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5 **Stochastic LTRE analysis of the effects of herbivory on the** 6 **population dynamics of a perennial grassland herb**

7
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25 **Abstract**

26
27 Herbivores can have strong deleterious effects on vital rates (growth, reproduction, and
28 survival) and thus negatively impact the population dynamics of plant species. In practice,
29 however, these effects might be strongly correlated, for example as a result of trade-offs
30 between vital rates. To get better insights into the effects of herbivory on the population
31 dynamics of the long-lived grassland plant *Primula veris* population projection matrices were
32 constructed from demographic data collected between 1999 and 2008 (nine annual
33 transitions). Data were collected in two large grassland populations, each of which was
34 subjected to two treatments (grazing by cattle vs. a mowing treatment), yielding a total of 36
35 matrices. We applied a lower-level vital rate life table response experiment (LTRE) using the
36 small noise approximation (SNA) of the stochastic population growth rate to disentangle the
37 contributions of changes in mean vital rates, variability in vital rates, correlations between
38 vital rates and vital rate elasticities to the difference in the stochastic growth rate. Stochastic
39 growth rates ($a = \log \lambda_S$) were significantly lower in grazed than in mown plots ($a = 0.0185$
40 and 0.1019 , respectively). SNA LTRE analysis showed that contributions of differences in
41 mean vital rates by far made the largest contribution to the observed difference in a between
42 grazed and control plots. In particular, changes in sexual reproduction rates made the largest
43 contributions to lower the stochastic growth rate in grazed plots: both adult flowering
44 probabilities and flower and seed production were importantly lower in grazed populations,
45 but these negative effects were largely buffered by increased establishment and seedling
46 survival rates. Among the stochastic terms of the SNA decomposition, contributions of
47 changes in covariance and correlations between vital rates had the largest impact, whereas
48 contributions of changed elasticities were smaller. The strongest correlation driver was the
49 association between adult survival and seedling establishment, suggesting that environmental

1 conditions favouring adult survival also are beneficial for seedling establishment. Overall, our
2 results show that herbivory had a strong negative effect on the long-term population growth
3 rate of *P. veris* that was primarily mediated by differences in fecundity (flower and seed
4 production) and germination.

5
6 *Key words: herbivory; life table response experiment (LTRE); Primula veris; small noise*
7 *approximation (SNA); stochastic population growth rate (λ_s).*
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9

10 **Introduction**

11
12 The precise factors that determine the population dynamics and long-term population growth
13 rate of plant species subject to grazing are diverse, complex and often interdependent. In
14 general, the impact of grazing animals on plant population dynamics varies depending on the
15 plant species that is grazed and on the animal species that consumes the plant (Maron and
16 Crone 2006). Grassland plants are particularly prone to the negative effects of consumers,
17 whereas forest herbs are less affected (Maron and Crone 2006). On the other hand, the impact
18 of grazers is not dependent on life-history traits such as reproductive mode or longevity
19 (Maron and Crone 2006, but see Hayes and Holl 2003).

20 In practice for natural populations, it is difficult to untangle the direct consumptive
21 effects of herbivores from indirect effects, as they often appear to be interrelated (Crawley
22 1983, McNaughton 1983). Given that correlations between vital rates may have a strong
23 impact on basic demography and long-term population viability (Wisdom et al. 2000, Menges
24 2000, Jongejans et al. 2010), better insights into these correlations are indispensable for
25 assessing the underlying dynamics of plant populations subject to grazing. Reductions in seed
26 production due to grazing, for example, may strongly impact the number of germinating seeds
27 in the next season, but treading by grazing animals may increase seedling establishment and
28 survival as a result of the higher availability of suitable micro-sites. Similarly, reductions in
29 growth may affect the probability of flowering, but at the same time incur costs to survival,
30 growth and reproduction in the next season, leading to trade-offs between current
31 reproduction and future survival, growth or fecundity (Stearns 1989).

32 Most studies investigating the effects of herbivory on the population dynamics of plant
33 species have a short duration (< 4 years) (Menges 2000, Maron and Crone 2006, Crone et al.
34 2011), and therefore may fail to detect trade-offs in life history traits. Particularly in long-
35 lived, iteroparous species with overlapping generations, assessing the impact of trade-offs on
36 plant population dynamics has proved challenging (Doak 1992, Obeso 2002). Due to their
37 short duration, most studies also largely ignore the fact that demographic rates may vary over
38 time. The abundance of grazers and grazing intensity, and the timing of grazing may vary
39 substantially from one year to the next, which in turn may lead to strong variation in vital
40 rates between years (Crawley 1983, Buckley et al. 2010) and therefore contribute negatively
41 to the long term growth rate of grazed populations (Cohen 1979). Moreover, differences in
42 environmental conditions between years may also directly impact population dynamics and
43 these impacts may be mediated by grazing (Bastrenta et al. 1995).

44 In this case, classic life table response experiments (LTREs) using deterministic
45 estimates of the population growth rate, such as the dominant eigenvalue of the mean
46 projection matrix (λ_0) or the intrinsic growth rate ($r = \log \lambda_0$), may fail to accurately assess the
47 effect of herbivores on the long-term growth rate (Cohen 1977, Tuljapurkar and Orzack
48 1980). Instead, the stochastic growth rate, $a = \log \lambda_s = E\{\log \lambda_0(t)\}$, provides a better way to

49 describe the long-term demographic behaviour of plant populations in varying environments

1 (Tuljapurkar 1990), whereas recent extensions of life table response experiments for
2 stochastic population growth allow us to assess the various demographic and environmental
3 factors that contribute most to variation in the stochastic growth rate (Caswell 2010, Davison
4 et al. 2010, 2011).

5 In this study, we investigated the impact of herbivory on the population dynamics of
6 the long-lived perennial grassland plant *Primula veris*. In a previous study, Brys et al. (2011)
7 showed that herbivory by grazing animals (cattle) had a strong impact on the size of
8 individuals of this species and that belowground biomass of grazed plants was about 20%
9 smaller than that of plants in the same population that were exposed to mowing. The number
10 of leaves and the size of leaves were significantly smaller in grazed plants than among plants
11 in mown plots. Reduced numbers of leaves and smaller leaf areas affect survival probabilities,
12 and may also impact future flowering behaviour, as the amount of carbohydrates that can be
13 relocated to belowground storage organs decreases with leaf area, possibly leading to resource
14 depletion and reduced performance in the next year. Short-term experiments in which a
15 proportion of the leaves was removed at different times in the growing season have indeed
16 shown that removal of 50% of the leaves during flowering (early defoliation) negatively
17 affected current reproductive performance (fruit set and total seed production) and future
18 growth, whereas middle defoliation (removal of 50% of the leaves during fruit development)
19 only reduced future flowering probability and growth, and late defoliation (removal of 50% of
20 the leaves during fruit maturation) did not affect any fitness component (García and Ehrlén
21 2002). These observations suggest that damage to above-ground tissue during the growing
22 season not only results in the destruction of flowering stalks and fruits, but may also reduce
23 flowering probabilities and performance of adult individuals in the next growing season,
24 depending on the developmental stage of the plant (García and Ehrlén 2002, Brys et al. 2004).
25 However, the long-term effects of herbivory on the population dynamics remain poorly
26 understood.

27 For the present study, population projection matrices were constructed from
28 demographic data collected between 1999 and 2008 (nine annual transitions). Data were
29 collected from two populations, each of which was subjected to two treatments (cattle grazing
30 vs. mowing), yielding a total of 36 matrices. We applied lower-level vital rate LTRE analyses
31 using the small noise approximation of the stochastic growth rate (Davison et al. 2011) to
32 untangle the direct consumptive effects of herbivores from a variety of indirect effects acting
33 on the population dynamics of this grassland species. This technique has the particular
34 advantage that it allows us to quantify the effects of differences in mean vital rates, in
35 variability in vital rates, in correlations between vital rates and in elasticities of vital rates
36 (Davison et al. 2011).

37 **Material and Methods**

38 *Study species*

39
40
41
42 *Primula veris* (Primulaceae) is a small perennial herb with a wide distribution in Europe (Brys
43 and Jacquemyn 2009). It typically occurs in nutrient-poor, calcareous grasslands, in which it
44 can be locally abundant, but it may also be found in dune grasslands and hay-meadows. Early
45 in spring, plants produce a rosette of several leaves and one (though, rarely, two or more)
46 flowering stalks bearing between 4 and 15 yellow flowers displayed in an umbel (García and
47 Ehrlén 2002). Flowers are distylous (Wedderburn and Richards 1990) and mainly pollinated
48 by bees and bumblebees (Ornduff 1980, Brys and Jacquemyn 2009). In the study area,
49 flowering starts at the end of April and lasts about three to four weeks. Seeds ripen 8–10
50 weeks after fertilization and seed shed takes place from mid-July to September. Seeds lack

1 any specific dispersal mechanisms and in most cases fall in the direct neighbourhood (< 15
2 cm) of their mother plants (Richards and Ibrahim 1978).

3 The majority of seeds survive winter and germinate in spring (from the end of April
4 until mid-May). Although seeds can accumulate in the soil seed bank (Milberg 1994), our
5 own experiments suggest that recruitment from the seed bank is very limited (Brys and
6 Jacquemyn 2009, Jacquemyn et al. 2011). This species is characterised by the occurrence of a
7 rhizome, which produces numerous fibrous roots that thrust through living leaf bases and
8 which can be up to 15 cm long. This rhizome is thought to function as a storage organ and
9 may buffer compensatory responses following herbivory and/or reproductive costs in the
10 short term (Brys and Jacquemyn 2009).

11 *Data collection and experimental design*

12
13
14 To investigate the effects of herbivory on the population dynamics of *P. veris* the fate of each
15 *P. veris* individual was monitored annually between 1999 and 2008. The design of this
16 experiment is detailed by Brys et al. (2011). Two comparable sites, both displaying optimal
17 growth conditions and containing > 10.000 flowering individuals of *P. veris*, were selected in
18 Voeren (Eastern Belgium). The populations are about 1 km apart and located in calcareous
19 grasslands on a south-facing slope (inclination 20°). Before sites were selected, it was
20 ascertained that they had a similar history of grassland management.

21 At each site, ten permanent plots (3 × 3 m²) were established in the winter of 1999,
22 yielding a total of 20 plots. All plots were laid out in the central and most homogenous part of
23 each population. Half of the plots were grazed and the other half were fenced and mown
24 annually at the end of the growing season (the second half of August). At this time, *P. veris*
25 leaves had already started to degenerate and most of the aboveground resources were
26 reallocated to the rhizomatous roots. Cattle grazing started at the end of May and lasted
27 intermittently until the end of September. Average cattle density numbered 15 cows ha⁻¹ and
28 was similar across sites. Fenced plots were mown mechanically (2-4 cm above the ground
29 surface) and all litter was removed afterwards. Each of the plots received the same
30 management throughout the entire study period (1999-2008), but the timing of grazing varied
31 throughout the study period. Whereas in the beginning of the study period (1999-2001)
32 grazing started already in May, later during the experiment cows were allowed to graze only
33 from the middle of June (see Brys et al. 2004 for more details).

34 At the beginning of the experiment (1999), each plant was meticulously mapped using
35 a 5 × 5 cm² grid and its life-history state was determined. Following Brys et al. (2004), plants
36 were classified into one of four categories: seedlings (all plants younger than one year);
37 juveniles (more than 1 year and the number of leaves ≤ 3 and/or length of the largest leaf < 2
38 cm); vegetative individuals (more than 1 year and the number of leaves > 3 and /or length of
39 the largest leave ≥ 2 cm); and reproductive individuals (more than 1 year and bearing
40 flowers). For a detailed description of the life cycle and all life cycle transitions we refer to
41 Brys et al. (2004).

42 To avoid edge effects and damage due to demographic monitoring, only the central 1
43 × 1 m² area within each 3 × 3 m² plot was surveyed for demographic analyses. In subsequent
44 years, all plots were monitored again, and the fate of each mapped plant was determined. New
45 seedlings arising in the population were also mapped annually and the state of each plant was
46 characterized during ten consecutive years. During this period, a total of 4594 plants was
47 monitored. For flowering plants, the number of flowers per plant and the number of seeds per
48 fruit were determined each year for twenty plants per treatment and site. Plants were
49 randomly selected in the plots, and for each selected plant the number of flowers was counted.
50 To assess seed set, three mature fruits were harvested from each selected plant and in each

1 fruit the number of seeds was counted. For each year and treatment, the average number of
 2 flowers and average seed set were used in all subsequent analyses.

4 *Data analysis*

6 For each year, site and treatment we constructed population projection matrices, resulting in a
 7 total of 36 matrices (see Appendix S1) describing annual population projections (Caswell
 8 2001). In these projections, n_t is the number of individuals in each stage class at time t and \mathbf{A}
 9 is the population projection matrix ($\mathbf{A}=\{a_{ij}\}$). Matrix elements a_{ij} describe the annual per-
 10 capita contribution of stage i individuals made by stage j individuals and $(n_{t+1} = \mathbf{A}n_t)$ describes
 11 the population projection:

$$12 \quad n_{t+1} = \mathbf{A}n_t = \begin{pmatrix} L(t+1) \\ J(t+1) \\ V(t+1) \\ F(t+1) \end{pmatrix} = \begin{pmatrix} 0 & 0 & 0 & \mu\pi\epsilon \\ \sigma_L(1-\gamma_L) & \sigma_J(1-\gamma_J) & 0 & 0 \\ \sigma_L\gamma_L & \sigma_J\gamma_J(1-\phi_J) & \sigma_V(1-\phi_V) & \sigma_F(1-\phi_F) \\ 0 & \sigma_J\gamma_J\phi_J & \sigma_V\phi_V & \sigma_F\phi_F \end{pmatrix} \begin{pmatrix} L(t) \\ J(t) \\ V(t) \\ F(t) \end{pmatrix} \quad (1)$$

13 Here, L is the number of seedlings, J the number of juveniles, V the number of vegetative
 14 plants and F the number of flowering plants in a given year. Because matrix elements are
 15 compounds of different vital rates, demographic comparisons among populations were made
 16 using vital rates rather than matrix elements and matrix elements were explicitly written as
 17 functions of different vital rates (Caswell 2001, Franco and Silvertown 2004). In equation 1, σ
 18 refers to survival, γ to growth conditional on survival, and ϕ refers to the probability of a plant
 19 flowering in the next year. The terms in the fecundity element (a_{14}) refer to the average
 20 number of flowers (μ), the average number of seeds per fruit (π) and the proportion of seeds
 21 that germinate and successfully establish as a seedling (ϵ).

22 Based on these matrices, we calculated the long-term stochastic growth rate ($a = \log$
 23 λ_s) in two ways for each site and treatment: 1) by simulation (of 100,000 years, discarding the
 24 first 2,000 years to exclude initial transient dynamics) and 2) by using the small noise
 25 approximation (Tuljapurkar 1990). In the latter case, the stochastic growth rate can be written
 26 as the deterministic growth rate minus a product containing vital rate elasticities (e),
 27 coefficients of variation (c) and correlations between vital rates (ρ) (Haridas and Tuljapurkar
 28 2005, Jongejans et al. 2010, Davison et al. 2011):

$$29 \quad a = \log \lambda_s \approx r - \frac{1}{2} \sum_{k,l} e_k e_l c_k c_l \rho_{k,l} \quad (2)$$

30 The second term in (2) describes the stochastic component of the population growth rate and
 31 shows depreciation of the deterministic growth rate by each of the different terms.

32 We applied vital rate LTRE analysis using the small noise approximation of the
 33 stochastic growth rate (Davison et al. 2011) to study the impact of herbivory on the overall
 34 population growth rate and to assess contributions of mean vital rates, variance in vital rates
 35 and correlations between vital rates to differences in the stochastic growth rate. For these
 36 analyses we used vital rates averaged over the two sites for each treatment-year combination.
 37 Following Davison et al. (2011), the difference in stochastic growth rates (Δa) between the
 38 mowing and grazing treatment can be written as a difference of a sum of products:

$$39 \quad \Delta a = a^{(g)} - a^{(m)} \approx r^{(g)} - r^{(m)} - \frac{1}{2} \left(\sum_{k,l} \{e_k e_l c_k c_l \rho_{k,l}\}^{(g)} - \sum_{k,l} \{e_k e_l c_k c_l \rho_{k,l}\}^{(m)} \right) \quad (3)$$

40 Using the Kitagawa decomposition (Kitagawa 1955), Davison et al. (2011) showed that this
 41 difference can be approximated by the summation of four components:

$$42 \quad 1) \text{ contributions of differences in vital rate means: } \sum_k \bar{e}_k (\log \mu_k^{(g)} - \log \mu_k^{(m)}) \quad (4)$$

1 2) contributions of differences in vital rate elasticities: $-\frac{1}{2} \sum_{k,l} [\overline{c_k c_l \rho_{kl}}] \Delta \{e_k e_l\}$ (5)

2 3) contributions of differences in coefficients of variation: $-\frac{1}{2} \sum_{k,l} [\overline{e_k e_l}] (\overline{\rho_{k,l}} \Delta \{c_k c_l\})$ (6)

3 4) contributions of differences in correlations: $-\frac{1}{2} \sum_{k,l} [\overline{e_k e_l}] ([\overline{c_k c_l}] \Delta \{\rho_{k,l}\})$ (7)

4
5 Please note that this double Kitagawa decomposition of the stochastic term (resulting in the
6 latter three contributions) is a perfect decomposition that contains all the components of
7 stochastic population growth (Davison et al. 2011).

8
9 **Results**

10
11 *Flower and seed production*

12
13 The mean number of flowers per plant was significantly smaller in grazed than in mown
14 treatments ($F_{1,36} = 88.66, P < 0.0001$), but it was significantly different between sites ($F_{1,36} =$
15 $0.12, P = 0.73$) (see Appendix A for vital rate values for all site-treatment-year combinations).
16 Similarly, average seed production per fruit was significantly higher in mown plots than in
17 grazed plots ($F_{1,36} = 92.67, P < 0.0001$), but did not differ between sites ($F_{1,36} = 0.18, P =$
18 0.67). There were also no significant interaction effects between site and treatment ($F_{1,36} =$
19 0.08 and $0.51, P > 0.05$). Plants produced an average of 4.7 flowers in grazed treatments,
20 whereas in mown treatments plants had, on average, 8.7 flowers. Similarly, the average
21 number of seeds per fruit varied between 12 and 23 in grazed plots (mean: 16.9), and between
22 23 and 45 in mown plots (mean: 36.8).

23
24 *Matrix analyses*

25
26 The effects of grazing, compared to mowing, were similar between sites. In grazed plots,
27 annual projected deterministic population growth rates varied between 0.8402 and 1.1529 in
28 Site 1 and between 0.6538 and 1.2345 in Site 2, whereas population growth rates of the mown
29 treatments varied between 0.9924 and 1.2950 in Site 1 and between 0.9531 and 1.3224 in Site
30 2. The corresponding intrinsic growth rates ($r = \log \lambda_0$; calculated with mean vital rates) were,
31 respectively, 0.0285 and 0.0322 in grazed sites, and 0.0994 and 0.1202 in mown sites.
32 Consistent with earlier findings (Buckley et al. 2010) and with theoretical expectations
33 (Cohen 1979), simulated stochastic growth rates ($a = 0.0110$ and 0.0124 in grazed sites, and
34 0.0861 and 0.1117 in mown sites) were consistently smaller than those of the corresponding
35 deterministic growth rates.

36
37 *SNA LTRE analyses*

38
39 Small-noise approximations were close to the simulated stochastic growth rates ($a_{\text{simulated}} =$
40 $0.0187, a_{\text{SNA}} = 0.0234$ for grazed plots; $a_{\text{simulated}} = 0.1018, a_{\text{SNA}} = 0.1069$ for mown plots,
41 respectively). Overall, LTRE decomposition using the SNA approximation also fitted the
42 difference in stochastic growth rates well: the difference between the simulated $\Delta a = a^{(g)} -$
43 $a^{(m)}$ and the SNA-LTRE sum was only 0.55% (Fig. 1). Decomposition of the stochastic
44 growth rates of grazed vs. mown populations showed that differences were mainly due to
45 mean vital rates. However, contributions of stochastic component were important, since their

1 exclusion worsens model fit more than tenfold to a 5.79% difference (Fig. 1). The largest
2 stochastic contributions were made by differences in correlations between vital rates in grazed
3 vs. mown populations and by differences in variability of vital rates (Fig. 1). Contributions of
4 differences in elasticities, on the other hand, were smaller (Fig. 1).

5 The contributions of means showed that vital rates related to fecundity made by far the
6 largest contributions (Fig. 2). There was a large positive effect of higher seedling
7 establishment in grazed sites, but this was outweighed by the pronounced negative
8 contribution of lower flower and seed production in grazed sites. Furthermore, the lower
9 probability of a vegetative plant flowering and of a flowering plant remaining in flower made
10 a substantial negative contribution among grazed sites. Interestingly, in grazed plots higher
11 seedling and juvenile survival had a positive, albeit small contribution to differences in
12 stochastic population growth rates, whereas lower survival of non-flowering adults had a
13 negative effect (Fig. 2). Finally, differences in growth of seedlings and juveniles made no
14 noticeable contribution.

15 The stochastic components contributing most to the difference in stochastic population
16 growth rates of grazed vs. mown populations were the correlations among vital rates and
17 variability of vital rates. In particular, variability in vegetative adult survival had a strong
18 negative contribution to differences in stochastic population growth rates in grazed compared
19 to mown populations. Similarly, the correlation between survival of non-flowering adults (σ_V)
20 and seedling establishment (ε) had a large negative effect on Δa . This correlation was
21 negative ($\rho = -0.57$) in mown plots, but positive ($\rho = 0.52$) in grazed plots (Fig.3). The strong
22 contribution was partly because of the large $\Delta\rho$, partly because σ_V had the largest mean
23 elasticity value ($\bar{e} = 0.497$), and partly because ε had an above-average CV ($\bar{c} = 0.509$).
24 Grazed populations also suffered lower growth rates due to negative contributions of
25 differences in the correlations between the survival of juveniles and non-flowering adults (σ_J
26 and σ_V) as well as between adult flowering probabilities (ϕ_V and ϕ_F) and seed set (π)
27 (contributions are listed in order of decreasing impact: σ_V - ε , σ_F - ε , σ_J - σ_V , σ_J - ϕ_V , ϕ_F - π and ϕ_V -
28 π). However, 76% of the total (-0.0064) negative impact of grazing that was due to higher
29 correlation coefficients was buffered by the combined positive effect (+0.0049) of lower
30 correlation coefficients in the grazed plots (Fig. 1).

31 **Discussion**

32 *Disentangling the contribution of mean effects and stochastic factors*

33
34 Consistent with previous studies (reviewed in Maron and Crone 2006), herbivory had a strong
35 and significant impact on the population dynamics and long-term growth rate of the perennial
36 grassland herb *P. veris*. Although other studies have tried to untangle the different effects of
37 herbivory on the population dynamics of this species (e.g. Garcia and Ehrlén 2002, Brys et al.
38 2004, Ehrlén et al. 2005), this is the first to consider different aspects of the life cycle
39 simultaneously by decomposing the projection matrix into lower level vital rates and at the
40 same time incorporating correlations between demographic rates. Moreover, because data
41 were collected over ten consecutive years and in different sites, this allowed us to characterize
42 the variance-covariance structure of vital rates. Accordingly, results should be less dependent
43 on year or site effects and therefore provide robust results and strong support to our findings.

44 Using a recently developed variance decomposition technique (Davison et al. 2011),
45 we showed that differences in the long-term stochastic growth rate of grazed and mown
46 populations were mainly due to differences in mean vital rates and to a lesser extent to
47 differences in correlations between vital rates and variability in vital rates. Our results also
48 showed that local selection pressures, as encapsulated in the between-treatment differences in
49
50

1 vital rate elasticity values (Benton and Grant 1996), did not contribute substantially to the
2 difference in the stochastic growth rate, suggesting that grazing does not lead to divergent
3 selection pressures imposed on this species.

4 5 *The impact of grazing on population demography*

6
7 Previous analysis clearly demonstrated that grazing significantly reduced the size of *P. veris*
8 individuals (Brys et al. 2011), which was also associated with pronounced reductions in
9 flower and seed production. Plants in grazed conditions had about half of the flowers of plants
10 in mown conditions, and produced on average only a third of the number of seeds. Mean total
11 seed production can therefore be considered six times smaller in grazed conditions than in
12 mown conditions. Our LTRE analysis showed that lower flower and seed production had a
13 pronounced negative impact on the population growth rates of grazed vs. mown sites. Similar
14 results have been reported for the long-lived woodland orchid *Orchis purpurea*, in which
15 differences in flower and seed production caused by different light environments also had a
16 strong effect on population growth rates (Jacquemyn et al. 2010a).

17 The LTRE analysis further showed that the effects of low flower and seed production
18 were largely counterbalanced by higher seedling establishment success in grazed plots, and
19 that this buffering reduced the difference in stochastic population growth rates between
20 grazed and mown plots. Although there were fewer recruits per m² in grazed than in mown
21 plots, establishment on a per-seed basis was higher when sites were grazed. There are four
22 mutually non-exclusive reasons that may explain these observations. First, treading by
23 grazing cattle disturbs the soil and creates numerous small openings in the vegetation, which
24 appeared to be suitable micro-sites for germination and survival of *P. veris* seedlings. In
25 mown plots, where such small-scale openings in the vegetation were less apparent, seeds
26 mostly germinated in larger openings that were often created by the activity of moles. Second,
27 the amount of light penetrating to the soil was significantly higher in grazed than in mown
28 plots (Jacquemyn et al. 2003), which may increase seed germination and seedling
29 establishment. Third, seed addition experiments (Brys et al. 2005) showed that when seed
30 density increases, the proportion of seedlings that successfully establishes decreases. Thus,
31 with higher seed rain, per-capita establishment of seedlings is lower due to negative density-
32 dependence. Similar results have been reported by Ehrlén et al. (2005), who found negative
33 density-dependence in seedling establishment and also found that establishment increased
34 when the vegetation was removed by manual clipping. Finally, it has been shown that
35 seedling establishment under field conditions is positively related to seed weight. Lehtilä &
36 Ehrlén (2005), for example, showed that 57% more seedlings were produced from heavier
37 seeds (average seed mass = 1.24 mg) than from lighter ones (average seed mass = 0.73 mg).
38 Although we did not measure the weight of the seeds, it is reasonable to assume that, due to
39 seed number/seed size trade-offs, seeds in grazed sites are heavier than those from mown
40 sites, and that this may contribute to the higher establishment success of seeds in grazed
41 conditions.

42 43 *Correlations and trade-offs*

44
45 Although differences in mean vital rates contributed by far the most to the difference between
46 stochastic growth rates of grazed and mown plots, the SNA-LTRE revealed interesting and
47 important effects due to vital rate correlations as well. By considering differences in both
48 deterministic and stochastic parameters, this recently developed technique can unravel such
49 otherwise obscure effects of covariation among demographic rates. Though the stochastic
50 effects of grazing were small, their inclusion did improve the model fit of the SNA-LTRE

1 almost ten-fold, suggesting that it includes additional factors that are significant to population
2 dynamics.

3 As we found with mean vital rates, we found strong buffering at the level of the vital
4 rate correlations. The lower stochastic growth rates of grazed populations, for instance, were
5 buffered by negative vital rate correlations that were strongly positive in mown sites.
6 However, correlation differences that lowered the stochastic growth rate in grazed plots had a
7 larger impact, mostly due to the positive correlation between adult survival and seedling
8 establishment in grazed plots that was negative under mowing. Especially important
9 contributions were made by differences in two temporal correlations. First, the correlation
10 between ϕ_F and ε was positive in mown sites, but negative in grazed sites, suggesting that
11 differences in the drivers or cues for flowering and seedling establishment buffered grazed
12 population growth rates. Second, σ_J - σ_L and σ_V - π correlations were positive in mown sites, but
13 close to zero in grazed sites, suggesting that grazed populations experienced a considerable
14 buffering effect due to absence of positive correlations of the mortality risks of seedlings and
15 juveniles, as well as due to the absence of synchrony between seed set and adult survival
16 (while these vital rates were positively correlated in mown sites).

17 Although some of these correlation contributions are relatively easy to explain (e.g.
18 correlation between seedling and juvenile survival in mown sites), others are less
19 straightforward. For example, the positive correlation between seedling establishment and
20 survival of non-flowering individuals in grazed plots may be the result of variation in grazing
21 intensity among years. In years with high grazing pressure, many small, non-flowering plants
22 may have died, but at the same time many flowering plants may have been damaged, which
23 may have decreased germination due to low fruit set. In years of relatively low grazing
24 pressures, mortality of non-flowering plants will be low, but seedling establishment will be
25 higher due to higher fruit production. In mown sites, on the other hand, the lack of
26 disturbances may explain the negative correlations between adult survival and seedling
27 establishment.

28 29 *Costs of reproduction*

30 We found limited evidence for costs of reproduction affecting population dynamics of *P.*
31 *veris*. Costs of reproduction have been notoriously difficult to detect in natural populations,
32 particularly in long-lived perennial plants (Obeso 2002), and the extent to which costs affect
33 long term population growth rates is also not well understood (but see Jacquemyn et al.
34 2010b). In the case of *P. veris*, non-flowering plants showed higher mortality than flowering
35 plants and survivorship curves for non-flowering plants were always lower than those for
36 flowering plants (results not shown). The reason for this might be that non-reproductive adults
37 are much smaller than reproductive plants (Brys et al. 2011). Because small plants generally
38 have lower survival chances than large plants, size-dependent mortality may explain why
39 costs of reproduction were not observed in this system. Moreover, experiments conducted by
40 Lethilä and Syrjänen (1995) have shown that flowering plants, when cut or pollinated with
41 surplus pollen, actually had higher survival and flowering probabilities in the next year,
42 suggesting that some kind of compensatory mechanism determines survival rates. García and
43 Ehrlén (2002), who used clipping experiments and pollen addition experiments to investigate
44 costs of reproduction in *P. veris*, also found no evidence for costs of reproduction in this
45 species. These responses may be at least partly explained by the fact that this species invests
46 considerable resources in above-ground growth and carbohydrate production each spring
47 (Syrjänen & Lehtilä 1993), and because the starch content in its roots is very low during
48 flowering (Mestenhauser 1961).

49
50

1 *Conclusion*

2
3 The SNA-decomposition of differences in stochastic growth rates allowed us to discern the
4 impact of deterministic and stochastic factors on the long-term population growth rate in both
5 grazed and mown sites of the perennial grassland herb *P. veris*. At the same time, this
6 decomposition also allowed us to identify the vital rates that contributed most to differences
7 in population growth rate and provided insights into contributions of correlations between
8 vital rates. We have clearly demonstrated that grazing had a strong impact on population
9 dynamics and that this effect was primarily due to changes in mean vital rates and to a lesser
10 extent to differences in the variance-covariance structure between grazed and mown sites.
11 Reductions in flower and seed production and lower flowering probabilities were the most
12 important vital rates explaining the lower growth rates in grazed sites, whereas these effects
13 were partly buffered by increased germination probabilities.

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13

14 **List of Figures**

15

16 Figure 1. Results of the stochastic life table response experiment using the small noise
17 approximation: summed contributions to the stochastic growth rate of mean vital rates ($\Delta\mu$),
18 variability of vital rates (Δc), elasticities (Δe) and correlations between vital rates ($\Delta\rho$) in
19 grazed and mown populations of the perennial grassland herb *Primula veris*.

20

21 Figure 2. a) Decomposition of the differences in stochastic population growth rate (a) of
22 grazed vs. mown populations of the perennial grassland herb *Primula veris* into contributions
23 by the differences in the vital rate means and b) by the differences in the stochastic
24 components (coefficients of variation of vital rates, vital rate elasticities, and correlations
25 between vital rates) (see Appendix B for all values). σ refers to survival, γ to growth
26 conditional on survival, and ϕ refers to the probability of a plant flowering in the next year. μ
27 represents the average number of flowers, π the average number of seeds per fruit and ε the
28 proportion of seeds that germinate and successfully establish as a seedling.

29

30 Figure 3. Contributions of differences in temporal correlations between vital rates of the
31 grazed and mown populations. The height and shading indicate the difference in vital rate
32 correlation: the white boxes indicate higher correlation coefficients (indicated with an
33 upward-pointing triangle) in the grazed populations than in the mown populations (bottom of
34 the white box). The grey boxes signal lower correlation coefficients (downward-pointing
35 triangle) in the grazed populations than in the mown populations (top of the grey boxes). The
36 grey horizontal lines correspond to a correlation coefficient level of 0. Maximal positive (1)
37 and negative (-1) correlation coefficient levels are halfway these grey horizontal lines. The
38 width (not the area) of a box is a relative measure of the contribution of the correlation
39 difference to the difference in stochastic population growth rate, Δa . Please note that increases
40 (white boxes) in correlation coefficients have a negative contribution to Δa . Symbols are
41 similar as in Figure 2.

Figure 1.

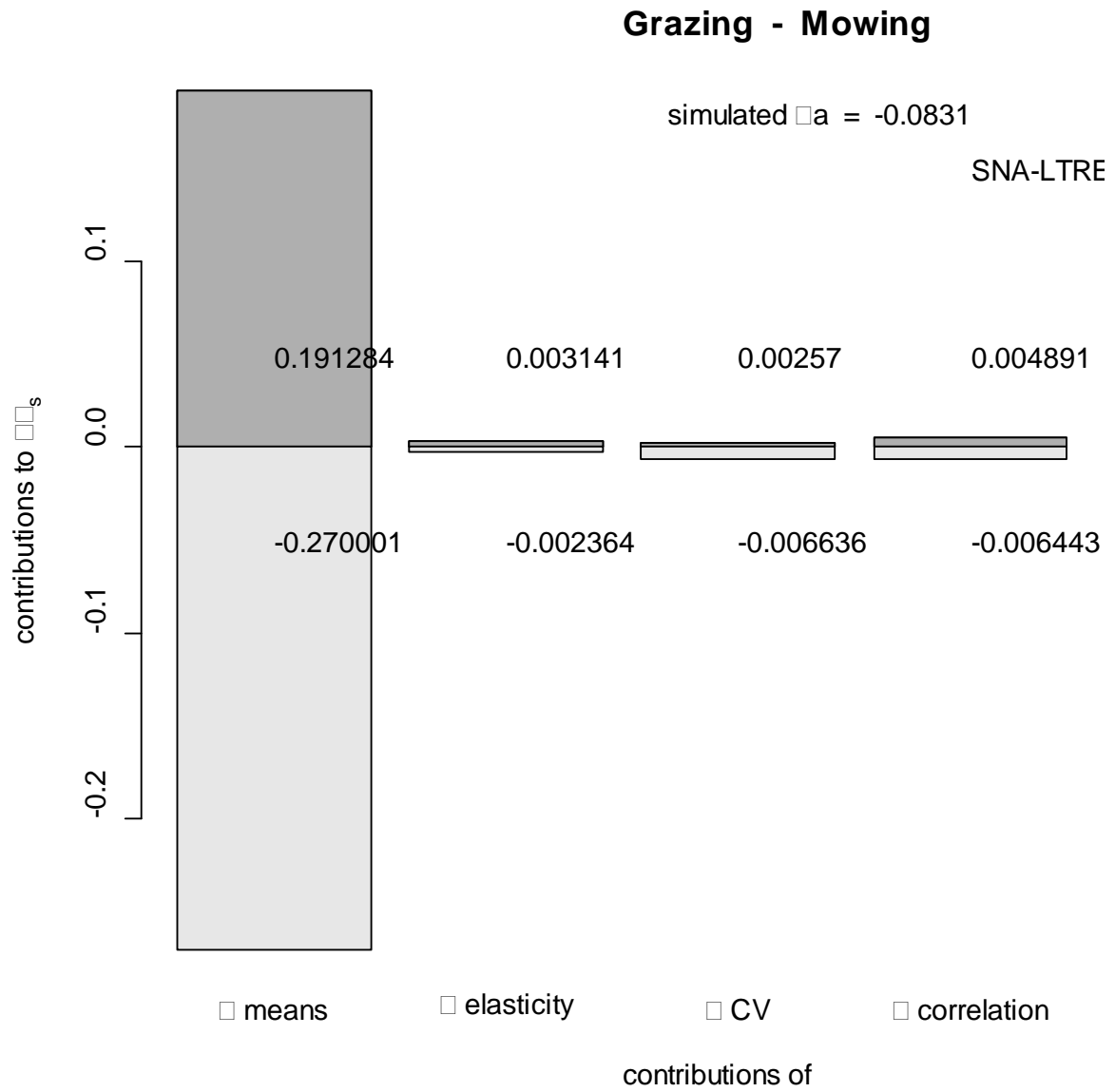
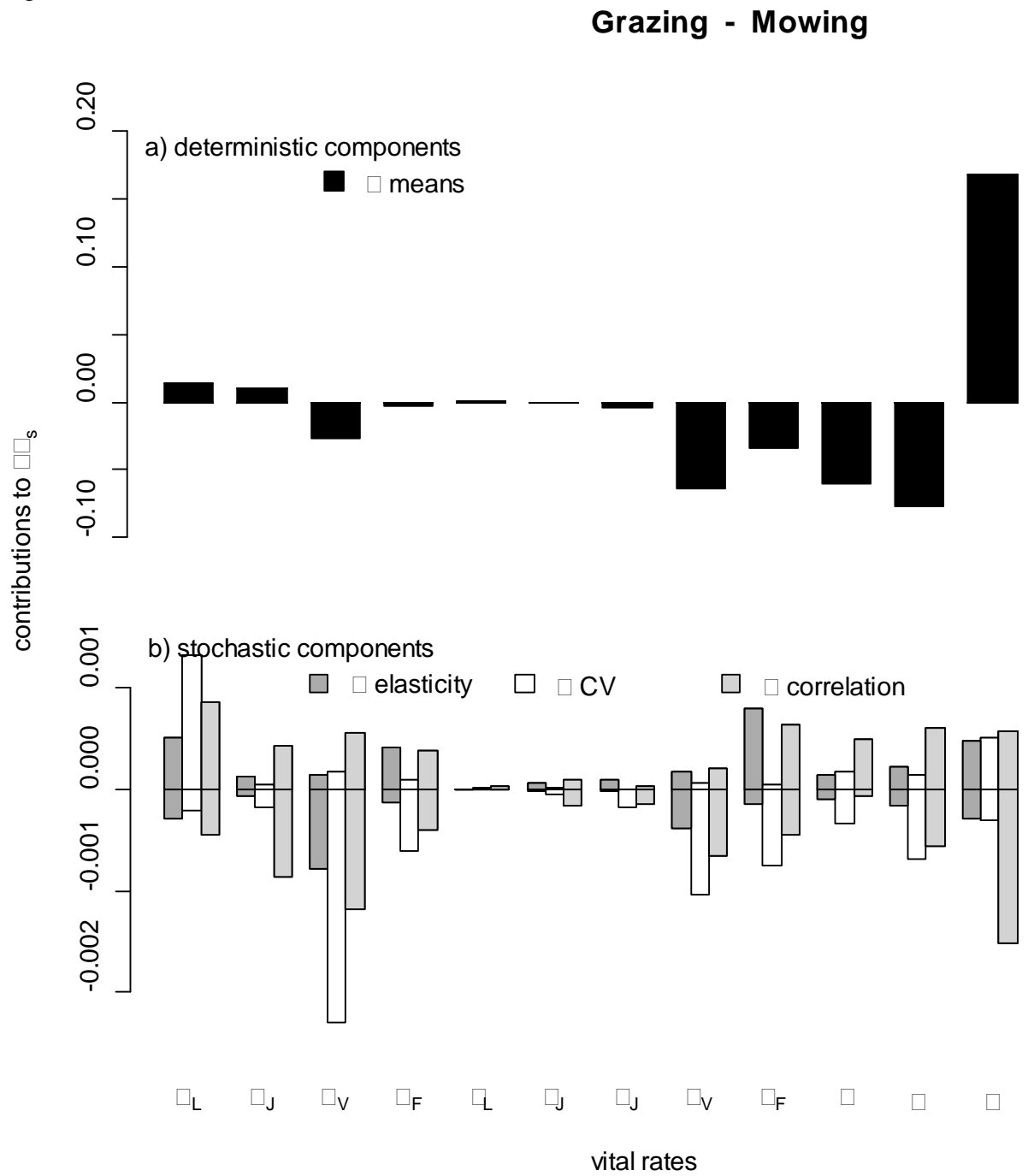


Figure 2.



Appendix A. Vital rates used to construct matrix models of mown and grazed *Primula veris* populations. Data were collected in two sites during ten consecutive years (1999-2008).

	sigmaL	sigmaJ	sigmaV	sigmaF	gammaL	gammaJ	phiJ	phiV	phiF	mu	pi	epsilon
1G99	0.86956522	0.8461538	0.8000000	0.7428571	0.0000000	0.9090909	0.0000000	0.11764706	0.2692308	5.54	22.77	0.004076915
1G00	0.72222222	0.8181818	0.7373737	0.8666667	0.0000000	0.9444444	0.0000000	0.08219178	0.3076923	3.44	13.56	0.024296266
1G01	0.82352941	1.0000000	0.9569892	1.0000000	0.0000000	0.9285714	0.15384615	0.12359551	0.0000000	3.94	12.45	0.032617781
1G02	0.75000000	1.0000000	0.9595960	1.0000000	0.0000000	0.8000000	0.0000000	0.14736842	0.1538462	4.22	6.36	0.054455366
1G03	0.36842105	0.8000000	0.8557692	1.0000000	0.0000000	0.8333333	0.0000000	0.03370787	0.1875000	5.60	9.71	0.016091658
1G04	0.28571429	0.6666667	0.9174312	1.0000000	0.0000000	1.0000000	0.0000000	0.15000000	0.1666667	4.54	12.17	0.030164930
1G05	0.20000000	0.7500000	0.9270833	0.9375000	0.0000000	0.3333333	0.0000000	0.17977528	0.0000000	5.02	15.18	0.027065650
1G06	0.30303030	1.0000000	0.9550562	0.9375000	0.0000000	1.0000000	0.2500000	0.31764706	0.2000000	4.67	21.30	0.032044515
1G07	0.27450980	0.9000000	0.9726027	1.0000000	0.0000000	1.0000000	0.11111111	0.32394366	0.5483871	5.67	26.73	0.016175953
1M99	0.61538462	0.8148148	0.8596491	0.9047619	0.0000000	1.0000000	0.0000000	0.30612245	0.4210526	5.53	22.72	0.006190448
1M00	0.51020408	0.8750000	0.9325843	0.8974359	0.0000000	1.0000000	0.0000000	0.16867470	0.2857143	6.04	41.80	0.003351476
1M01	0.54545455	0.6400000	0.9405941	0.9166667	0.0000000	1.0000000	0.3750000	0.47368421	0.6818182	10.56	34.75	0.002952184
1M02	0.80769231	0.6111111	0.9701493	1.0000000	0.0000000	1.0000000	0.0000000	0.38461538	0.3787879	12.15	52.48	0.001568303
1M03	0.40909091	0.7619048	0.9347826	1.0000000	0.0000000	0.8750000	0.21428571	0.44186047	0.8400000	8.59	33.12	0.011669563
1M04	0.10240964	0.5862069	0.9253731	0.9540230	0.0000000	0.7647059	0.15384615	0.48387097	0.8915663	8.02	35.16	0.008478536
1M05	0.11057692	0.7142857	0.9807692	0.9622642	0.0000000	1.0000000	0.2000000	0.27450980	0.3823529	9.12	38.12	0.005074439
1M06	0.12299465	0.6956522	0.9553571	0.9642857	0.0000000	0.8750000	0.21428571	0.66355140	0.5555556	8.89	34.67	0.005156397
1M07	0.19101124	0.6800000	0.9577465	0.9615385	0.0000000	0.9411765	0.0000000	0.72058824	0.5300000	10.07	40.93	0.002776147
2G99	0.76363636	0.7948718	0.8909091	0.9473684	0.19047619	0.5806452	0.02777778	0.25510204	0.1111111	5.00	22.66	0.019510382
2G00	0.43181818	0.4583333	0.6126761	0.6896552	0.10526316	0.8787879	0.03448276	0.16091954	0.2000000	4.56	18.46	0.004506072
2G01	0.54545455	0.5714286	0.9480519	1.0000000	0.0000000	0.9166667	0.09090909	0.30136986	0.2857143	4.12	15.67	0.086297925
2G02	0.58974359	1.0000000	0.9878049	1.0000000	0.0000000	0.8571429	0.0000000	0.02469136	0.0400000	3.89	14.89	0.022098646
2G03	0.34375000	0.7500000	0.8897638	1.0000000	0.0000000	0.7777778	0.0000000	0.02654867	0.0000000	4.89	13.67	0.069811892
2G04	0.28571429	0.4666667	0.8677686	1.0000000	0.0000000	0.8571429	0.0000000	0.06666667	0.0000000	5.23	17.89	0.046313763
2G05	0.23076923	1.0000000	0.9279279	0.8571429	0.0000000	0.8000000	0.0000000	0.16504854	0.1666667	4.82	21.67	0.025986609
2G06	0.31578947	1.0000000	0.9494949	0.9444444	0.0000000	1.0000000	0.0000000	0.28723404	0.6470588	5.01	18.18	0.028667759
2G07	0.25531915	0.8333333	0.9358974	0.9743590	0.0000000	1.0000000	0.2000000	0.12328767	0.3684211	5.12	21.63	0.027783705
2M99	0.84615385	0.9200000	0.9333333	0.8518519	0.03030303	0.8260870	0.13157895	0.35714286	0.6086957	5.47	23.71	0.010851779
2M00	0.52631579	0.8604651	0.9560440	0.9772727	0.0000000	0.8918919	0.0000000	0.21839080	0.2093023	6.04	34.57	0.001959221
2M01	0.66666667	0.9583333	0.9851852	1.0000000	0.0000000	0.9565217	0.18181818	0.44360902	0.6551724	9.58	37.46	0.005669186
2M02	0.72881356	0.9230769	0.9619048	0.9523810	0.04651163	0.7500000	0.0000000	0.47524752	0.5875000	9.60	45.37	0.003525903
2M03	0.48062016	0.9318182	0.9387755	0.9690722	0.01612903	0.8536585	0.11428571	0.28260870	0.4255319	9.67	36.75	0.007832641
2M04	0.12222222	0.5810811	0.9415584	1.0000000	0.0000000	0.6976744	0.13333333	0.33793103	0.5571429	8.54	34.68	0.013505885
2M05	0.09642857	0.5217391	0.9215686	0.9456522	0.0000000	0.6666667	0.06250000	0.19148936	0.3678161	8.99	39.36	0.007157367
2M06	0.22317597	0.6857143	0.9567568	0.9677419	0.0000000	0.8750000	0.14285714	0.50847458	0.5500000	9.23	36.76	0.004706156
2M07	0.19191919	0.6181818	0.9166667	0.9682540	0.0000000	0.8823529	0.06666667	0.38842975	0.3606557	9.66	40.86	0.003217170

Appendix B. Contributions of mean vital rates, variance in vital rates, vital rate elasticities and correlations between vital rates to differences in the stochastic growth rate of grazed and mown sites.

a. contributions of changes in mean vital rates

```

sigmaL  0.0135276913
sigmaJ  0.0098908769
sigmaV -0.0263700967
sigmaF -0.0033853494
gammaL  0.0003816191
gammaJ -0.0008416968
phiJ   -0.0038412609
phiV   -0.0643659036
phiF   -0.0338492888
mu     -0.0599747165
pi     -0.0773725207
epsilon 0.1674834566

```

b. contributions of changes in mean vital rate elasticity values

	sigmaL	sigmaJ	sigmaV	sigmaF	gammaL	gammaJ
sigmaL	3.895956e-04	4.819036e-05	4.430658e-05	-9.640628e-05	-3.037239e-06	1.344498e-05
sigmaJ	4.819036e-05	3.012401e-05	-4.374052e-05	4.987965e-06	-6.337593e-08	2.676209e-08
sigmaV	4.430658e-05	-4.374052e-05	-5.391553e-04	8.030200e-05	4.443426e-06	4.073886e-07
sigmaF	-9.640628e-05	4.987965e-06	8.030200e-05	1.357137e-04	-1.086563e-06	5.519632e-06
gammaL	-3.037239e-06	-6.337593e-08	4.443426e-06	-1.086563e-06	-1.443056e-07	-2.595598e-08
gammaJ	1.344498e-05	2.676209e-06	4.073886e-07	5.519632e-06	-2.595598e-08	7.933563e-06
phiJ	-8.933959e-06	2.540050e-06	-5.521959e-06	8.969481e-06	7.519433e-08	3.811647e-06
phiV	1.388858e-05	-6.174172e-06	-1.052017e-04	-1.374862e-06	2.293494e-08	4.278729e-06
phiF	-8.294780e-05	3.382508e-05	6.767143e-06	-1.747611e-05	1.086377e-07	2.660033e-05
mu	-2.763332e-05	-6.745203e-06	-1.943754e-05	3.096792e-05	-8.453858e-08	-1.978661e-06
pi	-1.613920e-05	-4.838568e-07	-1.129961e-05	-1.979289e-05	-5.468113e-07	1.567598e-06
epsilon	-5.193293e-05	-5.390856e-06	-6.332170e-05	1.417142e-04	1.442312e-06	-7.830229e-06
	phiJ	phiV	phiF	mu	pi	epsilon
sigmaL	-8.933959e-06	1.388858e-05	-8.294780e-05	-2.763332e-05	-1.613920e-05	-5.193293e-05
sigmaJ	2.540050e-06	-6.174172e-06	3.382508e-05	-6.745203e-06	-4.838568e-07	-5.390856e-06
sigmaV	-5.521959e-06	-1.052017e-04	6.767143e-06	-1.943754e-05	-1.129961e-05	-6.332170e-05
sigmaF	8.969481e-06	-1.374862e-06	-1.747611e-05	3.096792e-05	-1.979289e-05	1.417142e-04
gammaL	7.519433e-08	2.293494e-08	1.086377e-07	-8.453858e-08	-5.468113e-07	1.442312e-06
gammaJ	3.811647e-06	4.278729e-06	2.660033e-05	-1.978661e-06	1.567598e-06	-7.830229e-06
phiJ	6.292202e-06	-5.912207e-07	4.684835e-05	2.487288e-06	5.423339e-06	1.079871e-05
phiV	-5.912207e-07	-2.302138e-04	1.445882e-04	-1.002265e-05	-2.371794e-05	1.375768e-05
phiF	4.684835e-05	1.445882e-04	3.801309e-04	3.982705e-05	1.209168e-04	-4.002477e-05
mu	2.487288e-06	-1.002265e-05	3.982705e-05	3.744414e-05	2.762547e-05	-3.054864e-05
pi	5.423339e-06	-2.371794e-05	1.209168e-04	2.762547e-05	6.470503e-05	-8.766888e-05
epsilon	1.079871e-05	1.375768e-05	-4.002477e-05	-3.054864e-05	-8.766888e-05	3.064777e-04

c. contributions of changes in coefficients of variance

	sigmaL	sigmaJ	sigmaV	sigmaF	gammaL	gammaJ
sigmaL	1.008092e-03	2.819679e-05	1.443885e-04	6.899048e-05	1.103360e-06	-9.841795e-06
sigmaJ	2.819679e-05	-5.831310e-05	-8.271952e-05	1.383050e-05	-2.340121e-07	-8.022575e-06
sigmaV	1.443885e-04	-8.271952e-05	-1.314633e-03	-2.786340e-04	5.923992e-06	-7.351987e-06
sigmaF	6.899048e-05	1.383050e-05	-2.786340e-04	-1.439009e-04	1.819318e-06	1.985776e-06
gammaL	1.103360e-06	-2.340121e-07	5.923992e-06	1.819318e-06	-8.804769e-08	7.565956e-08
gammaJ	-9.841795e-06	-8.022575e-06	-7.351987e-06	1.985776e-06	7.565956e-08	-9.463779e-06
phiJ	4.226581e-06	-2.842241e-06	-4.318806e-05	-1.081691e-05	3.783822e-07	-3.437364e-06
phiV	1.342043e-05	-6.635841e-06	-2.294759e-04	-2.935225e-05	9.038257e-08	-9.521280e-06
phiF	3.965884e-05	-1.129107e-05	2.610662e-07	-2.102133e-05	-1.445701e-07	-7.699733e-06
mu	-1.213441e-04	-9.458795e-06	-8.907478e-05	-1.551072e-05	1.112577e-07	4.065540e-07
pi	6.641386e-06	8.950380e-06	-2.442918e-04	-3.033946e-05	-1.141724e-06	-1.095220e-06
epsilon	-8.143906e-05	1.333496e-06	1.966440e-05	-8.430983e-05	4.849361e-07	1.213233e-05
	phiJ	phiV	phiF	mu	pi	epsilon
sigmaL	4.226581e-06	1.342043e-05	3.965884e-05	-1.213441e-04	6.641386e-06	-8.143906e-05
sigmaJ	-2.842241e-06	-6.635841e-06	-1.129107e-05	-9.458795e-06	8.950380e-06	1.333496e-06
sigmaV	-4.318806e-05	-2.294759e-04	2.610662e-07	-8.907478e-05	-2.442918e-04	1.966440e-05
sigmaF	-1.081691e-05	-2.935225e-05	-2.102133e-05	-1.551072e-05	-3.033946e-05	-8.430983e-05
gammaL	3.783822e-07	9.038257e-08	-1.445701e-07	1.112577e-07	-1.141724e-06	4.849361e-07
gammaJ	-3.437364e-06	-9.521280e-06	-7.699733e-06	4.065540e-07	-1.095220e-06	1.213233e-05
phiJ	-1.231620e-05	-3.609319e-05	-4.825491e-05	5.613029e-07	-4.673539e-06	-1.143119e-05
phiV	-3.609319e-05	-3.949058e-04	-2.047478e-04	9.638121e-06	-1.229304e-04	3.281201e-05
phiF	-4.825491e-05	-2.047478e-04	-3.534037e-04	-1.374693e-05	-5.950966e-05	-3.750041e-05
mu	5.613029e-07	9.638121e-06	-1.374693e-05	1.443077e-04	1.630763e-05	-8.781959e-05

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pi      -4.673539e-06 -1.229304e-04 -5.950966e-05  1.630763e-05 -2.153610e-04  1.036724e-04
epsilon -1.143119e-05  3.281201e-05 -3.750041e-05 -8.781959e-05  1.036724e-04  3.431485e-04

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d. contributions of changes in correlation coefficients

	sigmaL	sigmaJ	sigmaV	sigmaF	gammaL	gammaJ
sigmaL	0.000000e+00	3.959845e-04	1.106629e-04	-3.908995e-05	1.666587e-06	6.126573e-05
sigmaJ	3.959845e-04	0.000000e+00	-2.523277e-04	-7.388602e-05	3.558012e-06	2.648334e-05
sigmaV	1.106629e-04	-2.523277e-04	0.000000e+00	-2.020807e-05	5.296889e-06	4.936679e-06
sigmaF	-3.908995e-05	-7.388602e-05	-2.020807e-05	0.000000e+00	2.034930e-06	-1.769552e-05
gammaL	1.666587e-06	3.558012e-06	5.296889e-06	2.034930e-06	0.000000e+00	2.749011e-07
gammaJ	6.126573e-05	2.648334e-05	4.936679e-06	-1.769552e-05	2.749011e-07	0.000000e+00
phiJ	-1.281698e-05	-2.151754e-05	-1.513413e-05	-5.636850e-07	-2.615332e-07	-7.017861e-06
phiV	-8.188845e-05	-2.053849e-04	-5.118243e-05	8.902800e-05	-6.606295e-07	-1.790123e-05
phiF	7.666012e-05	-8.704408e-05	-2.621554e-05	7.146379e-05	-1.148363e-07	-4.309880e-05
mu	1.505158e-04	-6.630922e-05	1.151587e-04	5.649653e-05	-6.797636e-08	1.596876e-06
pi	6.866067e-05	-8.991239e-05	3.211381e-04	1.586739e-04	-1.881544e-06	-5.302645e-06
epsilon	-3.198378e-04	-6.349895e-05	-8.171297e-04	-2.412886e-04	1.002891e-05	-7.464899e-05
	phiJ	phiV	phiF	mu	pi	epsilon
sigmaL	-1.281698e-05	-8.188845e-05	7.666012e-05	1.505158e-04	6.866067e-05	-3.198378e-04
sigmaJ	-2.151754e-05	-2.053849e-04	-8.704408e-05	-6.630922e-05	-8.991239e-05	-6.349895e-05
sigmaV	-1.513413e-05	-5.118243e-05	-2.621554e-05	1.151587e-04	3.211381e-04	-8.171297e-04
sigmaF	-5.636850e-07	8.902800e-05	7.146379e-05	5.649653e-05	1.586739e-04	-2.412886e-04
gammaL	-2.615332e-07	-6.606295e-07	-1.148363e-07	-6.797636e-08	-1.881544e-06	1.002891e-05
gammaJ	-7.017861e-06	-1.790123e-05	-4.309880e-05	1.596876e-06	-5.302645e-06	-7.464899e-05
phiJ	0.000000e+00	-3.940798e-05	-5.391617e-06	7.967399e-06	-4.825123e-05	2.792318e-05
phiV	-3.940798e-05	0.000000e+00	-5.764093e-05	1.054188e-04	-1.936819e-04	1.613018e-05
phiF	-5.391617e-06	-5.764093e-05	0.000000e+00	9.942797e-06	-2.231707e-04	4.799230e-04
mu	7.967399e-06	1.054188e-04	9.942797e-06	0.000000e+00	2.407896e-05	1.871958e-05
pi	-4.825123e-05	-1.936819e-04	-2.231707e-04	2.407896e-05	0.000000e+00	2.394632e-05
epsilon	2.792318e-05	1.613018e-05	4.799230e-04	1.871958e-05	2.394632e-05	0.000000e+00

Appendix C. SNA-LTRE analysis of the difference in stochastic population growth rate between site 2 and site 1.

