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Reproductive rates, survival, dispersal and cyclicity in *Clethrionomys* species: Some theoretical considerations

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The literature is surveyed with respect to proximate factors determining reproduction in *Clethrionomys*. On this basis models for predicting evolutionarily optimal rates are discussed: several ideas which have been misunderstood are restated in a more clear form. A section with technical recommendations on how various parameters entering these evolutionary models best should be estimated is included. Ideas for how the study of optimal reproduction and optimal dispersal may be intergrated are also presented. Recommendations for further work are given: these relate to both theoretical and empirical issues.

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1. Introduction

In this paper we draw together some current ideas on the evolution of demographic rates (and particularly of reproductive rates) in small rodents living in heterogeneous habitats: we emphasize the relation between optimal reproductive rates and population dynamics. Hence, this paper is the theoretical counterpart to the paper by Hansson & Henttonen (1985) (and also Henttonen & Hansson 1985).

To understand why particular demographic schedules (or rates) evolve is important in order to deduce precise testable predictions (or hypotheses). However, in addition to these evolutionary "why-questions" (*sensu* Mayr 1961), the "how-questions" (*sensu* Mayr 1961) are equally important for improving our understanding of the demography of stable and cyclic small rodent populations. Hence, we first review how reproductive rates are determined by physiological and ecological factors. On this basis we review models for the evolution of reproductive rates (i.e., the "why-questions"). Throughout we offer some pedagogical notes on how to relate population data to the theoretical predictions discussed in this paper.

As we are primarily concerned with populations living in patchy, or heterogeneous, habitats, we also discuss how dispersal and demography — in an evolutionary sense — may be related to each other. Unfortunately, we are unable to provide any detailed predictions regarding how — again, in an evolutionary sense — demography, dispersal and cyclicity are expected to be related. However, we hope that our discussion might suggest possible ways of approaching this issue.

We end the paper by listing what needs to be done in order to obtain a better understanding of the evolution of reproductive strategies in *Clethrionomys* species.

2. Reproductive rates

2.1. The patterns

2.1.1. *Preamble - some definitions and advice regarding the description of the ecological patterns*

Consider a *cohort* of animals (i.e., a group of individuals born at approximately the same time) from birth at time 0 (on a relative time scale) to some physiological maximum age w. Let l_x be the survivorship function at age x; i.e., the proportion of the cohort that survives from birth to age x (usually we only consider the female part of the population). The survival, s_x, from an age x to $x + \Delta x$ then becomes $s_x = l_{x+\Delta x}/l_x$. Let further m_x be the fecundity of individuals of age x measured as the number of female offspring produced by individual females of age x. These demographic schedules or functions (l_x and m_x) are, in general, functions of density, i.e., $l_x(N)$ and $m_x(N)$ where N is the density of the population under consideration. However, if the survivorship function (of age) and the fecundity function (of age) do not change through time, then the population will (after relatively few generations; see, e.g., Lotka 1925, Pielou 1969, Collier et al. 1973) grow at an exponential rate r, and attain a stable age structure characteristic for the value of r and the l_x- and m_x-functions (for a formal proof of this, see Pielou (1969) and Williamson (1972)); notice that r may be equal to zero in which case we have a stable population. Then, given *approximate* density independence of the l_x- and m_x-functions (an assumption which only is of particular importance for species — or populations — exhibiting greatly varying densities; see below), we may write (see, e.g., Christiansen & Fenchel 1977: 30)

$$\sum_{x=0}^{w} l_x m_x e^{-rx} = 1; \qquad (1)$$

this is Lotka's (1907a,b) famous equation for the birth-pulse situation (see Caughley 1977). Knowing the l_x- and m_x-functions, we may find r by solving Eq. (1) numerically, and write

$$\mathrm{d}N/\mathrm{d}t = rN. \qquad (2)$$

By a step-wise approximation to the actual population growth curve, we may solve (1) for r under various densities; hence, we may obtain $r = r(N)$ on the basis of empirical data. Alternatively, but less appropriately, $r = r(N)$ may be obtained by a similar step-wise estimation procedure based on Eq. (2) directly.

How then should w, l_x and m_x be estimated on the basis of data? The physiological maximal age, w, should be estimated from laboratory observation; however, this quantity is of little or no importance in the present context since, under most (or all) natural conditions, m_x is likely to become approximately equal to zero (and for all practical purposes identical to zero) long before the age w is reached.

As pointed out by, for example, Southwood (1978: 356) there are two conceptually different ways of constructing an l_x—m_x-table (or what we call a life-table or demographic schedule) which theoretically should give the same result but in practice often does not.

The age-specific (or horizontal) life table is based on the fate of a *real* cohort. In this case, the population may either be stationary or fluctuating.

The time-specific (or vertical) life table is based on the fate of an *imaginary* cohort found by determining the current age-structure of a sample of individuals from what is assumed to be a stationary population with overlapping generations (either one with *constant density* or one growing at a *constant specific rate*).

Since most — or all — *Clethrionomys* populations hardly can be assumed to have a stable age distribution, and since we only rarely are able to determine individuals' age precisely and accurately in a statistical sense (see, e.g., Hansson 1983), the *age-specific life table* is generally more applicable than the *time-specific life table* in our case. Hence, we recommend the application of the former in studies on microtine rodents; see Caughley (1977) and Southwood (1978) for valuable technical recommendations.

Obviously, any life table obtained on the basis of data on organisms living in a seasonal environment must necessarily be seasonal-specific; valuable technical recommendations for how to handle such effects are given by Caughley (1977: 98–99). Below, we will mainly refer to the main breeding season during summer, even though we briefly review data on winter reproduction in *Clethrionomys* species. Only the reproductively active females (i.e., the territory holders; see, e.g., Bujalska 1985) should be referred to when defining m_x. Thus defined, this quantity incorporates the frequency of litter productions by an average territorial female. The frequency of litter productions therefore directly influences the population growth rate since there is an absolute limit to the number of breeders; hence, it is an important quantity to study by itself. Following Davis & Golley (1963: 214) and Caughley (1977: 78–79), the mean number of litters produced per female over the main reproductive season may be estimated in two steps: the first step requires an estimate of the mean prevalence of pregnancy, $\bar{P}$, over the reproductive season. The prevalence of pregnancy

— or the proportion of females pregnant at any particular time (incorporating both the proportion of territory holders and the frequency of litter productions of those females) — is estimated on the basis of samples taken on several occasions during the reproductive period. These estimates are then averaged to give the value, $\bar{P}$; according to Caughley (1977) this ought to be an unweighted mean.

The second step in the estimation of the mean number of litters produced requires an estimate of the duration of pregnancy. Let $\bar{D}$ be the mean duration of visible pregnancy relative to the length of the main breeding season. From this, the incidence of pregnancy, I, or the number of times an average female (in the total population) produces a litter *during the reproductive season*, may be found as

$$I = \bar{P}/\bar{D} \tag{3}$$

(see, e.g., Caughley 1977). As pointed out by Caughley (1977), it may easily be seen that overestimating the *length* of the main breeding season does not affect the accuracy of I as long as samples for estimating $\bar{P}$ are taken over the same time interval.

2.1.2. *Maturation*

Clethrionomys females seem to be able to reach sexual maturity, and to be successfully inseminated, at an age of 25-30 days (Gustafsson et al. (1983) for *C. glareolus*; Martell & Fuller (1979) for *C. rutilus*). However, such rapid maturation does not occur in all females. The proportion varies with time of the year and is maximal for animals born in spring and early summer and at low population densities.

It is further known that young females do not reach maximal fertility immediately after becoming physiologically capable of mating: Westlin & Gustafsson (1984) report that only 20 per cent of 30-40 days old female *C. glareolus*, being mated for the first time, were fertile. Fertility increases, however, with age (Westlin & Gustafsson 1985) and with sexual experience (Westlin & Gustafsson 1983). Field data (Westling & Nyholm 1982) suggest that most females had mated 1-3 times before becoming pregnant. It is not known whether the frequency of sterile matings is related to population density or other aspects of the population dynamics: Ims (1985) reported sterile matings in *C. rutilus* and *C. rufocanus* for both a peak and a non-peak year. However, Wallgren et al. (1983) report that sterile matings only occurred during peak years in *C. rutilus*. On the other hand, sterile matings were observed to occur at similar frequencies in all years in a cyclic population of *C. glareolus* (Gustafsson, unpubl. data).

Several *Clethrionomys* populations show evidence of a strong density-dependent suppression of sexual maturation (e.g, Bujalska 1985). For example, an almost complete blockage of maturation at high densities has been reported for *C. rutilus* in the USSR (Koshkina & Korotkov 1975), for *C. rufocanus* in Finland (Kalela 1957) and for *C. glareolus* in Northern Sweden (Gustafsson 1983a). Furthermore, Martell & Fuller (1979) — working in the Canadian taiga — report an almost complete inhibition of maturation of male *C. rutilus* at low densities; they observed much less — or no — inhibition of sexual maturation at high densities.

At lower densities, most young in the early-born cohorts reach sexual maturity; density dependence in the rate of sexual maturation is only seen in the cohorts born during and after mid-summer (see, e.g., Fuller (1979) working on *C. gapperi*). In *C. glareolus* in western Europe, including Denmark and South Sweden, this pattern seems to be the typical one for most years independent of density (Gustafsson 1983a). Despite much higher population density, a similar pattern was observed in the Polish island population described by Bujalska (1973, 1985). The suppression of maturation seen in late born cohorts in all these *Clethrionomys* populations thus probably results from a combination of social factors and food quality and quantity. In *C. glareolus*, Bujalska (1973) found, by removing early cohort females, an increase in the number of maturating late cohort females. In the same population, adding food resulted in intensive winter reproduction, rapid maturation of winter-born individuals, and very high population densities (Andrzejewski 1975). Similarly, Jensen (1982) and Gustafsson (1983a) associated winter breeding and maturation of winter-born individuals with good food supply in the form of a good crop of beech nuts.

Sexual maturation of *Clethrionomys* species may also be affected by co-existing species. Viitala (1984), for example, reports that C.

Table 1. Breeding season in four *Clethrionomys* species. Approximate period for which pregnant females are found in the population. Phase of cycle: i = increase, p = peak.

Species and location		Breeding period (days)	Source
C. gapperi			
Canada	61N 117W	103–105	Fuller 1969
Canada	61N 117W	103–128	Mihok 1979
Canada	49N 85W	>102	Martell 1983
Canada	50N 97W	~160	Perrin 1979
USA	39N 106W	220*	Merritt & Merritt 1979
C. rutilus			
Canada	61N 117W	104(+)–110(+)	Fuller 1969
Canada taiga	68N 133W	108–133	Martell & Fuller 1979
Soviet	54N 88E	90–135	Koshkina & Korotkov 1975
C. rufocanus			
Finland	69N 21E	90–150	Kalela 1957
C. glareolus			
Sweden	66N 16E	147 i	Stenseth et al. 1985
Sweden	66N 16E	100 p	
Sweden	64N 15E	147 i	
Sweden	64N 15E	< 94 p	
Sweden	60N 17E	<150 i/p	
Sweden	56N 13E	169	
Norway	59N 8E	147–175	Wiger 1979
Poland island	~54N 22E	180–200	Bujalska 1973
Wales Skomer Island	52N 5W	110	Coutts & Rowland 1969

* "signs of breeding" during this period (Merritt & Merritt 1979)

Table 2. Data form Koshkina & Korotkov (1975) and Gustafsson (1983a) on litter size of over-wintered females. Numbers in parentheses represent number of females on which estimate is based.

Species	Density	May	June	July	August
C. rutilus[1]	low	7.3 (33)	7.5 (190)	6.5 (112)	6.0 (9)
	high	8.2 (166)	7.2 (265)	6.1 (157)	
C. glareolus[2]	low	5.7 (15)	6.0 (7)	7.3 (6)	
	peak	6.5 (34)	6.4 (20)	5.8 (85)	

1) stable population
2) cyclic population

rutilus in northern Finland produced fewer litters in years of intense competition from *C. rufocanus* and *Microtus agrestis*. In northern Norway, maturation of *C. rutilus* was suppressed in a year with high density of *C. rufocanus*, despite the fact that density of *C. rutilus* was low (Ims 1985).

2.1.3. *Length of main breeding season*

The lengths of the main breeding season (i.e., the summer breeding season) for various *Clethrionomys* species are given in Table 1. Many authors (see review by Bujalska 1985) report a shortened main reproductive period during high density years.

2.1.4. *Litter size*

Time of the year

In all laboratory studies on microtines, litter size is larger in multiparous females than in primiparous ones (see, e.g., Gustafsson et al. 1980, 1983b). Thus, we would expect, all other factors remaining unchanged, litter size to be lower in spring than later in the main breeding season.

The patterns seen in natural populations are, however, much more variable. Some authors (e.g., Martell & Fuller (1979) for a taiga population of *C. rutilus*; and Martell (1983) for *C. gapperi*) reported larger 2nd than 1st litters, while others (e.g., Zejda (1967) for *C. glareolus*; and Stenseth et al. (1985) for cyclic and non-cyclic populations of *C. glareolus*) reported maximum litters in spring. The observed differences may partly be explained as a result of differences in densities of the various populations being studied (see, e.g., Table 2; Koshkina & Korotkov 1975, Gustafsson 1983a). These variations in litter sizes may, further, be due to the opposing effects of increasing parity and deteriorating food supply, possibly with social factors influencing litter size as well.

Food supply

There are no quantitative laboratory data on reproduction and food. Supplementary feeding is, however, known to result in more intensive winter breeding (see below), and a larger fraction of females being in breeding condition (Andrzejewski 1975, Jensen 1982), but it is not known how and whether intervals between litters, litter size or proportion of adult females participating in breeding are affected. See Gustafsson & Batzli (1985) who, on the basis of a laboratory study where semi-natural food was used, could not find any effect of food on reproduction.

Photoperiodicity

Clethrionomys species are found to respond to photoperiod by maturating more rapidly during long than during short day-lengths (Tähkä 1978). However, reports on winter reproduction (see Section 2.1.6) indicate that this effect is easily suppressed by a good food supply. It may be that *Clethrionomys* use a long photoperiod to "decide" when it is time to start maturating in spring when food is scarce, but that they use food and density cues at other times. Obviously, much more work is needed on this issue.

Density

Litter size is strongly influenced by body size (Kalela 1957: *C. rufocanus;* Zejda 1966, Gustafsson 1983a: *C. glareolus*). However, when litter size is corrected for body size, maximal litter size in *C. glareolus* was observed in pre-peak years, while there was essentially no difference between peak and low density years (Gustafsson 1983a: pre-peak year, 7.2 (42); peak year 6.1 (78); and low year 6.0 (15)). Again, it is not known whether these differences could be related to differences in food supply or in social factors.

Density variations

Hansson & Henttonen (1985) (see also Henttonen & Hansson 1985) have provided a thorough review of this issue. See also discussion of the theoretical aspects below.

Age

For captive individuals of *C. glareolus*, age does not seem to influence litter size (except by influencing it through change in body size (Gustafsson et al. 1980)). For natural populations, some workers (e.g., Kalela 1957, Koshkina & Korotkov 1975) report larger litters in overwintered females than in young of the year, while others (e.g., Gustafsson 1983a) do not. Rather than being a simple effect of age, it seems, however, most likely that these differences may be explained as a result of differences in body weight distribution of the cohorts in various populations, and by the fact that young of the year have their litters later in the season than the overwintered individuals.

Effects of exposure to strangers

Gustafsson (1985) discusses in detail the available data on this issue. There are possibly two mechanisms for regulating sexual maturation of *Clethrionomys* (Gustafsson unpubl. data):

1) Females need an exclusive home range (or territory) in order to maturate; and

2) maturation is suppressed by contact with unknown animals, either by their own dispersal, or by meeting other dispersing animals.

Pattern 1) seems to apply to female *C. glareolus* in Poland (Bujalska 1973) and Finland (Viitala, pers. comm.), to female *C. gapperi* in Canada (Bondrup-Nielsen 1985), to female *C. rufocanus* in Japan (Saitoh 1983), and to male *C. glareolus* in North Sweden (Gustafsson et al. 1983b) and Finland (Viitala 1977). South Swedish *C. glareolus* on the other hand, do not seem to need an exclusive home range (Gustafsson et al. 1983a) in order to breed; however, the South Swedish *C. glareolus* are sensitive to contacts with unknown (i.e., dispersing) individuals (Gustafsson 1983b).

2.1.5. *Frequency of births*

Most workers seem to agree that postpartum estrus is common (see review by Hasler 1975). Some, possibly all, *Clethrionomys* species have delayed implantation when lactating (e.g., Andersson & Gustafsson 1979); this would result in some 20–30 days between litters. On the other hand, Martell & Fuller (1979) reported approximately 40–50 days between mean dates of birth of the first and second litter of the season. However, they do not seem to have considered the possibility of three or more litters being produced in a season; then, if their second litters in fact are the second and third litters, a 20-30 days interval between litters result.

Koshkina & Korotkov (1975) reported that 2.5-3 litters were, on average, produced per overwintered female per year; they apparently found no relation between the frequency of litter production and population density.

These conclusions may, however, have to be revised when more reliable data on frequency of birth become available. In the future, we recommend that data on frequency of litters be reported as incidence of pregnancy, I (as defined by Eq. (3) in Sect. 2.1.1.).

2.1.6. *Winter reproduction*

Winter reproduction in response to good autumn food supplies seems to be common for *C. glareolus* in western and central Europe (Jensen 1982). In areas with a thick snow cover, the occurrence of winter reproduction is, however, insufficiently studied, but occasional cases of winter reproduction in northern Sweden are reported by Larsson et al. (1973) for *C. glareolus* and *C. rufocanus*, and by Gustafsson (1983a) for *C. glareolus*. Gustafsson (1983a) found, however, that winter reproduction was quantitatively much less important in a cyclic North Swedish population of *C. glareolus* than in a non-cyclic South Swedish one. In a subalpine forest in Colorado, USA, *C. gapperi* usually starts breeding long before the seasonal snow-melt (Merritt & Merritt 1979).

2.2. The evolution of reproduction rate

2.2.1. *Demography in stable and cyclic populations - the overall pattern*

Ugland & Stenseth (1985) expressed r, given in (2), as

$$r(N) = r_c(N) + r_e(N) \tag{4}$$

where $r_c(N)$ is the density-dependent component which may be modified through selection, and $r_e(N)$ is the density-dependent component which cannot be modified in this way; it follows that $r_e(N)$ must be a nonselective mortality factor (see Stenseth 1978). Then, with reference to model (4) (and hence model (2)), a possible way of representing opportunistic population dynamics (see, e.g., Southwood 1977, Pianka 1978) is given in Fig. 1A; the comparable equilibrium population dynamics (see, e.g., Southwood 1977, Pianka 1978) are given in Fig. 1B.

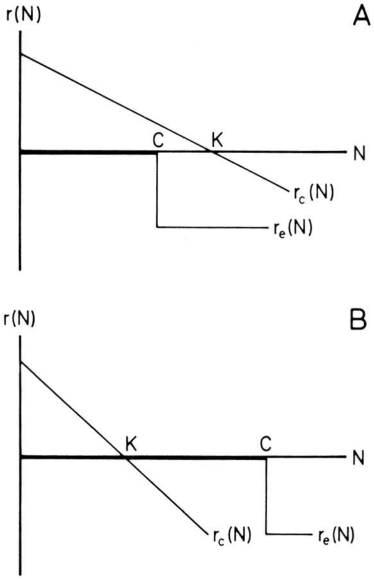

Fig. 1. The two components of the realized net population growth rate, $r(N)$, as defined by Eq. (4); $r_c(N)$ is the density-dependent component which may be modified through evolution by natural selection and $r_e(N)$ is the density-dependent component which cannot be modified through evolution. $r_c(N)$ is then the function commonly discussed by evolutionary arguments as, for example, the *r-K* selection theory (see, e.g., Pianka 1978). — A depicts a situation for which cyclic population dynamics result. B depicts a situation for which stable population dynamics result. — See main text and Ugland & Stenseth (1985) for further discussion and interpretation. (Modified from Ugland & Stenseth (1985)).

Two parameters, in addition to the slope of the r_c-function, are important in this argument; these are the equilibrium density K, determined by intrinsic factors of the population, and the critical density level, C, above which extrinsic (and random) factors play an important role in the model. These correspond, we believe, to what Lidicker (1978) calls "equilibrium density" and "limiting density", respectively.

Obviously, the critical aspect of our view depicted in Fig. 1 is the form of the r_e-

function; i.e., a critical point is the existence of a $C<K$ so that extrinsic factors are only of importance above the density C. There is some support for this view: For example, mammalogists studying the microtine density cycle have found that in one crash, disease may be the most important factor; in another crash of the same population, the responsible factor may be malnutrition; in a third, it may be due to vertebrate predators; in a fourth, it may be due to adverse environmental conditions, and so on (e.g., Krebs & Myers 1974, Krebs 1978). Similar conditions led Errington (1946) to propose the concept of compensatory mortality. Obviously, in such cases, it is impossible to improve evolutionarily so as to resist any of the many factors that may cause the crash.

The mystery is, however, why such a compensatory system of mortality factors exists and why it is operative only on or above a certain density-level, C. However, this is not the issue under discussion in this paper. In the present context it suffices to know that models (2) and (4) and Fig. 1 give appropriate descriptions of the population dynamics of the cyclic population under study. Then, we may ask: "Given a particular consistent pattern of density fluctuation, what reproductive rates will be favoured by natural selection?". In summary then, population ecologists trying to explain the occurrence of the density cycle (and also why so many populations are stable) are primarily concerned with understanding the r_e-function. Evolutionary biologists, on the other hand, trying to understand *why* populations are like they are, will primarily be concerned with the r_c-function. In this paper, we are primarily concerned with the evolutionary questions; hence, we treat the r_e-function as one with fixed parameter values.

Assuming a fairly slow increase and a rapid crash (e.g., Stenseth 1978: fig. 4), the analysis performed by Ugland & Stenseth (1985) demonstrates that the expected value of r — as found by solving (1) numerically — is predicted to be positively correlated with the coefficient of variation in density, CV, defined as

$$CV = [\mathrm{var}(N)]^{1/2}/\mathrm{E}(N) \qquad (5)$$

where var(N) is the variance in density from one year to another and E(N) is the average density at that time of the year over all studied years. Furthermore, this r is predicted to be positively correlated with the index proposed by Williamson (1972) and Stenseth (1977a) and defined as

$$SD(\log(N)) = [\mathrm{var}(\log(N))]^{1/2} \qquad (6)$$

where "log" is the logarithm with base 10.

Notice that the demographic (or reproductive) rate to be compared with the density variation indices is r as defined implicitly by Eq. (1); unfortunately this has not been stated precisely enough in earlier writings.

In order to test these predictions, we would need detailed data on the l_x m_x schedules of *several* populations of the same species with different population dynamic patterns, but under otherwise similar conditions. Data pertaining to this issue derived from the literature on small rodents are summarized by Ugland & Stenseth (1985). Unfortunately, such data are, as far as we know, not available for any *Clethrionomys* species.

2.2.2. *Reproduction in stable and cyclic populations*

The optimal reproductive rate in small rodent populations has been discussed by, for example, Stenseth (1978) and Stenseth et al. (1985) on the basis of Fisher's (1930), Williams' (1960), and Pianka & Parker's (1975) more general analyses. From this theory a positive correlation between current average reproductive rate, R, defined by $R=\sum_x m_x$ (or $\bar{m}_x$), and the degree of density variation is expected. Notice that the predicted causation is that given a population increasing in density most of the time (but with non-selective density crashes from time to time; see Sect. 2.2.1. and Stenseth 1978: fig. 4), there will be selection for increased reproductive output "here-and-now", i.e., increased R. Essentially, these predictions derive from a generalized ESS-argument (see, e.g., Lawlor & Maynard Smith 1976, Reed & Stenseth 1984). In a specific environment with a given CV (see Eq. (5)), we ask what characterizes the reproductive strategy which cannot be invaded by any mutant strategy; this strategy is defined as the optimal one and is the one assumed to be favoured by natural selection. That is, we ask which optimal reproductive strategy is such that it "matches" the particular CV being determined by the particular dynamics of the population.

Stenseth (1978, 1980) gives a full account of the predictions derived from this theory. The most important one is:

$$\text{increased } CV \rightarrow \text{increased } R^* \tag{7}$$

where R^* is the ESS-value corresponding to either an average rate, or a rate specified for a particular age. This prediction (7) may also be derived from Lomnicki's (1980: sect. 5) model: he found the ESS-reproductive rate, R^*, to be

$$R^* = 1 + E/k \tag{8}$$

where k is a coefficient expressing the cost of increasing litter size (relating to fitness sets (see Levins 1968) as, for example, derived by Stenseth et al. (1980) and discussed by Stenseth & Framstad (1980: fig. 4); a large k implies a convex fitness set, whereas a small k implies a concave fitness set). Furthermore, E is the probability of extinction for a local population; this quantity then relates to the r_e-function of Section 2.2.1. The probability E relates positively to the degree of density variation, CV (see Stenseth 1977b: 547-548): particularly at low density levels E may be high (see MacArthur & Wilson 1967: fig. 27). Furthermore, it is reasonable to assume that E decreases as the environment becomes structurally more complex (see arguments in Stenseth 1979: sect. 4.2; and in Stenseth 1980: sect. 3). On the basis of Eq. (8) it can then be seen that R^* will increase with increasing E independent of the value of k, i.e., presumably independent of the form of the fitness set. For further discussion, see Stenseth (1980).

Notice, as pointed out by Stenseth et al. (1985), that a positive relation between R^* and CV is only expected if everything else is the same in the populations being compared. However, in general both food supply *as well as* environmental uncertainties (or population dynamics as measured by CV) vary from one place to another. However, from arguments in Stenseth et al. (1985) it follows that we expect litter size to increase with food supply and that cyclicity will *enhance* this difference.

To test these predictions we would need data on the plateau-value of the m_x-curves, or the R-value as defined above together with data on density variation. Such information is needed for several populations, preferably of the same species, and in any case under otherwise identical — or almost identical — conditions. Such analyses were performed for *C. rutilus* by Stenseth & Framstad (1980); the validity and generality of their results were later questioned by Henttonen & Hansson (1985). See Hansson & Henttonen (1985) for a summary of additional data pertaining to these predictions; notice, however, that conditions are *not* similar for the populations being compared by Stenseth & Framstad (1980) and by Henttonen & Hansson (1985); in fact, Henttonen & Hansson (1985) and Hansson & Henttonen (1985) discuss this very issue.

Small rodents — and in particular *Clethrionomys* — are well suited for testing these predictions. Hence, it is encouraging to observe that available data in fact are analyzed with these predictions in mind.

2.2.3. *Age-specific reproductive schedules in stable and cyclic populations*

The optimal age-specific reproductive rates have been analyzed by Stenseth & Framstad (1980) and Stenseth & Ugland (1985). A variety of patterns may emerge (see Stenseth & Ugland 1985). However, for small rodents it seems that with increasing CV, maturation should always occur at a progressively earlier age, and the age-specific increase in m_x should be faster (see Fig. 2): unfortunately, there has been some confusion over this prediction in the literature — we hope that Fig. 2 and the accompanying figure legend will prevent further confusion.

Stenseth & Ugland (1985) also found that the l_x-curve always is expected to be more of a Type I curve for the equilibrium population, whereas it is expected to be more of a Type III curve for the opportunistic population. These patterns are found to emerge from the theory regardless of the specific forms of the fitness set functions being assumed. That is, the average length of life is expected to be shorter in more unstable populations. But again, it is important to remember that the presumption "under otherwise similar conditions" must hold, at least approximately.

Using data on *C. rutilus*, Stenseth & Framstad (1980: figs. 6 and 7, and table 1) found support for the derived prediction; again the validity and generality of this pattern were questioned by Henttonen & Hansson (1985). See Hansson & Henttonen (1985) for a summary discussion.

Again it should be pointed out that small

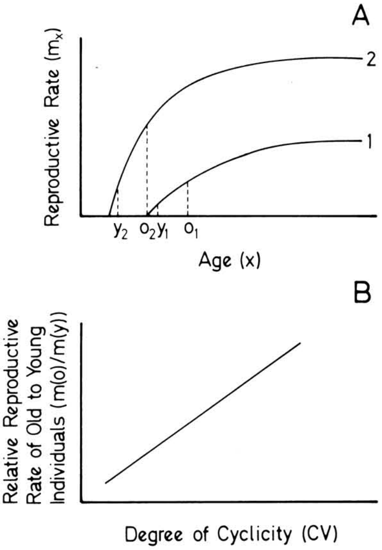

Fig. 2. In A, predicted m_x-schedules for a stable (curve 1) and a highly cyclic (curve 2) population; predictions are derived on the basis of the model developed and analyzed by Stenseth & Ugland (1985). On the basis of these curves, the expected relation between $m(o)/m(y)$ and the degree of cyclicity, *CV*, where $m(o)$ is the reproductive rate of older individuals and $m(y)$ is that of younger individuals: this relation is depicted in B. Notice, however, that "older" and "younger" is relative to the age of maturation; see A. — See main text and literature referred to there for further discussion.

rodents, and particularly *Clethrionomys*, are highly suited for testing these predictions (e.g., Bujalska 1985, Viitala & Hoffmeyer 1985). Laboratory — or field — studies for estimating the l_x-schedule should, of course, also be carried out in order to test these predictions; see in this respect the study of Morrison et al. (1977).

The topic of optimal life history models should not be left without referring to the general models discussed by Maynard Smith (1982: ch. 11): these models might — if reanalyzed in the light of cyclic/stable population dynamics — provide refined predictions. Much work remains to be done in this field.

3. Reproduction and dispersal

In 1977, S. Iwao wrote:

> Spatial pattern, the way in which individuals of a given species are distributed in habitat space, is an important aspect of population structure, and is determined jointly by the intrinsic properties of species concerned and the habitat conditions under which it lives.

		TIME	
		NOW	LATER
SPACE	HERE	$S\cdot(1-D)\cdot(r_1 \pm V_1)$	$S\cdot(1-D)\cdot(r_2 \pm V_2)$
	ELSEWHERE	$S\cdot D\cdot p\cdot(r_3 \pm V_3)$	$S\cdot D\cdot p\cdot(r_4 \pm V_4)$

Fig. 3. The habitat templet as defined by Southwood (1977) constituting the basis for analysis of the joint evolution of optimal reproductive and optimal dispersal rates. See main text for further discussion. (Modified from Southwood (1977)).

The same year, T. R. E. Southwood wrote:

> In the course of evolution the members of a species will evolve those strategies that maximize the number of their descendants in their habitat which must be viewed from the two dimensions emphasized by several ecologists ... Briefly, the choice open to any organism with respect to its breeding may be expressed in a two by two matrix with "now" and "later" on the time axis and "here" and "elsewhere" on the space axis.

Reproduction and dispersal are obviously closely related. Most commonly reproductive strategies and dispersal strategies are treated as two separate fields of study (but see Bondrup-Nielsen 1985). However, as argued by both Iwao (1977) and Southwood (1977), they *are* not. Further, dispersal may also proximally influence the reproduction performance of resident individuals (see Sect. 2.1.4.).

For summary references to the dispersal literature on small rodents, see Lidicker (1975), Gaines & McClenaghan (1981) and Stenseth (1983).

Southwood (1977) (see also Southwood et al. 1983) has provided a general theoretical framework for studying the interaction between dispersal and reproduction (or demography). The central idea is that any organism's habitat is heterogeneous in time and space (e.g., May 1973, Stenseth 1977b, 1983, Anderson 1980); hence, "space" and "time" become the axes in the so-called reproduction matrix (Fig. 3). In the following we suggest how to modify and extend this approach originally due to Southwood.

Consider two instances in time and two discrete habitat patches. In Fig. 3, *D* is the probability of dispersing; S is the probability of surviving from one instance in time to a later instance in time, given that the individual does not disperse; p is the probability that a dispersing individual will both survive the dispersing phase *and* be able to enter the other patch; r_1, r_2, r_3 and r_4 are the long-term expected specific rates of population growth (see (1) and (2) above) in the particular patch as given by the appropriate entry in Fig. 3; finally, the corresponding V-values express the variation in the specific population growth rates over time or space due to environmental variation. The effect of seasonality could be incorporated directly into the r's; similarly, the effect of mating with close relatives and with unrelated individuals could be incorporated directly into the r's (see, e.g., Bengtsson 1978). The effect of non-predictable environmental changes, on the other hand, could be incorporated into the V's. For this purpose much detailed biological reasoning would be essential.

As pointed out in Sect. 2.2.1, the r_i's are density dependent rates. Utilizing the technique developed by Ugland & Stenseth (1985), we may then find the joint optimal reproductive and dispersal strategies given a certain (overall) pattern of density change, a certain hostility of the transition habitat (p; *sensu* Stenseth 1983), and a certain level of environmental variation (V_i). Presumably, natural selection would — following Ugland & Stenseth (1985) — favour those strategies minimizing the time required to grow from a low density just after a crash to the critical density level, C, discussed in Sect. 2.2.1.

Within the general conceptual framework discussed above, it is obvious that what is the optimal strategy for any given individual will depend upon what other individuals do. This is so because any given individual may go to a patch of strangers, or strangers may — through dispersal — come to the patch of the considered individual. Situations like this should be treated by an ESS-type of argument (see, e.g., Maynard Smith 1982).

4. Conclusion: What next?

We hope that this review provides a framework for further work on both the proximate and ultimate causes of demographic strategies (and particularly, reproductive strategies). Even though much remains to be done on the theoretical aspects, we believe that several of the deduced predictions are sufficiently detailed to warrant further empirical testing. For this purpose, *Clethrionomys* is, because of its reasonably homogeneous biology throughout its range, extremely well suited. For testing of the derived preditions, *C. glareolus* along a north-south gradient in Scandinavia — or circumboreal *C. rutilus* — could be used (see, e.g., Henttonen et al. 1985). Whenever such testing is performed, great care should be exercised to estimate the appropriate test statistics — and then to do this correctly; we hope that the discussion in Section 2.1.1. will be helpful in this connection.

Repeatedly we have been emphasizing that the reproductive strategies of cyclic and noncyclic populations of the same species should be compared *under otherwise similar conditions.* Obviously such conditions for comparison are hard — or impossible — to find. In fact, Henttonen & Hansson (1985) suggested that some of the differences seen in reproductive strategies in various populations of *C. rutilus* could be explained as a result of the different conditions in the general biogeographic region where the various populations were found. One way of testing whether the degree of cyclicity is important — as argued above — might, however, be to perform a multiple correlation analysis where some measure of reproduction is the dependent variable and factors such as degree of cyclicity, food availability, predation pressure, abiotic condition of the site etc. are the independent variables. We believe that such an analysis would be of great value in our efforts to understand *why* organisms are doing what they are doing.

We also hope that studies on dispersal and on reproductive strategies will be more closely linked than they commonly are today: again we hope that our discussions may suggest a basis, first for some badly needed theoretical work, then for some challenging empirical work. In particular, we feel it is very important to ask what disperses do to the resident — possibly territory-holding — individuals they come in contact with. Gustafsson and coworkers (see summary in Gustafsson 1985) have provided a start in this respect. Much work remains to be done, though.

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