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Distribution of the field mice *Apodemus flavicollis* and *A. sylvaticus* in Norway

Harald Lura, Gunnar Langhelle, Tore Fredriksen & Ingvar Byrkjedal

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Examination of specimens of yellow-necked and wood mice in Norwegian museum collections showed that yellow-necked mice are confined to areas with a continental climate, east and northwest of the South Norwegian watershed. The range of wood mice overlapped extensively with that of yellow-necked mice, but contrary to yellow-necked, wood mice also inhabited the most oceanic parts of western and southernmost Norway. Wood mice seem more or less absent in the most continental areas, where yellow-necked mice have their stronghold. Both species are rare in the Trøndelag counties, north of the South Norwegian mountains, and they are absent further north. A discriminant function analysis described the occurrence of yellow-necked mice by low January mean temperatures, low annual precipitation, less productive vegetation zones, and high April temperatures, and wood mice by long growth season and low April temperatures. The analysis alters the Norwegian range maps for both species.

Harald Lura[1], Gunnar Langhelle, Tore Fredriksen & Ingvar Byrkjedal, Museum of Zoology, University of Bergen, Muséplass 3, N-5007 Bergen, Norway.

[1] Present address: Miljøvernavdelingen, Fylkesmannen i Rogaland, P.O. Box 59, N-4001 Stavanger, Norway.

INTRODUCTION

Distributed over major parts of Europe, yellow-necked and wood mice, *Apodemus flavicollis* and *A. sylvaticus*, show a large geographical overlap (e.g. Niethammer & Krapp 1978). Yet wood mice extend their range westwards to the Atlantic seaboard whereas yellow-necked mice are generally confined to the less oceanic parts of Europe. Both species inhabit the southern part of the Scandinavian Peninsula. Here, yellow-necked mice appear from published distribution maps (e.g. Siivonen 1967, Niethammer & Krapp 1978, Semb-Johansson & Ims 1990) to be exceptional by inhabiting also the extremely oceanic parts of western Norway. These are among the most oceanic regions on the European continent (Ouren et al. 1987-93). However, trappings at a limited number of localities seem to indicate wood mouse to be the only species of *Apodemus* present in southwestern Norway (Linn 1959, Christiansen 1983).

We examine the Norwegian distribution of these two species from identified material kept in museum collections, and compare the distribution with climatic and climatically related environmental parameters. We also discuss factors likely to determine the distribution of these species and point out issues in need of further study.

MATERIAL AND METHODS

We obtained copies of specimen cards for all wood and yellow-necked mice held in the collections of the four Norwegian university museums (in Oslo, Trondheim, Tromsø, and Bergen). This material comprised 120 specimens of yellow-necked mouse and 609 specimens of wood mouse, representing 40 and 106 localities, respectively.

For each locality we extracted environmental and climatic variables, using the maps in Ouren et al. (1987-93). On these maps the variables precipitation, snow cover, growth season, and temperature, are shown as zones, each zone representing an interval (e.g., 500-700 mm annual precipitation). We used the middle values of these intervals, instead of intrapolation. The following variables were used:

(1) Annual precipitation (range: 350-3750 mm)
(2) Mean temperatures in each of the months January (range: -10-2 °C), April (range: -2-6 °C), July (range: 6-18 °C), and October (range: -2-10 °C)
(3) Mean number of days with snow cover (range: 38-232 days)
(4) Length of the growth season, defined from the date of daily temperature (24 h) passing 5 °C and increasing (beginning) to the date of daily temperature passing 5 °C and decreasing (range: 78-230 days)
(5) Vegetation zones, arranged according to increasing productivity and complexity: 1, low alpine; 2, north boreal; 3, mid boreal; 4, south boreal; 5, boreonemoral (including heather moor region of western coast northwards from Rogaland); 6 nemoral (incl. heather moor region eastwards from Vest-Agder)
(6) Agriculture/forestry-areas, arranged according to increasing productivity: 1, no forestry or agriculture; 2, less productive forest; 3, productive forest; 4, agriculture.

Also, (7) elevation (m above sea level) was entered as a variable in the analysis.

Variables 1-6 were chosen apriori as being strongly related to the oceanic-continental climatic gradient. We compared the occurrence of the two species by discriminant function analysis (DFA) of the variables listed above using stepwise variable selection from minimized Wilk's Lambda. The variables were entered for each locality at which any of the species of *Apodemus* had been collected. Analysis was run for yellow-necked mice using all the wood mouse localities as reference points, and vice versa. We only considered presence or absence, sampling effort being unknown for most of the localities. Prior probabilities were chosen according to sample proportion of cases actually falling into each group. Since a number of localities had both species, DFA yielded different solutions for yellow-necked and wood mice, neccessitating separate analysis for each species. Localities less than 1 km apart and with the same scores on all variables were entered as a single locality.

Museum specimens represent a fair amount of opportunistic sampling, and absence of a species in an area may be an effect of lack of sampling. To check for lack of sampling in such areas we recorded localities for which the museum material contained specimens of bank vole *Clethrionomys glareolus*, grey-sided vole *C. rufocanus*, short-tailed vole *Microtus agresits*, or root vole *M. oeconomus*, species usually collected by the same type of traps (small snap traps and live traps) as used for *Apodemus* mice. Many localities with vole catches within a region, but a lack of field mice specimens, would suggest that the latter are rare or absent. However, behavioural differences between voles and *Apodemus* mice (diurnal vs. nocturnal activity, use of cover, etc.; Bergstedt 1965, Niethammer & Krapp 1978) may create differences in trapabilities and the use of vole sites to reveal absence of *Apodemus* is only indicative. DFAs of *Apodemus* against voles were not performed.

The species identity, although stated on specimen cards, was checked for yellow-necked mouse from 35 % of the localities from which the species was recorded, and for wood mouse from 70 % of the localities. None of the specimens had been assigned to an incorrect species identity. Emphasis was laid on checking specimens from the border of the distributions. Unlike mid and southern Europe, where the two species show morphological convergence (e.g., Niethammer 1969, Britton-Davidian et al. 1991, Fernandes et al. 1991) yellow-necked and wood mice from Fennoscandia separate well on the sizes of yellow collar and pectoral spot, ventral colour, relative tail length, and to some extent body size (Barth 1955, Ursin 1956, Reinvaldt 1958, Niethammer & Krapp 1978).

The enormous population fluctuations normally found in rodents (see Christiansen 1983 for a Norwegian material on fluctuations of *Apodemus*) strongly influence the likelihood that a species is recorded at a locality in a given year. The museum collections used were spread over a period of more than 100 years, to some extent counteracting this effect, at least on a regional scale.

RESULTS

All of the localities at which *Apodemus* had been caught were below the timberline, but both species were distributed from sea level to the subalpine forest. Whereas yellow-necked mice were confined to areas east and northwest of the south Norwegian watershed, wood mice were found also along the southern and southwestern coast (**Figure 1**). Yellow-necked mice seem to become relatively more common than wood mice northwards in Eastern Norway; south of Lillehammer the ratio yellow-necked to wood mice was 0.4 (11/27) as regards number of localities, and 3.5 (21/6) north of Lillehammer. In spite of a high number of localities having been trapped for mice as well as voles, wood mice have not been obtained in the interior parts of the valleys Gudbrandsdalen and Østerdalen or eastwards in the Femunden-Røros area. In the northwestern region, north of Sognefjorden, the ratio yellow-necked to wood mice localities was 1.8 (7/4), while south of Sognefjorden only wood mice have been recorded.

In Sør- and Nord-Trøndelag (i.e., north of the South Norwegian mountains) both species are rare judging from the relatively large number of localities at which voles have been trapped (**Figure 1**). Yellow-necked mice have not been recorded north of Oppdal in the interior southernmost part of Sør-Trøndelag, whereas wood mice have only been recorded at two localities, one (Trondheim) coastal and lowlying and one (Tydal) at higher elevation in the interior.

Among the variables entered in the discriminant function analyses (DFA), occurrence of yellow-necked mice was identified by low January temperatures, low annual precipitation, less productive vegetation zones, and high April temperatures (**Table 1**). By these variables DFA correctly classified 82.2 % of the localities as to presence or absence of yellow-necked mice (**Table 2**). The wrong classifications tend to be centered around the discriminating value, yet there is a considerable spread of both classification groups (**Figure 2A**). The localities at which yellow-necked mice have been recorded in spite of the DFA predicting their absence are found in the northwestern and southernmost parts of the species' range (i.e., Sogn og Fjorane, Møre og Romsdal, Sør-Trøndelag, and Akershus southwestwards to eastern Telemark; **Figure 1A**). Localities predicting presence but lacking

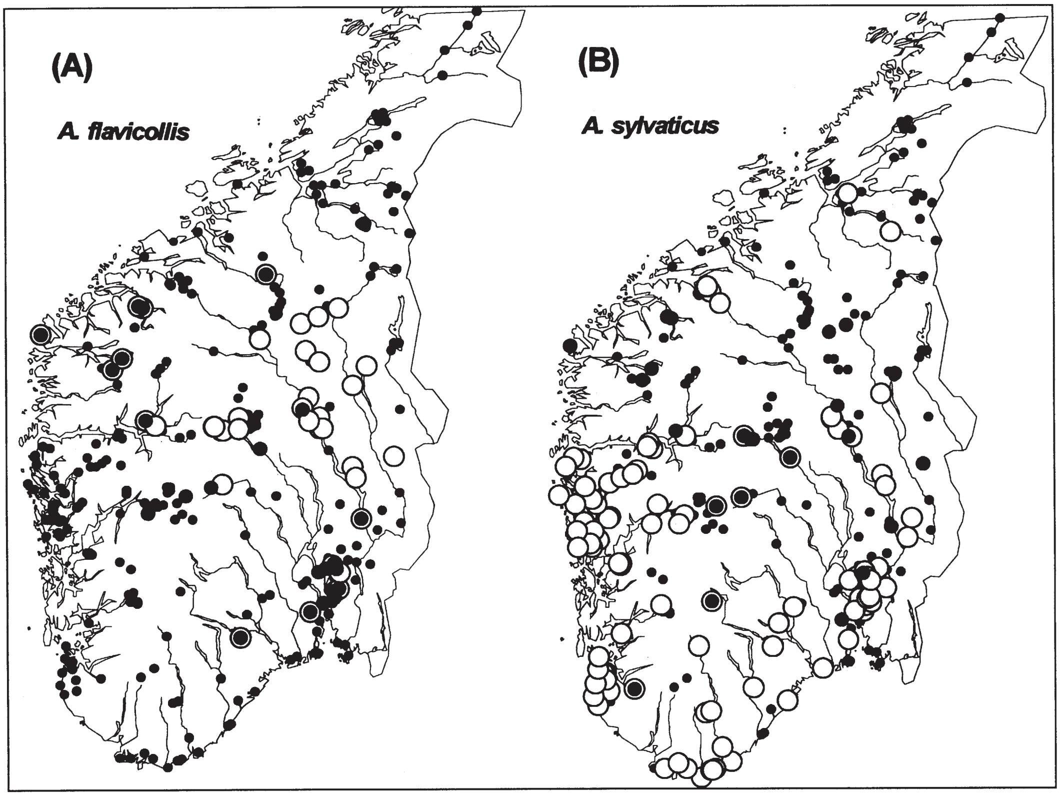

Figure 1
Norwegian localities of Apodemus flavicollis *(A) and* sylvaticus *(B) as documented by museum specimens. ○=Species found, presence predicted by discriminant function analysis (DFA). ◉=Species found, absence predicted by DFA. ● =Presence predicted by DFA, the other* Apodemus *species found only. •=Localities at which voles (not analyzed by DFA), or* Apodemus *of the other species have been caught, absence correctly predicted by DFA for species in question.*

recorded specimens are found in eastern Norway close to sites where the species has been found, with the exception of 2 localities (Vivelid, west of Hardangervidda, and Tydal, Sør-Trøndelag).

DFA identified wood mouse localities by a long growth season and a low April temperature (**Table 1**). In spite of a large spread in the discriminant scores, especially of localities with positive records of the species (**Figure 2B**), 83.7 % of the localities were correctly classified by the DFA (**Table 2**). The five wood mouse localities for which the DFA predicted the species to be absent, are all situated immediately east of the mountain region Hardangervidda-Hemsedalsfjella (**Figure 1B**). Ten of the 16 negative localities at which a presence of the species was predicted, are found east of the South Norwegian watershed, 8 of them close (1-10 km) to confirmed wood mouse localities. DFA also predicted presence at 7 localities distant (> 40 km) from known wood mouse localities, 5 in the northwest (Sogn og Fjordane-Møre og Romsdal) and 2 in the innermost part of Østerdalen valley.

Table 1. *Canonical coefficients from discriminant function analyses of presence or absence of field mice in relation to environmental variables at Norwegian localities. Variables are listed in descending importance, as entered by the analyses, and canonical correlation coefficients ($p < 0.001$, all cases) after each step are given. The discriminant functions gave a Wilk's Lambda of 0.605 for* Apodemus flavicollis *and 0.717 for* A. sylvaticus *($p< 0.001$ for both).*

Species and variables	Unstandardized coefficients	Standardized coefficients	Correlation coefficients
A. flavicollis			
January temperature	0.196	0.670	0.544
Annual precipitation	0.000938	0.529	0.594
Vegetation zone	0.470	0.479	0.610
April temperature	-0.168	-0.473	0.628
Constant	-0.908		
A. sylvaticus			
Length of growth season	0.0476	1.479	0.491
April temperature	-0.258	-0.734	0.532
Constant	-0.540		

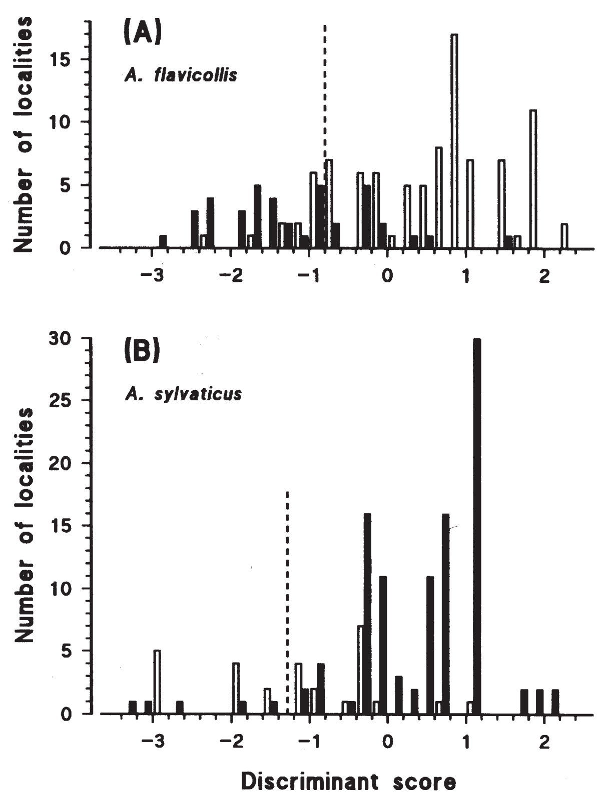

Figure 2
Canonical discriminant function diagram for Apodemus flavicollis *against* A. sylvaticus *(A) and vice versa (B). Black bars, species present; open bars, species absent. Points of discrimination are indicated by dashed lines.*

Table 2. Number of localities at which Apodemus flavicollis *and/or* A. sylvaticus *have been recorded, and their occurrence relative to predictions from discriminant function analyses (DFA) of environmental variables. Proportion of successful predictions by DFA are given as percentages.*

Observed	Predicted					
	Apodemus flavicollis			*Apodemus sylvaticus*		
	Absence	Presence	Proportion successfully predicted	Absence	Presence	Proportion successfully predicted
Absence	83	12	87.4	11	17	39.3
Presence	12	28	70.0	5	102	95.3
Total	95	40	82.2	16	119	83.7

DISCUSSION

Based on the actual records, potential ranges identified from DFA, ratios of yellow-neced/wood mice localities recorded in different regions, and by excluding mountain areas above the timberline, distribution maps crudely indicating abundance are suggested in **Figure 3**. Although the two species show overlapping ranges, their core areas are fairly well separated. While yellow-necked mice have a stonghold in the regions with a continental climate, wood mice are more confined to the milder, oceanic regions along the coast. Yet wood mice are found over a wider range of climatic zones than yellow-necked mice. Compared to the current Norwegian distribution maps (e.g. Semb-Johanson & Ims 1990) this pattern of distribution is more in line with what is found elsewhere in the westernmost parts of Europe (Niethammer & Krapp 1978). Two main discrepancies are evident from the new maps: (a) A lack of yellow-necked mice in the southern and southwestern parts of the country, as suggested by the trappings of Lind (1954) and Christiansen (1983), and (b) a range extention northwards, particularly for wood mice. We consider the former to be well-established from the present material on the basis of the high number of localities sampled in the south and west. The northern boundary, found to be in Sør-Trøndelag for both species may, however, extend further north than indicated in our material. *Apodemus* mice, probably yellow-necked, have been reported from Stod, Snåsa, Nord-Trøndelag (O. Hogstad, pers. comm.), but specimens confirming the records are lacking. Yet neither of the species appear to be regular even in most of Sør-Trøndelag (S. Haftorn, O. Hogstad, L. Løfaldli pers. comm; and present material).

In northwestern part of South Norway (Sogn og Fjordane, Møre og Romsdal) yellow-necked mice seem to be more common than wood mice, in spite of a more oceanic climate than east of the watershed (this study and A.O. Folkestad pers. comm.). Whether maintenance of populations of yellow-necked mice in the region, which may be climatically sub-optimal judged from the DFA, actually depend on more or less regular influxes from the east, deserves further study. Westward dispersals from high-density to low-density areas are likely to occur during population peaks in the east, by two forested valleys (Lærdal-Valdres and Romsdalen) connecting the region to the core areas in the east over only a few tens of kilometres. Moreover, a dispersal could rapidly penetrate far into the northwestern region, as in this region forest and agricul-

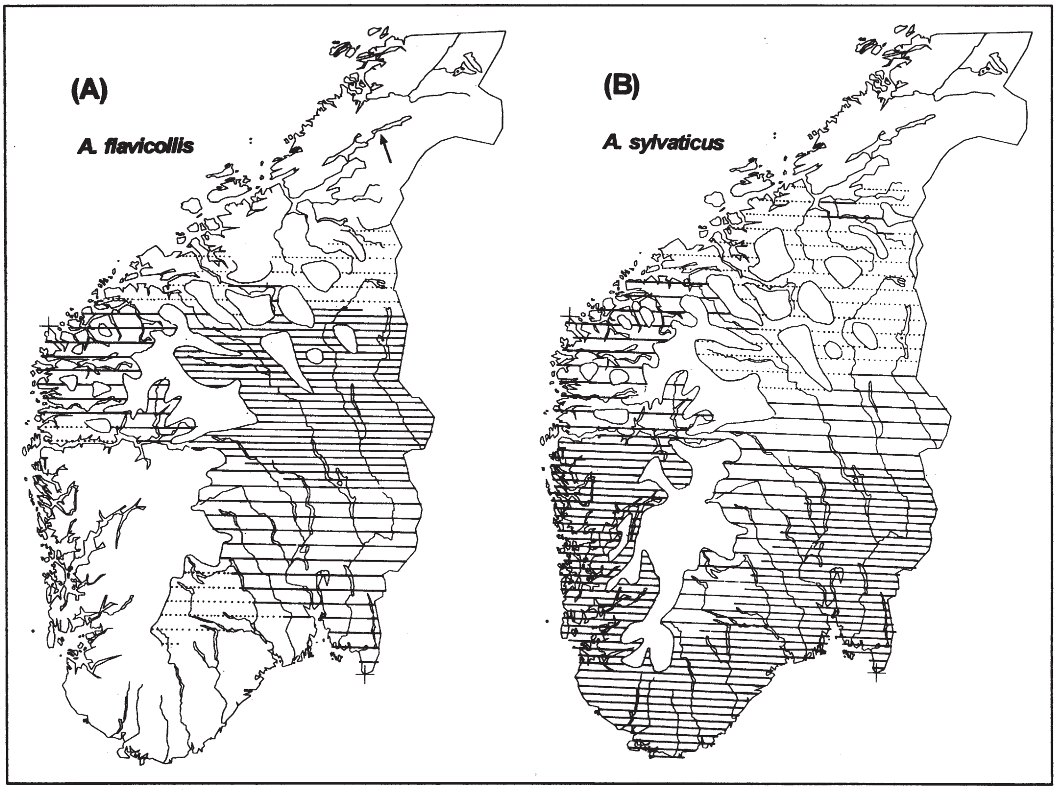

Figure 3
Distribution of Apodemus flavicollis *(A) and* A. sylvaticus *(B) in Norway, as judged from positive records, discriminant function analyses, and area below the tree line. Dense hatching, high abundance; less dense hatching, lower abundance; dotted hatching, possible occurrence. Open areas inland are areas above the tree line. Arrow = Stod, Snåsa (cf. text).*

tural land is largely distributed as narrow habitat corridors along fjords and valleys, due to the topography. This is a situation different from that in the southern parts of eastern Norway, where dispersals westwards are likely to be less notable, due to (a) a swamping effect of a broad zone of potential habitat in Telemark and Aust-Agder and (b) apparently a generally lower abundance of yellow-necked mice in the southern part of the range. In spite of the long time span represented by these museum collections, the material at hand was insufficient to demonstrate any dispersal effects as discussed above, mainly due to a an apparent temporally uneven sampling in the marginal areas.

Distribution depends on physical and ecological dispersal barriers. None of the species are likely to disperse across notable stretches of bare mountain. However, barriers constituted by the South Norwegian mountains are incomplete and in the long run insufficient to prevent the species' from dispersing between east and west; besides, both species could occasionally be carried between regions by human activities (e.g. in loads of grain, hay, etc.). Clearly, ecological factors are involved. The discriminant function analyses classify the two species as largely belonging to different climatic zones, but the functions do not neccessarily identify environmental variables which, through a direct action on a species' reproduction and survival, explain why. Most of the variables used were strongly intercorrelated, making the separate effect of each one becoming less firmly established; moreover the variables were measured on fairly crude scales.

Crucial variables are presumably those determining availability of food. Studies outside Norway show a substantial dietary overlap between the two species, but wood mice subsist to a greater extent on grass seed, green vegetable matter and even invertebrates than do yellow-necked mice, which feed more on tree seed (e.g., Pfeiffer & Niethammer 1972, Hoffmeyer 1976, Hansson 1985, Montgomery & Montgomery 1990, Gorman et al. 1993). Long seasonal access to green vegetation and invertebrates does relate to the length of the growth season, the most important variable in the discriminant function for wood mice. Differences between continental and oceanic regions in availability of tree seed is less obvious; trees like oak *Quercus* spp., pine *Pinus sylvestris*, spruce *Picea abies*, and hazel *Corylus avellana*, that may be of special importance to yellow-necked mice, are widely distributed in the southern and western regions where this species is lacking (Sjörs 1967). Both species cache food for the winter (Niethammer & Krapp 1978). A dry climate with cold winters might be more favourable for food storing, on which yellow-necked mice, being the more specialized, may depend more strongly for their winter survival (cf. Flowerdew 1985, Hansson 1985). However, the winter ecology of these species and their dependence on caches seem not to have been studied (cf. Bergstedt 1965, Niethammer & Krapp 1978).

The two species are potential competitors. According to Swedish studies, yellow-necked mice seem to be dominant over the slightly smaller wood mice, and a high abundance of the former is able to affect the habitat use of the latter in areas where they co-occur (Hoffmeyer 1973, Hoffmeyer & Hansson 1974). Competitive exclusion effects ought to be larger in structurally simple habitats, such as subalpine forest, than in lowland forests and farmlands with a higher habitat and food source diversity. To what extent this explains the rarity of wood mice in northern East Norway in spite of their predicted presence in parts of the area from the DFA, remains to be seen. Here yellow-necked mice inhabit subalpine birch and coniferous forests, often far from cultivated fields (Collett 1911-12, Barth 1955).

Climatically both species should be able to extend their distribution 2-3 latitudinal degrees further north than shown in this study. However, nowhere in other parts of the range do their northern limit go notably beyond what is found in Norway, except wood mice in Iceland (Niethammer & Krapp 1978). Increasingly light summer nights northwards could possibly be of some consequence for nocturnal animals like field mice (Bergstedt 1965, Niethammer & Krapp 1978) that move in a rather unconcealed manner (Bergstedt 1965). In Iceland low abundance of predators on rodents may relax this effect (Bengtson & Rundgren 1989).

In order to explain the distribution of field mice in Norway, more information on their basic biology is needed (food, habitat, diurnal rhythm, population dynamics, and dispersal patterns), both in areas of sympatry and in areas where only one of the species occur. Yellow-necked mice living in subalpine forest may differ in food and habitat use from what has been found in studies in lowland areas abroad. Comparing the biology of the two species in Norway would hold much promise, as environmental conditions vary strongly along gradients over short distances.

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SAMMENDRAG

Utbredelsen av stor og liten skogmus i Norge

Til nå har publiserte utbredelseskart framstilt stor skogmus som utbredt fra indre Østlandsstrøk, rundt Sørlandskysten og oppover Vestlandet like til Sør-Trøndelag, mens utbredelsen til liten skogmus har vært avgrenset nordover på Østlandet til Mjøstraktene og på Vestlandet til Bergen. Dette syntes overraskende ut fra artenes øvrige europeiske utbredelse, for selv om utbredelsen viser stort overlapp, er liten skogmus den arten som går ut i regioner med kystklima, mens stor skogmus holder til i områder med mer utpreget innlandsklima. Ved å sjekke alt norsk museumsmateriale av disse artene, fant vi at stor skogmus mangler på Vestlandet sør for Sognefjorden, og at arten heller ikke finnes på Sørlandet. Utbredelsen går fra Nordvestlandet og sørligste strøk av Sør-Trøndelag og nedover hele Østlandet, med hovedbastion på indre Østlandet. Liten skogmus finnes fra sentrale Østlandet, rundt Sørlandskysten og oppover til Nordvestlandet og Sør-Trøndelag. Den er vanligst på Sørlandet og den delen av Vestlandet der stor skogmus ikke forekommer. En diskriminantanalyse ut fra klimavariabler og klimarelaterte variabler viste at lokalitetene for stor skogmus kan karakteriseres ut fra lav januartemperatur, lav årsnedbør, vegetasjonssoner med lavere produktivitet, og høy apriltemperatur. Tilsvarende analyse for liten skogmus gir utslag for lang vekstsesong og lave apriltemperaturer. De to artene er m.a.o. utbredt hos oss i henhold til kyst-innlandsklima som forventet ut fra den øvrige europeiske utbredelsen. Forekomstene av stor skogmus på Nordvestlandet, som har et mer maritimt klima enn Østlandet, kan være betinget av stadige innvandringer østfra, da det er liten avstand fra kjerneområdene gjennom de skogkledde dalførene Romsdalen og Valdres-Lærdal. På Nordvestlandet vil en slik spredning kunne gå raskt, da skog og dyrket mark forekommer som habitatkorridorer langs fjordene og dalene. Snaufjell anses som spredningsbarrierer. Tidvise spredninger av stor skogmus vestover fra sørlige deler av Østlandet vil lettere kunne absorberes i en bred sone med potensielt habitat. Ut fra utenlandske studier av artenes levevis kan en spekulere over hvilke miljøparametre som begrenser utbredelsen. Stor skogmus lever mer av trefrø enn liten, og innlandsklima (tørt, kaldt) kan være gunstig for dens vinterforråd. Liten skogmus lever mer av grønne planter og insekter, og slik næring vil være mer tilgjengelig i områder med lang vekstsesong. Det kan heller ikke utelukkes at artene påvirker hverandres forekomst gjennom konkurranse, noe som er påvist fra Sør-Sverige. Imidlertid er artenes levevis enda ikke tilstrekkelig detaljstudert i vårt land til at en kan ha en klar oppfatning om hva som styrer utbredelsen. Sider ved levesettet kan skille seg fra det en har funnet i andre deler av Europa, hvor studier særlig av stor skogmus er gjort i frodigere skogstyper. Undersøkelse av artenes føde, habitatvalg og populasjonsdynamikk i Norge er sterkt ønskelig.

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