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Changes in home range size during growth and maturation of the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*)

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Summary. A field study was carried out during winter and spring of 1982/83 to determine changes in home range size with increasing body weight and maturation in the wood mouse (*Apodemus sylvaticus*) and the bank vole (*Clethrionomys glareolus*). Individual home range sizes in males increased and in females decreased with increasing body weight. Relating these changes to changed energetic requirements failed. In these species behavioral aspects seem to be a more important determinant of home range size than body weight.

The possession of a home range is a vital need for small mammals. Every individual tries to maintain such a "home" (Burt 1943, Viitala 1977, Korn 1983) and returns to it quickly when translocated (e.g. Schmid 1936, Schleidt 1951, Jezierski 1967, Applegate 1977, Graves 1977, Sullivan and Sullivan 1980). Current home range theory of mammals predicts that the major factors determining home range sizes are the types of food eaten, the animal's body weight and depending on that its energetic requirements (McNab 1963, Harestad and Bunnell 1979, Mace and Harvey 1983). All these studies have in common that for each species average home range size values are taken into account. In small mammals it is well known that average male home ranges are larger than average female home ranges (Brown 1956, Kulicke 1960, Kikkawa 1964, Bergstedt 1966, Jewell 1966, Crawley 1969, Radda 1969a, 1969b, Zejda and Pelikan 1969, Andrzejewski and Mazurkiewicz 1976) with extreme single values differing often fifty times or more.

By looking at single species the type of food eaten as an important factor for home range size determination can be omitted. When individuals of *Apodemus sylvaticus* and *Clethrionomys glareolus* grow and reach maturity they may change their home range sizes to fulfil their needs. The objective of this study is to observe these changes and to relate them to changes in body weight or energetic requirements due to breeding condition.

Methods

The field work was carried out on a 5.4 ha lot situated near the Biology Dept. of the Philipps University in Marburg, West Germany. This large grid was used to avoid biases in home range size calculations due to edge effects (Bondrup-Nielsen 1983). The lot is made up of small patches of different vegetation types. There are some patches of older forest and some of different successional stages as a result of clearcutting without reaforestation. Several logging roads cross the site. To a large extent the plot is surrounded by asphalt roads, which seem to be a major barrier for small rodents (Mader 1979; Mader and Pauritsch 1981). The eastern part is bounded by the Chemistry Dept., spruce forest, and patches of almost barren ground in early succession. Within the plot 251 trapping sites were chosen 5–20 m apart, depending on the vegetation and small-scale points of view (e.g. log piles, tree trunks, shrubs). About 45 trapping sites were chosen randomly for each day of trapping. This method enables one to sample a large area with a small number of traps (Layne 1954). Also the mice and voles cannot get habituated to any one place and return there every time. At each site one to three livetraps were set: wire cages 150 × 50 × 50 mm, fitted with a snap door and baited with hazelnuts. Trapping took place on 62 days between Nov. 19, 1982 and May 20, 1983 and lasted from late afternoon to midnight. Traps were checked every 2–4 h depending on weather conditions.

Occupied traps were replaced by newly baited ones, and the trapped animals were carried to the nearby laboratory inside their traps. All animals were individually marked by toe-clipping, a maximum of two toes being removed. At the end of the trapping period (usually after midnight) all mice and voles were released at their original trapping sites.

Home range calculations were made on a Commodore 8032 microcomputer using the "Minimum Area Method" described by Brown (1956). Only animals captured ten or more times with no obvious shift in home range were considered for calculations of home range size. Single exploratory sallies (Crawley 1969) far outside of normal home ranges were omitted. Data were recorded as recommended by Petrusewicz and Andrzejewki (1962). Population parameters were obtained by direct enumeration (Krebs 1966). A total of 145 *Clethrionomys glareolus*, 201 *Apodemus sylvaticus*, 23 *A. flavicollis*, 9 *Microtus agrestis*, 20 *Sorex araneus*, 14 *S. minutus* and 5 *Parus major* were captured 2075 times. Average capture rates for *C. glareolus* and *A. sylvaticus* were 7.9 and 4.1 times. All shrews were removed from the study plot. Captured great tits (*P. major*) were released immediately.

A heave tree seed crop in fall of 1982 (especially acorns) provided an excellent food supply for small rodents throughout the winter and spring. During the study period

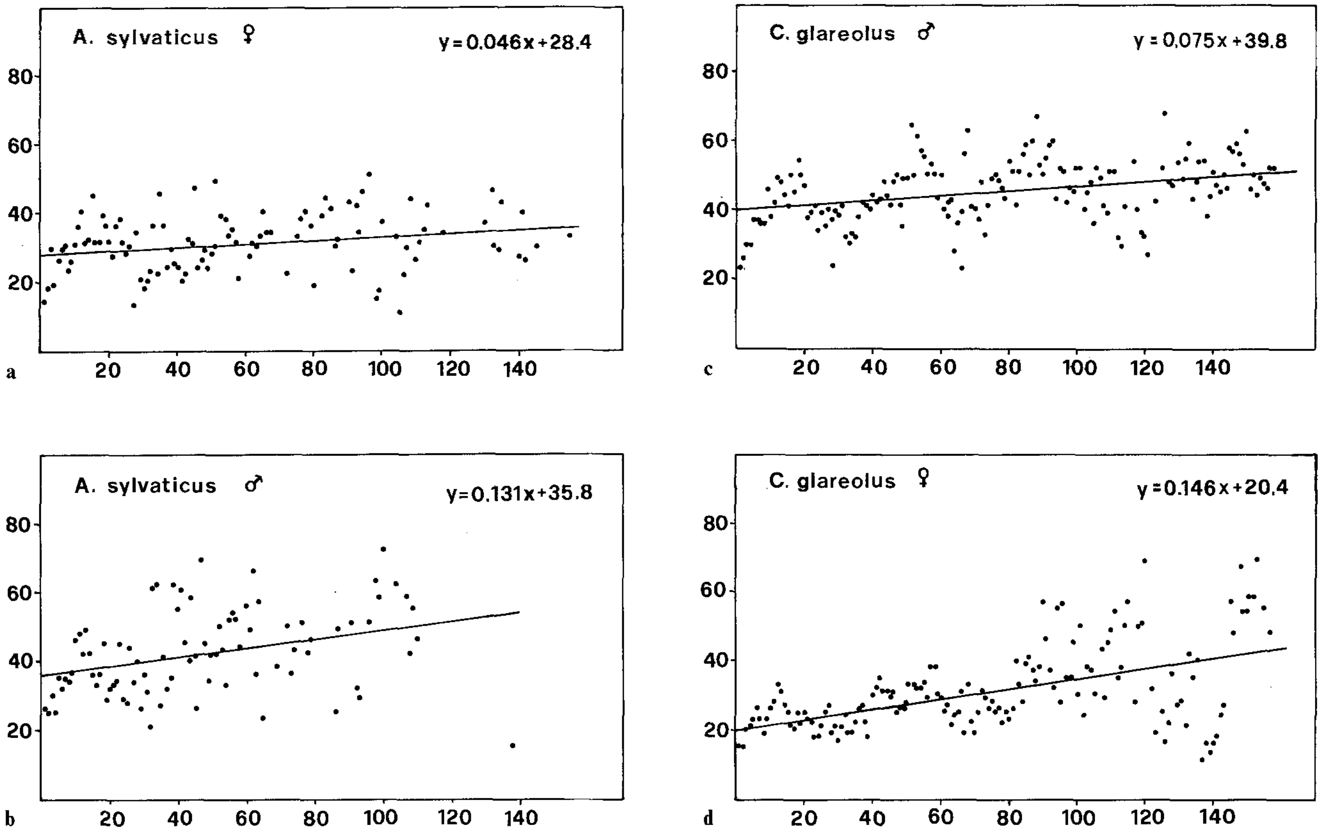

Fig. 1a–d. Average distance moved from original point of trapping over time for male and female *Apodemus sylvaticus* and *Clethrionomys glareolus*. Data pooled for entire study. Abscissa: days after initial capture. Ordinate: average distance moved in m

weather conditions were extraordinally favourable. The winter was extremely mild and only in February and again from mid-March to mid-April was there a closed snow cover.

Results

The number of voles and mice remained very stable from December 1982 to the onset of spring in March 1983. Average densities were about 15 *Apodemus sylvaticus* and 12 *Clethrionomys glareolus* per hectare. After a spring decline, in which *A. sylvaticus* was more affected than *C. glareolus*, densities leveled off at approximately 7 to 8 individuals per hectare in both species. Male and female numbers did not differ significantly from a 1:1 ratio, but there was some evidence that males declined more in spring than females. No significant difference was observed between sexes in trappability or residence time. Winter breeding was observed in *A. sylvaticus*, *A. flavicollis*, *C. glareolus* and *M. agrestis*.

According to different authors (e.g. Kikkawa 1964, Crawley 1969, Radda 1969a, b; Mares et al. 1980) at least ten captures of an individual mouse or vole are necessary for determining the size of its home range. Special attention must also be paid that no home range shift occurs during the course of the study. Figure 1a–d show that males as well as females of both species were very sedentary during the winter of 1982/83. Therefore, as long as no obvious home range shifts occurred, no upper time limit was there for an animal to be included in calculations. Average home range sizes differed significantly between sexes (*C. glareolus*: $t = 4.680$, $df = 33$, $P < 0.001$, *A. sylvaticus*: $t = 2.225$, $df = 15$, $P < 0.05$) (Table 1).

Table 1. Home ranges of voles and mice observed for more than two months and with at least 10 captures

	C. glareolus		*A. sylvaticus*	
	male	female	male	female
Number of individuals	17	18	7	10
Average number of trappings	20.6	18.2	11.9	12.4
Max. number of trappings	31	28	19	17
Average home range size (m^2)	4,120	1,280	3,230	1,530
Min. home range size (m^2)	1,200	150	1,025	275
Max. home range size (m^2)	11,000	4,850	6,250	3,375

The largest individual home range was observed in a large male *A. sylvaticus*. It extended over at least 1.4 ha, but the calculation was based on only nine trappings and is therefore not included in Table 1. Maximum home range sizes for each sex are approximately 5–15 times larger than minimum sizes. Between sexes there is a large range of overlap (Table 1). The entire range of home range sizes occurring within a population is divisible in three groups: (1) females with extremely small home ranges, (2) males and females with intermediate home ranges, and (3) males with very large home ranges.

Changes in home range sizes occurred with the onset of breeding or even before. Female *C. glareolus* show a tendency to decrease their individual home ranges during puberty with increasing body weight (Fig. 2). Sexually ac-

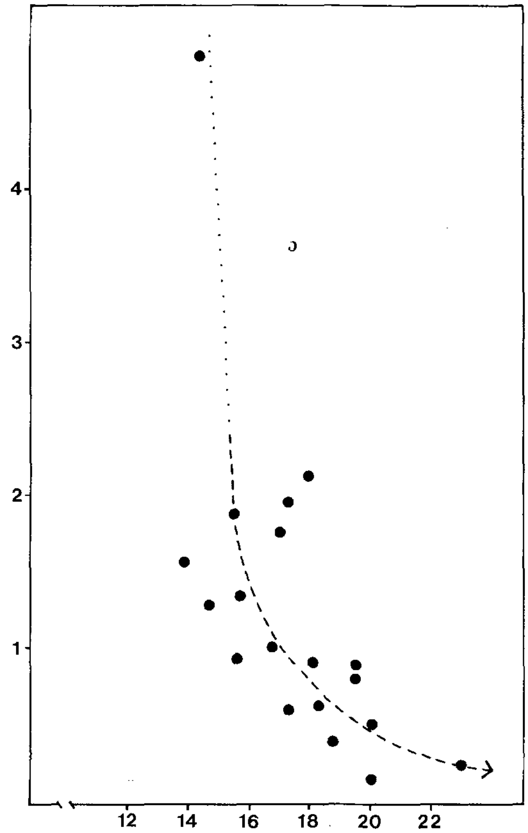

Fig. 2. Body weights of female *C. glareolus* at first capture plotted against final home range size after at least ten captures. Curve is fitted by eye. Abscissa: body weight in grams. Ordinate: home range size in 1,000 m^2

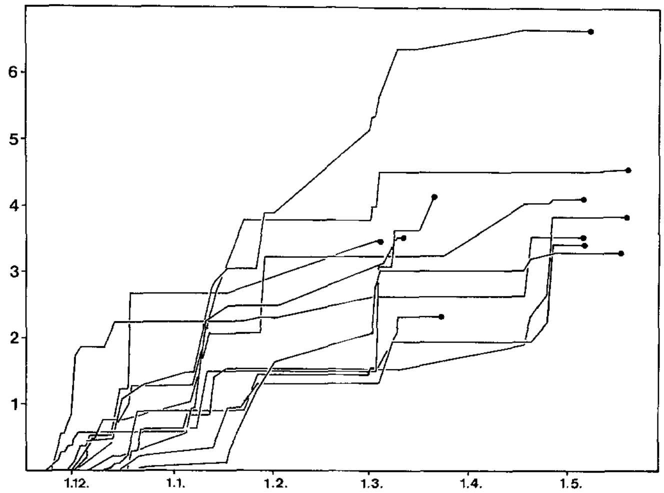

Fig. 3. Increase of individual home range sizes in eleven male *Clethrionomys glareolus* over time and with increasing number of captures. Only animals with records extending more than three months and at least 15 captures are represented. Abscissa: date. Ordinate: home range size in 1,000 m^2

tive females had the smallest home ranges. The extreme was a female bank vole that after 18 trappings had visited only three trap locations. The ultimate home range size was thus calculated to be 150 m^2. This animal never left its home range during 100 days. Intensive trapping just outside was fruitless but placement of traps inside the animal's home range led to 100% trapping success within hours

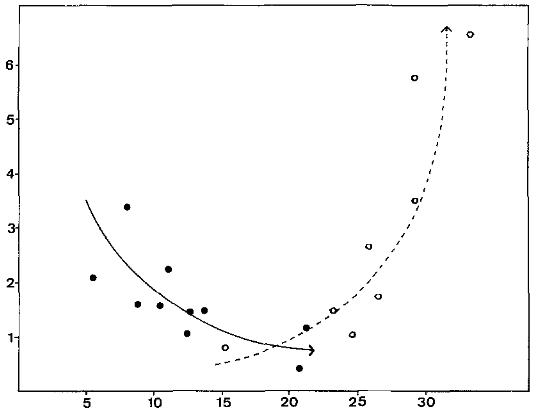

Fig. 4. Weight of female *Apodemus sylvaticus* at first capture and maximum weight of male *A. sylvaticus* are plotted against final home range size. Only animals with at least ten captures are included. Curves are fitted by eye. The arrows mark the direction of growing individuals. Dots represent females, open circles represent males. Abscissa: body weight in grams. Ordinate: home range size in 1,000 m^2

Males of *C. glareolus*, in contrast to females, extend their ranges when reaching maturity. In winter and spring these extensions occurred at different times which were always associated with periods of mild, favourable weather in January, early March and mid-April. The increase in male home range size in March coinceded with the spring decline. Four of the eleven best documented males disappeared during this time (Fig. 3). In spite of different rates of increase in home range sizes, in May all males, except one, had home ranges that extended over about 4,000 m^2. Four males that had already reached this value in March increased it only slightly or not at all in April. The ranges of these eleven male bank voles were all located around the center of the study plot and overlapped extensively.

In *A. sylvaticus* the same change in home range sizes can be observed at the onset of breeding as in *C. glareolus*. With increasing body weights during puberty males increase and females decrease their range of movements (Fig. 4) and thus show opposite trends.

Discussion

Body weight is a rough indicator of the social status of an individual within a population. Breeding mice and voles tend to be heavier than non-breeders (Brown 1969, Tanton 1969, Iverson and Turner 1974, Fairbairn 1977, Taitt 1981), and aggression and dominance relationships are also positively correlated with body weight in many species of small rodents (Turner and Iverson 1973, Fairbairn 1977, Semb-Johansson et al. 1979, Schwagmeyer and Brown 1983). After an initial period of fast growth in young animals, weight is fairly independent of age. In high density populations maturation and weight increase are suppressed (Kalela 1957, Christian 1963, Ashby 1967, Zejda 1967, Autrum and v. Holst 1968, Fuller 1969, Christian 1971a, b, Bujalska 1973, Saitoh 1981). Therefore we can attribute different home range sizes to animals with different social status, indicated by body weight (Figs. 2 and 4). The shortcomings of home range size determinations by means of trapping are well known. Supposingly the bias is the same for all animals we can still make valid comparative analysis within the same study. Clearly in *A. sylvaticus* the heaviest and presumably dominant males possess the largest home ranges (Fig. 4). They may thus gain access to more sexually active females and increase their fitness by producing more offspring. Krebs, Redfield and Taitt (1978) suggest that spacing behaviour causes population changes in *Microtus townsendii*, and Beacham (1980) pointed out that it is the most likely explanation for rapid decrease in survival at the start of the breeding season. These suggestions are consistent with my observation that four out of eleven male *C. glareolus* died or disappeared in spring when there was a general tendency in males to increase home range sizes (Fig. 3).

In spite of the large degree of overlap in home ranges (Korn 1982) subordinate males could be excluded and forced to migrate (Taitt 1981). The mechanism for this is not clear yet.

When females mature they gain weight and decrease home range sizes (Figs. 2 and 4). The final state is a small, defended territory (Korn 1982). Female territoriality has been found previously in microtine species (Getz 1961, Bujalska 1973, Wiger 1982). The results were based on live trapping data but have also been confirmed by ratio-telemetry (Madison 1979, 1980, Webster and Brooks 1981). Comparative results for murid rodents are not available.

Female *C. glareolus* come into breeding condition only when they possess a territory (Bujalska 1973, Viitala 1977). If the number of available breeding territories is limited this could impose an upper limit on population size. The size of these territories could therefore be an important factor in the population biology of the species.

If home range or territory size in these species are related to energy requirements (McNab 1963, Harestad and Bunnell 1979, Mace and Harvey 1983) they should range in size from the smallest – those of immature, light-weight animals of both sexes – through those of heavy, sexually active males to the largest – those of breeding females with their increased nutritional demands for pregnancy and lactation. In *C. glareolus* and *A. sylvaticus* the size order is reversed. In general, individual home range sizes exhibited by a small mammal species within one study site can differ in magnitude by fifty or more (Brown 1956, 1966, Zejda and Pelikan 1969, present study). Different energetic requirements due to different body weights and breeding conditions can only account for a small fraction of that variability. Home ranges have been reduced by increasing cover (Blair 1951, Getz 1961, Birney et al. 1976, Abramsky and Tracy 1980, Taitt et al. 1981), increasing population density (Stickel 1960, Sanderson 1966, Van Vleck 1969, Zejda and Pelikan 1969, Krebs 1970, Maza et al. 1973, Abramsky and Tracy 1980, Fitzgerald et al. 1981, Mazurkiewicz 1981, Gaines and Johnson 1982), or increasing food supply (Andrzejewsky and Mazurkiewicz 1976, Mares et al. 1976, Taitt 1981, Taitt and Krebs 1981, Taitt et al. 1981, Sullivan et al. 1983). The ranking pattern of home range sizes should in all these cases stay the same even that average values vary.

Caughley and Krebs (1983) suggested that small mammal populations tend to be regulated intrinsically. Food never gets so scarce, even at the worst time of the year, that animals die of starvation (Chitty et al. 1968). Grodzinski (1975) concluded that rodent populations consume only 0.6 to 5.5% of suitable food available in the majority of habitats. From this we can conclude that food availability and the bioenergetics of *A. sylvaticus* and *C. glareolus* cannot explain the observed home range size pattern. Present home range size theory is based on average values, irrespective of sex, season, method and duration of study (Harestad and Bunnell 1979, Mace and Harvey 1983, McNab 1963) and does not take into account behavioural aspects that may be more significant than energetical aspects, as shown in the present study.

Dividing the population into as many functional groups as possible is a first step to show that average values can be misleading and do not contribute to our understanding of what we observe.

In evaluating our results we should measure the quality of home ranges or territories in number of weaned offspring rather then observing short them changes in the behaviour of residents.

To the better understanding of population processes in small mammals in future more emphasis should be placed on the role of the individual animal instead of diluting interesting, often extreme, values by the formation of averages.

An experimental approach is needed to test which home range or territory size is favourable under which circumstances.

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