Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species

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The seasonally determined demographic structure of two semi-arid rodents, both agricultural pest species (the leaf-eared mouse (*Phyllotis darwini*) in Chile and the multimammate mouse (*Mastomys natalensis*) in Tanzania), is analysed using capture–mark–recapture (CMR) statistical models and measures for elasticity (the relative change in the growth rate due to a relative unit change in the parameter of concern) derived from projection linear matrix models. We demonstrate that reproduction and survival during the breeding season contribute approximately equally to population growth in the leaf-eared mouse, whereas the multimammate mouse is characterized by a more clearly defined seasonal structure into breeding and non-breeding seasons and that reproduction contributes far more than survival during the breeding season. On this basis, we discuss evolutionary and applied (pest control) issues. Regarding the evolution of life histories (leading to a maximization of the overall net annual growth rate), we suggest that for the leaf-eared mouse, features favouring survival throughout the year will provide selective value, but that during the main breeding season, features favouring reproduction and survival are about equally favourable. For the multimammate mouse, features favouring survival are particularly important outside the breeding season, whereas during the breeding season features favouring reproduction are more important. Regarding pest control (aiming at reducing the overall net annual growth rate), we suggest that (ignoring economic considerations) affecting survival outside the main breeding season is particularly effective for the leaf-eared mouse, a feature that is even more the case for the multimammate mouse. In sum, we demonstrate through this comparative study that much is to be learnt from studying the dynamics of fluctuating small rodents—a focal issue within much of population ecology.

Keywords: between-year variability; seasonality; evolutionary consequences; applied consequences; Africa; South America

1. INTRODUCTION

The numerical fluctuations of small rodent populations have long fascinated population ecologists (Elton 1924; Elton & Nicholson 1942; Krebs & Myers 1974; Chitty 1996; Stenseth 1999) and is often considered one of the most fertile grounds to gain an understanding of animal population dynamics (cf. Leslie 1945, 1948; Kalela 1957; Schaffer & Tamarin 1973; Krebs & Myers 1974; Stenseth *et al.* 1998, 2002, 2003*a*; Stenseth 1999). Most, but certainly not all, studies on small rodent population dynamics have focused on the dynamic patterns (e.g. multiannual cycles or not) rather than on the underlying demographic mechanisms. Much information is currently being accumulated on the underlying demography in fluctuating rodent populations (see Brown & Zeng 1989; Leirs *et al.* 1997; Getz & Hofmann 1999; Lambin *et al.* 2000; Lima *et al.* 2001). The use of capture–mark–recapture (CMR) statistical modelling to obtain estimates for the elements of the Leslie (1945, 1948) population matrix models (see Yoccoz *et al.* 1998; Nichols *et al.* 2000) provides an ideal link between demographic mechanisms and population dynamics.

In highly seasonal environments, a seasonally structured population model seems obvious to improve our understanding of the interface between demography and the resulting population dynamics. For small rodents, seasonality implies most of all changing between two (seasonally determined) regimes or stages: a reproductive season (summer in the Northern Hemisphere, wet season in the semi-arid regions that we consider in this study) and non-reproductive season (winter in northern rodents, dry season in our semi-arid rodent). Both the level of the net population growth rate and the density-dependent structure varies between these two regimes (see Stenseth *et al.* 1998, 2002, 2003*a*; Hansen *et al.* 1999; Merritt *et al.* 2001), partly because reproduction typically occurs only in one of the two seasons but also because survival may differ greatly between the two seasons.

In addition, the social structure might differ profoundly between the two seasons—differences that typically affect the density-dependent structures in the two seasons. Differences in the seasonal structure of the vital rates may

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indeed represent the phenomenological causes for differences in population dynamics (see Stenseth *et al.* 1998, 2002, 2003a).

To better understand the consequence of seasonal demographic structure, we need a model for the net overall growth rate for the population under study. Population projection matrix models (Leslie 1945, 1948) are ideally suited for this purpose. The so-called elasticity coefficients of such models (cf. Caswell 2001; Caswell & Trevisan 1994) are ideally suited for helping us improve our understanding of the population dynamics consequences of the changing seasonal demographic structure and processes. This is so because such elasticity coefficients provide measures of the relative contribution of changes in survival and recruitment to the overall annual net population growth.

We use statistical CMR models and Leslie matrix population models to compare the seasonal and interannual population dynamics for two small rodent species inhabiting semi-arid and seasonal regions in Africa and South America—using the leaf-eared mouse (*Phyllotis darwini*) from Chile and the multimammate mouse (*Mastomys natalensis*) from Tanzania. Both species exhibit extensive numerical outbreaks that are correlated with unusually high rainfall and increased primary production (Leirs *et al.* 1996; Lima *et al.* 1999). For both species we have highly and uniquely comparable individual-based long-term data. First, we are interested in detecting at what temporal scale demography varies (interannual, interseasonal, between months). Second, we determine the main monthly and seasonal components of within-year variation in demography and use these to parameterize population matrix models. Third, we estimate the elasticities of these matrix models and estimate the relative contribution of survival and recruitment components to the realized population growth rates (see Pradel 1996; Nichols *et al.* 2000).

2. MATERIAL AND METHODS

(a) *The species and the study area*

The leaf-eared mouse (*Phyllotis darwini* (Waterhouse 1837)) is a small rodent widely distributed in the semi-arid and Mediterranean-type ecosystems of north central Chile (Meserve & Le Boulengé 1987; figure 1). This species is herbivorous with an average adult weight of 50 g. The breeding of the leaf-eared mouse is markedly seasonal; it starts in July and lasts until December or January (Meserve & Le Boulengé 1987). Females produce two or three litters with an average size of approximately 5.2 pups (Fulk 1975; Meserve & Le Boulengé 1987).

The Chilean study site, Las Chinchillas National Reserve at Aucó (31°30′ S; 71°06′ W), is located 300 km north of Santiago, Chile (figure 1). Situated in the coastal ranges, the Reserve has a rugged topography with numerous ridges dissected by deep ravines and with some flat areas. The rainfall pattern in central Chile is characterized by a strong seasonality, with 90% of the annual precipitation occurring during winter from May to August (Jaksic *et al.* 1997). As exemplified by the Illapel climatological station (figure 2*a*(i)). Mean annual precipitation is 175 mm but with extensive interannual variability (Jaksic *et al.* 1996) from 10 to 520 mm annually. The vegetation is a thornscrub community (Jiménez *et al.* 1992).

The multimammate mouse (*Mastomys natalensis* (Smith 1834)) is a common murid rodent in Africa south of the Sahara,

with an adult weight of *ca.* 40 g. It is an opportunistic omnivore, very common in and around agricultural fields, often causing serious pest problems in cereal crops (Makundi *et al.* 1999). Breeding is strictly seasonal, starting after the onset of the rainy season and continuing well into the dry season, with pregnancies observed from May to October. A remarkable characteristic is the very high reproductive rate (Leirs *et al.* 1993): litter size is very high, up to 24 young per litter, with an average of approximately 11; females typically have 4–5 consecutive litters in the breeding season. Adult animals die after the breeding season and young animals usually do not become reproductively active until the next wet season.

The Tanzanian study site is located at the campus of the Sokoine University of Agriculture in Morogoro, Tanzania (6°50′ S, 37°38′ E; see figure 1). The area is a large mosaic of agricultural fields interspersed with fallow land. The pattern of seasonal variation in rainfall at Morogoro is clearly bimodal, the wet season begins in October and lasts until May, with a first and often minor peak of rainfall during the first months ('vuli'-season), a drier period around the turn of the year, and heavy rains from March to May ('masika'-season) (figure 2*b*(i)). The average rainfall per year over the period 1980–2001 was 868 mm with a range of 608–1055 mm. The area is cultivated mainly with maize, which is planted in March and harvested in August.

(b) *Trapping design*

Leaf-eared mice were monitored through CMR methods on two opposite-facing slopes in each of two creeks 2 km apart. Trapping was performed regularly from October 1987 to January 1992, alternating between creeks on a monthly basis. Four trapping grids were used: two in opposite-facing slopes of the El Grillo creek (26 primary trapping sessions; *sensu* White & Burnham 1999), and two in El Cobre creek (26 primary trapping sessions). Within each creek, the two trapping grids were considered as one large grid because of the large number of individuals dispersing between slopes (Lima & Jaksic 1999) and we pooled data from both creeks considering that population trajectories and demographic rates were similar between creeks (Lima & Jaksic 1999). In May 1992 there was a single trapping occasion, but only in the two grids of El Cobre creek. From July 1992 to April 1996, live trapping was conducted in El Cobre every three months (January, April, July and October). From May 1996 to June 2001 trapping was conducted monthly in El Cobre. Each 7 × 7 trapping grid had 49 stations separated by 15 m. Grids were equipped with one Sherman trap at each station, with traps activated simultaneously on the xeric and mesic slopes of a each creek during five consecutive nights (secondary trapping sessions; *sensu* White & Burnham 1999). All traps were kept permanently in the field and closed when not in use. Traps were baited with rolled oats and checked every morning. Each individual captured was marked with a metal ear tag, and its body mass, reproductive condition (females were classified as immature, pregnant or lactating), sex and species were determined. Besides leaf-eared mice, three other small mammals were frequently captured: the didelphid marsupial *Thylamys elegans*, and the cricetid rodents *Akodon olivaceus* and *Oligoryzomys longicaudatus*.

Information about a population of the multimammate mouse also derives from a CMR study with monthly trapping sessions of three consecutive nights each (primary trapping sessions). From March 1987 until February 1989, this study was carried out in a fallow field of 1 ha; in June 1994 the study was resumed but the area extended to a 3 ha mosaic of fallow land with two
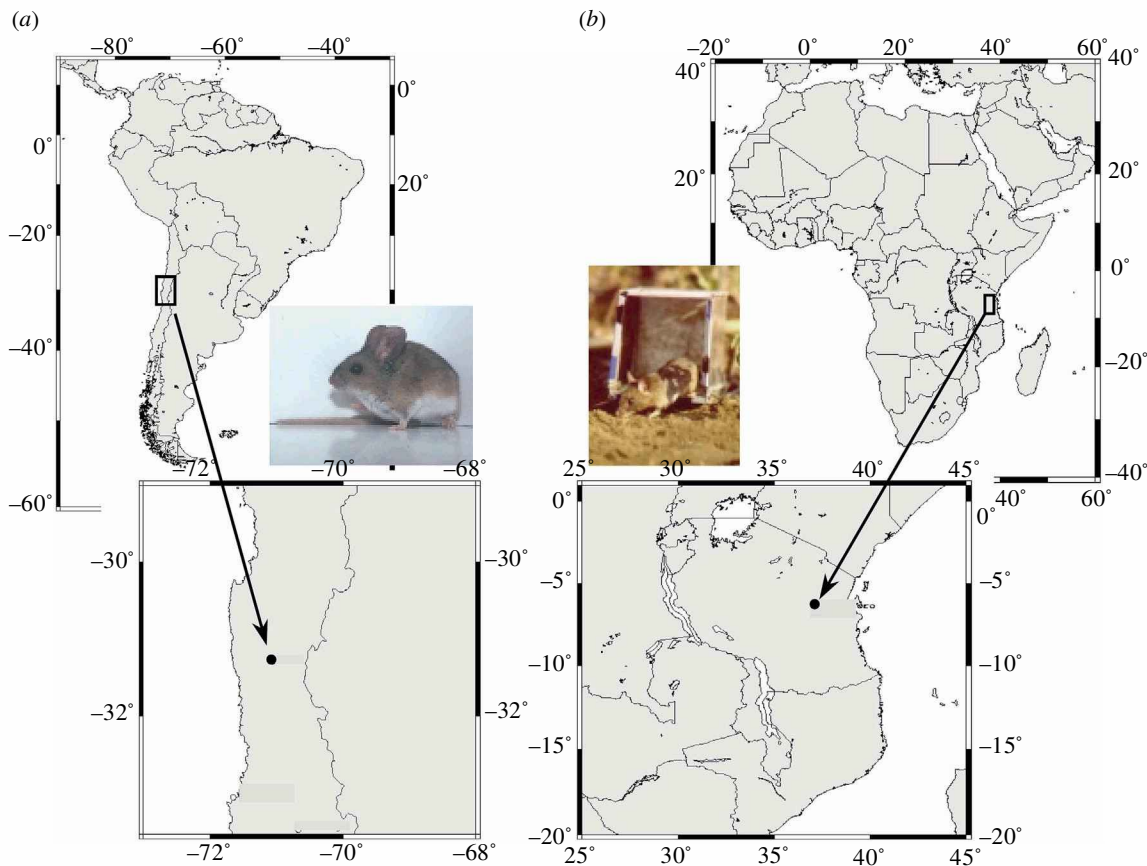
Figure 1. (*a*) Map of western South America with semi-arid Chile shown as a shaded area, and the study site for *Phyllotis darwini* at Reserva Nacional Las Chinchillas (31°30′ S; 71°06′ W). (*b*) Map of eastern Africa with Tanzania shown as a shaded area and the study site for *Mastomys natalensis* (Morogoro 06°50′ S 37°38′ E).

0.5 ha maize fields. Here, we used trapping results until June 2001. The study grids had permanent trapping stations 10 m apart. In the period 1987–1989, we used one to four Sherman traps at each trapping station, depending on the population density of rodents; since 1994, we have used a single trap per station. Sherman traps were baited with a mixture of peanut butter and maize bran, opened in the afternoon and checked in the morning. Each individual was marked with a toe clipping code, and its species, body mass, sex and reproductive condition were recorded. The animals were released again at the same station where they were trapped. Most (95%) of the trapped animals were *M. natalensis*. Other species included *Tatera robusta*, *Lemniscomys rosalia*, *Mus minutoides* and the shrew *Crocidura hirta*.

(c) Estimating demographic parameters

For both species the basic data for our comparative study consist of capture–recapture histories. For the leaf-eared mouse these histories were derived on the basis of 106 primary trapping sessions. The age category of each individual (juvenile or adult) was determined according to the body size recorded when first caught: individuals with body weight smaller than 35 g were classified as sub-adults (Meserve & Le Boulengé 1987). In this paper, we only consider the female section of the populations. We obtained 2081 captures corresponding to 853 adult females, and 699 captures corresponding to 298 sub-adult females. Population size was estimated by using closed CMR models (Lima *et al.* 2001).

For multimammate mice, the capture–recapture histories were obtained from 24 monthly trapping sessions between

March 1987 and February 1989, and 90 sessions from June 1994 to June 2001; for modelling demography we used only the 90 primary trapping sessions from the latter period. In total, we recorded 11 867 captures of 4623 individual females of *M. natalensis*. Females were considered as adults once they had displayed perforated vagina, lactating nipples or palpable pregnancy. Total population size was expressed as the percentage of successful traps in each session for the 1981–1989 period, from 1994 onwards closed-model population estimates were calculated for each 3-day trapping session using the jack-knife model for heterogeneous capture probability (Mh) in the software program CAPTURE (White *et al.* 1982).

Survival (ϕ), capture (p) and seniority probabilities (γ) or the resident fraction of the population (Pradel 1996) and population growth rate (λ) were estimated and modelled following the CMR methodology (Lebreton *et al.* 1992) and by the method developed by Pradel (1996) using the program MARK (White & Burnham 1999). In addition, the seniority probabilities are used to estimate other related demographic parameters, such as the recruitment component of population growth rate (see Nichols *et al.* 2000). The γ (or seniority) parameter is closely related to the concept of elasticity of λ (the growth rate) to changes in demographic rates (Nichols *et al.* 2000). For example, decomposing the expected population growth rate $E(\lambda_i)$, into the components related to survival $E(S_i)$ and recruitment $E(B_i)$, we can—according to Nichols *et al.* (2000)—compute an analogue of elasticity of the survival and recruitment components as

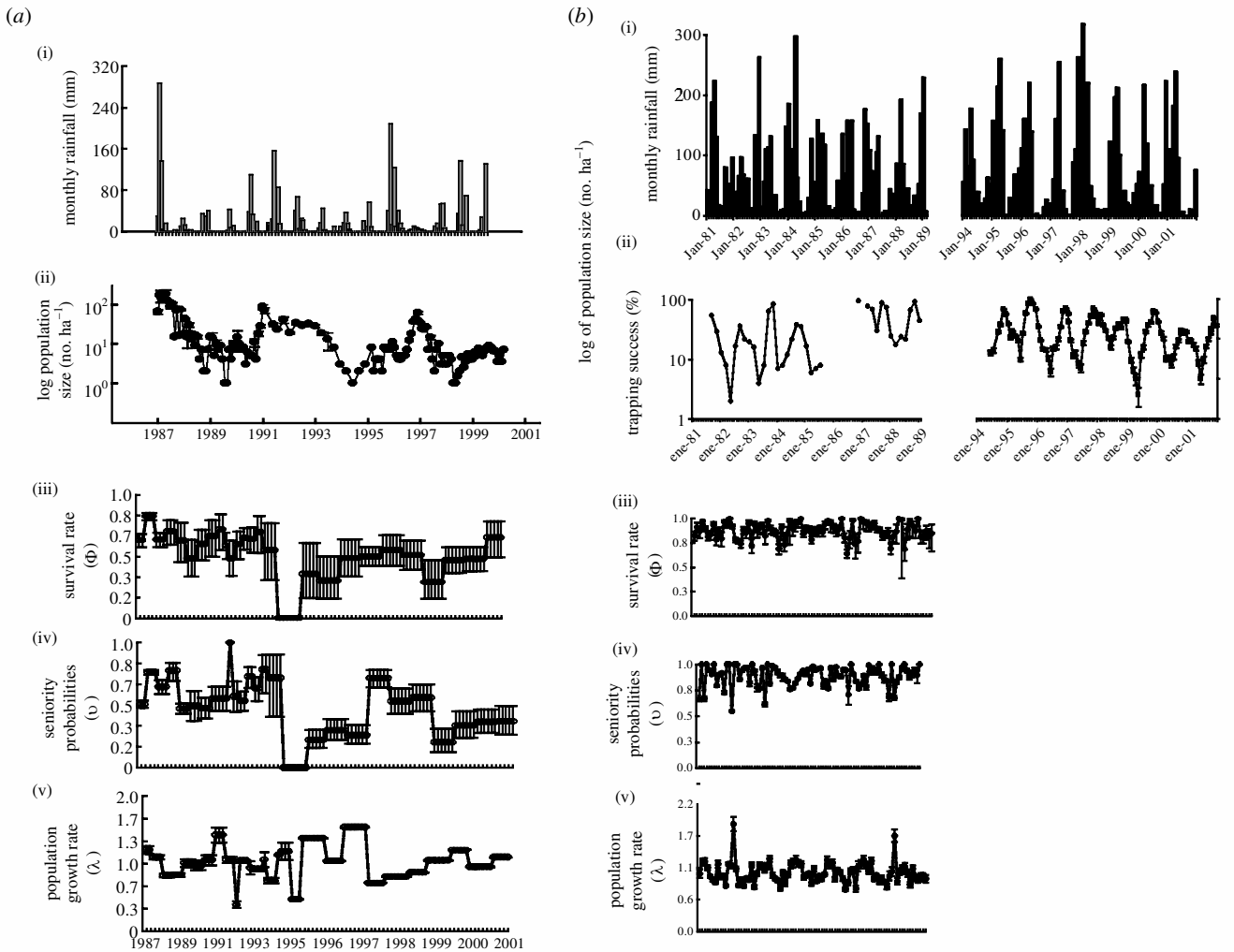$$\frac{\partial \log E(\lambda_i)}{\partial \log E(S_i)} = \gamma_{i+1}. \tag{2.1}$$

Figure 2. (*a*) *Phyllotis darwini*—Chile. (i) Monthly rainfall (bars) in Illapel (Chile). (ii) Leaf-eared mice (*P. darwini*) population dynamics. (iii) The survival rates of leaf-eared mouse females estimated from the model $\{\phi(\text{month} \times \text{year})\ p(\text{month} + \text{year})\}$. (iv) The relative contribution of the survival component of finite population growth rate of leaf-eared mouse females estimated from the model $\{\gamma(\text{month} \times \text{year})\ p(\text{month} + \text{year})\}$, where γ is the seniority probability. (v) The finite population growth rate (λ) of leaf-eared mouse females estimated from CMR data according to the statistical model $\{\phi(\text{month} \times \text{year})\ p(\text{month} + \text{year})\ \lambda(\text{month} \times \text{year})\}$. (*b*) *Mastomys natalensis*—Tanzania. (i) Monthly rainfall (bars) in Morogoro (Tanzania). (ii) Multimammate mouse (*M. natalensis*) population dynamics. (iii) The survival rates of multimammate mouse females estimated from the model $\{\phi(t)p(t)\}$. (iv) The relative contribution of the survival component of finite population growth rate of multimammate mouse females estimated from the model $\{\gamma(t)p(t)\}$. (v) The finite population growth rate (λ) of multimammate mouse females estimated from CMR data according to the statistical model $\{\phi(t)p(t)\lambda(t)\}$.

We modelled survival (ϕ), capture rates and seniority probabilities (γ) (Pradel 1996), and afterwards, using the best model for temporal variation in survival and capture rates, we modelled lambda (λ) using the Pradel (1996) survival and lambda model. Previous studies in *M. natalensis* showed full-time variation in capture rates (Julliard *et al.* 1999), therefore we used full-time variation in capture rates for all the *M. natalensis* models in addition to the seniority probabilities and recruitment rates. We estimated the time-specific rates of population growth (λ_t) using the approach of Pradel (1996).

Estimates were obtained through the maximum-likelihood method assuming a multinomial distribution of capture histories. For each of the demographic variables the overall time variation can be written as the sum of four components: month + year + year × month + error. The multinomial error was considered for parameter estimation. The basic CMR statistical models used the logit transformation for constraining the parameters θ, γ and p between 0 and 1, thus demographic rates can

be modelled as a linear logistic function of month (or seasons) and years.

The next step of the analysis was to estimate the proportion of variation accounted for by the within-year and between-year components. For these two rodents, the core of seasonality is the change between two reproductively defined periods: a reproductive season (July–December for *P. darwini* and May–October for *M. natalensis*) and non-reproductive season (January–June for *P. darwini* and November–April for *M. natalensis*). In consequence, we tested for no time variation; monthly variation (month); seasonal variation (season) and between-year variation (year) in the demographic parameters. For each demographic rate (survival, population growth, seniority and capture probability), we estimate the following models: (i) constant; (ii) monthly (month); (iii) month and year (month + year); (iv) seasonal (season); (v) season and year (season + year); (vi) only year effects (year); (vii) interaction between season and year (season × year); and (viii) full-time variation model (*t*).

To select the most appropriate model for describing demographic temporal variation we used a bias-corrected version of the Akaike's Information Criterion, AIC_c (Burnham & Anderson 1998) that is defined as

$$AIC_c = -2(\ln L) + 2K + \frac{2K(K + 1)}{n - K - 1}, \tag{2.2}$$

where $\ln (L)$ is the natural logarithm of the likelihood function evaluated at the maximum-likelihood estimates for a given model, K is the number of estimable parameters and n is the sample size. The model with the lowest AIC_c value represents the best choice to describe temporal variation in a given demographic rate.

3. POPULATION DYNAMIC MODELS

(a) *A monthly stage-structured matrix model*

To represent the rodent population dynamics we used a simple linear, time-invariant matrix model with monthly time-steps (Caswell 2001). Only the female fraction of the population was modelled. The basic stage-matrix model is given as

$$M_. = \begin{bmatrix} 0 & 0 & R_a \\ S_a & S_s \times (1 - \psi_s) & 0 \\ 0 & S_s \times \psi_s & S_a \end{bmatrix}, \tag{3.1}$$

where $R_a = $ [(per cent of reproductive females) $\times$ (0.5 $\times$ litter size)] represents the monthly reproductive rate per adult female (sex ratio at birth being assumed to be 0.5) and S_a represents the monthly adult survival rate. Survival from newly born to sub-adult, S_a, is assumed to be fully dependent on the mother's survival. Monthly survival rate of sub-adults was given by S_s. Monthly maturation rate from sub-adult to adult was given by ψ_s. The transition from the sub-adult stage to the adult stage was given by the product of maturation and sub-adult survival rates $(S_s \times \psi_s)$.

The parameters S_s, S_a and ψ_s of the matrix models were estimated from the multi-state (CMR) statistical models (Brownie *et al.* 1993) using monthly variation in demographic parameters. The seasonal reproductive rate per adult female (R_a) of leaf-eared mice was calculated from Lima *et al.* (1999; unpublished data), pregnancy rates were determined from 853 adult females, and litter size was estimated to be approximately three (Meserve & Le Boulengé 1987). The monthly reproductive rate per adult female (R_a) of multimammate mice was calculated from Leirs *et al.* (1993, 1997), pregnancy rates and litter size were determined from 5196 females captured in snap trapping studies.

To account for the within-year (monthly) variation in demography, we assumed month-specific matrices (see Yoccoz *et al.* 1998). Hence, the asymptotic properties of these seasonal models may be estimated separately. The annual matrix model can be given as

$$My = M_{12} \cdot M_{11} \cdot M_{10} \cdot M_9 \cdot M_8 \cdot M_7 \cdot M_6 \cdot M_5 \cdot M_4 \cdot M_3 \cdot M_2 \cdot M_1. \tag{3.2}$$

Assuming month-specific matrices then makes the linear and time-invariant matrix model of equation (3.1) a linear and time-variant model (Tuljapurkar & Caswell 1997):

$$M_{(t)} = \begin{bmatrix} 0 & 0 & R_{a(t)} \\ S_{a(t)} & S_{s(t)} \times (1 - \psi_{s(t)}) & 0 \\ 0 & \psi_{s(t)} \cdot S_{s(t)} & S_{a(t)} \end{bmatrix}, \tag{3.3}$$

where (t) denotes the monthly effects on the demographic parameters.

(b) *Elasticity*

The sensitivity coefficients (s_{ij}) are defined by absolute changes, whereas the elasticity coefficients (e_{ij}) are defined by the relative changes. Both coefficients are evaluated on the basis of the right and left eigenvectors and the dominant eigenvalue (population growth rate) of the matrix (Caswell 1978, 2001). For a given demographic parameter, a_{ij}, the sensitivity is defined as

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \tag{3.4}$$

and the elasticity as

$$e_{ij} = \frac{\partial \log (\lambda)}{\partial \log (a_{ij})} = s_{ij} \frac{a_{ij}}{\lambda}. \tag{3.5}$$

However, because small mammals typically are strongly affected by seasonal changes in the environment (Kalela 1957; Schaffer & Tamarin 1973; Krebs & Myers 1974), we evaluated the sensitivities (absolute and relative) of the annual population growth rate to changes in each demographic rate at each month during the year (see Caswell & Trevisan 1994; Yoccoz *et al.* 1998). The monthly sensitivities and elasticities were estimated according to Caswell & Trevisan (1994; eqn 6; p. 1300).

4. RESULTS

(a) *Population size*

Leaf-eared mouse numbers showed important temporal fluctuations, with population peaks closely associated with increases in annual rainfall (figure 2a(i)). In particular, three main outbreaks were evident in association with the ENSO events of 1986–1987, 1991–1992 and 1997–1998. In multimammate mice, seasonal fluctuations of population numbers were obvious with peaks every year around November (figure 2b(i)). Years with unusually high numbers (1984, 1986–1987, 1995) followed years with abundant rainfall early in the wet season.

Although the absolute densities are considerably larger in multimammate mice, the most striking difference between the two species is the relative magnitude of within-year variation. While multimammate mice reach high densities every year (albeit in some years higher than in other years), leaf-eared mice are very few in most years with a few clear outbreaks.

(b) *Demographic variability*

The goodness-of-fit test (GOF; see Choquet *et al.* 2003) for leaf-eared mouse female data showed no transient effects ($N(0,1)$ statistic for transients = 0.363; $p = 0.716$), but significant trap dependency (trap happiness; $N(0,1)$

Table 1. *The statistical best models are denoted according to each model-specific variation in the probabilities of survival (ϕ), seniority (γ), capture (p) and population growth rate (λ).*

(*t denotes full time-specific variation; s denotes seasonal time-specific variation; y denotes between-year variation; m denotes monthly variation; $+$ are additive effects and $\times$ an interaction term. The difference in AIC relative to the next best model is also given; AIC Akaike's information criterion. See, for details, table 3 in electronic Appendix A, available on The Royal Society's Publications Web site.)*

	Phyllotis darwini		*Mastomys natalensis*	
model	best model	ΔAICc with next-best	best model	ΔAICc with next-best
survival models	$\{\Phi(s \times y)p(m + y)\}$	−10.51	$\{\Phi(t)p(t)\}$	−33.39
recruitment models	$\{\gamma(s \times y)p(m + y)\}$	−16.17	$\{\gamma(t)p(t)\}$	−277.61
lambda and survival models	$\{\Phi(s \times y)p(m + y)\lambda(s \times y)\}$	−8.97	$\{\Phi(t)p(t)\lambda(t)\}$	−3050

signed statistics for trap dependency $= -5.71$; $p < 0.000\,01$). In consequence, we transformed the capture histories by splitting them for trap-dependency analyses using the U-CARE software (Choquet *et al.* 2003). By contrast, the GOF test for multimammate rat female data showed significant transient effects ($N(0,1)$ statistic for transients $= 3.63$; $p = 0.0003$) and significant trap dependency (trap happiness; $N(0,1)$ signed statistics for trap dependency $= -9.49$; $p < 0.000\,01$). In consequence, the model selection process for multimammate rats is less reliable than for leaf-eared mouse.

The best models for describing temporal variation in survival and seniority probabilities and population growth rate of leaf-eared mice showed an interaction between season and year (table 1; figure 2*a*(iii–v)). By contrast, the full-time variation models were the best for describing the pattern of variation in survival and seniority probabilities and population growth rate for multimammate mice (table 1; figure 2*b*(iii–v)), which is consistent with the presence of transients and trap-dependency problems. In fact, owing to the stronger seasonal component of variation in population dynamics in multimammate rats, we expected to find a clear-cut seasonal structure in demographic models.

The analysis of the pattern of monthly variation in demography for leaf-eared mice is revealed in figure 3. Survival rates (sub-adults and adults) were higher during the non-breeding season (January–June), but they tend to be lower during the middle of the breeding season (September–November), with a peak in sub-adult survival rates during the end of the year (figure 3*a*). By contrast, maturation rates showed a weak seasonal variation, this rate tends to be higher during the rainfall season (figure 3*a*). Reproductive rates (fraction of reproductive females) are higher in the months following the rainy seasons (September–December) and peaked in October (figure 3*a*). The analysis of the pattern of variation in demography for multimammate mice revealed strong within-year variability, especially in maturation and reproductive rates, but not in survival rates. Maturation rates were very high during the major rainy season ('masika') and reproductive rates were high immediately after the 'masika' rainfalls (figure 3*b*). Survival rates (sub-adult and adult) do not exhibit any clear seasonal pattern (figure 3*b*).

(c) *Within-year matrix models*

The monthly matrices characterizing the dynamics of leaf-eared mouse are shown in table 2. The annual overall
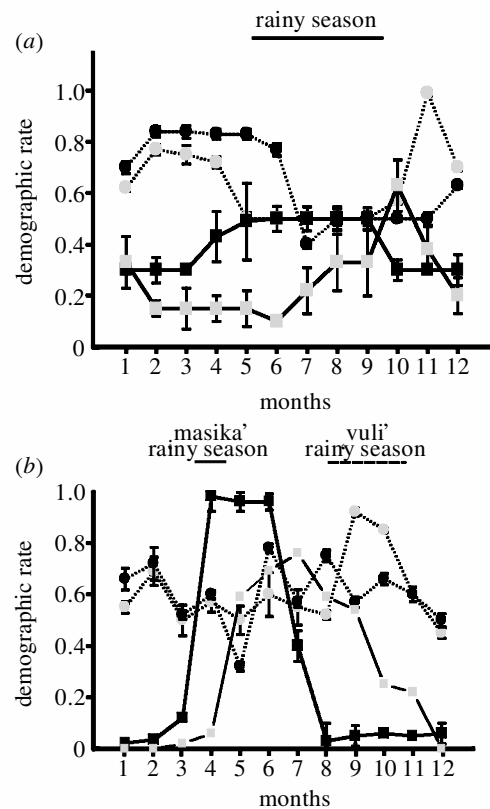

Figure 3. Within-year female variation in demographic rates. (*a*) *Phyllotis darwini*—Chile. (*b*) *Mastomys natalensis*—Tanzania. (*a*) Adult survival rates (filled circles and dotted line), sub-adult survival rates (grey circles and dotted line), maturation rates (filled squares and solid line) and reproductive rates (grey squares and solid line).

growth rate was 0.96, indicating a decreasing population trend during the 14 years of study. The monthly elasticities of the annual population growth rate are shown in figure 4*a*. Survival rates had a higher impact from December to June (figure 4*a*), while reproductive rates had a similar impact on both population growth rate and survival during the breeding season (August–November) (figure 4*a*).

The monthly matrix models for the multimammate mouse are shown in table 2. The overall annual growth rate was 0.99, indicating almost a stationary population growth pattern in the long term. Survival rates of multimammate mice had a very large impact on annual

Table 2. Monthly demographic rates used to parameterize the periodic matrix models.
(R_a = [(per cent of reproductive females) × (0.5 × litter size) × 1.33 × 1.50] (according to Leirs *et al.* 1997) represents the monthly reproductive rate per adult female (sex ratio at birth being assumed to be 0.5) and S_a represents the monthly adult survival rate. Survival from newly born to sub-adult, S_a, is assumed to be fully dependent on the mother's survival. Monthly survival rate of sub-adults was given by S_s. Monthly maturation rate from sub-adult to adult was given by ψ_s. The transition from the sub-adult stage to the adult stage was given by the product of maturation and sub-adult survival rates ($S_s \times \psi_s$).)

month	*Phyllotis darwini*				*Mastomys natalensis*			
	R_a	ψ_s	S_s	S_a	R_a	ψ_s	S_s	S_a
January	1.88	0.30	0.62	0.70	0.00	0.02	0.55	0.66
February	0.85	0.30	0.77	0.84	0.00	0.04	0.69	0.72
March	0.85	0.30	0.75	0.84	0.34	0.12	0.50	0.52
April	0.85	0.43	0.72	0.83	0.98	0.98	0.57	0.60
May	0.85	0.49	0.50	0.83	10.07	0.98	0.50	0.32
June	0.57	0.50	0.50	0.77	13.21	0.96	0.60	0.78
July	1.25	0.50	0.50	0.40	14.24	0.12	0.50	0.57
August	1.88	0.50	0.50	0.50	9.87	0.03	0.52	0.75
September	1.88	0.50	0.50	0.50	6.80	0.05	0.92	0.57
October	3.58	0.30	0.57	0.50	2.54	0.05	0.85	0.66
November	2.16	0.30	0.98	0.50	2.28	0.06	0.60	0.60
December	1.14	0.30	0.70	0.63	0.00	0.05	0.45	0.50

population growth rates before the major rainy season ('masika'): from May to June reproduction was more important and from July to September both components showed similar impact (figure 4*b*). Thereafter survival elasticity increases towards December (figure 4*b*).

Although both small rodent species show a seasonal pattern, there are several differences in the within-year variation of elasticities. Multimammate mice exhibit stronger changes in the relative importance of the different demographic parameters throughout the year, basically because of a large within-year variation in reproduction and maturation which is consistent with the extensive within-year variability exhibited by this species compared with leaf-eared mice.

5. DISCUSSION

(a) *General*

Our results point to the importance of understanding the consequences of the seasonal structure of rodent dynamics. One of the most striking differences between both rodent species in this study is the magnitude of the within-year changes in elasticity coefficients and the demographic contributions to population growth. In addition, leaf-eared mice showed important between-year variability in the relative contributions of the components of population growth (an issue dealt with elsewhere; Lima *et al.* 2002). In the following, we will first discuss the implications of our findings using both the CMR demographic and the matrix modelling approach for the understanding of rodent demography. We will then focus on the specific case of leaf-eared mice in western South America and multimammate mice in eastern Africa.

Although there is an analogy between the proportional seniority contributions (γ) and the elasticities derived from projection matrices, there are several differences in the meaning of the two quantities (Nichols *et al.* 2000). One of the most obvious is that elasticities are derived from the asymptotic properties of the matrix models (Caswell 2001; Tuljapurkar & Caswell 1997), while the γ parameters have

a time-specific interpretation (from t to $t + 1$) (Nichols *et al.* 2000). In addition, the use of the proportional seniority contributions has the advantage that the estimates do not rely on strong assumptions, unlike the matrix elasticity estimates, and they can be statistically modelled using external covariates (weather, density, enemies) (Nichols *et al.* 2000).

As expected in both species, the time-specific growth rates (monthly growth rates) showed a more important component of recruitment during the breeding season months, which is not a surprising finding. However, an important result of our demographic analyses, using CMR modelling, is the substantial variation observed in the demographic components of population growth. Therefore, understanding the nature and magnitude of temporal demographic variability may represent a challenge for small-rodent population ecologists. For example, the best model characterizing demographic variation in leaf-eared mice was one with a season × year interaction and full-time variation for multimammate rats. This pattern of temporal variation implies that within- and between-year variability in demographic rates may be somewhat difficult to disentangle. In particular, this may be interpreted as a consequence of changes in the length and timing of the breeding period between different years. It is known that the timing of the start and end of the breeding season (basically the length) in small rodents is highly variable between years (Leirs *et al.* 1994; Tkadlec 2000). In particular, the leaf-eared mouse showed large changes in the length of the breeding seasons during wet and dry years (Lima & Jaksic 1999), which may explain the season × year interaction observed in the seniority contributions.

By contrast, elasticity analyses derived from whole-year matrix models are likely to yield more reasonable approximations to numerical fluctuations showing strong within-year variability in relation to between-year variability (Nichols *et al.* 2000). The use of periodic elasticities (Caswell & Trevisan 1994) derived from the monthly matrix models may be very useful for understanding the
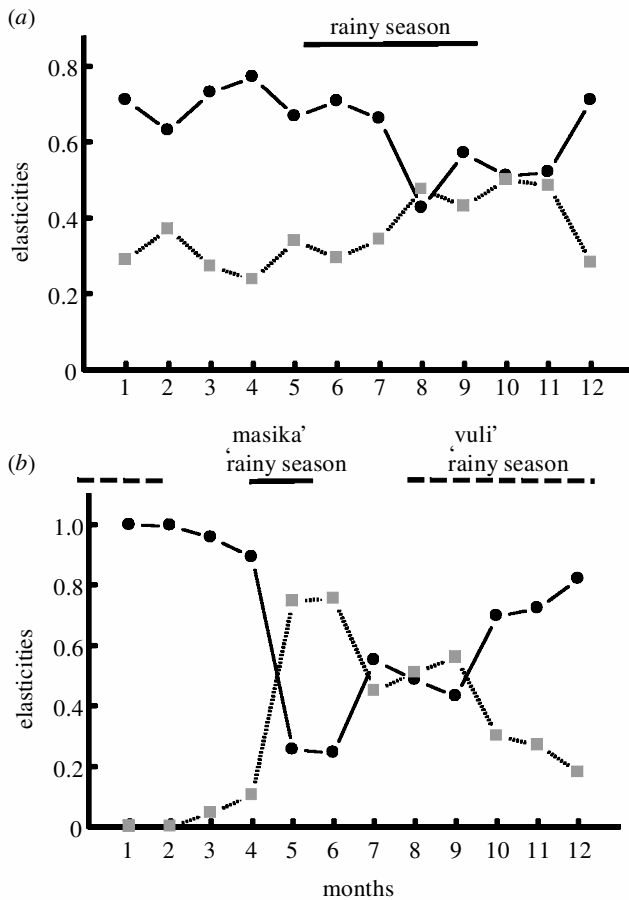
(a)

(b)

Figure 4. Monthly elasticity coefficients estimated from the matrix models. Survival elasticity component $[S_a + (S_s \times \psi_s) + (S_s \times (1 - \psi_s))]$ (filled circles) and reproduction elasticity component $(R_a + S_a)$ (grey squares). (a) *Phyllotis darwini*—Chile. (b) *Mastomys natalensis*—Tanzania.

demographic machinery of these small rodents. When analysing the within-year pattern of demographic variation using monthly elasticities, we found a consistent pattern for both rodent species studied here. The pattern of seasonal variation in elasticity coefficients taken from matrix asymptotic properties suggests that factors influencing survival will have larger impacts on population growth rate during the non-breeding season. Multimammate mice exhibit stronger variation in elasticity coefficients but there is a similar general trend. During the breeding season the more important changes in population growth rates are due to variation in reproduction, while variation in survival rates is more important for determining population growth in other months. Despite the general trend, it is worth observing the differences in the magnitude of the changes in monthly elasticities between the two rodent species. Because the within-year elasticities reflect, in part, the changes of the age structure of the population through the year, the pattern and magnitude of demographic variation represent a key element to be understood in rodent dynamics. These observations indicate that large numerical changes in rodent populations (from very low densities to outbreak densities) may be due to very different demographic mechanisms, such as small variations in several demographic rates during different seasons, large vari-

ations in one demographic rate during some months or seasons, and then sudden changes to another demographic parameter.

(b) Seasonality

Although seasonality typically is recognized as an important feature in demographic studies on small rodents (see Kalela 1957; Schaffer & Tamarin 1973; Krebs & Myers 1974), it is often ignored in population modelling of small rodents (but see Stenseth *et al.* 1998, 2002, 2003*a*). This study demonstrates the importance of incorporating seasonality into population dynamics models. Although it is somewhat obvious that reproduction as well as survival is important during the main breeding period, whereas only survival is the key demographic component outside the main breeding period, it is not clear how much these life-history components contribute during the breeding period to the overall annual population growth rate. The two species studied in this paper do indeed exhibit profound differences in this respect: whereas a distinctly seasonal breeder such as the multimammate mouse is characterized by a more profound contribution from reproduction than from survival to the overall population growth during the breeding period, a less distinct seasonal breeder such as the leaf-eared mouse is characterized by an approximately equal contribution from reproduction and survival.

(c) Evolutionary issues: maximizing λ

Through evolution, the overall net population growth rate (λ) is—under prevailing environmental conditions—being maximized (see Pianka 1983). Such evolutionary changes are achieved through evolutionary changes in the reproductive performance as well as survival of the individuals within the population. The sensitivity and elasticity quantify the relative importance of these two evolutionary avenues. Our analysis suggests that for the leaf-eared mouse, features favouring survival throughout the year will provide selective value, but that during the main breeding season, features favouring reproduction and survival are about equally beneficial. For the multimammate mouse, features favouring survival are particularly important outside the breeding season, whereas during the breeding season features favouring recruitment are particularly important. This may contribute to the extremely large litter size that is known for these species (and the large number (24) of nipples in females).

(d) Applied issues: reducing the population growth rate (λ) or the population (N)?

Pest control aims at reducing the damage that organisms cause to agricultural produce, other assets or health. The most common strategy for doing this is to reduce the population size of these organisms—directly or indirectly. In terms of this paper, this means that we are interested in either reducing the overall net population growth rate (λ) or reducing the equilibrium population density (or size) of the pest species. Although the two objectives may appear similar, analysing matrix elasticities demonstrates that we are clearly dealing with different quantities. Whereas the elasticities of λ represent the proportional change in annual population growth rate that results from a proportional change in the matrix elements

(demographic rates; Caswell 2001), the elasticities of the population size (density-dependent elasticities) are the slopes of the log population size at equilibrium (or some measure of average population size) as a function of log of the demographic rates:

$$e_{ij}(N) = \frac{\partial \log (N_{\text{equilibrium}})}{\partial \log (a_{ij})}. \qquad (5.1)$$

In fact, both types of elasticity may give very different results in several situations, especially for populations fluctuating around their equilibrium level (Grant & Benton 2000). As a result, what is the best tool within pest control depends on the kind of population dynamics and the focus of the management plans. For example, in the case of chronic pests (Berryman 1999), we should use the elasticities of the equilibrium population size because the objective will be to reduce this equilibrium density. By contrast, in rodent pests characterized by irruptive responses (pulse dynamics; *sensu* Berryman 1999) of rodent density to some external factor (e.g. rainfall), the control should aim at reducing the population growth rate following the exogenous perturbation. Because in most cases, during the increasing phase, the pest rodent populations exhibit exponential growth, the use of linear elasticities may represent an adequate analysis for implementing or deducing management actions. In particular, we maintain that the two species analysed in this paper are good examples of pulse-kind dynamics with strong responses to an exogenous factor such as is rainfall in these two semi-arid environments.

The reduction of the overall net annual population growth rate (λ) is attempted through the reduction of survival and, in some cases, through the reduction of reproduction. Again elasticity values quantify the relative importance of these two control avenues and can therefore be used to investigate which strategies could be more effective. In the case of leaf-eared mice, and from an ecological point of view, factors that reduce survival (e.g. predation) would be efficient throughout the year, particularly during autumn and early winter, whereas ecological factors influencing reproduction should be more important in late winter and spring (breeding season). In the case of multimammate mice, reducing reproduction will only be efficient during May–September; in the other months it is only efficient to reduce survival. Although it may seem trivial to conclude that in both species a reduction of reproduction will only be efficient during the reproductive season, it is less trivial to see that the reduction of survival may be effective throughout the year in one species, but only outside the breeding period in another species. The elasticity analysis in figure 4*b* shows that in May–June a proportional reduction of reproduction in multimammate rats will have a high effect, in all other months a similar reduction of survival will have a similar or much larger effect on population growth. This questions the argument that for highly fecund species (and multimammate rats certainly belong in this group), fertility control necessarily always is the more appropriate control strategy (Chambers *et al.* 1997). Whereas this is probably a very valuable strategy to stop outbreaks building up over a short period within a year, our study suggests that it may be less powerful as an exclusive technique for minimizing annual population growth. Theoretical con-

siderations of rodent population management approaches should therefore always consider very carefully the precise kind of intervention that is targeted.

Finally, how to develop and implement a controlling strategy for rodent pest populations represents a complex problem (Singleton 1994; Singleton & Petch 1994; Singleton *et al.* 1999; Stenseth *et al.* 2003*b*). We found large within- and between-year variation in the relative contributions of both components and in the elasticity coefficients indicating a more complex scenario in both rodent pests. It is important to take into account that elasticities reflect, in part, the age structure of the population, which are consequences of the changes in demographic rates during the year (Lima *et al.* 2001). For the case of rodent outbreaks the present study shows that using only one type of control strategy may not be effective, because of the large within- and between-year variability in demography and the influence of different factors on population dynamics. A mixed control strategy (reducing survival and fertility) that considers temporal variability in demographic rates should be more rewarding. Of course, this discussion assumes that it is equally easy to obtain similar reductions of survival or reproduction. At present, this is not possible with the availability of relatively cheap and efficient rodenticides, and fertility control is still not yet available for practical use (Buckle & Smith 1994; Chambers *et al.* 1999).

The use of CMR demographic analysis and matrix modelling has great potential in rodent management studies (Stenseth *et al.* 2001). In sum, the development of statistical models for demographic analyses based on CMR data, and the matrix population dynamics models, represent two related approaches for the study of rodent populations. It has been recently demonstrated that the link between demography and population dynamics can be very useful for gaining an understanding of rodent population fluctuations (Leirs *et al.* 1997; Yoccoz *et al.* 1998; Lima *et al.* 1999). We consider that the unification of both approaches should also be very useful for studying applied issues, such as control strategies in rodent-pest species (Nichols *et al.* 2000; Stenseth *et al.* 2001). However, to perform this kind of analysis, long-term CMR data are required and, therefore, an important commitment to long-term monitoring of rodent pest populations is needed.

6. CONCLUSION

We have demonstrated in this paper, through a comparative analysis, the profound effect of seasonality on the dynamics of small rodents living in arid environments. We have demonstrated that reproduction and survival contribute approximately equally to population growth following the rainy season in the leaf-eared mouse, whereas the multimammate mouse is characterized by a more clearly defined seasonal structure into breeding and non-breeding seasons and that reproduction contributes far more than survival following the main rainy seasons. This insight is of importance for both basic (ecological and evolutionary) studies as well as for more applied issues (such as pest control). Our studies have provided yet another example of there being much to be learnt of general value from studying the dynamics of fluctuating small rodents.

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