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Living slow and dying young? Life-history strategy and age-specific survival rates in a precocial small mammal

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Summary

1. Mammalian life histories can be ordered along a slow–fast continuum from slow-developing, long-lived species with low reproductive rates at one end to rapidly developing, short-lived species with high reproductive rates at the other. Body size and mortality rate are strong correlates of the slow–fast axis, whereby juvenile and adult mortality rates correlate positively but are linked to certain life-history traits with differing strengths. The strong covariation of life-history traits renders it difficult to evaluate the adaptive value of single life-history elements. Species that deviate from the common pattern might help to identify specific selected strategies.

2. Caviomorph rodents show an unusual combination of life-history traits. Like slow-living mammals, they produce few precocial young after long gestation periods, but they have the early maturation potential of their fast-living counterparts. This combination of life-history traits suggests low levels of juvenile mortality but high adult mortality rates, and thus an unusually low ratio of juvenile to adult mortality compared to other small mammals. To test these predictions, we modelled age-specific survival probabilities using capture–recapture data from a wild population of *Cavia magna*.

3. Patterns of age-specific survival rates were in accordance with the predictions, but atypical for small mammals. Levels of adult survival were low, and comparable to those of much smaller rodent species. Juvenile survival probabilities were high relative to those reported for other small mammals and reached adult levels after only 1 month. The ratio of adult to early juvenile survival depended strongly on the date of birth. Whereas survival of young from the first birth cohort in spring did not differ from that of adults, early survivorship of later cohorts was lower.

4. Our results fit expectations from life-history theory and suggest that high levels of adult mortality selected for the early onset of reproduction in wild cavies. The comparatively low juvenile mortalities are probably a consequence of the precocial state of the cavy offspring. We suggest that the reproductive strategy of cavies represents a different solution to the trade-off between fecundity and juvenile survival compared to altricial small mammals.

Key-words: altricical–precocial dichotomy, cavies, fecundity–juvenile survival trade-off, small mammals, slow–fast continuum.

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Introduction

Comparative analyses have brought some order to the ‘chaos of life’. Within taxonomic classes, basic life-history parameters covary in a predictable pattern (reptiles: Dunham & Miles 1985; birds: Saether 1988; mammals: Stearns 1983). For mammals, a prominent axis of life-history variation is the slow–fast continuum: some lead a fast, others a slow life (Eisenberg 1981; Gaillard *et al*. 1989; Read & Harvey 1989; Promislow & Harvey 1990). The fast living species show short gestation and lactation periods, mature at an early age,

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produce large litters of small offspring and die after a short life span – in contrast to their slow counterparts (Harvey, Read & Promislow 1989; Gaillard *et al*. 1989; Read & Harvey 1989). It has long been recognized that body size plays a crucial role in determining the time-scale of mammalian life histories: almost all life-history parameters correlate with body size, with small mammals living fast and large ones living more slowly (Blueweiss *et al*. 1978; Western & Ssemakula 1982; Stearns 1983; Calder 1984). This pattern underlies the hypothesis that body size, or another strongly correlated variable such as brain size (Sacher & Staffeldt 1974) or metabolic rate (McNab 1980, 1983), is the true target of selection, and that other life-history parameters simply covary according to allometric scaling rules.

However, after removing the effects of body size from the comparative analysis, the slow–fast continuum remains intact, and species can then be ordered along another gradient – mortality (Harvey *et al*. 1989; Read & Harvey 1989; Promislow & Harvey 1990; Harvey & Nee 1991). The importance of mortality in shaping life histories is also borne out by theoretical models, and these suggest further that it is the relationship between mortality rates of the different age-classes that is particularly important (Schaffer 1974; Michod 1979; Charlesworth 1994). The mortality rates of juveniles and adults are highly correlated across mammals, but juvenile mortality is usually higher and more variable than adult mortality (Charnov 1986). For a given size, juvenile mortality is correlated most closely with gestation period, litter and offspring size, whereas adult mortality is correlated most strongly with age at maturity (Sutherland, Grafen & Harvey 1986; Promislow & Harvey 1990).

Deviations from the slow–fast axis of life-history variation are rare, implying constraints on the independent evolution of life-history traits (Ricklefs & Wikelski 2002). Species with an unusual combination of life-history parameters could help to disentangle this 'life-history nexus' and enable us to relate specific ecological factors to single life-history traits. One example of 'atypical' mammals is the wild cavies (Caviidae), a family of precocial rodents. As Harvey & Nee (1991) put it, they might be expected to follow the strategy of 'living fast, dying young and leave a good looking corpse behind'. Wild cavies can mature very early in the laboratory, i.e. with less than 50% of the adult body mass, are weaned at an early age and predation pressure is reportedly high in natural populations (Rood 1972; Jaksic 1986; Cassini 1991; Kraus & Rödel 2004). Such factors are suggestive of a fast-living small mammal. However, in contrast to most small mammals, cavies have a disproportionately long gestation period of approximately 2 months and they produce small litters of large, highly precocial young. This is consistent with a slow life-history strategy. The life history of the cavies does not appear to conform to either stereotype, but rather jumps along the slow–fast continuum.

Given this combination of life-history traits, we can predict the patterns of age-specific mortality rates in populations of wild cavies based on the empirical relationships described above. The early age at maturity points towards high adult mortality, whereas the long gestation period and the small litters of large offspring imply low juvenile mortality. Adult and juvenile mortality rates should thus be somewhat decoupled; that is, the ratio of juvenile to adult mortality should be low compared to other small mammals (but still > 1). Here we test if these predictions hold in a wild population of *Cavia magna* (Ximénez). If cavies do, indeed, have an atypically low ratio of juvenile vs. adult mortality, this might be one piece of the puzzle explaining the strange life history of these precocial small mammals.

Methods

STUDY SPECIES AND STUDY POPULATION

C. magna is a recently described cavy species, confined to the wetlands of northern Uruguay and southern Brazil (Ximénez 1980). *C. magna*, a 500-g rodent, is one of the most extreme examples for precocial reproduction in small mammals, and thus is an especially suitable study subject to answer the questions raised in the Introduction. After a gestation period of, on average, 64 days, they give birth to just one or two offspring which already weigh almost 20% of their mother's weight at birth (C. Kraus, unpublished data). Sexual dimorphism is small and, in captivity, females may mature when only about 30 days old (F. Trillmich, unpublished data).

In our study population, reproduction was seasonal and rather synchronized, with young of the first cohort being born in early spring. The duration of the breeding season, and thus the number of birth cohorts, varied among years, with individual females producing up to four litters annually (Kraus, Künkele & Trillmich 2003; C. Kraus, unpublished data). *C. magna* lives solitarily in overlapping home ranges in an apparently promiscuous mating system (Kraus *et al*. 2003).

STUDY AREA

We conducted this study in the national park 'Refugio de Fauna Laguna de Castillos', situated near the Atlantic coast in the province of Rocha, Uruguay. Populations of two wild cavy species (*C. magna* and *C. aperea*) co-inhabited an extensive *caraguatal* (*c*. 3·3 ha), a typical wetland vegetation with the key species *Eryngium pandanifolium* (a tall spiny shrub). The surrounding short and adjacent long grassland was used by the cavies for feeding, but they relied on the *caraguatal* and always returned to it for shelter. Thus, they formed a distinct, island-type population, and this enabled us to collect data of the whole cavy population and minimize any edge effects. Gambarotta, Saralegui & Gonzáles (1999) provide a detailed description of the reserve and its fauna.

CAPTURE–MARK–RECAPTURE

To distribute our capture efforts evenly within the study site we built a grid system (250 × 200 m) marking the intersections at 10-m distances with wooden stakes. The systematic capture–mark–recapture study lasted from May 1999 to January 2001. Two hundred live traps (Tomahawk, USA) were distributed on the grid system, and each was placed within 5 m of a particular grid stake. The complete *caragatual* and the surrounding parts of the grassland were trapped to ensure that the trapping area covered the whole cavy population. Twice monthly (at approximately biweekly intervals), for two consecutive nights, unbaited traps were placed on the most heavily used runways. They were set 2 h before sunset and again at night 2 h before sunrise, because twilight phases were identified as the cavies' main activity periods. Traps were checked 4–5 h after setting and then left closed during the remainder of the night and day to minimize stress for the animals due to confinement in traps and adverse weather conditions. Between trapping sessions traps were left open but inactivated to habituate the cavies to the traps and to prevent them from changing their preferred runways. Animals caught for the first time were marked individually by injecting a transponder (Trovan, UK) subcutaneously and additionally, to minimize estimation bias due to tag loss, by attaching a numbered metal tag to the ear (National Band and Tag Co., USA). Before release body mass and body length were measured, each individual was sexed and its reproductive state was noted.

MODELLING OUTLINE

To model age-specific survival rates we used the Cormack–Jolly–Seber (CJS) approach for open populations (Cormack 1964; Jolly 1965; Seber 1965) implemented in the program MARK (White & Burnham 1999). Model selection was based on Akaike's information criterion (AIC) as described by Burnham & Anderson (1998). Because of the small sample sizes ($n/K_{GM} < 40$, K_{GM}: number of parameters of the global model), we employed the second-order variant AIC_c and in the presence of extra-binomial variation the quasi-likelihood modified QAIC_c, respectively (Anderson, Burnham & White 1994). We report (Q)AIC differences (Δ_i = (Q)AIC$_i$ – minimum (Q)AIC) to compare the support the different models had of being the estimated best approximating model in the set. According to Burnham & Anderson (1998) models with $\Delta_i \leq 2$ have substantial support and models with $4 < \Delta_i < 7$ achieve some support, whereas models with $\Delta_i > 10$ have little support or fail to account for some important explainable variation in the data and might be omitted from further consideration. Additionally, we use normalized Akaike weights (w_i) to assess the relative likelihood of competing models. We compare the relative importance of structural elements common to more than one model by summing up their AIC weight.

To account for model selection uncertainty we employed model-averaging techniques, which weigh the impact of a given model on the estimated parameter value according to its AIC weight (Buckland, Burnham & Augustin 1997; Burnham & Anderson 1998). We report these model-averaged values for maximum likelihood estimates and their unconditional standard errors (unconditional on a certain model selected, but conditional on the candidate set of models). All survival probability estimates are given as monthly rates (30 days). The models' notation is based on Lebreton *et al*. (1992).

GOODNESS OF FIT

The CJS model assumes only binomial variation to be present. However, real capture–recapture data are often somewhat overdispersed, resulting in an underestimation of the variances (Anderson *et al*. 1994). We assessed the goodness of fit of our global models for age-specific survival rates using the parametric bootstrap procedure available in program MARK to estimate the variance inflation factor [$\hat{c}$ = *deviance* (global model)/mean *deviance* (1000 simulated models)]. This factor is a measure of the extra-binomial variance (overdispersion) present in the data, which is caused by unequal capture or survival probabilities within groups (Anderson *et al*. 1994). Model selection statistics, standard errors and confidence intervals of the maximum likelihood estimates (MLEs) were adjusted according to the $\hat{c}$. We are aware that the bootstrap estimator of $\hat{c}$ might be negatively biased (White 2002). However, the biology of our study species does not suggest any serious overdispersion likely to be present in the data. Cavies in our study population moved solitarily and randomly with respect to each other (Kraus *et al*. 2003). Young cavies are fully mobile within hours after birth and even nibble solid food on their first day of life (Rood 1972).

CANDIDATE SET OF MODELS

The multivoltine, but seasonal temporal breeding pattern in our cavy population precluded the application of the commonly used structure of age-class models (e.g. Cooch & White 1999), because these assume that the time interval between encounter occasions corresponds to the time required for an animal to enter the next age class and that all age classes considered are present at every trapping session. Because these assumptions were not met, we chose a different approach based on the relatively synchronized birth pulses we observed (Kraus *et al*. 2003). Captured juveniles and subadults were assigned to one of the major birth pulses on the basis of their body weight. Animals that could not be assigned unequivocally and those of the late, but small, birth pulse in February 2000 were omitted from the analysis. These age-cohorts were treated as groups in the basic model structure. By following the 'fate' of the age-cohorts through time and comparing their survival rate for the same time interval, we were able to obtain age-specific survival rates not confounded by time-dependence. The ratio of adult to juvenile survival for a given time interval for the different juvenile pulses also enabled us to identify cohort-specific characteristics of survival.

Because the age-cohorts were drained by mortality over time, we restricted our analysis to time-windows for which enough animals were left in each cohort to estimate their survival. The first data set represents winter survival and spans from May to September 1999. It includes 179 individual *C. magna* (88 females, 91 males) which were caught 573 times (only one capture per trapping session considered). These were subdivided into the four age-cohorts of adults, subadults from the first birth pulse around October 1998 (~7 months old), subadults from the second birth pulse around December 1998 (~5 months old) and the late-born juveniles of May 1999. The second period, from October 1999 to April 2000, includes the main birth season of our wild cavy population. This data set includes 206 individual *C. magna* (94 females, 112 males), which were caught 702 times (only one capture per trapping session considered). During this period animals from the first data set were considered to be adults (all older than 5 months). Thus, the three age-cohorts considered were adults, juveniles born in October 1999 and juveniles born in December 1999. Because the last cohort was not present during the first 2 months of this data set, we constrained their parameter values to equal those for the October juveniles for these months. During the reproductive season of 2000/2001 animal numbers were too low to model age-specific survival rates.

The time-scale chosen for survival rates $\phi(T)$ differed from that of recapture rates $p(t_i, i = 1, 2, \dots k$th trapping session), because biweekly time intervals would have been too fine-grained (we would hit many boundary estimates of $\phi_i = 1$). We kept the first 2 months of life separate, because the first month corresponds to the period when the offspring depend on the mother (lactation lasts around 25 days in *C. magna*; C. Kraus, unpublished data) and during the second month, females can potentially mature. Males probably attain sexual maturity within 3 months (F. Trillmich, unpublished data). After that we considered bimonthly time intervals. Thus, for survival analysis, the May–September data set has the temporal structure 1 month/1 month/2 months and the October–April set 1 month/1 month/2 months/2 months (but 1 month/1 month/1 month/1 month/2 months for the December cohort). We constrained parameters to be constant over the interval considered.

Given the patterns of age-specific mortality rates described in the Introduction, we expected survival of young wild cavies to increase with age until adult levels were reached. To determine at which age this transition occurred in our population, we used the following basic modelling strategy: in the global model all age-cohorts were allowed to have different survival rates over time; that is, juvenile survival rates could potentially differ from those of adults for up to 7 (May–September) and 6 months (October–April), respectively. For the competing models in the set, we constrained survival parameter values to be identical with those of adults after successively shorter time-periods until no age-effect on survival remained. Sex was implemented as a potentially interactive or additive factor. In total, the model set for May–September consisted of 126 candidate models and that for October–April of 105. The notation of the candidate models and their biological meaning is shown in Table 1.

Results

GOODNESS OF FIT

The bootstrap goodness-of-fit tests indicated that some overdispersion was present in our data sets (May–September: $P = 0{\cdot}005$, October–April: $P = 0{\cdot}07$). Therefore, we adjusted the model selection statistics, standard errors and confidence intervals with the corresponding estimates of $\hat{c}$ (May–September: $\hat{c} = 1{\cdot}12$, October–April: $\hat{c} = 1{\cdot}09$).

MODEL SELECTION

For both time periods, model selection suggested that survival of juvenile wild cavies rapidly reached adult levels: models allowing for only 1 month of distinct juvenile survival rates achieved the most support (Table 2). For the data set from May to September 1999, five of the seven models with $\Delta_i \leq 2$ had this model structure; only two allowed for two months of distinct juvenile survival. Models with 1 month of different juvenile and adult survival rates were 2·5 times more likely than those with 2 months ($\Sigma w_{1\text{ month}} = 0{\cdot}62$ vs. $\Sigma w_{2\text{ months}} = 0{\cdot}25$), and together these had 7·7 times more support than models allowing for 4 months of lowered juvenile survival ($\Sigma w_{4\text{ months}} = 0{\cdot}11$). Models without an age-effect on survival and those with different juvenile survival for over 4 months were relatively unlikely ($\Sigma w_{\text{no age effect}} = 0{\cdot}01$, $\Sigma w_{>4\text{ months}} = 0{\cdot}004$). Similarly all three 'best' models ($\Delta_i \leq 2$) for the period between October 1999 and April 2000 allowed for only 1 month of distinct juvenile survival rates. Models in the candidate set with this structure were 3·7 times more likely than those with age-specific survival for 2 months ($\Sigma w_{1\text{ month}} = 0{\cdot}55$, $\Sigma w_{2\text{ months}} = 0{\cdot}15$). Together they were 5·7 times more likely than models with 4 months of distinct juvenile survival rates ($\Sigma w_{4\text{ months}} = 0{\cdot}12$). Models without age structure achieved similar support ($\Sigma w_{\text{no age effect}} = 0{\cdot}13$). Models with up to 6 months of age-specific survival were relatively unlikely ($\Sigma w_{6\text{ months}} = 0{\cdot}05$). In summary, the model selection results provide strong evidence that shortly after weaning (lactation lasts approximately 25 days), young wild cavies in our population already had survival rates indistinguishable from those of adults.

Table 1. Candidate set of models and their biological significance for age-specific survival of wild cavies. Factors considered are age (a), sex (s) and time (T for ϕ, t for p). The global models are highlighted in bold type

ϕ	Apparent survival is …	p	Recapture is …
May–September 1999			
$4a * T$	Age-specific for around 7 months	$\mathbf{s * 4a * t}$	Time-, age- and sex-specific, all factors considered interact
$3a * T$	Age-specific for around 5 months	$s * t$	Sex- and time-specific
$2a * T$	Age-specific for at least 4 months	$4a * t$	Age- and time-specific
$2a(2\text{mon}) * T$	Age-specific for up to 2 months	$s + 2a + t$	Time-specific with additive effects of sex and age (juvenile vs. adult)
$2a(1\text{mon}) * T$	Age-specific for 1 month only	$s + t$	Time-specific with an additive effect of sex
T	Only time-dependent	$2a + t$	Time-specific with an additive effect of age (juvenile vs. adult
		t	Time-specific
$s + 4a * T$	Combined with the models above with an additional additive effect of sex		
$s + \ldots$			
$\mathbf{s * 4a * T}$	Ditto, with an additional interactive effect of sex		
$s*\ldots$			
(b) October 1999–April 2000			
$3a(6\text{mon}) * T$	Age-specific for at least 6 months	$\mathbf{s * 4a * t}$	Time-, age- and sex-specific, all factors considered interact
$3a(4\text{mon}) * T$	Age-specific for up to 4 months	$s * t$	Sex- and time-specific
$3a(2\text{mon}) * T$	Age-specific for up to 2 months	$4a * t$	Age- and time-specific
$3a(1\text{mon}) * T$	Age-specific for 1 month only	$s + 2a + t$	Time-specific with additive effects of sex and age (juvenile vs. adult)
T	Only time-dependent	$s + t$	Time-specific with an additive effect of sex
		$2a + t$	Time-specific with an additive effect of age (juvenile vs. adult)
		t	Time-specific
$s + 3a * T$	Combined with the models above with an additional additive effect of sex		
$s + \ldots$			
$\mathbf{s * 3a * T}$	Ditto, with an additional interactive effect of sex		
$s * \ldots$			

Model notation: * interaction, + additive effect (parallel lines on a logit-scale).

PARAMETER ESTIMATES AND INFERENCE

Figure 1 shows the model-averaged survival rate estimates of the age-cohorts considered and their unconditional standard errors. Winter survival of subadult animals from the beginning of the reproductive season 1998/2000 was indistinguishable from that of adults (Fig. 1a). Young wild cavies suffered lowered survival only during their first month of life (Fig. 1a: May 1999 cohort, Fig. 1b: December 1999 cohort). The effect of age on survival depended strongly on the time of birth: while the first-born young of the reproductive season survived as well as adults from birth onwards (Fig. 1b: October 1999 cohort), juveniles from later birth cohorts had progressively lower survival prospects for their first month of life. The ratio of adult to juvenile survival was 1·02 (both sexes) for the October 1999 cohort, 1·52 (males: 1·56) for the December 1999 cohort and 2·33 (males: 2·41) for the late-born young of May 1999.

Survival rates were relatively constant over the austral winter of 1999, but during the following spring and summer they showed considerable temporal variation. Survival was lowest during the late, dry summer months. Some of the high-ranking models supported an additive effect of sex on survival, with males surviving somewhat less well than females. However, the size of this effect was small in comparison to the impact of early age and time. The maximum difference between female and male survival was 0·084 for the juvenile cohort from May 1999 and 0·054 for that of December 1999 based on the highest-ranking model incorporating an effect of sex. These models had little impact on the model-averaged estimates: the maximum difference in survival between the sexes across all time intervals and age-cohorts was 0·036 for the juveniles during May 1999. Therefore, we present only model-averaged estimates for females in Fig. 1; male curves would not be visibly different.

Discussion

Patterns of age-specific mortality in our study population of *C. magna* were atypical for a small mammal, but consistent with the predictions derived from the unusual combination of life-history traits of this precocial rodent species. Adult mortality rates were high and varied substantially. Survival rates of juvenile wild cavies were not much lower than adult survival rates and after the first month of life age no longer affected the survival probabilities of young cavies. The effect of early age on survival probabilities depended mainly on

Table 2. Summary of model selection statistics for some models of age-specific survival of wild cavies from (a) May to September 1999 and (b) October 1999 to April 2000. Factors considered are age (*a*), sex (*s*) and time (*T* for ϕ, *t* for *p*). The number of estimable parameters (*K*), the quasi-likelihood adjusted deviance (QDEV), the quasi-likelihood modified Akaike's information criterion for small samples (QAIC$_c$), the difference between the minimum QAIC$_c$ of the top model and the model considered (Δ_i) and Akaike weights (w_i) are given for each model. The best approximating models of the sets (based on (QAIC$_c$), are highlighted in bold type. After the top model, all models up to $\Delta_i \leq 2$ are listed, followed by those which share the recapture model of the top model and finally the global model. See Table 1 for abbreviations

Model	*K*	QDEV	QAIC$_c$	Δ_i	w_i
(a) May to September 1999					
$\phi_{2a(1\mathrm{mon}) * T}, p_t$	**12**	**658·407**	**1222·398**	**0**	**0·129**
$\phi_{2a(1\mathrm{mon}) * T}, p_{2a+t}$	13	656·374	1222·476	0·078	0·124
$\phi_{2a(1\mathrm{mon}) * T}, p_{s+t}$	13	657·432	1223·534	1·136	0·073
$\phi_{s+2a(1\mathrm{mon}) * T}, p_t$	13	657·503	1223·605	1·207	0·071
$\phi_{2a(1\mathrm{mon}) * T}, p_{s+2a+t}$	14	655·416	1223·637	1·239	0·069
$\phi_{s+2a(1\mathrm{mon}) * T}, p_{2a+t}$	14	655·419	1223·640	1·243	0·069
$\phi_{2a(2\mathrm{mon}) * T}, p_{2a+t}$	14	655·885	1224·106	1·709	0·055
$\phi_{2a(2\mathrm{mon}) * T}, p_t$	13	658·227	1224·329	1·932	0·049
$\phi_{4a * T}, p_t$	20	656·156	1237·287	14·889	0·000
$\phi_{3a * T}, p_t$	17	657·460	1232·094	9·696	0·001
$\phi_{2a * T}, p_t$	14	657·855	1226·077	3·679	0·021
ϕ_T, p_t	11	667·998	1229·887	7·490	0·003
$\phi_{s * 2a(1\mathrm{mon}) * T}, p_t$	16	656·045	1228·532	6·134	0·006
$\phi_{s * 4a * T}, p_{s * 4a * t}$	88	602·217	1356·617	134·219	0
(b) October 1999 to April 2000					
$\phi_{3a(1\mathrm{mon}) * T}, p_{s+2a+t}$	**20**	**1003·302**	**1648·331**	**0**	**0·227**
$\phi_{s+3a(1\mathrm{mon}) * T}, p_{s+2a+t}$	21	1002·284	1649·445	1·115	0·123
$\phi_{3a(1\mathrm{mon}) * T}, p_{2a+t}$	19	1006·629	1649·532	1·201	0·124
$\phi_{3a(6\mathrm{mon}) * T}, p_{s+2a+t}$	25	997·063	1652·821	4·491	0·024
$\phi_{3a(4\mathrm{mon}) * T}, p_{s+2a+t}$	24	997·724	1651·323	2·993	0·051
$\phi_{3a(2\mathrm{mon}) * T}, p_{s+2a+t}$	22	1001·661	1650·962	2·631	0·061
ϕ_T, p_{s+2a+t}	18	1010·412	1651·195	2·864	0·054
$\phi_{\mathrm{s}+3a(1\mathrm{mon}) * T}, p_{s+2a+t}$	21	1002·284	1649·445	1·115	0·123
$\phi_{s * 3a(1\mathrm{mon}) * T}, p_{s+2a+t}$	26	997·767	1655·692	7·361	0·006
$\phi_{s * 3a * T}, p_{s * * * t}$	86	942·091	1743·705	95·374	0

Model notation: * interaction, + additive effect (parallel lines on a logit-scale).

the date of birth: offspring born at the beginning of the reproductive year survived as well as adults from birth onwards, but young born later incurred progressively higher mortality risks.

Most mortality data for mammals used in comparative studies (Millar & Zammuto 1983; Promislow & Harvey 1990; Purvis & Harvey 1995) are derived from life tables for which strong assumptions need to be satisfied to provide unbiased estimates (Caughley 1977). First, life tables are likely to confound detection and survival probabilities; second, cohort life tables cannot distinguish between time and age effects; and finally, the assumption of a stationary age distribution required by time-specific life tables are unlikely to be met, particularly in small mammals (see Anderson, Burnham & White 1985; Messier 1990; Gaillard *et al.* 1994 for problems with life-table methods). Stochastic modelling approaches such as capture–recapture may often be used to obtain reliable estimates of demographic parameters, even in fluctuating populations (Lebreton *et al.* 1992; Gaillard, Festa-Bianchet & Yoccoz 1998). Therefore, we restrict our comparisons here mainly to studies that have used capture–recapture or known fates data (e.g. radiotelemetry) to estimate age-specific survival probabilities.

AGE-SPECIFIC SURVIVAL RATES

The most common pattern of age-specific mortality rates is one of relatively high juvenile mortality followed by somewhat lowered adult mortality rates (Charnov 1986; Promislow & Harvey 1990; Sibly *et al.* 1997). Monthly probabilities of adult survival were low and variable in our cavy population. During the year from May 1999 to April 2000 they ranged from 0·66 during times of strong population decline to 0·94 when the population size was relatively stable. These values translate into time-dependent adult life expectancies of only 2·4–16 months. Thus, considering that in the laboratory wild cavies might live up to 8 years (Nowak 1999), their conspecifics in the field die young indeed. Compared to other small mammals, levels of adult survival were similar to those found in natural populations of the much smaller microtines (Table 3). There is still a lack of data for species of the size-class around 500 g, probably due partly to a lack of species, as this mass lies at the upper edge of the body size distribution for rodents (Caughley & Krebs 1983). For the somewhat larger lagomorphs (> 1 kg) monthly survival rates of adults are at the higher end for small mammals (Table 3).

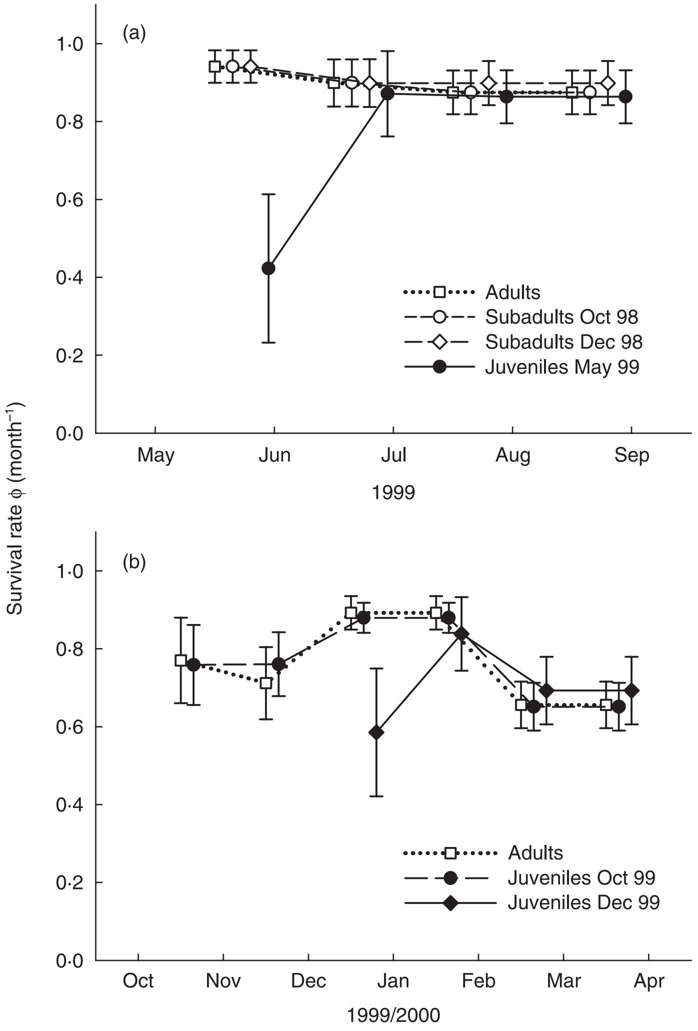

Fig. 1. Monthly survival rates of female *C. magna* for different age-cohorts from (a) May–September 1999 and (b) October 1999–April 2000. Estimates from identical time intervals are offset slightly to ensure that overlapping points are distinctly visible. Patterns for males (not shown here) are analogous, with values only slightly below those of females. Depicted are model-averaged estimates and their unconditional standard errors.

Table 3. Estimates of age-specific survival probabilities of small mammals in comparison (no life-table data included). Species are ordered by their adult body size (ascending). Juvenile survival estimates correspond to the first month of life. Data for birth cohorts other than the first were only available for two species and are shown in brackets

Species	Adult survival (month^{-1})	Juvenile survival (month^{-1})	Adult/juvenile survival ratio	Source
Mediterranean pine vole *Microtus duodecimcostatus*	0·88			Paradis, Guedon & Pradel (1993)
Bank vole *Clethrionomys glareolus*	0·42–0·83			Crespin *et al*. (2002)
Townsend's vole *M. townsendii*	0·72	0·39–0·51	1·4–1·8	Lambin & Yoccoz (1998) (avian predation prevented)
Red squirrel *Tamiasciurus hudsonicus*		0·57		Larsen & Boutin (1994)
Wild cavy ***C. magna***	**0·66–0·94**	**0·75 (–0·42)**	**1·0 (–2·3)**	
Snowshoe hare *Lepus americanus*	0·90	0·46	1·96 (–6·0)	Gillis (1998) (adults) O'Donoghue (1994) (juveniles)
European rabbit *Oryctolagus cuniculus*	0·96	0·37	2·5	H. Rödel, personal communication
Brown hare *Lepus europaeus*	0·95			Marboutin & Peroux (1995) Marboutin & Hansen (1998)

Because most small mammalian species hide their young in nests or burrows until weaning or independence, field estimates of early juvenile survival are notoriously difficult to obtain and are consequently rare in the literature. Newborn wild cavies are fully mobile within a few hours after birth and some of the young we marked were caught together with their mother still in postpartum oestrous. Of course, not all young were caught this early. Thus, if the survival probability increases over the first few days, our estimates are inevitably somewhat high. However, other studies assessing early juvenile survival in altricial rodents probably include a similar systematic bias. Lactation lasts around 25 days in the laboratory and perhaps slightly longer in the field (C. Kraus, unpublished data). Thus, our survival estimates for the first month of a birth-cohort should reflect approximately the probability of survival to weaning.

At up to 0·75 month^{-1}, early juvenile survival of *C. magna* was among the highest documented for a small mammal (Table 3). For altricial small mammals, estimates of survival over the first month of life for the first (or single) birth cohort of the reproductive season range from 0·37 to 0·57. In the precocial snowshoe hare the survival chance of offspring was not much better than that of similar-sized altricial rabbits. However, snowshoe hares are much less precocial than wild cavies. Although adults are more than twice as heavy as *C. magna* females, neonate weights are lower (40–60 g against 66–100 g; Nowak 1999; C. Kraus, unpublished data) and young are parked together by their mothers for the first few days of life (O'Donoghue 1994).

Many small mammals produce more than one litter per breeding season. If birth dates are synchronized among females, distinct cohorts are produced. As every cohort experiences a different environment, cohort-specific life-history attributes can be expected (Negus & Berger 1988). Accordingly, these species often show a high plasticity in some life-history parameters, such as growth (Negus & Berger 1988), age at maturity (Prévot-Julliard *et al*. 1999; Lambin & Yoccoz 2001) or survivorship (O'Donoghue 1994). Young wild cavies from successive cohorts had progressively lower survival probabilities over their first month of life: 0·75 for the first-born young of the reproductive year, 0·58 for the second and only 0·42 for those born last in autumn. Decreasing food quantity and/or quality and later on cold weather, as well as frequent storms and flooding of the study site, might all have added to this temporal pattern of survivorship, which coincided with an analogous change in growth rates and maturation probabilities (C. Kraus, unpublished data). The first birth cohort is likely to have had a greater impact on population growth than later cohorts, due not only to the higher juvenile survival and maturation probability, but also because it is largest, as the percentage of breeding females was lower for later cohorts.

Theory predicts that the ratio of juvenile to adult mortality will be a particularly relevant variable to understand life-history evolution (e.g. Cole 1954; Charnov & Schaffer 1973; Charlesworth 1994). In our study population, young cavies of the first cohort survived as well as adults from birth onwards. We are not aware of any small mammal for which such a low ratio of adult to juvenile survival (i.e. 1·0) has been reported (Table 3). However, for subsequent cohorts the ratio increased to 1·5 and 2·3, respectively. Whereas in many altricial mammals lowered survival probabilities persist for some time after weaning (e.g. Mediterranean pine vole: Paradis *et al*. 1993; wood mice *Apodemus sylvaticus* and bank voles: Telfer *et al*. 2002), survival rates of young cavies rapidly reached adult levels, independent of the time of birth. The same pattern has been documented for other precocial species. A comparison among degu *Octodon degus* age-groups showed no significant differences between survival times of individuals first caught as juveniles or subadults (Meserve, Gutiérrez & Jaksic 1993). Similarly, once weaned, juvenile snowshoe hares survived as well as adults (Gillis 1998).

LIVING SLOW AND DYING YOUNG?

One of the strongest correlations between life-history parameters independent of body size is that of age at maturity and reproductive life span; that is, adult mortality (Sutherland *et al*. 1986; Promislow & Harvey 1990). Thus, it fits well that wild cavies, despite being about 25 times as heavy, are able to mature at an age similar to those of microtine rodents. Female *C. magna* can conceive successfully within about 30 days (earliest age observed: 19 days, C. Kraus, unpublished data). Intuitively, it makes sense to begin reproduction early if there is a high probability of dying young, so as to decrease the chance of leaving no descendents at all.

The relatively high juvenile survival is likely to be a consequence of the well-developed state of cavy offspring. Promislow & Harvey (1991) argue that species with high adult mortality should produce altricial young, as they have to raise their young as quickly as possible under the risk of death before the offspring reach independence. This does not seem to hold for wild cavies, which produce precocial young despite high adult mortalities. Two special features might allow caviomorph rodents to escape from this problem. Whereas pre- and postnatal investment in individual offspring is generally correlated positively (Read & Harvey 1989; Pontier, Gaillard & Allainé 1993), precocial rodents have relatively short lactation periods (Derrickson 1992). In addition, young cavies start to take solid food very early. In the domestic guinea pig, young are able to survive without milk after only 4 days of lactation (Laurien-Kehnen 2002).

Models of life-history evolution predict that relatively low adult survival, in combination with high juvenile survival, will select for an early and high reproductive effort (e.g. Charnov & Schaffer 1973; Michod 1979; Charlesworth 1994). At first that seems to be contradicted by the slow aspects of the cavies' life-history strategy. However, reproductive effort and reproductive output are not equivalent, although the two terms are often confounded (e.g. Promislow & Harvey 1991). Reproductive effort as measured in terms of energy expenditure might be similar for altricial and precocial mammals with similar patterns of age-specific mortality rates. Thus, not the absolute reproductive effort, but how it is partitioned between fecundity and juvenile survival, might be what distinguishes precocial small mammals from their altricial relatives. Consequently, to explain the altricial–precocial dichotomy we have to ask which factors would favour a shift from high fecundity to high juvenile survival.

Life histories are the result of age-specific mortality and fecundity schedules (Partridge & Harvey 1988). In the long term, mortality must be balanced by fecundity for a population to persist (Sutherland *et al*. 1986). If we assume that extrinsic adult mortality (e.g. by predation; Kraus & Rödel 2004) is generally high, theoretically wild cavies have several possibilities to adapt their life-history. Different combinations of age at maturity, litter size, inter-litter interval, and juvenile survival can all increase recruitment to compensate for adult mortality. The typical rodent solves the problem by maturing early and producing a large number of small, vulnerable offspring within a short time period. In contrast, wild cavies seem to opt for quality instead of quantity; they maximize juvenile survival via a high level of maternal investment into each of a few offspring. However, the present short-term study can provide but a snapshot of the demographic processes in a wild cavy population, and more field studies are needed to evaluate whether the patterns described here are, indeed, typical for precocial small mammals. If a high reproductive rate characterizes altricial small mammals and high adult survival large mammals, we hypothesize that high prereproductive survival plays a key role in the life-history strategy of precocial small mammals.

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