VITAL RATES, THEIR VARIATION AND NATURAL SELECTION: A CASE FOR AN ATLANTIC FOREST MARSUPIAL

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Abstract: Evolutionary theory predicts that viable wild populations confront environmental variation by maintaining the variance of the most important vital rates low, a phenomenon also known as demographic buffering. However, patterns diverging from the demographic buffering hypothesis have also been reported. Here we used Population Matrix Models to test the hypothesis of buffering in the early survival of an Atlantic Forest marsupial. We used sensitivity analyses, which allow quantifying the effects that perturbations in specific vital rates could have on the population's growth rate. We obtained the sensitivities, elasticities, and second-order derivatives of the discrete population growth rate with respect to different vital rates for a population of the black-eared opossum (*Didelphis aurita*, Marsupialia, Didelphidae) in a preserved Atlantic Forest, the state of Rio de Janeiro, Brazil. The second-order derivatives offer an insight into the selection forces occurring during the life cycle, clarifying the processes behind the common pattern of early-survival importance. We found evidence of buffering in early survival, however, in one of the cohorts, early survival displayed evidence of opposed behavior to the expected under demographic buffering, thus revealing that established life-history patterns can be quickly modified by a small change in one vital rate.

Keywords: life cycle; life history; matrix population model; sensitivity of sensitivity; selection pressures.

INTRODUCTION

Evolutionary demography has been growing exponentially during the last decades (Coulson *et al.* 2010, 2016) and one of the reasons for such expansion is addressing the intriguing questions like How do wild-living populations of plants and animals cope with environmental variation (Sutherland *et al.* 2013, Rodríguez-Caro *et al.* 2021)? Theory predicts that wild populations confront environmental variation by maintaining the variance of the most important vital rates (*e.g.*, survival, fertility) low (Pfister 1998, Hilde *et al.* 2020). The important vital rates will modify population growth rate most effectively (into both directions) should they be perturbed, and as such, these important vital rates should be kept constant and have their variance minimized by natural selection (Pfister 1998). This means that if a value of an important vital rate changed, the response of the

population growth rate (its increase or decrease) would be stronger than if a less important vital rate changed.

Variation in vital rates is as important as their relative contribution to the population growth rate and should be an inherent part of evolutionary biology studies (Phillips & Arnold 1989, Pfister 1998). Temporal variation in the most important vital rates for the population growth rate (λ hereafter, a discrete-time population growth rate) will tend to decrease the long-term population growth rate (Gaillard & Yoccoz 2003, Reed & Slade 2012). This phenomenon, whereby the most important vital rate(s) in a population is (are) temporally constrained against variation, is known as demographic buffering (Pfister 1998), and it has been assumed as a key strategy to deal with environmental variability.

However, recent reports have emerged on species whose most important vital rates vary wildly with environmental fluctuations, while remaining demographically viable (Koons *et al.* 2009, McDonald *et al.* 2017, le Coeur *et al.* 2022). This puzzling observation has been formalized into the demographic lability hypothesis (Koons *et al.* 2009), whereby if the most important vital rates vary coinciding with optima in certain environmental regimes, the long-term population growth rate may remain non-negative. Nevertheless, a general pattern, where long-lived species tend to have the most important vital rates buffered in order to sustain environmental variability - while the opposite holds for short-lived organisms - remains (Gaillard & Yoccoz 2003, Nilsen *et al.* 2009).

Within this general pattern, the life histories of didelphid marsupials - resembling the fast end of the slow-fast continuum, characterized by large litters and short life spans (Ferreira *et al.* 2013, Fisher *et al.* 2013) - would not be expected to have their growth rate influenced mostly by survival, but rather by fertility. Nonetheless, a study on the same species as here showed that the most important vital rate for *Didelphis aurita* population growth rate in a rural area was early survival, and as such, should have its variance minimized.

Within population ecology, Matrix Population Models (MPMs hereafter) join the (st)age specific contributions in terms of fertility and survival into a system of equations representing the entire population (Caswell 2001). Among the many advantages the MPMs offer, they allow quantifying the effect that a perturbation in one (st)age specific vital rate (*e.g.*, fertility or survival) might have on the entire population's growth rate, λ. Furthermore, in a constant environment, λ can be equalled to fitness (Tuljapurkar 1982) since it includes the information regarding all (st)age specific contributions of survival and fertility at the same time (Lande 1982, Coulson *et al.* 2006). Thus, a first partial derivative of λ with regard to a (st)age specific vital rate (*i.e.*, the sensitivity of λ to changes in a vital rate), represents the selection gradient acting on that vital rate (Lande 1982, Shyu & Caswell 2014). A sensitivity analysis (represented by the first partial derivatives of λ with regard to a vital rate) allows identifying those vital rates to which λ is most sensitive (*i.e.*, have the highest sensitivity value, (Pfister 1998, Ebert 1999, Caswell 2001). Elasticities offer similar information as sensitivities, but in a proportional way (so that the contributions of all the vital rates in a life cycle sum to one - which is not the case for sensitivities (Ebert 1999).

The first partial derivatives of λ offer information regarding how λ will respond to a perturbation in a vital rate - whether λ will increase, decrease or remain constant (Ebert 1999). The derivative informs what would happen to λ if a vital rate should change (Caswell 2001). They offer information regarding linear selection – because they represent the linear selection gradients – an information which can be associated with the concept of directional selection, whereby selection dislocates the vital rate's *mean value*. However, the first derivatives have two shortcomings: 1) they assume that the relationship between a vital rate and the consequent response of λ is linear; and 2) they withhold any information of how the sensitivity of λ itself might change after a change in a vital rate (Shyu & Caswell 2014). In other words, if a value of a vital rate changes in time, does λ's sensitivity to that vital rate change too? Once the vital rate with the highest sensitivity is identified, the crucial question is *what affects this sensitivity*? The self-second derivatives (when not equal to zero) quantify this change in vital rate's sensitivity when the value of the vital rates is modified (Caswell 1996). The second order derivatives represent *locally* the quadratic selection gradients on λ (as opposed to the linear selection gradients represented by the first-order derivatives)

(Phillips & Arnold 1989, Caswell 1996). The quadratic selection gradients embody non-linear selection, which can be: 1) convex: increasing vital rate *variance*, representing evolutionary unstable singular strategy, also associated with the concept of disruptive selection; or 2) concave: decreasing vital rate *variance*, representing evolutionary stable singular strategy, also associated with the concept of stabilizing selection (Shyu & Caswell 2014, Kawano 2020).

Because concave selection implies in a reduction of temporal variance of a vital rate, it can also be used as a form of evidence of demographic buffering. There is also a third type of nonlinear relationship between a vital rate and λ, which can be represented by the cross-second derivatives. When the cross-second derivatives with respect to two different vital rates are non-zero, this implies in an increase of correlation between the two vital rates (when the cross-second derivatives > 0), or in a decrease of correlation between the two vital rates (when the cross-second derivatives < 0) (Shyu & Caswell 2014, Caswell 2001).

Despite the extensive theoretical advances (Caswell 1996, McCarthy *et al.* 2008, Shyu & Caswell 2014) and the valuable evolutionary-demographic insights that second derivatives of λ provide, they have been rarely applied to empirical data (see for example Shyu & Caswell 2014). Here we analysed a wild population of a neotropical mammal, the black-eared opossum *Didelphis aurita* Wied 1826 (Marsupialia, Didelphidae). This species represented a perfect MPM model, since individuals could be captured in all the life stages (age classes), including juveniles inside the mother's marsupium, making it possible to estimate vital rates at the moment of weaning.

The black-eared opossum is abundant in Atlantic Forest and has been interpreted as a key species because of its influence on the space used by other small mammals (Fonseca & Robinson 1990, Moura *et al.* 2009). Its population dynamics have been studied under various aspects (Cerqueira *et al.* 1993, Bergallo 1994, Gentile *et al.* 2000, 2004, Kajin *et al.* 2008, Mendel *et al.* 2008) including sensitivity and elasticity analysis in a rural area (Ferreira *et al.* 2013). Here we report the sensitivities and elasticities of population growth rate to each vital rate, the second-order derivatives of λ with respect to each vital rate and comment on the

evolutionary-demographic insights these results offer. Based on the life table analysis of the same data (Kajin *et al.* 2008) and on the demographic pattern observed in didelphid marsupials (Ferreira *et al.* 2013), we hypothesize that the survival of the early stages of *D. aurita* will result in the highest values of first and lowest values of second order derivatives, indicating demographic buffering in early survival. This means that early survival is the most important vital rate within the opossum's life cycle, and selection forces its variance to remain low (*i.e.*, is being buffered against environmental variability).

METHODS

Study site and field methods

A population of black-eared opossums was studied in a preserved area of coastal forest of the Serra do Mar, a subdivision of the Atlantic Forest biome (Dinerstein *et al.* 1995). The study site is located in the mountain range of Serra dos Órgãos, in the Parque Nacional da Serra dos Órgãos (PARNASO), municipality of Guapimirim, State of Rio de Janeiro. Brazil (22º28'28" S. 42º59'86" W). A more detailed description of the area is given by Mendel & Vieira (2003). The climate is mild humid mesothermic (Nimer 1989). During the study, the mean minimum and maximum monthly temperatures were 10.7 ºC and 30.5 ºC, respectively, and the total monthly rainfall was between 0.2 and 508 mm. Black-eared opossums have been captured-recaptured in this locality continuously since October 1997 in bimonthly trapping sessions of five consecutive nights as part of a long-term study by the Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro. Trapping details can be found in Mendel & Vieira (2003). All procedures were in accordance with the American Guidelines for the Capture, Handling and Care of Mammals (Sikes & Gannon 2011) and approved by the Brazilian Institute for Environment and Renewable Natural Resources (IBAMA) under license # 02001 004671/98-51.

The model species

Didelphis aurita is an abundant marsupial with a wide distribution ranging from north-eastern

Brazil in the north to northern Argentina in the south (Cerqueira 1985, Cerqueira & Lemos 2000). Characterized as occasionally arboreal and mostly terrestrial generalist species. it is found in all habitat types of the Atlantic Forest, as well as urban and rural areas often being considered a dominant species in the small-mammal community (Cerqueira *et al.* 1990, Fonseca & Robinson 1990, Gentile & Fernandez 1999, Cunha & Vieira 2002, Vieira & Monteiro-Filho 2003). These opossums reproduce seasonally, where the end of the reproductive season coincides with the peak of resource abundance, which occurs at the end of the rainy season (Cerqueira 2005). Pregnancy is short, lasting around 13 days. Right after the birth, bean-sized new-borns crawl until reaching the mother`s pouch, where they remain lactating for approximately 100 days until weaning. Females have a well-defined pouch with an average of 13 nipples; the average litter size for this population was 7.3 young/litter, with a minimum of 6 and a maximum of 10 offspring (Kajin *et al.* 2008). They are iteroparous, a single female can have up to two litters per reproductive season; their generation time was estimated between 232 to 470 days and the sex ratio did not differ from 1:1 (Kajin *et al.* 2008). Their nutritional habit is generalist, their diet considered fructivorous-omnivorous, composed primarily of terrestrial arthropods, fruits, and occasionally small vertebrates (Caceres & Monteiro-Filho 2001, Paglia *et al.* 2012, Santori *et al.* 2012). Competition by indirect interference with other small mammal species has been detected in the same population studied here, characterizing this opossum as an opportunistic predator and suggesting the occurrence of intra-guild predation (Moura *et al.* 2009).

Obtaining the estimates of vital rates

Eight cohorts (1997–1998, 1998–1999, 1999–2000, 2000–2001, 2001–2002, 2002–2003 2003–2004, 2004–2005) of female *D. aurita* were established and followed from birth until the last individual had disappeared from the study area. Five age classes were defined that corresponded to five life stages: (0) pouch young, 0–4 months; (1) weaned young, 4–8 months; (2) sub-adults (reproductively active), 8–12 months; (3) adult, 12–14 months; and (4) aged females, 14–18 months (Kajin *et al.*

2008). Therefore, the intervals between capture occasions (two months) were proportional to the period between the subsequent age classes (four months between two strata). We used MARK software (Cooch & White 2017) to estimate survival and capture probabilities, which varied in time and between age classes. The most plausible models were selected with the Akaike Information Criterion corrected for small samples, AICc (Burnham & Anderson 1998). Since survival is always related to the interval between age classes, for simplicity, we labelled the survival of a certain class by referring to the interval that followed that class, *e.g.,* pouch-young survival refers to surviving the transition from the pouch-young class to the weaned class, and so forth for all the classes.

A multi-strata model with age classes as strata was used to obtain age-specific survival rates (P_i, i=0, 1, 2, 3). The fecundity rates (m_j, j=2, 3, 4, i.e., lower-level parameters) were estimated following Caswell (2018), and fertility rates (F_i, *i.e.,* upper-level parameters) were composed of fecundity and pouch survival ($F_i = P_0 m_j$). With five age classes (but only three of them reproductively active), the life cycle of *D. aurita* was composed of four nodes and three loops (Figure S1, Supplementary Material). We tested the goodness-of-fit based on the global model (which included all the possible variation in survival and capture probability), by comparing the global model's deviance to the deviance of 1,000 simulated input matrices (a goodness-of-fit function within program MARK. The inflation factor was calculated dividing the observed deviance by the average value of the expected deviances obtained in the simulations (Cooch & White 2017).

First and second order sensitivity analysis of the discrete population growth rate (λ)

The sensitivity of the population growth rate (λ) to changes in vital rates P_i and F_j (*i.e.*, upper-level parameters) was obtained by calculating the first partial derivatives of λ with respect to P_i and F_j ($\partial\lambda/\partial P_i$ and $\partial\lambda/\partial F_j$). A non-zero first-order derivative for a certain vital rate quantifies the importance that this vital rate has for λ (*i.e.*, the sensitivity of λ to changes in that vital rate). If the first partial derivative of a vital rate were

positive, any perturbations in that vital rate would cause a linear increase in λ. If it were negative, a perturbation in that rate would cause a linear decline of λ. Elasticity - representing a relative sensitivity (Ebert 1999, Caswell 2001) - permits a comparison of the relative impact on λ among vital rates that occur on different scales, such as survival (always ranging from 0 to 1) and fertility (ranging from 0 to ∞).

The self- and cross- partial derivatives of λ were calculated with respect to each matrix entry (*i.e.*, upper-level parameters), where $\partial^2\lambda/\partial P_i\partial P_j$ represents the change that a perturbation of survival (P_j) would cause on the *sensitivity of λ to changes in P_i* ($\partial\lambda/\partial P_i$). A self-partial derivative is denoted as $\partial^2\lambda/\partial P_i^2$. The $\partial^2\lambda/\partial F_i\partial P_j$ represents the change that a perturbation of survival (P_j) would cause on the *sensitivity of λ to changes in F_i* ($\partial\lambda/\partial F_i$). Similarly, the second derivative of form $\partial^2\lambda/\partial F_i\partial F_j$ represents the change that a perturbation of fertility (F_j) would cause on the *sensitivity of λ to changes in F_i* ($\partial\lambda/\partial F_i$), and so on. All the derivatives were calculated following Caswell (1996) and Ebert (1999).

RESULTS

Among the eight cohorts followed, only five cohorts (namely cohorts 1997-1998, 1998-1999, 2000-2001, 2001-2002, and 2004-2005) could be included in the analysis because the remaining three cohorts failed to register reproduction or had no individuals recaptured after weaning. Within the five complete cohorts, a total of 189 females were marked still inside their mothers' pouches. From the total of 189, 20 were caught later as adult and/or as aged.

Estimates of vital rates

The modelling procedure in program MARK used to obtain the age specific survival rates indicated that survival varied with age, while capture probability among different age classes was constant. Thus, the model with the lowest QAICc values (where QAICc stands for adjusted AIC for small samples after adjusting the inflation factor c-hat (Burnham & Anderson 1998), see below) included survival varying through time (*i.e.,* between the age classes), and the differences in QAICc (ΔQAICc) to the next most plausible model were >> 2 for all cohorts (results not shown here). Thus, evidence

for survival's variation among age classes was undisputable. We used the best-ranked model to obtain the survival estimates to populate the MPMs (for estimated values see Table 1). Little evidence of lack of fit was detected in the global model including all possible types of variation (survival and capture probability varying in time). The inflation factor was corrected to *c-hat* = 1.136 to maximize models' fit. In general, the lowest survival estimates in all five cohorts were for pouch young (P_0), increasing in later classes (ranging from 0.21 to 1.00) (Table 1). Capture probability varied from 0.32 (in 1997-1998 cohort) to 0.59 (in 2001-2002 cohort). Fecundity rates varied from 0 to 4.5 young females per female (Table 1).

First- and second-order sensitivity analyses

The sensitivity of λ to survival rates ($\partial\lambda/\partial P_i$) was high for early survival (weaned and sub-adult, *i.e.*, P_1 and P_2) in all cohorts (Figure 1a), thus in concordance with our hypothesis. Cohort 2000-2001 presented a distinct high value for the P_1 sensitivity (Figure 1a). Similarly, elasticities identified early survival as the most influential vital rate for the population growth rate, although two cohorts (namely 2004-2005 and 2000-2001) also presented high values for fertility (Figure 1b).

The self-second derivative with respect to survival of weaned, $\partial^2\lambda/\partial P_1^2$, displayed a positive value for the 2001-2002 cohort (Figure 2a, indication with a black arrow), indicating convex selection, which was not expected following our hypothesis. For the remaining cohorts the value of $\partial^2\lambda/\partial P_1^2$ was negative (expected) and had distinctly low value for the 2000-2001 cohort (Figure 2a, indication with a black arrow), designating concave selection and reduction in rates' variance. The self-second derivative for sub-adult survival, $\partial^2\lambda/\partial P_2^2$, resulted in negative values for all the cohorts (Figure 2b, indication with a black arrow). The second derivatives with respect to adult survival, $\partial^2\lambda/\partial a_i\partial P_3$, were characterised by the absence (or a very weak presence) of nonlinear selection, where all the second derivative values were close to zero (Figure 2c). The remaining self and cross-second derivatives presented relatively consistent patterns with no major deviations among the cohorts regarding the sign of the values (either all negative or all positive) (Figure 2a, d, e, f).

Table 1. Vital rate values (used for populating the MPMs) and their descriptive statistics for five *D. aurita* female cohorts in South-eastern Brazil. P1 = survival of weaned; P2 = survival of sub-adult; P3 = adult; m2 = fecundity rate of sub-adult; m3 = fecundity rate of adults; m4 = fecundity rate of aged females.

Cohort	Survival estimates				Fecundity rates		
	Pouch young (P_0)	Weaned (P_1)	Sub-adult (P_2)	Adult (P_3)	Sub-adult (m_2)	Adult (m_3)	Aged (m_4)
1997-1998	0.211	1.000	0.500	1.000	1.000	4.500	1.750
1998-1999	0.222	0.750	1.000	1.000	1.000	3.000	2.500
2000-2001	0.172	0.200	1.000	1.000	0.000	3.500	0.000
2001-2002	0.250	0.670	1.000	1.000	0.000	0.000	4.500
2004-2005	0.159	0.714	0.200	1.000	4.250	6.000	0.000
Variance	0.001	0.085	0.138	0.000	3.063	4.925	3.563
SD	0.037	0.291	0.371	0.000	1.750	2.219	1.887
Mean	0.203	0.667	0.740	1.000	1.250	3.400	1.750
CV	18.336	43.600	50.200	0.000	140.000	65.272	107.855

Effects of trade-offs could be seen in the following cross-second derivatives: $\partial^2\lambda/\partial P_1\partial F_2$ (indicating positive correlational selection forces, enhancing the correlation between survival of weaned (P_1) and sub-adult fertility (F_2), Figure 2d, black arrow pointing upwards), $\partial^2\lambda/\partial P_2\partial F_2$ (indicating negative correlational selection forces, decreasing the correlation between survival of sub-adult (P_2) and sub-adult fertility (F_2), Figure 2d, black arrow pointing downwards), $\partial^2\lambda/\partial P_1\partial F_3$ (indicating positive correlational selection forces between survival of weaned (P_1) and adult fertility (F_3), Figure 2e, left black arrow pointing upwards), $\partial^2\lambda/\partial P_2\partial F_3$ (indicating positive correlational selection forces between survival of sub-adult (P_2) and adult fertility (F_3), Figure 2e, right black arrow pointing upwards)), $\partial^2\lambda/\partial P_3\partial F_4$ (indicating positive correlational selection forces between survival of adult (P_3) and aged adult fertility (F_4), Figure 2f, black arrow pointing upwards), and $\partial^2\lambda/\partial F_3\partial F_4$ (indicating positive correlational selection forces between fertility of adult (F_3) and aged adult fertility (F_4), Figure 2f, black arrow pointing downwards).

DISCUSSION

Our results are in concordance with a study on *D. aurita* in a rural area (Ferreira *et al.* 2013), where survival of weaned had been identified as the most important vital rate within this opossum's life cycle. As such - following the demographic buffering hypothesis - survival of weaned would be expected to have its variance reduced by natural selection. However, we found an unexpected positive value for the self-second derivative of survival of weaned ($\partial^2\lambda/\partial P_1^2$) in one of the cohorts (2001-2002), indicating absence of demographic buffering. In the cohort 2001-2002, the expected pattern of concave selection, reducing the variance in P_1, was not only absent, but replaced by convex selection, where P_1 variance tends to be increased. Thus, our results show that selection acting on one vital rate, the P_1, shifted from one type (concave selection) in one cohort, to a different type of selection (convex selection) in the following cohort. This leads us to conclude that the pattern of concave selection - which resembles demographic buffering for implying a variance reduction in a vital rate – is dynamic rather than fixed.

It is important to distinguish among two concepts of temporal variance: the realised and the potential variance. The realised variance can be calculated for every vital rate as the variance among multiple MPMs (one for each cohort, reported in Table 1) to quantify how much a certain vital rate varied through time *de facto*. The potential variance, on the other hand, is revealed
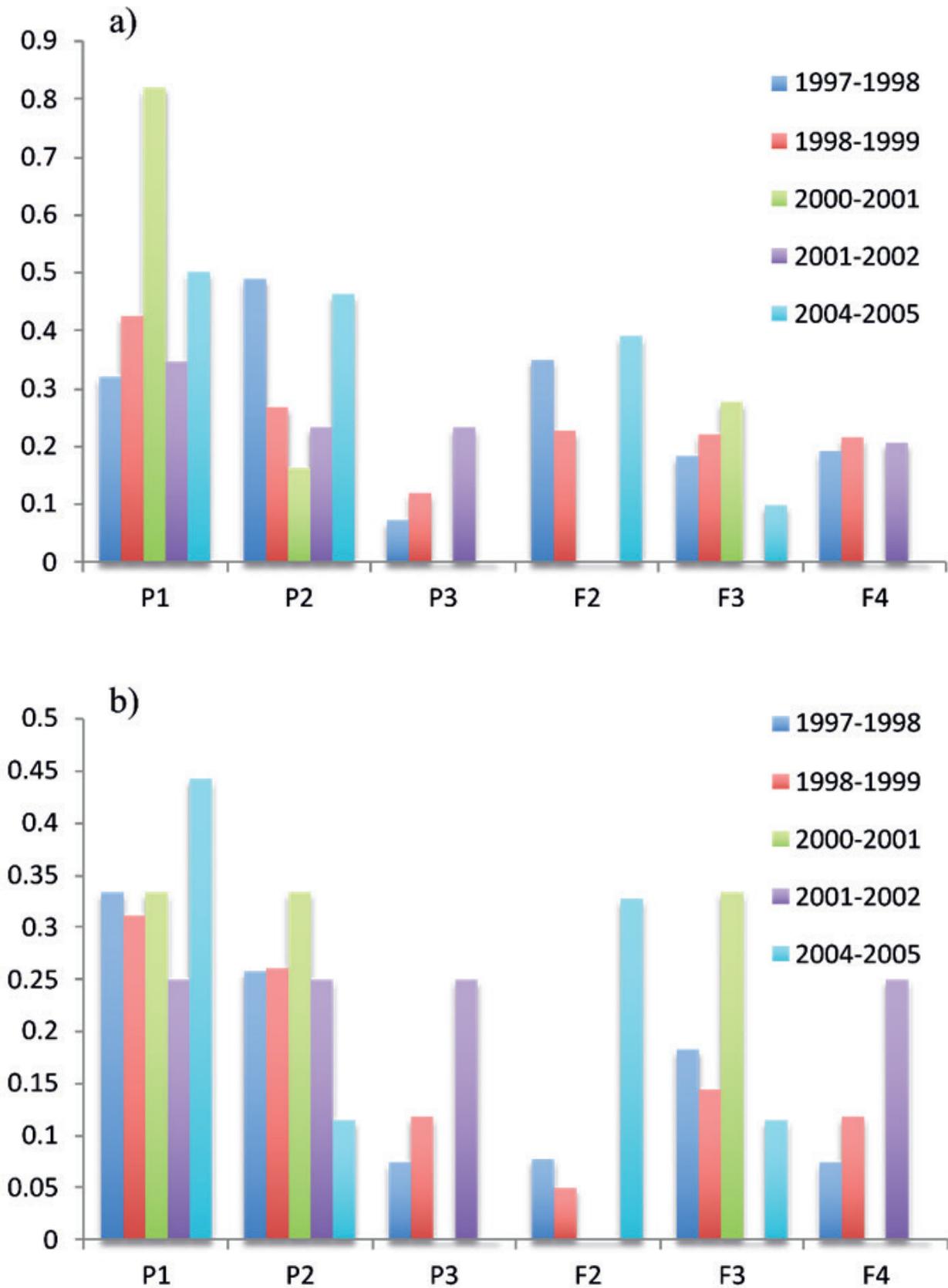
Figure 1. Sensitivities (a) and elasticities (b) of population growth rate with respect to seven vital rates (upper-level parameters). Data from five female *Didelphis aurita* cohorts. P_1 = survival of weaned; P_2 = survival of sub-adult; P_3 = adult; F_2 = fertility rate of sub-adult; F_3 = fertility rate of adults; F_4 = fertility rate of aged females. Note that the scales of y-axes in a) and b) are different.

by the second-order derivatives. Thus, the second-order derivatives provide information on what would happen to vital rate variance in every cohort if that vital rate was perturbed (*i.e.*, changed by the environment). As such, they express the non-linear selection pressures acting on vital rate variance, which can be convex or concave.

The sign shift in the $\partial^2\lambda/\partial P_1^2$ derivative is a consequence of the change in P_1 survival value. Thus, for the 2000-2001 cohort, all the vital rates
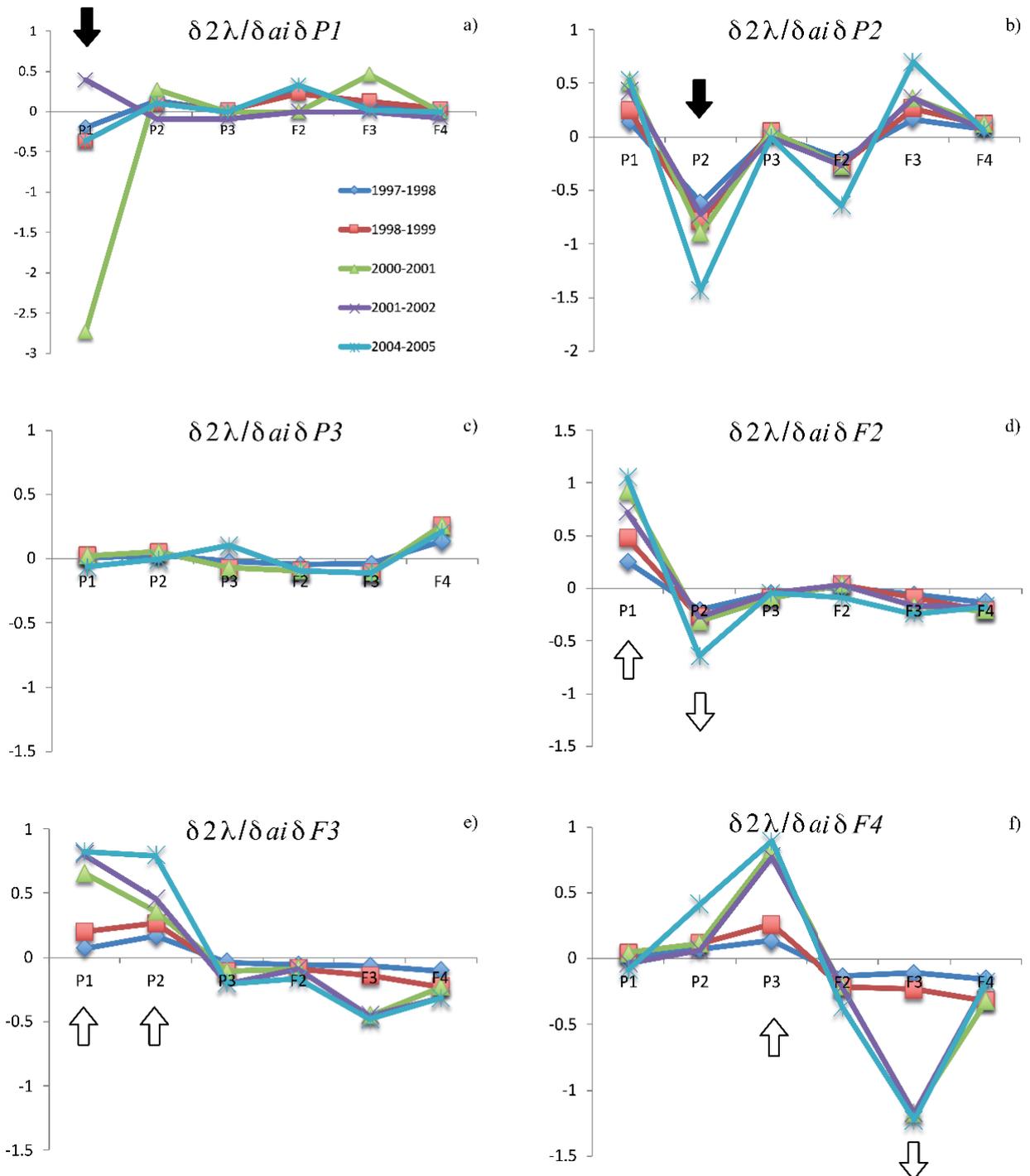
Figure 2. Second-order derivatives of *D. aurita* population growth rate with respect to a) P_1 (survival of weaned); b) P_2 (survival of sub-adult); c) P_3 (survival of adult females); d) F_2 (fertility of sub-adult); e) F_3 (fertility of adult), and f) F_4 (fertility of aged adult females) from four cohorts in Atlantic Forest, South-eastern Brazil. The self-second derivatives are marked with a black arrow and the cross-second derivatives with a black-lined white arrow. Note that the y-axis scale is different in a.

of subsequent age classes (after the class of weaned) are being 'filtered' by low early survival. When P_1 increased in the following 2001-2002 cohort, the demographic strategy of the entire life cycle changed and buffering on P_1 vital rate was completely absent. Correspondingly, the sensitivity of λ to changes in P_1 also changed from the 2000-2001 cohort to the 2001-2002 cohort. The fast shifting of the $\partial^2\lambda/\partial P_1^2$ derivative sign from one cohort to the next evidences how the patterns of selection forces acting on a life history can be modified by a small change in only one vital rate.

A consistent buffering pattern across all the cohorts was identified for the survival of sub-adult (P_2), resulting in negative self-second derivative $\partial^2\lambda/\partial P_2^2$ values, thus supporting our initial hypothesis. This means that despite the weaker importance of P_2 for λ (as compared to P_1, Figure 1a, b), this importance can quickly change if P_2 were to be perturbed. This change happens in a nonlinear manner and reveals a "secondary" importance of P_2 vital rate that had not been revealed by first-order sensitivity values. Because the self-second derivatives $\partial^2\lambda/\partial P_2^2$ are negative, any change in P_2 would cause a quick change in λ's sensitivity to P_2. Thus, even if λ is not as sensitive to P_2 as to P_1, the sensitivity of P_2 itself is very sensitive to any changes in the value of P_2.

The biological reasons for low early survival (P_1 and P_2) and their high sensitivity/elasticity values are two: firstly, at the moment of weaning and until the adult age, young are much easier prey for predators than adults (Hossler *et al.* 1994). Secondly, young individuals recently weaned or which left the nest would compete for resources, where the most limited resource in the study area is probably space. Food resources were probably not the most limiting factor for this species in the study area because of the generalist feeding habit of the opossum, the relatively high abundance in food resources year-round, and the timing of weaning, which coincides with the wet season and the peak in the food resource abundance. However, until the females reach their adult age, they are subjected to intra-specific competition (*i.e.*, density-dependence) for space, since they are known to avoid each other, are unsocial and can present violent behaviour towards other species or frequently towards conspecifics, or even infanticide (Pires *et al.* 2010). Frequently, changes in den localities have been reported (Allen

et al. 1985). Females have been found to modify their movement patterns in the study area as a result of increased density dependence, which corroborates the studies on movement patterns and use of space and its relationship with the reproductive season (Almeida *et al.* 2015). The competitive pressures at the early ages are also enacted by other small mammal species. In addition, young are under strong pressure from predation. This pressure is even stronger in absence of top predators, when the only predators left are snakes and rapines, which both select for smaller prey (young individuals) if compared to bigger predators.

A different pattern was found for the survival of adults (P_3) in all five cohorts, where only weak or no selection forces were identified as well as little or no nonlinearity of λ's response to perturbations in P_3. Once the females survive the critical moments early in the life cycle (pass the P_1 and P_2), they become established within the population, their survival increases and stabilizes, and consequently, selection forces on this vital rate (P_3) are minimized. Caswell (1996) shows a similar pattern for human demographic data, where early survival is under concave selection forces, while survival at later age classes has little or no effect on the sensitivity of λ. Weaker selection forces on vital rates at late age classes imply in survival related senescence, which is expected to occur in *D. aurita* as the phenomenon is widely present in mammals (Jones *et al.* 2008).

The cross-second derivatives revealed the selection forces behind the survival-fertility trade-off. These can also be called the "cost of reproduction". While selection forces the variance of P_2 to be reduced, at the same time, forces the correlation between P_2 and F_2 to decrease. Selection force operating on the pair of vital rates P_2 and F_2 is correlational and this is evidenced by the negative values of the cross-second derivative of form $\partial^2\lambda/\partial F_2\partial P_2$, where selection reduces the strength of correlation between P_2 and F_2. This is so because P_2 and F_2 are engaged in a trade-off, where an increase in one causes a decrease in another (Table 2, significant negative correlation for the pair P_2 and m_2). Thus, if P_2 is to have its variance reduced to maintain the long-term population growth rate >1, the selection must act in the direction of reducing the strength of correlation between P_2 and F_2 - since F_2 (and its component m_2) vary substantially (Table 1).

However, selection acts on increasing the strength of correlation between weaned survival (P_1) and sub-adult fertility (F_2), since the cross-second derivative of form $\partial^2\lambda/\partial P_1\partial F_2$ resulted in positive values. An investment in reproduction by sub-adult females would lead to an increased influence of the first age-class survival on the population growth, since F_2 represents one of the direct feeds into the first age class (generating new weaned individuals, see Figure S1 in Supplementary Material).

The positive values for the cross-second derivative of form $\partial^2\lambda/\partial P_1\partial F_3$ and $\partial^2\lambda/\partial P_2\partial F_3$ indicate selective forces acting towards increasing the strength of correlation between P_1 (survival of weaned), P_2 (sub-adult survival) and F_3 (adult fertility). An increase in F_3 would increase λ's sensitivity to P_1 and P_2, because more females would be generated into the age classes 1 and 2. Similarly as the F_2, F_3 too represents a direct feed into the class of weaned females, thus influencing directly the sensitivity of λ to early survival. An interesting pattern that emerged is that any increase in the fertility of sub-adult and adult females does not increase the sensitivity of λ to fertility, but to early survival, because females must first survive to at least sub-adult age in order to realize their fertility.

An increase in aged females' fertility (F_4) would reduce the sensitivity of λ to changes in sub-adult fertility (F_3), as indicated by the negative cross-second derivative $\partial^2\lambda/\partial F_3\partial F_4$ (denoted by the black arrow in Figure 2f). An increase in investment in reproduction by adult females would lead to a reduction in the influence of reproduction of the previous age class on population growth, that is, some females would have a reproductive strategy of greater fecundity at older ages, which would not affect survival rates, but rather the fecundity of younger females. The latter pattern evidences a lack of reproductive senescence (*i.e.*, the fertility does not decrease with age), which had been showed to occur in small mammals (Jones *et al.* 2008).

D. aurita has already been shown as atypical within the slow-fast continuum. It displays the characteristics of a slow-end organism – where survival is more important for the population growth rate than fertility (Ferreira *et al.* 2013). Given its relatively short life span, large litters and short periods of parental care, the expected pattern for this opossum would be a pattern typical of a fast-end organism, where fertility would play a more

Table 2. Correlations among vital rates for the five cohorts of *Didelphis aurita* in Northeastern Brazil. Significant value (p ≤ 0.05) is in bold.

	P_0	P_1	P_2	m_2	m_3
P_1	0.39				
P_2	0.56	-0.47			
m_2	-0.61	0.30	**-0.87**		
m_3	-0.84	0.15	-0.80	0.76	
m_4	**0.98**	0.37	0.50	-0.51	-0.86

important role for the population growth rate. Our results confirmed the greater importance of early survival for the opossum's population growth rate than fertility. However, we showed that within the position the opossum takes inside the fast-slow continuum, the importance of survival is *dynamic*. Consequently, the patterns of selection pressures acting on survival might change from one cohort to another. Such sudden change in selection pressure patterns was promoted by a change in the value of one vital rate (P_1). The value of P_1 was modified by a change in the environment, which caused a shift in the patterns of selection pressures. Namely, the selection pressures on P_1 changed from *concave* to *convex*. The latter change implies in selection acting in an opposite form on temporal variance of P_1. However, the first order sensitivities only revealed that λ was less sensitive to P_1 in cohort 2001-2002 as compared to cohort 2000-2001. What the first order sensitivities did not reveal, is that the way selection acted on P_1 had shifted from one cohort to another.

In conclusion, the hypothesis that early survival is a key point for the demography of this species, which was observed in previous studies, was supported and elucidated by the second derivative analyses. However, the second derivative approach allowed for a more detailed insight into the selection patterns on each vital rate (the self-second derivatives) as well as on the strength of correlations among the vital rates (the cross-second derivative). The latter feature is exclusive to the second-order derivative approach, which makes it a promising tool in evolutionary demography. Its major potential lies in the ability to identify the pairs of vital rates where the strength of correlation among vital rates might increase as a function of environmental change.

The organisms on the slow-end of the slow-fast continuum have been shown as more susceptible to

changes in vital rates provoked by the environment (Morris *et al.* 2008, Albaladejo-Robles *et al.* 2022). *D. aurita* was classified as a slow-end organism, however, we showed that the importance of survival, classifying the species as a slow-end organism, can easily change from year to year.

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SUPPLEMENTARY MATERIAL

Figure S1. The life-cycle graph for *Didelphis aurita* population in Atlantic Forest, Southeastern Brazil. The four circles represent the age classes. The population was structured into five age classes (see text for details), whereby the zero age class, when the animals are still inside the pouch, was represented by the four-month transition from the reproductively active classes to the first age class of weaned young. Each transition's duration is approximately four months. The estimates for survival transitions (P_i) were obtained from capture-recapture data using program MARK.