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

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Abstract

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

Introduction

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

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

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

Here, we present a comprehensive review of published studies of red fox demography. With 70 years of published studies, collating these extensive data for the first time provides a unique resource for assessing the worldwide variability in the demography of this common and often intensively-managed species. We use the collated data to construct matrix projection models to determine basic demographic descriptors. Given that the fox is a generalist occurring over a wide range of habitat conditions, harvest levels, and population densities, we predict that life history speeds of distinct populations of this carnivore will be highly variable, with a gradient of fast to slow with increasing latitude (Ferguson and Larivière 2002). We expect that the importance of vital rates with low variation will appear greater when using traditional perturbation analyses than when using LSA, because the latter incorporates observed parameter variability. We also predict that as foxes are highly adaptable, modelled population growth rates will be sensitive to substituting the most variable life history rates between fox populations. We show that data for relatively few fox populations are adequate for detailed demographic analyses. However, those examined suggest important population-level differences in fox life history, with implications for erroneous management prescriptions when using surrogate data.

Methods

Data Collection, Fox Life Cycle, and Matrix Element Calculation

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

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

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

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

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

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

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

$$m_x = M_x B_x SR \tag{3}$$

where M_x is the proportion of pregnant females, B_x is mean litter size and SR is the sex ratio (Caughley 1977, p. 82). Based on empirical evidence (Vos and Wenzel 2001), we assumed a 1:1 birth sex ratio. Females are able to mate when they are about 10 months old and produce one litter per year thereafter (Englund 1970). Consequently, we formulated a post-breeding 'birth-pulse' model (Caswell 2001). We calculated age-specific matrix elements for fecundity:

$$F_x = P_x m_x \tag{4}$$

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

Life-History Speed

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

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

$$F = \frac{\sum_{x=\alpha}^{\omega} w_x F_x}{\sum_{x=\alpha}^{\omega} w_x} \tag{5}$$

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

$$T_b = \sum_x x l_x m_x \lambda^{-x} \tag{6}$$

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

Perturbation Analyses

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

$$e_{ij} = \frac{a_{ij}}{\lambda}\frac{\delta\lambda}{\delta a_{ij}} \tag{7}$$

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

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

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

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

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

Data Substitution

We illustrated the consequence of substituting data between populations from the same country with two urban UK populations (Bristol and London), one subjected to control measures and the other not, and two USA populations (Midwest and East), both subject to hunting. Previously, data have been substituted between populations in Australian and the USA (e.g. Pech, et al. 1997). Consequently, we also examined the consequences of this intercontinental substitution. For each case study, we sequentially replaced matrix components of survival, fecundity, probability of breeding, and litter size from one population to another: we substituted Bristol data for the London population, USA (Midwest population) data for the USA (East) population and USA (Midwest population) data for the hunted Australia (Hunted) population. The last example illustrates an alternative approach for data substitution, by using vital rates averaged from all eight populations to substitute into the Australia (Hunted) population. Using the above methods, we generated 95% confidence intervals for the resultant mean stochastic λ estimates for each simulation. All analyses were conducted using R 2.12.0 (R Development Core Team 2010).

Results

Data review

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

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

Life history speed

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

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

Perturbation analyses

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

Data substitution

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

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

Discussion

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

Inter-population variation in life history speed

The determination of life-history speed along the fast-slow continuum has been much debated (Bielby, et al. 2007, Gaillard, et al. 2005, Oli 2004). Intraspecific studies have used both generation time (Nilsen, et al. 2009) and the F/α ratio (Bieber and Ruf 2005). We found that both metrics correlated with λ, suggesting that as Oli and Dobson found (2005), both are at least partially indicative of a fox population's current trajectory. We illustrate the calculation of confidence intervals for the most commonly used metrics of the fast-slow continuum, and suggest that the use of confidence intervals should be routine before making inferences about the extent to which populations differ in life history speed.

Phylogeny and body mass typically account for much of the variation in life history variables (Gaillard, et al. 2005) and, consequently, within-species variation in demographic tactics is generally expected to be limited. A practical application of defining a population's position on the fast-slow continuum is to provide a measure of the population's response to perturbations and adaptability to the local environment. This 'interpopulation' approach (Nilsen, et al. 2009) merits further attention for comparing population responses to specific pressures and exploring evidence of trade-offs between recruitment and survival. Recent comparisons show that roe deer do not exhibit this trade-off, slowing down their life history in harsher environments because they cannot increase reproduction when faced with increased mortality in adverse conditions (Nilsen, et al. 2009). In wild boar, by contrast, the contribution of life history tactics shifted from juvenile to adult survival as conditions changed from poor to good (Bieber and Ruf 2005). Similarly, Servanty et al. (2011) found that wild boar increased life history speed by increasing fecundity when facing higher hunting pressure. Tasmanian devils *Sarcophilus harrisii* show increased reproduction in young age classes as a response to disease mortality (Jones, et al. 2008). Here, however, our results point towards substantial variation in fox life history speed; although the majority of fox populations that we modelled would be classified as 'fast' by either metric, two of the eight populations (both from Sweden) lay outside that category (one of them substantially). Compared to other hunted fox populations, the Australia (Hunted) population shows surprisingly low λ considering its short generation time. This suggests that is it unable to respond to the hunting pressure by increasing reproduction. However, at the time of data collection the population was experiencing a drought, which had a negative effect on reproduction (McIlroy, et al. 2001), highlighting the conflicting response to anthropogenic versus climate pressures. Conversely, the faster speed of the London population compared to the non-hunted Bristol population suggests a possible compensatory response to hunting, although the lack of additional data on immigration and density hinders assigning causation to this variation. The population with the slowest life history (by both metrics) is the Sweden (North) population, probably reflecting the harsh winter conditions and food limitations that it experiences (Lindström 1989), although fluctuations in this populations' density may violate assumptions of a stable population size. Slower species are expected in habitats with low productivity but high environmental variation (Ferguson and Larivière 2002). In foxes, the relationship between the environment and life history rates is complex: environmental variability is an important determinant of lifetime productivity (Soulsbury, et al. 2008b), and body condition, driven partly by climatic conditions, is an important factor affecting both survival (Gosselink, et al. 2007) and fecundity (Cavallini 1996). Bartoń and Zalewski (2007) found fox density was negatively correlated with an index of seasonality within Eurasia, suggesting that such an index could also be used to explain variation in life history speed between populations. However, using latitude as a proxy for seasonality, we found no correlation. Similarly, previous studies have failed to demonstrate a relationship between litter size and latitude (Lord 1960).

Vital rate contributions and life-history characteristics

That younger age classes are important to growth is unsurprising for a species with a relatively fast life history and is consistent with the observation that juveniles comprise an average of 60 % of fox populations (Lloyd, et al. 1976, Marlow, et al. 2000, Nelson and Chapman 1982). Although juvenile foxes are particularly susceptible to anthropogenic control (Englund 1970, Pils and Martin 1978), heterogeneity in hunting effort generates source populations (Baker and Harris 2006), and together with constant immigration from dispersers (Rushton, et al. 2006), helps to explain why some populations remain stable or grow despite hunting pressure. While compensatory responses in productivity are thought to occur in areas of high hunting pressure (Cavallini 1996, Harris 1977), our results provide little evidence for this for the populations analysed here (see previous section). Thus, as McLeod and Saunders (2001) conclude, targeting the youngest age class is likely to be the most effective form of management when the aim is to decrease the population.

Traits that have a large impact on λ are predicted to be buffered against variation (Pfister 1998), but demographic analyses of mammals are not always consistent with this theory (e.g. Creel, et al. 2004, Henden, et al. 2009). In our analyses, λ was equally sensitive to the contributions of fecundity and survival. Foxes are expected to have higher contributions to λ from fecundity than survival, but we found that fecundity is more variable than survival, possibly because fecundity is influenced more than survival by complex factors, which include food limitation, body mass, and social factors (Cavallini 1996, Iossa, et al. 2008, Lindström 1988). However, when considering demographic contributions in the context of the fast-slow continuum, the equal sensitivity of λ to both rates corresponds to that expected with a medium speed. We also found that the relative contribution of vital rates varied among populations, especially in the youngest age class, which drive growth. Changes in relative elasticities between demographic rates have been demonstrated as a response to environmental conditions (Bieber and Ruf 2005), with potential management implications if demographic traits are to be targeted based on data from fluctuating conditions. Given that variation is an important factor driving population dynamics, it is advantageous to incorporate as high a degree of realism as possible into models (Mills, et al. 1999, Wisdom, et al. 2000). Studies using multiple demographic analyses, such as those in this study, have illustrated how predicted life history contributions can differ with the inclusion of variation (Wisdom, et al. 2000, Johnson, et al. 2010); our results reinforce that conclusion.

Validity of using substitute demographic parameters

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

Data substitution is often inevitable in situations concerning highly endangered, elusive, or data-deficient species, highlighting the need for long-term research. It occurs in many forms, such as using data from species of the same family (Finkelstein, et al. 2010), species sharing similar attributes (Schtickzelle, et al. 2005), or making assumptions about a parameter based on a different (Peck, et al. 2008) or captive (Martinez-Abrain, et al. 2011) population. Githiru et al. (2007) evaluated the applicability of substituting data from a common species for a critically endangered thrush *Turdus helleri*; both species responded to habitat disturbance with higher fluctuating asymmetry and lower effective population density. The sensitivity of λ estimates to surrogate demographic parameters illustrated by our case studies suggests a finer scale approach is required compared to the broad measures of similarity applied in Githiru et al.'s (2007) approach. Based on our results, we agree with Caro et al. (2005) that surrogate data should be used only when similar traits can be identified; following Johnson et al. (2010), we caution against substituting data between demographically distinct populations.

Data quality implications and recommendations

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

The rarity with which quantifiable study attributes such as habitat, environmental, and anthropogenic variables were reported also limits analysis of the impact of these factors on inter-annual variability in population processes. Covariates, such as hunting effort, and those that enable scaling from an urban to rural gradient (e.g. human or road density), are easy to measure and can be important predictors in more powerful models (Mladenoff, et al. 1995). As with other studies (Wisdom, et al. 2000, Rice and Gay 2010, Nilsen, et al. 2011), quantification of inter-annual variation in vital rates is possible for few of the fox populations studied (but see Appendix 2). This is disappointing, given the importance of stochasticity for populations (Melbourne and Hastings 2008) and the advances in demographic modelling for incorporating variation (Kendall 1998, White 2000, Akçakaya 2002, Udevitz and Gogan 2012). In this regard, studies are limited both by their relatively short durations and by their sample sizes. The seasonal variation that exists in trap capture rates between age and sex classes, which also mirrors the susceptibility to culling (Baker, et al. 2001), implies that important classes are underrepresented at key times of years. These differences are due to behavioural changes throughout the year, such as vixens being harder to catch when breeding. We suggest best practice for measuring inter-annual variation in key demographic rates is to sample during the dispersal period (October to December in the northern hemisphere). Samples during this period would show (i) how many cubs survive to independence (the ratio of cubs to adults); (ii) annual proportions of adult vixens that bred from placental scar counts; (iii) mean annual litter sizes (from placental scar counts); (iv) annual variations in both cub and adult sex ratios; and (v) annual variations in adult survival. Whilst such samples may be skewed towards dispersing subadults, particularly males, they are the least biased samples available, and presenting data for this specific period separately would facilitate comparisons between populations. Currently, few studies make it clear how sampling effort varied through the year; biases in sampling effort skews samples towards the age and sex classes that were most vulnerable during the main collection period.

Most available data on red foxes are from mortality studies, which have associated assumptions (for a review see Caughley 1977). Ultimately, however, mortality data such as hunting bag returns will remain an important source of information for fox populations. Four particular issues arise when presenting the data from these studies, all of which should be straightforward to remedy. First, studies differ in their definition of age classes. Factors affecting uncertainty in ageing methods and their minimisation have been discussed extensively elsewhere (Allen 1974, Harris 1978). Whether the first year after birth is described as age class zero, or one, leads to confusion in interpreting published age-specific data, as does dividing the first year into shorter periods, such as pre-and post-weaning, or into 3-month segments, although there are biological and ecological arguments justifying this division (Marlow, et al. 2000). Similarly, the term ‘juvenile’ is not consistently linked to a specific age class; an appropriate definition includes all individuals under the age of one i.e. cubs and subadults (Soulsbury, et al. 2008b). Second, inconsistent determination of fecundity is a major source of confusion surrounding the conversion of vital rates to matrix elements (Noon and Sauer 1992). The interpretation and definition of techniques to determine litter size have been extensively reviewed (Allen 1984, Englund 1970, Harris 1979, Lindström 1981). It is unclear whether guidelines for using placental scars to determine litter size (Englund 1970) are widely followed but explicit reference to these guidelines would promote greater confidence in the data obtained from specific studies. Third, of the components driving reproductive output, the proportion of breeding females varies more widely between populations than litter size (Harris 1979, Zabel and Taggart 1989), often due to complex social factors (Macdonald 1979, Iossa, et al. 2009). The definition of “barren” females is an area of particular uncertainty and great variability. "Barren" can indicate animals that are unable to reproduce, as well as those that are capable of reproducing but fail to do so in a particular year. In addition, reproductive failure could occur at various points: failure to mate; failure to implant fertilised ova; death of the entire litter during pregnancy; and loss of an entire litter immediately following parturition, due to infanticide or other social factors. We recommend that, rather than using the ill-defined term “barren”, future studies define the proportion of females experiencing reproductive failure at any given stage, as has been done for Eurasian badgers *Meles meles* (Cresswell, et al. 1992). Fourth, "hunting" samples vary between countries depending on legal restrictions and local practices. At the moment, for instance, it is unclear how samples taken by driven shoots, night shoots, snaring, leghold traps or digging out of dens differ: data from different collection methods should be presented separately and by time of year to facilitate analyses on the impact of sampling method on demographic parameters. Furthermore, demographic data are often restricted to technical reports (e.g. Whitlock, et al. 2003), representing a substantial source of more directly useable raw data.

Conclusion

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

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

Acknowledgements

We thank Durham University and the Dulverton Trust for financial support. We thank the Durham University Ecology Group for insightful discussion and three anonymous reviewers for their constructive comments.

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

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

[1]Saunders et al 2002; [2] Marlow *et al* 2000; [3]Harris and Smith 1987: [4]Englund 1980; [5]Pils and Martin 1978; [6]Nelson and Chapman 1982. CA: cementum annuli (of molars or canines); TE: tibia epiphysis closure; EW: eye lens weight; SM: skull measurements; Mixed: Combination of shooting, trapping, gassing, baiting and 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 increasing control (1977) and if possible, by information provided by each study on the presence or level of hunting.

Table 2. Summary of mean fecundity rates, F_x, for eight fox populations.

	Australia (hunted)	***Australia (non-hunted)***	***UK (Bristol)***	***UK (London)***	***Sweden (North)***	***Sweden (South)***	***USA (Midwest)***	***USA (East)***
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

[1]Saunders et al 2002; [2]McIlroy et al 2001; [3]Marlow *et al* 2000; [4]Harris and Smith 1987: [5]Harris 1979; [6]Englund 1980, [7]Pils and Martin 1978; [8]Nelson and 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 entire embryos; NVP: no visible signs of pregnancy; PPIL: pre and post implantation loss; - method not given. * see text for explanation. † Placental scar grades refer to the level of fading, with dark scars (5-6) being the most reliable (see Lindström 1981).

Table 3. Age-specific elasticities and coefficients of determination of the LSA for eight fox populations. Elasticities and r^2 are the 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

Figures

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

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

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

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

populations. NS = no substitution; P_x = survival; F_x = fecundity; M_x = probability of breeding; B_x= litter size.

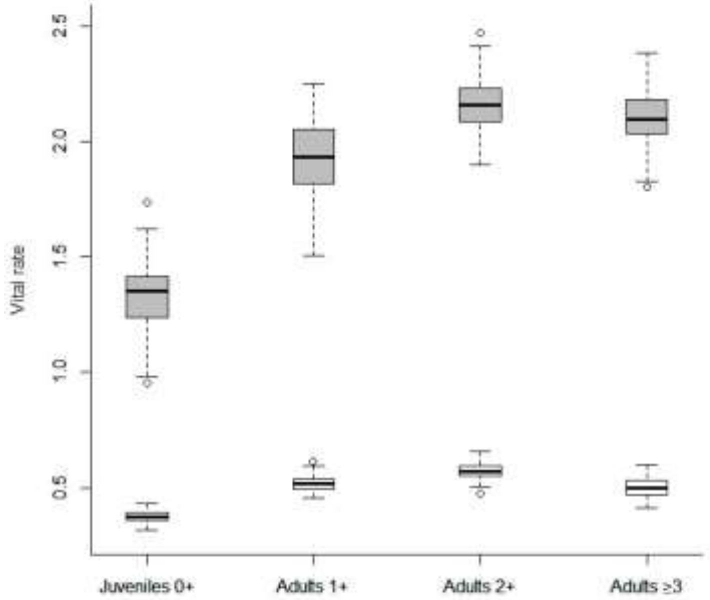
Vital rate
2.5
2.0
1.5
1.0
0.5
Juveniles 0+
Adults 1+
Adults 2+
Adults ≥3

Figure. 1

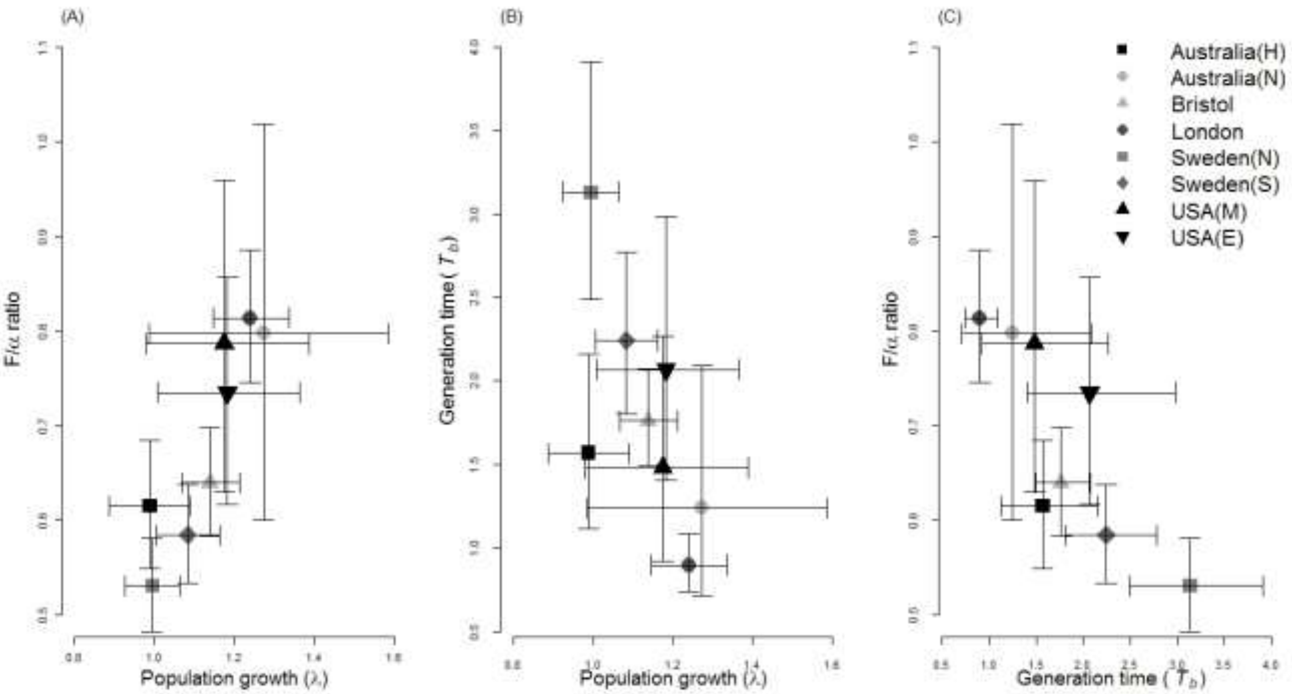
(A)
(B)
(C)
F/α ratio
Generation time (T_b)
Population growth (λ)
Generation time (T_b)
0.5
0.6
0.7
0.8
0.9
1.0
1.1
0.8
1.0
1.2
1.4
1.6
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
■ Australia(H)
● Australia(N)
▲ Bristol
◆ London
■ Sweden(N)
◆ Sweden(S)
▲ USA(M)
▼ USA(E)

Figure 2

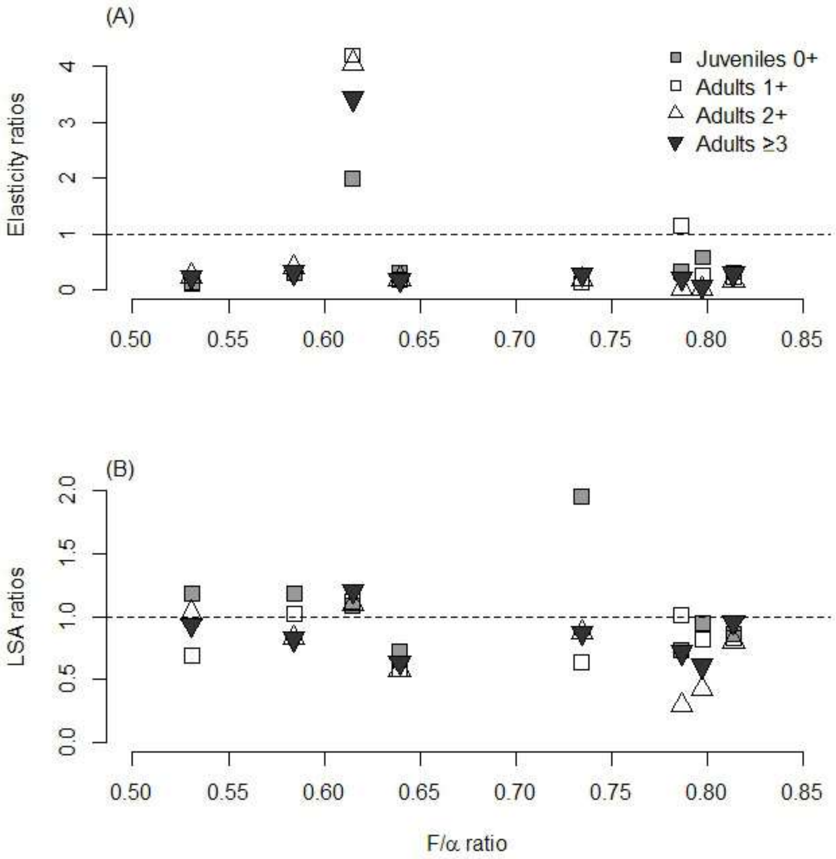
(A)
Elasticity ratios
0
1
2
3
4
Juveniles 0+
Adults 1+
Adults 2+
Adults ≥3
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
(B)
LSA ratios
0.0
0.5
1.0
1.5
2.0
0.50
0.55
0.60
0.65
0.70
0.75
0.80
0.85
F/α ratio

Figure 3.

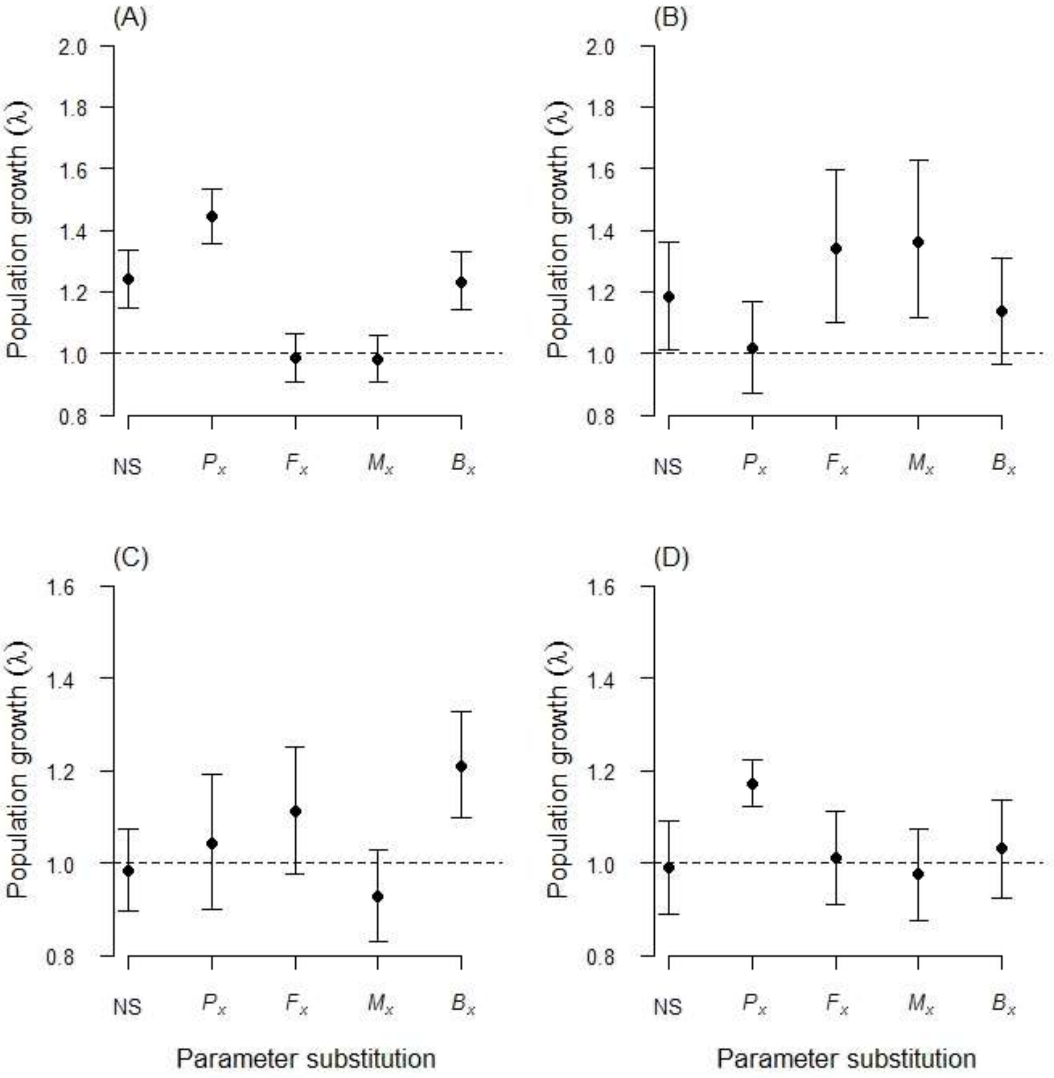
(A)
(B)
(C)
(D)
Population growth (λ)
2.0
1.8
1.6
1.4
1.2
1.0
0.8
NS
P_x
F_x
M_x
B_x
Parameter substitution

Figure 4.

Appendix 1. 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, Englund 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

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

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:

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

The total log-likelihood is the natural logarithm of equation (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 $\overline{\pi}$ 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 & 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.

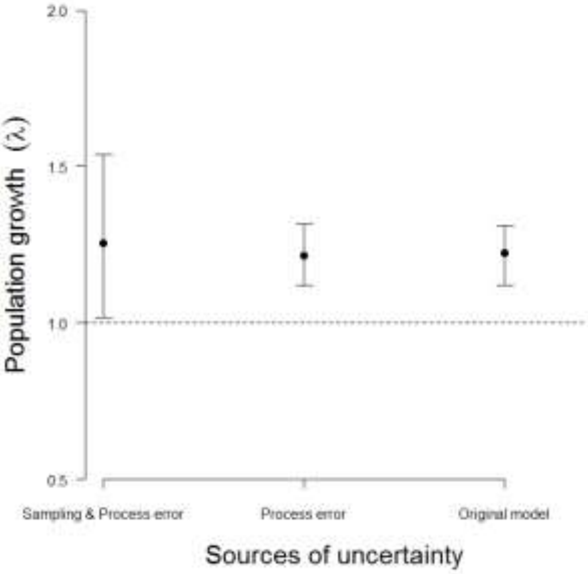

Figure A1. Population growth rates for the Sweden (South) population with both process and sampling variance included, sampling error removed, and the estimate from our original model. Error bars are 95% confidence intervals determined from the matrix replicates (see Methods).

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 (± standard deviations, where provided). Underlined populations were selected for demographic analysis.

Study #	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	**UK: London**	1, 2, 3	MD	6	1618	1141	4	1 : 0.96*		
2	**UK: London**	4	CMR, SS	6	7.6	209	4		2.33 ± 0.39 1.03*	1.65
3	**UK: Bristol**	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± 8.34 1.82*	0.51 ± 0.48
4	**UK: Oxford**	13, 14, 15, 16	RT	10	9.17	>120	3,4		2.15 2.5**	0.92 ± 0.66
5	**UK: Wales**	17, 18	CMR,	6	580	476	1,2	1:82**	1.85 ± 1.27 0.90 ± 0.57*	2.35 ± 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 ± 0.97
8	**UK**	21, 22	MD	3	2322	656	1,2	1 : 1**	0.94 ± 0.85	
9	**UK: Scotland**	23, 24	MD	23	48760	4765	1,2		1.09 ± 0.67	
10	**Ireland**	25, 26	CMR	2	-	292				
11	**Belarus**	27	SS	3	300	-	2		0.92 ± 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 ± 0.75
14	**France**	33		-	-	-				
15	**Germany**	34	MD, BE	15	130	955	2	1.5: 1**	0.73 ± 0.25 0.55 ± 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 ± 1.28
18	**Netherlands**	39	RT	5	-	150	2		0.55*	3.48 ± 3.77
19	**Netherlands**	40, 41	RT	6	300	311	2			
20	**Norway**	42	SS	3	18	2	2			5.47 ± 0.46

Table A1 contd.

Study #	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**	67	SS, RT	2	41.44	32				6.993 ± 1.372
38	**USA (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 #	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	**USA (East): Maryland**	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	**Australia (Hunted): NSW**	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	**Australia (Non-hunted): Western**	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

[1] Data type: MD: Mortality data; CMR: Capture-mark-recapture; RT: Radiotelemetry; SS: Sign surveys; BE: Behavioural observations; G: Genetic. – Data not provided

[2] Habitat: 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 #	**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	**UK: London**	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	**UK: Bristol**	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 #	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	1	NA	3.8 (2.7 - 4.5)* 5.5^					
23	**Russia**	1	0.62:0.38	0+ 0.34 1+ 0.49 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 #	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	**Sweden(South)**	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	**Sweden(North)**	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 #	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 #	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	**Australia (Hunted): NSW**	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	**Australia (Non-hunted): Western**	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		

[1] Age 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.

[2] Litter 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.

[3] Breeding 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.

[4] Litter 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 Tables A1 and A2).

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

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).