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Spacing behaviour and male reproductive ecology in voles of the genus *Clethrionomys*

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The literature on the relationships between social behaviour, population density and the suppression of sexual activity in male microtine rodents, and in particular the genus *Clethrionomys*, is reviewed. Data from laboratory cages, from laboratory and outdoor enclosures, from islands and from natural populations are considered.

Although it has been shown that, in males of many vole and lemming species, social behaviour and/or high population density can suppress sexual maturation of immature individuals, can suppress adult sexual activity, and can shorten the breeding season, the potential that this has for limiting the density of populations of these animals, at least in those species that are polygynous, is slight (compared with females).

The evolutionary significance of this widespread phenomenon in male microtine rodents remains to be clarified.

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1. Introduction

A large body of literature on the relationships between social behaviour and ecology of rodents exists (for reviews, see, e.g., Krebs 1978, Lidicker 1978, Christian 1980, Gaines & McClenaghan 1980, Tamarin 1983); in this article, I concentrate on the genus *Clethrionomys*, but will often refer to the literature on other Microtines and less often the other members of Cricetidae.

I concentrate on the role played by spacing behaviour in the reproductive ecology of rodent populations, and particularly on the ways it affects male reproductive ecology. Bujalska (1985) reviews the literature on females. I also attempt in this review to ask some questions about the ways in which different methods of looking at the relationship between behaviour and male reproduction have affected the interpretation of results and to draw attention to ways in which unjustified conclusions may have been made.

There are three major phenomena associated with control of sexual activity of male microtine rodents by population density:

1) Delay of first maturity.
2) Regression of sexually mature animals.
3) Winter breeding. (This is the opposite to suppression, but is of interest since population density may play a part in its control).

2. Spacing behaviour

First, spacing behaviour must be defined. In neutral arena tests in the laboratory, aggressive and amicable interactions between pairs of small mammals may readily be observed, and the frequencies, latencies and durations of various behavioural states and actions may be quantified (e.g., within the genus *Clethrionomys*: Johst 1967, Ashworth 1973, Alder 1975, Mihok 1976, 1981, Mitchell-Jones 1979, Perrin 1981, De Jonge 1983, Gipps 1983, 1984). All neutral arena tests have a fault in common, namely that escape by either of the test animals is impossible. The frequency or intensity of so-called aggressive postures or acts may therefore be atypical or exaggerated when compared to similar acts when they occur in the field. Thus, any information on components of behaviour that have been derived from laboratory neutral arena studies must be treated with caution; although it is likely that they resemble in quality events that occur in the field, the relative occurrence of various components may be different.

In attempts to avoid this problem, some workers have resorted to observing the behaviour of individuals in large laboratory colonies or field enclosures (*C. glareolus*: Oldfield 1968, Evans 1975, Gipps 1981, De Jonge 1980, 1983). Enclosed populations of voles have always reached very high densities (the so-called "fence effect" of Krebs (1966)) so that the quality and quantity of aggressive interactions have again almost certainly been different from those that occur in unenclosed field populations. Few workers have tried to observe directly meetings between voles in the field, and in all cases their efforts have necessarily been restricted to observation of above-ground interactions at traps or bait points (*C. glareolus*: Andrzejewski & Olszewski 1963, Kikkawa 1964, Gipps 1981). Interactions that occur within the animal's burrow systems cannot be observed, so that, again, biased data must inevitably have been obtained.

In the field, the spatial consequences of aggressive interactions that constitute spacing behaviour are more readily observed than the behavioural components themselves, and many authors using live traps to study the population ecology of *Clethrionomys* have drawn conclusions about home ranges and territoriality (*C. glareolus*: Crawley 1969, Zejda & Pelikan 1969, Mazurkiewicz 1971, 1981, Andrezjewski & Mazurkiewicz 1976; *C. gapperi*: Perrin 1979; *C. rufocanus*: Kalela 1957, Viitala 1977; *C. rutilus*: Koshkina & Korotkov 1975). The likely errors that may result from inferring spatial relationships from live trapping data alone are considerable, since, once caught, an animal is effectively immobilised and therefore unable to reveal its true, unrestricted home range. Tracking methods, such as those used by Randolph (1977) or radio-tracking (e.g., Madison 1978, 1980b) are therefore needed.

It is clear from the above that there is a wide range of behavioural phenomena that fall into the categories of aggression and spacing behaviour; definitions are therefore difficult, but in this article, I assume that spacing behaviour includes any form of social interaction that leads to animals spacing themselves regularly rather than at random or which leads animals to disperse (sensu Stenseth 1983). I presume that this includes all the forms of aggressive interaction mentioned above, plus scent marking (Evans 1975, Johnson 1975, De Jonge 1980, Hoffmeyer 1982).

3. Ecology

3.1. Introduction

All free-living populations of voles in temperate areas go through an annual cycle in numbers. In optimal habitat, the most common form of this cycle consists of a low density in the late spring and early summer, an increase through recruitment by births during late summer and autumn which ends when the last young born at the end of the summer breeding season are weaned and recruited, a peak in the late autumn, and a decline in numbers in late winter and early spring; this annual cycle is the most commonly observed pattern in the four *Clethrionomys* species whose ecology has been most thoroughly studied (Alibhai & Gipps 1985, see also Stenseth 1985, fig. 1-4). Some, however, also exhibit multi-annual cycles (e.g., Krebs & Myers 1974) in parts of their ranges (e.g., in *C. glareolus*: Hornfeldt 1978, Nyholm & Meurling 1979, Henttonen & Hansson 1985). In this review I will focus on what conditions are both necessary and sufficient to *stop* the increases and to *cause* declines.

Ecological studies on aspects of the reproductive ecology of *Clethrionomys* have been done on small groups of animals (less than 10) in laboratory cages; on larger, freely growing groups in laboratory or outdoor enclosures; on populations on islands; and on unenclosed field populations. As noted above, the effects on demography of frustrating dispersal are profound (Krebs 1966, and many others; see Gaines & McClenaghan 1980, and Stenseth 1983, for reviews). The extrapolation of results from the artificial situation in the laboratory or enclosure to the field situation must be done with great care.

It should be noted that all the results from studies mentioned in this review have required assessment of breeding condition in live animals. In females, this is usually fairly straightforward (Twigg 1975). Breeding condition in males is much less easy to determine in the field. It ultimately depends on whether viable spermatozoa are being produced by the testes, and this depends on testis size (e.g., Rowlands 1936). Field workers have usually resorted either to defining breeding males as those with scrotal testes, or those with large testes. The former method is poor at identifying breeding males accurately, the latter is subjective and also prone to inaccuracy (Jameson 1950, Woodall 1982).

How do the various forms of spacing behaviour (observed in the laboratory, enclosure or in the field) affect reproductive ecology? For males, age at first sexual maturity and the length of the breeding season are the most important aspects of reproductive ecology, and those most likely to be affected by social behaviour. Several questions concerned with sexual maturity and its possible mediation by social behaviour and population density present themselves.

1) Is attainment of sexual maturity by immature animals affected by population density during the breeding season?

2) Do late cohorts of young ever mature in the year of their birth?

3) Do previously sexually mature animals become reproductively inhibited at high densities?

4) Does high density shorten the breeding season by delaying its start or advancing the end?

3.2. Small groups in the laboratory (Table 1A)

Several studies on Cricetids other than from the genus *Clethrionomys* have shown that basic reproductive variables can be profoundly affected by social conditions in small laboratory groups. Sexual maturity of males can be suppressed by the presence of adult males, by their odour, or simply by high population density (*Peromyscus* spp.: Rogers & Beauchamp 1976, Bediz & Whitsett 1979, Lawton & Whitsett 1979; *Microtus* spp.: Christian 1956, Lecyck 1967, Batzli et al. 1977).

Studies of this sort on *Clethrionomys* species are few. Gustafsson and his coworkers (see Gustafsson 1985) have concentrated on the role of male social behaviour in the reproductive ecology of *Clethrionomys glareolus* and found that in the laboratory, male sexual maturation could be retarded by exposure to a strange adult male (Gustafsson & Andersson 1980), and by high density grouping (4/cage compared with 1 or 2/cage) but, in the latter case, only in animals derived from a strongly cyclic natural population (Gustafsson et al. 1983). In contrast to previous work on *Mus musculus* (Vandenbergh 1971) Gustafsson (1984) found that male maturation could also be retarded by the presence of adult females.

3.3. Freely growing populations in enclosures (Table 1B)

At high densities in large enclosures, several rodent species have exhibited delayed attainment of first sexual maturity of young males. Additionally, in some of these studies, high density within enclosures has led to an early end to the breeding season, in comparison with respect to free-living populations (Krebs et al. 1969, Lidicker 1979).

In *Clethrionomys glareolus*, sexual maturation of males was effectively blocked in young born in both of two large field enclosures at high density (Gipps & Jewell 1979). In one of the enclosures, approximately 80% of the founding, adult males had been castrated (thereby rendering them docile in comparison with intact, adult males; Gipps 1983). There were no differences between the two enclosures in the degree to which sexual maturation was repressed, suggesting either that high density alone was responsible for the observed effects, or that female behaviour (which was not experimentally made different between the two enclosures) was responsible. When densities built up to high levels, there was also considerable suppression of reproductive activity in animals that had previously bred in the enclosures; in effect, there was an early end to the breeding season in comparison with field populations studied at the same time.

3.4. Island populations (Table 1C)

Populations on *small* islands are similar to artificially enclosed populations in that immigration and emigration are usually absent. Islands used in studies of small mammal population dynamics have varied widely in size, from very small (<1 ha) with more or less homogeneous habitats, to large (>250 ha) with distinctly patchy habitat. In general, island populations of microtines live at high densities compared with mainland populations, and exhibit relatively lower reproductive output. A relatively short breeding season has commonly been observed (see Crowell 1983, Gliwicz 1980, for general reviews).

Perhaps the best known island on which voles of the genus *Clethrionomys* have been studied is Crab Apple Island in Poland (Gliwicz et al. 1968, Bujalska 1971, 1973, 1979, 1985, Mazurkiewicz 1972, Gliwicz 1975, 1980); up to the present, there has been emphasis on the role of females in the dynamics of this population (Bujalska 1985). On Skomer Island, Wales, bank voles (*C. glareolus skomerensis*) exhibit a much shortened breeding season, and very few animals of either sex come into breeding condition in the year of their birth (Jewell 1966, Healing, pers.-comm.). There is no evidence that high density directly inhibits breeding in males or females, but the numbers of males in the middle of the breeding season is more constant from year to year than the numbers of females (Healing, pers.comm.; see also Bujalska 1985).

3.5. Free-living populations (Table 1D)

Delayed attainment of sexual maturity by young males at high density has been observed in both cyclic and non-cyclic *Microtus* populations. Within the genus *Clethrionomys*, several examples of reproductive inhibition or delayed male maturation at high density in free-living populations exist.

At peak and declining population densities, a shortened breeding season has been observed in several species of *Microtus*, *Clethrionomys glareolus* (in both cyclic and annually fluctuating populations), *C. rufocanus* and *C. rutilus*. This phenomenon was not observed in an annually fluctuating population of *C. glareolus* (Nyholm & Meurling 1979), nor could Viitala (1977) find any correlation between early cessation of breeding and population density in *C. rufocanus* (nor in *Microtus agrestis*).

3.6. Summary

What Table 1 shows most clearly is that the phenomenon of sexual suppression at high population density in males is widespread in microtine rodents. Most of the gaps in the table are almost certainly not because the phenomenon did not occur, but because the relevant data were not collected. Many studies have described marked suppression of sexual activity in females, but have been omitted from the table because they present no data on males (e.g., Chitty 1952, Clarke 1955 and others).

4. Discussion

In polygynous mating systems in mammals, females are predicted to be resource-limited, whereas males are not and are therefore assumed to compete so that each may mate with the maximum number of females (Eisenberg 1966, Orians 1969, Wittenberger & Tilson 1980, Tamarin 1983). Several microtine species appear to be polygynous at least at moderate and high densities (Hasler 1975, Getz 1978, Getz & Carter 1980, Jannett 1980, Lidicker 1980, Madison 1980a, Wolff 1980, Wiger 1982). Amongst female voles, the possession of territory-like home ranges during the breeding season has been demonstrated for some *Microtus* species (Getz 1961, Jannett 1980, Madison 1980b) and for *Clethrionomys rufocanus* (Kalela 1957, Viitala 1977), *C. rutilus* (Koshkina & Korotkov 1975), *C. gapperi* (Perrin 1979, 1981) and *C. glareolus* (Bujalska 1970, 1973) (see also Bondrup-Nielsen & Karlsson 1985). By adopting this strategy, they secure sufficient resources for the successful rearing of litters. It is proposed that male voles, on the other hand, have larger home ranges which tend to overlap each other more than those of females. Males are presumed to be competing for oestrous females to inseminate, so that a male's home range must be large enough to include those of several sexually mature females. Males are more overtly aggressive, but their large home ranges are not mutually exclusive territories.

In *Clethrionomys*, therefore, the potential that suppression of female sexual activity has to regulate breeding density is high, since their spacing behaviour, manifest as territoriality, can impose an upper limit on population density; it is hard to envisage such a discrete level in the density of sexually mature males, above which the failure of males to mature could have a significant role in population limitation, and I think that it is fair to conclude that it has no such role. Our understanding of the social organization of most species of *Clethrionomys* is still meagre, and the effects of failure to mature on males' inclusive fitness (because of social factors and/or high population density) need investigations.

Within the genus *Clethrionomys*, the details of the effects of the social behaviour of each sex upon the population dynamics of the other, and the differences in demography between them, also remain largely to be

Table 1. Suppression of sexual activity in male rodents of the subfamily Microtinae (Rodentia, Cricetidae). Authors' comments and/or descriptions of mechanisms of suppression are given.
Y = suppression of sexual maturation in young males. A = suppression of sexual activity in adult males.
L = late start of breeding season. E = early end of breeding season.
Y, A, L, E alone: Suppression studied and observed; Y-, A-, L-, E-: Suppression studied but not observed.

A. Laboratory groups
Microtus californicus: Y-; caged with strangers cf littermates: grew more slowly. (1)
M. ochrogaster: Y; caged with strangers cf littermates: growth and sexual maturation inhibited. (1)
M. pennsylvanicus: Y-; caged with strangers cf littermates: neither growth nor sexual maturation inhibited. (1)
M. arvalis: Y. (27)
Clethrionomys glareolus: Y; exposure to strange male. (14)
C. glareolus: Y; high cage density (4/cage cf 1 or 2); animals from cyclic populations only. (15)
C. glareolus: Y; exposure to strange male daily and exposure to strange female daily. (13)

B. Freely growing populations
Microtus californicus: Y, A; high density (cf natural populations). (28)
M. pennsylvanicus: Y; high density (cf natural populations). (25)
M. ochrogaster: Y; high density (cf natural populations). (25)
M. arvalis: Y; high density (cf natural populations). (4)
Clethrionomys glareolus: Y, A-, E; high density (cf natural populations). (10)

C. Island populations
Microtinae: L, E; reviews. (12, 6)
Clethrionomys glareolus skomerensis: Y, A, L, E; Skomer Island: high density cf mainland. Subspecies. (17, 16)
C. rutilus: Y; proportion maturing in year related to density. (3)
Microtus breweri: Y, A, E; high density (non-cyclic). (35)

D. Free-living populations
Lemmus trimucronatus: Y, L-, E; cyclic peak and decline. (23)
L. trimucronatus: Y, L, E-; cyclic peak. (31)
Dicrostonyx groenlandicus: Y, L-, E; cyclic peak and in decline. (23)
D. groenlandicus: Y; cyclic peak. (9)
Microtus pennsylvanicus: Y, A-; high density. (5)
M. pennsylvanicus: Y, L*; high density, * in decline. (19)
M. pennsylvanicus: Y, L, E; cyclic peak and decline. (35)
M. ochrogaster: Y, L*; cyclic peak, *in decline. (19)
M. californicus: Y; cyclic peak. (29)
M. californicus: L*, E; cyclic peak, * in decline. (24)
M. townsendi: Y, A, L-, E-; experiments: low density led to earlier maturation and greater % scrotal. (2)
M. townsendi: Y, A-, L-, E-; experiments: low male density led to earlier male maturation. (33)
M. townsendi: Y-, A, L, E- experiments: decline: early breeding on area with low male aggression. (11)
M. townsendi: Y; control grid: weight at sexual maturity proportional to density (weak evidence). (26)
M. oregoni: A; high density: no differencies between different habitat grids at different densities. (34)
Clethrionomys rufocanus: Y, L*, E; high density, * in decline. (18)
C. rufocanus: Y, E-; high density. (36)
C. rufocanus: Y; high density. (21)
C. rutilus: Y, L, E; cyclic peak. (20)
C. rutilus: Y; cyclic peak. (22)
C. rutilus: Y; weak relationship. (30)
C. gapperi: Y-, A-; spring or summer density. (8)
C. gapperi: Y, L, E; decline. (7)
C. glareolus: Y, E; cyclic peak. (32)
C. glareolus: Y, E-; high density (non-cycling population). (32)
C. glareolus: Y, L, E; cyclic peak. (37)
C. glareolus: Y; high density. (38)
C. glareolus: Y, L, E; high density. (39)
C. glareolus: Y; cyclic peak. (21)

Sources: 1) Batzli et al. 1977; 2) Boonstra 1978; 3) Burns 1981; 4) Chelkowska 1978; 5) Christian 1971; 6) Crowell 1983; 7) Fuller 1969; 8) Fuller 1979; 9) Fuller et al. 1975; 10) Gipps & Jewell 1979; 11) Gipps et al. 1981; 12) Gliwicz 1980; 13) Gustafsson 1984; 14) Gustafsson & Andersson 1980; 15) Gustafsson et al. 1983; 16) Healing, pers. comm.; 17) Jewell 1966; 18) Kalela 1957; 19) Keller & Krebs 1970; 20) Koshkina 1965; 21) Koshkina 1966; 22) Koshkina & Korotkov 1975; 23) Krebs 1964; 24) Krebs 1966; 25) Krebs et al. 1969; 26) LeDuc & Krebs 1975; 27) Lecyk 1967; 28) Lidicker 1979; 29) Lidicker 1980; 30) Martell & Fuller 1979; 31) Mullen 1968; 32) Nyholm & Meurling 1979; 33) Redfield et al. 1978; 34) Sullivan & Krebs 1981; 35) Tamarin 1977; 36) Viitala 1977; 37) Wiger 1979; 38) Zejda 1964; 39) Zejda 1967.

clarified. This can only be done successfully by removal experiments and by experiments in which the behaviour of one or other sex is modified. Although several studies of this sort have been done with other microtine rodents (Boonstra 1978, Gaines et al. 1979, Gipps et al. 1981, Baird & Birney 1982, Boonstra & Rodd 1983) and on enclosed or island populations of *Clethrionomys* (Bujalska 1973, Gipps & Jewell 1979), there is a need for similar experiments on natural, unenclosed *Clethrionomys* populations.

Social organisation in any small mammal requires complex systems for communication between individuals. Visual, auditory and chemical signals must all play a part, but it is likely that the most important of these for cryptic rodents is chemical (Bronson 1974, 1983, Richmond & Stehn 1976, Brown 1979). Unfortunately, there has been relatively little work on pheromonal communication in *Clethrionomys* species except in the laboratory (see references above), and this is a further area where manipulative field experiments associated with accurate knowledge of movements of individuals could be most profitable in unravelling the intricacies of social organisation.

In conclusion, although suppression of male breeding in natural populations of *Clethrionomys* may be an important factor in their social organisation, it is, on the present evidence, unlikely to have the same importance in density regulation. That phenomenon appears to be the preserve of mature females, and to be mediated by their resource-controlled spacing behaviour.

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