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Variability in number and distribution of *Apodemus flavicollis* (Melch.) and *A. sylvaticus* (L.) in South Sweden

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1. Introduction

Apodemus sylvaticus (L.) is a very common small rodent in South Sweden which in most autumns occurs in large numbers in forest habitats (HANSSON 1967). The species also appears regularly on open fields (HANSSON 1968). *Apodemus flavicollis* (Melch.) is usually found in considerably smaller numbers and almost only appears in forest habitats, but may during certain years reach high numbers (cf. HANSSON 1967).

During a study of habitat selection and behaviour of the two *Apodemus* species at the Stensoffa Ecological Station in southernmost Sweden (cf. e. g. HOFFMEYER 1973), *A. flavicollis* was found in large and increasing numbers during 1972. An opportunity was thus presented to examine the population increase and the habitat distribution of *A. flavicollis* and the possible effects on the *A. sylvaticus* population. Long-term population studies in the area were used for the analyses and some particular examinations were also performed.

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2. Methods

2.1. Small quadrat catches

The Stensoffa area was used as one of the sampling localities for a pan-Nordic monitoring programme concerning small rodents. Trapping was performed in four habitats with small quadrats (Myllymäki et al. 1971) during the autumn, late winter, spring and high summer. Population structure, reproduction and weight were determined for the animals caught.

2.2. Unsystematic live-trapping

Live-traps were put in the "best positions» in the forests and on grasslands in order to obtain as many animals as possible for the experiments. The trapping was non-regular but as there was a great trapping effort the catches are believed to be comparable in 1971 and 1972.

2.3. Long-term removal

Twenty live-traps were located in the garden of the Stensoffa Station since 1967. The station is situated in about the middle of a 10 ha abandoned field, mainly surrounded by forests but connected with other extensive abandoned fields. The shortest distance to a forest is about 75 m. The project and results will be treated in another context but it may be stated here that the catches partly reflect the population pressure for various species.

2.4. Examination of occurrence on fields in relation to distances to forests

2.4.1. Removal lines

Six lines of 14×2 live-traps were placed starting from inside beech forests and out onto sandy, abandoned fields for two days during September 1972. The distance between trap stations was 15 m with 3 stations in the forest, 1 station on the forest edge and 10 stations thus extending 150 m out onto the fields.

2.4.2. Random quadrats

Ten small quadrats with live-traps were radomly distributed on sandy, abandoned fields during August and October 1972 so that the distance to the nearest forest was variable. Animals were trapped for four days and removed each day.

3. Habitats

3.1. Beech forests

This habitat consisted mainly of pure mature beech, *Fagus silvatica,* but some mature oaks, *Quercus robur,* and pines, *Pinus silvestris,* were also present. The field layer was rather poor and contained low herbs and *Rubus idaeus.*

3.2. Reforestations

These areas had been reforested with spruce, *Picea abies,* after the beech forest had been cut. A luxuriant field layer dominated by *Chamaenerion angustifolium* and *R. idaeus* was also present.

3.3. Abandoned fields on mineral soil

These habitats were sandy, dry areas with a rather open grass cover dominated by *Dactylis glomerata.*

3.4. Abandoned fields on peat soil

This habitat type consisted of wet areas with a luxuriant vegetation cover of mainly grasses and sedges, e. g. *Deschampsia caespitosa* and *Carex nigra.*

4. Results

4.1. Small quadrat catches in four habitats during 1971—73

In all four habitats examined, there was a change in the proportions of *A. flavicollis* and *A. sylvaticus* trapped during 1971–73 (Fig. 1). The number of *A. sylvaticus* decreased rapidly from autumn, 1971 to late winter and spring, 1972. There

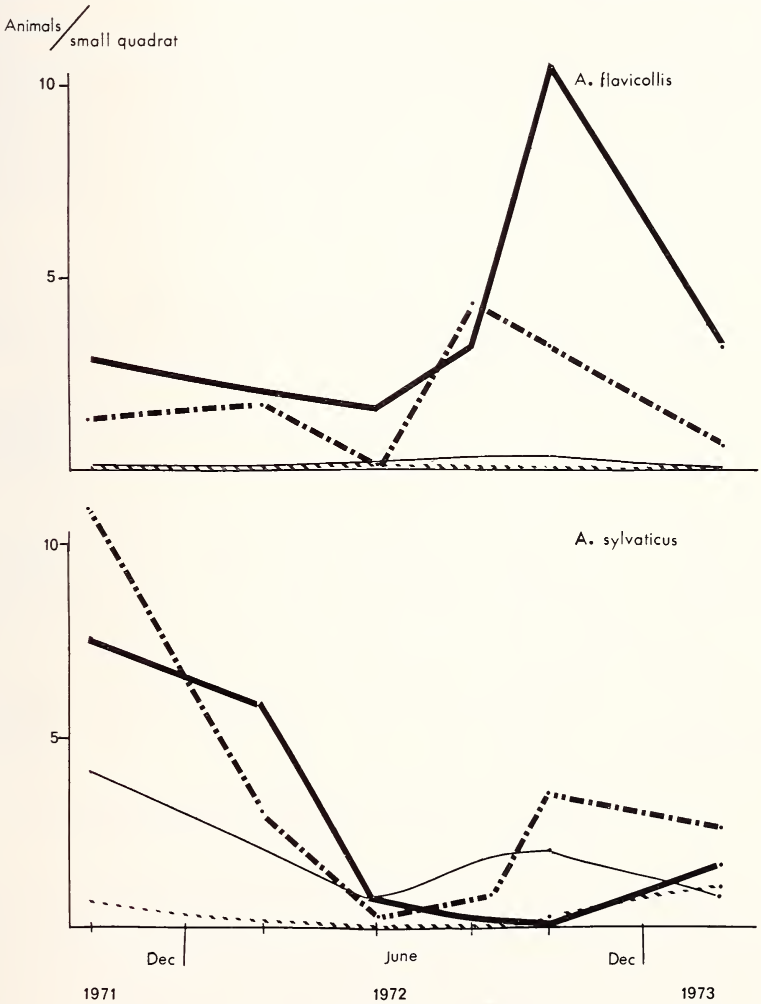

Fig. 1. Mean number of animals caught per small quadrat in four habitats during 1971—73. About ten small quadrats were randomly distributed in each habitat during each trapping period ——— = beech forest; –.–.– = reforestation; ——— = sandy, abandoned fields; — — — = abandoned fields on peat soil

was only a slight increase in "field" habitats (with generally more captures on sandy than on peat soil) during the summer-autumn period of 1972 and a further decrease for the beech forest. For *A. flavicollis*, there was a slight decrease until the spring of 1972 and thereafter a rapid increase, especially for the beech forest. For both species, highest numbers were obtained during the autumns of 1971 and 1972 in the same habitats, i. e. in the beech forest for *A. flavicollis* and in the reforestations for *A. sylvaticus*. However, during 1972 as compared with 1971, there were significantly more *A. flavicollis* caught per quadrat in the beech forests ($t = 3.24$, $p < 0.01$) and fewer *A. sylvaticus* in the beech forests ($t = 4.73$, $p < 0.001$) and the reforestations ($t = 5.58$, $p < 0.001$). During the late winter of 1973, there was a pronounced decrease in the *A. flavicollis* population. The *A. sylvaticus* population was now more evenly distributed in the four habitats and there was an increase in the numbers present in the beech forest.

The inverse relations for catches of *A. flavicollis* and *A. sylvaticus* could have been due to e. g. competition for traps or differences in the selection of micro-habitats. Both these conditions ought to have resulted in negative correlations between catches of the two species in the quadrats. Examination showed insignificant correlations for the beech forest ($r = -0.54$) and the reforestations ($r = +0.04$) for the autumn of 1971, but a significant positive correlation for the reforestations for the autumn of 1972 ($r = +0.64$, $P < 0.05$). These were the only habitats and times with considerable numbers of animals of both species.

Table 1

Population structure and weights of *A. flavicollis* and *A. sylvaticus* caught in small quadrats in various habitats during the autumns of 1971 and 1972

Habitat	Year	Juv.	Ad.	Subad.	Post repr.	Σ speci-mens	Weight of subadults ($\bar{x} \pm SE$)
A. *A. flavicollis*							
Beech forest	1971	2	12	11	6	31	30.0±1.4
Beech forest	1972	1	37	33	24	95	27.9±0.8
Reforestations	1971	0	3	4	3	10	26.9±1.2
Reforestations	1972	0	8	15	7	30	31.1±1.3
B. *A. sylvaticus*							
Reforestations	1971	4	2	62	8	76	17.5±0.3
Reforestations	1972	3	4	17	10	34	16.2±0.3
Abandoned fields	1971	4	11	20	12	47	16.2±0.5
Abandoned fields	1972	8	3	28	8	47	16.0±0.4

The population structures during the two autumns were examined for the beech forests and the reforestations for *A. flavicollis* and in the reforestations and on abandoned fields for *A. sylvaticus* (Tab. 1). As only one *A. sylvaticus* was caught in the beech forest during the autumn of 1972, a comparison was impossible for this habitat. The population structures of *A. flavicollis* were very similar for the two years while there was a considerably lower proportion of *A. sylvaticus* subadults in the reforestations during 1972. (When compared to the rest of the catches, $\chi^2 = 11.57$, $P < 0.001$). The weights of these subadults were also significantly lower in 1972 than in 1971 ($t = 3.24$, $P < 0.01$). On abandoned fields with very few *A.*

flavicollis, there were no such changes. Subadults of *A. flavicollis* in the reforestations weighed more during 1972 than as compared to 1971 ($t = 2.34$, $P < 0.05$).

4.2. Live-trapping during the autumns 1971 and 1972

The unsystematic live-trapping (Tab. 2) revealed the same pattern of distribution for the two species, i. e. *A. sylvaticus* was most common in both the beech forests and on the abandoned fields during the autumn of 1971, and *A. flavicollis* appeared in large numbers in the forests during 1972, while *A. sylvaticus* was almost only found in the fields. Live-trapping (multiple-catching traps) yielded a relatively larger number of *A. flavicollis* in the forests during 1972 than of *A. sylvaticus* in 1971.

4.3. Long-term removal

The number of continuous removal catches (Fig. 2) differed for the two years mainly in the great number of *A. flavicollis* caught from June until November–December, 1972. In 1971, there were only rather occasional catches of *A. flavicollis* for the same period. For both years there were a great number of *A. sylvaticus* caught. In 1972 the summer-autumn increase was delayed, i. e. the first animals were not caught until the middle of August, whereas the increase in 1971 started during June. A comparison of the distribution of catches of *A. sylvaticus* for the two years showed a significant difference ($\chi^2 = 37.62$, $P < 0.001$). However, in both years the peak fell in September, which was also the case for *A. flavicollis* in 1972.

4.4. Distributions on fields of the two species during the autumn of 1972

The lines of traps extending from forests and onto the fields (Fig. 3) showed that this year the forest edge was a clear limit for the penetration of the grassland-living *A. sylvaticus.* Specimens were caught in trap stations at each unit distance outside the forest but in none inside the forest. *A. flavicollis* was caught in great numbers inside the forests but a few were also caught on the fields. The numbers caught at

Table 2

Catches from unsystematically placed live-traps during August—October 1971 and 1972

	Beech forest						Abandoned fields					
		1971			1972			1971			1972	
	Σ trap nights	Σ animals	$\bar{x}$, animals trap	Σ trap nights	Σ animals	$\bar{x}$, animals trap	Σ trap nights	Σ animals	$\bar{x}$, animals trap	Σ trap nights	Σ animals	$\bar{x}$, animals trap
A. flavicollis	1428	99	0.07	1032	217	0.21	1470	20	0.01	2172	35	0.02
A. sylvaticus		140	0.10		7	0.01		212	0.14		188	0.09

the two ends of the lines were due to an edge effect appearing when the distance between trap stations is smaller than the home ranges of the species.

When the correlations were examined between catches in quadrats on the fields and the distances to the forests (Tab. 3), significant negative correlations were found for *A. flavicollis* and for *A. sylvaticus* during August. No *A. flavicollis* were captured in the fields during October. The correlation to the distance to the beech mast/acorn forests was not better than the correlation to only the nearest forest edge. Obviously *A. flavicollis* only penetrated the fields in the near vicinity of the forests. There was a tendency of *A. sylvaticus* to gather close to the forests.

5. Discussion

In 1972, the numbers of *A. flavicollis* increased very greatly but there was no noticeable change in the habitat distribution from 1971. The increase only occurred in the beech forests and in the forest-like reforestations. On the other hand, the change in habitat distribution of *A. sylvaticus* from 1971 to 1972 was very distinct. There was a marked decrease in the forest populations in 1972. However, this species seemed to prefer forest-like habitats, as even in this year the largest numbers were caught in the reforestations. The number of *A. sylvaticus* caught on abandoned fields was almost unchanged at the time of the decrease in the forests.

The population structure and physiology of *A. sylvaticus* were affected in habitats where *A. flavicollis* occurred, i. e. in the reforestations. There seems to have been a low recruitment in high and late summer, 1972 as few subadults were caught later on. However, reproduction and spring survival appeared to be normal with the usual number of post-reproductive animals present during the autumn 1972. The low summer recruitment might be the reason for the delayed immigration to the Stensoffa garden traps.

Fig. 2. Animals caught by continuous removal trapping at the Stensoffa Ecological Station. ——— = *A. flavicollis*; - - - = *A. sylvaticus*

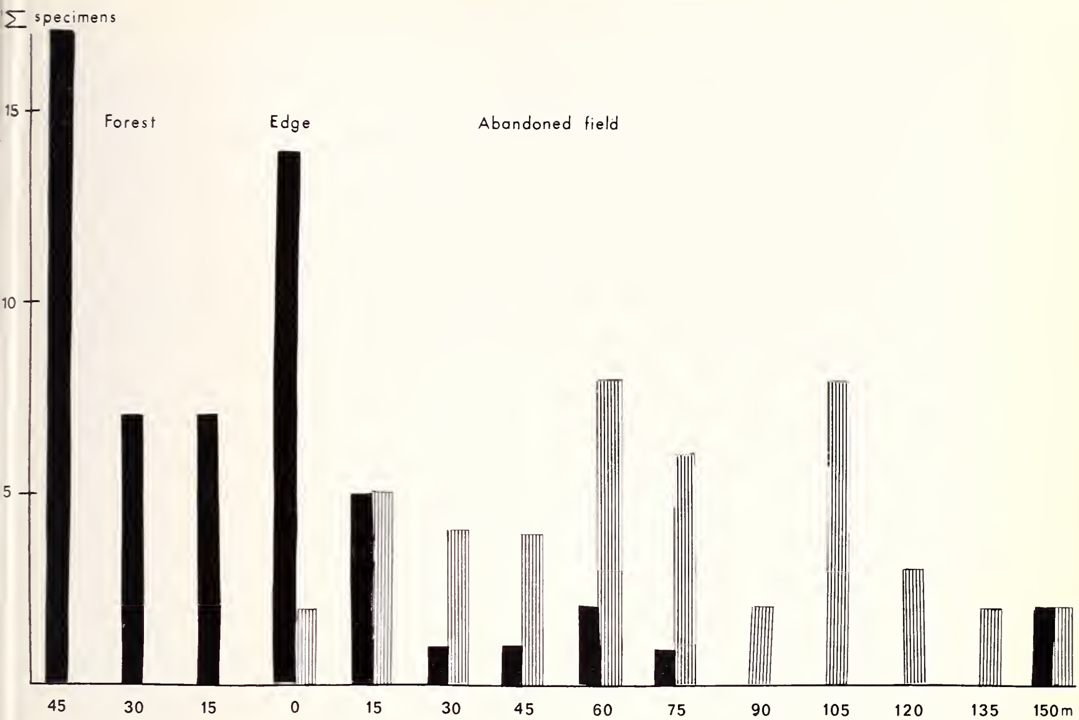

Fig. 3. Distribution of catches in six removal lines extending from beech forest out onto sandy, abandoned fields. ▮ = *A. flavicollis* ‖‖ = *A. sylvaticus*

There are thus clear indications that *A. sylvaticus* was negatively affected by *A. flavicollis* during the peak occurrence of the latter. HOFFMEYER (1973) experimentally found that *A. flavicollis* were able to dominate *A. sylvaticus* in a passive way. Such a dominance, perhaps enhanced by aggressiveness (it has been demonstrated that breeding animals are more aggressive than nonbreeding, SADLEIR 1965, WATSON, MOSS 1970) — may explain the decrease of *A. sylvaticus* in the forests and the limitation of this species to the fields during the summer of 1972. Early summer may be a critical period for *A. sylvaticus* with regard to food conditions (HANSSON 1971). *A. flavicollis* in general eats the same kinds of food, and a domi-

Table 3

Correlation between small quadrat captures on abandoned fields and the distances to forest habitats

NS = non-significant

Distance	A. sylvaticus				A. flavicollis	
	August		October		August	
	r	P	r	P	r	P
Forests generally	—0.64	<0.05	—0.47	NS	—0.72	<0.05
Beech/oak forests	—0.62	NS	—0.52	NS	—0.64	<0.05

nating behaviour on its part might affect food availability for perhaps especially the young of *A. sylvaticus.*

Environmental conditions which cause an out-break of *A. flavicollis* might include weather and food. The 1970–71 and 1971–72 winters were both mild, although there was much snow in November, 1971 and low temperatures in March, 1971 and January, 1972. There was no authoritative registration of the acorn and beech-mast productions for the autumns 1970—72, but personal observations agreed with those of foresters that there was a peak production in 1971 and a low in 1972. The cone production of spruce was locally abundant in 1971 (SIMAK, ANDERSSON 1971) and there is a positive correlation of the production of spruce and beech (HANSSON 1971).

HANSSON (1971) showed that in an area where there were no *A. flavicollis* present, a good beech-mast crop resulted in an increase in the *A. sylvaticus* population during the same autumn and the following year. In an area where *A. flavicollis* was also present, there was an increase in the *A. sylvaticus* population the same autumn whereas only *A. flavicollis* increased the following year. In forests where the species *A. sylvaticus* was not present, the number of *A. flavicollis* increased during the year after a peak beech-mast or acorn crop (GRODZINSKI et al. 1966; BOBEK 1971). The more rapid reactions of *A. sylvaticus* might be due to invasions from fields and perhaps also to a higher turnover rate. It thus appears that a peak tree seed crop causes increases in the populations of small granivorous rodents. For populations of *A. sylvaticus,* the increase may occur both during the same year and the next year, and for *A. flavicollis,* just the next year. If, however, *A. flavicollis* and *A. sylvaticus* are both present, the former will suppress the nextyear increase in the latter.

Similar conditions have been observed for *Microtus oeconomus* (Pall.) and *M. agrestis* (L.) where the subordinate species was driven out from grasslands (TAST 1968).

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Summary

During the occurrence of a peak number of *Apodemus flavicollis* there was a pronounced decrease in the number of *Apodemus sylvaticus* in forest habitats while it remained normal in field habitats. In the autumn population of *A. sylvaticus* there was a low number of subadults and with low body weights, in areas where this species shared habitats with *A. flavicollis.* This evidence of a low and poor summer recruitment was supported by a low population pressure in *A. sylvaticus* during the summer. Distinct borders for the distribution of *A. sylvaticus* further indicated that the presence of *A. flavicollis* affected the number and distribution of *A. sylvaticus.*

It appears that peak crops of beech-mast or acorn are generally followed by large forest populations of *Apodemus* spp., but that *A. flavicollis* will suppress the nextyear increase of *A. sylvaticus* when both are present.

Zusammenfassung

Variabilität in Zahl und Verteilung von Apodemus flavicollis (Melch.) und A. sylvaticus (L.) in Süd-Schweden

Bei hoher Dichte von Gelbhalsmäusen *(Apodemus flavicollis)* nahm die Zahl von Waldmäusen *(Apodemus sylvaticus)* im Waldbiotop ab, wogegen sie im Feldbiotop unverändert blieb. Die Herbstpopulation von Waldmäusen enthielt in Gebieten, in denen auch Gelbhalsmäuse vorkamen, nur wenige und kleinwüchsige Jungtiere. Gleichzeitig war der Populations-

druck von *A. sylvaticus* schwach. All dies spricht für eine nur schwache Vermehrung der Waldmaus im voraufgegangenen Sommer. In einem Fall hoher Dichte von Gelbhalsmäusen im Wald bildete der Waldrand eine scharfe Grenzlinie für das außerhalb des Waldes regelmäßige Auftreten von Waldmäusen. Dies spricht dafür, daß die Gegenwart von Gelbhalsmäusen das Vorkommen von Waldmäusen negativ beeinflußt.

Jahre reicher Eichel- oder Buckeckernmast haben gewöhnlich eine Zunahme von *Apodemus* im Wald zur Folge. Bei Vorkommen beider Arten werden jedoch nur die Gelbhalsmäuse häufiger, wogegen die Waldmäuse zurückgehen.

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