atlas des poils de Mammifères d'Europe.* Institut de Zoologie (Ed.), Université de Neuchâtel, Suisse. 208 p.

DEBROT, S., et C. MERMOD, 1981. — *Cranial helminth parasites of the stoat and other mustelids in Switzerland.* Worldwide Furbearer Conf. Proc., Frostburg, Maryland, August 1980. Vol. II : 690-705.

FITZGERALD, B.M., 1977. — Weasel predation on cyclic population of the montane vole (*Microtus montanus*) in California. *J. Anim. Ecol.*, 46 : 367-397.

HEWSON, R., 1972. — Changes in the number of stoats, rats and little owls in Yorkshire as shown by tunnel trapping. *J. Zool.*, 168 : 427-429.

KALLIO, P., 1975. — Kevo, Finland. *In : Structure and function of tundra ecosystems* (T. ROSSWALL and O.W. HEAL, Eds), *Ecol. Bull.*, 20 : 193-223.

KING, C.M. (Ed.), 1975. — *Biology of Mustelids, some soviet research : volume 1.* British Lib. Lend. Div., Boston Spa. 266 p.

KING, C.M. (Ed.), 1980. — *Biology of Mustelids, some soviet research : volume 2.* Sciences Information Division, Dpt. Scientific and Industrial Research, Wellington, New Zealand. 214 p.

KING, C.M., 1980. — Population biology of the weasel *Mustela nivalis* on British game estates. *Holarctic Ecol.*, 3 : 160-168.

KING, C.M., et P.J. MOORS, 1979. — On co-existance, foraging strategy and the biogeography of weasels end stoats (*Mustela nivalis* and *M. erminea*) in Britain. *Oecologia*, 39 : 129-150.

KOPEIN, K.I., 1970. — The effect of hunting on the sex ratio and population density of ermine. *In* C.M. KING (Ed.), 1980 : cf. *supra.*

LAVROV, N.P., 1944. — Effect of helminth invasions and infectious diseases on variations in numbers of the ermine (*Mustela erminea* L.). *In* C.M. KING (Ed.), 1975 : cf. *supra.*

LAVROV, N.P., 1956. — Characteristics and causes of the prolonged depression in numbers of the ermine in forest-steppe and steppe zones of USSR. *In* C.M. KING (Ed.), 1975 : cf. *supra.*

OSTBYE, E., 1975. — Hardangervidda, Norway. *In : Structure and function of tundra ecosystems* (T. ROSSWALL and O.W. HEAL, Eds), *Ecol. Bull.*, 20 : 225-264.

REMMERT, H., 1980. — *Arctic animal ecology.* Springer-Verlag, Berlin, Heidelberg, New York : 250 p.

TIKHVINSKAYA, M.V., et P.K. GORSHKOV, 1971. — (The trophic relations of foxes and *Arvicola terrestris* L. in different landscape regions of the Tatar ASSR). *Bull. Mosk. Obshch Isp. Prir. Otd. Biol. SSSR,* 76 : 33-43. En russe.

VERSHININ, A.A., 1972. — The biology and trapping of the ermine in Kamchatka. *In* C.M. KING (Ed.), 1980 : cf. *supra.*

WOOD, M.S. (Ed.), 1979. — *Second report of the Joint Otter Group.* S.P.N.C., Lincoln, England : 58 p.

EXTRAIT DE

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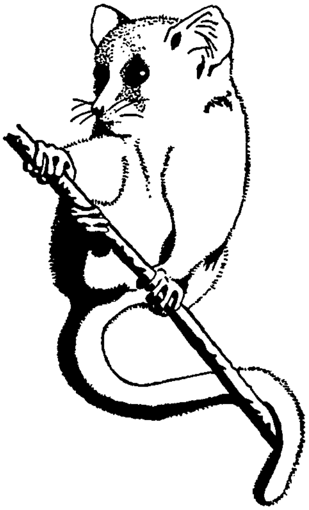

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The day and night activity pattern of the stoat (*Mustela erminea* L.) *

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Au cours d'une étude par piégeage de 1976 à 1983 en Suisse romande, 625 captures d'hermines ont été obtenues, réparties tout au long de l'année. La proportion d'animaux trouvés lors du contrôle du matin fournit une estimation de la répartition de l'activité entre le jour et la nuit. Les hermines sont essentiellement nocturnes en hiver et diurnes en été. De plus, le changement de rythme nycthéméral, s'il se produit simultanément pour les deux sexes en novembre, survient plus tôt au printemps chez les mâles (entre février et mars) que chez les femelles (entre avril et juin). Cette différence est à mettre en relation avec la stratégie spatiale particulière des mâles au printemps. De même, une activité de déplacements accrue serait à l'origine du rythme nycthéméral plus diurne chez les juvéniles que chez les adultes à la fin de l'été et en automne.

INTRODUCTION

The activity rhythm of animals has been widely studied, and much is known about its variations in relation to seasons, environment, ontogeny or artificial light-dark cycle (Aschoff, 1964). However, data on carnivores are not easily accessible in the nature and little has been published on the day and night activity pattern of the stoat (Saint Girons, 1966; Erlinge, 1979). The aim of this paper is to contribute to this part of the biology of the stoat.

METHODS

The data are part of a long term study of stoat populations initiated in 1976. The animals were live-trapped, marked, sexed and released at their site of capture (Debrot and Mermod, 1981). The age was determined by external examination (development of the testes, lactation) and X-rays radiographs (Mermod and Debrot, 1978). The stoats were considered as juveniles if they were born during the year. Thus, only adults were caught from January to May.

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Three regions were investigated in the western part of Switzerland. The first one, trapped from December 1976 to November 1982 is the Brévine Valley (Jura Moutains). The second, the Val de Ruz, is an other Jura Valley, at a lower altitude, and was investigated from April 1978 to March 1983. One of us (P.M.) studied the stoats in the fore-Alps from Novembre 1981 to November 1982.

Live-trapping occurred all over the year but the trapping effort was not constant each month. The traps were controlled twice a day, after sunrise and just before night fall. As the stoats found in the traps in the morning were caught during their night activity and the others during the day, it was possible to estimate the proportion of night activity of the population, or of a particular class (e.g. juveniles, adults, females or males) during defined periods (i.e. month, season).

When not specified, the statistical test used to compare proportions is the Fisher exact probability test, and its results are expressed by the probability p of signification.

RESULTS

On the whole, 625 captures have been recorded from 379 different stoats, 235 in the Brévine Valley, 308 in the Val de Ruz and 82 in the fore-Alps. One third (30.7 %) of the animals have been found in the traps during the morning control. The monthly proportions are illustrated in figure 1. Little trapping effort was achieved in May in order to reduce the disturbance during the reproduction period.

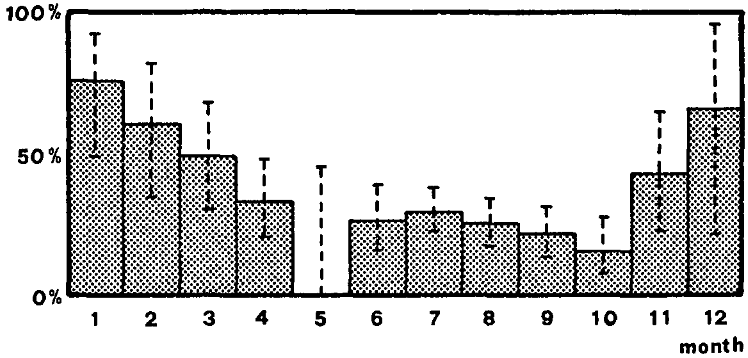

Fig. 1. — Day-night activity rhythm of the stoat in western Switzerland, estimated by the proportion of captures during the night. Broken lines indicate confidence limits (p = 0.05).

The seasonal (¹) activity rhythms were not significantly different between the three regions except in autumn, when the stoats were more nocturnal in the fore-

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(1) Meteorological seasons were used (i.e. spring = March + April + May).

Alps ($p = 0.004$). This is due to the fact that, in this region, 7 of the 8 captures achieved in autumn have been recorded during the second half of Novembre, when the stoats were already mainly nocturnal.

The figure 2 compares the seasonal proportions of captures achieved during the night between males and females. A significant difference was found in spring

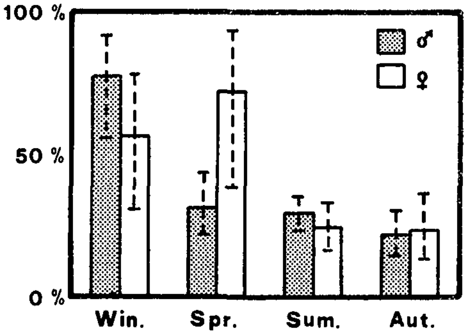

Fig. 2. — Comparison between the sexes of the seasonal day and night activity rhythm of the stoat. Broken lines indicate confidence limits ($p = 0.05$).

($p = 0.016$) : the males appeared to be less active during the night in March and April.

Significant differences were also found when the activity rhythm was compared between the two age classes (Fig. 3). The juveniles were more active during the day from August to November ($\chi^2 = 9.81$, $p < 0.005$).

DISCUSSION

Stoats have been seen at all hours of the day, however their part of nocturnal activity is difficult to estimate by direct observation. Herter (1858), quoted by Saint Girons (1966), mentioned from studies in zoological gardens, a low activity phase from 4 p.m. to 1 a.m. and two maxima at 3 a.m. and 11 a.m. Müller's observations (1970) differed notably, with one period of activity from 8 to 11 a.m. and a second one from 5-6 to 8 p.m. In fact, captive stoats modified their activity rhythms when the feeding time was changed (Debrot, personal observation) and it is difficult to compare day-night cycles of captive stoats with wild ones.

Bäumler (1973) observed *in natura* that stoats are nocturnal in winter and reported an inversion of the activity cycle in March. A more shaded pattern appears from our results (Fig. 1), with a decreasing proportion of the nocturnal locomotor activity from January to October. Erlinge (1979) observed that a radio-tracked male stoat was more active by night in February (it was active 32 % of the night time and 18 % of the day time) than another one in May (respectively 29 % and 38 %) or than a third one in October (80 % of its activity occurred during the day). These results fit ours and confirm that our method provides a good estimation of the day and night activity pattern of the stoat.

The juveniles, who generally behave as transients, have a tendency to display a larger part of their activity in travelling movements (Erlinge, 1977). As such, locomotor activity appears to be essentially performed during the day (Erlinge, 1979), this could explain the differences observed between adults and juveniles in late summer and autumn (Fig. 3).

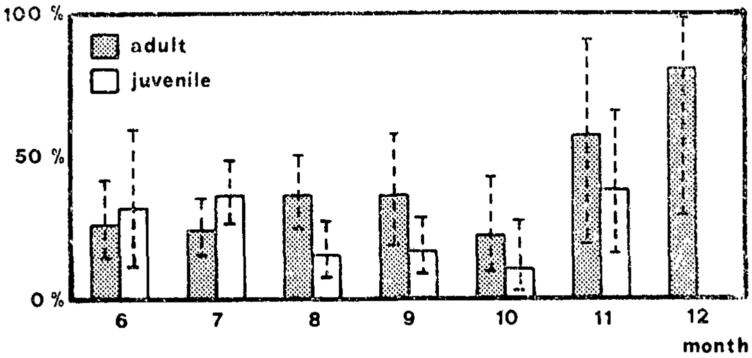

Fig. 3. — Comparison between two age classes of the day and night activity rhythm of the stoat. Broken lines indicate confidence limits (p = 0.05).

In March and April, the male stoats exhibit intensive locomotor activity due to a modification in the spacing pattern of the population (Erlinge, 1977 ; Debrot, in press). It is assumed that this change of behaviour, peculiar to the males, is related to the difference observed in the activity rhythm between the sexes (Fig. 2). Whereas the females appear to keep the « winter activity pattern » until April, the males become more diurnal already in March, when a specific behaviour appears. This was predicted by Erlinge (1977, 1979) who emphasized that the type of locomotor activity (e.g. hunting, territorial patrolling, movements for reproductive purposes) was not equally affected by seasonal changes in the day-night rhythm.

Thus, the stoats of both sexes change from a diurnal to a nocturnal activity pattern in November, whereas the inverse change occurs earlier in males (February-March) than in females (April-June). Alternatively dark and light active species have already been described (Aschoff, 1964). *Microtus agrestis* for exemple were found active during the night in summer and more active during the day in winter (Erkinaro, 1961). It would be interesting to determine if the day-night rhythm observed in the stoat is involved in a prey-predator relationship.

ACKNOWLEDGEMENTS

We thank the « Inspectorat de la chasse et de la pêche » (Neuchâtel) and the « Conservation de la faune » (Vaud) for the trapping licences.

SUMMARY

During a live-trapping program, conducted from 1976 to 1983 in western Switzerland, 625 captures of stoats were achieved throughout the year. The rate of captures recorded during the morning control provides an estimation of the day and night activity pattern. The stoats are mainly nocturnal in winter and diurnal in summer. Moreover, the changes of the day-night cycle, if it occurs simultaneously in November for both sexes, appear earlier in spring in males (between February and March) than in females (between April and June). This difference has to be related with the particular spacing pattern of the males in spring. In the same way, intensive movements could be responsible for the more diurnal activity rhythm observed by juveniles in late summer and autumn.

BIBLIOGRAPHY

ASCHOFF, J., 1964. — Die Tagesperiodik licht- und dunkelaktiver Tiere. *Rev. suisse Zool.*, 71 : 528-558.

BÄUMLER, W., 1973. — Ueber die Activitätsperiodik des Iltisses (*Mustela putorius*) und des Hermelins (*Mustela erminea*) sowie über dessen Farbwechsel. *Säugetierk. Mitt.*, 21 : 31-36.

DEBROT, S., in press. — The spatial and temporal distribution pattern of the stoat (*Mustela erminea* L.). *Oecologia.*

DEBROT, S., and C. MERMOD, 1981. — *Cranial helminth parasites of the stoat and other mustelids in Switzerland.* Worldwide Furbearer Conf. Proc., Frostburg, Maryland, August 1980. Vol. II : 690-705.

ERKINARO, E., 1961. — The seasonal change of the activity of *Microtus agrestis. Oikos,* 12 : 157-163.

ERLINGE, S., 1977. — Spacing strategy in stoat *Mustela erminea. Oikos,* 28 : 32-42.

ERLINGE, S., 1979. — *Movements and daily activity pattern of radio tracked male stoats,* Mustela erminea. *In :* A handbook on biotelemetry and radio tracking (C.J. AMLANER Jr. and D.W. MACDONALDS, eds.). Pergamon Press, Oxford and New York : 703-710.

HERTER, K., 1958. — Die Säugetierkundlichen Arbeiten aus dem zoologischen Institut der Freien Universität, Berlin. *Z. Säugetierk.*, 23 : 1-32.

MERMOD, C., and S. DEBROT, 1978. — Morphométrie crânienne par radiographie. I : Problèmes techniques. *Rev. suisse Zool.*, 85 : 730-738.

MÜLLER, H., 1970. — Beiträge zur Biologie des Hermelins (*Mustela erminea* L.). *Säugetierk. Mitt.*, 18 : 293-380.

SAINT GIRONS, M.-C., 1966. — Le rythme circadien de l'activité chez les mammifères holarctiques. *Mémoires du Muséum National d'Histoire Naturelle,* Série A, Zoologie, 40 : 101-187.

DYNAMIQUE DU RENOUVELLEMENT ET STRUCTURE D'AGE D'UNE POPULATION D'HERMINES (*MUSTELA ERMINEA*)

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Caractériser une population d'hermines (*Mustela erminea* L.) est une tâche rendue particulièrement ardue par sa faible densité et la labilité de ses structures liée à une grande mobilité, une piégeabilité inégale et une adaptabilité remarquable des individus qui la composent. L'application des techniques de capture-marquage-recapture à l'étude de ce petit Carnivore a cependant permis une meilleure compréhension de sa répartition spatiale (Erlinge, 1977 ; Simms, 1979 ; Debrot et Mermod, 1983), de la dynamique de ses populations (King, 1981 ; Debrot, 1981, 1983) et de sa dispersion (King et McMillan, 1982). La nature des données reste cependant un facteur limitant important dans l'acquisition de connaissances plus détaillées concernant certains aspects de la biologie des hermines, tels que la structure et le renouvellement des populations.

Dans ce travail, nous avons développé une méthode d'analyse originale, adaptée à la structure de nos données, afin d'estimer quelques paramètres fondamentaux de la population étudiée.

TERRAIN D'ETUDE ET METHODES

Une population d'hermines a été étudiée par la capture-marquage-recapture sur un terrain de 616 ha dans le Val de Ruz (47° 02' N., 6° 55' E. ; alt. 670-740 m). Cette vallée du Jura neuchâtelois (Suisse), dont les cultures couvrent les 3/4 de la surface, est parcourue par une rivière alimentée par plusieurs ruisseaux. Les sites de piégeage ont été principalement choisis le long des allées buissonnantes bordant les cours d'eau, dans les haies et à la périphérie de quelques petites forêts mixtes. D'avril 1978 à avril 1981, 27 sessions de piégeage ont été organisées sur le terrain d'étude et 18 aux alentours. Une

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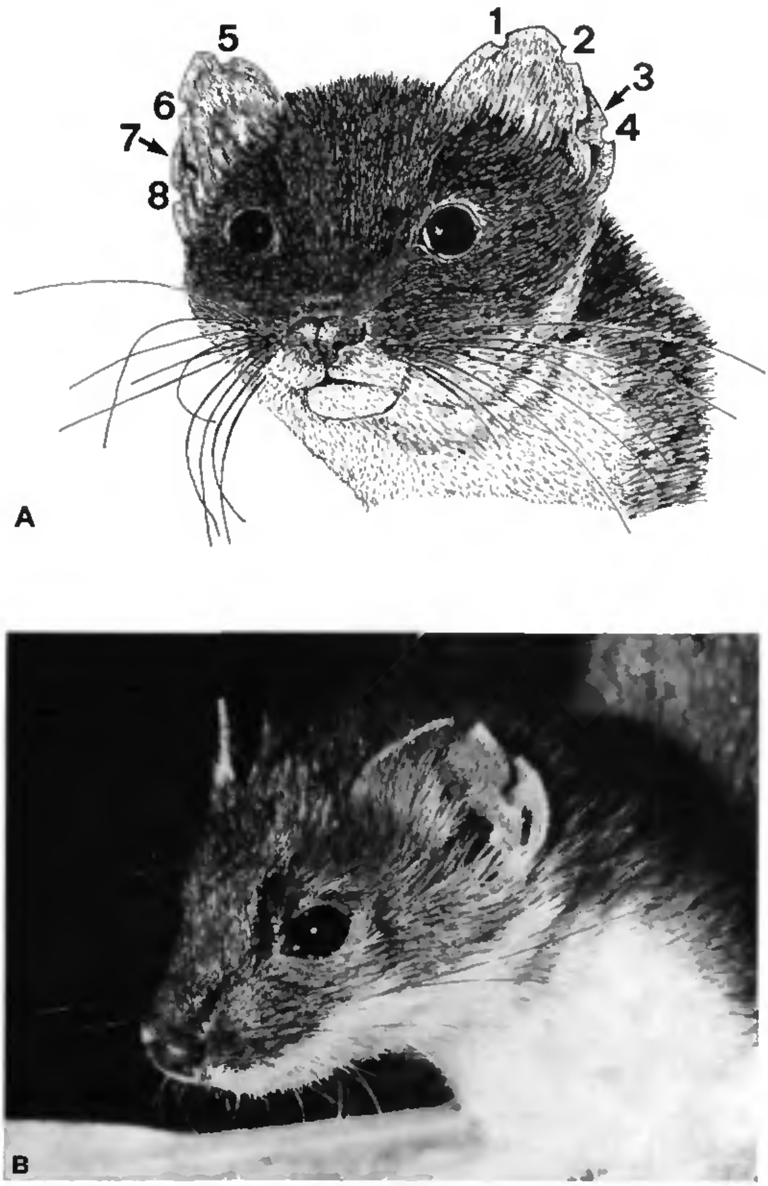

Figure 1. — Système de marquage des hermines par découpage d'encoches dans les lobes des oreilles. A. Numérotation des 8 positions de marquage (dessin G. Fivaz). B. Portrait de l'Hermine n° 70 ($2^{2-1} + 2^{3-1} + 2^{7-1}$), marquée en position 2, 3 et 7 (la marque en position 7 n'est pas visible).

session de piégeage consiste dans la règle en la pose de 60 pièges à bascule, tendus du lundi au vendredi (soit 240 unités-piège).

Dans les limites du terrain d'étude, 147 captures de 76 hermines ont été réalisées avec un effort de piégeage de 5 724 unités-piège, alors que 31 captures supplémentaires et 19 nouveaux individus ont été obtenus en périphérie avec un effort de piégeage additionnel de 1 516 unités-piège.

Les pièges ont été contrôlés matin et soir, et les captures transférées au laboratoire pour être anesthésiées, examinées et marquées (Debrot et Mermod, 1981). Tous les animaux ont ensuite été relâchés sur le lieu de leur capture.

L'âge et le sexe ont été déterminés par l'examen des organes génitaux et par radiographie (Mermod et Debrot, 1978). Le terme juvénile désigne les animaux sevrés, nés dans l'année (1).

Le marquage, par *ear clipping* (Erlinge, 1974 ; Twigg, 1978), effectué sous anesthésie, consiste à découper des encoches dans les lobes des oreilles. Nous avons élaboré un sytème de codage binaire sur 8 positions (Fig. 1 A). A chaque position, numérotée dans un ordre défini, correspond une valeur telle qu'à la position *n* corresponde la valeur 2^{n-1}. Ainsi le numéro d'une Hermine sera la somme des valeurs 2^{n-1} attribuées à chacune des positions *n* présentant une marque (Fig. 1 B). Ce système permet de distinguer 255 (2^8—1) individus.

CALENDRIER DES CAPTURES

Théoriquement, si toutes les hermines sont également piégeables et que la probabilité de recapture des individus présents sur le terrain (piégeabilité) est constante, la distribution des fréquences du nombre de captures par Hermine doit suivre une distribution de Poisson : $T(i) = N . e^{-M} . M^i/i!$ où T (i) est la fréquence théorique de la classe des hermines capturées i fois, N la population totale et M le nombre moyen de captures par individu. Notons que l'approximation avec une distribution de Poisson plutôt qu'une distribution binomiale est considérée comme bonne lorsque N est grand et $M < 5$ (Dagnelie, 1973), ce qui est notre cas.

La distribution expérimentale est une *zero-truncated distribution* (Caughley, 1977) de moyenne m. Elle est significativement différente (2) de la distribution de Poisson de moyenne M telle que $m = M / (1 - e^{-M})$: $\chi^2 = 23{,}77$ pour 3 degrés de liberté ; $p < 0{,}001$ (cf. Debrot, 1982, pour plus de détail). Ceci implique que la piégeabilité constante et égale n'est pas vérifiée. King et McMillan (1982) sont arrivés à la même conclusion lors de l'analyse de leurs données, obtenues entre le 15 et le 25 janvier 1980 sur deux lignes de pièges en Nouvelle-Zélande. Ils concluent que la piégeabilité inégale observée peut exister entre individus et/ou entre groupes d'hermines (classes de sexe ou d'âge). Nos observations personnelles suggèrent que les déviations peuvent éga-

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(1) La maturité sexuelle n'est pas atteinte simultanément par les deux sexes : les femelles juvéniles sont accouplées pour la première fois à l'âge de 2 à 3 mois (cf. revue par King et Moody, 1982) alors que les mâles ne sont fertiles que l'année suivante. Ainsi, pour des raisons d'ordre essentiellement pratique, les jeunes hermines sont considérées comme adultes, par définition, dès le premier janvier.

(2) Pour ce test, les données d'une autre station de piégeage (Debrot, 1981) ont également été prises en considération.

lement intervenir selon la saison ou le nombre de recaptures (modification du comportement par apprentissage). Ce résultat préliminaire nous empêche d'employer les techniques classiques d'analyse des données issues des méthodes de capture-marquage-recapture (Caughley, 1977).

Nous avons donc choisi une autre approche en basant notre analyse sur un *calendrier de captures* (Petrusewicz et Andrejewski, 1962 ; Debrot et Mermod, 1981). Il repose principalement sur les approximations selon lesquelles une Hermine entre dans le terrain d'étude le mois de sa première capture, qu'elle y reste présente entre deux recaptures et qu'elle y meurt le mois de sa dernière recapture. Un tel calendrier de captures donne ainsi une bonne idée de la dynamique de la population minimum formée par les hermines actives piégeables (à l'exclusion en particulier des jeunes au nid).

Conformément aux observations d'Erlinge (1977), les relevés de traces sur neige ont montré que le calendrier de captures traduit de façon adéquate l'évolution réelle de la population.

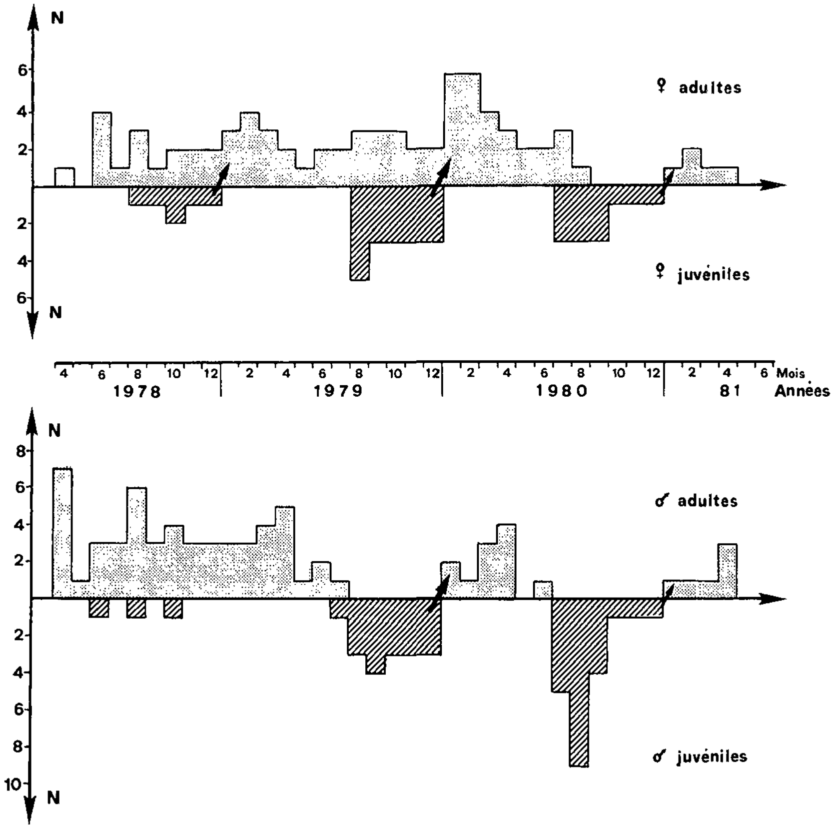

Figure 2. — Calendrier de captures de la population des hermines au Val de Ruz, par classes de sexe et d'âge. Les flèches soulignent l'arrivée de la cohorte des juvéniles dans la classe des adultes.

DYNAMIQUE DE POPULATION

Le calendrier de captures (Fig. 2) a mis en évidence une population relativement stable au cours des 3 années d'étude.

1. — POPULATION MOYENNE

Pour chaque mois de l'année, le nombre moyen d'adultes et de juvéniles, estimés présents sur le terrain d'étude, a été calculé (Fig. 3). La valeur obtenue pour le mois de mai peut paraître aberrante. Elle s'explique cependant par le profond remaniement observé dans la distribution spatiale des hermines (Debrot et Mermod, 1983) entre le printemps et l'été, et par le fait qu'il n'y a pas eu de piégeage en mai, pour éviter de perturber la population pendant la phase la plus sensible de la reproduction.

Les nombres d'adultes estimés présents ($N = 33$), déduits du calendrier de captures pour chaque mois, de juin 1978 à avril 1981 (mai excepté), ont permis de calculer la droite de régression (Fig. 3) $Na(m) = 6{,}20 - 0{,}35\ m$ où $Na(m)$ est le nombre moyen d'adultes estimés présents au mois m. Elle donne une estimation de la diminution de la population des adultes et le coefficient de corrélation ($r = 0{,}495$) indique une relation linéaire significative ($p < 0{,}01$) entre le mois considéré et le nombre d'adultes présents.

2. — TAUX DE MORTALITÉ

De la droite de régression, on peut calculer un taux de mortalité annuel des adultes :

$$TMa = \frac{Na(1.1) - Na(31.12)}{Na\ (1\ .\ 1)} = 0{,}68$$

où $Na(1.1)$ et $Na(31.12)$ représentent les nombres moyens d'adultes estimés présents respectivement au début et à la fin de l'année.

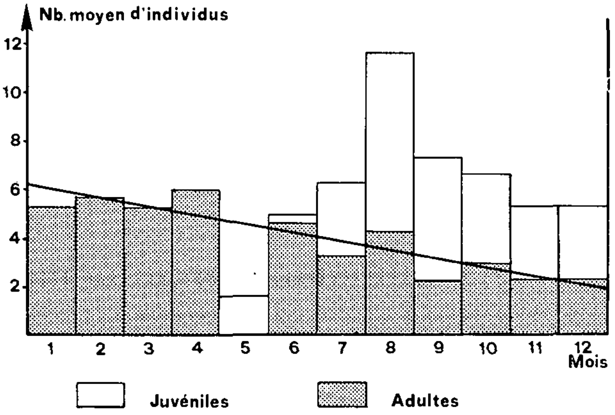

Figure 3. — Diagramme expérimental de la dynamique annuelle moyenne de la population des hermines du Val de Ruz et droite de régression $Na(m) = 6{,}20 - 0{,}35\ m$.

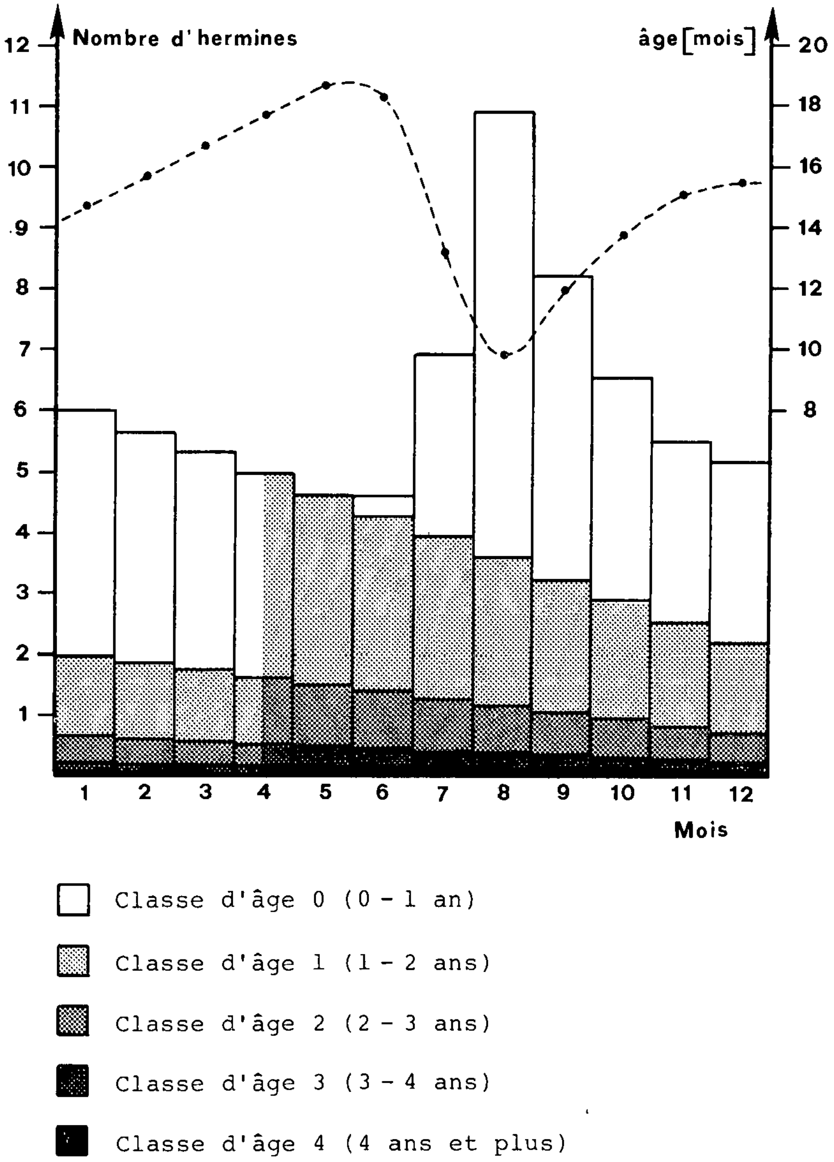

Figure 4. — Evolution mensuelle de la pyramide des âges et de l'âge moyen (en trait discontinu) de la population des hermines du Val de Ruz. Diagramme établi à partir des nombres moyens observés de juvéniles, de la droite de régression Na(m) = 6,20 — 0,35 m et d'un taux de mortalité constant des adultes TMa = 0,68.

La valeur trouvée pour TMa signifie que, selon cette estimation, 2/3 des hermines adultes vivantes à un moment précis de l'année mourront au cours des 365 jours à venir.

TMa peut être considéré comme indépendant de l'immigration-émigration si on admet que la répartition des hermines est de type aléatoire dans la région étudiée. Une telle distribution a été vérifiée en phase de forte densité dans la vallée de la Brévine (Debrot et Mermod, 1983) et paraît plausible au Val de Ruz également, bien que la dimension de la superficie et le nombre de données n'en permettent pas une vérification statistique.

3. — TAUX DE RENOUVELLEMENT

Le taux de renouvellement des hermines adultes (TRa) exprime la proportion des individus présents à un moment donné de l'année, qui ne sont plus là 365 jours plus tard. TRa tient donc compte de la mortalité, comme TMa, mais également de la dispersion (émigration).

Pour chaque mois de l'année, nous avons calculé le nombre d'hermines adultes estimées présentes (selon le calendrier de captures), ainsi que le nombre de celles-ci qui sont encore présentes dans les limites du terrain d'étude une année plus tard. Ainsi TRa = 0,93 ; et l'intervalle de confiance est de 0,88 à 0,97 ($p = 0{,}05$).

Ce résultat exprime clairement le *turnover* élevé auquel a été soumise la population des hermines du Val de Ruz. Il permet également de comprendre le relatif faible taux de recaptures (avec une moyenne de 2,33 captures/Hermine) : en plus d'un taux de mortalité élevé, la dispersion est intense et seulement 7 % environ des hermines adultes ont séjourné plus d'une année sur le terrain d'étude.

STRUCTURE DE POPULATION

1. — STRUCTURE D'AGE

Nous avons vu qu'un taux de mortalité moyen constant des adultes était une approximation satisfaisante. Posons l'hypothèse que TMa est également constant pour chaque classe d'âge. En d'autres termes que la probabilité de survie d'une Hermine adulte est constante quel que soit son âge. Une telle hypothèse a déjà été émise par Quick (1963) et reprise par van Soest et van Bree (1970), qui ont calculé une pyramide des âges théorique avec un taux de mortalité de 0,75.

La population estimée à partir de la droite de régression $Na(m) = 6{,}20 - 0{,}35\, m$ (Fig. 3) peut alors être décomposée en classes d'âge (la classe i étant représentée par les individus ayant entre i et i+1 ans d'age) pour chaque mois de l'année (Fig. 4) :

$$Na(m)_i = Na(m) \,.\, Tma \,.\, (1 - TMa)^i.$$

Le taux de mortalité des juvéniles TMj ne pouvant pas être considéré comme constant, les nombres moyens mensuels de juvéniles Nj(m) extraits du calendrier de captures ont été utilisés pour compléter le diagramme de la structure d'âge de la population (Fig. 4).

2. — AGE MOYEN

La population moyenne estimée étant décomposée en classes d'âge, il est possible de calculer l'âge moyen de la population, si on considère que toutes les hermines naissent, en moyenne, à la mi-avril. Cette estimation de la date de naissance, basée sur les données de Deanesly (1943), Müller (1970), Gulamhusein et Thawley (1974) et sur des observations personnelles correspond assez précisément à la date moyenne calculée à partir des données de King et Moody (1982), après correction de 6 mois pour compenser le changement d'hémisphère.

Dès lors, l'âge moyen des adultes Aa(m) au mois m sera :

$$Aa(m) = \frac{\sum_i Na(m) \, . \, Tma \, . \, (1 - TMa)^i \, . \, (m + 8 + 12i)}{\sum_i Na(m) \, . \, TMa \, . \, (1 - TMa)^i}$$

Pour calculer l'âge moyen de la population active totale A(m), il faut prendre en considération le collectif des juvéniles :

$$A(m) = \frac{Nj(m) \, . \, (m - 4) + \sum_i Na(m) \, . \, TMa \, . \, (1 - TMa)^i \, . \, (m + 8 + 12i)}{Nj(m) + \sum_i Na(m) \, . \, TMa \, . \, (1 - TMa)^i}$$

A(m) ainsi estimé a été illustré à la Fig. 4.

Un échantillonnage aléatoire effectué sur la population décrite à la Fig. 4 conduirait à la mesure d'un âge moyen global de 14,4 mois.

DISCUSSION

1. — DYNAMIQUE DE POPULATION

La densité de population a été relativement constante au Val de Ruz de 1978 à 1981, les variations observées au cours de cette période étant principalement imputables à la méthode d'échantillonnage. En effet, nous avons observé que les conditions météorologiques (pluviosité, vents dominants, couverture de neige, etc.), les variations saisonnières de la couverture végétale et les ressources alimentaires (Debrot, 1981) ont une influence sur les résultats de piégeage. Tous ces facteurs externes à la population des hermines, additionnés aux facteurs internes (variations saisonnières de la répartition des classes d'âge, piégeabilité inégale et non exhaustivité des sessions) justifient l'utilisation d'un calendrier de captures dans l'analyse des caractéristiques de la population étudiée.

La fréquence des sessions, l'intensité des efforts de piégeage, l'utilisation de pièges efficaces et les contrôles par le relevé des traces sur neige permettent de considérer que le calendrier de captures concerne la majorité des hermines sédentaires et des sédentaires temporaires (*residents* et *temporary residents* selon Lockie, 1966), auxquelles s'ajoute une partie malheureusement inestimable des erratiques (*transients*) ayant traversé le terrain d'étude. Il donne donc une bonne idée des fluctuations de population (Debrot et Mermod, 1981) et indique pour chaque mois une estimation minimale de la population et de sa composition (Fig. 2), même lorsqu'aucun piégeage n'a eu lieu.

De plus, l'examen de l'évolution annuelle d'une population moyenne présente plus d'intérêt que celui d'une situation unique. Il faut cependant relever que la stabilité de la population, observée pendant 3 années, reflète une situation particulière plutôt que la règle (King, 1981 ; Debrot, 1983), et qu'une forte augmentation de population a été observée en 1982-1983 sur le même terrain d'étude (Mermod, *com. pers.*).

2. — TAUX DE MORTALITÉ ET DE RENOUVELLEMENT

Le taux de mortalité estimé des adultes TMa = 0,68 exprime l'intense pression de sélection à laquelle a été soumise la population étudiée. Il est en accord avec la forte proportion de juvéniles observée d'août à décembre (entre 55 % et 67 %).

Le rapide renouvellement de la population des adultes (TRa = 0,93) permet de mieux comprendre le faible taux de recaptures à moyen et à long terme enregistré au cours de l'étude. Il faut cependant remarquer que TRa est d'autant plus élevé que la surface d'étude est petite (théoriquement, TRa = TMa dans une population fermée).

Un haut degré de dispersion et une mortalité élevée chez les adultes ont également été observés par King et McMillan (1982), alors que les travaux d'Erlinge (1977) et de Simms (1979) suggèrent un renouvellement important par les forts pourcentages de juvéniles qui ont été mis en évidence.

3. — AGE MOYEN

Van Soest et van Bree (1970) ont étudié la structure d'âge d'une population d'hermines dans une région de dunes des Pays-Bas, par l'application de différentes techniques de détermination de l'âge, en particulier l'analyse des couches concentriques de cément des canines. A partir de leurs données nous avons calculé que l'âge moyen de la population mâle était de 11,9 mois, en considérant que l'échantillonnage (N = 87) a été effectué au hasard tout au long des trois années d'étude (soit que la classe 0 est constituée d'individus ayant en moyenne 6 mois d'âge, la classe 1 d'individus de 18 mois, etc.).

Kukarcev (1978) a étudié de la même manière l'âge des hermines piégées pour leur fourrure dans le district de Berezov (T'umen, U.R.S.S.). Comme la saison de piégeage s'étend essentiellement de novembre à février, on peut considérer que les hermines de la classe 0 étaient âgées en moyenne de 8,5 mois, celles de la classe 1 de 20,5 mois, etc. (naissance : mi-avril, date moyenne de capture : fin décembre). Ainsi, l'âge moyen calculé de l'échantillon (N = 730) est de 13,0 mois. Kukarcev (1978) précise cependant que la proportion de chaque classe d'âge varie d'une année à l'autre.

Ces deux estimations de l'âge moyen de populations d'hermines donnent des valeurs comparables bien qu'inférieures à celle trouvée pour la population du Val de Ruz. Ceci confirme la validité de notre approche et la justesse des estimations faites (TMa constant, naissance à mi-avril, TMJ ≠ TMa, etc.).

Il est possible d'avancer une hypothèse permettant d'expliquer pourquoi l'âge moyen calculé avec les données du Val du Ruz est plus élevé que ceux extraits des données de la littérature : en effet, les deux études de van Soest et van Bree (1970) et de Kukarcev (1978) ont été réalisées sur du matériel récolté pendant plusieurs années par piégeage suppressif, même à but exhaustif dans le premier cas. Cette méthode d'échantillonnage doit certainement modifier la structure de la population étudiée en favorisant la reproduction et/ou en stimulant l'immigration. Le biais ainsi introduit devrait se traduire par une surreprésentation de la classe 0 par rapport à une population naturelle ou étudiée par capture-marquage-recapture.

4. — PYRAMIDE DES AGES

Pour comparer la répartition en classes d'âge de la population étudiée par Kukarcev (1978) avec nos estimations, nous avons calculé pour le Val de Ruz la proportion représentée par chaque classe d'âge par rapport à la population totale du mois de janvier (Fig. 5). La classe 0 (jeunes adultes) est sous-représentée au Val de Ruz, alors que les collectifs des classes 1 et 2 y sont plus grands que ceux de la population chassée étudiée par Kukarcev (1978). La longévité de cette dernière est donc effectivement plus faible.

L'échantillonnage de van Soest et van Bree (1970) s'étalant tout au long de l'année, nous le comparons, de la même manière, à la proportion moyenne de chaque classe d'âge par rapport à la population totale moyenne du Val de Ruz (Fig. 5). Dans ce cas, la différence de répartition des individus dans la pyramide des âges est encore plus marquée, ce qui pourrait traduire la pression de chasse très forte exercée sur la population étudiée par ces auteurs.

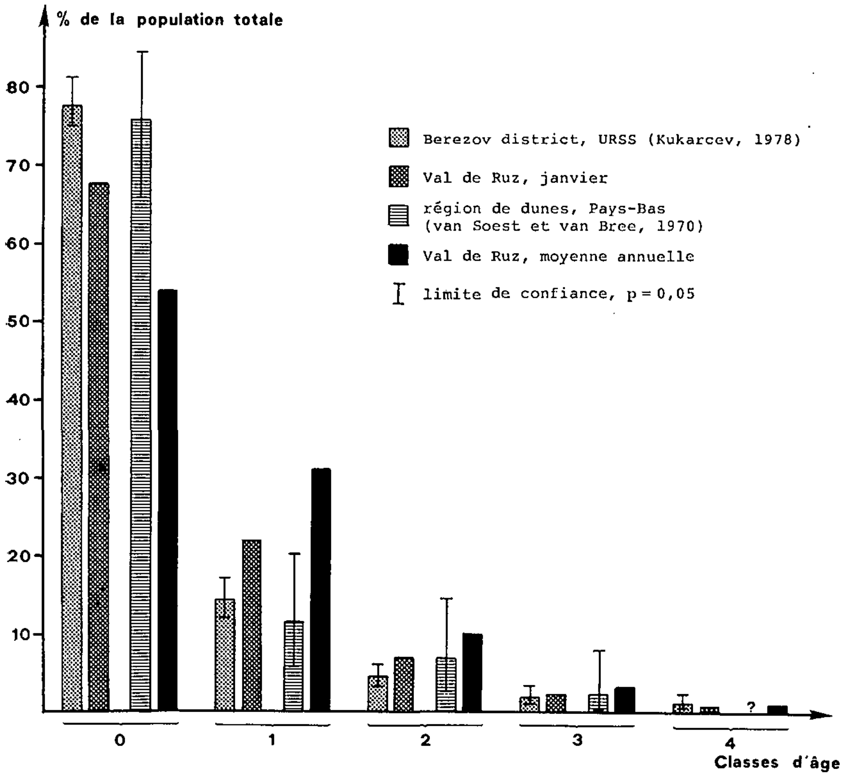

Figure 5. — Diagramme comparatif de la décomposition en classes d'âge de 3 populations d'hermines. Les deux premières colonnes de chaque classe d'âge correspondent à des situations hivernales. Les deux autres colonnes illustrent des structures moyennes de population.

CONCLUSION

Ce travail propose une méthode originale d'analyse des données obtenues par capture-marquage-recapture chez *M. erminea*. Certes elle s'appuie sur quelques approximations qui mériteraient d'être vérifiées dans la mesure du possible par des travaux ultérieurs, afin d'affiner les résultats obtenus et d'en préciser la fiabilité. Cette étude a cependant permis de mettre en évidence un taux de mortalité élevé, associé à un brassage de population important et une reproduction intense. Bien que les hermines du Val de Ruz semblent vivre plus longtemps que celles des populations exploitées, l'âge moyen estimé est étonnamment faible par rapport à la longévité potentielle de l'espèce, qui est certainement supérieure à 8 ans (Müller, 1970).

RESUME

L'étude d'une population d'hermines (*Mustela erminea*) dans le Val de Ruz (Jura neuchâtelois, Suisse) a permis la capture et le marquage de 95 individus d'avril 1978 à avril 1980. La structure mensuelle moyenne de la population a été établie à partir d'un *calendrier de captures* intégrant les 178 captures et recaptures réalisées. Un taux de mortalité (TMa ; estimé constant) de 0,68 et un taux de renouvellement (TRa ; dépendant de l'émigration) de 0,93 caractérisent la labilité de la population des adultes. TMa est en accord avec la proportion élevée de juvéniles. TRa traduit le large rayon de dispersion des adultes par rapport aux dimensions du terrain d'étude (616 ha). L'âge moyen de la population active estimée a été calculé pour chaque mois. Il oscille entre 9,8 mois en août et 18,7 mois en mai. La longévité estimée est un peu plus élevée que les valeurs trouvées dans des populations intensivement chassées, mais inférieure à la longévité potentielle de l'espèce. Les hermines du Val de Ruz paraissent donc être soumises à une pression de sélection élevée.

SUMMARY

A population study of the Stoat (*Mustela erminea*) in the Val de Ruz (Swiss Jura mountains) led to the capture and marking of 95 individuals from April 1978 to April 1980. The structure of the population has been established on a monthly basis from a *calendar of captures* integrating the 178 captures and recaptures recorded. A death rate (TMa ; assumed to be constant) of 0.68 and a renewal rate (TRa ; emigration-dependant) of 0.93 characterize the lability of the adult population. The high proportion of juveniles recorded correlates well with the TMa value. TRa expresses the large dispersal range of the adults compared with the size of the study area (616 ha). The average age of the estimated active population was calculated for each month ; it ranges from 9.7 months in August to 18.7 months in May. The estimated age structure is compared with data from the literature. Our estimates for longevity are somewhat higher than the values for populations that are extensively hunted, but they are low when compared with the potential longevity of the species. The stoats of the Val de Ruz therefore appear to be under severe selective pressure.

BIBLIOGRAPHIE

Caughley, G. (1977). — *Analysis of vertebrate populations.* John Wiley and Sons, New York, 234 pp.

Dagnelie, P. (1973). — *Théorie et méthodes statistiques, applications agronomiques : Volume I.* Les Presses Agronomiques de Gembloux, Gembloux, 378 pp.

Deanesly, R. (1943). — Delayed implantation in the Stoat (*Mustela mustela*). *Nature,* 151 : 365-366.

Debrot, S. (1981). — Trophic relations between the Stoat (*Mustela erminea*) and its prey, mainly the Water Vole (*Arvicola terrestris scherman*). In *Worldwide Furbearer Conf. Proc., Vol. II.* Chapman J.A., Pursley D. (eds), Frostburg, Maryland, August 1980, pp. 1259-1289.

Debrot, S. (1982). — *Ecologie de* Mustela erminea *L. : dynamique des composantes structurales, trophiques et parasitaires de deux populations.* Thèse de doctorat non publiée, Neuchâtel, 279 pp.

Debrot, S. (1983). — Fluctuations de populations chez l'Hermine (*Mustela erminea* L.). *Mammalia,* 47 : 323-332.

Debrot, S., Mermod, C. (1981). — Cranial helminth parasites of the Stoat and other mustelids in Switzerland. In *Worldwide Furbearer Conf. Proc., Vol. II.* Chapman J.A., Pursley, D. (eds), Frostburg, Maryland, August 1980, pp. 690-705.

Debrot, S., Mermod, C. (1983). — The spatial and temporal distribution pattern of the Stoat (*Mustela erminea* L.). *Oecologia,* 59 : 69-73

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

Erlinge, S. (1977). — Spacing strategy in Stoat *Mustela erminea. Oikos,* 28 : 32-42.

Gulamhusein, A.P., Thawley, A.R. (1974). — Plasma progesterone levels in the Stoat. *J. Reprod. Fert.,* 36 : 405-408.

King, C.M. (1981). — The reproductive tactics of the Stoat (*Mustela erminea*) in New Zealand forests. In *Worldwide Furbearer Conf. Proc., Vol. I.* Chapman J.A., Pursley, D. (eds), Frostburg, Maryland, August 1980, pp. 443-468.

King, C.M., McMillan, C.D. (1982). — Population structure and dispersal of peak-year cohorts of stoats (*Mustela erminea*) in two New Zealand forests, with special reference to control. *New Zealand J. Ecol.,* 5 : 59-66.

King, C.M., Moody, J.E. (1982). — The biology of the Stoat (*Mustela erminea*) in the National Parks of New Zealand. IV. Reproduction. *New Zealand J. Zool.,* 9 : 103-118.

Kukarcev, V.A. (1978). — The structure of an Ermine (*Mustela erminea*) population at different densities. In *Abstracts of papers, II. Congressus Theriologicus Internationalis.* Obrtel, R., Folk, C., Pellantova, J. (eds). Brno, Czechoslovakia, June 1978, p. 328.

Lockie, J.D. (1966). — Territory in small carnivores. *Symp. zool. Soc. Lond.,* 18 : 143-165.

Mermod, C., Debrot, S. (1978). — Morphométrie crânienne par radiographie. I : Problèmes techniques. *Rev. suisse Zool.,* 85 : 730-738.

Mueller, H. (1970). — Beiträge zur biologie des Hermelins (*Mustela erminea* L.). *Säugetierk. Mitt.,* 18 : 293-380.

Petrusewicz, K., Andrzejewski, R. (1962). — Natural history of a free-living population of house mice (*Mus musculus* L.), with particular reference to groupings within the population. *Ekologia Polska,* Seria A, 10 : 86-122.

Quick, H.F. (1963). — Animal population analysis. In *Wildlife Investigational Techniques,* Mosby, H.S. (ed.), pp. 190-228.

Simms, D.A. (1979). — Studies of an Ermine population in southern Ontario. *Can. J. Zool.,* 57 : 824-832.

Twigg, G.I. (1978). — Marking mammals by tissues removal. In *Animal marking, recognition marking of animals in research,* Stonehouse, B. (ed.), The MacMillan Press, London, pp. 109-118.

Van Soest, R.W.M., Van Bree, P.J.H. (1970). — Sex and age composition of a Stoat population (*Mustela erminea* Linnaeus, 1758) from a costal dune region of the Netherlands. *Beaufortia,* 17 : 51-77.