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THE BANK VOLE POPULATION IN CRABAPPLE ISLAND

ABSTRACT: The results of studies on demography of an island population of *Clethrionomys glareolus* are presented. Population numbers and structure were estimated 5 times a year in 1966–1999. Two patterns of seasonal changes in population size were found: either continuous, slow increase from April (beginning of the breeding season) to October, with maximum density below 50 individuals per hectare, or rapid increase resulting in a July/September peak with maximum density up to 153 individuals per ha. The highest variations in numbers occurred in April (Whittaker's CF=2.05) and decreased with advancement of the breeding season: in September CF=1.49. The mechanism accounting for the decrease was territoriality of mature females. Fluctuating July population numbers revealed cyclic changes, namely a 3.8-year as well as a 9.4-year cycle. It is postulated that social relations between neighboring individuals rather than mean population density affect changes in population numbers.

KEY-WORDS: reproduction, survival, population numbers, cycling, space-dependence

1. INTRODUCTION

A starting point for studies of population ecology often involves data on changes of its size. Population dynamics seem to be considered as a result of various driving forces leading, *via* negative feedback, to an equilibrium between the population size and the environmental capacity. The density-dependent processes are supposed to be the efficient means of maintaining the equilibrium.

On the other hand, however, such an approach that neglects spatial aspects of population structure as well as individual features, has not provided answers to most important questions. Some of these are "mystery of cycles", range of population fluctuation or even increase or decrease population numbers at the same density. Contrary to that Den Boer's (1968) concept of "interaction groups" opens a new vista: the interaction groups may have different histories, namely some of them increase, others decrease or even become extinct. Thus, population survival depends on recolonization of the places with extinct interaction groups rather than on maintenance of the equilibrium. This concept makes it possible to construct models of population dynamics without the acceptance of the idea of density-dependence (e.g., Bujalska and Grüm 1989). Besides, it is also close to the approach of Petrusewicz (1966), who tried to explain population dynamics by study of its structure and organization. Both Petrusewicz (1966) and Bujalska (1985a) draw attention to various importance of different categories of individuals (dominants, subordinates, males, females, mature, pregnant, immature, etc.) for changes of population numbers. At present it is often stressed that neglect of attention to individual differences results in false conclusions, and hence modelling of population dynamics should be based on recognition among individuals (Murdoch and Nisbet 1996).

All the above outlined concepts were applied to investigations on population dynamics of *Clethrionomys glareolus*. This rodent species is a particularly appropriate object of such studies because of its well-recognized biology, behavior and physiology as well as its extensive geographic distribution (Bashenina 1981, Petrusewicz 1983).

Here, I present a review of studies on bank vole demography, conducted in Crabapple Island, which were the subject of many publications incrementally improving understanding of the regularities and mechanisms that affect population fluctuations. An attempt to answer the question whether or not population numbers is a subject of regulation.

2. STUDY AREA AND SAMPLING PROCEDURE

Demography of Crabapple Island population of *Clethrionomys glareolus* has been continuously studied since 1966. The island, located in Bełdany Lake, NE Poland, is covered by a mixed deciduous forest with predominant association of *Tilio-Carpinetum*. Rich understory and shrubs as well as abundant herb layer (Photo.1) make this habitat favorable for bank voles (Pucek 1983).

Crabapple Island, 4 ha in area and 120 m distant from the mainland, makes the local bank vole population well isolated from nearby representatives of that species, though neither emigration nor immigration cannot be excluded. One can suppose that emigration from the island is more probable than immigration: a male marked in the island was caught in the mainland in late summer. During the entire study period a few unmarked bank voles, i.e. of unknown origin, were found (among several hundred marked individuals, recaptured concurrently) in April 1994, 1996 and 1997. Therefore, one can safely assume that the studied population consists of individuals born in the island. Individuals born there disappear; however, it is impossible to distinguish between the quantities dying and emigrating (Grüm 1997).

In 1982–84 and in 1988 *Microtus agrestis* and *Microtus oeconomus* appeared, and in 1983–84 also *Apodemus flavicollis* was present. Since 1994 the latter species has been continuously present at the island (Bujalska, in press, Grüm, in press, Grüm and Bujalska 2000, this volume).

The same sampling scheme was applied during the entire study period. Each year 5 series of captures were conducted in 6-week intervals, beginning with mid April and ending with the end October. A series lasted at 7 days at least, and live traps were inspected twice daily at 7 a.m. and 7 p.m. This way all individuals present during the series were caught at least once (Bujalska 1985a). Their numbers were assessed using the method of the common census that, according to Bujalska (1985a), provided estimates higher by 4.2% than those obtained with the method by Jolly (1965). Live traps formed a grid with rows and columns spaced in 15-m distance. All in-

Photo 1. *Tilio-Carpinetum* associatioin in Crabapple Island
(Photo G. Bujalska)

dividuals were marked by toe-clipping at first capture. Among males immature and mature were distinguished: abdominal *versus* scrotal testes. Females with closed vaginal orifice were considered sexually immature. Vaginal smears were taken from females with perforate vaginae, and microscopic inspection of smears provided means to distinguish between pregnant and non-pregnant voles (Bujalska 1970, 1985a).

Current year voles usually started to appear in June. They were arbitrarily divided (Gliwicz *et al.* 1968) into cohorts K_1 (June), K_2 (July), K_3 (September) and K_4 (October). Cohorts K_1 and K_2 born in the first part of the breeding season were named spring generation, and the two cohorts born in the second part of the season formed the autumn generation (Bujalska 1985a). This division is consistent with the generations distinguished by Schwarz *et al.* (1963).

The applied sampling procedure provided data on population numbers (N), numbers of mature, pregnant, and immature females as well as mature and immature males. Also age structure was estimated, for each cohort consisted of voles differing 3 weeks at most (at the first appearance of a cohort it consisted of individuals 3 to 6 weeks old).

From 1975 onward the herb layer biomass was estimated for each series of captures. This parameter was informative for the potential food abundance for bank voles (Bujalska 1985a, 1994). In 1969, 1972, 1973 and 1974 the bank vole population of Crabapple Island was a subject of field experiments (Bujalska 1985b).

3. RESULTS

3.1. PATTERNS OF POPULATION DYNAMICS

For 34 years (1966–1999) patterns of population dynamics of the bank voles inhabiting Crabapple Island have been analyzed (Fig. 1), with particular attention to the growth rate and its impact on seasonal and multi-annual changes in numbers (Bujalska 1985a, 1994). In the years 1975–1999 population numbers showed two patterns of seasonal changes:

1) continuous increase of numbers from spring till autumn, with the highest numbers in October, not exceeding 50 individuals per hectare. This pattern occurred in 6 years.

2) relatively rapid increase from spring till a peak (at most 153 individuals per hectare) in July or September (occurred in 18 years) (Fig. 2). Only once (in 1990) the peak occurred in June.

The dependence of the population numbers in June (when the current year (K_1) individuals enter the trappable fraction) on the numbers in April, that is, on the basic stock overwintered at the start of the breeding season, can be described by the regression formula: $Y = -14.9 + 3.713X - 0.0143X^2$, $R = 0.722$, $n = 22$, $p < 0.0001$ (Bujalska 1994). The rate of population growth in this period is, however, more instructive: it is lowest when the basic stock does not exceed 5 individuals per ha, and the highest at 23 basic stock individuals per ha (Fig. 3). The regression of population growth rate on the numbers of basic stock can be described by the
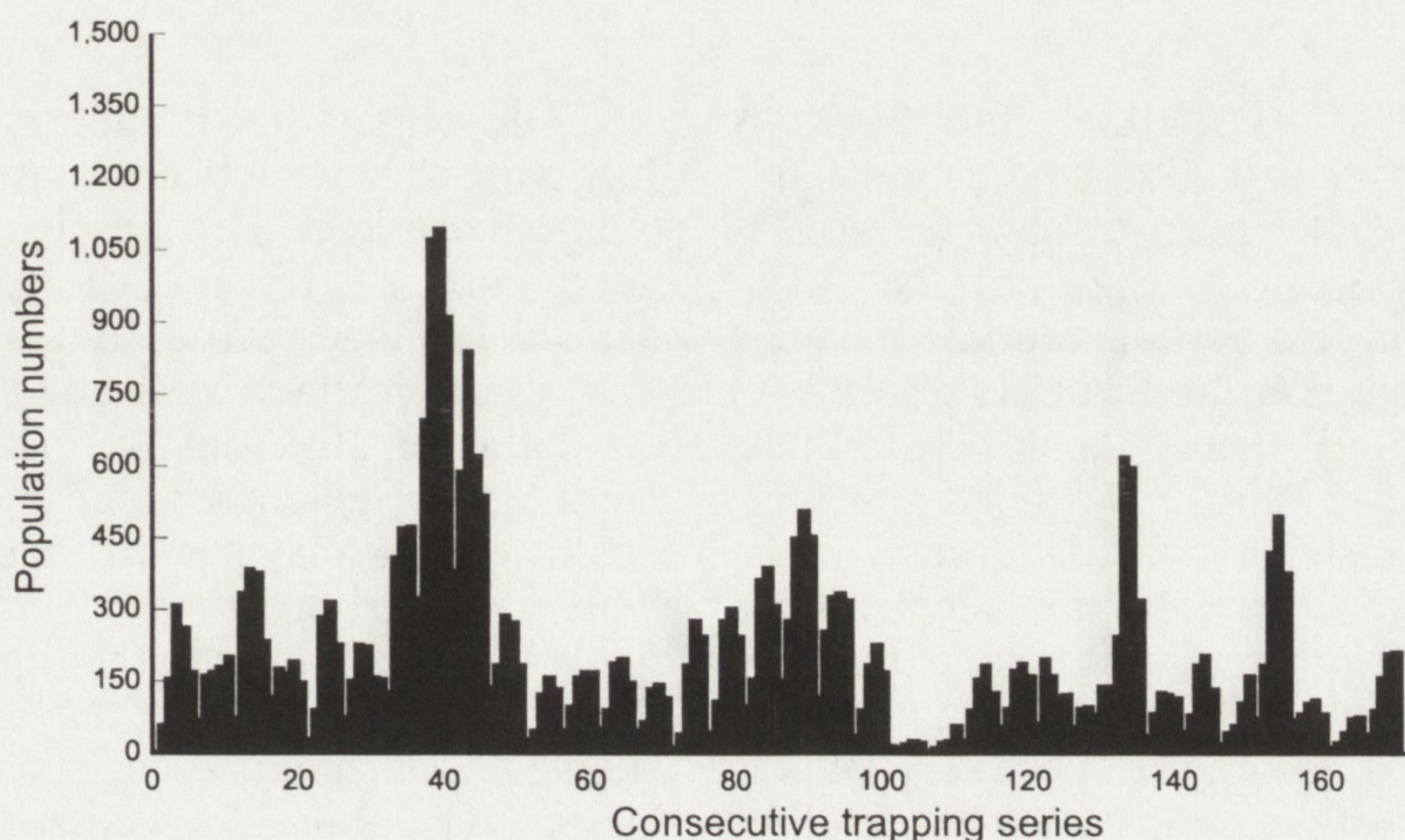

Fig. 1. Multi-annual dynamics of bank voles in Crabapple Island (5 trapping series a year in the period 1966 to 1999)
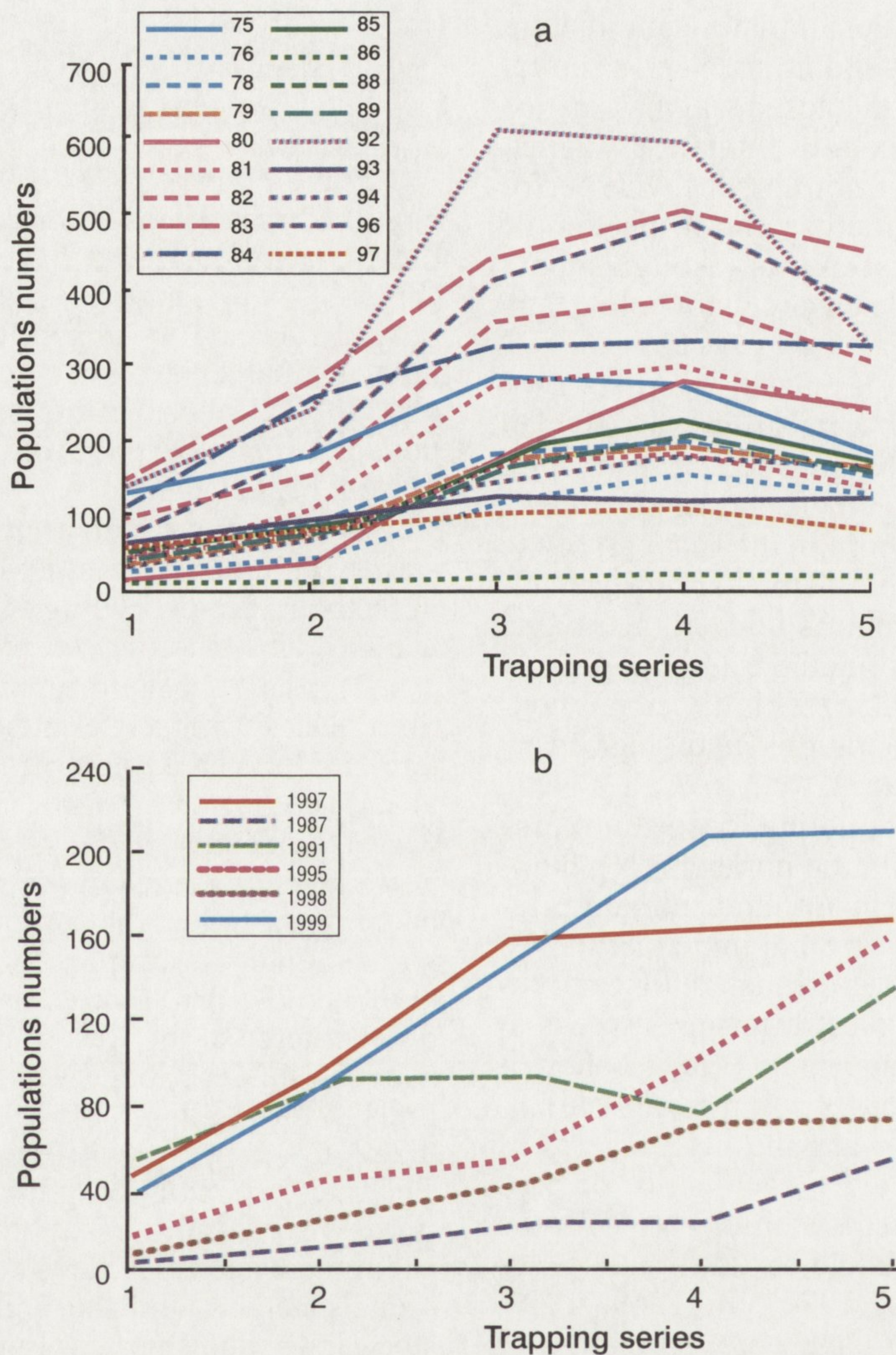
Fig. 2. Frequent patterns of seasonal dynamics (5 trapping series a year). a) years with summer peak, b) years with continuous increase

formula: $Y = 1 - [1/(0.43 + 0.00536X - 0.0000489X^2)]$, $R = 0.532$, $n = 22$, $p < 0.03$ (Bujalska 1994). This formula emphasizes "subminimal population size" of the basic stock, with numbers born not counterbalancing the numbers that die (Bujalska 1994), possibly resulting in the population extinction. On the other hand, basic stock numbers exceeding a threshold of about 23 per ha also indicate a retarded growth rate. Acceleration or inhibition of the population growth rate depend on numbers born of cohort K_1 and on the mortality rate of nestlings (Bujalska 1994). Nestling mortality depends on the mortality of their mothers (Bujalska 1985a), though it may be influenced by other factors, such as predators or diseases.

The population numbers in April and July were only weakly correlated, and no correlation between the numbers in April and September or April and October could be evidenced for that period (Bujalska 1985a). That was confirmed by the data sampled later on, that is till 1998 (unpubl.). The population numbers in September and in October were positively correlated with those in July: $r = 0.93$, $p < 0.001$ and $r = 0.71$, $p < 0.01$, respectively. This indicates that the changes in numbers in the second part of the breeding season showed substantial inertia (Bujalska 1985a). The above, as well as the features of the population growth rate from April to June leads to the conclusion that in the period June-July the fluctuations of numbers are be-
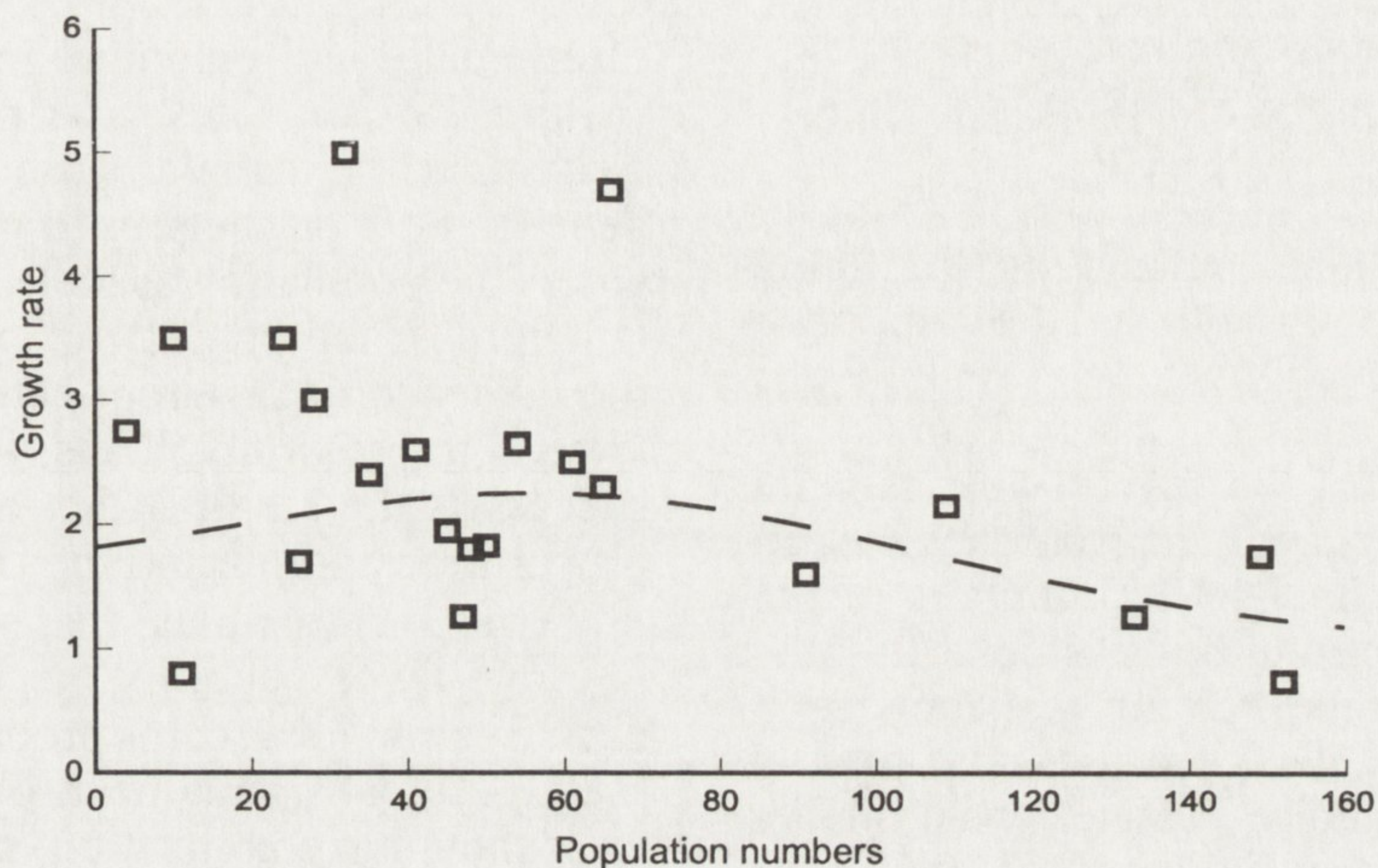
Fig. 3. Population growth rate (ratio of July to April numbers) as a function of population numbers in April (changed from Bujalska 1994). Regression formula
$Y = 1 - [1/(0.43+0.00536X-0.0000489X2)]$. $R = 0.532$, $n = 22$, $F = 3.76$, $p < 0.03$

ing damped (Bujalska 1985a). Such a conclusion is supported by the application of the CF index by Whittaker (1975): it steadily decreases in the breeding season, that is from April to September (Tab. 1) (Bujalska 1988, Bujalska and Saitoh 2000, this volume).

Table 1. Seasonal changes in fluctuations of population numbers as illustrated by Whittaker's (1975) CF after Bujalska (1988)

April	June	July	Sept.
2.05	1.84	1.53	1.49

3.2. FACTORS AFFECTING POPULATION DYNAMICS

The exclusive population process affecting the size of the basic stock, and therefore influencing the population success in the next breeding season, is winter survival. Winter breeding was noted only once during the entire study period (Bujalska 1997a). Winter survival was estimated from the difference between the population numbers in October and in April, next year. There is a significant linear correlation between the numbers of the basic stock in April and the population numbers in October previous year, calculated for the data sampled in 1966–1969 and 1974–1994: $r = 0.509$, $p < 0.004$. However, this correlation explains only 25% of the variation of the numbers in April (Bujalska 1997b).

The analysis of possible influence of winter climatic conditions (like duration of winter indicated by the number of days with snow cover, number of days with temperatures below $-10°C$, etc.) as well as food availability in early spring (indicated by standing crop of herb layer biomass in April) shows that the most significant environmental factor is the duration of snow cover. Thus, the best explanation of variability of the basic stock numbers in April is given by the formula: $Y = 77.062 + 0.192X_1 - 0.679X_2$, $R = 0.646$, $p < 0.003$, where: X_1 – population numbers in the October, X_2 – duration of snow cover in days. Addition of the 3rd factor, e.g. the herb layer biomass did not significantly increase the correlation coefficient ($R = 0.692$, $p < 0.018$) as shown by Bujalska (1997b). No differences between winter survival of sexually mature and immature females and immature males were found. The only difference found was better survival of mature than immature males (Bujalska 1997b).

The following course of seasonal changes in the population numbers of bank voles inhabiting Crabapple Island can be hence outlined: in the accord with earlier opinions (Bujalska 1985a, 1985b) the period April-July shows substantial dynamics with variable rate of changes in numbers leading to a decrease of the amplitude of multi-annual changes. On the contrary, the period July-October exhibits an inertia in the population numbers, relying on replication of the numbers in July. Also the winter period (October to April) shows some inertia in the changes of the population size.

3.3. MECHANISMS RESPONSIBLE FOR CHANGES IN POPULATION NUMBERS

The mechanism accounting for limitation of population growth and the damping of population fluctuations in July-September is territoriality of mature females. Namely, the maturation rate of the current-year females, and their subsequent reproduction, is inversely proportional to the numbers of mature females in the basic stock. In other words, more of the current year females attained maturity when the area occupied by overwintered mature females was smaller. Such a relationship indicates that the resulting population dynamics depends on space-related social structure rather than on the mean population density (Bujalska 1985a, Bujalska and Grüm 1989).

Lifetime reproductive success of females is approximately twice as high in spring generation individuals (number of pregnancies per female amounts up to 0.743) as in autumn generation females (0.368). This is a result of a lifespan usually longer in spring – than in autumn-generation females, because only very rarely (a few cases in 34 years) does a female survive 2 winters (Bujalska 1997c). On the other hand, it should be pointed out that home ranges of females being pregnant in at least 50% of the series of captures were larger (961 m² on the average) than the home ranges of females never found to be pregnant (845 m² on the average). Additionally, successful females had more mature males in the neighborhood, while the unsuccessful ones were surrounded by many mature females and immature individuals (Bujalska 1997c). Thus, it is possible to conclude that the female reproductive success depends both on the season when the female enters the population as well as on the spatial structure of the population, as expressed by the presence of different categories of individuals in proximity. Thus, female breeding success is the result of her appearance in a proper time and place (Bujalska 1997c).

One may postulate that stable reproductive rate favors stability of population numbers. Such an idea seems probable because no mass outbreaks have been observed in species showing stabilization of reproduction (Bujalska 1981, Bujalska and Saitoh 2000). Nevertheless, an increase of population numbers was coupled with increased survival rates (Bujalska 1985a) (Fig. 4), and that may have a more general relevance (Adler and Wilson 1987).

It is also necessary to consider exceptional, very rarely observed phenomena that therefore remain unexplained. For instance, in spring 1975 the earlier-introduced individuals of *Apodemus agrarius* (Andrzejewski, unpubl.) were removed from Crabapple Island. The same year the population numbers of *C. glareolus* increased by 100% from April to July (which remains within the observed range of the population growth) and concurrently there occurred exceptionally high numbers of mature females combined with higher than usual overlap of their home ranges. Bujalska and Janion (1981) interpreted this in terms of "relaxation" following the removal of the other species.
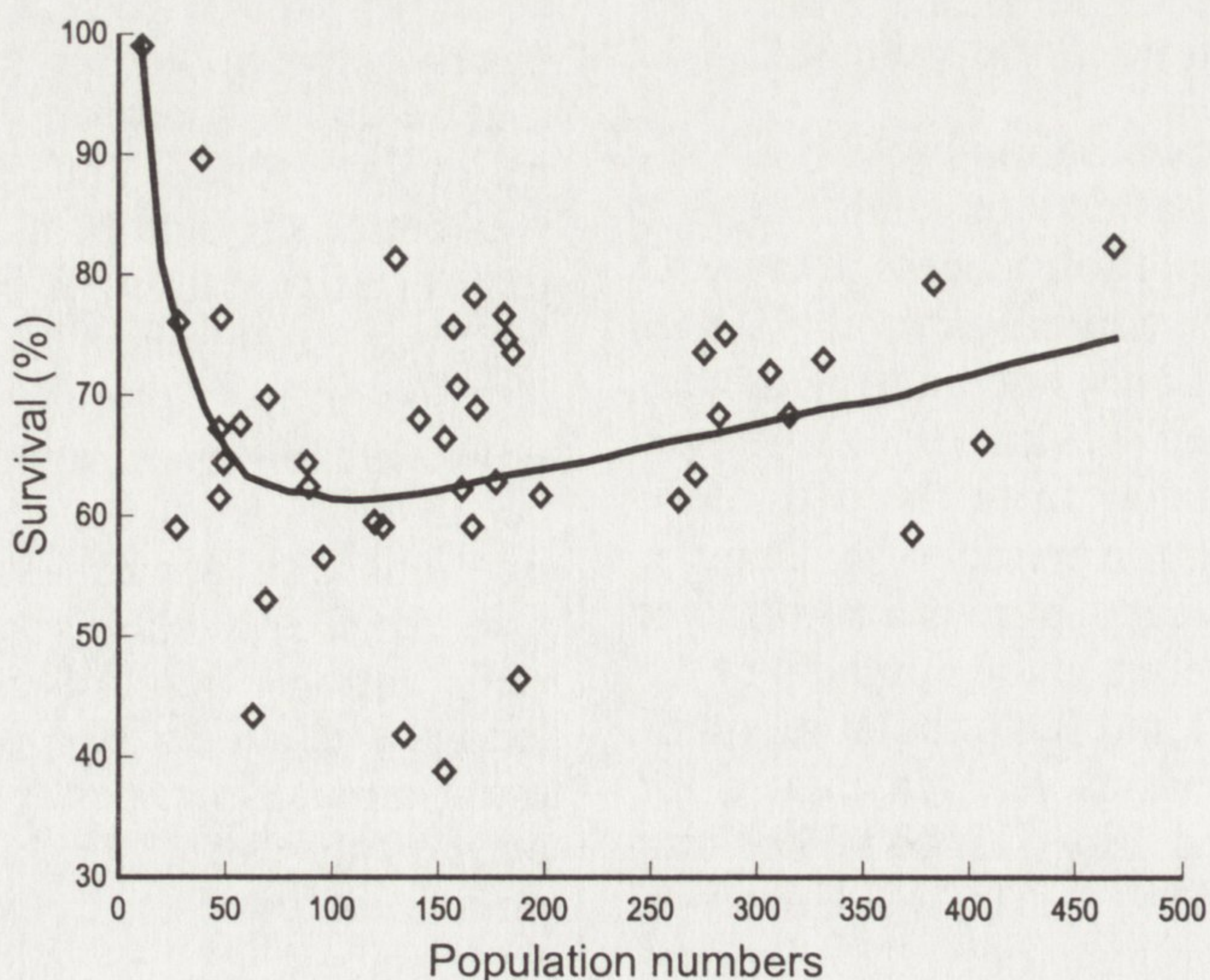

Fig. 4. Survival of trappable individuals per 6 weeks plotted against population numbers (changed from Bujalska 1985)

Another single event was winter reproduction (in 1991–1992) of bank voles in Crabapple Island (Bujalska 1997a). As a result an "additional" early spring cohort appeared (Bujalska 1997d). Concurrently the number of mature females amounted to 119 and 116 individuals in June and July 1992, respectively. This resulted in very high crowding of the mature females: on the average 3 home ranges occupied the same place. However, the spatial distribution of the home ranges showed places with many of them overlapping as well as places occupied by single mature females. Therefore, even at very high numbers mature females were able to hold their territories (Bujalska 1997d).

One can conclude from the above that two different ecological situations, i.e., removal of a potential competitor and winter reproduction, resulted in a similar response, namely increased numbers of mature females accompanied by changes in their social and spatial organization. The population numbers in the two mentioned exceptional years were high: 284 individuals in July 1975 and 613 in July 1992 (Fig. 1). These numbers can be associated with the increased numbers of pregnant voles: 30 (i.e., 39% of mature females) in June 1975, and 79 (i.e., 66% of mature females) in June 1992 (Tab. 2). The numbers of newly recruited bank voles belonging to the spring generation reflect the number of pregnant females: 274 in 1975 and 665 in 1992.

Population dynamics in 1966–1999 was shaped by "natural", though not always recognized, extrinsic and intrapopulation factors.

Table 2. Percentages of pregnant among mature females

Year	April	June	July	Sept.
1975	63	39	28	17
1976	87	64	66	19
1977	84	55	45	33
1978	91	61	48	24
1979	82	60	34	26
1980	67	88	47	27
1981	91	51	22	6
1982	61	49	26	16
1983	54	59	40	24
1984	80	49	19	25
1985	71	67	40	19
1986	–	–	–	–
1987	–	–	44	25
1988	61	50	26	17
1989	100	62	33	5
1990	94	41	27	51
1991	88	58	49	78
1992	75	66	45	8
1993	84	57	55	43
1994	95	49	61	0
1995	–	38	74	56
1996	87	58	56	7
1997	21	68	41	29
1998	–	–	48	43
1999	81	61	25	25

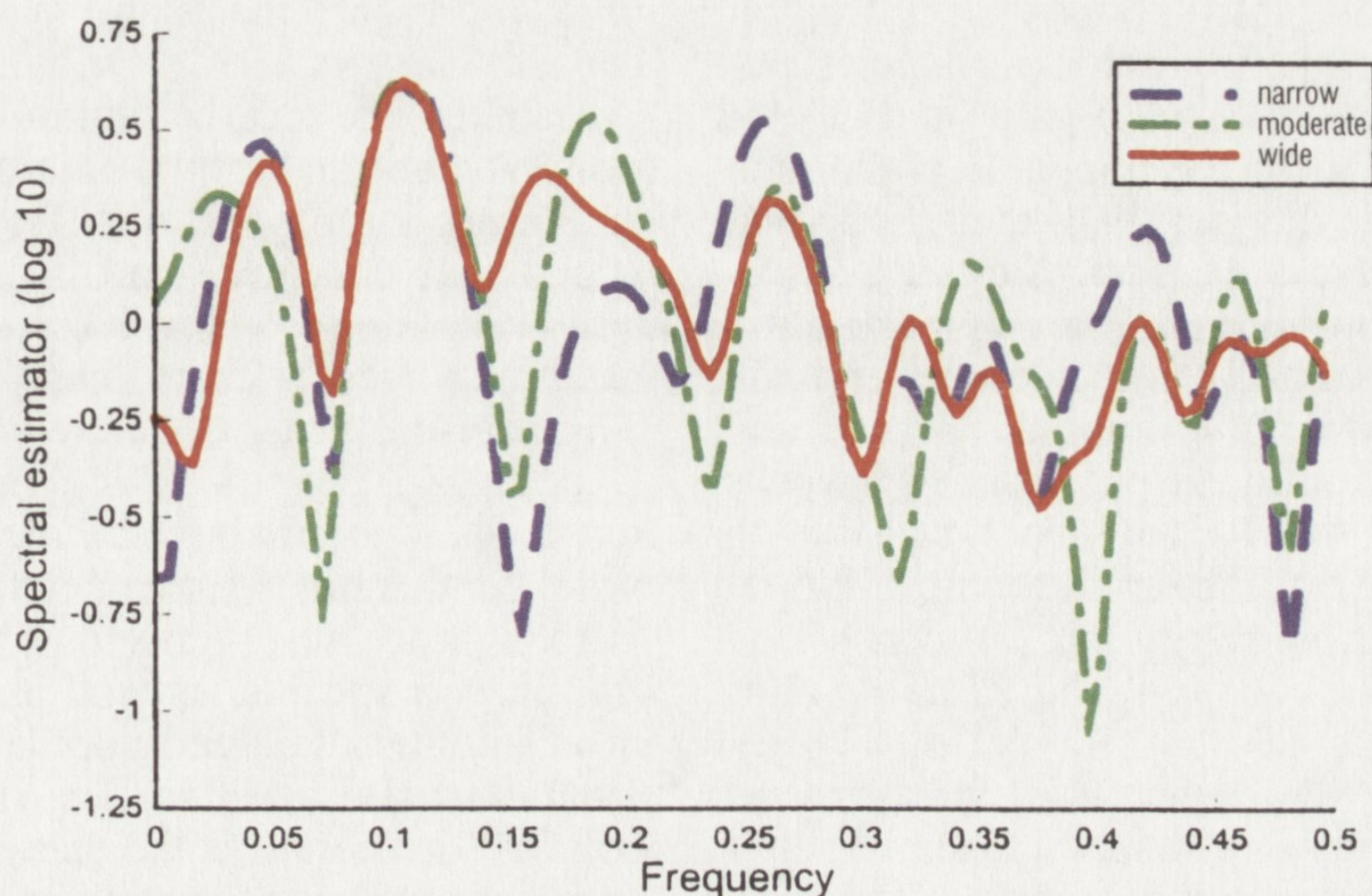– not estimated when number of mature females was less than 10.

Fig. 5. Cycles of population numbers in July

Natural regularities, exceptional events and experimental manipulation are intermingled. Are the two latter resulting in normal range of the population variation? If so, then a question arises whether or not the peaks of numbers show cyclicity? An analysis following the methods advocated by Finerty (1980) revealed a 3.8 year and also a 9.4 year cycle (on the average) in July numbers (Fig. 5).

4. DISCUSSION

The analyses presented above indicate relations between potential reproduction, expressed in terms of numbers of mature females, and population numbers. The actual reproduction, as indicated by the numbers of pregnant, is always lower than the potential one and it changes in the course of the breeding season: at the beginning of the breeding season almost all mature females are pregnant, and the proportion of the pregnant among mature females tends to decrease in the breeding season. Bujalska and Grüm (1989) proposed a model that explains the decrease as a result of increasing incompatibility in spatial distribution of mature females and mature males in the second part of the breeding season. That incompatibility may be due to the "sit and wait" strategy of immature bank voles that seemingly limits the ability of maturing males to find a place with reproductive female (Bujalska and Grüm 1994).

It is often overlooked but important for considerations about the importance of reproduction rate for the population dynamics, that the numbers of pregnant cannot be higher than those of territorial mature females (Bujalska 1985a, Bujalska and Saitoh 2000). Another demographic variable affecting population numbers is survival. Especially important for the trappable population numbers is nestling survival, that is survival in the period between parturition and recruitment (first capture). In the studied population on Crabapple Island that period depends on the frequency of the trapping series, and hence the maximum age of recriuts is 6 weeks (Bujalska 1985a). It was not possible to evaluate mortality factors in the nestling period. However, mortality rates in that period seem to be correlated with the mortality rates of the mothers (Bujalska 1975, 1985a). Nevertheless, the latter does not explain variations in nestling survival, usually better prior to a peak numbers in summer. Probably, a number of unrecognized factors is involved in the nestling survival, as indicated by large unexplained variation, i.e. low correlation coefficients with the investigated factors (Bujalska 1985a).

Reproduction rate and nestling survival rate satisfactorily explain the population numbers in the first part of the breeding season. The population numbers in the second part of the breeding season can be regarded as replicates of the numbers in July (Bujalska 1985a).

The described sequence of changes in the population numbers, resulting from relations within the distinguished categories of individuals (e.g., within females) or the relations between different categories (e.g., between mothers and their progeny), with different vulnerability to intrinsic (e.g., competition for space) and extrinsic (e.g., predation) factors, excludes interpretation in simple terms of density dependence. Moreover, the paradigm of regulation of numbers seems to be doubtful as a kind of interpretation of the population dynamics. The population dynamics remains reduced to a byproduct of reproduction limited by female territoriality and unexplained, stochastic changes in survival (Bujalska 1985a). The formal, mathematical analysis may suggest a kind of density dependence, but the actual mechanisms affecting the changes in population numbers depend rather on social relations between the neighboring individuals. If the latter is neglected then one can unsuccessfully search for a Holy Grail (Krebs 1992).

Survey of the literature on demography of rodent populations does not help to solve the dilemma whether or not the demographic processes found in island populations, as exemplified by the population of Crabapple Island, represent "the island syndrome" (Adler and Levins 1994). Or, whether they are present in the nearby "mainland" populations. According to some opinions both short- and long-term processes differ in the case of island (i.e. confined) and open populations (Gliwicz 1980). However, such opinions seemingly result from hasty conclusions. This is also the case of behavioral differences (Adler and Levins 1994). In spite of that, territoriality of mature females of the bank vole, fundamental for understanding demographic processes, seems to be typical of *Clethrionomys* species, as well as existing both in island and mainland populations (Saitoh 1981, Bujalska 1985c, Bujalska and Saitoh 2000). Therefore, the delayed maturation cannot be limited to island populations. It is a consequence of territoriality and not the out-

come of differential selection resulting from reduced dispersal, as suggested by Adler and Levins (1994). The same authors predicted increased body size in the island populations, which is opposite the changes in mean body mass found in the bank vole of Crabapple Island: Grüm *et al.* (1997) provided evidence of a progressive dwarfing of the island individuals.

Also cycling population numbers is not the exclusive property of mainland populations of bank voles. The simulation of multiannual dynamics of numbers of the island population of bank voles showed cyclic peaks every 2.6 years (Bujalska 1985a). At present, the data sampled during 34 years show a 3.8-year cycle length in the bank vole population of Crabapple Island. Both of the above figures are close to those given by Krebs and Myers (1974) for open populations: the vole cycle is often 3–4 years. Thus, it cannot be claimed that island populations always show more stable density, as seems to appear from the literature survey made by Gliwicz (1980). A generalized picture of differences between island and mainland populations cannot be based on random information, sampled from different areas and species living under different habitat conditions (both in islands and mainland). It should not resemble joining a puzzle from parts originating in different collections, as the final result may only be superficially consistent.

Surprizingly, 34-year data reveal a 9.4-year cycle that has never been reported for *C. glareolus*. There is evidence for 10-year cycles in Canadian populations of the snowshoe rabbit (*Lepus americanus*), the muskrat (*Ondatra zibethicus*) and some predators like the mink (*Mustela vison*) (Finerty 1980). Bulmer (1975) suggested that the muskrat cycle was due to predation by mink. It is a very interesting hypothesis for an attempt to recognize possible factors affecting bank vole cyclicity, because since the beginning of 80 the mink has been continuously present in Crabapple Island. It may, perhaps, mean that the mink forced also the 9-year cycle of fluctuations of the bank vole numbers. 9-year cyclity of bank voles in Novosibirsk is reported also by Moshkin *et al.* (2000).

5. CONCLUSIONS

1. To interpret changes in bank vole population numbers it is not necessary to recall the ideas of density-dependence and population regulation.

2. Interrelations between neighboring individuals competing for place to occupy and breed affect reproduction and mortality of breeding individuals. Thus, space-dependence within local breeding colonies is postulated as a mechanism affecting changes of the population numbers.

3. Cyclic fluctuations of population numbers are not the evidence for regulation. Population numbers depend on regulated reproduction rate and randomly varying mortality rate of immature individuals.

4. Hypothetic differences between mainland and island (open versus confined) populations should be verified using concurrent data sampled from populations of the same species and geographic region.

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