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Survival-variation within and between functional categories of the African multimammate rat

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Summary

1. By identifying ecological factors specific to functional categories of individuals, it may be possible to understand the mechanisms underlying life-history evolution and population dynamics. While empirical analyses within the field of population biology have focused on changes in population size, theoretical models assuming differential sensitivities of population growth rate or fitness to demographic parameters have mostly been untested, particularly against data on small mammals.

2. Statistical modelling of capture–mark–recapture data on the multimammate rat (*Mastomys natalensis*) from Tanzania shows that: (i) females survive slightly better than males and subadults survive much better than adults; (ii) temporal variation of survival of all individuals is similarly related to the rainfall of the month; (iii) subadults exhibit a strongly density-dependent low persistence rate in the population immediately after their first capture; (iv) subadults survival in later months is, however, positively related to density; and (v) adult survival shows negative density-dependence.

3. Both density-dependent and density-independent factors simultaneously determine stage-dependent survival variation of the multimammate rat. Whereas environmental factors in this population seem to affect survival rates of all individuals in a similar manner, density-dependent relationships are more complex.

4. The patterns of survival variation in small mammals may be different from those observed in large mammals.

5. Further studies of demography in small mammals should aim at understanding how much of the variability in population growth rate is accounted for by the variability of the demographic rates resulting from limiting (density-independent) and regulating (density-dependent) factors, respectively. This study emphasizes the use of robust and accurate statistical methods as well as stage- or age-structured population modelling.

Key-words: capture–mark–recapture statistical modelling, density dependence, *Mastomys natalensis*, state-dependent life history, tropical rodent demography.

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Introduction

Recent empirical and theoretical studies have claimed that it is necessary to appreciate the existence of both density-dependent and density-independent factors in order to understand population dynamics (e.g. Royama 1977; Clobert *et al.* 1988; Lebreton & Clobert 1991; Turchin 1995; Stenseth, Bjørnstad & Saitoh 1996). Many studies have focused on testing the presence of density-dependent effects on population dynamics or demographic parameters (e.g. Slade 1977; Vickery & Nudds 1991; Saitoh, Stenseth & Bjørnstad 1997), and therefore, they may have lost sight of the *relative* quantitative importance of density-dependent and density-independent factors.

Density-dependent and density-independent factors may affect differently the various demographic parameters, depending on the state of the individuals (see e.g. McNamara & Houston 1996). In large mammals, for example, adult survival is known to have a much larger relative impact on population growth rate than juvenile survival as measured by the relative sensitivity (elasticity; *sensu* de Kroon *et al.* 1986). At the same time, density dependence is mainly found in juvenile survival, and has rarely been detected in adult survival (Gaillard, Festa-Bianchet & Yoccoz 1998). Indeed, Eberhardt & Siniff (1977) pointed out that density-dependence should primarily affect reproductive traits, such as age at first reproduction or early survival, and lastly adult survival. This was also assumed by Charnov (1991) in his theoretical analysis of life-history evolution of mammals. This is also related to the theoretical expectation that traits with large impact on fitness should be under stronger stabilizing selective pressures and buffered against environmental variability (Stearns & Kawecki 1994). On the other hand, the short generation time of small mammals (Fowler 1988) should result in juvenile survival having a larger impact than adult survival, both for population dynamics and evolution of life histories (Lebreton & Clobert 1991). J.-M. Gaillard & N.G. Yoccoz (unpublished information) thus hypothesized (and provided some empirical evidence in support of the view) that in small mammals, adult survival should show relatively larger variation than juvenile survival, the opposite of what is found in large mammals.

None of the above-cited studies quantified the relative importance of density-dependent and density-independent factors for different demographic parameters. It is of particular interest to investigate this problem in a species where both density-independent and density-dependent factors are expected to have a large impact because of extensive and unpredictable environmental variability coupled with extensive changes in population size. The population dynamics of the African multimammate rat [*Mastomys natalensis* (Smith 1834)] are known to be affected both by rainfall and density (Leirs *et al.* 1997). Using statistical modelling of capture–recapture data, this report gives a detailed description of survival variation in the population of multimammate rats studied by Leirs *et al.* (1997). The overall aim of the present study is to investigate the relative importance of density-dependent and density-independent factors in explaining the variation of survival rates of different functional categories of individuals.

Materials and methods

THE MULTIMAMMATE RAT LIFE HISTORY

The multimammate rat, with an adult weight of about 40 g, occurs in natural grasslands and bushy areas, cultivated areas, and human habitations (Delany 1986). It is the most common murid rodent in sub-Saharan Africa and a major pest to agriculture and public health (Fiedler 1988). Its environment is characterized by predictable (seasonal) and unpredictable variation, mainly steered by rainfall (Leirs *et al.* 1996a); population density varies greatly, and does not seem much limited by territorial behaviour (Leirs, Verheyen & Verhagen 1996b). The life history of the multimammate rat in the study area in Morogoro, Tanzania, has been described in detail elsewhere (Leirs, Verhagen & Verheyen 1993). An individual *Mastomys*, in common with most other rodent species (e.g. Myllymäki 1977; Prévot-Julliard *et al.* 1999), typically experiences three functional stages during its life. The juvenile stage corresponds to the period from birth to independence, which is closely followed by the earliest age of possible sexual maturation. This corresponds approximately to the first month of life, during which individuals remain very elusive and difficult to trap. The adult stage corresponds to the period from maturation to death. However, between independence and maturation, an individual may remain immature for a longer period than expected from its age. This period corresponds to the subadult stage.

For *Mastomys*, breeding is highly seasonal and usually starts in April (1 month after the usual peak rainfall), lasting until September. Each adult female produces a maximum of five to six litters, each consisting of 11–12 young. Young individuals do not normally mature before the next rainy period (April) and thus remain subadults for several months. However, if rainfall late in the year is abundant, subadults mature and may breed as early as in January. Young born in such early breeding seasons grow fast and mature in their third month, starting to breed during the main breeding period. Hence, the length of time between birth and maturation may last from 2 to 10 months (Leirs *et al.* 1990). The present study focuses on the variation of survival rate of subadults and adults. From the life-table built on average values it could be calculated that the population growth rate is highly sensitive to variation in these parameters. Furthermore, elasticity for subadult survival is between one and three times higher than elasticity for adult survival, depending on density and rainfall (Leirs *et al.* 1997; unpublished analysis).

STUDY AREA AND TRAPPING DESIGN

The study site is located on the campus of the Sokoine University of Agriculture in Morogoro, Tanzania (06°51′S, 37°38′E). The capture–mark–recapture (CMR) grid was situated in fallow land near agricultural fields (mostly maize). During the study period, yearly rainfall averaged 835 mm, with two distinct seasons (dry from June to October and wet from November to May). However, monthly rainfall during the rainy season showed important interannual variation (e.g. rainfall in November–December ranged from 60 to 370 mm between 1981 and 1988). On the other hand, temperature varied little (mean monthly temperature range from 23° C in July to 28° C in February), with virtually no variation among years.

A square trapping grid of 1 ha with 100 trapping stations (10 m from each other) was used. A study grid of this size, larger than in several other small mammal studies (Taitt & Krebs 1985), was used in order to minimize edge effects; remaining variation in capture heterogeneity was taken into account by the statistical modelling of capture rate (see below). Furthermore, the regional dynamics of multimammate rats are highly geographically correlated because plague years occur at the same time over several 100 km^2 (Leirs *et al.* 1996a); hence, the demographic parameters estimated on a 1-ha grid may indeed be representative of the demography on a larger scale. Trapping data collected from March 1987 to February 1989 were used. Each month, for three consecutive nights, Sherman live traps baited with peanut-butter and maize scraps were laid out. Traps were checked the following morning, and each rat was identified by toe-clipping. Dead animals were rarely found in the traps [21 deaths recorded out of 5574 captures (0·4%) of 2071 individuals (1%)]. Sex and reproductive condition were recorded. Animals were considered as subadults as long as they did not show any signs of reproductive activity (scrotal testes for males; perforated vagina, lactating nipples or visible pregnancy for females); animals showing such signs were considered to be adults in all consecutive captures. The number of traps varied between one and four per trapping station, depending on rodent densities; nevertheless, during high density periods a high proportion of individuals could not be caught because of saturation of the traps (see below).

The studied population was clearly open to large amounts of migration (Leirs *et al.* 1996b). However, once settled in the population, individual movements were rather small, rarely exceeding 30 m from one capture to the next (Leirs *et al.* 1996b). Such observations may be biased by the limited grid size in the trapping study; however, telemetric observations also indicated small home ranges ($\approx 1000\,\mathrm{m}^2$). The home ranges of individuals (studied by radio-telemetry) overlapped greatly. Home range size and movements between consecutive captures were similar for the two sexes (Leirs *et al.* 1996b).

CAPTURE–MARK–RECAPTURE DATA SET

The data comprise capture–recapture histories (CH; see Table 1) of individuals caught in either of two different states (subadult and adult). State-specific survival was defined according to the state of the individual at the beginning of the month. Because maturation rates are not strictly age-dependent (see above), the subadult state cannot be considered as an age-class of constant length. Subadult and adult survival rates were therefore estimated with two separate subsets of the data corresponding to the CH of subadults and adults, respectively.

The adult subset contained two types of individuals: those caught only as adult [CH of types (C) and (D) in Table 1], and those captured previously as subadult [CH of types (E) and (F) in Table 1]. Only the part of CH starting from the first occasion the individual was caught as adult was used in the latter case. Altogether, there were 462 captures of 304 adult males and 440 captures of 225 adult females.

The subadult subset was constructed in the same way as for adults. However, subadults recaptured as adults are known to have survived through the subadult stage. Hence, the subadult section of such CH ended with a specific code, indicating that these individuals were not released upon last capture (Table 1). However, defining which capture session is considered as the last capture of a subadult is not simple. By definition such individuals have survived as subadult during the month of maturation. Hence, if individuals were removed from the data set at the occasion they were last seen as subadults [see Table 1, first kind of splitting of type (F) CHs], subadult survival estimates would be underestimated whenever individuals matured during that month; for example, in the extreme case where all subadults mature in a given month, no individuals would be recorded to have been seen again, and the subadult survival for that month would be estimated to be zero (yet at least all those known to have matured, have survived). To solve this problem, an additional capture event was created in the subadult part of the CH [the second way of splitting type (F) CHs in Table 1]. Altogether, 106 capture events were thus created for a total of 1411 captures of 744 subadult females, and 93 capture events for a total of 1352 captures of 794 subadult males.

Individuals found dead in the trap (see above) were coded as not being released on that occasion.

MODELLING SURVIVAL AND CAPTURE RATES

For small mammals, the relation between density and variation in survival has often been studied using

Table 1. Hypothetical capture–recapture histories (CH) found in the data set, and their biological meanings. Two ways of organizing the data are proposed to deal with individuals known to have matured. Symbols: 0 = not captured; 1 = captured as a subadult; 2 = captured as an adult; C = captured but not released (thus, this individual is not taken into account to estimate survival after that occasion)

	Time step									
Type of CH	1	2	3	4	5	6	7	8	9	Biological interpretation
(A)	1	0	0	0	0	0	0	0	0	Subadult never recaptured: a proportion of them may be transient
(B)	1	1	0	1	0	0	0	0	0	Subadult never recaptured as adult: may have died as subadult, emigrated, died during maturation, or matured but escaped capture as adult
(C)	0	0	0	2	0	0	0	0	0	Individual first caught as adult and never recaptured again: a proportion of them may be transient
(D)	0	0	0	2	0	2	2	0	0	Individual first caught as adult and caught again at least once
(E)	1	1	0	1	2	0	0	0	0	Subadult which matured between time step 4 and 5, and which survived as subadult between these two time steps. The absence of recapture after maturation may result from emigration
(F)	1	1	0	1	0	2	0	2	2	Subadult which matured either between time steps 4 and 5 or between time steps 5 and 6. Such an individual has survived as a subadult at least between time steps 4 and 5
Two ways of splitting capture history of type (F)										
(1)	1	1	0	C	0	0	0	0	0	
	0	0	0	0	0	2	0	2	2	
(2)	1	1	0	1	C	0	0	0	0	
	0	0	0	0	0	2	0	2	2	

regression of the proportion of individuals surviving on initial number of individuals (e.g. Ostfeld & Canham 1995). However, such approaches generally give biased estimates because they do not account for capture rate (Pollock *et al.* 1990; Clobert & Lebreton 1991). For this reason, capture–mark–recapture statistical modelling (CMR) is most appropriate (Burnham *et al.* 1987; Lebreton *et al.* 1992). Analysing the effect of quantitative (density, climate) and categorical (sex, reproductive status) variables on survival through capture–recapture modelling has the flexibility and philosophy of linear models (Lebreton *et al.* 1992).

Three quantitative variables were selected based upon their *a priori* strong biological importance (Leirs 1995): (i) rainfall of the current month; (ii) cumulative rainfall over the three previous months; and (iii) density at the beginning of the month (measured as the number of individuals present on the 1-ha grid). Rainfall data were obtained from the Morogoro Meteorological Station, located 2 km from the study site. The robust design of the capture sessions (three consecutive nights of capture separated by one month; Pollock 1982) allows estimation of the population size on the grid (i.e. density) at the time of capture (Schnabel method; cf. White *et al.* 1982; Pollock *et al.* 1990). These three variables were largely independent; the combination of two of them did not explain more than 28% of the variation of the third one.

Capture–mark–recapture data sets often show an excess of individuals captured only once [CH of types (A) and (C) in Table 1]. This may be because of a variety of reasons: presence of transient individuals (Pradel *et al.* 1997), low probability of settlement, and/or capture heterogeneity (Prévot-Julliard, Lebreton & Pradel 1998). A cohort of newly captured individuals may thus be a mixture of individuals with different probabilities of persistence in the population: zero for transients, low for settlers, and equal to survival of resident individuals for others. Such low persistence rate will show up in survival estimates following first capture (Pradel *et al.* 1997). To obtain estimates of survival not affected by this initial persistence rate, we built a model with two classes for survival. These survival classes correspond to survival of newly marked individuals in the month following their first capture (here called survival of 'unmarked individuals'), and to survival from the second month following first capture (here called survival of 'marked individuals'). Altogether, eight categories of survival were considered according to sex, maturation status (adult or subadult) and marked/unmarked status.

Capture–mark–recapture models assume equal probability of capture for all individuals in a given category and capture occasion. However, some individuals may be 'trap-shy', yet others may seek the baits and have a higher than average capture probability. Another common problem, known as the edge effect, is that individuals with only part of their home range on the grid have a lower probability of being captured. The violation of the capture homogeneity assumption, known as capture heterogeneity may substantially bias survival estimates (e.g. Francis & Cooke 1993; Pradel 1993; Prévot-Julliard *et al.* 1998). Individuals with high capture probabilities tend to be captured (and recaptured) first, and individuals with low capture probabilities tend to be captured (and recaptured) later. Hence, apparent recapture probability is high at the occasion following a capture, and, if the individual has not yet been recaptured, apparent recapture probability tends to be lower on following occasions. Pradel (1993) has proposed to take into account this phenomenon by allowing for separate estimates between first and later occasion of recapture. This model called 'trap-dependence' reduces the negative bias on survival estimates as a result of capture heterogeneity (Pradel 1993).

The most general model used for the present study (denoted [$\phi_{t*M*G*S}$, $p_{(t+m)*G*S}$]); see Appendix for notation] assumed independent time-variation in survival rates for the eight categories mentioned above, and in capture rates for sex and group with an additive effect of trap-dependence. The temporal variation in trapping efficiency (caused, for example, by trap-saturation at high rodent density) is likely to affect all individuals similarly. A common temporal variation of capture rates across sex and group was therefore sought (i.e. additive affects of time and group). This approach may improve the precision of both capture and survival estimates by reducing the number of parameters to be estimated. Then, for each of the eight categories, the coefficients were estimated relating survival to all three external variables. This allowed us to test for the effect of each variable adjusted for the effect of the others. Nonsignificant variables (see below) were then successively removed as in a backward stepwise selection procedure (e.g. Draper & Smith 1981). The selected model provided the best description of survival variation for any given category. These patterns were then compared between categories by testing for interactions between qualitative and quantitative variables.

STATISTICAL ANALYSIS

Leirs *et al.* (1997) showed that the model [ϕ_t, p_t] fitted the data satisfactorily. There is no simple formulation for a goodness-of-fit test of the most general model used (i.e. [ϕ_{M*t}, p_{t+m}]). However, because this model is less constrained than [ϕ_t, p_t] (we allowed survival to vary according to marked/unmarked status, and for certain types of capture heterogeneity), it was assumed that its goodness-of-fit was satisfactory too. Nested models without environmental variables were compared with likelihood ratio test (LRT; e.g. Lebreton *et al.* 1992). Testing how much variables explain survival or capture rates temporal variation is more subtle. In the general case, three sources of variation may affect parameter estimates: sampling variability (which is assumed to follow a multinomial distribution), extra-multinomial variability resulting from heterogeneity in the capture and survival rates, and temporal variability, the latter only being of interest here. To evaluate the effect of the external variables on temporal variation of parameter estimates, three models are available: model assuming full time-dependence (with deviance DEV_T, number of identifiable parameters df_T), model assuming constancy over time (DEV_C, df_C), and model assuming a linear effect of the external variables (DEV_{EV}, df_{EV}). The quantity $DEV_{EV}-DEV_T$ measures the adequacy of external variables to explain all temporal variability of the parameter considered, but the sampling binomial variability. The quantity DEV_C-DEV_{EV} measures the effect of external variables, assuming that there is no other source of variability (but sampling binomial variability). Hence, both these measures cannot tell properly whether external variables indeed explained a significant part of the temporal variation of the parameter estimates. Assuming that extra-multinomial variability inflates similarly the deviance of the three models considered, then $DEV_{EV}-DEV_T$ can be assumed to be proportional to the temporal variability not explained by external variables, while DEV_C-DEV_{EV} can be assumed to be proportional to the temporal variability explained by external variables (R. Julliard & N.G. Yoccoz, unpublished information). Hence, by analogy with analysis of deviance (McCullagh & Nelder 1989; Skalski, Hoffman & Smith 1993), the effect of the external variables was tested by a Fisher ratio test: $F(df_{EV}-df_C, df_T-df_{EV}) = \{(DEV_C-DEV_{EV})/(df_{EV}-df_C)\}/\{(DEV_{EV}-DEV_T)/(df_T-df_{EV})\}$.

The variances of the estimates of the coefficients were multiplied by $(DEV_{EV}-DEV_T)/(df_t-df_{EV})$. The ratio (estimated coefficient)/(corrected error estimate) is then analogous to a Wald test (Breslow 1990). These tests appear unbiased and robust to heterogeneity in the data (R. Julliard & N.G. Yoccoz, unpublished information).

Results

CAPTURE RATES

Models with similar time-variation of capture rates between groups and/or sexes fitted the data as well as models with independent time-variation [$p_{(t+m)*G}$ vs. p_{t+m*G}, $p_{(t+m*G)*S}$ vs. $p_{t+m*G*S}$; $P > 0{\cdot}5$]. However, the overall time variation was strongly significant (e.g. $p_{t+m*G*S}$ vs. p_{G*m*S}, $\chi^2_{22} = 118{\cdot}67$; $P < 0{\cdot}0001$; range of capture rate estimates: 45–100%). The acceptance of the model with parallel time-variation of capture rates may have been an artefact of one or more of the data sets being small. However, for a given sex, constraining capture rates of one group to be constant through time always increased the deviance more than constraining capture rates of the two groups to vary in parallel, yet changes in d.f. were the same (e.g. adults males capture rate being constant, p_{t+m} vs. p_m: change in deviance = 24·44; same variation of time for adult and subadult males, $p_{(t+m)*G}$ vs. p_{t+m*G}: change in deviance = 12·93; change in d.f. = 21). We can thus conclude that the temporal variation in capture rates was remarkably similar for all individuals.

The trap-dependence effect was additive on groups ($p_{t+m*G*S}$ vs. $p_{t+m+G*S}$, $\chi^2_3 = 1{\cdot}69$; $P = 0{\cdot}64$). Capture rate could even be considered equal across categories ($p_{t+m+G*S}$ vs. p_{t+m}, $\chi^2_3 = 5{\cdot}57$; $P = 0{\cdot}13$). The effect of trap-dependence was large (p_{t+m} vs. p_t, $\chi^2_1 = 36{\cdot}75$; $P < 0{\cdot}0001$), suggesting that capture heterogeneity was important.

SURVIVAL RATES

Level of variation

Multimammate rat survival exhibited extensive temporal variation (see below). Hence, direct comparison of average survival level between categories is not straightforward. However, assuming consistent and additive effects, we may compare the level of variation between categories beyond temporal variation. For this purpose, we built the model $\phi_{t+G*S*M}$, which constrained survival rates of the various categories to vary in parallel in time, yet at eight different levels. This model did not fit the data ($\phi_{t*G*S*M}$ vs. $\phi_{t+G*S*M}$, $\chi^2_{134} = 195{\cdot}65$, $P = 0{\cdot}0004$), but the residual time variation was still large ($\phi_{t+G*S*M}$ vs. ϕ_{G*S*M}, $\chi^2_{22} = 209{\cdot}29$), suggesting that a large amount of temporal variation of survival was similar for the different categories; survival estimates varied from 15 to 100% between months. Nonsignificant third-order and second-order interactions were then removed successively (i.e. we simplified $G*S*M$, in the model $\phi_{t+G*S*M}$). The thus selected model was $\phi_{t+S+G*M}$. This model suggested that females survived significantly better than males (difference of $\approx 0{\cdot}05$; $P = 0{\cdot}03$), independently of marked/unmarked status and group. Furthermore, unmarked subadults had a lower survival than marked subadults (difference of $\approx 0{\cdot}14$, $P = 0{\cdot}0001$). Unmarked and marked adults, however, have similar survival ($P = 0{\cdot}54$). Overall, adult survival was slightly lower than unmarked subadult survival, and thus much lower than marked subadult survival ($\approx 0{\cdot}20$ less).

Temporal variation

Male and female subadults showed very similar patterns of variation (coefficients with same sign within marked/unmarked categories; see Table 2). However, coefficients for males appeared higher than for females. This was probably an artefact, because coefficients could be constrained to be equal for male and female subadults (Table 3). Environmental variables explained a smaller part of survival variation of adults and without any clear pattern. Combining all adults, however, revealed a significant effect of density and rain of the month (Table 2). The fit was markedly increased when unmarked adult females were not taken into account to estimate the coefficient of rain of the month, yet we had no *a priori* justification for doing so.

Rain of the month affected all categories of survival similarly (except for unmarked adult females; Tables 2 and 3 and Fig. 1). All categories were also affected by density but not always in the same way: there was a positive density-dependence for marked subadults survival, and a negative density-dependence for unmarked subadults and for adults (Tables 2 and 3 and Fig. 1). Marked subadults survival was further affected by the rain of the three previous months (Tables 2 and 3 and Fig. 1). On the whole, we were thus left with five coefficients (Table 3) to describe the survival variation of multimammate rat, accounting for 134·07 units of deviance (270·87 were not explained with 151 remaining d.f.). We have thus explained 33% of survival variation (which is unusually high in such survival analysis, see, e.g. Lebreton *et al.* 1992).

The partial *R*-squares were 25% and 14% for density-independent and density-dependent factors, respectively.

Discussion

ESTIMATING SURVIVAL RATES FOR TWO STATES WITH A 'ONE-STATE' CMR-STATISTICAL MODEL

Potential bias

By manipulating capture histories (CH), survival estimates may have been biased. First, there are many reasons why a subadult may not be seen again (cf. CH (B) in Table 1); for example, a subadult which disappeared may have matured and not be captured as adult. It may even have survived additional time steps as an adult, yet still not be captured. Therefore, the probability corresponding to no recapture after the last capture of a subadult is a complex function of subadult capture and survival rates (as usual), but also of adult capture and survival rates. If adults have different survival rates and, especially, different capture rates as compared to subadults, subadult survival estimates would be biased. Fortunately, capture rates were very similar between adults and subadults. Adult survival was, however, consistently lower than subadult survival. The consequent bias (towards an underestimation of subadult survival) was mitigated by the relatively high capture rate (average of 80%). Therefore, very few subadults were likely to have survived two additional time steps (the second one as an adult) without being captured. Hence, this source of bias seems negligible.

Second, several subadult capture events were created even though the individuals were captured as adults, or even not captured (cf. CH (F) in Table 1). This may bias estimates of subadult capture rate. However, adult and subadult capture rates were found

Table 2. Modelling survival variation for each category of individuals. The coefficients ($*10^4$) ± SE (with appropriate correction, see Methods), and associated *P*-values, relating survival (on a logit scale) and environmental variables were first estimated in Model 1 when all three variables were included. Nonsignificant variables were then successively removed, if necessary (Model 2 and Model 3). The last two columns give the deviance explained by the selected model (in bold) and the remaining deviance not explained by the model

	Model 1	Model 2	Model 3	Deviance explained (d.f.)	Deviance not explained (d.f.)
(a) Sub-adults					
Unmarked female				10·99 (2)	32·71 (18)
Density	–20 ± 12	**–19 ± 10** *P* = 0·06			
Rain of the month	–59 ± 33	**–65 ± 34** *P* = 0·05			
Rain 3 months	–2 ± 13 *P* = 0·86				
Unmarked male				60·43 (2)	42·45 (15)
Density	–41 ± 17	**–32 ± 16** *P* = 0·04			
Rain of the month	–165 ± 36	**–180 ± 37** *P* < 0·0001			
Rain 3 months	–27 ± 19 *P* = 0·15				
Marked female				25·17 (1)	48·16 (20)
Density	+30 ± 13	+18 ± 13 *P* = 0·16			
Rain of the month	–95 ± 29	–75 ± 27	**–90 ± 17** *P* < 0·0001		
Rain 3 months	+43 ± 29 *P* = 0·14				
Marked male				55·25 (3)	39·31 (18)
Density	**+48 ± 19** *P* = 0·01				
Rain of the month	**–170 ± 45** *P* = 0·0001				
Rain 3 months	**+153 ± 62** *P* = 0·01				
(b) Adults					
Unmarked female				–	44·78 (14)
Density	–96 ± 56	–61 ± 40	–54 ± 36 *P* = 0·14		
Rain of the month	+73 ± 58	+34 ± 55 *P* = 0·54			
Rain 3 months	–63 ± 62 *P* = 0·31				
Unmarked male				6·14 (1)	21·43 (20)
Density	–13 ± 20 *P* = 0·50				
Rain of the month	–115 ± 60	–95 ± 44	**–93 ± 42** *P* = 0·03		
Rain 3 months	–21 ± 23	–14 ± 19 *P* = 0·46			
Marked female				22·65 (2)	25·01 (19)
Density	–30 ± 20	**–23 ± 12** *P* = 0·06			
Rain of the month	–180 ± 56	**–177 ± 60** *P* = 0·003			
Rain 3 months	–14 ± 27 *P* = 0·60				
Marked male				–	26·75 (21)
Density	–5 ± 21 *P* = 0·82				
Rain of the month	–51 ± 34	–47 ± 36 *P* = 0·19			
Rain 3 months	+27 ± 30	+31 ± 20	+22 ± 16 *P* = 0·22		
Adults combined			Special model*	27·39 (2)	118·76 (75)
Density	–19 ± 11	–19 ± 8 *P* = 0·02	**–23 ± 8** *P* = 0·006		
Rain of the month	–58 ± 26	–59 ± 27 *P* = 0·03	**–112 ± 34** *P* = 0·0008		
Rain 3 months	+1 ± 15 *P* = 0·97				

*Unmarked females were not used for estimating the coefficient for rain of the month.

to be similar, which minimizes such biases. Only 18 and 19 capture events for females and males, respectively, were created for individuals not being observed either as an adult or as a subadult at that time (as for individuals of type (F) in Table 1). These numbers have to be compared with the total of 1411 and 1352 captures of female and male subadults, respectively. Furthermore, this could result in a slight overestimation of subadult survival, counterbalancing the slight underestimation as a result of the low adult survival (see above). Leirs *et al.* (1997) found that maturation rate was higher in months with low density, and in months with high rainfall during the previous 3 months. If maturation rate had affected the estimates in the present study of subadult survival, it should have induced opposite trends. It is noticeable that the same trend was actually found for the rainfall effect on marked subadult survival. Altogether, it seems that this bias also was negligible in the case reported here.

Table 3. Comparison of pattern of survival variation between categories

	Interactions tested	Model retained		
		variable	slope	P-value
Between sexes for unmarked subadults		Density	−24 ± 9	$P = 0\cdot006$
(density)–(sex)	$P = 0\cdot58$	Rain of the month, female	−81 ± 29	$P = 0\cdot005$
(rain of the month)–(sex)	$P = 0\cdot04$	Rain of the month, male	−173 ± 40	$P < 0\cdot0001$
Between sexes for marked subadults		Density	+36 ± 12	$P = 0\cdot003$
(density + rain of the month + rain 3 months)–(sex)		Rain of the month	−115 ± 23	$P < 0\cdot0001$
	$P = 0\cdot29$	Rain 3 months	+64 ± 29	$P = 0\cdot03$
Between marked and unmarked subadults		Density, unmarked	−25 ± 8	$P = 0\cdot001$
(density)–(mark class)	$P = < 0\cdot0001$	Density, marked	+41 ± 14	$P = 0\cdot003$
(rain of the month)–(mark class + (sex). (M1))	$P = 0\cdot33$	Rain of the month	−125 ± 15	$P < 0\cdot0001$
(rain 3 months)–(mark class)	$P = 0\cdot01$	Rain 3 month, marked	+69 ± 25	$P = 0\cdot006$
Between adults and subadults		**Density, subadult unmarked**	−21 ± 7	$\mathbf{P = 0\cdot001}$
(rain of the month)–(group)	$P = 0\cdot72$	**Density, subadult marked**	+36 ± 10	$\mathbf{P = 0\cdot0005}$
		Density, adults	−21 ± 8	$P = 0\cdot009$
		Rain of the month	−129 ± 13	$P < 0\cdot0001$
		Rain 3 month, marked	+64 ± 23	$P = 0\cdot006$

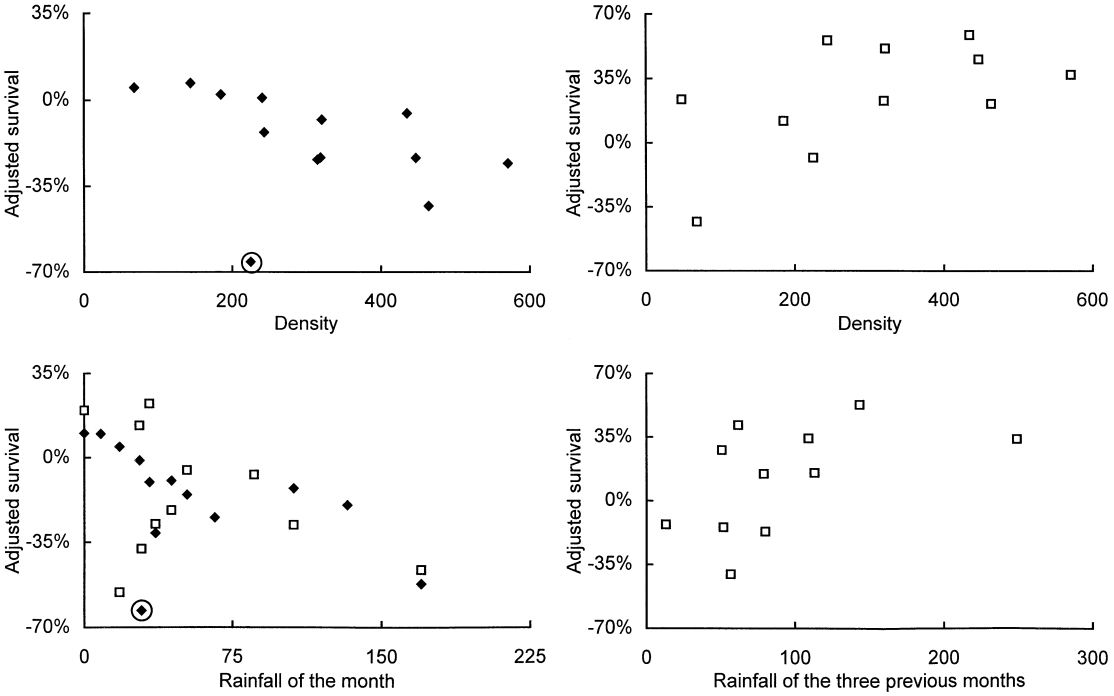

Fig. 1. Relationships between subadult survival and external variables. For each graph, survival was adjusted for variation in other variables: fitted values were calculated from coefficients obtained in Table 3 omitting the variable of interest. These values are subtracted to estimates from the model $\phi_{M*t+M*S}$, i.e. unfitted estimates (partial residual plots; Larsen & McCleary 1972). Only estimates with S.E. < 0·15 are shown. Full squares: survival of unmarked subadults; open squares: survival of marked subadults. The outlying data points (circled) correspond to survival between December 1987 and January 1988 when a strong reduction of population density occurred.

Potential benefits

There is often a temptation not to model variation in capture rates (Clobert 1995). Modelling of capture rate variation can, however, substantially improve the precision of survival estimates and the power of tests; for example, the test for temporal variation of survival for marked subadult males (LRT ϕ_t vs. ϕ) increased from 50·21 to 94·56 when assuming capture rate to have additive time variation over categories (the reverse was not true; the LRT of additive variation on capture rate decreased when constraining survival). The strong heterogeneity of capture revealed by the model p_{t+m} led, interestingly, to a substantial decrease of time dependence on survival (e.g. LRT ϕ_t vs. ϕ for marked subadult males decreased from 104·41 to

94·56 when allowing for capture heterogeneity). This suggests that capture heterogeneity induced extraneous temporal variation of survival. Even more interestingly, such modelling of capture rate not only improved the fit of the general model, but also increased the significance of the relationship between survival and environmental variables; for example, the three environmental variables accounted for 58% ($P = 0{\cdot}001$) of the deviance for marked subadult males when capture rate was fully modelled (Table 2), 55% ($P = 0{\cdot}002$) without additive temporal variation on capture rate, and 49% ($P = 0{\cdot}006$) without correction for capture heterogeneity. Hence, the relationships found are not likely to be artefacts associated with heterogeneity in the data.

THE DETERMINANTS OF SURVIVAL

For fluctuating small mammal populations, there has been a peculiar neglect in asking whether demographic rates depend on density or not (but see Ostfeld & Canham 1995); for that group, there is generally a focus on what cyclic phase the population is in (increasing, peak, low, etc.; see, e.g. Krebs & Myers 1974). Recently, Leirs *et al.* (1997) showed that density-dependent and density-independent factors affect demographic rates of a highly fluctuating population of multimammate rats. However, their method did not allow comparison between functional groups, nor did it allow for proper modelling of capture rates. They furthermore used only rough categories of 'high' and 'low' densities. By analysing the same and additional data in an alternative way, we have qualitatively confirmed the conclusions of Leirs *et al.* (1997). However, the precise forms of the relationships between the survival rates of different functional classes and density and rainfall were investigated. Male and female survival rates varied similarly with respect to time, but females survived slightly better than males. Once settled, subadults survived with a much higher probability than adults. Survival of three categories of individuals, unmarked subadults, marked subadults, and adults, were similarly related to one environmental variable (rain of the month). Beyond this similarity with respect to density-independent determinants of survival, different density effects on survival for these different categories were found: a negative effect on adults and unmarked subadults survival, and a positive effect on marked subadults survival. Furthermore, marked subadults survival was positively correlated to the cumulative rainfall over the three previous months, which was not the case for the other categories. As suggested in Fig. 1, the relation between survival and its determinants appeared continuous and linear on a logit scale.

Survival or dispersal?

Local persistence rate in the population estimated with capture–mark–recapture data represents the combined effect of survival and emigration. When included in a Leslie matrix type of model, multimammate rat estimated survival rates (together with given fecundity rates) are able to sustain a population (Leirs *et al.* 1997), suggesting that they may indeed be reasonably close to actual survival schedules. This suggests that emigration rate after settlement may be low, a conclusion supported by the short distances between successive captures of the same individual (Leirs *et al.* 1996b). Such philopatry after settlement has been observed in several other rodents (Lambin 1997).

Different survival of newly marked individuals

Newly marked subadults had a lower survival with a particular pattern of variation in the month following their first capture, compared to survival in later months (when they become 'marked' subadults). This was not the case for adults. Heterogeneity of capture may induce a lower survival estimate after first capture (Francis & Cooke 1993; Prévot-Julliard *et al.* 1998). However, a substantial bias is found only when a large number of individuals have a low capture rate, which is unlikely here because capture rate was, on average, relatively high. Furthermore, despite similar trap-dependence effect as compared to subadults, adults did not show reduced survival after first capture. Therefore, the low survival estimate of unmarked subadults is here unlikely to be only an artefact of capture heterogeneity. It is rather a result of the presence of transient individuals (i.e. individuals accidentally trapped in the area but which normally do not live there), or to a low probability of settling in the population for new individuals, or to a combination of these effects. The negative effect of density on survival of unmarked subadults is then reasonable, suggesting that settlement was increasingly difficult when density increased. This could be a major phenomenon regulating population size, and its importance could be explicitly investigated by incorporating estimated parameters into a population dynamics model.

Density-independent effects on survival

Survival of all individuals was equally negatively correlated with the rain of the month. This could be considered as the common pattern of variation of survival linked to the part of the environment acting similarly on all individuals. This relationship may reflect a direct effect of heavy rain showers on the survival of the rats, but it is more likely to be a proxy for the advancement of the season. It would be worthwhile studying the effect of rainfall beyond the normal seasonal variation of survival. This would require additional data (i.e. more years). However, the seasonal variation of the environment as measured by rainfall, clearly induced seasonal survival variation.

The most striking result was the different relation between density and survival of marked subadults and adults, and the low survival of adults compared to subadults. The positive density effect on subadult survival could originate from at least two phenomena: inhibited dispersal, and hence higher probability of persistence in the population at high density (Lidicker 1975; Stenseth 1983; Brant 1992; Stenseth & Lidicker 1992), or reduced predation rates through a saturation effect at high density. The former is not supported by observational data: the number of new individuals is usually high at high density, and between-capture movements are small both within and between capture sessions and are not related to density (Leirs 1995; Leirs *et al.* 1996b). On the other hand, telemetry observations have shown that avian predation is a primary cause of mortality in the multimammate rat (H. Leirs, unpublished data). If small subadults are more prone to predation than adults (as found by, e.g. Sinclair, Olsen & Redhead 1990 for predation on mice, *Mus domesticus* L. 1758), it could further explain the different density effect between adults and subadults.

In *Mastomys*, subadults have, on average, a higher survival than adults. In addition, the population growth rate is relatively more sensitive to variation of subadult survival than to variation of adult survival (elasticity analysis from data in Leirs *et al.* 1997). Subadult survival should thus be under stronger selection pressure than adult survival. The present study did indeed find that density affects demographic parameters differently under different selection pressure as predicted by theory of life history evolution (e.g. Schaffer 1974; Charlesworth 1994).

Conclusion

For multimammate rats, density seems to affect survival of adults more than survival of subadults (as suggested by Ostfeld & Canham 1995 for the meadow vole *Microtus pennsylvanicus*). This is the opposite of what is generally found for large mammals (Gaillard *et al.* 1998), and supports the hypothesis of J.-M. Gaillard & N.G. Yoccoz (unpublished information) for a different pattern in demographic sensitivities between large and small mammals. This result, together with the higher survival of subadults compared to adults, shows that mammals cannot be assumed to be a homogeneous group with respect to demographic patterns (contra Charnov 1991). The results presented here rely on the analysis of survival by capture–recapture statistical modelling: for example, ignoring that newly caught subadults may have a lower persistence rate than other subadults caught at the same time, would have hidden most of this pattern. Hence, it is not clear whether these unexpected results are a result of special features of the multimammate rat (such as the large litter size or the lack of territorial defence), or to the use of less modern methodologies in previous studies.

Highly fluctuating populations—such as many small rodents—are amenable to the study of density-dependence in both demographic rates and the resulting population dynamics. In this paper the *relative* effects of density-dependence and density-independence on the multimammate rat demography have been demonstrated; earlier Leirs *et al.* (1997) demonstrated that the combination of the estimated density-dependence and density-independence might mimic the observed dynamics in the field. One major criticism of the ‘density-dependent paradigm’ is that ‘population density is not a mechanism’ explaining how population is regulated (Krebs 1995). By comparing density-dependent effects between functional categories, beyond the common pattern of survival variation, we may indeed prepare the ground for discussing state-specific mechanisms acting on survival depending upon density.

Finally, to assess the relative importance of density-dependent and density-independent mechanisms in population dynamics and life-history evolution necessitates: (i) proper statistical methods to obtain robust estimates as well as estimates of sampling variability (Link & Nichols 1994); (ii) theoretical age- or stage-structured models, including different sources of stochasticities (demographic and environmental) as well as density-dependence (see Dennis *et al.* 1995; Engen, Bakke & Islam 1998). We hope our results will stimulate such an integrated research effort and show that small mammals could indeed be a suitable empirical model for analysing population dynamics.

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Appendix: notation

We used notations recommended by Lebreton *et al.* (1992):

ϕ	survival rate
p	capture rate
t	model with time dependence
G or S	model with a group (subadult vs. adult) or sex effect
M	model with two mark classes, this separate survival immediately after first capture (unmarked) vs. later (marked)
m	model with capture heterogeneity (only for p); capture rate on the occasion following capture differs from capture rate on later occasions
*	model with an interaction (includes main effects and interactions)
+	model with additive effects

Example:

$\phi_{M*(t+G)}$, p_{G*m} survival modelled with two mark classes with independent time-variation. However, within mark class, time variation is similar between groups yet at different levels (parallel variation); capture rate without time variation but different for the different groups, and with a capture heterogeneity effect different for the different groups.