

6. ECOLOGICAL STRUCTURE OF THE POPULATION

6.1. Sex Ratio

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Sex ratio, the mechanisms of its formation, variability of its range, and significance to the population dynamics have frequently been theoretically analysed, but less frequently studied empirically.

Theoretical bases for the concept of the evolution of optimal sex ratio in diploid animals with sexual reproduction were developed by Fisher (1959). According to his theory, the optimal sex ratio in steady-state populations should approximate 50 : 50.

This hypothesis was tested by means of the mathematical modelling of empirical data for *Microtus ochrogaster* and *M. pennsylvanicus* populations (Myers & Krebs, 1971). The effect on sex ratio of differences in recruitment rate, survival, trappability, and individual growth between males and females was analysed. The conclusion was that despite all these differences sex ratio should be 1 : 1, as predicted by Fisher.

It is not difficult to find some deviations from the "ideal" sex ratio frequently recorded in rodent populations (e. g. Pelikán, 1965, 1970; Kalela & Oksala 1966; Kalela, 1971; Myllymäki, 1975, 1977; Adamczewska-Andrzejewska & Nabagło, 1977; Hansson, 1978, and others).

According to the phases of individual development, sex ratios have been classified into primary (at the time of conception), secondary (at birth), tertiary (soon after leaving the nest), and quaternary (in reproducing animals) (Kalela & Oksala, 1966; Pianka, 1974). In practice, however, it is frequently difficult to differentiate the tertiary and quaternary sex ratios (in the case of animals for which the time of leaving the nest is unknown). Therefore, in free-living populations we can determine the sex ratio for immature and mature individuals. But most often only the sex ratio of all the males and females in the population as a whole is examined.

Sex ratio in the bank vole has not been thoroughly analysed. This paper presents a review of the literature on this subject, and also

emphasize gaps in our knowledge of the sex ratio in the bank vole relative to published data for other rodents. At the present state of knowledge it is difficult to postulate a synthesis of this issue, or to show relationships between the processes of sex ratio formation and other processes determining population dynamics.

As the primary sex ratio has not been studied in the bank vole at all, I shall start this review with the secondary sex ratio.

6.1.1. Secondary Sex Ratio

Secondary sex ratio in the bank vole was studied by Buchalczyk (1970) under laboratory conditions. Among newborn animals there were 656 males and 636 females. Litters in which some young died consisted of 195 males and 184 females. The observed prevalence of males is not statistically significant, thus the secondary sex ratio is 1 : 1.

Similar results were obtained by Kalela and Oksala (1966) for *C. glareolus* and *C. rufocanus*. In the latter species males accounted for 49.6% of 256 embryos. Also Zejda (1967) examined sex ratios in embryos prior to birth, and found that the proportion of males was 53%.

The estimated data for an island population of the bank vole (Bujalska, 1981b) show that the proportion of males at birth can vary from 44.4 to 72.0%, with an average of 54.7%. A particularly high predominance of males occurred in cohort K₃ (born in the second half of the breeding season) in 1967 and 1968, the respective values being 70.1 and 72.0%. In the other seven cases that were analysed, the upper limit of male proportion did not exceed 59.0%. These values, calculated on the assumption that the number of young decreased exponentially in the period from birth to an age of about three months, can contain some error. However, the thesis that the secondary sex ratio can vary seems reasonable. Even more so since the secondary sex ratio greatly deviates from 1 : 1 in *Myopus schisticolor* (Kalela & Oksala, 1966).

6.1.2. Tertiary Sex Ratio

The tertiary sex ratio is generally determined for immature individuals. Interesting data on this issue are presented by Kalela (1971) for a population of *C. rufocanus* living in Finnish Lapland. He analysed sex ratios for immature and mature animals in successive months from May to September and in different phases of the population cycle over 15 years. In July the sex ratio for immature individuals was 1:1 (47% males), while in August males significantly predominated (64.9%), while in September their numbers fell (55.4%) but remained statistically significant.

Males predominance among immature individuals of an island bank vole population was observed in June-July of 1975 and in June-September of 1977 (Bujalska, 1981b). In June, July, and September of 1975 the proportions of males were 53.3, 55.5, and 49.6%, respectively, and in 1977 the respective figures were 82.1, 60.6, and 66.2%. Thus in 1975, the sex ratio in immature voles was rather stable and near 1:1, while in 1977 the proportion of males tended to decrease. In 1976, when the population was very low, the sex ratio in July (data for June are lacking) was characterized by a smaller proportion of males (44.9%), while in September this proportion was more equalized (49.1%). It can thus be suggested that a higher proportion of males among immature individuals occurs at higher population densities.

Kalela (1971), who analysed the effect of population factors on sex ratio in *C. rufocanus*, found that males predominated in August and September (61.6%) during years of high population densities. In the years of low population densities the proportion of males in the same months was 53.6% and thus not statistically different from the 50:50 ratio. These consistent results for *C. glareolus* and *C. rufocanus* imply that this pattern may also occur in other representatives of this genus.

6.1.3. Quaternary Sex Ratio

Quaternary sex ratio, that is, in mature individuals, was studied by Kalela (1971) with reference to seasonal changes and population dynamics of the bank vole. The sex ratio of adults was 1:1 late in May and in June (51.9% males) and also in July (50.5% males), and then the proportion of males declined in August and September (35.2 and 28.0%, respectively).

Regression of the number of mature males and females on the total trappable population of an island showed that the female curve was always higher than that of males and the sex ratio declined (Bujalska, in print.).

In years of a high *C. rufocanus* population density, the proportion of males among adult individuals was lower in August and September (28.7%) and equalized in May-July (50.4% males). In low population density years, sex ratio was 50:50 in both May-July (54.8%) and August-September (48.9% males).

Overwintered voles were usually (in 17 out of 30 cases analysed) predominated by females in April, that is, when formed the reproducing stock of the population. This female predominance already occurred in the autumn of the preceding year, thus did not result from differences in winter mortality between males and females (Bujalska, in print.).

It seems that the sex ratio in mature, thus capable of reproduction, individuals is particularly important to population dynamics. In this respect the analysis of sex ratio in immature voles would be less important. It would characterize, however, the relations in the "reserve" that they represent for the reproducing part of the population. This reserve accounts for the maintenance of the sex ratio observed in the adult population.

6.1.4. Sex Ratio in Selected Age Classes

Another type of analysis was done by Ivanter (1975) on the basis of long-term data for a bank vole population inhabiting north-western regions of the USSR. He analysed the sex ratio in overwintered voles

Table 6.1.
Percentage of males in three categories of bank voles
in 1958—1972 (after Ivanter, 1975).

Month	Category of individuals		
	Overwintered	Current-cohorts	
		Early	Late
March	60.0	—	—
April	62.5	—	—
May	68.7 ¹	100	—
June	62.4 ¹	65.1 ¹	—
July	58.5 ¹	66.5 ¹	55.4
August	49.0	62.9 ¹	59.9 ¹
September	11.1	31.7 ¹	60.3 ¹
October	—	20.0 ¹	54.3
November	—	—	48.3
December	—	—	53.3
January	—	—	50.0
February	—	—	—
Mean	58.7 ¹	60.5 ¹	57.3 ¹

¹ Denotes statistically significant deviation from 50:50.

and in the current-year cohorts recruited into the population early and late in successive months of the year (Table 6.1). At first the proportion of males in overwintered animals was high, and it gradually declined after May. Current-year cohorts were usually predominated by males in the early months of their lives. In older cohorts the proportion of males gradually dropped, while in younger cohorts the sex ratio was 1:1 from the time when they accounted for more than 90% of the population (from October to January of the following year).

Moreover, Ivanter (1975) found that the proportion of males of the early current year-cohort tended to increase with increasing population

density in spring (from 56.2% at the beginning to 66.7% later on). He suggests that this may be explained by a higher number of males born to overwintered animals in response to the high population density. The predominance of males among overwintered voles was noted in the years of average population densities, and among the cohorts later recruited

Table 6.2.

Percentage of males in three categories of bank voles at various population numbers (after Ivanter, 1975).

Population numbers	Category of individuals		
	Overwintered	Current-year cohorts	
		Early	Late
Low spring numbers and rapid increase until autumn	54.7	56.2 ¹	56.7 ¹
Intermediate spring numbers and moderate increase until autumn	62.4 ¹	61.7 ¹	57.5 ¹
High spring numbers and slow increase until autumn	57.8	66.7 ¹	55.0

¹ Denotes statistically significant deviation from 50:50.

Table 6.3.

Mean male : female ratio (\bar{z}) in spring and autumn generations of the bank vole (after Bujalska, 1981b).

Year	Generation			
	Spring		Autumn	
	\bar{z}	95% confidence limits	\bar{z}	95% confidence limits
1966	1.0407	0.9801—1.1013	0.8662	0.3289—1.4035
1967	1.2855	1.1298—1.4412	1.4266	1.2442—1.6090
1968	1.1221	0.9736—1.2706	0.8607	0.5418—1.1796
1969	—	—	0.9328	0.8363—1.0293
1970	0.9683	0.8255—1.1511	0.5342	0.5204—0.5480
1972	0.9123	0.8060—1.0196	1.0245	0.9272—1.1218
1975	0.8362	0.7806—0.8916	0.8690	0.6143—1.1237
1976	0.5995	0.4822—0.7168	0.9340	0.8153—1.0527
1977	1.1366	0.8704—1.4028	0.9704	0.7314—1.2094

to the population in the years of low and average population densities in spring (Table 6.2). Instead, the sex ratio in the spring and autumn generations of an island bank vole population (Bujalska, 1981b) rarely deviated from the 1:1 ratio (Table 6.3), suggesting that these deviations are independent of the population density.

6.1.5. Total Sex Ratio

As indicated above, sex ratios for different categories of individuals can vary. In some cases males predominate, in some others females. To understand the role of this variation, it may be important to know whether it intensifies in the population considered as a whole, or the differences compensate for each other.

There is a statistically significant tendency of diminished departure of sex ratio from 1:1 with increasing population numbers (Bujalska, 1981b) (Fig. 6.1), and this may suggest the occurrence of some compen-

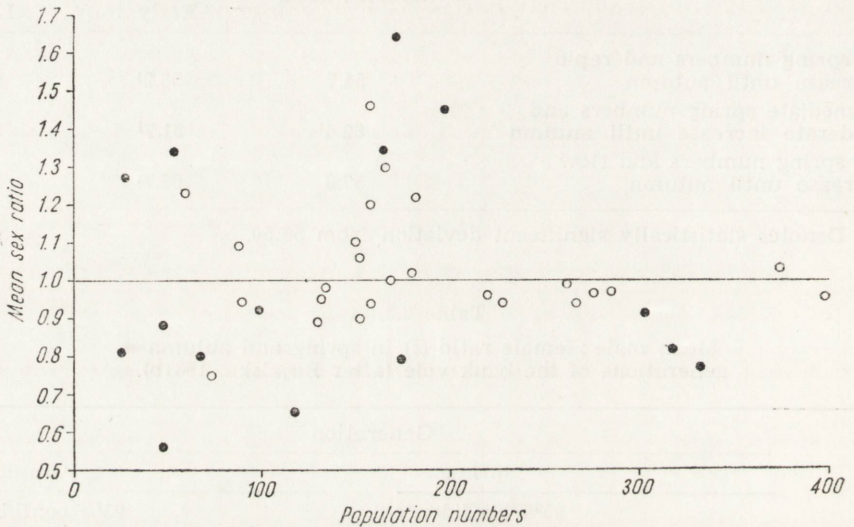


Fig. 6.1. Mean values and 95% confidence limits for sex ratio in various censuses versus population density of the bank vole.

Open circles — 95% confidence limits include 1.0, closed circles — 95% confidence limits do not include 1.0 (after Bujalska, 1981b).

satory processes at the population level. A similar relationship was found for *Microtus arvalis* (Bujalska, 1981a). It is thus possible that the 1:1 sex ratio can be established only when the population numbers reach some critical level.

It is worth reviewing the total sex ratio found by other authors for different populations. In a population of *C. rufocanus* (Kalela, 1971) it was 1:1, ranging from 47.9% males in September to 52.6% males in August (statistically insignificant differences), though there were seasonal changes in this ratio for immature and mature individuals. The same pattern was observed in different phases of the population cycle.

Despite significant differences in sex ratio of immature or of mature individuals, the total sex ratio approximated 1:1, ranging from 49.8 to 51.1% males (insignificant deviation).

Similarly interpreted data by Ivanter (1975) on seasonal changes in the sex ratio of the bank vole show a total predominance of males approximate from March to September, thus in the breeding season, while from Oct. to Dec. the sex ratio is about 1:1. In view of the mechanisms of sex ratio formation in the population, it would be interesting to know whether this is a functional regularity or merely a methodological artifact due to a higher mobility of males during the breeding season, thus the possible overestimation of their number.

Also Zejda (1967) found an equal sex ratio in a bank vole population before the breeding season (51.8% males). In April males predominated (61.0%), this being the case by the end of that month (62.5%). In the following months, overwintered voles were predominated by females and the current year voles by males.

Similarly, Bergstedt (1965) observed the predominance of males in a bank vole population in spring, while females predominated in summer. Hansson (1978), however, noted an equal sex ratio in three bank vole populations inhabiting southern, central, and northern Sweden during 1971—1975 (the only exception being females predominance in an increasing population in central Sweden in 1973).

6.1.6. Discussion

The above results of the studies on sex ratio in the bank vole show that it may differ for particular vole categories. These differences generally compensate for each other so that the resultant sex ratio in the population does not deviate from 1:1. In view of this fact we should know whether it is the result of a simple mathematical relationship due to the size of the analysed vole categories, or an effect of intrapopulation processes. Many data show that the equalizing of sex ratio occurs as a result of population mechanisms, namely, differentiated recruitment and mortality of males and females being members of different vole categories, generally age groups. To prove this, we should recognize the causal relation between recruitment and survival for males and females of successive cohorts or generations.

The deviation from the 1:1 sex ratio predicted by Fisher's theory, though generally not occurring in the bank vole populations, is rather common in populations of other species such as *Microtus arvalis* or *Myopus schisticolor*. This may be related to different strategies of number regulation in the populations of these species. An increase in

the density of bank vole populations is limited due to the decline in reproduction. Among other things, this is related to sex ratio establishment among mature voles through their territorial tendency, thus independent of the population numbers. In populations producing outbreaks (e.g. *Microtus arvalis* populations), reproduction is reduced at much higher densities than in other populations. Hence, an unlimited maturing of voles is observed in these populations (Adamczewska-Andrzejewska *et al.*, 1979; Bujalska, 1981a).

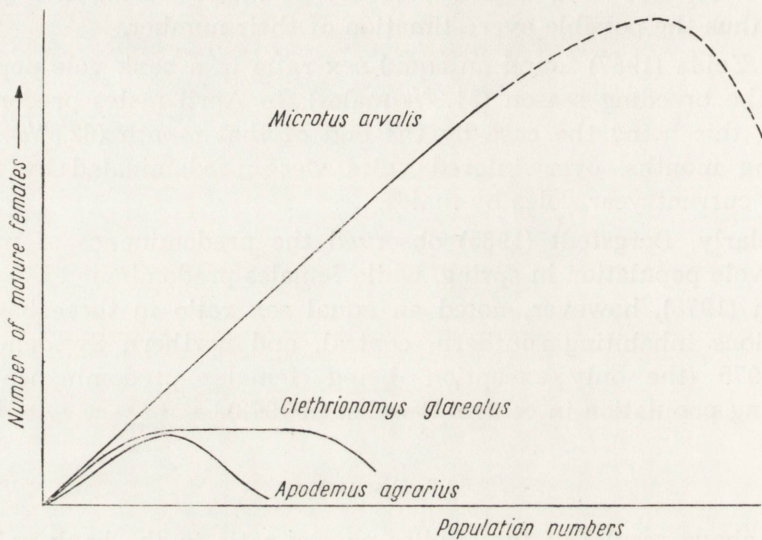


Fig. 6.2. Three curves describing relations between the number of adult females and population density (after Bujalska, 1981a).

As an illustration of changes in the number of mature individuals with changes in population densities of different species, we may quote the results obtained for *C. glareolus*, *Apodemus agrarius*, and *M. arvalis*. These species are characterized by different critical density values above which sexual maturity is delayed (Bujalska, 1981a, 1981b) (Fig. 6.2). There are differences in the rate of this process between males and females, which determine sex ratio in mature individuals at a given population density. These differences can be due to a differential "sensitivity" of males and females to a tolerable number of encounters with other individuals of the same sex. They may also be related to usually differential spatial requirements of reproducing males and females. Consequently, the sex ratio among immature individuals would depend on the number of males and females born, rate of their recruitment to

the mature population and on their mortality. An analysis of the behaviour of this population "reserve" can provide information on the ways of compensation for the deviation from 1:1 the sex ratio in the entire population.

Using this approach, the categories of mature and immature individuals would be the axis of the structural division of the population, and the analysis of sex ratio in the cohorts making up these two categories would seem to be one of the most promising ways of obtaining insight into the mechanisms underlying the variability of sex ratio in the population.

6.2. Age Structure

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The age structure of a population at any given moment is the result of birth rate and death rate prior to this moment. It can be modified by migrations if there are differences in migratory tendencies among particular age classes. In turn, the age structure itself largely determines future birth rate and death rate. Therefore, knowing age structure, we can reconstruct some processes that have occurred in the population in the immediate past and also predict some future changes in its population dynamics. Consequently, it is not surprising that much attention is paid to this element in population studies.

It is not easy, however, to study age structure, especially in the wild. We can use one of two basic methods, but each of them serves slightly different purposes. Studying a poorly known population, we can use morphological and anatomical indices which vary with age and do not depend much on the condition of the animal. A critical review of such indices is given by Pucek & Lowe (1975) (see also section 2). The best indices of age in the bank vole are changes in the length of the roots of M_1 (Wasilewski, 1952; Pucek & Zejda, 1968) and changes in weight of the eye lens (Lord, 1959; Adamczewska-Andrzejewska, 1971). But to collect the material for calculating these indices, it is necessary to kill animals, and this is inconsistent with *CMR* methodology. Thus the age of living animals is determined from such indices as body weight or tail