

# Appendix 1 for 'Density-dependent selection and the maintenance of colour polymorphism in barn owls'

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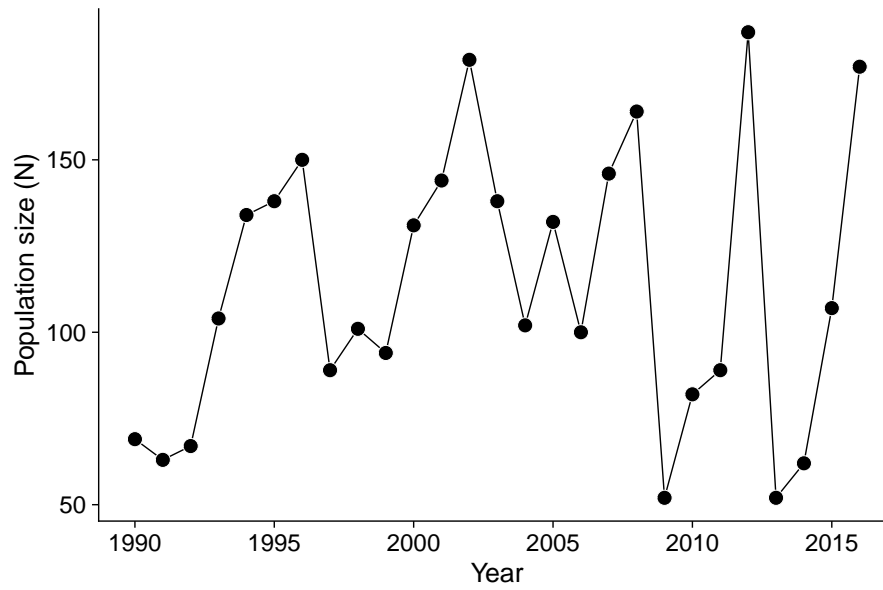
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Main paper: Kvalnes, T., Sæther, B.-E., Engen, S. and Roulin, A. 2022. Density-dependent selection and the maintenance of colour polymorphism in barn owls. *Proc. R. Soc. B* (doi: 10.1098/rspb.2022.0296).

## Annual population sizes



*Figure A1: Estimated annual total population sizes with pre-breeding census for barn owls on the plains south-west of lake Neuchâtel in western Switzerland ( $46^{\circ} 49'N$ ,  $06^{\circ} 56' E$ ) in the period 1990-2016. Estimated as the annual number of individuals (both sexes) known to be alive that were recorded to breed within the study area in the period.*

# Density dependence and vital rates for barn owls

Table A1: Parameter estimates  $\pm$  standard error (SE) and 95% confidence intervals for analyses of the effect of age and population density on variation in recruit production and survival of female barn owls in western Switzerland in the period 1990-2015. Separate generalized linear models (GLMs) were fitted for each fitness component. For recruit production **(a)** we fitted a GLM with Poisson error distribution, a log link function, and an offset of  $\ln 2$  and weights 1/2 to account for sexual reproduction (on average, half of the recruits are females). For survival **(b)** we fitted a GLM with binomial error distribution and a logit link function.

	Estimate $\pm$ SE	Confidence Interval	
		Lower	Upper
<b>(a) Recruits</b>			
Intercept	-2.2606 $\pm$ 0.1386	-2.5435	-1.9994
Age 2	-0.0830 $\pm$ 0.2233	-0.5348	0.3442
Age 3	0.1771 $\pm$ 0.2338	-0.2986	0.6223
Age 4	0.1559 $\pm$ 0.2664	-0.3954	0.6554
Age 5	0.3252 $\pm$ 0.3039	-0.3152	0.8861
Age 6	0.4364 $\pm$ 0.3748	-0.3791	1.1098
Age 7	0.0589 $\pm$ 0.5154	-1.1323	0.9428
Age 8	0.1677 $\pm$ 0.6448	-1.4056	1.2310
$\Delta N/N$	1.6314 $\pm$ 0.1707	1.2967	1.9662
<b>(b) Survival</b>			
Intercept	-0.7293 $\pm$ 0.1016	-0.9308	-0.5323
Age 2	0.5600 $\pm$ 0.1729	0.2211	0.8994
Age 3	0.6592 $\pm$ 0.1939	0.2792	1.0400
Age 4	0.9487 $\pm$ 0.2311	0.4985	1.4063
Age 5	0.9518 $\pm$ 0.2835	0.4010	1.5166
Age 6	1.3543 $\pm$ 0.3770	0.6334	2.1238
Age 7	0.4911 $\pm$ 0.4450	-0.3966	1.3674
Age 8	0.4170 $\pm$ 0.5303	-0.6586	1.4560
$\Delta N/N$	1.3767 $\pm$ 0.1580	1.0717	1.6914

Table A2: Age-specific fecundity ( $f_x$ ) and survival ( $s_x$ ) (estimate $\pm$ SE) with pre-breeding census for female barn owls in western Switzerland in the period 1990-2015. **a**, The observed mean vital rates. **b**, Vital rates estimated at  $K$  (using the observed changes in population size). In **c**, Fecundities are scaled by a konstant of 5.16 to account for emigration such that we have a projection matrix,  $\mathbf{l}$ , with stable dynamics.  $n_x$  = number of individuals in age class  $x$ . The stable age distribution ( $u_x$ ) and reproductive values ( $v_x$ ) are estimated as the scaled left and right eigenvector of  $\mathbf{l}$  populated by the age-specific vital rates for each section **a-c** in the table. Individuals in age class 1 are recruits (one year old individuals) and age class 8 collects all individuals aged  $\geq 8$  years.

Age ( $x$ )	Fecundity ( $f_x$ )	Survival ( $s_x$ )	$u_x$	$v_x$	$n_x$
<b>(a)</b> $\lambda = 0.62$ (observed)					
1	0.13 $\pm$ 0.01	0.33 $\pm$ 0.02	0.25	0.80	508
2	0.12 $\pm$ 0.02	0.47 $\pm$ 0.03	0.13	1.20	242
3	0.16 $\pm$ 0.03	0.49 $\pm$ 0.04	0.10	1.38	161
4	0.17 $\pm$ 0.03	0.59 $\pm$ 0.05	0.08	1.48	103
5	0.20 $\pm$ 0.04	0.60 $\pm$ 0.06	0.08	1.31	65
6	0.21 $\pm$ 0.06	0.67 $\pm$ 0.08	0.07	1.09	38
7	0.16 $\pm$ 0.09	0.48 $\pm$ 0.11	0.08	0.75	25
8	0.16 $\pm$ 0.09	0.44 $\pm$ 0.13	0.21	0.70	16
<b>(b)</b> $\lambda = 0.57$ (at $K$ )					
1	0.10 $\pm$ 0.01	0.33 $\pm$ 0.02	0.21	0.87	508
2	0.10 $\pm$ 0.02	0.46 $\pm$ 0.04	0.12	1.25	242
3	0.12 $\pm$ 0.03	0.48 $\pm$ 0.04	0.10	1.38	161
4	0.12 $\pm$ 0.03	0.56 $\pm$ 0.05	0.08	1.41	103
5	0.14 $\pm$ 0.04	0.56 $\pm$ 0.07	0.08	1.26	65
6	0.16 $\pm$ 0.06	0.65 $\pm$ 0.08	0.08	1.07	38
7	0.11 $\pm$ 0.06	0.44 $\pm$ 0.11	0.09	0.72	25
8	0.12 $\pm$ 0.08	0.42 $\pm$ 0.13	0.26	0.72	16
<b>(c)</b> $\lambda = 1$ (scaled at $K$ )					
1	0.60 $\pm$ 0.08	0.33 $\pm$ 0.02	0.61	0.87	508
2	0.55 $\pm$ 0.11	0.46 $\pm$ 0.04	0.20	1.08	242
3	0.71 $\pm$ 0.15	0.48 $\pm$ 0.04	0.09	1.31	161
4	0.70 $\pm$ 0.17	0.56 $\pm$ 0.05	0.04	1.45	103
5	0.82 $\pm$ 0.23	0.56 $\pm$ 0.07	0.02	1.52	65
6	0.92 $\pm$ 0.33	0.65 $\pm$ 0.08	0.01	1.46	38
7	0.63 $\pm$ 0.32	0.44 $\pm$ 0.11	0.01	1.01	25
8	0.70 $\pm$ 0.45	0.42 $\pm$ 0.13	0.01	1.06	16

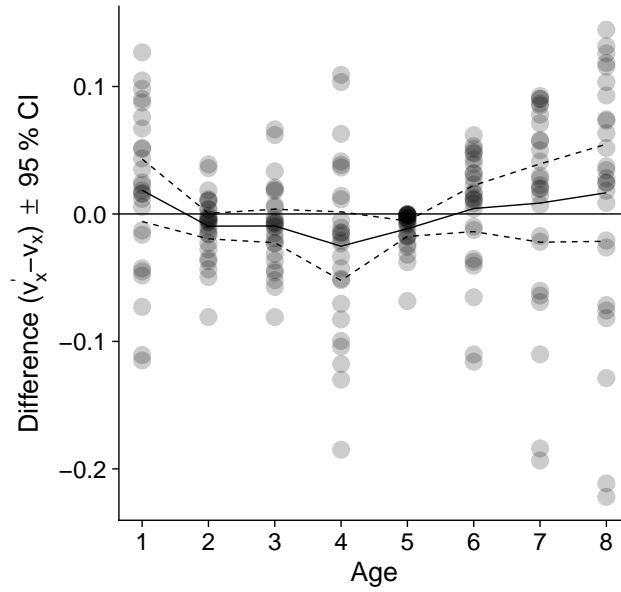
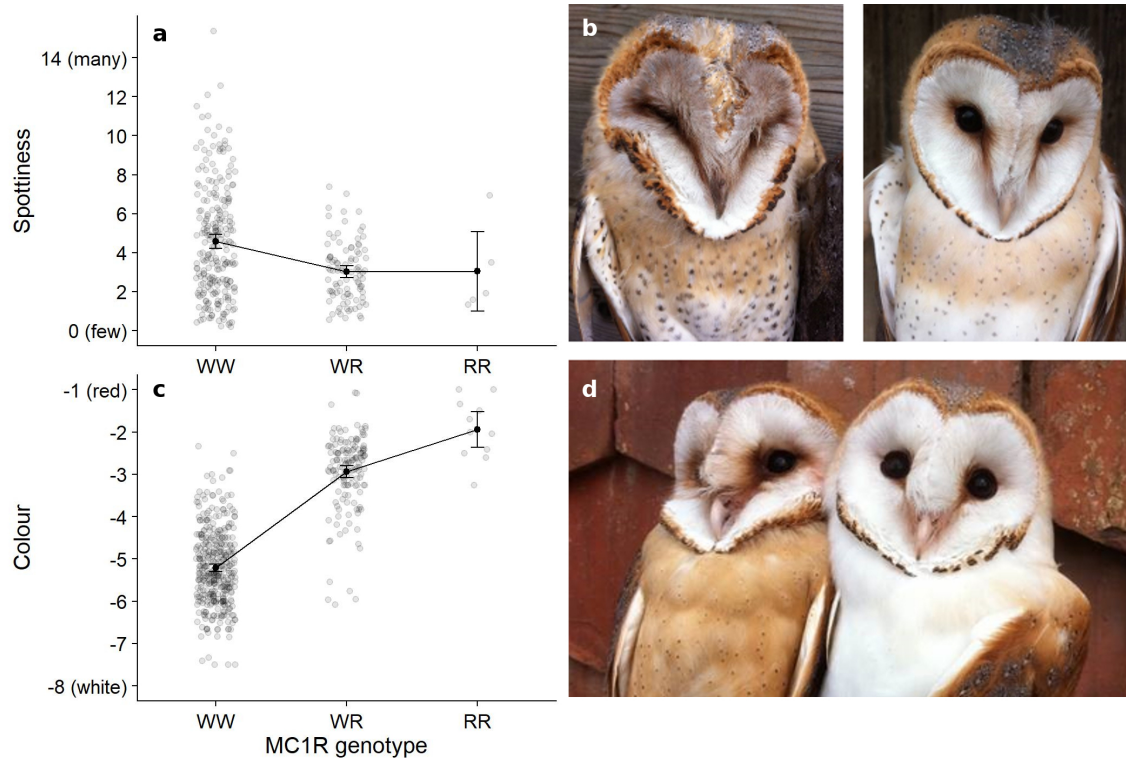


Figure A2: Differences between reproductive values at observed population densities ( $v'_x$ ) and equilibrium reproductive values ( $v_x$ ,  $\lambda = 1$ , Table A2c) in female barn owls on the plains south-west of lake Neuchâtel in western Switzerland ( $46^\circ 49'N$ ,  $06^\circ 56' E$ ) in the period 1990-2015. The solid and dashed lines show the mean differences  $\pm 95\%$  confidence intervals (CIs). The lower and upper bounds of the CIs were estimated as  $\pm 1.96$  standard errors.

## Colouration, spottiness and MC1R-genotype



*Figure A3: The relationship between variation in two melanin-based plumage traits, spottiness (a) and the degree of reddish colouration (c), and the genotype at the melanocortin-1 receptor (MC1R) gene in female barn owl fledglings in western Switzerland. Small displacements have been added to the data points to avoid overlapping and improve visualisation. Images show examples of the observed plumage variation in spottiness (b) and the reddish coloration (d).*

## Density-dependent selection

Table A3: Parameter estimates and 95% confidence intervals for analyses of the effect of phenotypes and population density on variation in individual fitness ( $\Lambda$ ) of female barn owls in western Switzerland. Log-linear mixed-effects models with a random intercept for year were fitted to estimate the strength of density dependence on each of two melanistic phenotypes, the degree of reddish colouration (**a**) and spottiness (**b**). The model for individual  $i$  in year  $t$  was the form  $\ln\tilde{E}(\Lambda_{it}) = \beta_1 + \beta_2 z_i + \beta_3 z_i^2 + \beta_4 N_t + \beta_5 N_t z_i + u_t$ , where  $z_i$  is the mean centered trait,  $N_t$  is population size,  $u_t$  is the random effect and  $\tilde{\cdot}$  denote reproductive value weighting. The random intercept with a mean of 0 and variance  $\sigma_e^2$  was estimated for year to account for environmental stochasticity. Parameters which are significantly different from zero are given in bold.

		Confidence Interval	
Estimate		Lower	Upper
<b>(a) Colour</b>			
$\beta_1$	0.3381	-0.3421	0.9994
$\beta_2$	0.1830	-0.0301	0.3980
$\beta_3$	-0.0032	-0.0475	0.0394
$\beta_4$	<b>-0.0076</b>	<b>-0.0130</b>	<b>-0.0023</b>
$\beta_5$	<b>-0.0018</b>	<b>-0.0035</b>	<b>-0.0001</b>
$\sigma_e^2$	0.1543	0.0693	0.3512
<b>(b) Spottiness</b>			
$\beta_1$	-0.6332	-1.4954	0.1889
$\beta_2$	-0.1857	-0.3815	0.0021
$\beta_3$	-0.0007	-0.0139	0.0100
$\beta_4$	-0.0010	-0.0078	0.0057
$\beta_5$	0.0011	-0.0003	0.0026
$\sigma_e^2$	0.1454	0.0485	0.3967

Table A4: Parameter estimates and 95% confidence intervals for analyses of the effect of MC1R-genotypes and population density on variation in individual fitness ( $\Lambda$ ) of female barn owls in western Switzerland. Log-linear mixed-effects models with a random intercept for year were fitted. The model for individual  $i$  in year  $t$  was the form  $\ln\tilde{E}(\Lambda_{it}) = \beta_1 + \beta_2x_{WRi} + \beta_3x_{RRi} + \beta_4N_t + \beta_5N_tx_{WRi} + \beta_6N_tx_{RRi} + u_t$ , where  $x_{kl}$ 's are dummy variables which take to value 1 for individuals of genotype  $kl$  (otherwise 0),  $N_t$  is population size,  $u_t$  is the random effect and  $\tilde{\cdot}$  denote reproductive value weighting. The random intercept with a mean of 0 and variance  $\sigma_e^2$  was estimated for year to account for environmental stochasticity. Parameters which are significantly different from zero are given in bold.

	Estimate	Confidence Interval	
		Lower	Upper
$\beta_1$	0.2581	-0.5163	1.0091
$\beta_2$	0.3202	-0.3444	0.9770
$\beta_3$	2.8426	-0.2387	7.2082
$\beta_4$	<b>-0.0067</b>	<b>-0.0129</b>	<b>-0.0004</b>
$\beta_5$	-0.0030	-0.0084	0.0024
$\beta_6$	<b>-0.0275</b>	<b>-0.0723</b>	<b>-0.0006</b>
$\sigma_e^2$	0.1934	0.0856	0.4537



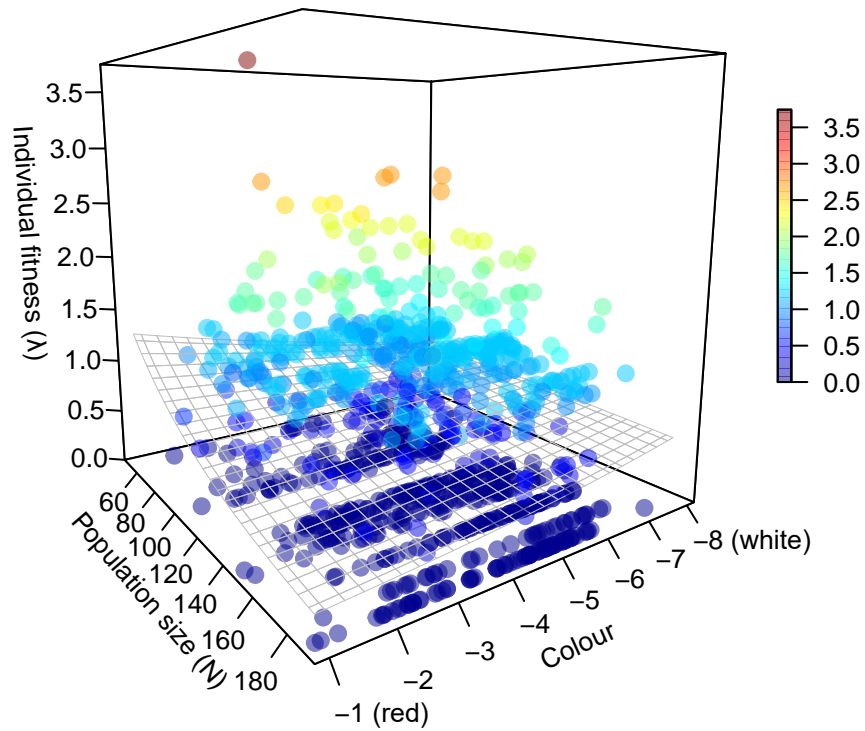


Figure A4: Estimated density-dependent selection surface for the degree of reddish colouration in female barn owls on the plains south-west of lake Neuchâtel in western Switzerland ( $46^{\circ} 49'N$ ,  $06^{\circ} 56' E$ ) in the period 1994-2015. Red individuals are favoured at low population densities while white individuals are less sensitive to population density and have the highest individual fitness at high densities.

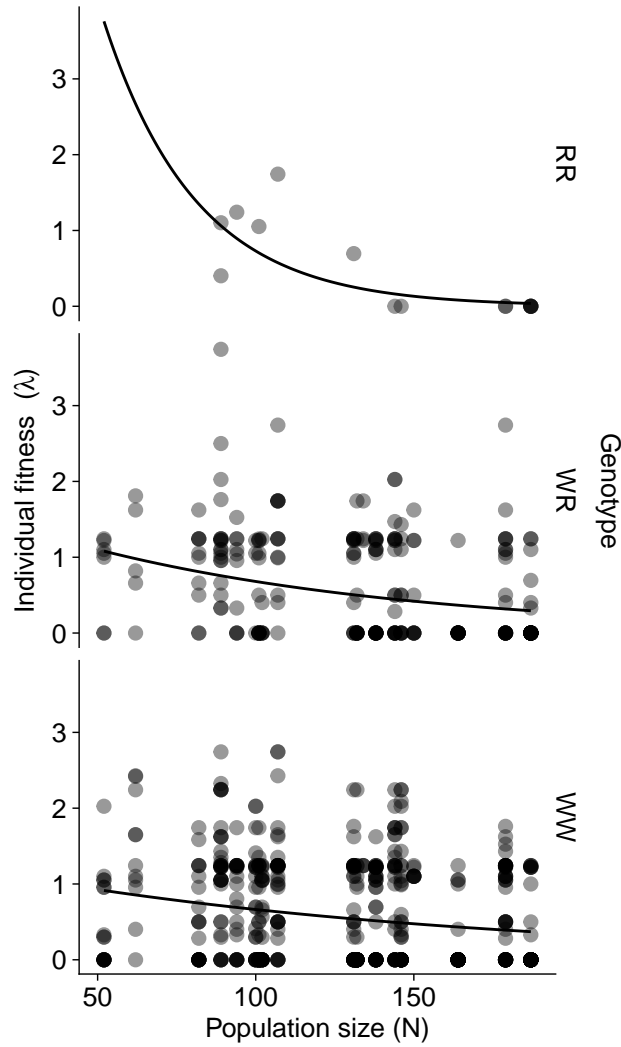


Figure A5: Estimated density-dependent selection on the melanocortin-1 receptor (MC1R) genotype in female barn owls on the plains south-west of lake Neuchâtel in western Switzerland ( $46^{\circ} 49'N$ ,  $06^{\circ} 56' E$ ) in the period 1996-2015. The red genotype (RR) is shown to be most sensitive to changes in population density, such that WW is favoured at high densities and RR is favoured at low densities.

# Dynamics of reproductive values under density dependence

In exponentially growing populations, reproductive values are defined as the expected contribution of an individual of a given age to the future population growth [1]. In such populations, weighting individual fitness, phenotypes and allele frequencies by reproductive values, as originally proposed by Fisher [1], allows unbiased estimates of selection and adaptive evolutionary changes [2–7]. Given an expected projection matrix  $\bar{\mathbf{L}}$ , reproductive values and the stable age distribution may be estimated as the left and right eigenvectors of  $\bar{\mathbf{L}}$  scaled to  $\sum u_x = 1$  and  $\sum v_x u_x = 1$  [2].

In density-dependent populations we have  $\mathbf{L}(N) = \bar{\mathbf{L}}(N) + \boldsymbol{\varepsilon}$ , where  $\bar{\mathbf{L}}(N)$  is the expected projection matrix at population size  $N$  and  $\boldsymbol{\varepsilon}$  is an environmental noise term. At the equilibrium population size or carry capacity, the equilibrium projection matrix  $\hat{\mathbf{L}} = \bar{\mathbf{L}}(K)$  with growth rate  $\lambda = 1$  given by its real dominant eigenvalue. The stable age distribution  $\mathbf{u}$  and reproductive values  $\mathbf{v}$  at equilibrium are given as the left and right eigenvectors of  $\hat{\mathbf{L}}$  scaled as above [2, 8–10].

Here we use simulations to show that weighting by equilibrium reproductive values (rv-weighting) allows unbiased estimates of phenotypic changes and responses to selection at the carry capacity and dampens the fluctuations observed in arithmetic means due to fluctuating age distribution (Fig. A6). Hence, weighting by reproductive values at equilibrium provides accurate estimates of the dynamics of total population size and change in phenotypes following selection given that the fluctuations around the carry capacity are not very large.

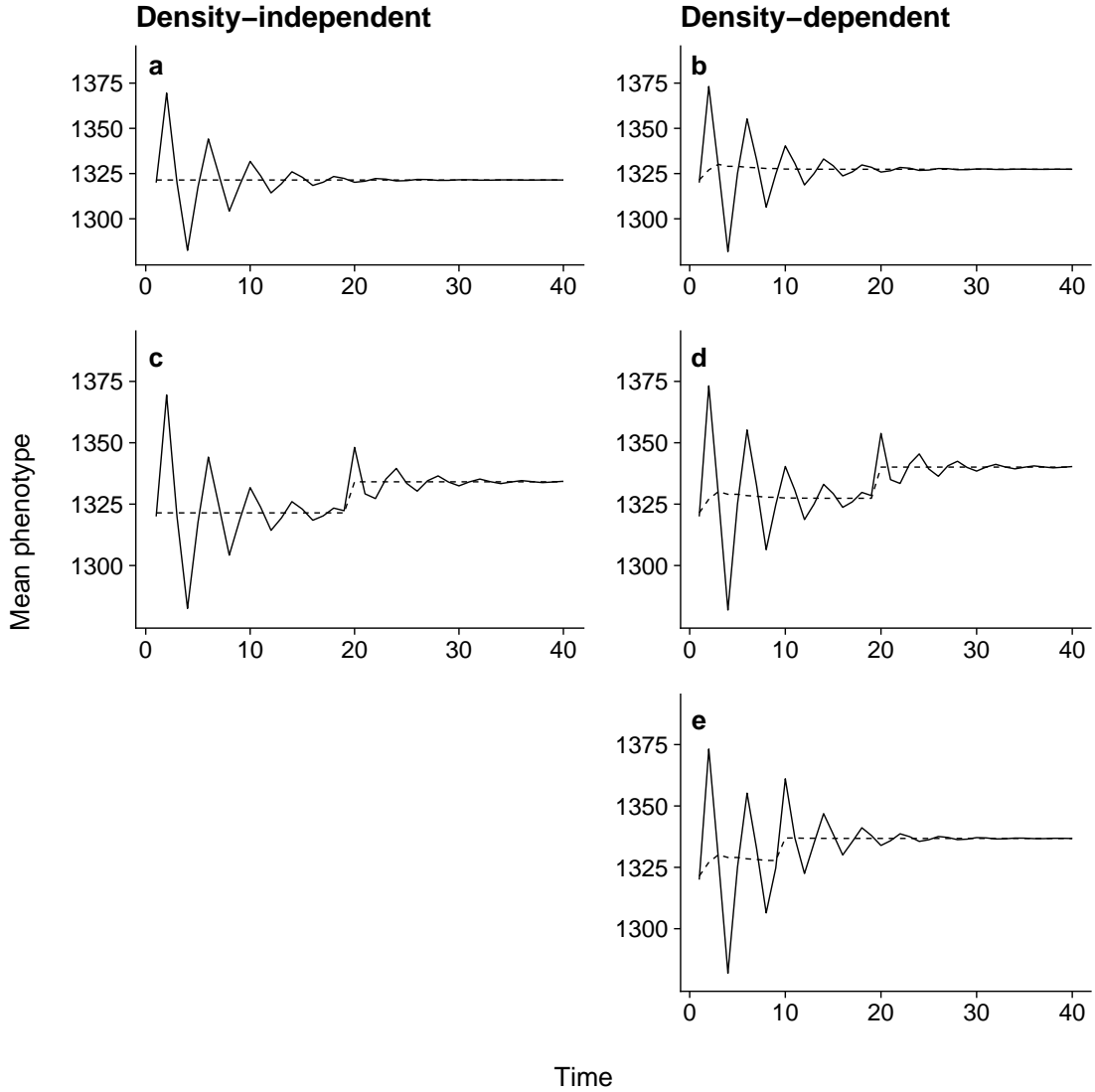


Figure A6: Simulations of arithmetic (solid line) and rv-weighted (dashed line) mean phenotype in an age-structured population under density-independent (**a** and **c**) and density-dependent (**b**, **d** and **e**) population dynamics. The simulated populations had initially 2000 individuals in each of five age classes and initial phenotype vector  $z_0 = (1200, 1200, 1300, 1400, 1500)$ . For the density-independent population the population growth was governed by the expected projection matrix  $\bar{\mathbf{L}}$  with growth rate  $\lambda = 1$ .  $\bar{\mathbf{L}}$  had non-zero elements given by fecundities  $\bar{L}_{1,1} = \bar{L}_{1,2} = 0$ ,  $\bar{L}_{1,3} = 1.76$ ,  $\bar{L}_{1,4} = 2.64$  and  $\bar{L}_{1,5} = 1.76$  and survival rates  $\bar{L}_{2,1} = 0.3$ ,  $\bar{L}_{3,2} = 0.6$  and  $\bar{L}_{4,3} = \bar{L}_{5,4} = 0.9$ . The growth of the density-dependent population was given by the projection matrix  $\bar{\mathbf{L}}(N)$  with growth rate  $\lambda = 1.5$  in the limit as  $N \rightarrow 0$  (with no density regulation).  $\bar{\mathbf{L}}(N)$  had non-zero elements given by fecundities  $\bar{L}(N)_{1,1} = \bar{L}(N)_{1,2} = 0$ ,  $\bar{L}(N)_{1,3} = 5.84g_f(N)$ ,  $\bar{L}(N)_{1,4} = 8.76g_f(N)$  and  $\bar{L}(N)_{1,5} = 5.84g_f(N)$  and survival rates  $\bar{L}(N)_{2,1} = 0.34g_s(N)$ ,  $\bar{L}(N)_{3,2} = 0.68g_s(N)$  and  $\bar{L}(N)_{4,3} = \bar{L}(N)_{5,4} = 1g_s(N)$ .  $g_f(N) = e^{-aN} = e^{-0.00010N}$  and  $g_s(N) = e^{-bN} = e^{-0.00001N}$ , which are the density regulatory functions for fecundity and survival.  $a$  and  $b$  measures the sensitivities of the vital rates to population density. At the carry capacity,  $\bar{\mathbf{L}}(K) = \bar{\mathbf{L}}$ .

# Maximization principle for allele frequency under density-dependent selection

In a large population with a single diallelic locus we have allele frequencies  $p$  and  $q = 1 - p$  for alleles  $B$  and  $b$ . Let the tree genotypes  $BB$ ,  $Ba$  and  $bb$  have expected genotypic values  $a_m$ ,  $d_m$  and  $-a_m$  for Malthusian fitness ( $m$ ), where  $a_m = m_{BB} - m_0$ ,  $-a_m = m_{bb} - m_0$  and  $d_m = m_{Bb} - m_0$  [11]. Here  $m_0$  is the midpoint between the expected Malthusian fitness of the homozygotes. Following Falconer [11], the mean Malthusian fitness of the population is then given by  $\bar{m}(p) = a_m(p - q) + 2pqd_m + m_0$ .

Allowing for density-dependence, we assume that the locus is pleiotropic and separate mean Malthusian fitness into a density-independent  $\bar{r}(p)$  and a density-dependent  $\bar{\gamma}(p)$  component, such that  $\bar{m}(p, N) = \bar{r}(p) - \bar{\gamma}(p)N$ . Then we define  $\bar{r}(p) = a_r(p - q) + 2pqd_r + r_0$  and  $\bar{\gamma}(p) = a_\gamma(p - q) + 2pqd_\gamma + \gamma_0$ , where  $r_0$  and  $\gamma_0$  are the midpoint between the genotypic values of the homozygotes.

In fluctuating environments, the variance in mean Malthusian fitness between years is  $\sigma_e^2$ , which reduce the average growth rate of the population such that  $\bar{m}_e(p, N) = \bar{s}(p) - \bar{\gamma}(p)N$ , where  $\bar{s}(p) = \bar{r}(p) - \frac{1}{2}\sigma_e^2$  [8]. At the equilibrium population size  $N = N^*$ , the mean Malthusian fitness  $\bar{m}_e(p, N^*) = 0$  such that

$$N^* = \frac{\bar{s}(p)}{\bar{\gamma}(p)}. \quad (1)$$

Following Fisher [1], the change in allele frequency can be given as  $\frac{dp}{dt} = pq\alpha_m$ , which can be rewritten to  $\frac{d}{dt}\text{logit}(p) = \alpha_m$ . Here  $\alpha_m = (1/2)(d\bar{m}/dp)$  is the average effect of a gene substitution on mean Malthusian fitness with no inbreeding [1]. Using that  $\alpha_m = \alpha_s - \alpha_\gamma N$  we write

$$\begin{aligned}
\frac{d}{dt}\text{logit}(p) &= \alpha_s - \alpha_\gamma N \\
&= \frac{1}{2}\left(\frac{d\bar{s}}{dp} - \frac{d\bar{\gamma}}{dp}N\right) \\
2\frac{d}{dt}\text{logit}(p) &= \frac{d\bar{s}}{dp} - \frac{d\bar{\gamma}}{dp}N.
\end{aligned} \tag{2}$$

At the equilibrium population size  $N = N^*$  (eqn. 1) we then have

$$\begin{aligned}
2\frac{d}{dt}\text{logit}(p) &= \frac{d\bar{s}}{dp} - \frac{d\bar{\gamma}}{dp}N^* \\
&= \frac{d\bar{s}}{dp} - \frac{d\bar{\gamma}}{dp}\frac{\bar{s}(p)}{\bar{\gamma}(p)} \\
&= \bar{\gamma}(p)\frac{d}{dp}\frac{\bar{s}(p)}{\bar{\gamma}(p)} \\
&= \bar{\gamma}(p)Q'(p),
\end{aligned}$$

where  $Q'(p) = (d/dp)(\bar{s}(p)/\bar{\gamma}(p))$ . Thus, equivalent to the maximization principle  $Q(\bar{z})$  for the mean phenotype  $\bar{z}$  under density-dependent selection derived by Engen et al. [12], the evolution of the mean allele frequency is governed by the function  $Q(p) = \bar{s}(p)/\bar{\gamma}(p)$ , where  $Q(p)$  give the maximum expected population size as function of allele frequency. Adaptive evolution is expected towards allele frequency  $p_{opt}$  at which  $(d/dt)\text{logit}(p_{opt}) = 0$  and the  $Q$ -function has its maximum.

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