

Devenish-Nelson, E. S., Harris, S., Soulsbury, C. D., Richards, S. A. and Stephens, P. A. 2013. Demography of a carnivore, the red fox, *Vulpes vulpes*: what have we learnt from 70 years of published studies? – Oikos 122: 705-716.

Appendix A1

Selection of populations for demographic analysis

To select populations for demographic modelling, we only used data from study populations for which all the required demographic data were available. This meant eliminating some populations where the age-specific data (e.g. litter size or probability of breeding) were incomplete. We only used data from populations for which age or stage- (i.e. juvenile, adult) specific values were provided for all vital rates. Stage-specific vital rates were deemed acceptable because, typically, the most significant differences exist between juveniles and adults (Fig. 1). Survival rates were based on standing age distributions; most studies only reported an overall mean number of individuals in each age class, which were used to infer survival estimates. This approach was necessary because most studies were of less than 5 years duration and estimating inter-annual variation from short time periods is unreliable.

Appendix 2

Estimating process error using Kendall's (1998) method: an example using a Swedish population

To assess the relative contributions of process and sampling error to observed uncertainty in demographic rates we followed Kendall's (1998) method. The only population that had sufficient data to apply this technique was the Sweden (South) population. Age distribution data for this population were available for six consecutive years, and the probability of breeding was available for four of those six years (Englund 1970, 1980). Kendall's method was applied to the survival and breeding probabilities. The contributions of sampling and process error to these vital rates can be estimated by assuming that a beta distribution describes between-year variation in the survival or breeding probability, with the number of survivors and breeders for a given year drawn randomly from the binomial distribution (Kendall 1998). For example, if the probability parameter of interest is π , then the likelihood that the long-term probability is $\bar{\pi}$ and variation in π among years is $\sigma^2(\pi)$, given the data in year t , is

$$L_t(\bar{\pi}, \sigma^2(\pi)) = \binom{N_t}{m_t} \frac{B(m_t + a, N_t - m_t - b)}{B(a, b)} \quad (\text{A1})$$

where N_t is the total number of trials (individuals) in year t , m_t is the number of successes (survivors or breeders), B is the beta function, and a and b are the parameters of the beta distribution derived from the mean and variance:

$$a = \bar{\pi} \left[\frac{\bar{\pi}(1 - \bar{\pi})}{\sigma^2(\pi)} - 1 \right] \quad \text{and} \quad b = (1 - \bar{\pi}) \left[\frac{\bar{\pi}(1 - \bar{\pi})}{\sigma^2(\pi)} - 1 \right]$$

The total log-likelihood is the natural logarithm of Eq. A1 summed across all years of data. Maximum likelihood was then used to find the best parameter estimates for $\bar{\pi}$ and $\sigma^2(\pi)$, with the latter quantifying the variance due to process error.

The relative contributions to uncertainty in λ caused by process and sampling error were estimated as follows. First, to determine the contribution of process error alone, we sampled the survival and breeding probabilities for the matrix element replicates from beta distributions. For both survival or breeding probability, the parameters of the relevant beta distribution were denoted as the mean $\bar{\pi}$ and variance σ^2 , both estimated as described above (i.e. with the sampling error removed). The LSA method was then used to determine λ from the matrix replicates (see 'Process error' in Fig. A1). Next, to determine the combined contributions of process and sampling error, we used the LSA method as in the original model. Importantly, however, for each replicate matrix elements were drawn from the beta distributions of the sampling error associated with data from a randomly chosen year (see 'Sampling and process error' in Fig. A1).

There is good agreement between the mean λ estimates for the Sweden (South) population for all of the three methods used to account for uncertainty in vital rates. As expected, the uncertainty in λ is largest when both sources of variance are included (Fig. A1). Process error and sampling error contributed similar uncertainty to our estimates of λ .

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Doak, D. F. et al. 2005. Understanding and predicting the effects of sparse data on demographic analyses. – *Ecology* 86: 1154–1163.

Kendall, B. E. 1998. Estimating the magnitude of environmental stochasticity in survivorship data. – *Ecol. Appl.* 8: 184–193.

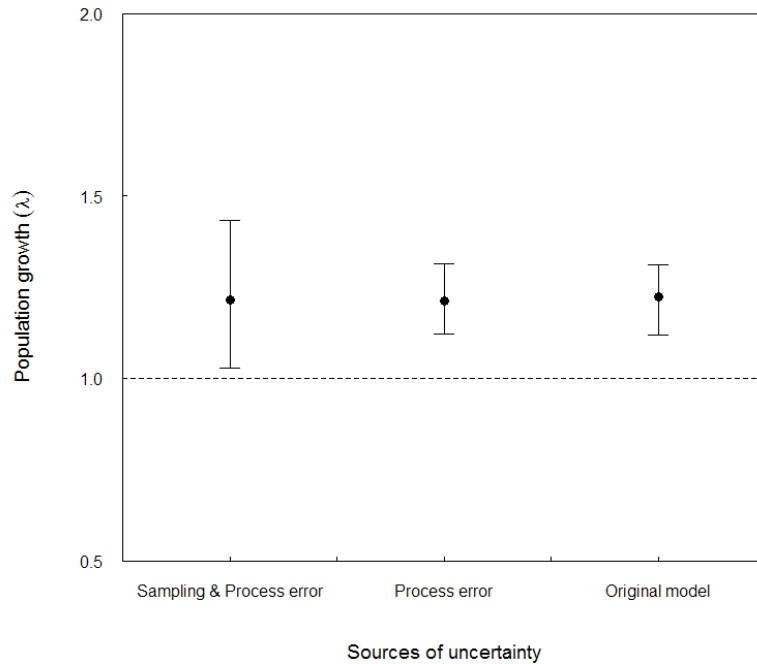


Figure A1. Population growth rates for the Sweden (South) population with both process and sampling variance included, sampling error removed, and the estimate from our original model. Error bars are 95% confidence intervals determined from the matrix replicates (Methods).

So, how representative of other fox populations is the Sweden (South) population? The Sweden (South) population most likely falls towards the higher end of the process error spectrum, coming from an area that is prone to environmental fluctuations, although not as extreme as experienced farther north in Sweden but there were less data available for this population. However, it is known to be subject to high inter-annual variation owing to regulation by prey cycles (Lindström 1989). As many fox populations are likely to experience

less environmental variation, we expect the process variation in these populations to be less pronounced. However, our results should be interpreted with caution, given that Doak et al. (2005) suggest that studies of less than five years duration are inadequate to quantify sources of variation, and that sample sizes for the Sweden (South) population were small in some years.

Table A1. Summary of a review of global fox population dynamics (\pm standard deviations, where provided). Underlined populations were selected for demographic analysis.

Study no.	Study population	References	Data type ¹	Total study duration (years)	Max study area (km ²)	Max sample size (from one study)	Habitat ²	Sex ratio: all ages*; adults**; juveniles^; embryos^^	Density km ⁻² (individual, litter* or group**)	Home range (km ⁻²)
1	<u>UK: London</u>	1, 2, 3	MD	6	1618	1141	4	1 : 0.96*		
2	UK: London	4	CMR, SS	6	7.6	209	4		2.33 \pm 0.39 1.03*	1.65
3	<u>UK: Bristol</u>	5, 3, 6, 7, 8, 9, 10, 11, 12	MD, RT, BE, SS, CMR, G	30+	116	1701	4	1 : 0.81* 1.2:1.0**	14.00 \pm 8.34 1.82*	0.51 \pm 0.48
4	UK: Oxford	13, 14, 15, 16	RT	10	9.17	>120	3,4		2.15 2.5**	0.92 \pm 0.66
5	UK: Wales	17, 18	CMR,	6	580	476	1,2	1:82**	1.85 \pm 1.27 0.90 \pm 0.57*	2.35 \pm 2.33
6	UK: Hampshire	19	BE	1	53	124	2		0.57*	
7	UK: Dorset	20	RT, SS	2	11	14	2			2.43 \pm 0.97
8	UK	21, 22	MD	3	2322	656	1,2	1 : 1**	0.94 \pm 0.85	
9	UK: Scotland	23, 24	MD	23	48760	4765	1,2		1.09 \pm 0.67	
10	Ireland	25, 26	CMR	2	-	292				
11	Belarus	27	SS	3	300	-	2		0.92 \pm 0.93	
12	Belgium	28	MD	2	589	314	3,4	0.95:1*		
13	France: North-eastern	29, 30, 31, 32	RT, SS, MD, G	7	250	1259	1,3			1.18 \pm 0.75
14	France	33		-	-	-				
15	Germany	34	MD, BE	15	130	955	2	1.5: 1**	0.73 \pm 0.25 0.55 \pm 0.17*	7.00
16	Germany	35, 36	MD, CMR	5	1012	1371	1,2		0.74 0.31*	
17	Italy	37, 38	RT, MD	2	2448	317	1,2,4	1 : 0.96^^		1.98 \pm 1.28
18	Netherlands	39	RT	5	-	150	2		0.55*	3.48 \pm 3.77
19	Netherlands	40, 41	RT	6	300	311	2			
20	Norway	42	SS	3	18	2	2			5.47 \pm 0.46

Table A1 contd.

Study no.	Study population	References	Data type ¹	Total study duration (years)	Max study area (km ²)	Max sample size (from one study)	Habitat ²	Sex ratio: all ages*; adults**; juveniles^; embryos^^	Density - individual/ litter*/ group**/ km	Home range (km)
21	Poland	43, 44	SS, MD, BE	9	89	113	1,2	1.17 : 1**	0.71 ± 0.18 0.0.94-0.171*	
22	Poland	45	SS	3	66	-	1,2		1.30 ± 0.31 0.31 ± 0.02*	
23	Russia	46	MD	5	-	759				
24	Spain: Doñana	47, 48	MD, SS	4	500	116	-	0.9:1^^	1.70	
25	Spain: Ebro	49	MD	7	-	413	1,2	1:0.76*		
26	Sweden: South	50, 51	MD, CMR	6	-	799	1,2			
27	Sweden: North	50, 51	MD, CMR	4	-	870	1,2			
28	Sweden	52	BE	6	3	13	1,2			4.00 ± 1.84
29	Sweden	53, 54, 55, 56, 57	MD, RT, SS	17	130	874	2			
30	Switzerland	58, 59, 60	MD, SS	8	30	88	1,2		0.4 - 3.2 0.37 ± 0.04*	5.66 ± 11.68
31	Japan	61	MD	4	6800	690	1,2			
32	Japan	62	RT	1	24	4		1 : 0.65** 1 : 0.74^		3.95 ± 1.98
33	Japan	63		1	-	6				4.94 (3.57-6.31)
34	USA: New York State	64		2	-	175		0.95 : 1^^		
35	USA: Indiana		MD	1	-	104				
36	USA: Midwest USA	65, 66	MD, SS, CMR, RT	9	84	2049	1,2	1 : 0.79** 1 : 0.82^ 1 : 0.96^^		9.71
37	USA: Minnesota USA	67	SS, RT	2	41.44	32				6.993 ± 1.372
38	(Midwest): Wisconsin	68, 69		4	83.73	-		1 : 1.04^	0.09 ± 0.03**	
39	USA: Illinois	70	RT, MD	5	3000	611	1,4			

Table A1 contd.

Study no.	Study population	References	Data type ¹	Total study duration (years)	Max study area (km ²)	Max sample size (from one study)	Habitat ²	Sex ratio: all ages*; adults**; juveniles^; embryos^^	Density - individual/ litter*/ group**/ km	Home range (km)
40	USA: New York State	71, 72, 73	CMR, MD	5	26	2848	1,2	1.06:1** 1.35:1^	0.74 0.97 ± 0.09**	
41	<u>USA (East): Maryland</u>	74	MD	3	-	210	1,2	1:1*		
42	USA: North Dakota	75, 76	MD, RT	5	-	363	1,2	1.33:1** 1: 0.93^^	0.10 ± 0.04**	
43	USA: Alaska	77	CMR, BE	4	3	30	2		9.53 ± 0.45	
44	Canada: Alberta	78	SS, BE	9	21	-	1,2			
45	Canada: Ontario	15, 79	RT	8	-	120	1		0.54 ± 0.65	9 (5.00-20.00)
46	Canada: Ontario	80	RT	1	4	7	3		0.57**	0.77 ± 0.39
47	Australia: Canberra	81		2	-	437	-	1:0.87*		
48	Australia: NSW	82		5	-	838				
49	Australia: Victoria	83, 84	MD	4	24	317		1: 0.79**	2.7 ± 1.38	2.56 ± 2.30
50	Australia: Melbourne	85, 86, 87	RT, MD, SS	5	21	50	4		5.99 ± 4.93 1.18 ± 0.96*	0.28 ± 0.12
51	<u>Australia (Hunted): NSW</u>	88, 89	RT, MD, SS	3	-	534	1,2	1 : 0.72* 1:0.72^		
52	Australia: NSW	90		2	77	21	2,4			1.35 ± 0.042
53	Australia: NSW	91	SS,MD	2	108	276	1			
54	<u>Australia (Non-hunted): Western</u>	92	MD, SS,	1	200	204	1	1:1*	0.46–0.52	
55	Australia: south	93	SS	10	20 km transect	-	2,4		0.60	
56	Australia: Melbourne	94	RT	2	26	9	2,3			0.45 ± 0.13

¹Data type: MD: mortality data; CMR: capture–mark–recapture; RT: radiotelemetry; SS: sign surveys; BE: behavioural observations; G: genetic. – Data not provided

²Habitat: 1 – rural agricultural; 2 – rural non-agricultural 3: low population density; 4 – high population density

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Table A2. Demographic parameters from a review of global fox populations. Study numbers refer to Table A1, ± standard deviations, where provided.

Studies from Table A1 that do not report relevant information are omitted. Underlined populations were selected for demographic analysis.

Study no.	Study population	Age definition ¹	Juvenile: adult ratio	Survival (age-specific)	Litter size definition ²	Breeding probability definition ³	Litter size ⁴ (mean - all ages)	Litter size (age-specific)	Percent non-breeding (mean)	Percent non-breeding (age-specific)	Percent dispersing - juvenile males (mean)	Percent dispersing - juvenile females (mean)
1	<u>UK: London</u>	1	0.53:0.47	0+0.38 1+0.43 2+0.49 3+0.44	1	1		0+4.6 1+5.0 2+4.9 3+4.9		0+ 24.6 1+8.1 2+4.9 3+3.5		
2	UK: London	3			2	NA						
3	<u>UK: Bristol</u>	1	0.50:0.50	0+ 0.44 1+0.53 2+ 0.52 3+0.51	1	1		0+4.5 1+4.9 2+4.8 3+4.7		0+24.4 1+17.1 2+19.1 3+2.9	44.0 ± 25.9	22.7 ± 12.6
4	UK: Oxford	NA			1	2			40.6± 25.5			
5	UK: Wales	1		0.75-1: 0.45 1.75-2: 0.43 2.75-3: 0.44 3.75-4: 0.43 4.75-5: 0.50	1	1	4.6**		20.5		25.0 ± 16.2	32.5 ± 1.7
7	UK: Dorset	NA			1	NA	5.8 ± 1.9^					
8	UK	1		0+ 0.45 1+ 0.45 2+ 0.30 3+ 0.45	1	1	5.55 ± 0.98		9.7 ± 13.72			
9	UK: Scotland	1	0.67:0.33	0+ 0.34 1+ 0.45 2+ 0.43 3+ 0.13	1	NA	5.0**					
10	Ireland	3	0.64:0.36		1	3			9.8 ± 2.8		30.0	20.0
12	Belgium	1	0.51:0.49	0+ 0.42 1+ 0.51 2+ 0.63 3+ 0.92 4+0.36	NA	NA						

Table A2 contd.

Study no.	Study population	Age definition ¹	Juvenile: adult ratio	Survival (age-specific)	Litter size definition ²	Breeding probability definition ³	Litter size ⁴ (mean - all ages)	Litter size (age-specific)	Percent non-breeding (mean)	Percent non-breeding (age-specific)	Percent dispersing - juvenile males (mean)	Percent dispersing - juvenile females (mean)
14	France	1	0.54:0.46		NA	NA						
15	Germany	1	0.66:0.34	0+ 0.35 1+ 0.34 2+ 0.35 3+ 0.32 4+ 0.23	2	NA	4.8 ± 1.1* 6.8 ± 0.9**'					
16	Germany	1	0.56:0.44		1	1	4.6*	0+ 4.5^ 1+ 5.3 2+ 4.7 3+ 4.9		0+ 24 1+ 17.9 2+ 0.0 3+ 6.8		
17	Italy	1	0.52:0.48		1	2	4.0 ± 1.3^ 3.9 ± 1.6**		20			
21	Poland	1	0.54:0.46	0-0.167: 0.69 0.167-0.5: 0.76 0.5-1: 0.45 1+ 0.56 2+ 0.428 3+ 0.38 4+ 0.32 0+ 0.34 1+ 0.49	1	NA	3.8 (2.7 - 4.5)* 5.5^					
23	Russia	1	0.62:0.38	2+ 0.52 3+ 0.50 4+ 0.60	2	NA						
24	Spain: Donana	1			1	1	3.1 (2.5- 3.6)* 3.3 ±0.7 **		13.2			
25	Spain:Ebro	2	0.58:0.42	1+ 0.56 2+ 0.52 3+ 0.55 4+ 0.64	1	1	3.6 ± 0.4^		10.5 ±12.5			

Table A2 contd.

Study no.	Study population	Age definition ¹	Juvenile: adult ratio	Survival (age-specific)	Litter size definition ²	Breeding probability definition ³	Litter size ⁴ (mean - all ages)	Litter size (age-specific)	Percent non-breeding (mean)	Percent non-breeding (age-specific)	Percent dispersing - juvenile males (mean)	Percent dispersing - juvenile females (mean)
26	<u>Sweden(South)</u>	1	0.60:0.40	0+ 0.43 1+ 0.53 2+ 0.75 3+ 0.55	1	1		0+ 3.93^ 1+ 4.77 2+ 4.53 3+ 4.20		0+ 46 1+ 62 2+ 81		
27	<u>Sweden(North)</u>	1	0.54:0.46	0+ 0.33 1+ 0.71 2+ 0.50 3+ 0.59	1	1		0+ 4.17^ 1+ 4.30 2+ 4.77 3+ 4.20		0+ 59 1+ 48 2+ 33		
28	Sweden	NA			1	2	4.8 ± 0.7*		50			
29	Sweden	1		0+ 0.53 1+ 0.67 2+ 0.66 3+ 0.61 4+ 0.66	1	NA	4.1 ± 0.5^					
30	Switzerland	NA			2	NA	3.9 ± 0.4*					
31	Japan	2	0.70:0.30	0+ 0.19 1+ 0.51 2+ 0.53 3+ 0.40 4+ 0.75	NA	NA						
32	Japan	1	0.62:0.38	0+ 0.20 1+ 0.88 2+ 0.43 3+ 0.70	NA	NA						
34	USA: New York State	NA			1	2	5.4 (1-9)**		4.7			
35	USA: Indiana	NA			2	2	6.8 ± 0.3		40			

Table A2 contd.

Study no.	Study population	Age definition ¹	Juvenile: adult ratio	Survival (age-specific)	Litter size definition ²	Breeding probability definition ³	Litter size ⁴ (mean - all ages)	Litter size (age-specific)	Percent non-breeding (mean)	Percent non-breeding (age-specific)	Percent dispersing - juvenile males (mean)	Percent dispersing - juvenile females (mean)
36	USA: Midwest	1	0.64:0.36	0+ 0.35 1+ 0.53 2+ 0.80 3+ 0.80 4+ 0.86	1	3	4.2 ± 0.1* 7.1 ± 1.9^ 6.8 ± 0.1**				87.4 ± 9.2	44.6 ± 11.5
38	USA (Midwest): Wisconsin	1	0.59:0.41	1+ 0.33 2+ 0.40 3+ 0.95 4+ 0.43	1	2		0+ 5.9** 1+ 5.4 2+ 6.8 3+ 5.3 4+ 8.0		0+ 41 1+ 10 2+ 11 3+ 25 4+ 0		
39	USA: Illinois	3		0+ 0.27 1+ 0.35	NA	NA						
40	USA: New York State	1	0.69:0.31	0+ 0.63 1+ 0.33 2+ 0.57 3+ 0.25 4+ 0.58	NA	NA					58.3 ± 14.0	47.5 ± 26.7
41	USA (East): Maryland	2	0.55:0.45	0+ 0.34 1+ 0.87 2+ 0.56 3+ 0.63 4+ 0.58	2	2	0+ 5.32^ 1+ 6.68 2+ 6.26 3+ 6.10			0+ 83 1+ 17		
42	USA: North Dakota	2	0.44:0.56		1	1		0+ 3.1±2.3 1+ 4.7±2.2 2+ 4.9±2.2 3+ 5.6±1.9 4+ 4.8±1.3		0+ 28.3 1+ 7.7 2+ 7.7 3+ 5.3 4+ 0.0	62.0± 10.1	31.0 ± 34.7
43	USA: Alaska	3			2	2	4.2 ± 0.2*		78.8 ± 14.1			
44	Canada: Alberta	3			NA	NA	5.0*					
45	Canada: Ontario	3	0.79:0.21	Juv+ 0.20 1.5+ 0.40 2.5+ 0.83	2	3	8.0^				90.5	77.0

Table A2 contd.

Study no.	Study population	Age definition ¹	Juvenile: adult ratio	Survival (age-specific)	Litter size definition ²	Breeding probability definition ³	Litter size ⁴ (mean - all ages)	Litter size (age-specific)	Percent non-breeding (mean)	Percent non-breeding (age-specific)	Percent dispersing - juvenile males (mean)	Percent dispersing - juvenile females (mean)
47	Australia: Canberra	3			2	3	3.8 (1-8)* 4.3 (1.8)^ 3.8 (1-6)**		2.6	3		
48	Australia: NSW	2			2	3	3.7 ± 1.5^ 4.0 ± 1.6**		30			
49	Australia: Victoria	1	0.55:0.45		1	NA	3.3*				31.0	23.5
50	Australia: Melbourne	1			1	NA	4.4 ± 0.2* 4.6^					
51	<u>Australia (Hunted): NSW</u>	1	0.61:0.39	0+ 0.29 1+ 0.38 2+ 0.55 3+ 0.64 4+ 0.70	1	3		0+ 3.0 ± 1.8 1+ 3.9 ± 1.5 2+ 4.8 ± 1.3 3+ 4.1 ± 2.0 4+ 5.2 ± 1.8		0+30.6 1+14.8 2+13.3 3+8.3 4+8.3		
53	Australia: NSW	1			NA	NA						
54	<u>Australia (Non-hunted): Western</u>	1	0.54:0.46	0+ 0.39 1+ 0.65 2+ 0.92 3+ 0.17 4+ 0.5	1	2		0+ 3.5^ 1+ 3.9 2+ 3.1 3+ 4.5 4+ 3.0		0+ 0 1+ 0 2+ 0 3+ 0 4+ 0		

¹Age definition: 1 – well defined: clear description of technique, with juveniles clearly defined; 2 – adequately defined: technique stated, but juveniles poorly defined; 3 – poorly defined: no definition provided.

²Litter size definition: 1 – well defined: clear description of technique, e.g. defining grades of placental scars, or live embryos; 2 – adequately defined: technique stated but lack of detail; 3 – poorly defined: no definition provided. NA – not applicable for study purpose.

³Breeding probability: 1 – well defined: clear description of technique, e.g. stating inclusion of post-implantation loss/reabsorptions; 2 – adequately defined: technique stated but lack of detail; 3 – poorly defined: no definition provided.

⁴Litter size: ^placental scars; *direct counts; ** embryos

Table A3. Coefficients of variation for age-specific survival (P_x) and fecundity (F_x) across matrix replicates for eight fox populations (study number refers to study population in Table A1 and A2).

Study no.	Population	P_0	P_1	P_2	P_3	F_0	F_1	F_2	F_3
51	Australia (Hunted)	0.08	0.13	0.14	0.08	0.10	0.15	0.18	0.10
54	Australia (Non-hunted)	0.17	0.16	0.10	0.42	0.21	0.21	0.21	0.56
3	Bristol	0.04	0.05	0.06	0.07	0.07	0.09	0.13	0.12
1	London	0.05	0.07	0.10	0.10	0.06	0.09	0.12	0.12
26	Sweden (North)	0.02	0.03	0.04	0.03	0.03	0.04	0.05	0.05
27	Sweden (South)	0.06	0.05	0.08	0.06	0.11	0.11	0.11	0.11
38	USA (Midwest): Wisconsin	0.06	0.07	0.06	0.07	0.11	0.11	0.10	0.11
41	USA (East): Maryland	0.11	0.17	0.06	0.18	0.20	0.21	0.16	0.26

Figure A2. Correlation between mean matrix replicates for survival and fecundity for eight fox populations. (A) Juveniles 0+ ($r^2 = 0.20$, $p = 0.23$); (B) Adults 1+ ($r^2 = 0.51$, $p = 0.03$); (C) Adults 2+ ($r^2 = 0.56$, $p = 0.02$); (D) Adults ≥ 3 ($r^2 = 0.64$, $p = 0.01$).

