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1 Title: Demography of a carnivore, the red fox, *Vulpes vulpes*: what have we learnt from 70 years of  
2 published studies?

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24 **Abstract**

25 Populations of the same species often face different selection pressures and, increasingly, the  
26 demography of populations within a species has been shown to be highly variable. Knowledge of such  
27 intraspecific differences has implications for substituting demographic data, a practice that is often  
28 necessary for population modelling due to missing parameters. The red fox *Vulpes vulpes*, a widely-  
29 studied, widespread and economically important species, offers an opportunity to consider the  
30 degree of intraspecific variability in the demography of a carnivore and to test the consequences of  
31 interpopulation data substitution. We use published life history data to review the extent and quality  
32 of demographic data for fox populations. Using demographic descriptors, matrix models, and  
33 perturbation analyses, we identify important demographic properties and classify interpopulation  
34 variation along the fast-slow continuum. We also illustrate the consequences of data substitution in  
35 demographic models. Data quality varies substantially between reviewed studies. Sufficient data exist  
36 to model the demography of eight of 57 study populations. Modelled populations have a tendency  
37 towards positive population growth, with survival and fecundity of the youngest age class  
38 contributing most to that growth. Metrics point to strategies ranging from medium to fast life  
39 histories. While broad demographic similarities exist among fox populations, our results imply  
40 considerable demographic variation between populations. We show that significant differences in  
41 model outcomes based on substituted data are dependent on the parameter replaced, and that  
42 geographic proximity does not imply demographic similarity. Superficially, the red fox appears to have  
43 been well studied, yet there are remarkably few usable demographic data from much of its range.  
44 Despite 70 years of published studies, we were unable to examine the effects on demographic  
45 parameters of harvesting regimes, density, and weather. We propose improvements to enhance the  
46 value of demographic data, both for foxes and for other species.

## 47 **Introduction**

48 Demographic modelling is widely used in conservation and management (Mills, et al. 1999, Fieberg  
49 and Ellner 2001) but data availability frequently imposes significant limitations on modellers (Caro, et  
50 al. 2005). Data are often patchily reported because they have been collected for purposes other than  
51 to derive demographic parameters (Baker, et al. 2004, Imperio, et al. 2010, Joly, et al. 2009).  
52 Moreover, demographic parameters are often missing for a focal population, requiring modellers to  
53 rely on surrogate data from other populations of the same species (Pech, et al. 1997, Peck, et al.  
54 2008), or even from similar species (Githiru, et al. 2007, Schtickzelle, et al. 2005). Whilst the  
55 consequences of these problems can be hard to determine, well-studied species are increasingly  
56 being used to gain insights into the consequences of demographic differences between species  
57 (Coulson, et al. 2005) or populations (Johnson, et al. 2010, Nilsen, et al. 2009).

58         The insights gained from recent analyses of multiple populations within a species suggest a  
59 high degree of inter-population variability in demography. For example, Nilsen et al. (2009) showed  
60 population-specific demography of roe deer *Capreolus capreolus* resulting from distinct climatic  
61 conditions, predation and harvest levels, and Servanty et al. (2011) found variation along the fast-slow  
62 continuum among wild boar *Sus scrofa* populations facing different hunting pressure. Similarly,  
63 Johnson et al. (2010) demonstrated substantial differences in vital rate contributions between  
64 populations of Sierra Nevada bighorn sheep *Ovis canadensis sierra* in various phases of population  
65 growth. To date, these cross-population comparisons have focused on large herbivores and some bird  
66 species (Frederiksen, et al. 2005, Tavecchia, et al. 2008). Indeed, Nilsen et al. (2009) speculated that  
67 the high degree of intraspecific variation in life history speed that they observed in roe deer might be  
68 a characteristic of large herbivore dynamics. Here, we consider whether there are similar patterns of  
69 intraspecific variability in a widely-studied carnivore.

70 Red foxes are the most widespread, extant, terrestrial mammal (Schipper, et al. 2008) and are  
71 also a species of great economic, cultural, and disease importance (Baker, et al. 2008). Hence, many  
72 years of sampling effort have been devoted to the red fox to gain insight into its life history for both  
73 management purposes (Smith and Harris 1991) and studies of sociality (Soulsbury, et al. 2008a).  
74 Despite this intensive effort, successful management of foxes often remains difficult (Saunders, et al.  
75 2010) and demographic analyses of many fox populations are lacking. Recent deterministic models of  
76 red foxes have suggested that demographic traits, particularly age-specific contributions to  
77 population growth, are highly consistent across a sample of populations (McLeod and Saunders 2001).  
78 However, whether this pattern is robust to the method used to assess contributions to population  
79 growth, such as classical perturbation (Caswell 2001) or incorporating variation through life-stage  
80 simulation analyses (LSA) (Wisdom, et al. 2000), is unknown. It is also unclear whether the apparent  
81 consistency of age-specific contributions to population growth translates into high consistency of life  
82 history speed, because there are only a few estimates of life history speed metrics for foxes (see Oli  
83 and Dobson 2003). Foxes are found across many habitats, from tundra to arid environments, and with  
84 rural and urban populations (Pils and Martin 1978, Harris and Smith 1987, Lindström 1989, Saunders,  
85 et al. 2002). Given this diversity, with evidence of within population inter-annual variation of body  
86 mass and reproductive strategies (Soulsbury, et al. 2008b, Harris and Whiteside, *pers.comm.*) and the  
87 potentially sensitivity of life history rates to anthropogenic pressure (Lloyd, et al. 1976), differing  
88 demographic tactics may be expected between populations.

89 Here, we present a comprehensive review of published studies of red fox demography. With  
90 70 years of published studies, collating these extensive data for the first time provides a unique  
91 resource for assessing the worldwide variability in the demography of this common and often  
92 intensively-managed species. We use the collated data to construct matrix projection models to

93 determine basic demographic descriptors. Given that the fox is a generalist occurring over a wide  
94 range of habitat conditions, harvest levels, and population densities, we predict that life history  
95 speeds of distinct populations of this carnivore will be highly variable, with a gradient of fast to slow  
96 with increasing latitude (Ferguson and Larivière 2002). We expect that the importance of vital rates  
97 with low variation will appear greater when using traditional perturbation analyses than when using  
98 LSA, because the latter incorporates observed parameter variability. We also predict that as foxes are  
99 highly adaptable, modelled population growth rates will be sensitive to substituting the most variable  
100 life history rates between fox populations. We show that data for relatively few fox populations are  
101 adequate for detailed demographic analyses. However, those examined suggest important  
102 population-level differences in fox life history, with implications for erroneous management  
103 prescriptions when using surrogate data.

## 104 **Methods**

### 105 **Data Collection, Fox Life Cycle, and Matrix Element Calculation**

106 We collated life history data from 57 fox populations, totalling 96 papers published since the 1940s.  
107 Searches were conducted in Web of Science (<http://webofknowledge.com>, July 2010) using the  
108 search terms “red fox”, “demography”, “population ecology” and “life history”. We summarised  
109 demographic rates from these papers and, as a measure of data quality, we recorded study attributes  
110 including sample size, duration, size of study area, and data type (see supplementary Table A1). We  
111 classified methods of determining age, litter size and proportion of barren females as well -,  
112 adequately-, or poorly-defined (see supplementary Table A2). This classification included, for  
113 example, how post-implantation loss was classified in the description of barren females, or if full  
114 descriptions of ageing methods were provided.

115 From this data review, we were able to obtain sufficient age-specific vital rates for eight  
 116 populations (studies 1, 3, 26, 27, 38, 41, 51 and 54 in Tables A1 and A2; see Appendix 1 for additional  
 117 information as to how populations were chosen) to construct density-independent, time-invariant,  
 118 age-classified matrix models (Caswell 2001). Age-specific models are appropriate for modelling fox  
 119 population dynamics because attributes such as litter size have been shown to vary significantly with  
 120 female age (Harris 1979, McIlroy, et al. 2001). Populations were assumed to be stable in size (Englund  
 121 1970, Nelson and Chapman 1982, Harris and Smith 1987, Marlow, et al. 2000, Saunders, et al. 2002).  
 122 The data had been collected predominantly from hunting returns, reported as standing age  
 123 distributions, with survival determined from the age frequencies,  $f_x$ , for age class  $x$  (Caughley 1977, p.  
 124 91). As it is unusual for individuals to survive past four years (Harris and Smith 1987, Pils and Martin  
 125 1978, Stubbe 1980) we used four age classes in the matrix,  $\mathbf{A}_t$ , (eqn 1), where juveniles are age class  
 126 0+, and adults are age classes, 1+, 2+ and  $\geq 3$  respectively.

$$127 \quad \mathbf{A}_t = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & P_3 \end{bmatrix} \quad (1)$$

128 Age-specific matrix elements for survival were calculated as (Caswell 2001):

$$129 \quad P_x = \frac{f_{x+1}}{f_x} \quad (2)$$

130 where  $P_x$  is the probability of survival from  $t$  to  $t+1$  of females in class  $x$ . To avoid issues of small  
 131 sample size in the older classes, and to account for any individuals older than four, we created a  
 132 composite final age class for all age classes beyond three ( $\geq 3$ ). We calculated survival ( $P_3$ ) for this age  
 133 class by  $P_{x^*} = f_{x>x^*} / (f_x + f_{x>x^*})$ , where  $x^*$  is the final age class.

134 We calculated productivity  $m_x$ , the expected number of female births per female of age class  $x$ :

135 
$$m_x = M_x B_x SR \quad (3)$$

136 where  $M_x$  is the proportion of pregnant females,  $B_x$  is mean litter size and  $SR$  is the sex ratio (Caughley  
137 1977, p. 82). Based on empirical evidence (Vos and Wenzel 2001), we assumed a 1:1 birth sex ratio.

138 Females are able to mate when they are about 10 months old and produce one litter per year  
139 thereafter (Englund 1970). Consequently, we formulated a post-breeding ‘birth-pulse’ model (Caswell  
140 2001). We calculated age-specific matrix elements for fecundity:

141 
$$F_x = P_x m_x \quad (4)$$

142 where  $F_x$  is the expected number of female offspring at time  $t+1$  per female in class  $x$  at  $t$ .

### 143 **Life-History Speed**

144 Life-history ‘speed’ is determined by how a species resolves the evolutionary trade-off  
145 between reproduction and survival, in response to extrinsic mortality and environmental stochasticity  
146 (Bielby, et al. 2007). Oli and Dobson (2003) proposed the ratio of fertility rate to age at first  
147 reproduction ( $F/\alpha$ ) (i.e. the level of reproduction in relation to the onset of reproduction) as a  
148 measure of a **mammalian** species’ position on the fast-slow continuum: ‘fast’ species were deemed to  
149 have an  $F/\alpha$  ratio of  $> 0.6$ , whilst ‘slow’ species have an  $F/\alpha$  ratio of  $< 0.15$ ; those in between are  
150 considered ‘medium’. Gaillard *et al.* (2005) used generation time as a proxy to determine life-history  
151 speed **in mammals**; fast species typically have a generation time of under two years. We used both  
152 metrics to examine inter-population variation in life history speed of red foxes.

153 We calculated the mean weighted fertility rate as in Oli and Dobson (2003):

154 
$$F = \frac{\sum_{x=\alpha}^{\omega} w_x F_x}{\sum_{x=\alpha}^{\omega} w_x} \quad (5)$$



155 where age at first reproduction,  $\alpha = 1$ , age at last reproduction,  $\omega = 4$  (consistent with our matrix, eqn.  
156 1), and  $w$  is the stable age distribution determined from the projection model. We calculated  
157 generation time,  $T_b$ , determined according to Gaillard *et al.* (2005):

$$158 \quad T_b = \sum_x x l_x m_x \lambda^{-x} \quad (6)$$

159 where  $l_x$  is the proportion of individuals that survive from birth to age  $x$ . To calculate confidence  
160 intervals for the  $F/\alpha$  ratio and  $T_b$ , we used the approach described below to conduct resampling for  
161 10,000 matrix replicates.

## 162 **Perturbation Analyses**

163 Perturbation analyses provide a ranking of the relative importance of demographic rates, in  
164 the context of their effects on the population growth rate ( $\lambda$ ) (Caswell 2001). To decompose  
165 contributions to  $\lambda$  by life stage we calculated elasticity values ( $e_{ij}$ ) of  $\lambda$  to the matrix entry  $a_{ij}$  (Caswell  
166 2001):

$$167 \quad e_{ij} = \frac{a_{ij}}{\lambda} \frac{\delta \lambda}{\delta a_{ij}} \quad (7)$$

168 Traditional perturbation methods do not account for variability and uncertainty in vital rates,  
169 potentially masking the true importance of life stages (Mills, et al. 1999). High uncertainty in vital rate  
170 estimation stems from inherent spatiotemporal variation, as well as inevitable sampling and  
171 measurement error (Wisdom, et al. 2000). LSA includes uncertainty in the effects of variance on  
172 population growth. Classical elasticity analyses examine the effects of varying vital rates  
173 independently about point estimates of their values; in LSA, by contrast, vital rates are varied  
174 simultaneously, taking into account interactions in uncertainty in the values of each.

175 Following previous studies (Wisdom, et al. 2000) we performed LSA by constructing 10,000  
176 stochastic matrix replicates, using vital rates drawn from appropriate probability distributions.

177 Specifically, best estimates of age-specific survival were derived from standing age distributions using  
 178 a likelihood approach, assuming uncertainty around these estimates was beta-distributed (see Fig.1 in  
 179 Devenish-Nelson, et al. 2010). Similarly, the proportion of breeding females of each age-class and  
 180 age-specific litter sizes were drawn, respectively, from beta and shifted Poisson distributions  
 181 (Devenish Nelson et al. *unpublished*). Matrix replicates were constructed by resampling from these  
 182 distributions (Fieberg and Ellner 2001). To determine the degree of variation in  $\lambda$  explained by each  
 183 parameter (coefficient of determination,  $r^2$ ), we regressed  $\lambda$  against each individual transition  
 184 element (Wisdom, et al. 2000). From the matrix replicates, we generated 95% confidence intervals for  
 185 the mean stochastic estimates of  $\lambda$  for each population. To compare the inferences from the two  
 186 perturbation methods, we first determined the variance of  $\lambda$  explained by each vital rate (Horvitz, et  
 187 al. 1997). Following Coulson et al. (2005) the square of the elasticity ( $e_{ij}$ )<sup>2</sup> was multiplied with the  
 188 variance of a given age-specific matrix element  $V(a_i)$ :

$$189 \quad \chi_{ij}^{ind} = V(a_{ij})(e_{ij})^2 \quad (8)$$

190 Using equation (8) we were able to determine the age-specific contributions of survival ( $\chi_{ij}^p$ )  
 191 and fecundity ( $\chi_{ij}^f$ ) to the variance in  $\lambda$ . Hence, we were able to compare the elasticity variance ratios  
 192 ( $\chi_{ij}^p / \chi_{ij}^f$ ) with age-specific ratios based on the contributions of survival  $r^2$  to fecundity  $r^2$  ( $r_{p,x}/r_{f,x}$ ) to  $\lambda$   
 193 as determined by the LSA.

#### 194 **Data Substitution**

195 We illustrated the consequence of substituting data between populations from the same country with  
 196 two urban UK populations (Bristol and London), one subjected to control measures and the other not,  
 197 and two USA populations (Midwest and East), both subject to hunting. Previously, data have been  
 198 substituted between populations in Australian and the USA (e.g. Pech, et al. 1997). Consequently, we

199 also examined the consequences of this intercontinental substitution. For each case study, we  
200 sequentially replaced matrix components of survival, fecundity, probability of breeding, and litter size  
201 from one population to another: we substituted Bristol data for the London population, USA (Midwest  
202 population) data for the USA (East) population and USA (Midwest population) data for the hunted  
203 Australia (Hunted) population. The last example illustrates an alternative approach for data  
204 substitution, by using vital rates averaged from all eight populations to substitute into the Australia  
205 (Hunted) population. Using the above methods, we generated 95% confidence intervals for the  
206 resultant mean stochastic  $\lambda$  estimates for each simulation. All analyses were conducted using R 2.12.0  
207 (R Development Core Team 2010).

## 208 **Results**

### 209 **Data review**

210 Our review of 57 published demographic studies is summarised in supplementary Tables A1 and A2.  
211 This review exposes some significant weaknesses, both in the extent of data coverage and in  
212 inconsistent data presentation. For example, 23 of the studies reviewed gave average litter size, but  
213 only nine gave age-specific litter sizes (supplementary Table A2). Whilst age-specific survival was  
214 available for 22 populations (supplementary Table A2), 14 were from populations without  
215 corresponding survival rates, restricting demographic modelling to just eight studies. In terms of data  
216 quality, 31%, 29% and 61% of studies did not adequately define ageing, litter size and probability of  
217 breeding, respectively (supplementary Table A2); in general, these studies gave insufficient details of  
218 methodology and definitions. Also, 29% of studies included no details of study attributes such as  
219 study area (supplementary Table A1). Of the eight populations used for the matrix models, none had  
220 been studied for more than ten years' duration and age-specific demographic data from all but the  
221 Australian populations were collected between the 1960s and mid-1980s (Table 1).

222 Age-specific productivity ( $m_x$ ) is more variable than survival ( $P_x$ ) (Fig.1). The two parameters  
223 show similar patterns with age, with both parameters peaking in young adults (Fig. 1). Study  
224 attributes and vital rates for the eight populations used for analyses are presented in Tables 1 and 2.  
225 Again, coefficients of variation show that fecundity was more variable than survival (mean  $CV_F = 0.15$ ;  
226  $CV_S = 0.10$ , supplementary Table A3). These eight populations show a similar relationship to that seen  
227 in Fig. 1 (supplementary Table A3), with a positive correlation between fecundity and survival in the  
228 older age classes (strongest in age  $\geq 3$  ( $r^2 = 0.64$ ,  $p = 0.01$ ), supplementary Figure A2), suggesting that  
229 local conditions, rather than trade-offs between recruitment and survival, determine life history  
230 properties in foxes.

### 231 **Life history speed**

232 Relative to many other carnivores, red foxes mature early, are fairly short-lived and, as is  
233 typical of canids, have larger than average litter sizes; consequently, theory predicts that they should  
234 fall towards the fast end of the spectrum (Heppell, et al. 2000). In fact our analyses show wide  
235 variation in the speed of fox populations, from 'medium' to 'fast' species according to the  $F/\alpha$  ratio,  
236 and 'slow' to 'fast' species according to generation time (Fig. 2). There is large variation in speed  
237 within these classifications; the metrics increased by factors of 3.5 (generation time) and 1.5 ( $F/\alpha$   
238 ratio) between the 'slowest' fox population of north Sweden ( $F/\alpha = 0.53$ ,  $T_b = 3.13$ ), and the 'fastest'  
239 population, London ( $F/\alpha = 0.81$ ,  $T_b = 0.90$ ). The Australian hunted population (Australia (Hunted)) has  
240 a faster life history than would be expected from its population growth (Fig. 2). The  $F/\alpha$  ratio is  
241 positively correlated with  $\lambda$  ( $r = 0.83$ ,  $p = 0.01$ ) (Fig. 2A), and generation time ( $T_b$ ) is negatively  
242 correlated with  $\lambda$  ( $r = -0.86$ ,  $p = 0.01$ ) (Fig. 2B). Unsurprisingly, given that they are determined by the  
243 same life-history rates, there is a negative correlation between the  $F/\alpha$  ratio and  $T_b$  ( $r = -0.79$ ,  $p = 0.03$ )  
244 (Fig. 2C). No correlation was found between life history speed ( $F/\alpha$  ratio) and latitude ( $r = -0.34$ ,  $p =$

245 0.38). These results suggest that local conditions play a significant role in determining life history  
246 rates; for example, good conditions give rise to both high survival and high fecundity, resulting in  
247 higher population growth and faster speed.

## 248 **Perturbation analyses**

249 Life-history theory suggests that relatively early-maturing mammals, such as the fox, should  
250 have higher elasticity of fecundity than survival (Heppell, et al. 2000). Elasticity analysis and LSA reveal  
251 two main points: that the youngest age class makes the largest contribution to  $\lambda$ , and that, generally,  
252 fecundity is as important as survival (Table 3). Despite these patterns, both elasticity and LSA results  
253 reveal there is a great deal of inter-population variation in the contribution that vital rates make to  $\lambda$ .  
254 For example, there is a threefold difference in fecundity elasticity of the youngest age class (London  
255  $e_{F,1} = 0.35$ ; Sweden (South)  $e_{F,1} = 0.10$ ). Life history theory predicts higher sensitivity of  $\lambda$  to fecundity  
256 in 'fast' species, to survival in 'slow' species (Heppell, et al. 2000), and more evenly balanced  
257 sensitivity to both parameters in 'medium' species (Oli 2004). Therefore it is expected that, as  
258 recruitment drives fast populations, the sensitivity of  $\lambda$  to fecundity should increase as populations  
259 get faster (Oli and Dobson 2003). Age-specific variance ratios ( $V_{S,x}/V_{F,x}$ ) show a tendency to decrease  
260 across all age classes (strongest in juveniles 0+,  $r = -0.75$ ,  $p = 0.003$ ) with increasing speed (Fig. 3A),  
261 suggesting that fecundity contributions become more important in faster populations. LSA ratios  
262 ( $r_{P,x}/r_{F,x}$ ) did not show a significant relationship (strongest in adults 2+,  $r = -0.64$ ,  $p = 0.09$ ) with speed  
263 (Fig. 3B). Evaluating these two ratios ( $\chi_{ij}^P / \chi_{ij}^F$  and  $r_{P,x}/r_{F,x}$ ) highlights the importance of including  
264 variation when estimating the relative contributions of vital rates. When the reduced variability of  
265 survival is taken into account, the importance of survival for slower populations is reduced (Fig. 3).  
266 While it is possible that this reduced variability stems from errors in sampling rather than intrinsic

267 variation, our results are consistent with the prediction of higher variability in the fecundity of this  
268 species.

### 269 **Data substitution**

270 The importance of accounting for inter-population variation in life history is highlighted by the  
271 substitution of vital rate parameters between fox populations; using surrogate data substantially  
272 changes the resultant population growth rate estimates (Fig. 4). The results are particularly striking  
273 when substituting Bristol data in the London population, even though both samples come from the  
274 same habitat in the same country; surrogate fecundity produces a 23% decrease in  $\lambda$ , whereas  
275 substituting survival data increases the  $\lambda$  estimate by 21% (Fig. 4A). A 23% decrease in  $\lambda$  occurs when  
276 only probability of breeding is used, but only a 1% increase in  $\lambda$  when replacing litter size, highlighting  
277 that the percentage of breeding females is lower in London, whereas there is no significant difference  
278 in litter size between these populations (Harris and Smith 1987). In the USA (Midwest) population  
279 breeding probability is higher and more variable than litter size, compared to the USA (East)  
280 population. Although the levels of uncertainty in  $\lambda$  are high, differences in mean  $\lambda$  estimates range  
281 from a 15% increase with the probability of breeding, to only a 3% decline when litter size is replaced  
282 (Fig. 4B). Many of the age-specific survival and fecundity rates are similar in the Australia (Hunted)  
283 and USA (Midwest) populations, leading to smaller differences resulting from data substitution.  
284 However, replacing fecundity data produces a 13% increase in  $\lambda$ , and substituting litter size increases  
285  $\lambda$  by 20% (Fig. 4C), highlighting the dependency of the model outcome on the chosen surrogate  
286 parameter. Figure 4D illustrates that the population growth rate estimates using the parameter range  
287 from the eight populations are closer to the Australia (Hunted)  $\lambda$  estimate than when using surrogate  
288 data from just one population, with the exception of when replacing survival data. Noticeably, the

289 Australia (Hunted) population is the only population where survival elasticity was consistently greater  
290 than fecundity (Fig.3), indicating that this population is sensitive to changes in survival rates.

## 291 **Discussion**

292 Our review highlights the large sampling effort expended on the red fox but, with only eight of 57  
293 studies providing sufficient data for age-specific demographic modelling, also identifies how much  
294 more could yet be learned about interpopulation variability in demography. Recruitment in red fox  
295 populations appears to be consistently more variable than, but correlated with, survival across age-  
296 classes and populations. Population growth rates were sensitive to changes in both survival and  
297 fecundity. Our analyses showed large intraspecific variation in demography, in both life history speed  
298 and the contribution of vital rates to  $\lambda$ . **Our results are indicative of the potential role of**  
299 **environmental conditions for determining life history rather than trade-offs between recruitment and**  
300 **survival.** Variation in demographic rates between populations allowed us to illustrate the  
301 consequences of data substitution between populations. Inferences gained from population models  
302 are likely to be highly sensitive to the practice of data substitution, and this will vary with the vital rate  
303 replaced. We discuss the outcomes of our study in the context of four broad issues: emerging  
304 recognition of the variation in life history among populations within a species; perturbation analyses  
305 and their implications for management; data substitution in demographic modelling; and  
306 recommendations for ongoing studies of demography in red foxes and similar species.

## 307 **Inter-population variation in life history speed**

308 The determination of life-history speed along the fast-slow continuum has been much debated  
309 (Bielby, et al. 2007, Gaillard, et al. 2005, Oli 2004). Intraspecific studies have used both generation  
310 time (Nilsen, et al. 2009) and the  $F/\alpha$  ratio (Bieber and Ruf 2005). We found that both metrics  
311 correlated with  $\lambda$ , suggesting that as Oli and Dobson found (2005), both are at least partially indicative

312 of a fox population's current trajectory. We illustrate the calculation of confidence intervals for the  
313 most commonly used metrics of the fast-slow continuum, and suggest that the use of confidence  
314 intervals should be routine before making inferences about the extent to which populations differ in  
315 life history speed.

316 Phylogeny and body mass typically account for much of the variation in life history variables  
317 (Gaillard, et al. 2005) and, consequently, within-species variation in demographic tactics is generally  
318 expected to be limited. A practical application of defining a population's position on the fast-slow  
319 continuum is to provide a measure of the population's response to perturbations and adaptability to  
320 the local environment. This 'interpopulation' approach (Nilsen, et al. 2009) merits further attention  
321 for comparing population responses to specific pressures and exploring evidence of trade-offs  
322 between recruitment and survival. Recent comparisons show that roe deer do not exhibit this trade-  
323 off, slowing down their life history in harsher environments because they cannot increase  
324 reproduction when faced with increased mortality in adverse conditions (Nilsen, et al. 2009). In wild  
325 boar, by contrast, the contribution of life history tactics shifted from juvenile to adult survival as  
326 conditions changed from poor to good (Bieber and Ruf 2005). Similarly, Servanty et al. (2011) found  
327 that wild boar increased life history speed by increasing fecundity when facing higher hunting  
328 pressure. Tasmanian devils *Sarcophilus harrisii* show increased reproduction in young age classes as a  
329 response to disease mortality (Jones, et al. 2008). Here, however, our results point towards  
330 substantial variation in fox life history speed; although the majority of fox populations that we  
331 modelled would be classified as 'fast' by either metric, two of the eight populations (both from  
332 Sweden) lay outside that category (one of them substantially). Compared to other hunted fox  
333 populations, the Australia (Hunted) population shows surprisingly low  $\lambda$  considering its short  
334 generation time. This suggests that it is unable to respond to the hunting pressure by increasing



335 reproduction. However, at the time of data collection the population was experiencing a drought,  
336 which had a negative effect on reproduction (McIlroy, et al. 2001), highlighting the conflicting  
337 response to anthropogenic versus climate pressures. Conversely, the faster speed of the London  
338 population compared to the non-hunted Bristol population suggests a possible compensatory  
339 response to hunting, although the lack of additional data on immigration and density hinders  
340 assigning causation to this variation. The population with the slowest life history (by both metrics) is  
341 the Sweden (North) population, probably reflecting the harsh winter conditions and food limitations  
342 that it experiences (Lindström 1989), although fluctuations in this populations' density may violate  
343 assumptions of a stable population size. Slower species are expected in habitats with low productivity  
344 but high environmental variation (Ferguson and Larivière 2002). In foxes, the relationship between  
345 the environment and life history rates is complex: environmental variability is an important  
346 determinant of lifetime productivity (Soulsbury, et al. 2008b), and body condition, driven partly by  
347 climatic conditions, is an important factor affecting both survival (Gosselink, et al. 2007) and fecundity  
348 (Cavallini 1996). Bartoń and Zalewski (2007) found fox density was negatively correlated with an index  
349 of seasonality within Eurasia, suggesting that such an index could also be used to explain variation in  
350 life history speed between populations. However, using latitude as a proxy for seasonality, we found  
351 no correlation. Similarly, previous studies have failed to demonstrate a relationship between litter  
352 size and latitude (Lord 1960).

### 353 **Vital rate contributions and life-history characteristics**

354 That younger age classes are important to growth is unsurprising for a species with a relatively fast  
355 life history and is consistent with the observation that juveniles comprise an average of 60 % of fox  
356 populations (Lloyd, et al. 1976, Marlow, et al. 2000, Nelson and Chapman 1982). Although juvenile  
357 foxes are particularly susceptible to anthropogenic control (Englund 1970, Pils and Martin 1978),

358 heterogeneity in hunting effort generates source populations (Baker and Harris 2006), and together  
359 with constant immigration from dispersers (Rushton, et al. 2006), helps to explain why some  
360 populations remain stable or grow despite hunting pressure. While compensatory responses in  
361 productivity are thought to occur in areas of high hunting pressure (Cavallini 1996, Harris 1977), our  
362 results provide little evidence for this for the populations analysed here (see previous section). Thus,  
363 as McLeod and Saunders (2001) conclude, targeting the youngest age class is likely to be the most  
364 effective form of management when the aim is to decrease the population.

365         Traits that have a large impact on  $\lambda$  are predicted to be buffered against variation (Pfister  
366 1998), but demographic analyses of mammals are not always consistent with this theory (e.g. Creel, et  
367 al. 2004, Henden, et al. 2009). In our analyses,  $\lambda$  was equally sensitive to the contributions of  
368 fecundity and survival. Foxes are expected to have higher contributions to  $\lambda$  from fecundity than  
369 survival, but we found that fecundity is more variable than survival, possibly because fecundity is  
370 influenced more than survival by complex factors, which include food limitation, body mass, and  
371 social factors (Cavallini 1996, Iossa, et al. 2008, Lindström 1988). However, when considering  
372 demographic contributions in the context of the fast-slow continuum, the equal sensitivity of  $\lambda$  to  
373 both rates corresponds to that expected with a medium speed. We also found that the relative  
374 contribution of vital rates varied among populations, especially in the youngest age class, which drive  
375 growth. Changes in relative elasticities between demographic rates have been demonstrated as a  
376 response to environmental conditions (Bieber and Ruf 2005), with potential management implications  
377 if demographic traits are to be targeted based on data from fluctuating conditions. Given that  
378 variation is an important factor driving population dynamics, it is advantageous to incorporate as high  
379 a degree of realism as possible into models (Mills, et al. 1999, Wisdom, et al. 2000). Studies using  
380 multiple demographic analyses, such as those in this study, have illustrated how predicted life history

381 contributions can differ with the inclusion of variation (Wisdom, et al. 2000, Johnson, et al. 2010); our  
382 results reinforce that conclusion.

### 383 **Validity of using substitute demographic parameters**

384 The use of substitute data in demographic modelling is often necessary but requires great caution,  
385 even at the intraspecific level. Bristol and London foxes might be expected to share similar properties,  
386 being urban populations in relatively close proximity. However, at the time of data collection the  
387 London fox population was subject to hunting (Harris 1977), illustrating that geographical proximity of  
388 populations is no guarantee of the validity of this approach. Pech et al. (1997) used USA data for their  
389 model of an Australian population to test the impact on  $\lambda$  of reducing the fecundity of an invasive  
390 population. Our results illustrate how replacing fecundity, and its component elements, could have  
391 led to flawed outcomes. In the case of foxes, recruitment is the most variable life history rate, so  
392 should be substituted with great caution. If in doubt, the most comprehensive approach might involve  
393 substituting data from across the range of available values, and acknowledging the resultant  
394 uncertainty.

395 Data substitution is often inevitable in situations concerning highly endangered, elusive, or  
396 data-deficient species, highlighting the need for long-term research. It occurs in many forms, such as  
397 using data from species of the same family (Finkelstein, et al. 2010), species sharing similar attributes  
398 (Schtickzelle, et al. 2005), or making assumptions about a parameter based on a different (Peck, et al.  
399 2008) or captive (Martinez-Abraín, et al. 2011) population. Githiru et al. (2007) evaluated the  
400 applicability of substituting data from a common species for a critically endangered thrush *Turdus*  
401 *helleri*; both species responded to habitat disturbance with higher fluctuating asymmetry and lower  
402 effective population density. The sensitivity of  $\lambda$  estimates to surrogate demographic parameters  
403 illustrated by our case studies suggests a finer scale approach is required compared to the broad

404 measures of similarity applied in Githiru et al.'s (2007) approach. Based on our results, we agree with  
405 Caro et al. (2005) that surrogate data should be used only when similar traits can be identified;  
406 following Johnson et al. (2010), we caution against substituting data between demographically  
407 distinct populations.

#### 408 **Data quality implications and recommendations**

409 As the most widespread terrestrial mammal, the red fox has been subject to extensive study  
410 throughout its range. Despite the constraints on studying carnivores, data exist for an impressive  
411 number of red fox populations; however, for the amount of sampling effort, surprisingly few  
412 populations can be described by a matrix model with all necessary vital rates. Further, demographic  
413 data were biased towards collection during the 1970s. The quality of data is also restricted, in some  
414 published papers, by unclear methodologies, inconsistent definitions of key parameters, and issues  
415 related to basic study attributes. Sampling design is a direct source of bias for parameter estimation,  
416 but is often beyond the control of researchers due to funding and logistical limitations. However, it is  
417 important to take into account that sample size (Gross 2002), duration (Fieberg and Ellner 2001), and  
418 area (Steen and Haydon 2000) can have repercussions for the precision of demographic estimates.

419         The rarity with which quantifiable study attributes such as habitat, environmental, and  
420 anthropogenic variables were reported also limits analysis of the impact of these factors on inter-  
421 annual variability in population processes. Covariates, such as hunting effort, and those that enable  
422 scaling from an urban to rural gradient (e.g. human or road density), are easy to measure and can be  
423 important predictors in more powerful models (Mladenoff, et al. 1995). As with other studies  
424 (Wisdom, et al. 2000, Rice and Gay 2010, Nilsen, et al. 2011), quantification of inter-annual variation  
425 in vital rates is possible for few of the fox populations studied (but see Appendix 2). This is  
426 disappointing, given the importance of stochasticity for populations (Melbourne and Hastings 2008)

427 and the advances in demographic modelling for incorporating variation (Kendall 1998, White 2000,  
428 Akçakaya 2002, Udevitz and Gogan 2012). In this regard, studies are limited both by their relatively  
429 short durations and by their sample sizes. The seasonal variation that exists in trap capture rates  
430 between age and sex classes, which also mirrors the susceptibility to culling (Baker, et al. 2001),  
431 implies that important classes are underrepresented at key times of years. These differences are due  
432 to behavioural changes throughout the year, such as vixens being harder to catch when breeding. We  
433 suggest best practice for measuring inter-annual variation in key demographic rates is to sample  
434 during the dispersal period (October to December in the northern hemisphere). Samples during this  
435 period would show (i) how many cubs survive to independence (the ratio of cubs to adults); (ii) annual  
436 proportions of adult vixens that bred from placental scar counts; (iii) mean annual litter sizes (from  
437 placental scar counts); (iv) annual variations in both cub and adult sex ratios; and (v) annual variations  
438 in adult survival. Whilst such samples may be skewed towards dispersing subadults, particularly  
439 males, they are the least biased samples available, and presenting data for this specific period  
440 separately would facilitate comparisons between populations. Currently, few studies make it clear  
441 how sampling effort varied through the year; biases in sampling effort skews samples towards the age  
442 and sex classes that were most vulnerable during the main collection period.

443 Most available data on red foxes are from mortality studies, which have associated  
444 assumptions (for a review see Caughley 1977). Ultimately, however, mortality data such as hunting  
445 bag returns will remain an important source of information for fox populations. Four particular issues  
446 arise when presenting the data from these studies, all of which should be straightforward to remedy.  
447 First, studies differ in their definition of age classes. Factors affecting uncertainty in ageing methods  
448 and their minimisation have been discussed extensively elsewhere (Allen 1974, Harris 1978). Whether  
449 the first year after birth is described as age class zero, or one, leads to confusion in interpreting

450 published age-specific data, as does dividing the first year into shorter periods, such as pre-and post-  
451 weaning, or into 3-month segments, although there are biological and ecological arguments justifying  
452 this division (Marlow, et al. 2000). Similarly, the term 'juvenile' is not consistently linked to a specific  
453 age class; an appropriate definition includes all individuals under the age of one i.e. cubs and  
454 subadults (Soulsbury, et al. 2008b). Second, inconsistent determination of fecundity is a major source  
455 of confusion surrounding the conversion of vital rates to matrix elements (Noon and Sauer 1992). The  
456 interpretation and definition of techniques to determine litter size have been extensively reviewed  
457 (Allen 1984, Englund 1970, Harris 1979, Lindström 1981). It is unclear whether guidelines for using  
458 placental scars to determine litter size (Englund 1970) are widely followed but explicit reference to  
459 these guidelines would promote greater confidence in the data obtained from specific studies. Third,  
460 of the components driving reproductive output, the proportion of breeding females varies more  
461 widely between populations than litter size (Harris 1979, Zabel and Taggart 1989), often due to  
462 complex social factors (Macdonald 1979, Iossa, et al. 2009). The definition of "barren" females is an  
463 area of particular uncertainty and great variability. "Barren" can indicate animals that are unable to  
464 reproduce, as well as those that are capable of reproducing but fail to do so in a particular year. In  
465 addition, reproductive failure could occur at various points: failure to mate; failure to implant  
466 fertilised ova; death of the entire litter during pregnancy; and loss of an entire litter immediately  
467 following parturition, due to infanticide or other social factors. We recommend that, rather than using  
468 the ill-defined term "barren", future studies define the proportion of females experiencing  
469 reproductive failure at any given stage, as has been done for Eurasian badgers *Meles meles*  
470 (Cresswell, et al. 1992). Fourth, "hunting" samples vary between countries depending on legal  
471 restrictions and local practices. At the moment, for instance, it is unclear how samples taken by driven  
472 shoots, night shoots, snaring, leghold traps or digging out of dens differ: data from different collection

473 methods should be presented separately and by time of year to facilitate analyses on the impact of  
474 sampling method on demographic parameters. Furthermore, demographic data are often restricted  
475 to technical reports (e.g. Whitlock, et al. 2003), representing a substantial source of more directly  
476 useable raw data.

## 477 **Conclusion**

478 Demographic analyses of red foxes highlight inter-population differences in life-history. Currently,  
479 however, data required to identify the drivers of these demographic patterns are lacking. We  
480 reiterate the difficulties of interpreting models based on uncertain data. While we recognise that, for  
481 many species, data are often limited both in quality and quantity, we caution against data substitution  
482 unless exploratory demographic analyses suggest high levels of consistency between populations.

483 Superficially, the red fox appears well studied. As a result, we might assume a good  
484 understanding of red fox demography. In reality, in spite of the fox's widespread distribution,  
485 abundance and economic importance, there are remarkably few usable demographic data from much  
486 of its range. Studies of other abundant and widespread species suggest that great insight can be  
487 gained by comparing intraspecific demography. Demographic research on the red fox lags behind that  
488 on ungulates, for example, studies of which have been used to examine the effects on population  
489 dynamics of harvesting regimes (Servanty, et al. 2011), quantitative trait variation (Pelletier, et al.  
490 2007), and climate (Coulson, et al. 2001). Few broad scale models of age-specific survival and  
491 fecundity of multiple carnivore populations have been conducted. Here, we have illustrated the range  
492 of analyses that can be performed using published data, but recommend further research to  
493 determine whether apparent inter-population differences are upheld in light of temporal variation  
494 and sampling bias. With improvements in reporting standards, much more remains to be learnt about  
495 this important and widespread carnivore.

496

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665

666



667 Table 1 Summary of mean survival rates,  $P_x$ , and population attributes for eight fox populations.  
 668

	<i>Australia</i>	<i>Australia</i>	<i>UK</i>	<i>UK</i>	<i>Sweden</i>	<i>Sweden</i>	<i>USA</i>	<i>USA</i>	
	<i>(hunted)</i>	<i>(non-hunted)</i>	<i>(Bristol)</i>	<i>(London)</i>	<i>(North)</i>	<i>(South)</i>	<i>(Midwest)</i>	<i>(East)</i>	
669									
670									
671	$P_0$	0.30	0.39	0.48	0.42	0.33	0.43	0.33	0.34
672	$P_1$	0.35	0.65	0.54	0.43	0.71	0.53	0.40	0.88
673	$P_2$	0.57	0.92	0.53	0.47	0.50	0.75	0.95	0.57
674	$P_3^*$	0.70	0.18	0.51	0.49	0.59	0.55	0.43	0.53
675	Sample size	538	99	1628	1110	1070	827	269	94
676	Study area (km <sup>2</sup> )	200	200	8.9	1618	-	-	83.73	-
677	Habitat type	Rural	Rural	Urban	Urban	Rural	Rural	Rural	Rural
678	Study Years	1992; 1994-97	1992	1977-85	1971-77	1966-70	1966-70	1971-75	1976-79
679	Major source of mortality data	Mixed	Baited	Roadkill	Mixed, shot	Shot	Shot	Mixed	Trapped
680	Aging method	CA	CA	CA	CA	TE, CA	TE, CA	CA	CA, EW,TE,SM
681	Level of control**	Intense	No	No	Light/Average	Light	Intense	Average	Average
682	Individual density/km <sup>2</sup>	-	0.46–0.52	29.5	-	-	-	-	-
683	Invasive	Yes	Yes	No	No	No	No	No	No
684	Latitude	-32	-24	51	51	63	59	44	38
685	References	1	2	3	3	4	4	5	6
686	Study number in Tables A1 and A2	51	54	3	1	26	27	38	41

684 <sup>1</sup>Saunders et al 2002; <sup>2</sup>Marlow *et al* 2000; <sup>3</sup>Harris and Smith 1987; <sup>4</sup>Englund 1980; <sup>5</sup>Pils and Martin 1978; <sup>6</sup>Nelson and Chapman 1982. CA: cementum annuli (of  
 685 molars or canines); TE: tibia epiphysis closure; EW: eye lens weight; SM: skull measurements; Mixed: Combination of shooting, trapping, gassing, baiting and  
 686 battues. \* see text for explanation. \*\* determined according to juvenile age ratios (Table A2), where an increasing juvenile to adult age ratio is an indication of  
 687 increasing control (1977) and if possible, by information provided by each study on the presence or level of hunting.  
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691 Table 2. Summary of mean fecundity rates,  $F_x$ , for eight fox populations.

	<i>Australia</i>	<i>Australia</i>	<i>UK</i>	<i>UK</i>	<i>Sweden</i>	<i>Sweden</i>	<i>USA</i>	<i>USA</i>
	<i>(hunted)</i>	<i>(non-hunted)</i>	<i>(Bristol)</i>	<i>(London)</i>	<i>(North)</i>	<i>(South)</i>	<i>(Midwest)</i>	<i>(East)</i>
$F_0$	0.37	0.686	0.55	0.72	0.29	0.30	0.58	0.40
$F_1$	0.61	1.271	0.77	1.00	0.79	0.72	0.96	1.46
$F_2$	1.21	1.426	0.71	1.09	0.79	1.35	2.88	0.89
$F_3^*$	1.58	0.332	0.74	0.89	0.83	0.92	0.97	0.81
Sample size	291	47	252	384	161	217	367	94
Method to determine litter size	EM; EM, PS	PS (excluded faded scars)	PS (grade 5 - 6)†	PS (grade 5-6)	EM; PS (grade5-6)	EM; PS (grade5-6)	PS (dark), EM	PS
Method to determine barren females	-	PS (excluded faded scars)	FL, FO, FI, LE	NVP	NVP, PPIL	NVP, PPIL	-	NVP
References	1,2	3	4	5	6	6	7	8
Study number in Tables A1 an A2	51	54	3	1	26	27	38	41

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693 <sup>1</sup>Saunders et al 2002; <sup>2</sup>McIlroy et al 2001; <sup>3</sup>Marlow *et al* 2000; <sup>4</sup>Harris and Smith 1987; <sup>5</sup>Harris 1979; <sup>6</sup>Englund 1980, <sup>7</sup>Pils and Martin 1978; <sup>8</sup>Nelson and

694 Chapman 1982; PS: placental scars; EM: number of embryos; DC: den counts; FL: failure to produce litter; FO: failure to ovulate; FI: failure to implant; LE: lost

695 entire embryos; NVP: no visible signs of pregnancy; PPIL: pre and post implantation loss; - method not given. \* see text for explanation. † Placental scar grades

696 refer to the level of fading, with dark scars (5-6) being the most reliable (see Lindström 1981).

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700 Table 3. Age-specific elasticities and coefficients of determination of the LSA for eight fox populations. Elasticities and  $r^2$  are the  
 701 mean values calculated across all replicates (study number refers to study population in Tables A1 and A2).

Study #	Population	Elasticity of survival ( $e_{P,x}$ ) and fecundity ( $e_{F,x}$ )								LSA survival $r^2$ ( $r_{P,x}$ ) and fecundity $r^2$ ( $r_{F,x}$ )							
		$e_{P,0}$	$e_{P,1}$	$e_{P,2}$	$e_{P,3}$	$e_{F,0}$	$e_{F,1}$	$e_{F,2}$	$e_{F,3}$	$r_{P,0}$	$r_{P,1}$	$r_{P,2}$	$r_{P,3}$	$r_{F,0}$	$r_{F,1}$	$r_{F,2}$	$r_{F,3}$
51	Australia (Hunted)	0.20	0.14	0.10	0.24	0.12	0.06	0.04	0.10	0.14	0.15	0.08	0.15	0.13	0.14	0.07	0.13
54	Australia (Non-hunted)	0.28	0.11	0.02	0.01	0.30	0.17	0.09	0.02	0.38	0.08	0.01	0.01	0.41	0.10	0.01	0.01
3	Bristol	0.27	0.12	0.06	0.05	0.25	0.15	0.06	0.06	0.23	0.10	0.04	0.03	0.32	0.17	0.07	0.05
1	London	0.25	0.09	0.03	0.02	0.35	0.16	0.06	0.03	0.30	0.12	0.03	0.01	0.35	0.14	0.04	0.01
26	Sweden (North)	0.27	0.12	0.05	0.04	0.25	0.15	0.07	0.05	0.28	0.12	0.04	0.03	0.30	0.14	0.05	0.03
27	Sweden (South)	0.26	0.16	0.09	0.13	0.11	0.10	0.07	0.09	0.23	0.07	0.09	0.10	0.20	0.11	0.09	0.11
38	USA (Midwest)	0.27	0.17	0.09	0.09	0.10	0.10	0.09	0.09	0.21	0.17	0.06	0.07	0.18	0.17	0.07	0.08
41	USA (East)	0.26	0.15	0.05	0.03	0.25	0.11	0.11	0.05	0.26	0.15	0.01	0.02	0.35	0.15	0.03	0.02

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706 **Figures**

707 Figure 1. Survival ( $P_x$ , open boxes) and productivity ( $m_x$ , grey boxes) for global fox  
708 populations showing variation and age-specific patterns. Boxes show the sample median,  
709 minimum and maximum. Error bars indicate the lower and upper quartiles. Sample sizes of  
710 the number of studies used to determine rates are: juveniles 0+ ( $P_x$  n=22;  $m_x$  n=9); adults 1+  
711 ( $P_x$  n=22;  $m_x$  n=9); adults 2+ ( $P_x$  n=21;  $m_x$  n=8); adults  $\geq 3$  ( $P_x$  n=20;  $m_x$  n=8).

712

713 Figure 2. The variation in life history metrics and population growth rate between fox  
714 populations, and the relationships between these measures, showing 95% confidence  
715 intervals. (A) Positive correlation between F/ $\alpha$  ratio and population growth rate ( $\lambda$ ); and  
716 negative correlations between (B) generation time ( $T_b$ ) and  $\lambda$ ; (C) F/ $\alpha$  ratio and  $T_b$ .

717

718 Figure 3. Age-specific variance decomposition ratios ( $\chi_{ij}^P / \chi_{ij}^F$ ) and life-stage simulation  
719 analysis ratios ( $r_{P,x} / r_{F,x}$ ) against life history speed metrics, F/ $\alpha$  ratio (A and B), for eight for  
720 populations, showing the change in contributions with the inclusion of uncertainty.

721

722 Figure 4. Effects of substituting matrix elements and fecundity components on the  
723 population growth rate between two urban, and two hunted fox populations, with 95%  
724 confidence intervals. (A) London population substituted with the Bristol population vital  
725 rates; (B) USA (East) population substituted with the USA (Midwest) population vital rates;  
726 (C) Australia (Hunted) population substituted with the USA (Midwest) population vital rates;  
727 (D) Australia (Hunted) population substituted with vital rates averaged from all eight

728 **populations.** NS = no substitution;  $P_x$  = survival;  $F_x$  = fecundity;  $M_x$  = probability of breeding;

729  $B_x$ = litter size.

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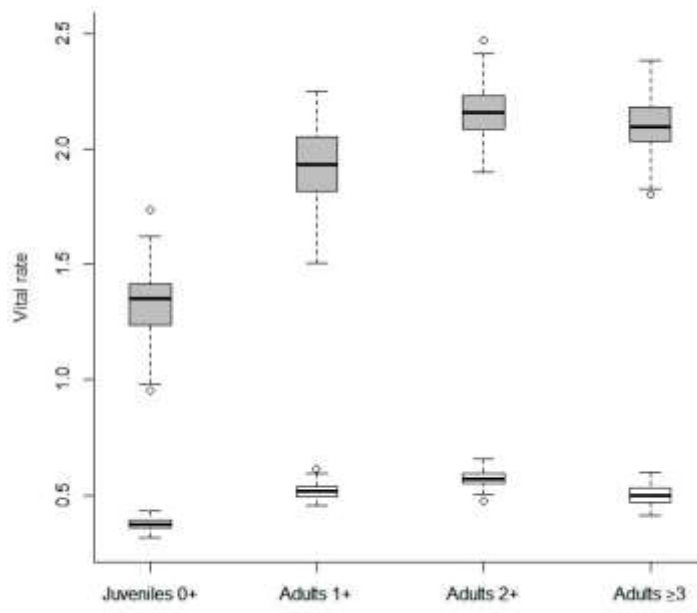


Figure. 1

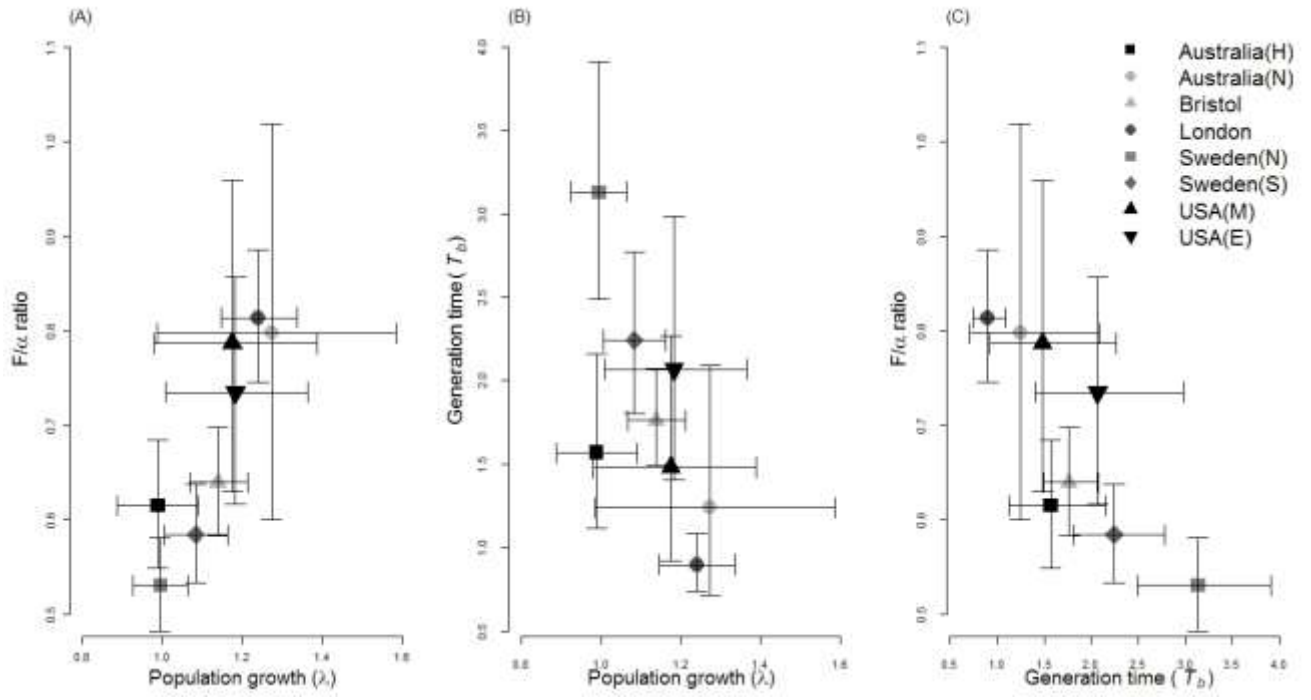


Figure 2

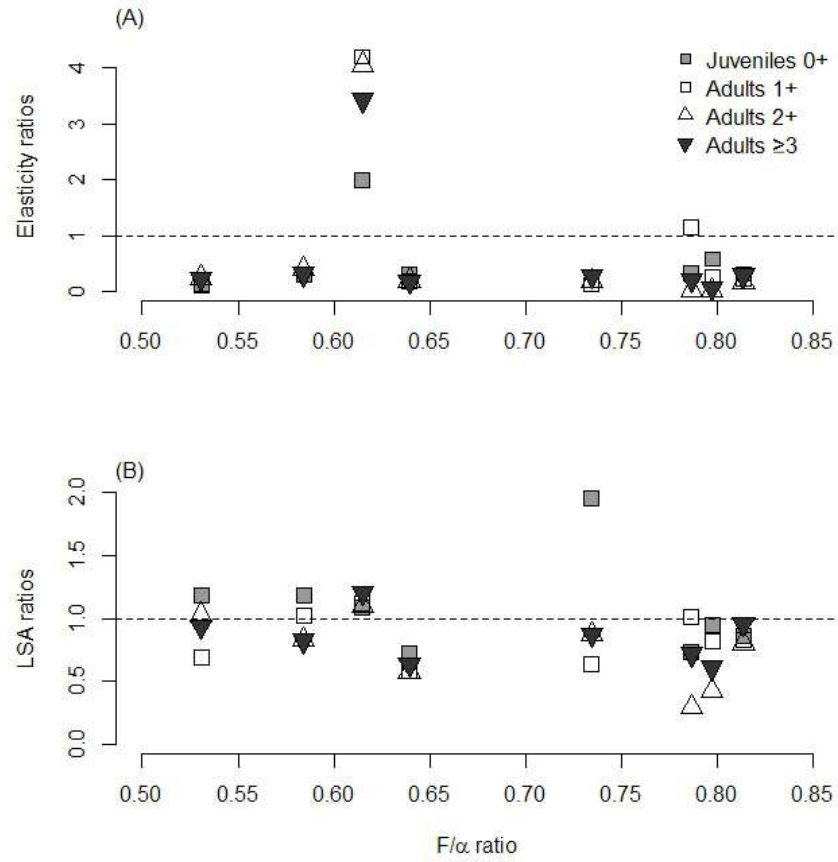


Figure 3.



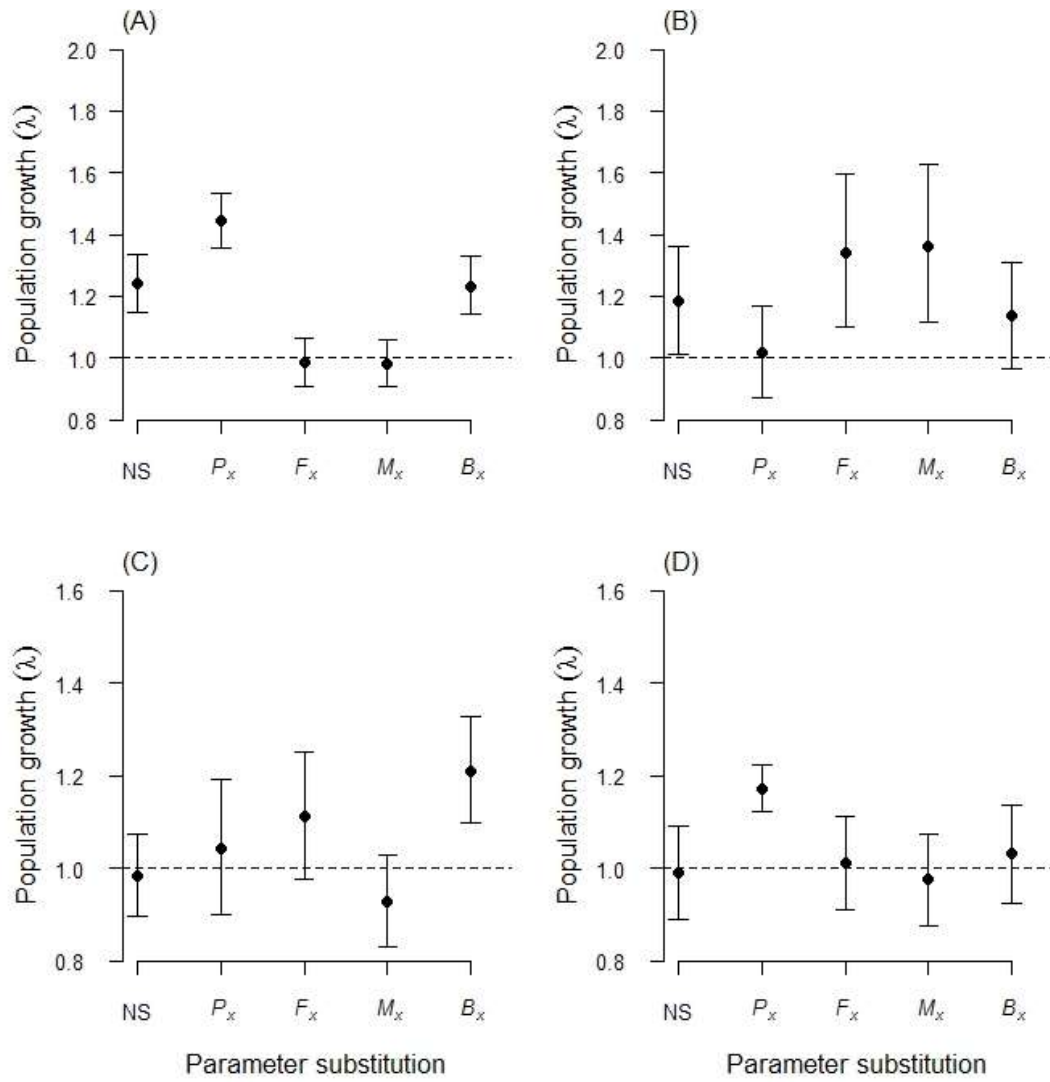


Figure 4.

745 Appendix 1. Selection of populations for demographic analysis

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

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782 Appendix 2. Estimating process error using Kendall's (1998) method: an example using a  
783 Swedish population

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

797

$$798 \quad L_t(\bar{\pi}, \sigma^2(\pi)) = \binom{N_t}{m_t} \frac{B(m_t + a, N_t - m_t + b)}{B(a, b)} \quad (A1)$$

799

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

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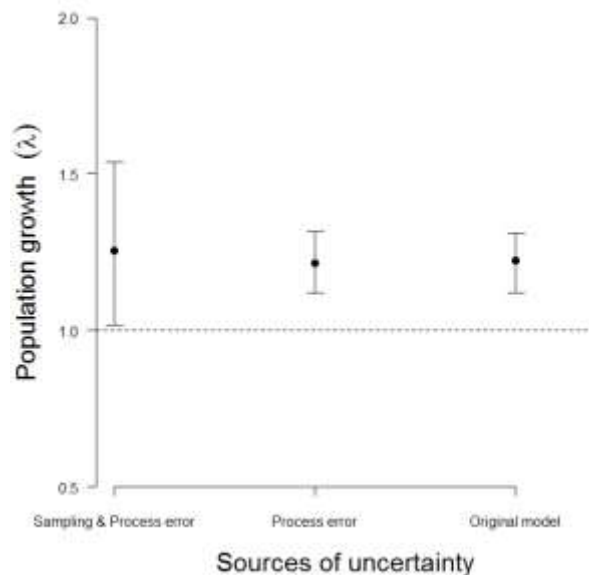
$$804 \quad a = \bar{\pi} \left[ \frac{\bar{\pi}(1 - \bar{\pi})}{\sigma^2(\pi)} - 1 \right] \quad \text{and} \quad b = (1 - \bar{\pi}) \left[ \frac{\bar{\pi}(1 - \bar{\pi})}{\sigma^2(\pi)} - 1 \right]$$

805

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

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

820 There is good agreement between the mean  $\lambda$  estimates for the Sweden (South)  
821 population for all of the three methods used to account for uncertainty in vital rates. As  
822 expected, the uncertainty in  $\lambda$  is largest when both sources of variance are included (Fig. A1).  
823 Process error and sampling error contributed similar uncertainty to our estimates of  $\lambda$ .  
824



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826  
827 Figure A1. Population growth rates for the Sweden (South) population with both process and  
828 sampling variance included, sampling error removed, and the estimate from our original model. Error  
829 bars are 95% confidence intervals determined from the matrix replicates (see Methods).  
830

831           So, how representative of other fox populations is the Sweden (South) population?  
832   The Sweden (South) population most likely falls towards the higher end of the process error  
833   spectrum, coming from an area that is prone to environmental fluctuations, although not as  
834   extreme as experienced farther north in Sweden but there were less data available for this  
835   population. However, it is known to be subject to high inter-annual variation owing to  
836   regulation by prey cycles (Lindström 1989). As many fox populations are likely to experience  
837   less environmental variation, we expect the process variation in these populations to be less  
838   pronounced. However, our results should be interpreted with caution, given that Doak et al.  
839   (2005) suggest that studies of less than five years duration are inadequate to quantify  
840   sources of variation, and that sample sizes for the Sweden (South) population were small in  
841   some years.  
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844 Table A1. Summary of a review of global fox population dynamics ( $\pm$  standard deviations, where provided). Underlined populations were  
 845 selected for demographic analysis.  
 846

Study #	Study population	References	Data type <sup>1</sup>	Total study duration (years)	Max study area (km <sup>2</sup> )	Max sample size (from one study)	Habitat <sup>2</sup>	Sex ratio: all ages*; adults**; juveniles^; embryos^^	Density km <sup>-2</sup> (individual, litter* or group**)	Home range (km <sup>-2</sup> )
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

847 Table A1 contd.

848

Study #	Study population	References	Data type <sup>1</sup>	Total study duration (years)	Max study area (km <sup>2</sup> )	Max sample size (from one study)	Habitat <sup>2</sup>	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	<u>Sweden: South</u>	50, 51	MD, CMR	6	-	799	1,2			
27	<u>Sweden: North</u>	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	67	SS, RT	2	41.44	32				6.993 ± 1.372
38	<u>(Midwest): Wisconsin</u>	68, 69		4	83.73	-		1 : 1.04^	0.09 ± 0.03**	
39	USA: Illinois	70	RT, MD	5	3000	611	1,4			

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Table A1 contd.

Study #	Study population	References	Data type <sup>1</sup>	Total study duration (years)	Max study area (km <sup>2</sup> )	Max sample size (from one study)	Habitat <sup>2</sup>	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

854 <sup>1</sup>Data type: MD: Mortality data; CMR: Capture-mark-recapture; RT: Radiotelemetry; SS: Sign surveys; BE: Behavioural observations; G:  
855 Genetic. – Data not provided

856 <sup>2</sup>Habitat: 1 – Rural agricultural; 2 – Rural non-agricultural 3: Low population density; 4 – High population density



857 References

858

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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 #	Study population	Age definition <sup>1</sup>	Juvenile: adult ratio	Survival (age-specific)	Litter size definition <sup>2</sup>	Breeding probability definition <sup>3</sup>	Litter size <sup>4</sup> (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						

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1036 Table A2 contd.  
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Study #	Study population	Age definition <sup>1</sup>	Juvenile: adult ratio	Survival (age-specific)	Litter size definition <sup>2</sup>	Breeding probability definition <sup>3</sup>	Litter size <sup>4</sup> (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						
				0+ 0.35			4.8 ±					
15	Germany	1	0.66:0.34	1+ 0.34	2	NA	1.1*					
				2+ 0.35			6.8 ±					
				3+ 0.32			0.9***					
				4+ 0.23								
16	Germany	1	0.56:0.44		1	1	4.6*	0+ 4.5^		0+ 24		
								1+ 5.3		1+ 17.9		
								2+ 4.7		2+ 0.0		
								3+ 4.9		3+ 6.8		
17	Italy	1	0.52:0.48		1	2	4.0 ±		20			
							1.3^					
							3.9 ±					
							1.6**					
21	Poland	1	0.54:0.46	0-0.167: 0.69		NA	3.8 (2.7 -					
				0.167-0.5: 0.76	1		4.5)*					
				0.5-1: 0.45			5.5^					
				1+ 0.56								
				2+ 0.428								
				3+ 0.38								
				4+ 0.32								
				0+ 0.34								
				1+ 0.49								
23	Russia	1	0.62:0.38	2+ 0.52	2	NA						
				3+ 0.50								
				4+ 0.60								
24	Spain: Donana	1			1	1	3.1 (2.5-3.6)*		13.2			
							3.3 ±0.7					
							**					
25	Spain:Ebro	2	0.58:0.42	1+ 0.56	1	1	3.6 ±		10.5 ±12.5			
				2+ 0.52			0.4^					
				3+ 0.55								
				4+ 0.64								

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1040 Table A2 contd.  
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Study #	Study population	Age definition <sup>1</sup>	Juvenile: adult ratio	Survival (age-specific)	Litter size definition <sup>2</sup>	Breeding probability definition <sup>3</sup>	Litter size <sup>4</sup> (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			

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1044 Table A2 contd.  
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Study #	Study population	Age definition <sup>1</sup>	Juvenile: adult ratio	Survival (age-specific)	Litter size definition <sup>2</sup>	Breeding probability definition <sup>3</sup>	Litter size <sup>4</sup> (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

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1048 Table A2 contd.  
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Study #	Study population	Age definition <sup>1</sup>	Juvenile: adult ratio	Survival (age-specific)	Litter size definition <sup>2</sup>	Breeding probability definition <sup>3</sup>	Litter size <sup>4</sup> (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		

1050  
1051 <sup>1</sup>Age definition: 1 – Well defined: Clear description of technique, with juveniles clearly defined; 2 – Adequately defined: Technique stated, but juveniles poorly  
1052 defined; 3 – Poorly defined: No definition provided.

1053 <sup>2</sup>Litter size definition: 1 – Well defined: Clear description of technique, e.g. defining grades of placental scars, or live embryos; 2 – Adequately defined: Technique  
1054 stated but lack of detail; 3 – Poorly defined: No definition provided. NA – not applicable for study purpose.

1055 <sup>3</sup>Breeding probability: 1 – Well defined: Clear description of technique, e.g. stating inclusion of post-implantation loss/reabsorptions; 2 – Adequately defined:  
1056 Technique stated but lack of detail; 3 – Poorly defined: No definition provided.

1057 <sup>4</sup>Litter size: ^Placental scars; \*direct counts; \*\* embryos

1058 Table A3. Coefficients of variation for age-specific survival ( $P_x$ ) and fecundity ( $F_x$ ) across matrix replicates for eight fox populations (study  
 1059 number refers to study population in Tables A1 and A2).  
 1060

Study #	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

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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  $\geq 3$  ( $r^2 = 0.64$ ,  $p = 0.01$ ).

