Environmental variation at the onset of independent foraging affects full-grown body mass in the red fox

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The period following the withdrawal of parental care has been highlighted as a key developmental period for juveniles. One reason for this is that juveniles cannot forage as competently as adults, potentially placing them at greater risk from environmentally-induced changes in food availability. However, no study has examined this topic. Using a long-term dataset on red foxes (*Vulpes vulpes*), we examined (i) dietary changes that occurred in the one-month period following the attainment of nutritional independence, (ii) diet composition in relation to climatic variation, and (iii) the effect of climatic variation on subsequent full-grown mass. Diet at nutritional independence contained increased quantities of easy-to-catch food items (earthworms and insects) when compared with pre-independence. Interannual variation in the volume of rainfall at nutritional independence was positively correlated to the proportion of earthworms in cub diet. Pre-independence cub mass and rainfall immediately following nutritional independence explained a significant proportion of variance in full-grown mass, with environmental variation affecting full-grown mass of the entire cohorts. Thus, weather-mediated availability of easy-to-catch food items at a key developmental stage has lifelong implications for the development of juvenile foxes by affecting full-grown mass, which in turn appears to be an important component of individual reproductive potential.

Keywords: climate variation; growth rate; invertebrates; *Lumbricus terrestris*; nutritional independence; phenotype

1. INTRODUCTION

Post-natal growth rates in mammals are influenced by, e.g. intra-litter processes, such as nutritional status and hormonal condition of the mother (Everitt 1968), milk quality (Kunz & Stern 1995), litter size (Bassett 1984), parasite burden (Stebbins 1968; Newman *et al.* 2001), and environmental processes that affect the availability of key food resources, such as variation in climate and temperature. Nutritional stress arising from changes in food availability can lead to reduced adult body size (Searcy *et al.* 2004), diminished survival (de Kogel 1997), slower brain development (Nowicki *et al.* 2002), prolonged immaturity and reduced secondary sexual characters (Ohlsson *et al.* 2002). In turn, these can affect individual reproductive potential by virtue of their effect on dominance rank, fecundity and offspring size (Brown & Brown 1998; Metcalfe & Monaghan 2001; Ohlsson & Smith 2001). Understanding how processes affect juvenile growth rates and, ultimately, full-grown body mass is, therefore, fundamental to understanding life-history variation.

Parental care has evolved, in part, to reduce the impact of environmental variation on offspring growth and survival (e.g. Adams *et al.* 1994; Rauter *et al.* 2000). However, the period following the withdrawal of parental

provisioning can be a key limiting stage in offspring development (Hauser 1994; Nislow & King 2006); juvenile animals often lack the appropriate knowledge and motor skills to locate and acquire foods as competently as adults (Sullivan 1988; Weathers & Sullivan 1989; Egorova & Petrov 1998), and poorly developed foraging skills can cause significant juvenile mortality (Daunt *et al.* 2007). One mechanism by which newly independent foragers may alleviate this potential problem is by focusing on more easily acquired food types while they hone the skills necessary to catch more difficult prey; such dietary shifts may also help reduce competition with adult conspecifics.

Red foxes (*Vulpes vulpes* L.) provision cubs from approximately one to three months of age, after which the cubs commence independent foraging (Baker *et al.* 1998). While being provisioned at the breeding den, their diet contains a greater proportion of larger prey items (Lindström 1994; Lovari & Parigi 1995), presumably because these are more favourable parcels for parents to deliver during the period of central place foraging. By contrast, there are few data on the diet of cubs after they begin to forage independently (but see Harris 1981). However, this is likely to be a difficult period for juveniles, since they have reduced access to the resources on their natal territory because their ranging behaviour during this transitional period is still focused around the immediate vicinity of den sites (Robertson *et al.* 2000). Furthermore, success rates of adults and older juveniles hunting common food sources are generally low (23% and 2% for

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mammalian and avian prey, respectively; Henry 1986), requiring well-coordinated capture techniques, e.g. small rodents are located by auditory cues and caught by a leap into the air with the forefeet landing precisely on the prey (Fox 1969; Henry 1986). Newly independent juveniles would, therefore, be expected to have even lower capture rates.

By contrast, earthworms (*Lumbricus terrestris*) and insects are relatively easily caught (Henry 1986), although earthworm availability at the soil surface at night is closely correlated with rainfall (Macdonald 1980; Askeew & Yalden 1985; Gruar *et al.* 2003). Consequently, spatial and temporal variations in environmental conditions during the transitional period following the attainment of nutritional independence could significantly affect the foraging success of newly independent juveniles. One corollary of this would be that interannual changes in prevailing weather patterns during the transitional period may significantly affect the patterns of juvenile growth, and that these changes may be carried through to adult body mass, which in turn could influence the individual's reproductive potential. Furthermore, such effects could be experienced by whole cohorts as well as specific individuals.

In this study, we identified those food types that increased in the diet of juvenile red foxes in Bristol, UK, as they attained nutritional independence and investigated whether these dietary components varied with prevailing weather conditions. We then examined how mean full-grown mass and skeletal measurements of cohorts of foxes were related to interannual variations in rainfall and diet. Finally, we examined the interrelationship between pre-nutritional independence body mass and rainfall as explanatory variables of full-grown body mass.

2. MATERIAL AND METHODS

(a) Study site and capture methodology

The study site initially (1978–1989) comprised the entire city of Bristol, UK (144 km²). To allow more intensive study of individual social groups, it was reduced to an area of approximately 1.5 km² in the northwest suburbs (pre-mange period: 1990–1994) before being expanded to approximately 15 km² during (epizootic period: 1994–1995) and following (enzootic/post-mange period: 1996–2004) an outbreak of sarcoptic mange *Sarcoptes scabiei* (Baker *et al.* 2000; Soulsbury *et al.* 2007a). The most important foraging habitat for urban foxes both pre- and post-mange was back gardens (Newman *et al.* 2003); during the course of this study, back gardens have shown a relatively small loss of area (e.g. 0.3%; Pauleit *et al.* 2005) and little conversion of 'conventional' gardens (*sensu* Hessayon & Hessayon 1973) to other habitats such as boarded decking, i.e. terraces made from wooden boards (4.9%; Smith *et al.* 2005). Thus, although the study encompasses 26 years, there has been no substantial change in the key foraging habitat for foxes in Bristol. Data on resource abundance throughout this period are absent, but proportions of key food items such as scavenged meat have remained consistent, suggesting little change in resource usage (Ansell 2004).

Foxes were captured by netting from den sites or in baited box traps placed in residential gardens (Baker *et al.* 2001a). All individuals were sexed, weighed, aged from tooth wear (Harris 1978) and ear tagged (Rototags, Dalton Supplies Ltd, Nettlebed, Henley-on-Thames, Oxfordshire, UK). The

foxes were classified as cubs (less than six months), subadults (6–12 months) or adults (more than 12 months; Harris & Trehwella 1988); cubs and subadults are referred to collectively as juveniles. The majority of females have given birth by the end of March, so date of birth of all animals was assumed to be 1 April (Harris & Smith 1987). Date of birth is related to photoperiod, not temperature, so is unlikely to vary interannually (Lloyd & Englund 1973); additionally, observations in Bristol also indicate no interannual variation in litter emergence.

(b) Diet composition during the transition to independent foraging

Stomach content data from 355 cub cadavers collected during May–September 1978–1989 were examined to determine whether diet composition changed during the transitional phase from provisioned to independent foraging. In Bristol, behavioural data show that adults stop provisioning cubs at the end of June (Baker *et al.* 1998); the transitional period following the cessation of parental provisioning was, therefore, taken to be the month of July. The mortality categories of cubs examined for stomach contents were: road traffic accidents (80.3%); control, i.e. dug out or snared (7.3%); fights with dogs, foxes or other animals (7.3%); illness (2.8%: excludes mange); misadventure, e.g. trapped by neck in fence (1.7%); and unknown (0.6%). Given these causes, the majority of individuals died in obvious locations and were recovered dead on the day they died.

Six food categories were recognized: earthworms (based on the volume of chaetae and earthworm fragments; see Harris 1981); insects and other invertebrates (hereafter 'insects'); wild and domestic birds; wild and domestic mammals; scavenged meat, including bone fragments; and scavenged bread. The last two categories originate primarily from householders specifically provisioning foxes or other animals, e.g. hedgehogs (*Erinaceus europaeus*) and badgers (*Meles meles*; see Baker *et al.* 2000), but may also have been obtained by scavenging on human refuse. The volume of each item in the stomach was scored from 0 (no item) to 5 (full stomach). The volume scores for each food type between the five months were compared using Kruskal–Wallis tests with *post hoc* comparisons calculated manually where appropriate (Siegel & Castellan 1988). The relative biomass (B) of each of the six food groups in the diet in a given year was calculated as: $B = (vd / \sum vd) \times 100$, where v is the mean stomach volume for a given food group in that year and d is the corresponding density of that food group (earthworms, 1.13 g ml⁻¹; insects, 0.43 g ml⁻¹; birds, 0.72 g ml⁻¹; mammals, 0.86 g ml⁻¹; scavenged meat, 1.04 g ml⁻¹; scavenged bread, 0.57 g ml⁻¹; after Ansell 2004).

During 1988–1991, kidney fat reserves of necropsied fox cubs were scored on a scale of 0 (no fat) to 5 (kidney completely covered in fat); kidney fat indices show a good correlation with total body fat and, hence, overall nutritional condition (Winstanley *et al.* 1998). Differences in kidney fat scores between months during May–September were analysed using a Kruskal–Wallis test.

(c) Environmental correlates of diet composition

The impact of environmental factors on cub diet composition was examined using Spearman rank order correlations to compare the stomach volume scores of each of the four most common items (earthworms, insects, scavenged meat and scavenged bread) of cubs recovered dead in July 1978–1989

versus (i) mean daily temperature and (ii) total monthly rainfall in July. As the availability of earthworms and insects in July may have been dependent on environmental conditions in the preceding months, we also examined the relationship between the volume scores of earthworms and insects in the stomachs of cubs during July and mean daily temperature and total monthly rainfall in June. Rainfall and temperature data were taken from three long-term weather stations located within the city of Bristol (www.bristolweather.org.uk).

In addition, we compared the volume of earthworms in cub stomachs with the number of 'worm nights'. Earthworm emergence on the soil surface depends on both temperature and moisture (Edwards & Lofty 1972). Worm nights are defined as those where temperature is higher than 0°C and rainfall in the preceding 72 hours is greater than 2 mm (Kruuk & Parish 1981). Minimum daily temperatures in July exceeded 10°C in all years, so rainfall was the primary driver of interannual variation in the number of worm nights. As rainfall in June would affect worm nights at the beginning of July, daily rainfall data from 28 June to 31 July were used to examine the relationship between the volume of earthworms in cub stomachs and total rainfall in the 72 hours prior to death using a Spearman rank order correlation. The mortality of cubs examined for stomach contents during July was road traffic casualties (91.3%), fights with dogs, foxes or other animals (5.0%), control (2.5%) and unknown (1.2%).

(d) *Environmental correlates of full-grown mass*

Red foxes attain full-grown mass during their first year of life. Since we were not able to recapture each cub every month to measure its exact rate of growth, the pattern of juvenile growth was estimated from the mean monthly body mass for all juveniles from the 1992 and 1993 cohorts captured each month from May (after first emergence) to March (attainment of adult age); these cohorts were selected because they comprised the most complete data on a subset of known individuals (males: 109 individuals, 177 captures; females: 73 individuals, 129 captures). Both years were climatically similar. The corresponding growth 'curve' was then used to identify the month (October: see §3) during which full-grown mass appeared to be attained. This was then tested by comparing the mass of individual male and female foxes that had been captured as a subadult in October and as an adult in April–May the following year using a Wilcoxon signed-rank test; pregnant females and individuals infected with sarcoptic mange were excluded. These analyses showed that mass at capture during October–March could be used as a reliable proxy for adult, i.e. full-grown mass for both males and females. After identifying the period in which individuals were still growing, we used recapture data to examine sex differences in growth rates. Daily growth rates (mass capture A – mass capture B/days between captures) were compared between males and females using an independent sample *t*-test.

Interannual changes in full-grown mass of males and females in relation to total July rainfall were quantified using linear regression. Data on full-grown mass were obtained from animals captured and those recovered dead within the city throughout 1978–2004. Since sarcoptic mange causes mass loss, muscle catabolism and eventually death (Newman *et al.* 2002), any animals caught from 1994 onwards with signs of mange infection were excluded from the analyses. Years where eight or fewer full-grown individuals of a given

sex were captured or recovered dead were excluded from the analysis for that sex. Eight individuals was seen as the minimum number required to reflect an adequate sample of the year's cohort; excluded years were predominantly post-sarcoptic mange outbreak (males, 7/7, females, 6/7), when only one to three animals not infected with mange were caught each year due to low population density and very low levels of productivity (Baker *et al.* 2001b). Excluded years post-sarcoptic mange outbreak did not have significantly lower July rainfall (Mann–Whitney *U*-test: males, $W=35.0$, $p=0.219$; females, $W=28.0$, $p=0.171$) nor was the number of individuals caught related to July rainfall in that year (Spearman rank order correlation: males, $r_s=0.166$, $p=0.627$; females, $r_s=0.330$, $p=0.322$). Thus, the excluded years did not differ in environmental conditions and would not affect the results. Nor was juvenile susceptibility to sarcoptic mange infection and mortality related to climate. Mange occurred in those litters where an adult in the group was infected, and then 93% of infected cubs died irrespective of year or climatic conditions (C. D. Soulsbury, G. Iossa, P. J. Baker and S. Harris 2008, unpublished data).

As the sarcoptic mange outbreak altered population density (Soulsbury *et al.* 2007a), we examined the effect of changes in density using a general linear model (GLM) in the statistical software R v. 2.5.1 (<http://www.R-project.org>), with full-grown mass (dependent variable), period (factor: pre-mange, post-mange), rainfall (independent variable) and their interaction as variables. We also examined whether full-grown body mass correlated with (i) total rainfall and average daily temperature in each month from May to September inclusive and (ii) the number of worm nights (see above). Data for males and females were analysed separately using Spearman rank order correlations.

Increased food availability may increase body mass by virtue of increasing physical, i.e. skeletal size and/or the extent of fat reserves. Since body mass is a relatively crude measure of body size, we further compared the lower jaw length (mm) of subadult cadavers with total July rainfall using a Spearman rank order correlation. Lower jaw length correlates significantly with body size (Harris & Trehwella 1988). Subadult foxes were examined during 1978–1989.

(e) *Environmental correlates of cub mortality*

The majority of cub mortality during July was through road traffic accidents (91%). However, any nutritionally limiting period may affect cub survival in the immediate or longer term. Therefore, we investigated whether there was a correlation between total July rainfall and the percentage of cubs that had been tagged before July that were subsequently recovered dead during (i) July, (ii) August–September, and (iii) post-July as a juvenile or adult. Data were analysed using Spearman rank order correlations.

(f) *Intra-litter variables, environmental variation and full-grown mass*

In addition to environmental variation, a range of other factors may also have affected patterns of growth and adult body mass, including, among others, sex, litter size, maternal condition, mass at birth, parental care, individual parasite load and social group size. Since obtaining such detailed information on large numbers of free-ranging individuals is problematic, we investigated the potential influence of some of these factors on growth and full-grown mass in two separate stages.

First, a generalized linear mixed-effects model (GLMM) with Gaussian error structure using the GLMMPQL procedure (MASS package) in R was used to examine the effects of maternal mass (independent variable), litter size (independent variable) and sex (factor) on the mass of cubs prior to the attainment of nutritional independence (dependent variable) using a subset of animals from the 2002 to 2004 cohorts where maternity had been assigned genetically (Soulsbury *et al.* 2007b; Iossa *et al.* in press). Since cub mass will tend to increase during the pre-nutritional independence phase, cub mass was controlled for age at first capture (cub mass/days since 1 April) prior to insertion in the model; vixen was included as a random factor in the model. We did not have data on individual parasite load.

Second, a general linear model (GLM run in R) was used to examine the effects of cub mass prior to the attainment of nutritional independence (independent variable), sex (factor) and total July rainfall (independent variable) on full-grown mass for those animals captured both during the pre-nutritional independence phase (i.e. aged less than three months, capture April–June) and when full-grown (i.e. aged six months or more; dependent variable). Again, cub mass was controlled for age at first capture (cub mass/days since 1 April) prior to insertion in the model. As there is the potential for animals of, e.g. different mass and sex to respond differently to changes in food availability, all first-order interaction terms were included in the initial model; non-significant terms were then removed sequentially in a backward stepwise manner. To illustrate the effect of total July rainfall in the year of birth on full-grown mass, the residuals from a multiple linear regression of full-grown mass against cub mass and age were plotted against total July rainfall. Residuals were calculated separately for males and females.

Except where stated otherwise, all data were analysed using MINITAB v. 14.0 (Minitab Inc.) or SPSS 12.0 (SPSS Inc.). Where appropriate, data were checked to confirm that they adhered to the underlying assumptions of the statistical tests used.

3. RESULTS

(a) Diet composition during the transition to independent foraging

There were no significant differences between months in the volume scores of mammalian prey (mean $\pm$ s.e. volume score = 0.35 ± 0.05 ; Kruskal–Wallis test, $H_4 = 1.89$, $p = 0.76$), scavenged meat (1.72 ± 0.08 ; $H_4 = 1.59$, $p = 0.81$) or scavenged bread (0.94 ± 0.07 ; $H_4 = 4.00$, $p = 0.41$) in the stomachs of cubs recovered dead ($n = 355$ in all cases). By contrast, the volume scores of earthworms ($H_4 = 20.27$, $p < 0.001$) and insects ($H_4 = 46.84$, $p < 0.001$) increased significantly in the diet of cubs after the attainment of nutritional independence, whereas the volume scores of avian prey ($H_4 = 47.10$, $p < 0.001$) declined significantly (figure 1). Kidney fat reserves varied significantly between months ($H_4 = 13.40$, $p = 0.009$, $n = 106$), being the lowest in July (*post hoc* analysis: May (mean $\pm$ s.e. fat score = 2.83 ± 0.24) $\geq$ August (2.09 ± 0.19) = June (2.31 ± 0.20) = September (2.09 ± 0.11) > July (1.82 ± 0.15)).

(b) Environmental correlates of diet composition

Mean ($\pm$ s.e.) stomach volume scores for each of the four most important items in the diet of fox cubs in July

Figure 1. Relative importance of earthworms, insects and avian prey in the diet of fox cubs during May–September. Figures are mean ($\pm$ s.e.) volume of prey in the stomach. Letters denote *post hoc* groupings. Sample sizes were: May, $n = 58$; June, $n = 80$; July, $n = 82$; August, $n = 82$; and September, $n = 53$.

($n = 81$) during 1978–1989 were: earthworms, 0.99 ± 0.16 (present in 41% of stomachs); insects, 1.43 ± 0.15 (78%); scavenged meat, 1.76 ± 0.17 (70%); and scavenged bread, 0.83 ± 0.15 (35%). There was a significant positive correlation between total July rainfall each year and stomach volume scores for earthworms (Spearman rank order correlation: $r_s = 0.31$, $n = 81$, $p = 0.01$) but not for insects ($r_s = -0.20$, $n = 81$, $p = 0.08$), scavenged meat ($r_s = 0.02$, $n = 81$, $p = 0.85$) or scavenged bread ($r_s = 0.03$, $n = 81$, $p = 0.82$). Mean daily July temperature was not significantly correlated with the volume scores for any diet component: earthworms, $r_s = -0.21$, $n = 81$, $p = 0.06$; insects, $r_s = 0.18$, $n = 81$, $p = 0.10$; scavenged meat, $r_s = -0.08$, $n = 81$, $p = 0.50$; scavenged bread, $r_s = 0.01$, $n = 81$, $p = 0.91$. Nor was there any significant correlation between total June rainfall or mean daily June temperature and earthworm (rainfall, $r_s = -0.07$, $n = 81$, $p = 0.52$; temperature, $r_s = -0.02$, $n = 81$, $p = 0.83$) or insect (rainfall, $r_s = -0.05$, $n = 81$, $p = 0.65$; temperature, $r_s = -0.01$, $n = 81$, $p = 0.95$) stomach volume scores in July. At a finer scale, there was a significant positive correlation between total rainfall in the 72 hours preceding death and the volume of earthworms in cubs' stomachs during July ($r_s = 0.28$, $n = 81$, $p = 0.011$). Thus, the prevalence of earthworms, but not insects, in the diet of cubs in July was influenced by prevailing environmental conditions in that month. In the 2 years of the lowest total July rainfall (both 22 mm), earthworms comprised 12.5% the diet by mass whereas scavenged meat, the major dietary component, comprised 39.3%. Conversely, in the year of the highest total July rainfall (109 mm), earthworms and scavenged meat constituted 34.4% and 41.1% of the diet by mass, respectively.

(c) Environmental correlates of full-grown mass

Juveniles reached asymptotic mass in October in the year of their birth (figure 2). Subadult mass in October was not significantly different from adult mass the following spring (April–May) for either males (Wilcoxon signed-rank test: $z = -0.07$, $n = 9$, $p = 0.94$) or females ($z = -0.51$, $n = 8$, $p = 0.61$). Males ($n = 21$; 30.19 ± 1.52 g d $^{-1}$) grew significantly faster than females ($n = 15$; 24.46 ± 2.20 g d $^{-1}$; independent sample t -test: $t_{26} = -2.14$, $p = 0.042$).

Figure 2. Mean ($\pm$ s.e.) monthly male and female body mass during their first year (males (circles): $n=109$ individuals, 177 captures; females (triangles): $n=73$ individuals, 129 captures).

Figure 3. Mean interannual male ($n=11$ years; circles) and female ($n=11$ years; triangles) full-grown body mass in relation to total rainfall during July. Regression lines (solid line) through all data points and 95% CIs are shown.

Full-grown body mass was significantly positively correlated with interannual variation in total July rainfall for both males (linear regression: $R^2=0.10$, $F_{1,229}=26.28$, $p<0.001$; $n=231$ individuals, $n>8$ for 11 years during 1987–2004) and females ($R^2=0.08$, $F_{1,109}=9.01$, $p=0.003$; $n=111$ individuals, $n>8$ for 11 years; figure 3). Variance in full-grown body mass between years was not significantly different for males (Levene statistic=1.15, $p=0.327$) or females (Levene statistic=0.90, $p=0.529$), indicating that variation in body mass for either sex did not increase or decrease significantly between years. Mean full-grown mass from the year with the highest July rainfall was 12% (males) and 11% (females) greater than the mean full-grown mass from the year with the lowest July rainfall. There was no effect of period (males: $t=-0.310$, $p=0.757$; females: $t=-1.083$, $p=0.281$) or its interaction with rainfall (males: $t=0.087$, $p=0.931$; females: $t=1.241$, $p=0.217$) on the observed patterns, with rainfall being the only significant parameter in both models (males: $t=4.262$, $p<0.001$, $F_{3,227}=8.368$, $p<0.001$; females: $t=2.438$, $p=0.016$, $F_{3,117}=5.334$, $p=0.001$). Additionally, the lack of any interaction between rainfall and period indicates that there was no temporal change in this pattern. Interannual variation in total rainfall or mean temperature in any month

other than July did not correlate significantly with the full-grown mass of males or females (table 1). However, there was a significant relationship between the full-grown mass of males ($r_s=0.310$, $n=231$, $p<0.001$) and females ($r_s=0.244$, $n=111$, $p=0.013$) and the number of worm nights in July. Total July rainfall was significantly correlated with lower jaw length in subadult males ($n=225$, $r_s=0.158$, $p=0.018$) but not females ($n=111$, $r_s=0.184$, $p=0.053$), although the latter result approached significance.

(d) Environmental correlates of cub mortality

There was no significant correlation between total July rainfall and the percentage of cubs recovered dead during July (Spearman rank order correlation: $r_s=0.375$, $p=0.207$), August–September ($r_s=-0.299$, $p=0.384$) or post-July as juveniles or adults ($r_s=-0.001$, $p=0.996$).

(e) Intra-litter variables, environmental variation and full-grown mass

Juvenile mass prior to the attainment of nutritional independence ($n=31$ cubs, 12 litters) was significantly associated with sex, but not maternal mass or litter size (table 2). Full-grown mass was significantly associated with sex, mass prior to the attainment of nutritional independence and total July rainfall in the year of birth (GLM: $n=16$ males, 9 years, $n=14$ females, 7 years, $F_{3,26}=21.29$, $R^2=0.71$, $p<0.001$); no first-order interaction terms were significant (table 3). Controlling for cub mass and age at first capture, full-grown body mass was significantly affected by July rainfall (figure 4a,b).

4. DISCUSSION

Factors impacting growth and subsequent adult body size are diverse and, in carnivores, can include litter size (Hofer & East 2008), parasite loads (Newman *et al.* 2001) and seasonal food abundance (Hofer & East 1993). Environmental variation has also been shown to have a significant impact on growth and body size in a range of taxa, mediated by variation in food abundance and availability (bats: Tuttle 1976, Hoying & Kunz 1998; carnivores: Russell *et al.* 2002; insectivorous birds: Emlen *et al.* 1991, McCarty & Winkler 1999; ungulates: Post *et al.* 1999, Knott *et al.* 2005). In our study, the full-grown mass of foxes was dependent on pre-nutritional independence cub mass and sex, but appeared to be affected to a greater degree by environmentally induced variation in the abundance of an important food resource, earthworms, during the transition to independent foraging. To the best of our knowledge, such a profound impact during this period has not been shown previously in mammals.

The increased reliance on earthworms in the month immediately following the withdrawal of parental provisioning observed in this study does not appear to be attributable to an increase in their abundance. In fact, earthworm availability is the lowest during summer (June–August; see Ansell 2004) and this is reflected in a decline in the proportion of earthworms in the diet of adult foxes (less than 10% in July; Harris 1981). Instead, the increased reliance on earthworms and insects by newly independent juvenile foxes was most likely due to differences in the relative catchability of invertebrate versus vertebrate prey (Henry 1986). For example, the

Table 1. Spearman's rank correlation coefficients for tests comparing total monthly rainfall and mean daily temperature against full-grown mass of male ($n=231$) and female ($n=111$) foxes. There is a significant negative collinearity between total July rainfall and mean daily July temperature ($r_s = -0.45$, $p < 0.01$), and mean daily August temperature ($r_s = -0.34$, $p = 0.05$), explaining the negative relationship between subadult male body mass and these variables.

		May	June	July	August	September
males	rainfall	$r_s = 0.07$, $p = 0.32$	$r_s = -0.06$, $p = 0.33$	$r_s = 0.33$, $p < 0.01$	$r_s = 0.08$, $p = 0.23$	$r_s = 0.11$, $p = 0.12$
	temperature	$r_s = 0.03$, $p = 0.61$	$r_s = 0.09$, $p = 0.16$	$r_s = -0.22$, $p < 0.01$	$r_s = -0.13$, $p = 0.05$	$r_s = -0.05$, $p = 0.48$
females	rainfall	$r_s = 0.06$, $p = 0.54$	$r_s = -0.10$, $p = 0.29$	$r_s = 0.28$, $p < 0.01$	$r_s = 0.02$, $p = 0.82$	$r_s = 0.02$, $p = 0.86$
	temperature	$r_s = 0.13$, $p = 0.19$	$r_s = 0.15$, $p = 0.14$	$r_s = -0.14$, $p = 0.17$	$r_s = -0.10$, $p = 0.33$	$r_s = 0.05$, $p = 0.60$

Table 2. Results of GLMMs model examining factors potentially affecting body mass prior to the age of nutritional independence.

factor	coefficients	t	p
sex	-0.003	3.59	0.002
maternal mass	0.0002	0.08	0.935
litter size	0.0091	-1.37	0.190

Table 3. Results of GLM examining factors potentially affecting full-grown mass for those animals captured as a cub aged less than three months and after the attainment of full-grown mass (six months or more).

factor	coefficients	t	p
cub mass at first capture	27.09	3.82	< 0.001
sex	0.70	2.32	0.028
total July rainfall	0.01	4.25	< 0.001

capture of small rodents and avian prey requires sophisticated foraging techniques.

By contrast, earthworms are easily caught at the soil surface but are only readily available following periods of rainfall (Edwards & Lofty 1972; Macdonald 1980; Askew & Yalden 1985; Gruar *et al.* 2003). Consequently, the proportion of earthworms in the diet of fox cubs following the attainment of nutritional independence was significantly positively correlated with interannual variation in the volume of rain falling during July. For example, earthworms constituted 12.5% and 39.3% of cub diet by volume in the driest and wettest summers, respectively. Conversely, other food items remained consistent in their importance, independent of variation in climatic conditions: scavenged meat, the most important food item, comprised 34.4% and 41.1% during these years, respectively.

The decline in kidney fat reserves in July indicates that this is a period of nutritional stress for cubs and/or a key period when resources are allocated to growth. Consequently, variation in July rainfall was also correlated with the subsequent full-grown mass of cohorts of cubs: cubs born in years with low July rainfall would tend to become small adults relative to those born in years with high July rainfall. Starvation, however, was never recorded as a source of mortality in this population, unless the animal was also either injured or diseased (Soulsbury *et al.* 2007a). Furthermore, our data indicated no apparent difference in mortality associated with wet or dry years. Thus, in this population, rainfall during the transitional period following the cessation of

Figure 4. Residual full-grown mass of individual (a) males and (b) females in relation to total July rainfall. Regression lines (solid line) through all data points are shown.

parental care appeared to modify cub diet and full-grown mass but did not influence demographic processes, in contrast to patterns observed in, e.g. badgers (Macdonald & Newman 2002).

Full-grown mass was, however, also influenced by sex, with the growth rates of males and females diverging early in their development, and the mass of the individual prior to the attainment of nutritional independence. The latter result indicates, therefore, that larger cubs within a cohort of cubs tended to become larger adults, but that they may be small or large relative to adults from other cohorts due to the influence of July rainfall. Conversely, litter size and maternal mass did not significantly affect pre-nutritional independence cub mass. We were not able to examine the effects of a range of other factors (e.g. parasite load, local resource use, local habitat quality, competitive interactions) that may also have influenced individual growth rates both pre- or post-independent foraging. However, July rainfall is demonstrably important in determining full-grown mass and has a significant impact across cohorts.

In conclusion, it is clear that environmental conditions at the attainment of nutritional independence were an

important factor influencing the development of juvenile foxes. Specifically, the results of this study are consistent with the hypothesis that climatic variation at the onset of nutritional independence significantly affected the availability of easy-to-catch prey items, which, in turn, affected the growth and the subsequent full-grown size and mass of individual foxes. This effect was not due to habitat changes, since the key foraging habitat for foxes, back gardens (Saunders *et al.* 1997; Newman *et al.* 2003), has shown little pattern of change in cover or usage (Pauleit *et al.* 2005; Smith *et al.* 2005).

Male mass exhibited a stronger relationship with July rainfall than female mass, and since body mass positively influences the reproductive success of male foxes in this population (Iossa *et al.* in press), life-history tactics of individual males may be significantly influenced by climatic variation during early stages of their development. Consequently, further studies on the impact of the development of foraging skills and the availability of different food sources on individual growth and subsequent reproductive potential in other species are warranted.

All capture and handling procedures were conducted in accordance with UK legislative requirements and with the approval of the ethical review board of the University of Bristol.

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