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Regulation of female maturation in *Clethrionomys* species, with special reference to an island population of *C. glareolus*

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Literature survey reveals that in *Clethrionomys* maturation is suppressed at high population densities. Territoriality of mature females appears to be responsible for this phenomenon. Suppression of female maturation begins when a habitable area is saturated with mature females. Hence, when a saturation density has been achieved (i.e., when all home ranges are occupied) neither the number of mature females nor suppression of maturation depend on changes in population density. The number of mature females may be modified by a variety of factors related to where in the geographical range of the species the population is, dominance relation to coexisting species, environmental capacity (especially food availability); all these factors seem to influence the home range size.

A long-term study on an island population of *C. glareolus* has provided data which are used to formulate an analytic model relating the number of mature females to the population density (or number). The model demonstrates the existence of certain density thresholds signifying shifts from a linear increase of number of mature females (accompanied by unlimited maturation) to relative stability of number of mature females (associated with suppression of maturation), and at last, decrease of number of mature females (accompanied by inhibited maturation and cessation of reproduction (i.e., anoestrus) in mature females). These thresholds may suggest a balance between population density and environmental capacity.

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1. Introduction

Spacing behaviour of various categories of individuals living together in rodent populations has been studied in some detail (Calhoun 1963a,b, Watson & Moss 1970). There seems to be some sort of "order" in the spatial distribution of individuals in populations that do not attain high densities and that do not exhibit social hierarchy (Anderson 1961). This pattern of space use shown by sexually mature individuals (i.e., those able to reproduce), has important consequences for natural control of population density (Kalela 1957). However, the latter idea seems often to be biased by the density-dependent approach: as appears from most demographic studies it is much easier to find data on percentages of sexually mature individuals in relation to population density, than to find information on the density of mature males and females. It is my opinion that knowledge on density of such categories of individuals is of equal importance for population studies as that on the total population density.

In particular, the density of mature females and their spacing behaviour — as shown by their spatial distribution and home range size — may contain information on a state of balance between the population and its environment (primarily characterized by food availability; Bujalska 1975) as well as on the sort of life strategy revealed by the population (Bujalska 1981, 1985).

Mature females of *Clethrionomys* show a distinct territorial behaviour, lacking in both mature and immature males as well as in immature females (Tanaka 1953, Koshkina 1965, Bujalska 1970, and others). The existence of such territoriality forms the basis for the assumption that maturation of young females depends on the degree of "saturation" of the habitat by already mature females (Koshkina 1965, Bujalska 1970, 1973).

The present paper is a review of data and ideas presented by several authors on territorial tendencies in mature females of *Clethrionomys*, and the impact of such territoriality on the maturation rate of young females. A model — based on a long-term study on an island population of *C. glareolus* — explaining the quantitative relations between the density of mature females and the total population density as a consequence of spacing behaviour is also presented. However, the main aim of this paper is to convince students of rodent populations that they ought to concentrate their efforts as much on the spacing behaviour of mature females as on the total population density. A companion review on males is provided by Gipps (1985).

2. Review and discussion of the literature

2.1. Criteria used

Based on literature data it is not easy to arrive at objective and consistent conclusions on inhibition of female maturation. Each author approaches the problem of reproduction in his or her own way. Some of the published data also seem to need statistical verification. Finally, some of the published conclusions seem to be of limited value. Nevertheless, a literature survey is unavoidable in order to understand where we are and where we need to go.

First, do all *Clethrionomys* species exhibit inhibition of female maturation at high density? If so, under what ecological circumstances, in particular at what range of seasonal and/or under what habitat conditions — ranging from optimal to pessimal ones — does it occur? I must confess that it was not always possible to find direct information of relevance for these issues. Therefore on several occasions my work was sort of a detective story based on direct deductions from the available data or comments made by the various authors. Hence, on the basis of the recommendations by Watson & Moss (1970) I might have drawn some unjustified conclusions regarding inhibition of female maturation. I hope, however, that the general picture is correct.

I have used the following criteria:

1) Inhibition of maturation takes place when

a) females from late cohorts do not attain sexual maturity in the year they are born, or the percentages of females attaining maturity are much lower than those in the earlier cohorts. I assume that immature females are able to attain sexual maturity in the year they are born, which at least is the case for *C. glareolus* (Bujalska 1973) and *C. rufocanus bedfordiae* (Saitoh 1981).

b) Mature females show tendency toward territoriality. In this case I assume, following Viitala (1977), that the home ranges of mature females can overlap only to a very limited extent, and certain part of the home range must always be free from visits of other territorial females. Koshkina (1965), for example, found in a highly overcrowded population of *C. rufocanus* as much as 50% of the home range of each mature female free. Such a free part I will, following Wiger (1982), call the breeding territory.

2) I assume that the tendency toward territoriality occurs when

a) mature females are distributed evenly in space, or

b) home ranges of mature females do not overlap completely.

The conclusion I have come to accept while surveying the literature is based on my firm belief that the density of mature females varies within much more narrow limits than the remaining part of the trappable population. The mechanism responsible for the relative stability of mature female density is their spacing behaviour resulting from their particular spatial requirements (Bujalska 1970, 1973, 1985).

There is no general agreement, however, that the territorial tendencies in mature females induce cessation of maturation in females. Bashenina (1981:240), for example, says that the number of mature females in an island population of *C. glareolus* in the eastern part of Lithuania is not stable, being twice as high in 1968 as in 1969 and 1970. That author suggests that this may be due to variation in home range size and in the degree of their overlapp. Unfortunately, neither the number of mature females nor the methods used for the assessment of spacing behaviour are presented by Bashenina.

2.2. Inhibition of female maturation

The first report on territoriality in mature females of *Clethrionomys* was, supposedly, provided by Tanaka (1953) who studied *C.*

rufocanus bedfordiae (see Appendix). A few years later Kalela (1957) described inhibition of sexual maturation of both males and females in an overcrowded population of *C. rufocanus.* Since then numerous papers have been published showing that inhibition of sexual maturation is associated with regulation of reproduction, and that this takes place after a certain threshold of population density has been reached. Such a threshold seems to be particularly important for our understanding of demography in rodent populations; I will deal with this topic in a later section.

It is commonly concluded that females born late in the breeding season (i.e., those belonging to the autumn generation in the sense of Schwarz et al. (1963)), do not attain sexual maturity in the year they are born. Such a conclusion is typical of those authors finding a summer peak of population density in the same year (Zejda 1964, Koshkina 1965, Jewell 1966, and others; see Appendix). However, others conclude that when population density is low, some or even all late-born young females of the year attain sexual maturity (Koshkina & Korotkov 1975, Mihok 1979, and others; see Appendix).

One may expect that such a pattern does not occur over the entire geographic range of the species. In populations living at the northern border of the species range, and hence exposed to extremely severe climatic and food conditions, females of the autumn generation never seem to attain sexual maturity the year they are born. The results reported by Fuller (1976) may serve as an example of this. Ivanter (1975) expresses the opinion that in the north-western part of the USSR taiga, mature and sexually active females of *C. glareolus* do not survive winter. Hence, the reproductive output during the subsequent year is entirely due to those females that did not reproduce the year before (i.e., those of the autumn generation). On the contrary, winter survival of *C. glareolus* in the north-eastern part of Poland does not depend on the age of the individuals nor on their previous reproductive effort (Bujalska, unpubl. data).

Koshkina & Korotkov (1975) suppose that in pessimal habitats located in the middle of the geographic range of *C. rutilus*, inhibition of sexual maturation does not occur. However, this opinion, though consistent with expectations arising from general ecological knowledge, is based on data that do not seem to be properly verified. Namely, it appears from the data presented by Koshkina & Korotkov (1975) that the population living in the pessimal habitat does not reach as high densities as those in the near-by optimal habitats where the inhibition of sexual maturation was observed.

Other ecological circumstances supposedly influencing maturation are also worth mentioning. Koshkina (1971) and Ivanter (1975) are convinced that inhibition of sexual maturation takes place in the population of a dominant species and does not occur in that of the subordinated species. Their conclusions are based on studies of *C. rutilus* and *C. glareolus*: in the Siberian taiga *C. rutilus* was the dominant species (Koshkina 1971), whereas in the European part of the USSR taiga the dominance order was reversed (Ivanter 1975). Ivanter contends that inhibition of maturation is a means of adapting the population to maintain a density close to a value preventing extinction. However, in my mind, this is a case which badly needs better evidence (perhaps, by field experiments) to clarify what is the main cause of the observed patterns: the pressure of the dominant species on the females of the subordinated one, or perhaps that the subordinate species could not achieve a sufficently high population density to reveal the inhibition of sexual maturation (by definition the subordinate species was the one with the lower density). But, apart from the above criticism, the suggestion expressed by Ivanter (1975), that adaptation to different conditions occurring in various parts of the species' range influences the demographic processes in populations of rodents, seems to be very interesting.

It may appear that the interspecific composition of the rodent community as a modifier of maturation rate, operates in a rather complex way, and may not necessarily be limited to a direct, "face to face", interaction. For example, the experiment carried out by Bujalska & Janion (1981) demonstrates that removal of an earlier introduced population of *Apodemus agrarius* resulted in an increase of both total population density and the density of mature females of *C. glareolus.* The latter increase was due to an increased mutual tolerance among the mature females.

Habitat conditions may also affect the maturation rate of females. For example, it can be concluded from the data on *C. glareolus* published by Newson (1963) that in two neighbouring habitats of different conditions, the densities of mature females were different.

In spite of numerous examples of territoriality manifested by mature females of *Clethrionomys* (Koshkina 1965, Bujalska 1970, 1973, Bujalska & Janion 1981, Viitala 1977, Saitoh 1981) it has until now been common to think of maturation rate in terms of its dependence on the total density of the trappable population. However, this hides, in my opinion, the complexity of the many regulatory processes, or mechanisms, their complex interrelations with the habitat (including coexisting species), and the complexity of the interaction between various members of the population (e.g., mature and immature). To me that simplification is a "dead-end street".

In accordance with earlier studies (for example those by Bujalska (1970, 1973, 1985) and Saitoh (1981)) I feel that the number of mature females is limited partly because of their spatial requirements and partly because of the environmental capacity. The latter means a limited quantity of resources (e.g., food, space, nesting places, etc.), or a limited rate of their renewal. Hence, newly born females are, for their sexual maturation the same year, dependent on the quantity of the free breeding territories (i.e., on the quantity of the space unoccupied by the females that have maturated earlier).

2.3. Relation between density of mature females and total population density

Because newly born females are, for their sexual maturation, dependent on the availability of free breeding territories, one can find a negative correlation between the number of the overwintered and the number of mature females born in the current year (Koshkina & Korotkov 1975), and similarly why the females of the autumn generation usually do not attain sexual maturity in the same year they are born. Nevertheless, it seems useful to relate the density of the mature females to the total population density, especially if one looks for explanation to changes in the population density. First, the number of mature females increases in direct proportion to the total population density (see Fig. 1): at low numbers of overwintered females all young females attained sexual maturity within a few days after weaning (Zejda 1964, Bujalska 1970). After some critical population density has been achieved, new females can attain maturity only when the mature ones die. It means that the number of dying mature females is counterbalanced by the number of females attaining maturity; the immature females thus become a "reserve". It implies inhibition of maturation of the current year's females to a variable extent, even though these females are potentially able to attain maturity (Bujalska 1973, Saitoh 1981). The time of maturation of such a "reserve" female is dependent upon the liberation of a breeding territory; this may benefit the entire population.

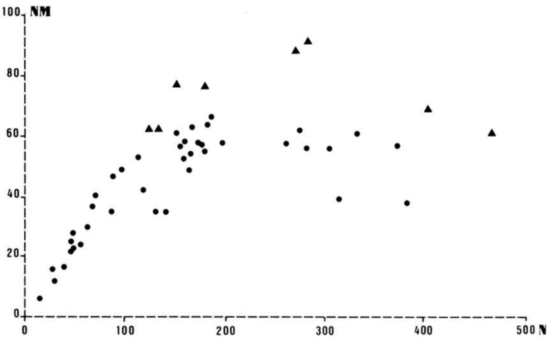

Fig. 1. Number of mature females plotted against total density. *NM* denotes the number of mature females per 4 ha, and *N* the population numbers per 4 ha. Triangles represent data from years of experimental manipulation (i.e., 1972 and 1975; either food added or a competitor removed), whereas circles represent data from 1966-1970 and 1976-1980. The entire data set can be described by the following regression: $NM = (-780.13 + 35.65N - 0.0616N^2)^{1/2}$, $R = 0.723$, $n = 48$, $F = 24.64$, $p < 0.001$. (Modified from Bujalska 1985).

I further believe that the idea of a mean level around which the density of mature females is stabilized (Bujalska 1970) while the entire density of the trappable population changes should be studied carefully.

At last, one can imagine another critical point, a "security" threshold, above which the density of the mature females is no longer stable: beyond this critical threshold the population density still increases (Fig. 1). In this case, I feel, it is justified to talk about the density dependence of the number of mature females on the population numbers (Bujalska 1970) due to an excessive number of encounters between mature and immature females. A physiological mechanism responsible for such a decline can be the stress syndrome, as described by Christian (1956) as

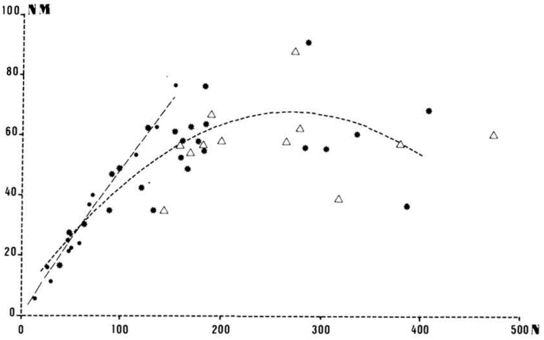

Fig. 2. Seasonal aspects of regressions of the number of mature females on the population numbers. *NM* denotes the number of mature females per 4 ha, and *N* the population numbers per 4 ha. Dots represent April, asterisks represent June and July, and triangles represent September. Straight line represents a section of a parabola describing the regression in April ($y = 0.463 + 0.497x - 0.000086x^2$, $R = 0.990$, $n = 12$, $p < 0.001$), whereas broken line represents a parabola describing the regression in June and July ($y = 5.72 + 0.46x - 0.00085x^2$, $R = 0.777$, $n = 24$, $p < 0.001$).

well as by Christian et al. (1965). This may lead either to closing vaginal orfice (anoestrus) in the previously reproducing females (Bujalska 1970) or to inhibition of maturation of juvenile females forming an overcrowded aggregation. It is possible that similar physiological phenomena contribute to the shortening of the breeding season in overcrowded populations of the voles (as, e.g., reported by Kalela (1957) and Bergstedt (1965).

The question, however, is whether or not the above is the only adequate description of reality. If so, it must be assumed that seasonality of maturation is a superficial phenomenon entirely due to the progressive accumulation of the number of female recruits in the course of the breeding season and to the existence of a limited number of breeding territories. This hypothesis reflects my way of thinking of the causes and effects involved in regulation of the female maturation. Consequently, I related the number of mature females mathematically to the total number of individuals in the population in April (i.e., beginning of the breeding season), in June and July (i.e., advanced breeding), and in September (i.e., end of the season).

The scatter of the data on the number of mature females ordinated along the population density axis for each of the months during 12 years resembles a parabola or a section of it (Fig. 2). However, in the second part of the breeding season a rather high scatter results for relatively small data sets ($n = 12$) which makes statistical inference inconclusive. The parabolic regressions in April (Fig. 2) and in June ($y = -1.823 + 0.616x - 0.00129x^2$, $R = 0.950$, $n = 12$, $p < 0.001$) were highly significant, even though for the April data a linear regression model also was acceptable ($y = 0.884 + 0.428x$, $r = +0.990$, $n = 12$, $p < 0.001$). The significance of the parabolic regression in July is questionable ($p < 0.08$), and that in September is insignificant ($p < 0.10$). A possible explanation of the nonsignificant regression is evidently narrower range of changes in the population numbers (in particular, a lack of low densities) and the relatively high variability of the number of mature females.

Nevertheless, in each data set there was an indication of inhibition of female maturation only when the population numbers exceeded approximately 40 individuals per hectare. Naturally, so high densities were never found in April (since there are no females born the same year to recruit to the population). In June, July and September a decreasing trend in the number of mature females was found provided that population density exceeded 80 individuals per ha. Such a decreasing trend was sometimes accompanied by anoestrus in previously mature females.

The following can be concluded:

1) At the beginning of the breeding season (April) there is no "reserve" of immatures. Regression of the number of mature females on total population density can be described by a section of a parabola or a straight line (Fig. 2). Population densities vary in their lower range.

2) Advanced breeding with variable number of immature females and a wide range of changes in population density (June and July data combined). This part of the season is characterized by a parabolic regression of the number of mature females on the population numbers (Fig. 2).

3) At the end of the breeding season (September) the population size varies in its upper range. No correlation between the number of mature females and the total number in the population has been found. However, the scatter of data points does not differ from that found in June - July (Fig. 2).

The general appearance of the data for the entire breeding season may then be described by a flattened 2nd order polynomial: this illustrates the idea of increase, independence and decrease of the number of mature females accompanying continuous increase of the total population density.

3. A model for regulation of number of mature females

The literature survey has shown suppression of maturation in *Clethrionomys* females at high population density. My own studies on an island population (part of which is published; see, e.g., Bujalska 1985) monitoring the whole trappable population reveal a more complex picture (Fig. 1): maturation is not suppressed at low population densities. Then when a threshold density of mature females is reached, the number of mature females remains relatively stable even with increasing population density — that is, maturation of immature females is suppressed. At last, the number of mature females decreases after another threshold in population density has been reached. In this case maturation is further inhibited.

Now, I will present a model for these changes in numbers of mature females. The empiric basis for the model are parameters estimated for the island population on the basis of data from 1966-1970 and 1976-1980 (1972 and 1975 data being excluded because of experimental disturbance that influenced spacing behaviour). The output from numerical evaluation of the model will then be compared with available empirical results.

Let the population area, $\bar{A}$, correspond to 159 trap sites, each of which covers 225 m^2; let further this area vary randomly in order to mimic (or simulate) changes in the habitable space. So, at any time, corresponding to a census of the island population) the total area, A_t, equals

$$A_t = \bar{A} \pm \rho \cdot A^{1/2} \qquad (1)$$

where $A = 159 \times 225\ \mathrm{m}^2 = 35.775\ \mathrm{m}^2$ and ρ is a random normal variable.

The home range size of mature females was estimated by the method of Wierzbowska (1972) four times a year during the study period. The mean of these estimates is 755 m^2 with a standard deviation equal to 140 m^2. Thus, at any time, t, the expected value of the home range size is

$$r_t = \bar{r} \pm \rho \cdot SD_r. \qquad (2)$$

Let us accept that the sex ratio in the trappable population (i.e., including both mature and immature voles) equals 1:1. Hence, the expected number of all trappable females, NF_t, at time t is

$$NF_t = 0.5 \cdot N_t \pm \rho \cdot (0.5 \cdot \mathrm{N}_t)^{1/2} \qquad (3)$$

where N_t is the population density.

As pointed out by Bujalska (1970, 1973), mature females are distributed evenly. For the sake of simplicity I therefore assume their distribution to be ideally even, and — following Koshkina & Korotkov (1975) — that the females avoid encounters and mutual interference. Thus, if $NF_t \cdot r_t \leq A_t$ then all females attain maturity, and as a consequence the number of mature females is a linear function of the population numbers (as shown by Fig. 1 at low population numbers): that is,

$$NM_t = NF_t. \qquad (4)$$

However, if $NF_t \cdot r_t > A_t$ where the "saturation" threshold is defined by $NF_t \cdot r_t = A_t$, then the home ranges of females have to overlap. Under such circumstances one can expect mutual interference between females — manifested by, for example, territorial fights (Koshkina 1965) — suppressing maturation to an extent which is assumed to be directly proportional to the degree of overlap between their home ranges. The degree of overlap is, according to Bujalska (1970), proportional to $NF_t \cdot r_t / A_t$. Thus, when the saturation threshold is reached, a further increase of population numbers produces a "surplus" of immature females: that is,

$$NS_t = (NF_t \cdot r_t - A_t) / r_t. \qquad (5)$$

Only a fraction of the surplus females will attain maturity: this fraction is assumed to be inversely proportional to the degree of overlap between female home ranges, that is, $NS_t \cdot A_t / (NF_t \cdot r_t)$. From this it appears that the number of mature females will increase asymptotically according to the formula

$$NA_t = A_t / r_t + NS_t \cdot A_t / (NF_t \cdot r_t). \qquad (6)$$

Immature females "wanting" to maturate represent some sort of pressure on the mature females: Let us imagine that the home ranges

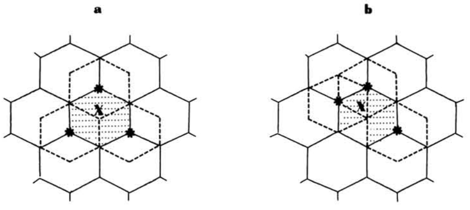

Fig. 3. A scheme of distribution and overlapping of home ranges. Habitable space is saturated with home ranges of mature females (represented by continuous lines); home ranges of immature females (broken lines) are distributed so that their centres (asterisks) fall in between the home ranges of mature females. — a) If immature females are distributed evenly, then the home range of mature females (X) would be entirely covered (dotted area) by home ranges of 3 neighbouring immature females. — b) If immature females were not distributed evenly, then home ranges of 3 immature females would not cover it entirely (dotted area).

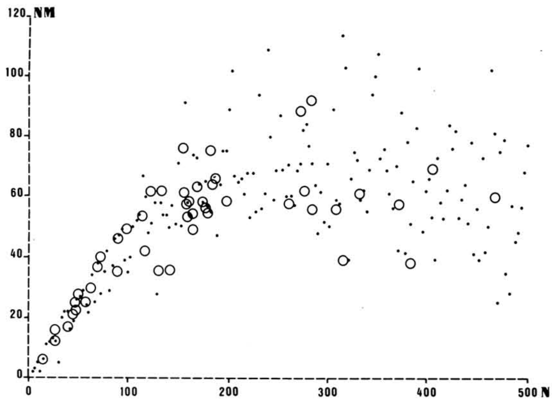

Fig. 4. Number of mature females plotted against total density: comparison between model output and empirical data. *NM* denotes the number of mature females per 4 ha, and *N* the population numbers per 4 ha. Open circles represent empirical data (the entire set), whereas dots represent model output.

of mature females are "covered" by those of the remaining immature ones. I further assume that when the home range of a mature female is entirely covered by home ranges of the immature females (so that there is no free breeding territory) the reproduction of the already mature female will become inhibited. Let us accept — in accordance with data presented by Bujalska (1975) — that the home ranges of the mature and immature females are equal in size. Immature females may prefer to stay "in between" the home ranges of the mature ones in order to avoid encounters with the latter (Fig. 3). Immature females are, however, assumed never to be distributed evenly; either they are randomly distributed or clumped (Bujalska 1970, 1973). In order to simplify calculations, I assume their distribution to be completely random (i.e., according to the Poisson distribution). If the spatial distribution of immature females is random, then all mature females whose home ranges are covered by i ($i = 0,1,2,3$) home ranges of immature females will still have some part of their ranges uncovered; hence, they may still own a free breeding territory (Fig. 3).

The number of home ranges of mature females covered by 0, 1, 2 or 3 home ranges of immature ones can be estimated on the basis of Poisson probability distribution: that is

$$P_i = (\lambda^i / i!) \cdot e^{-\lambda} \qquad (7)$$

where $\lambda = (NF_t - NA_t) / NA_t$ (representing the number of remaining immature females per expected number of mature ones assuming no pressure from the mature ones) and e is the base of natural logarithms.

Thus, when the saturation threshold has been reached, any further increase in the number of females will produce the following number of mature females:

$$NM_t = \sum_{i=0}^{3} p_i \cdot NA_t \pm \rho \, (\sum_{i=0}^{3} p_i \cdot NA_t)^{1/2} \qquad (8)$$

The random variability, ρ, in formula (8) is introduced in order to simulate slight deviations from the Poisson distribution.

The simulated number of mature females was obtained either from formula (4), used when the total density was below the saturation threshold, or from formula (8). These formulas were used for $N_t = 3, 6, 9..., 498$. This way the observed range of population densities was simulated. The resulting pattern resembles that found for the island population (Fig. 4). Hence, the assumed mechanisms seem able to explain the observed patterns. I would like, however, to point out that a variety of ecological and physiological phenomena may take part in regulation of the number of mature females. These are, presumably, different below and above the saturation threshold.

4. Conclusions

1) In most studied populations of the species belonging to the genus *Clethrionomys* sup-

pression of sexual maturation in females born the same year is evident. This suppression results from territoriality in mature females. Because the size of the home ranges — and, perhaps, the breeding territory size — depends on the environmental capacity (in a broad sense of the word) the number of mature females will be adjusted to that capacity.

2) Because the mechanism limiting the number of mature females essentially is based on the spacing behavior of mature females, the number of mature females is in fact independent of the trappable population density (except below the saturation threshold). The frequently described inverse proportionality between the percentage of mature females and the population density should not be assumed to be a causal relationship.

3) Ordination of the number of mature females along the axis of population numbers is recommended in order to understand the underlying mechanisms better. Such an approach makes it possible to reveal a variety of regulatory processes related to resources; this approach may be very useful when modelling changes in population numbers. It seems particularly important to locate various thresholds on the total density axis; that is,

a) the saturation threshold representing the beginning of suppression of maturation, and

b) the security threshold representing the beginning of the decrease in number of mature females (above this threshold the number of mature females is density-depedent). The latter threshold may prevent the population from becoming overcrowded.

4) These thresholds divide the population densities into 3 ranges: that is,

a) presaturation density, where increase in the numbers of mature females is directly proportional to the population numbers,

b) saturation density, where a relatively stable number of mature females is maintained despite of rather extensive changes in total population density, and

c) oversaturation density, for which a decrease in the number of mature females accompanies further increase of the total population density.

The suggested deterministic model simulates such a pattern closely.

5) The above attempt to analyze relationships between maturation, reproduction and population density in *Clethrionomys* may appear useful when comparing results obtained for various populations of the same species living in different habitats (i.e., under different environmental conditions). This approach may also be useful when evaluating mechanisms for regulation of population density in species of different evolutionary history and life strategies.

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Appendix. Literature data on maturation and territoriality in *Clethrionomys* species. — 1) Population density. — 2) Density of mature females, sexual maturation and reproduction. — 3) Comments made by the quoted author.

Clethrionomys gapperi
Fuller 1969: 1) 2-14/ha
2) Young females of June litters attain maturity, those born later probably do not maturate
3) Suppression of reproduction of the young of the year was not associated with higher densities.
Mihok 1979: 1) Low
2) All females attain maturity
3) Suppression of maturation was not found, probably because of low density of mature females.
Perrin 1979: 1) Not given
2) Only females of the first cohort attain maturity
3) Females participated in breeding during the same year they were born whenever overwintered ones die.

Clethrionomys glareolus
Newson 1963: 1) Low; no peak was observed
2) Only in April and July 100 % were mature, in the remaining months only 50-87 %
3) Grassland grid
Newson 1963: 1) High, with a peak in October
2) Percentages of mature were high, the current year females reproducing when large enough
3) Woodland grid
Zejda 1964:
— 1) 4 per 100 trapnights in April
2) 66 % of females younger than 3 months were sexually mature
— 1) 11 per 100 trapnights in May
2) 82 % of females younger than 3 months were sexually mature
— 1) 12 per 100 trapnights in June
2) 8 % of females younger than 3 months were sexually mature
— 1) 16 per 100 trapnights
2) 1.5 % of females younger than 3 months were mature
3) Sexual maturation of females born in May/June, and partly those born in April, were strongly suppressed.
Zejda 1967: 1) High (peak year)
2) 10 % of the females attained maturity the same year they were born; this percentage decreased when population density increased
3) The young of the 2nd and 3rd litters did not attain maturity.
Zejda 1976 (see also Zejda 1964, 1967): 1) Not given
2) Spring cohorts: 87 % of the females attained maturity; summer cohorts: 22 % of the females did; and females of the autumn cohorts did only attain sexual maturity in exceptional cases
3) Percentages of those attaining maturity changed depending on population density.
Bujalska 1970, 1973, 1982:
— 1) 36-85 per ha
2) 14-15 per ha
— 1) 97 per ha
2) 9 per ha
3) The number of mature females was stable in June - September; the percentage of females which maturated the same year they were born depends on the number of overwintered females.
Bujalska 1975: 1) more than 100 per ha
2) 17 per ha
3) Extra food offered.
Bujalska & Janion 1981: 1) 70 per ha
2) 22-23 per ha
3) A competing species was removed.
Ivanter 1975:
— 1) Low in spring followed by a rapid increase
2) Percentages of females attaining maturity: 50 % in June, 65 % in July, and 87 % in August
— 1) High in spring followed by a slightly increase later in summer
2) Percentages of females attaining maturity: 14 %, 40 %, 53 % in the same months as given above
3) The maturation rate in north-west of the USSR depends on the date of parturition: early born females attain maturity sooner than later born, adults and sexually mature do not survive the winter.
Nyholm & Meurling 1979:
— 1) No cycle found (South Sweden)
2) Females often attain maturity in the same year they are born, and take part in reproduction in summer and autumn.
— 1) Cycles occur (North Sweden)
2) Females do not attain maturity in the same year they are born under peak conditions.

Wiger 1979:
— 1) Pre-peak
2) 7.9 per 100 trap-nights in June; 7 per 100 trap-nights in August
— 1) Peak
2) 9.1 per 100 trap-nights in June; 9.3 per 100 trap-nights in August
— 1) Increase
2) All females attain maturity in the year they are born
3) In the pre-peak and peak years the number of mature females remained relatively constant, each mature female had an exclusive territory.
Wiger 1982:
— 1) Low (1st year of the cycle)
2) Females born till mid-August (i.e., cohorts K_1, K_2) attain maturity
— 1) Low (2nd year of the cycle)
2) Mostly females of K_1-cohort and only some of K_2-cohort attain maturity
— 1) High (3rd and 4th year of the cycle)
2) Females do not attain maturity in the same year they are born; overwintered predominate among breeding females
3) Low density of K_0 (overwintered cohort); in the pre-peak years overlapping of home ranges increased for breeding females; in the 3rd and 4th year, overwintered dominated breeding.
Gustafsson 1983:
— 1) No cycle found (South Sweden)
2) Females attain maturity in the same year they are born
— 1) Cycles occur (North Sweden)
2) Almost all females older than 2 months attain maturity
— 1) Peak numbers
2) Few females attain maturity in the same year they are born

Clethrionomys glareolus skomerensis
Jewell 1966:
— 1) July: about 150 individuals per ha caught in 14 days
2) Among them about 62 mature females
— 1) September: about 350 individuals per ha caught in 11 days
2) Among them about 52 mature females
3) 250 voles per ha appear to be crowded; most of the summer recruits remain in a state of physiological immaturity in their first season.

Clethrionomys rufocanus
Kalela 1957:
—1) 5–15 per 100 trap-nights
2) Almost all females of the first cohort attain maturity in the same year they are born
—1) About 23–50 per 100 trap-nights
2) Most of the females attain maturity in the same year they are born
—1) 155 per 100 trap-nights (Malla site, very high density)
2) No females attain maturity the same year they are born
3) Density-dependent suppression of maturation; control of reproduction takes place in mid-summer when food is superabundant.
Viitala 1977: 1) Not given
2) Maturation ceased when all habitable space was occupied
3) Density of mature females controlled by territorial behaviour; home range size equal to 900 m^2 in summer and 300 m^2 in September (equals 35 indiv./ha).

Clethrionomys rufocanus bedfordiae
Tanaka 1953: 1) Not given
2) Not given
3) Breeding females defend their territories against other females.
Saitoh 1981: 1) Not given
2) 10 per 0.5 ha
3) Stable number of mature females; their numbers are independent of the numbers of other female categories.

Clethrionomys rutilus
Koshkina 1965:
— 1) High density (peak)
2) Only overwintered females reproduce
— 1) Low density
2) Both overwintered and year-born females reproduce
3) In June breeding females occupied 75 % of sampling area (very high population density) or 50 % of the area (low density); high density was accompanied by smaller home range size which was overlapping greatly; territorial fights and wounded animals were observed.

Koshkina & Korotkov 1975:
— 1) 1-6 per 100 trap-nights in spring*
  2) 13.2-72% of the females attained maturity the same year they were born
— 1) 7-15 per 100 trap-nights in spring*
  2) 0.8-60.4% of the females attained maturity the same year they were born
— 1) Over 15 per 100 trap-nights in spring*
  2) No female attained maturity the same year they were born
  3) At low density home ranges of mature females did not overlap; maturation inhibited at high density.
Fuller 1969: 1) Density within the range of 2-20 per ha
  2) Some females of the early litters attain maturity during the summer of their birth
  3) Suppression of reproduction of young of the year does not accompany relatively high numbers.
Ivanter 1975: 1) 0-0.26 per 100 trap-nights
  2) Only females of early litters reproduce regularly the summer they are born; those born in July and later reproduce very rarely (in average 3%) the same year
  3) In the north-western taiga of the USSR *C. rutilus* is subordinated to *C. glareolus* and thus does not form dense populations; the subordinated species is characterized by high reproduction and maturation rates.

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* Recalculated from the original data by combining data for several habitat.

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