

# Interactive effects of exogenous and endogenous factors on demographic rates of an African rodent

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Exogenous and endogenous environmental factors can have simultaneous additive as well as interacting effects on life-history traits. Ignoring such interactions can lead to a biased understanding of variability in demographic rates and consequently population dynamics. These interactions have been the focus of decades-long debates on the mechanisms underlying small mammal population fluctuations. They have often been studied indirectly through seasonal effects, but studies considering them directly and more mechanistically are rare. We investigated the joint effects of exogenous (temperature, food availability) and endogenous (population density) factors on the demographic rates of a group-living diurnal rodent, the African striped mouse *Rhabdomys pumilio* using nine-year mark–recapture data from a population in the Succulent Karoo, South Africa. In general, higher temperatures and lower food availability were associated with higher survival, whereas high population densities were either beneficial or detrimental to survival depending on interacting food availability. High reproductive rates were related to lower temperatures, higher food availability and lower population density, and interactions among environmental factors mediated the strength of these relationships. Our study highlights the complex ways in which different environmental factors can interact to shape demographic rates and emphasizes the importance of explicitly including interactions among exogenous and endogenous factors into studies of population dynamics.

The relative importance of exogenous and endogenous environmental drivers in shaping population dynamics is a key topic in population ecology and has received particular attention in the past decades (reviewed by Krebs 2013). Exogenous (i.e. population extrinsic) factors, such as climate and resource availability, have been demonstrated to play a key role in the regulation of several animal populations (Batzli 1985, Oksanen et al. 2008), whereas in other studies, endogenous (i.e. population intrinsic) factors, including density-dependent regulatory mechanisms, have been proposed as the main force driving population fluctuations (Krebs 1978, Krebs et al. 2007). Today, there is broad agreement that neither exogenous nor endogenous factors alone are sufficient to explain population dynamics and the demographic variability underlying them (Krebs 2013). Both have to be studied simultaneously in order to gain a thorough understanding of population dynamics and to develop effective wildlife management strategies (Williams et al. 2001).

As a result of this synthesis, research in the past two decades has focused on investigating simultaneous effects

of environmental factors on population dynamics. This was mainly done by either considering additive effects of different, continuous environmental factors, or by looking at the effects of a discrete factor such as season. Here, the latter indirectly incorporates interacting effects of environmental factors (Turchin and Ostfeld 1997, Merritt et al. 2001). Modelling non-linear interactions among continuous factors directly has largely been ignored (Coulson et al. 2001, Crain et al. 2008). More recent studies have now highlighted the importance of including these interactions specifically in ecological research in order to gain a more mechanistic understanding of their effects (de Little et al. 2007, Crain et al. 2008, Griffiths et al. 2015). The interaction of two environmental effects can lead to greater or smaller responses than the sum of the individual effects (Crain et al. 2008), depending on the underlying biological processes, such as competition or energetic tradeoffs (Previtali et al. 2010, Griffiths et al. 2015). Ignoring such non-additive effects among exogenous and endogenous environmental drivers can lead to false conclusions about their roles in population regulation (Previtali et al. 2010). Previtali et al. (2010), for example,

demonstrated that while there was no individual effect of precipitation on deer mouse *Peromyscus maniculatus* survival and reproductive rates, the interactions of precipitation with season and environmental disturbance were very important. They showed that survival at disturbed sites was particularly low during summer, and the negative impact of disturbance on survival and reproduction was mitigated by high precipitation (Previtali et al. 2010). A different study found juvenile survival of elephant seals *Mirounga leonida* to decrease with population density when its interaction with climate was ignored, but this relationship disappeared when the interaction was considered, showing that stochastic environmental forcing dwarfed negative density feedbacks in this system (de Little et al. 2007). Consequently, identifying and quantifying interactions is crucial in the study of multifactor hypotheses of population regulation.

Small rodents represent suitable model systems for studying multifactor hypotheses on demographic rates variability, including interactions among exogenous and endogenous environmental factors. As fast life history species (i.e. shorter life spans and high offspring production with relatively low survival prospect), their individual life-history traits are highly sensitive to changes in both exogenous and endogenous environmental factors. This demographic sensitivity in combination with the wide geographical distribution of rodent species provides a unique opportunity to study the impacts of the same environmental factors interacting at both different time-scales and across habitat types and continents (Krebs 2013). This is highly valuable for generalizing hypotheses about interactive effects among environmental factors.

The aim of our study was to assess the interacting effects of exogenous and endogenous environmental factors on demographic rates of the African striped mouse *Rhabdomys pumilio* in the Succulent Karoo semi desert of South Africa. In addition to fast life histories, this species lives in arid and unpredictable habitats, providing a high level of environmental variability for many generations within a relatively short time period (Schradin and Hayes unpubl.). We used nine years (2005–2014) of monthly mark–recapture data to parameterize a multi-state mark–recapture model and generalized linear (mixed) models, tested several system-specific hypotheses regarding environment–demography relationships and investigated the role of interacting effects in population regulation.

For our analysis, we considered ambient temperature and food availability as exogenous factors, and population density as an endogenous factor. Exogenous factors investigated in multifactor studies frequently include temperature as an important climatic variable (Ferreira et al. 2006, Andreo et al. 2009). Rodents from dry environments are challenged with temperatures well above and below their thermoneutral zone, incurring thermoregulatory costs at both extremes (Haim and Izhaki 1995). As the thermoneutral zone of striped mice is rather high ( $32 \pm 1^\circ\text{C}$ , Haim and Fourie 1980), we hypothesized that particularly cold extremes might have a strong negative impact on their survival and reproduction as a result of high energetic costs. We further expected this detrimental effect of low temperatures to be counterbalanced by interactive effects of high food availability (more energy available for physiological thermoregulation) and

high population density (limited heat loss due to huddling at night; Scantlebury et al. 2006). Food availability generally determines the amount of energy available to an animal, and has been found to have a positive influence particularly on rodent reproduction (Dobson and Oli 2001, Pinot et al. 2014). We therefore hypothesized that high food availability would result in higher survival and reproductive rates. Among endogenous environmental factors, negative density-dependent feedbacks have been found to be important drivers of rodent population dynamics (reviewed by Krebs 2013). Furthermore, studies found that in habitats similar to that of our study population, population density acted in concert with exogenous factors in shaping demographic rates of rodent species (Leirs et al. 1997, Lima et al. 2003). We therefore hypothesized that high population density would decrease survival and reproduction of striped mice, particularly if it acted in concert with low food availability and thus increased intraspecific competition.

## Material and methods

### Study area

This study was conducted in Goegap Nature Reserve in the Succulent Karoo of South Africa ( $29^\circ 41' 42.5''\text{S}$ ,  $18^\circ 01' 33.4''\text{E}$ , 912 m a.s.l.). The Succulent Karoo semi-desert is a winter rainfall ecosystem where most of the annual rain (approximately  $192 \pm 51$  mm p.a. at our field site) falls between May and September. Vegetation cover is closely linked to rainfall patterns, and therefore has an annual peak in spring, following the winter rainfalls. Ambient temperatures also follow a seasonal pattern, and span a wide range from below  $0^\circ\text{C}$  in winter nights to over  $40^\circ\text{C}$  during summer days (Supplementary material Appendix 1 Fig. A1). Climatic conditions in the Succulent Karoo do not only have strong intra-annual fluctuations, but the amount and timing of rainfall and thus the availability of green vegetation ( $18.9 \pm 8.7$  percent ground coverage at the field site) can vary greatly between years (Supplementary material Appendix 1 Fig. A1).

### Study species

The African striped mouse *Rhabdomys pumilio* is a small, diurnal murid rodent (Schradin and Pillay 2004) inhabiting dry regions of southern Africa (Meynard et al. 2012). Striped mice form extended family groups with individuals of one group sharing one nest, but foraging solitarily during the day (Schradin and Pillay 2004). The main breeding season coincides with the annual burst of vegetation in the austral spring, usually between July/August and November/December, although reproduction can occur outside this window if sufficient rain falls in summer or autumn. Within the main breeding season, females can have up to three litters of 5.3 pups on average (Schradin and Pillay 2005). Offspring can reach sexual maturity as early as four weeks of age, but most stay with their natal group as philopatric helpers and delay reproduction (and dispersal in males) for several months until the next breeding season (Schradin et al. 2012). Few breeding mice survive to another breeding

season, such that striped mice typically breed only during the spring following the breeding season they were born in (Schradin and Pillay 2005).

### Trapping procedure

The striped mouse population has been monitored using a standard capture–mark–recapture protocol since 2001. Striped mice were trapped using metal live-traps which were placed in front of bushes that were used as nesting sites (revealed by direct observations and radio-tracking). Trapping was done during mornings and evenings, including the time intervals when family groups basked together outside their nests. Trapped mice were sexed, weighed and individually marked with metal ear tags as well as hair dye for individual recognition in the field during observations. During the study period (January 2005–September 2014), all mouse groups within the study area ( $19 \pm 4$  groups on average) were trapped for three consecutive days at least once and typically twice every month. Female striped mice were considered ‘reproductively active’ if a perforated vagina and/or nipples showing signs of lactation were observed. The trapping protocol has been described in detail elsewhere (Schradin and Pillay 2004, 2006). A total of 7745 individuals (2539 females and 5206 males) were caught and marked during the 117 trapping sessions within the study period. In our analyses of individual capture histories, we only considered the 1609 female striped mice whose date of birth had been estimated based on their body mass at a young age (method described in Schradin et al. 2009).

### Environmental factors

Our analysis considered three different environmental factors that are hypothesized to play an important role for our study species. They included 1) temperature and 2) food availability as exogenous factors, and 3) population density as an endogenous factor. All environmental factors were analysed on a monthly scale.

Mean monthly temperature was calculated by averaging daily minimum and maximum ambient temperatures (measured at the field station, 5 cm above ground) for each month. Food availability was estimated as the percentage of ground covered with succulents and ephemerals known to be edible by striped mice (34 species, Schradin and Pillay 2006). To calculate a study site mean of plant cover, we used data from plant surveys conducted on the 15th of each month and averaged the estimates from eight different  $2 \times 2$  m monitoring plots within the study area that were sampled following a standard protocol (Braun–Blanquet method, Werger 1974).

We calculated population density by dividing the total number of trapped adult mice of both sexes by the study area. Immature individuals were excluded from the calculations as they do not yet consume much vegetation, forage only very close to their nest (limiting competition with individuals from other groups) and do not partake in reproductive competition. We also included individuals of unknown age in the density calculations, and therefore defined the immature stage for individuals below 20 g of weight here (based on a mass-at-age regression, Schradin et al. 2009). This definition

of the immature stage using weight overlaps strongly with the definition based on age (Supplementary material Appendix 2 Fig. A2). Trapping directly at the nests, and combining this with field observations as done in our study, is expected to result in overall high capture probabilities. Based on this, the use of the number of trapped mice for calculating a proxy for density should be adequate even without correcting for variation in capture probabilities. Seven trapping sessions were known to have had very low sampling effort due to a lack of field assistants. To avoid bias caused by this, we used an average of the number of individuals trapped at the previous and next reliable trapping session to estimate density for these sessions. Low variability in recapture rates when discounting these sessions of known low sampling effort was later confirmed by the analyses (Supplementary material Appendix 2 Fig. A3). The size of the study site varied between 1 and 10 ha over the study period (depending on the distribution of the sleeping nests and on sampling effort), and we consequently estimated the size using a 100% minimum convex polygon (MCP) approach on the coordinates of the sampled nests at each trapping session. Our resulting measure of the minimum number of adult mice present divided by the study area represents a proxy for adult population density and not absolute population density; nonetheless, we will refer to this measure as population density in the remainder of this text. All three environmental variables were scaled and standardized to allow for a comparison of their relative effects. We checked for multicollinearity among environmental variables using Pearson correlations (Supplementary material Appendix 1 Table A1).

### Mark–recapture models

We built multi-state mark recapture models (MSMR models, Lebreton et al. 2009) to assess the effects of temperature, food availability and population density on female survival and maturation rates, while accounting for temporally variable recapture probabilities. Individuals were assigned to one of three different life stages: 1) immatures representing offspring younger than four weeks of age, 2) philopatrics which are offspring older than four weeks and which could have reached sexual maturity, but did not show signs of reproductive activity yet, and 3) breeders which showed signs of reproductive activity (perforate vagina or lactation) at least once before in their life (Fig. 1). An individual can only be encountered in the immature class once, as the trapping interval corresponds to four weeks. When an immature survives to the next month with a survival probability  $S_p$ , it will have a probability  $\Psi_{IP}$  to become a philopatric and a probability  $\Psi_{IB}$  (maturation rate) to become a breeder directly if it becomes reproductively active at the same time. Philopatrics survive with a probability  $S_p$  and have a maturation rate  $\Psi_{PB}$  to become breeders, but may also be re-encountered as philopatrics ( $1 - \Psi_{PB}$ ). Breeders survive with a probability  $S_b$  and can only be re-encountered as breeders. They also represent the only stage able to reproduce and therefore add new immatures to the population (R).

Our most general model included the recapture rates ( $p$ ) as a function of life stage and an interaction between year and season, to account for variation in sampling effort over time. Survival ( $S$ ) and maturation rates ( $\psi$ ) were modelled

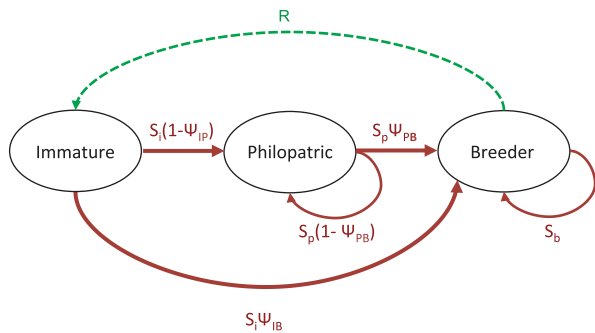


Figure 1. Life cycle of the African striped mouse. Survival probabilities are abbreviated as  $S$ , maturation probabilities as  $\psi$  and reproduction as  $R$ . The subscript denotes to which stage/transition a probability is specific ( $i$  = immature,  $p$  = philopatric,  $b$  = breeder,  $IP$  = immature to philopatric,  $IB$  = immature to breeder,  $PB$  = philopatric to breeder).

as functions of life stage, temperature, food availability and population density. The most general model for survival included all possible two-way interactions, as well as three-way interactions including life stage. The most general model for maturation on the other hand included only interactions between environmental factors but not with stage. We were unable to parameterize models with stage interactions due to data limitations. All three models were estimated with a logit link function. The corresponding linear predictors were thus transformed within their respective modelling framework using a logit (survival, recapture) or multinomial logit (maturation) function to obtain the actual rates.

We assessed the goodness of fit of our most general model by estimating the variance inflation factor  $\hat{c}$  using the median  $\hat{c}$  approach implemented in program MARK. The goodness of fit test indicated adequate fit of our global model to the data, with an estimated median  $\hat{c}$  of 1.09. Therefore, it was not necessary to account for over dispersion in our model selection (Anderson et al. 1994). Subsequently, we reduced the most general model for model selection. Model selection was based on the Akaike information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002). When alternative models were indistinguishable ( $\Delta AICc < 2$ ), the model with fewest parameters was retained. Our model selection procedure consisted of two steps. 1) We first identified the best model for recapture rate ( $p$ ), then proceeded with the model optimization for maturation rates ( $\psi$ ) and ultimately for survival rates ( $S$ ). 2) As the three models ( $p$ ,  $\psi$ ,  $S$ ) are linked, we tested for potential effects of the order of model selection by comparing the best recapture rate model with reduced recapture rate models, while keeping the selected best models for survival and maturation. We proceeded likewise with the maturation rate model and finally the survival rate model.

## Reproduction models

We modelled the probability of a breeder making a reproductive attempt (RA, indicated by perforate vagina or lactation) as a binomial generalized linear mixed model (GLMM). We considered temperature, food availability, and population density at the previous time-step (month) as fixed effects. Furthermore, we included individual identity and year as

random effects on the intercept to account for individual and temporal heterogeneity generated by repeated measurements on the same individual and the same year.

Since individual-based data on the number of immature individuals added to the population (recruits) per mother and breeding event was not available, we used a population mean at each time-step  $t$ . We calculated this as the number of immatures trapped at time  $t$  divided by the number of active breeders trapped at time  $t-1$ . Additionally, we corrected both the number of immatures and the number of breeders by the recapture rates obtained from the MSMR model. Because these data contained many entries of 0, we used two different models to approximate the relationship between recruitment and temperature, food availability and population density at the previous time-step (month). We modelled the probability of any successful recruitment occurring (0 or 1) as a binomial GLM, and number of recruits per female (given that it is larger than 0) as another GLM with a gamma distribution. Parameters were estimated on the logit (probability of reproductive attempt, recruitment probability) or log (recruit number) scale, and the corresponding linear predictors were transformed within the modelling framework using a logit or log function respectively. Model selection was based on AICc, as described before.

All analyses were run in R ver. 3.1.2 (<[www.r-project.org](http://www.r-project.org)>). MSMR models were fitted using the RMark package (Laake 2013) which calls upon program MARK for model fitting (White and Burnham 1999). The median  $\hat{c}$  test was performed in program MARK directly. GLMMs were fitted using the lme4 package for R (Bates et al. 2015). We used built-in prediction functions where possible, and resorted to manual prediction of point estimates combined with the delta method (as described by Williams et al. 2001) and bootstrapping approaches for calculating confidence intervals where necessary.

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.c1657>> (Nater et al. 2016).

## Results

### Survival

Our final model for survival rates included stage-specific effects of all three environmental covariates, as well as a two-way interaction between temperature and food availability and a three-way interaction between stage, food availability and population density (Supplementary material Appendix 4 Table A2). The estimates of monthly survival probability of immatures ranged from 0.50 to 0.98 (mean =  $0.80 \pm 0.13$ ) over the study period. Philopatric survival varied between 0.55 and 0.98 with a mean of  $0.83 \pm 0.08$ . Breeder survival had a mean of  $0.81 \pm 0.05$  and a range of 0.64 to 0.93. On average, our model predicted an association of high temperatures with higher survival of immatures ( $\beta = 0.54$ , 95% CI [0.05, 1.04]) and philopatrics ( $\beta = 0.25$ , 95% CI [0.09, 0.41]) but with lower survival of breeders ( $\beta = -0.11$ , 95% CI [-0.22, 0.01], Fig. 2A). Increasing food availability



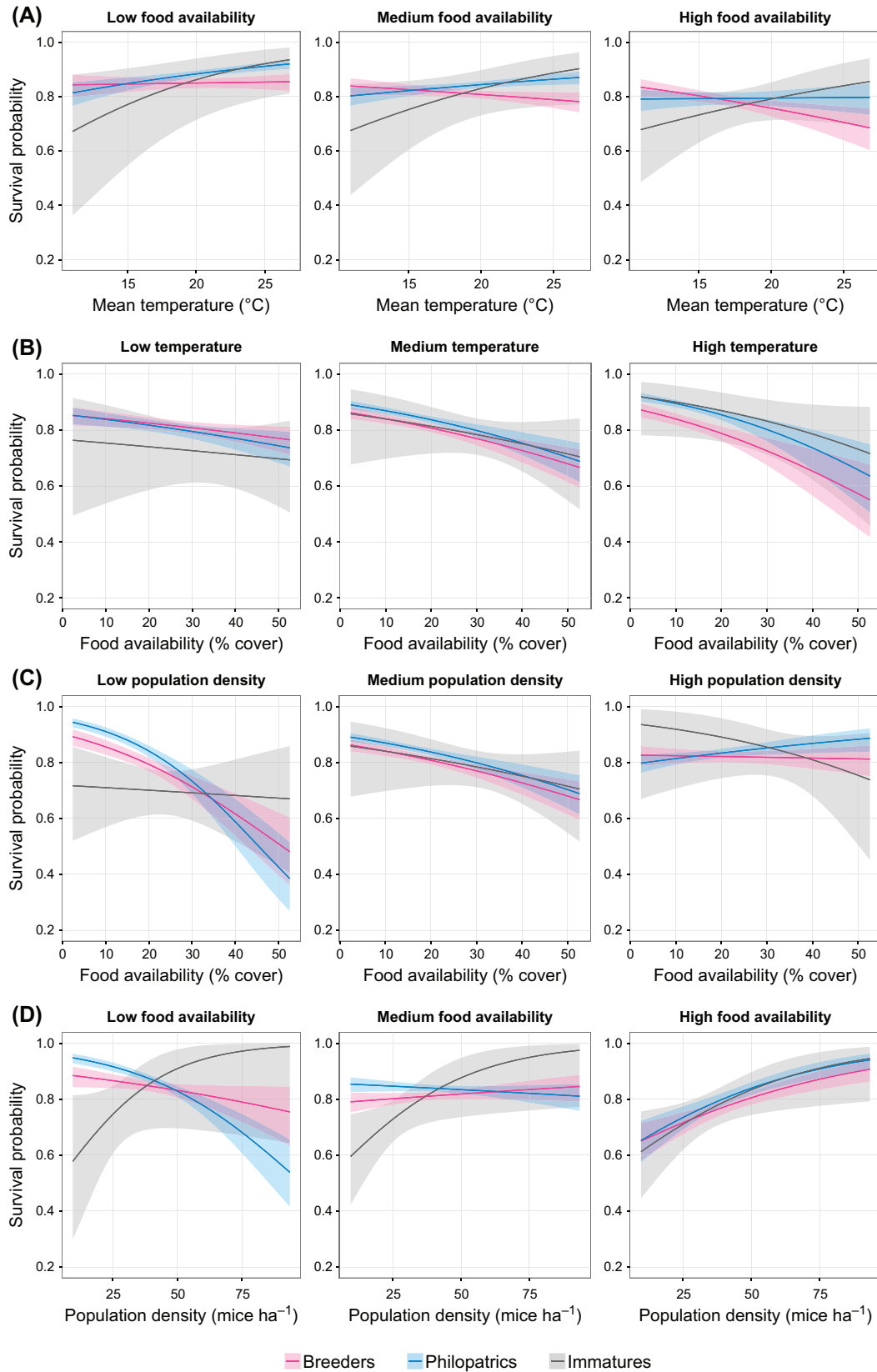


Figure 2. Model predictions for survival probability of immatures, philopatrics and breeders as functions of (A) temperature, (B) and (C) food availability and (D) population density. Solid lines represent point estimates predicted by the model; shaded areas are their 95% confidence intervals. The three panels in each row contain visualizations of the relationship at three different levels of one interacting covariate, from left to right: low (mean - SD), medium (mean) and high (mean + SD). All other covariates were set to the mean observed in the data.

was generally associated negatively with survival of all life stages (average  $\beta = -0.09$ , Fig. 2B–C). There were indications that the average effect of population density on survival was positive for immatures ( $\beta = 0.56$ , 95% CI [-0.03, 1.15]) and breeders ( $\beta = 0.07$ , 95% CI [-0.03, 0.18]) but negative for philopatrics ( $\beta = -0.13$ , 95% CI [-0.27, 0.01], Fig. 2D). An interaction between temperature and food availability resulted in the model predicting steeper declines in survival with increasing food availability if temperature was high (Fig. 2A–B). The interaction between food availability and population density was particularly strong and able to reverse the general pattern under high-density conditions: for philopatrics and breeders, the negative relationship between survival and food availability disappeared (Fig. 2C), and low food availability resulted in philopatric and breeder survival decreasing (instead of increasing) as population density became higher (Fig. 2D). Survival of immatures remained associated negatively with food availability and positively with population density, irrespective of variation in the other factor.

### Maturation

Our final model for maturation rates contained single effects of stage, temperature, food availability and population density as well as an interaction between temperature and population density (Supplementary material Appendix 4 Table A3). The monthly maturation rates estimated over the study period showed large variation and were slightly higher for immatures ( $\psi_{IB}$ : 0.003 to 0.66, mean =  $0.18 \pm 0.16$ ) than philopatrics ( $\psi_{HB}$ : 0.003 to 0.63, mean =  $0.16 \pm 0.15$ ). The selected model predicted that the maturation rates of immatures and philopatrics decreased with higher temperature ( $\beta = -0.94$ , 95% CI [-1.07, -0.81]), with lower food availability ( $\beta = 0.43$ , 95% CI [0.32, 0.54]) and with higher population density ( $\beta = -0.41$ , 95% CI [-0.55, -0.28], Fig. 3). Furthermore, the negative impacts of population density and temperature amplified each other through an interaction (Supplementary material Appendix 3 Fig. A4). Another model ranking within 2AICc units of the most

parsimonious one also provided support for an interaction between food availability and population density (Supplementary material Appendix 4 Table A3).

### Recapture

Our final model for recapture rates included a single effect of life stage and an interaction between season and year (Supplementary material Appendix 4 Table A4). Recapture rates ranged from 0.30 to 0.95 for breeders (mean =  $0.84 \pm 0.12$ ) and from 0.11 to 0.87 for philopatrics and immatures (mean =  $0.61 \pm 0.14$ ) during the study period. Particularly high or low recapture rates were not associated with specific months. However, variation in recapture rates appeared to be larger before 2009, often coinciding with the few months of known low sampling effort, and average recapture rates have slightly increased between 2011 and 2015.

### Reproductive attempts

Our final model for the probability of breeders making a reproductive attempt (RA) included single effects of all covariates as well as two-way interactions of temperature with food availability and temperature with population density (Supplementary material Appendix 4 Table A5). Monthly RA probabilities spanned a large range from 0.001 to 0.96. The mean RA probability was  $0.43 \pm 0.30$ . The model predicted that RA probability became higher as temperatures decreased ( $\beta = -0.94$ , 95% CI [-1.11, -0.76], Fig. 4A–B), as food availability increased ( $\beta = 0.82$ , 95% CI [0.58, 1.08], Fig. 4C) and as population density decreased ( $\beta = -0.44$ , 95% CI [-0.62, -0.26], Fig. 4D). Interactive effects resulted in RA probability at low temperatures being even higher if food availability was high at the same time and if population density was low.

### Recruitment

The probability of successful recruitment was explained best by a model containing only the additive effects of food availability and population density (Supplementary material

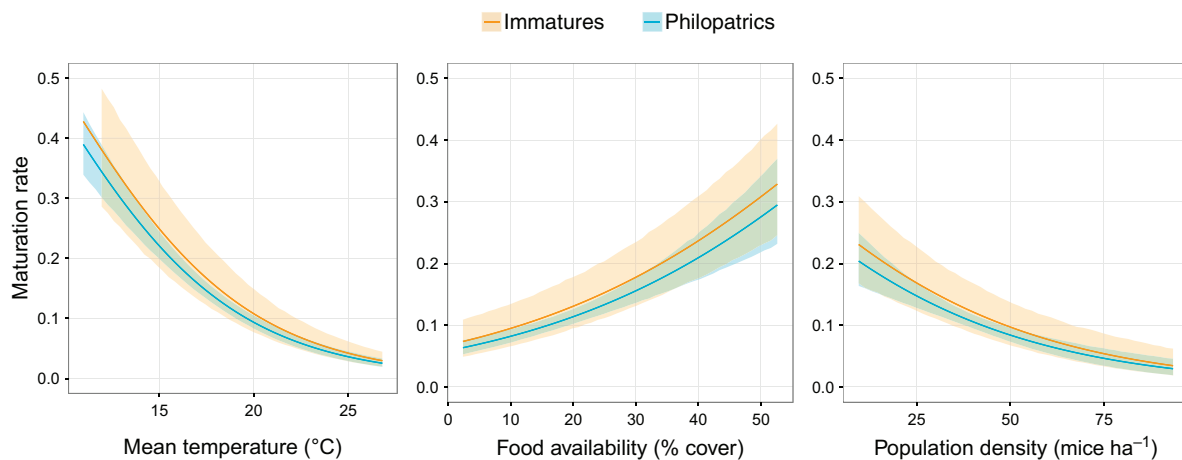


Figure 3. Model predictions for maturation rates of immatures and philopatrics as functions of temperature, food availability and population density. Solid lines represent point estimates predicted by the model; shaded areas are their 95% confidence intervals. All other covariates were set to the mean observed in the data.

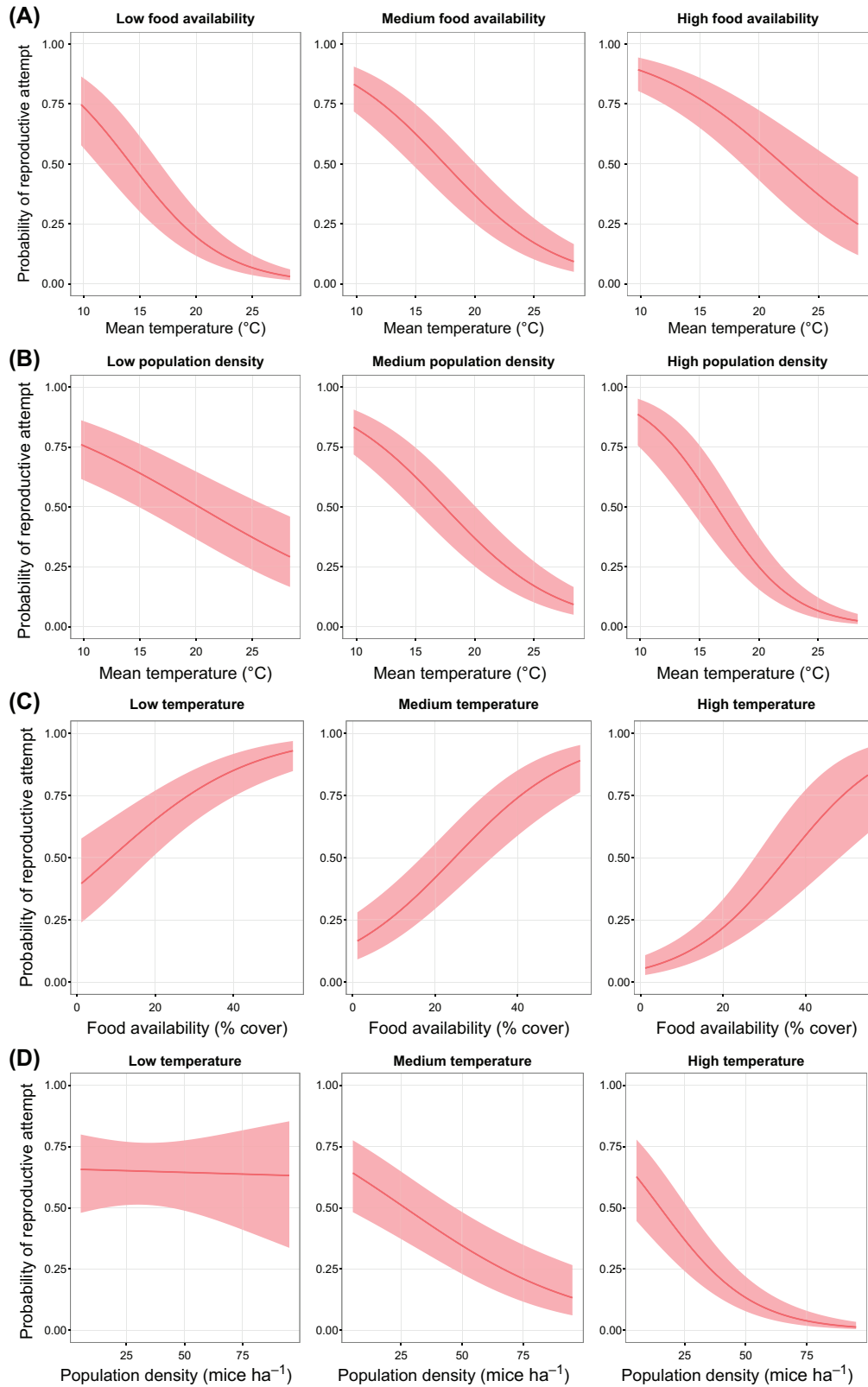


Figure 4. Model predictions for the probability of reproductive attempts of breeders as functions of (A) and (B) temperature, (C) food availability and (D) population density. Solid lines represent point estimates predicted by the model; shaded areas are their 95% confidence intervals. The three panels in each row contain visualizations of the relationship at three different levels of one interacting covariate, from left to right: low (mean - SD), medium (mean) and high (mean + SD). All other covariates were set to the mean observed in the data.

Appendix 4 Table A6). The probability of successful recruitment ranged from 0.08 to 0.97 (mean =  $0.45 \pm 0.26$ ). The model predicted successful recruitment to be more likely when food availability was high ( $\beta = 1.22$ , 95% CI [0.72, 1.80]) and population density was low ( $\beta = -0.52$ , 95% CI [-1.01, -0.07], Supplementary material Appendix 3 Fig. A5).

Our selected model for the number of recruits per breeding female consisted of the additive effects of temperature and population density (Supplementary material Appendix 4 Table A7). The average number of recruits per female ranged from 0.16 to 1.25 (mean =  $0.44 \pm 0.23$ ), and seemed to be larger under higher temperatures ( $\beta = 0.31$ , 95% CI [-0.05, 0.71]) and lower population density ( $\beta = -0.49$ , 95% CI [-0.99, 0.01], Supplementary material Appendix 3 Fig. A6). A second model containing an additional positive effect of food availability explained variation in the data almost equally well (Supplementary material Appendix 4 Table A7).

## Discussion

In this study, we investigated the combined effects of exogenous and endogenous factors on demographic rates of the African striped mouse. We found that temperature, food availability and population density jointly affected demographic rates, but that their impacts on specific rates varied considerably. Most importantly, we demonstrated that interactions between exogenous and endogenous factors were shaping environment–demography relationships. We found density-dependence in all demographic rates, and these density effects were sometimes offset (e.g. in breeding probability) or even reversed (e.g. in survival) by interactions with other environmental factors. Considering these interactions allows for drawing further inferences about the mechanisms underlying demographic variability and linking them to previously reported seasonal patterns (Schradin and Pillay 2004, 2005).

## Survival

Survival rates of all life stages were influenced considerably by temperature, food availability and population density. Furthermore, we showed that interactions among factors were crucial for understanding variability in survival rates. In accordance with our first hypothesis, survival was positively associated with temperature for immatures and philopatrics, indicating that higher costs of thermoregulation at low ambient temperature decrease survival probability. Larger energetic costs arising from hypothermia for earlier (hence smaller-bodied) life stages have previously been shown in field voles *Microtus agrestis* (Simons et al. 2011) and remain a likely explanation of the observed pattern. For breeders, on the other hand, warmer temperatures correlated with decreasing survival. This may be related to survival costs of past reproduction and individuals dying of old age: temperature increases are indicative of the onset of summer, and for breeders this will often coincide with the end of the spring breeding season of their second year (Schradin and Pillay 2004). Interactive effects of food availability resulted in

more negative impacts of increasing temperature, indicating that there may be additional survival costs associated with high food availability. This becomes more apparent when the explicit relationships between survival and food availability are considered. We found survival of all life stages to be lower when food availability was high. This stands in stark contrast with our initial hypothesis and appears counter-intuitive, as high food availability has been associated with increased survival in, for example, leaf-eared mice *Phyllotis darwini* (Lima et al. 2001), which are ecologically very similar to striped mice. It is likely that unaccounted factors that decrease survival are associated with high food availability in this system. As outlined below, potential explanations for these unaccounted factors can be drawn when considering density effects in addition to and interacting with food availability.

Population density was correlated positively with survival of immatures, producing a pattern opposite to the negative relationship we had expected. For philopatrics and breeders, high population density had a negative impact on the survival under low-food conditions, as we had hypothesized. Under high-food conditions, however, the interaction between population density and food availability reversed the trend, making high population density beneficial to survival. Consequently, the relationship between density and survival of striped mice is consistent with two contrasting results from other rodents inhabiting semi-arid environments depending on the amount of food available: a negative density–survival relationship found for multimammate rats (*Mastomys natalensis*, Leirs et al. 1997) and a positive density–survival relationship found for leaf-eared mice (Lima et al. 2001, 2003).

Lima et al. (2003) argued that the latter could be due either to a predator saturation effect decreasing the chance of each individual to be killed, or to inhibition of dispersal resulting in higher apparent survival. Both explanations would be plausible mechanisms to explain the complex survival patterns arising from the interaction of population density and food availability we observed for striped mice. As opposed to other systems where high plant cover can provide rodents with shelter from predators (Andreo et al. 2009, Schorr et al. 2009), high availability of annual food plants in the Succulent Karoo can prompt striped mice to spend more time foraging in open areas with little shrub cover (Schradin and Pillay 2006), exposing them to a higher risk of predation. A predator saturation effect could then explain why the negative association between food availability (= predation pressure) and survival disappears under high population densities. Alternatively, the pattern could also be explained through dispersal dynamics: when food availability is high (e.g. in the breeding season) dispersal of female striped mice is negatively density-dependent (Schoepf and Schradin 2012), and consequently increasing densities will result in reduced dispersal and therefore higher apparent survival. During the non-breeding season (lower food availability) female dispersal is density-independent and mostly absent (Schoepf and Schradin 2012) and a different mechanism (e.g. competition) could then be responsible for the negative density–survival relationship. Immature striped mice apparently survived better when population densities were high irrespective of interacting factors, potentially because



they do not disperse, may be exempted from strong resource competition with adults, and additionally benefit from increased protection and alloparental care in larger groups (McGuire et al. 2002, Schradin 2013).

Our final survival model did not contain an interaction between population density and temperature, even though we had hypothesized this to be important, as striped mice can save energy by huddling in groups, which are larger when population density is high. However, Scantlebury et al. (2006) found a reduction of energy expenditure with increasing huddling group size only up to six individuals, a size that can be reached at low to medium population densities. Energy saving due to huddling is believed to be the main cause of group-living in striped mice (Schradin et al. 2012), and striped mice may form groups of a minimum size to reach the maximal thermoregulatory benefit independent of population density (Schradin et al. 2006).

## Reproduction

Different demographic rates associated with reproduction (maturation rates, RA probability, recruitment probability, recruit number) were affected by the studied environmental factors in similar directions. Interactive effects on reproduction did buffer the strength of environmental impacts slightly, but did not reverse any environment–demography relationships as observed for survival.

The effects of temperature varied among different demographic rates related to reproduction. Maturation rates and reproductive attempts were negatively related to high temperatures, which could be a consequence of stress induced by hyperthermia, low water availability and low food quality. Additional stressors in the form of interacting low food availability and high population density exacerbated the negative effect of increasing temperature, supporting the notion that overall poor environmental conditions impair reproduction. For recruitment on the other hand, we found indications of a positive relationship with temperature: the number of recruits was slightly larger under higher mean temperatures. A similar trend was found by Ferreira et al. (2006) for the house mouse *Mus musculus*, and may relate to reduced survival of offspring between birth and weaning due to hypothermia. Alternatively, the positive association between recruitment and ambient temperature may be related to maternal condition: breeding female striped mice increase in body mass and age throughout the breeding season and therefore as temperature increases (Schradin unpubl.) and litter size is known to be larger for older and heavier females (David and Jarvis 1985).

Our observations of positive associations between increased food availability and reproduction are in accordance with our initial hypothesis as well as numerous studies on other rodent species (Taitt 1981, Dobson and Oli 2001) including the previously mentioned ecologically similar leaf-eared mouse (Lima et al. 2001) and multimammate rat (Leirs et al. 1997). Our results thus support previous evidence that the availability of small annual plants is an important driver of rodent reproduction in semi-arid environments (Previtali et al. 2009), as such plants provide the amount of dietary water, vitamins (Beatley 1969) and especially protein (Nel et al. 2015) necessary to cover the

physiological demands of reproduction. Furthermore, the relationship between reproduction and food availability was independent of temperature for all but one demographic rate, supporting the notion that striped mice are capable of opportunistic breeding at any time of the year if sufficient protein-rich food is available.

As predicted, all reproductive rates were negatively correlated with increasing population density. This result is intuitive, given that population density increases throughout the breeding season and peaks at its end. Concurrent with the increase in density in the course of the breeding season, the amount of protein found within food plants becomes less (because plants stop growing), resulting in gradual removal of the key physiological prerequisite of striped mouse reproduction (Nel et al. 2015). After the breeding season, the total availability of food plants and breeding territories decrease (Schradin et al. 2012), resulting in fewer resources per capita, and increasing competition, which could impair reproduction (Hestbeck 1982, Lima et al. 2001). This argument is further supported by our findings that maturation rate and probability of making a reproductive attempt are unaffected by density at cool temperatures (beginning of the breeding season) when resources are abundant, plants are growing (high protein content) and competition might therefore be lower. In sum, the negative relationship between population density and reproduction might either indicate a direct negative impact of population density on reproduction, or simply indicate that population density is at its highest when reproduction ceases due to other factors.

## Importance of interactions

Our study revealed the importance of considering interactions among environmental factors in the study of life-history variability and population processes. First, we reported strong interactive effects that both exacerbated or dampened demographic responses to environmental factors. These effects include, for example, how high temperature and low population density together resulted in even lower maturation rates, or how at lower temperatures the strength of the negative density feedback on the probability of reproductive attempts decreased, an interaction frequently reported in other rodent studies (Karels and Boonstra 2000, Previtali et al. 2010). Second, we also demonstrated that the strength of interactions may exceed simple modification of relationship strength (exacerbation or dampening) and affect even the general direction of environment–demography relationships. We showed this for the density feedback on survival in our study system, which is negative if food availability is low, and positive when food availability is high. Third, we demonstrated that the consideration of interactions has great potential for explaining contrasting environment–demography relationships between ecologically close-related species, such as the relationship between survival and population density outlined here for striped mice, leaf-eared mice and multimammate rats. Our comparison demonstrates that studies may find apparently opposite environment–demography relationships in similar species as a result of different and unaccounted levels of interacting covariates instead of fundamental differences in the mechanistic processes underlying those relationships.

Our findings thus concur with recent studies (de Little et al. 2007, Previtali et al. 2010, Griffiths et al. 2015) claiming that considering interactions is crucial for gaining a detailed understanding of the roles of environmental drivers in population regulation. Furthermore, considering the effects of interacting environmental factors on demographic variability will allow building population models including them as well. It will be important to investigate the role of interactive environmental effects on outcomes and precision of population projections, particularly under consideration of climate change. This constitutes a promising venue for future research for the study system presented here, as well as many others. While analytical tools for analysing demography and population dynamics are becoming more and more flexible, the study of interactions remains very data demanding, as illustrated by our analysis. Long-term individual-based data with considerable temporal resolution is required to parameterize demographic models including interactions. This highlights once more the great value and importance of starting, maintaining and continuing long-term monitoring programmes.

## Conclusion

Demographic rates, and consequently population dynamics, change in response to combinations of exogenous and endogenous environmental factors (Krebs 2013). In this study, we found that not only the independent effects of temperature, food availability and population density were important, but also that particularly interactions between the different environmental factors were crucial for explaining the observed demographic variability. As interactions affect population dynamics non-additively and sometimes unexpectedly, identification of the underlying mechanisms, for example using trait-based analysis (Coulson et al. 2001, Ozgul et al. 2010), is pivotal for forecasting species responses to environmental change (Griffiths et al. 2015).

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Supplementary material (Appendix oik-03384 at <[www.oikosjournal.org/appendix/oik-03384](http://www.oikosjournal.org/appendix/oik-03384)>). Appendix 1–4.