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Diet and bite force in red foxes: ontogenetic and sex differences in an invasive carnivore

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Abstract

Bite force is often used as a predictive indicator of an animal's feeding ecology, although the premise that there is a direct link between diet and cranial morphology can be difficult to test empirically. Studies that have examined this question tend to rely on generalizations of a species' diet, and age and sex differences are rarely considered. Red foxes (*Vulpes vulpes*) are introduced predators in Australia, allowing large sample size collection through culling for comparison of skull morphology (size, morphometry, weight), demographics (age, sex) and diet (stomach contents). Over half (57%) of the 540 animals we sampled were juveniles (<1 year old; dispersing from their natal sites) and most variation in skull morphometry was driven by age; adults had significantly more robust skulls than juveniles, with greater estimated bite force. Sexual dimorphism (body mass and body length) was reflected in longer, heavier skulls of males. We also recorded significant sex and age differences in diet. Sheep carrion comprised 47–65% of diet volume; however, adult females ate less sheep but had more mice and invertebrates in their diet than males or juveniles of both sexes. This dietary separation for adult females does not appear to be directly due to estimated bite force constraints, but probably rather prey availability, which may reflect feeding behaviour and space use patterns. Juveniles (both sexes) showed as much consumption of sheep carrion as adult males, despite their lower estimated bite force than adults. This is the first study that directly compares ontogenetic and sex differences in the diet of a carnivore together with their cranial morphology and estimated bite force, and highlights limitations of inferring diet partitioning from skull morphology alone.

Introduction

Because carnivorans rely heavily on their head and jaws for prey acquisition and ingestion of food, skull morphology and bite force can reflect diet specialization and competition (Radinsky, 1981; Carbone, Teacher & Rowcliffe, 2007; Van Valkenburgh, 2007). Bite force is often used as a predictive indicator of an animal's feeding ecology (Therrien, 2005; Christiansen & Wroe, 2007), although the premise that there is a direct link between diet and cranial morphology can be difficult to test empirically. Bite force is often estimated from dry skulls using lever models (Kiltie, 1984; Thomason, 1991), without data on the diet of the same animals. Studies that have examined this question therefore tend to rely on generalizations of a species' diet, while age and sex differences are rarely considered (e.g. Christiansen, 2008; Damasceno, Hingst-Zaher & Astua, 2013).

Canids that take larger prey items tend to have shorter and broader, more powerful jaws and specialized carnassial dentition (Slater, Dumont & Van Valkenburgh, 2009), for example, the culpeo (*Lycalopex culpaeus*), a large (~ 10 kg) South American canid (Segura, 2013). Short, thin jaws, such as in grey foxes (*Urocyon cinereoargenteus*) reflect a higher reliance on omnivory (Jaslow, 1987). Despite being the largest *Vulpes* species (Macdonald & Reynolds, 2004), red foxes (*Vulpes vulpes*) typically take small prey items and their skulls are characterized by relatively elongate jaws and generalist dentition, with fast-closing jaw muscles ideal for smaller prey (Goswami, 2006; Slater *et al.*, 2009).

Skull morphology changes with age, and these changes can influence accessibility of particular food items (e.g. Binder & Valkenburgh, 2000; Giannini *et al.*, 2010). It is therefore predicted that young animals can be handicapped with respect to the breadth of diet they can take compared with skeletally mature adults if they lack the mechanical strength required to deal with particular diets. For example, in spotted hyenas (*Crocuta crocuta*), younger animals lack the robust skull that would generate the bite force required to access food associated with heavy bones; mandibular maturity precedes maturation of cranial shape, with shape changes continuing beyond the stage of reproductive maturity, reflecting the mechanical demands of bone-cracking (Tanner *et al.*, 2010; La Croix *et al.*, 2011). Similarly, high mechanic strength of the mandible is achieved early in ontogeny in puma (*Felis concolor*) (Giannini *et al.*, 2010).

Sex differences in skull morphology can also influence diet partitioning. Sex differences in skull shape have been noted for a number of carnivorans (e.g. Loy, Spinosi & Carlini, 2004; Thom, Harrington & Macdonald, 2004; Jones & Goswami, 2010; Christiansen & Harris, 2012). Although sexual dimorphism is not as pronounced in canids as in other carnivorans (Gittleman & Van Valkenburgh, 1997), some trophic separation and concomitant morphological differences between the sexes may still occur (Prestrud & Nilssen, 1995; Travaini *et al.*, 2000).

Identifying the age and sex of animals as part of diet and cranial morphology analyses is therefore important for understanding the mechanistic constraints of bite force upon diet selection. However, such analyses require large sample sizes of fresh material, where diet can be analysed for the same individuals as skulls are collected. The red fox (*Vulpes vulpes*) inhabits the most expansive global range of any wild carnivore (Macdonald, 1987; Voigt, 1987). Red foxes were introduced into Australia from Europe during the second half of the 19th century (Saunders *et al.*, 1995), and are a threat to persistence of native species (e.g. Dawson *et al.*, 2017) and livestock (e.g. Fleming *et al.*, 2016) (reviewed by Saunders, Gentle & Dickman, 2010; Woinarski, Burbidge & Harrison, 2014). Their success as an invasive species reflects their highly adaptable and unspecialized ecology, with few specific habitat requirements (Saunders *et al.*, 1995; Bateman & Fleming, 2012), and their diverse opportunistic, generalist diet (Harris, 1981; Reynolds & Tapper, 1995). These animals are therefore controlled in Australia, with the potential for culling programmes to collect large numbers of animals over a short period of time.

In this study, we compare skull morphology and diet (stomach contents) of red foxes from Australian populations to investigate whether there is evidence of diet segregation by age or sex in this species, and whether diet is reflected in estimated bite force and ontogenetic changes in skull morphometry. Because carrion would require more mechanical processing compared with smaller diet items that can be swallowed whole, we predicted that cohorts of animals with a large proportion of sheep meat in their diet would also have greater estimated bite force compared with those feeding on invertebrates, fruit, grain, or even small mammals (e.g. mice) that can be swallowed whole.

Materials and methods

Life-history details for foxes

The red fox is monoestrus, vixens coming on heat only once during the breeding season and then for only 2–3 days (Saunders *et al.*, 1995). In Australia, most cubs are therefore born in August and September (Saunders *et al.*, 1995). Cubs are suckled until 4 weeks, then progressively weaned onto solids and both sexes become sexually mature from 10 months of age (Saunders *et al.*, 1995). The majority of dispersal occurs in sub-adult foxes, particularly males, commencing in late summer and continuing through to the onset of breeding in winter (Saunders *et al.*, 1995). During dispersal, they would face intraspecific competition for access to resources, including food. At the time we sampled (February and March 2010), foxes in their first year were therefore aged between 6 and 8 months, those in their second year between 18 and 20 months, etc. For the purposes of this study, these age cohorts are described as 1 year olds (1yo), 2 year olds (2yo) etc.

Skulls and stomachs were collected from 540 culled animals collected from 13 geographic locations across south-west Western Australia during February and March 2010 (See Fig. S1). The cull was carried out by regional natural resource management groups as part of the coordinated ‘Red Card for Rabbits and Foxes programme (RCRF 2016). Other data collected from each animal included geographic location, sex, body mass, and three measurements of body size: head length (from the tip of the nose to the atlanto-occipital joint), head-body length (tip of the nose to the base of the tail) and hind pes length. Stomachs were removed and stored frozen (−18°C) for later analysis, when they were thawed before dissection. Heads were removed from carcasses and soft tissue was removed from skulls by maceration at 30–40°C.

We have different numbers of individuals for each set of data due to collection issues: although we sampled and measured 540 individuals, we collected skulls and aged 476 but only 318 skulls were intact, and we collected stomachs that had sufficient contents to examine diet in 473 individuals.

Skull morphometry

Skull mass (SM) was obtained using digital scales. Fourteen two-dimensional craniodental measurements were made (Table S1) on 318 intact skulls (capital letters in Fig. 1). In total, 12 variables were included in analyses: skull measures were standardized for skull size by expressing each as a proportion of skull length (SL), while jaw height and width were used to calculate jaw cross-sectional area. Measurements were carried out by one person (JFH) to avoid inter-observer error. Mean coefficient of variation in three repeated measures of 10 skulls was found to be minimal (<2% measurement error) for all variables.

Estimated bite force – lever model calculations

Bite force was estimated using the dry skull method (Thomason, 1991; Damasceno *et al.*, 2013). This method has been used by many authors previously, enabling direct comparison between studies. Estimates derived from this approach show strong correlation with *in vivo* bite force (e.g. Thomason, 1991 for opossums), and are more repeatable than measurements that would rely on fresh muscle weights measured under field conditions. Digital photographs of each skull were made in dorsal, ventral and lateral views and measurements (lower case letters in Fig. 1) were made using ImageJ software following Damasceno *et al.* (2013): ventral skull length (sl), skull height (h),

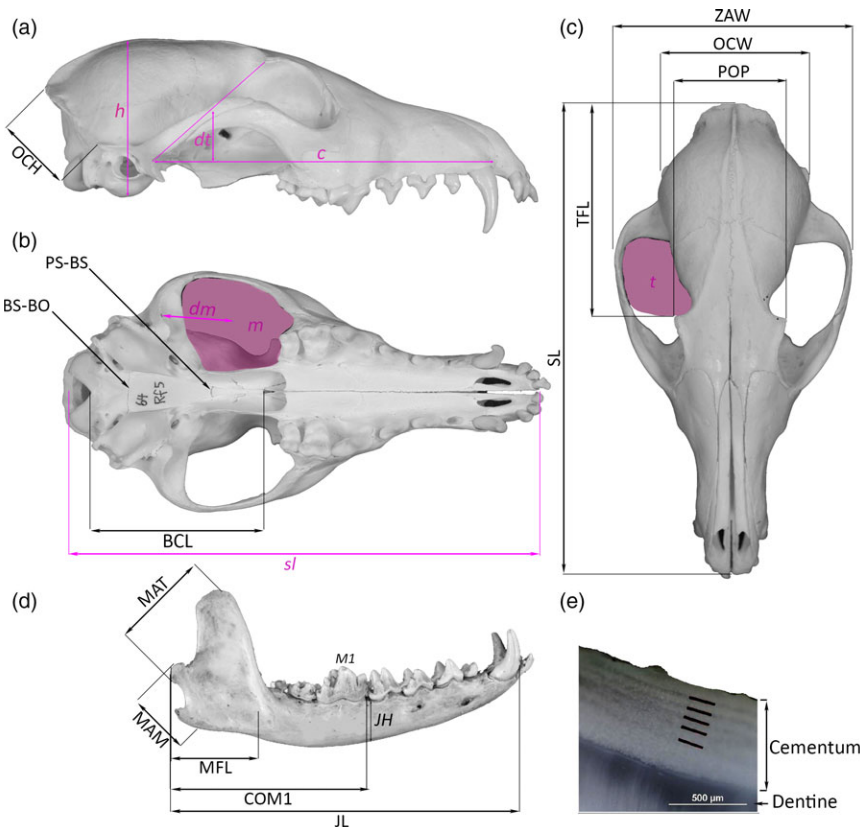

Figure 1 Measurements and landmarks on the skull of *Vulpes vulpes* used in this study. (a) Lateral, (b) ventral, (c) dorsal views of cranium; (d) lateral view of mandible and (e) lamination of canine cementum used for ageing adults. BCL, basicranial length; BS-BO, basisphenoid-basioccipital suture; COM1, jaw condyle to anterior border of first mandibular molar (M_1); JH, mandibular (jaw) height; JL, mandibular (jaw) length; MAM, moment arm of the m. masseter; MAT, moment arm of the m. temporalis; MFL, masseteric fossa length; OCH, occipital height; OCW, occipital width; POP, postorbital process width; PS-BS, presphenoid–basisphenoid suture; SL, skull length; TFL, temporal fossa length; ZAW, zygomatic arch width. Measurements used to calculate bite force indicated in pink (after Damasceno *et al.*, 2013): *c,* distance between bite force (canine) and TMJ; dm, distance between the centroid of *m* and the TMJ; dt, vertical distance between the centroid of t and height of the TMJ; *h*, cranial height; sl, ventral skull length; *m,* cross-sectional area of the m. masseter/m. pterygoideus; *t*, cross-sectional area of the m. temporalis.

distance between the canine and TMJ (c), distance between the centroid of the masseter (dm) and the temporomandibular joint (TMJ) and the distance between the centroid of the temporalis and TMJ (dt); cross-sectional areas of the m. masseter/m. pterygoideus (m) and m. temporalis (t).

All measurements were made in mm and estimated bite force (Newtons; N) given in N using the formula below. The estimated force of the two muscle groups are summed and then divided by the distance from TMJ to the canines (the estimated bite force output for our animals), which corresponds to the moment or out-lever arm (c). These values were multiplied by 2 to estimate the 'absolute' bite force (F; N) generated by muscle group on both sides of the skull:

$$F(\mathrm{N}) = 2 \times \frac{(\mathrm{dm} \times m \times \sigma) + (\mathrm{dt} \times t \times \sigma)}{c}$$

where σ is the isometric muscle stress value of 0.3 $\mathrm{N/mm^2}$ (Sakamoto, Lloyd & Benton, 2010). As the dry skull method has been shown to underestimate bite force, this absolute value was corrected (F_{corr}) (Sakamoto *et al.*, 2010):

$$F_{\mathrm{corr}} = 10^{(0.859 \times \log F + 0.559)}$$

Because skull size influences bite force, we standardized for skull size. Ventral skull length (sl) was a better predictor ($r^2 = 0.609$) of F_{corr} than was carcass mass ($r^2 = 0.584$). We therefore calculated residuals (F_{corr} as a proportion of the predicted force for a skull of the same length) that represent the SL-standardized bite force quotient (BFQ) for each skull:

$$\mathrm{BFQ} = \frac{F_{\mathrm{corr}}}{F_{\mathrm{predicted}}}$$

Ageing foxes

Animals less than 2 years old were aged via cranial sutures (Harris, 1978); foxes in their first year were determined by the presence of an open basisphenoid-basioccipital suture; foxes in their second year were indicated by the presence of a closed basisphenoid-basioccipital suture in conjunction with an open presphenoid-basisphenoid suture (Fig. 1b). Foxes older than 2 years were aged by microscopic analysis of the canine tooth dentine lamina (Fig. 1e) (Roulichova & Andera, 2007).

Statistical analyses

We tested for age and sex differences in body mass using multiple regression analysis. We calculated a body condition score (BCS) as the residual of intact body mass against head-body length (which showed a stronger correlation with body mass $r^2 = 0.56$ $P < 0.001$ than either head length: $r^2 = 0.26$ $P < 0.001$, or pes length: $r^2 = 0.28$ $P < 0.001$). We calculated BCS for males and females separately, since they showed significantly different slopes ($F_{1,534} = 5.44$, $P = 0.020$) (statistiXL 1.11; http://www.statistixl.com). We tested for age and sex differences in BCS using multiple regression analysis.

For 318 skulls with complete datasets, we carried out a Principal Components Analysis (PCA) (Statistica 8.0 StatSoft Inc., Tulsa, OK, USA) using a varimax normalized rotation to reduce the number of skull measures. Three PC dimensions had an Eigenvalue >1 ('Kaiser criterion' Kaiser, 1960) and were therefore considered biologically relevant. Type III SS mixed-model analyses were carried out comparing the independent variables of age (covariate), sex (fixed) and geographic location (random), with each of the three PC factors, bite force estimate (F_{corr}) and the bite force quotient (BFQ) as dependent variables. We tested the relationship between the PC factors and BFQ by regression analysis.

Diet analyses

For 473 foxes, stomach contents were emptied into two 20 cm-diameter graduated sieves (2-mm and 1-mm sieve intervals) and gently rinsed with running water. Individual food items were separated into broad categories (Table 2) and the percentage volume of each food category estimated. Fur and bones were oven dried (40 °C for 24–48 h) and contents unsuitable for drying were stored in 70% ethanol for later identification. Large body parts/whole animals were identified from field guides, and hair samples were identified using whole-mount techniques (Brunner & Triggs, 2002). Plant material was classified as either 'deliberately ingested' (green grass, figs, grapes, mulberries, corn, grains) or 'incidentally ingested' (dead grass, leaves, twigs, bark; these items were generally in low proportion and their identity suggested that they were probably partly present on/in other food items).

The age and sex differences in diet were expressed as diet overlap using Pianka's Measure of Overlap and Percentage Overlap measure (Krebs, 2002). The differences were visualized using non-metric multidimensional scaling analysis (N-M MDS) of the proportions of each food item (arcsine-square root transformed proportions of the total stomach contents) using PAST (Hammer, Harper & Ryan, 2001) and statistically tested using two-way PERMANOVA for sex (male and female) and age (two age categories: 1 and 2+ years old) cohorts. Similarity Percentage (SIMPER) analysis was carried out to determine the food categories that contributed to significant diet differences. The food items with the strongest correlation with each N-M MDS dimension axis were calculated by Spearman Rank Order Correlation analysis.

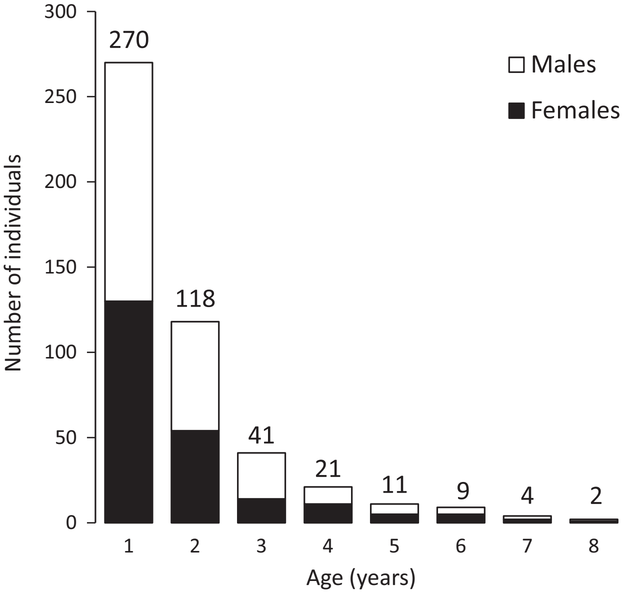

Figure 2 The number of foxes sampled in each age cohort.

General

Data are presented as means ± 1 SD and a statistical level of $\alpha \leq 0.05$ was used throughout.

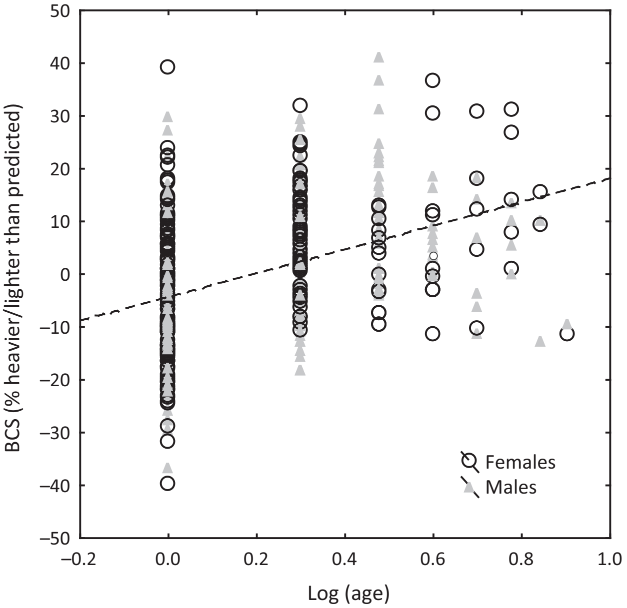

Figure 3 Body condition scores for foxes compared with their age.

Table 1 Summary of the PCA describing fox skull shape (each measure standardized by skull length, SL; Table S1)

Skull dimension	Description	PC1		PC2		PC3	
Jaw length	${}^{\mathrm{JL}}/_{\mathrm{SL}}$	**0.66**		−0.36		−0.33	
Jaw condyle to M_1	${}^{\mathrm{COM1}}/_{\mathrm{SL}}$	**0.61**		−0.30		−0.36	
Masseteric fossa length	${}^{\mathrm{MFL}}/_{\mathrm{SL}}$	**0.61**		−0.41		−0.11	
Moment arm of masseter	${}^{\mathrm{MAM}}/_{\mathrm{SL}}$	**0.69**		−0.13		−0.22	
Basicranial length	${}^{\mathrm{BCL}}/_{\mathrm{SL}}$	0.37		0.13		−0.40	
Moment arm of temporalis	${}^{\mathrm{MAT}}/_{\mathrm{SL}}$	0.57		0.03		−0.07	
Occipital width	${}^{\mathrm{OCW}}/_{\mathrm{SL}}$	0.03		**0.75**		−0.42	
Occipital height	${}^{\mathrm{OCH}}/_{\mathrm{SL}}$	0.17		**0.70**		−0.31	
Skull mass	${}^{\mathrm{cubrt\text{-}SM}}/_{\mathrm{SL}}$	**0.80**		0.18		0.36	
Zygomatic arch width	${}^{\mathrm{ZAW}}/_{\mathrm{SL}}$	**0.78**		0.27		0.30	
Temporal fossa length	${}^{\mathrm{TFL}}/_{\mathrm{SL}}$	0.44		0.16		**0.60**	
Jaw cross-sectional area	${}^{\mathrm{sqrt\text{-}JXA}}/_{\mathrm{SL}}$	0.58		0.22		0.22	
PCA results							
Eigenvalue		3.94		1.66		1.37	
% Total variation		32.85		13.80		11.38	
Correlation with Bite Force Quotient (BFQ)		**r^2 = 0.441, P < 0.001**		**r^2 = 0.017, P = 0.018**		**r^2 = 0.017, P = 0.019**	
Mixed-model regression for PC factors		*F*	*P*-level	*F*	*P*-level	*F*	*P*-level
Log(age)		**219.54**	**<0.001**	2.59	0.109	**46.95**	**<0.001**
Sex		2.41	0.148	**21.09**	**0.001**	**9.84**	**0.008**
Geographic area		2.99	0.084	1.02	0.487	3.14	0.075
Geographic area × sex		0.92	0.494	0.78	0.608	0.62	0.737
Mixed-model regression for Estimated bite force (Log F_{corr}; N)							
Log(age)		**248.16**	**<0.001**				
Sex		**53.20**	**<0.001**				
Geographic area		2.32	0.143				
Geographic area × sex		1.50	0.166				
Mixed-model regression for Bite Force Quotient							
Log(age)		**80.93**	**<0.001**				
Sex		1.61	0.222				
Geographic area		**9.09**	**0.004**				
Geographic area × sex		0.42	0.892				

Factor loadings greater than 75% of the largest loading (bold) were considered to contribute significantly to the PC (Mardia, Kent & Bibby, 1979). Bottom rows summarize mixed-model analyses of the three PC factors, estimated bite force and bite force quotient, with significant effects shown in bold.

Results

Body condition

The 540 foxes sampled weighed 5.3 ± 1.1 kg. No significant sex bias was present within the sample (males 52%, females 48%), but males (5.8 ± 1.1, range 2.1–8.9 kg, $n = 290$) were heavier than females (4.8 ± 0.8, range 2.9–7.4 kg, $n = 250$) ($t_{469} = 12.61$, $P < 0.001$) and older animals were heavier than younger animals (Log_{10}(age): $t_{469} = 14.42$, $P < 0.001$). Of 476 foxes aged, over half (57%) were in their first year, and 25% were in their second year. The remaining 18% ranged in age from 3 to 8 years (Fig. 2). Adults (2+ years old) were relatively heavier than 1-year-old animals in terms of the body condition score (BCS), that is, compared with their head-body length (Log_{10}(age): $t_{470} = 8.41$, $P < 0.001$), but there was no sex difference in body condition score (sex: $t_{470} = 1.46$, $P = 0.144$) (Fig. 3).

Skull morphology

Three PC axes together described 58.0% of the variation within the dataset (Table 1). PC1 (32.9% of the variation within the dataset) was positively correlated with six variables: jaw length, jaw condyle to M1 length, masseteric fossa length, moment arm of masseter, skull mass and zygomatic arch width. Foxes with higher PC1 scores have relatively larger jaw dimensions. PC2 (13.8% of variation) was positively correlated with two variables: occipital width and height. Foxes with high PC2 scores therefore had proportionally larger occipital areas relative to the overall size of the skull. PC3 (11.4% of variation) was positively correlated with temporal fossa length. Foxes with high PC3 scores had a longer temporal fossa, part of which is likely to be due to an increased sagittal crest height, and therefore more extensive attachment for the temporalis muscles on the skull.

There was a sex effect on PC2 and PC3; males had proportionally longer skulls relative to their occipital areas (PC2: $P = 0.001$) and a longer temporal fossa (PC3: $P = 0.008$) compared with females. There was a significant effect of age on PC1 and PC3; older animals had relatively larger jaws (PC1: $P < 0.001$) and relatively longer temporal fossae (PC3: $P < 0.001$). There was no significant effect of geographic location on any of the PC factors ($P > 0.05$ for each; Table 1).

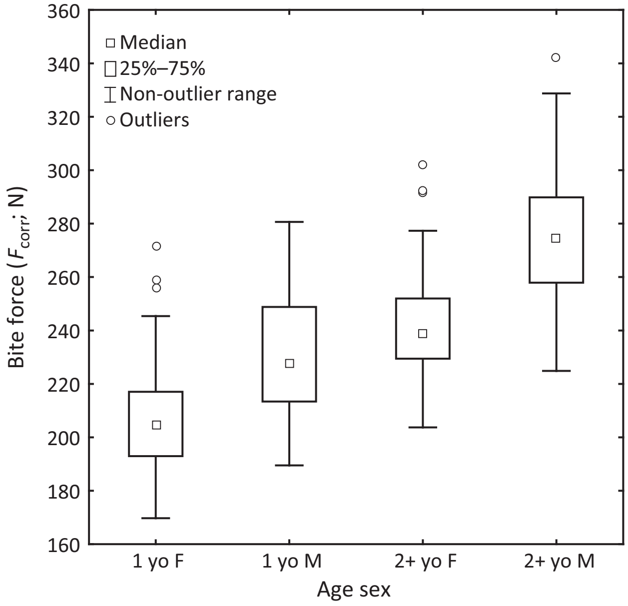

Figure 4 Estimated bite force (F_{corr}) for red foxes calculated using a lever model (Damasceno *et al.*, 2013). Although log-transformed values were used for statistical analyses, raw data are shown for clarity.

Bite force estimates were influenced by animal age ($P < 0.001$) and sex ($P < 0.001$), with estimated bite force for 1-year-old animals being weaker than that for adults, and males having greater estimated bite force than females (Fig. 4). The sex difference in estimated bite force was largely due to the larger skulls for males than females, because BFQ estimates (where differences in skull length were accounted for) showed no sex effect ($P = 0.222$). BFQ was greater for adults than 1-year-old animals ($P < 0.001$) and there was also a significant effect of geographic area on BFQ ($P = 0.004$), which could reflect regional differences in predominant diet. BFQ was strongly correlated with PC1 ($r^2 = 0.441$, $P < 0.001$), and to a lesser degree with PC2 ($r^2 = 0.017$, $P = 0.018$) and PC3 ($r^2 = 0.017$, $P = 0.019$).

Diet analyses

Diet composition for juveniles (1yo) and adult (2+ yo) male and females is summarized in Table 2. There was a significant sex effect (two-way PERMANOVA: $F_{1,475} = 3.94$, $P = 0.006$) and an age effect (juveniles *vs.* adults: $F_{1,474} = 3.28$, $P = 0.015$) on diet composition, with a significant interaction term ($F_{1,475} = -6.31$, $P = 0.030$) (MDS summarized in

Table 2 (a) Percentage composition of diet for foxes and (b) dietary overlap measures (Percentage Overlap and Pianka's Overlap indices). Asterisks indicate the main food materials that differentiate the diet separation of adult females from the other cohorts

	Females		Males		
a. Diet summary	1 yo (%)	2+ yo (%)	1 yo (%)	2+ yo(%)	
Sheep	60.38	46.81	64.59	61.91	*
Mouse	3.65	13.29	5.22	7.02	*
Rat	1.99	0.00	0.00	0.37	
Rabbit	2.66	1.07	4.40	0.93	
Brushtail possum	0.55	0.96	0.02	0.36	
Fat-tailed dunnart	0.00	0.00	0.00	0.28	
Cow	0.00	0.01	0.15	0.00	
Bird	3.84	1.45	5.32	2.36	
Reptile	0.49	1.47	0.29	0.28	
Amphibian	1.32	0.78	0.04	0.32	
Invertebrate	12.10	20.15	8.54	7.26	*
Plant material	13.03%	14.01%	11.44%	18.91%	*

b. Dietary overlap

	Pianka's Overlap	Percentage overlap			
Female 1 yo			80.5	91.2	87.2
Female 2+ yo		0.805		74.7	77.9
Male 1 yo		0.996	0.947		89.6
Male 2+ yo		0.990	0.953	0.896	

Yo, year old.

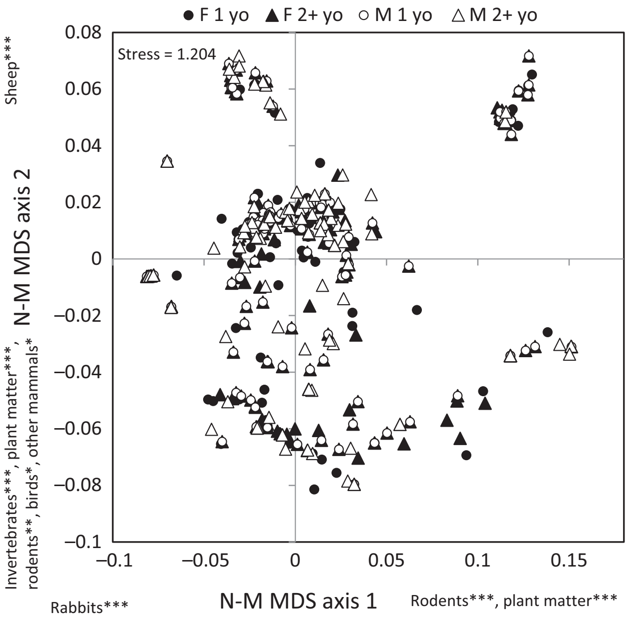

Figure 5 Output of Non-metric multidimensional scaling analysis (N-M MDS) of diet proportions for male (M) and female (F) red foxes in four age groups (1, 2, 3 and 4+ years old). The food items with the strongest correlation with each dimension axis (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$) and the output of the non-parametric MANOVA are indicated.

Fig. 5). The sex difference was largely determined (SIMPER percentage) by greater amounts of sheep carrion (43.0%) and plant material (18.0%) for males, but less invertebrates (16.2%) and rodents (10.0%) than females. The remaining food items, each contributed <10% of the difference between males and females. The difference between juveniles and adults was largely due to greater amounts of sheep for juveniles (42.8%), but less plant material (18.4%), invertebrates (15.9%) and mice (10.5%) than adults (Fig. 6). The significant interaction indicates that males eat sheep as juveniles and adults, whereas adult females shift from a diet dominated by sheep as juveniles towards other food such as invertebrates and mice as adults.

Discussion

We found significant sex and age differences in skull morphology for a large sample of red foxes across south-west Western Australia. Together, the variables describing the first PC factor capture the dimensions of the jaws and associated musculature and are strongly correlated with estimated bite force (Radinsky, 1981; Wiersma, 2001). PC2 describes relative size of neck muscle attachment, while PC3 describes the attachment area for the *temporalis* muscle; both these measures showed some correlation with estimated bite force, although the relationships were not as strong as those predicted by PC1. Skulls of both sexes become longer (mandible measures) and broader (zygomatic arch width) with age. Males have proportionally longer and broader (zygomatic arch width) skulls relative to their occipital areas, a longer temporal fossa (sagittal crest) and greater estimated bite force than females due to their larger skulls.

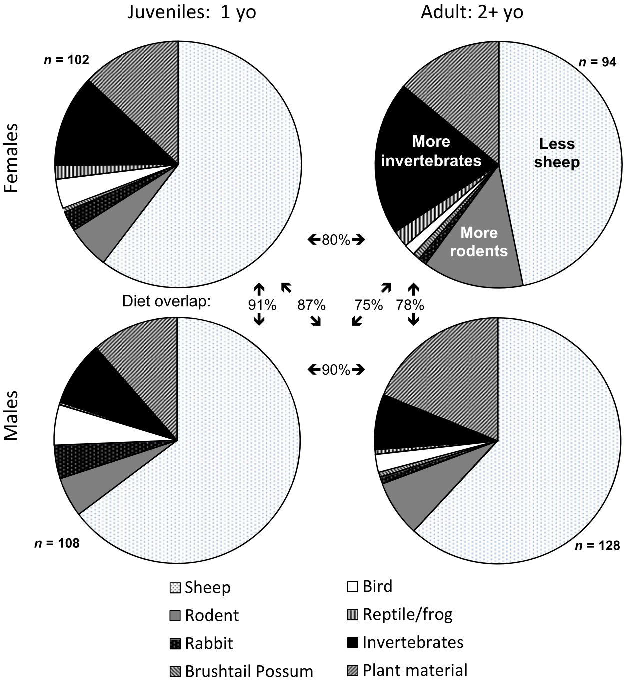

Figure 6 Pie charts showing diet composition for juvenile (1 year old) and adult foxes.

We also recorded sex and age differences in diet. Our data suggest that adult females show dietary separation from males and juveniles (of both sexes) with less sheep carrion and plant material, but more rodents and invertebrates in their diet. Similarly, a study from northern Italy showed that adult female foxes had more small mammals and invertebrates in their diet than did adult males (Cavallini & Volpi, 1996). Because sheep material would require more mechanical processing compared with smaller diet items that can be swallowed whole, we had predicted that animals with a large proportion of sheep meat in their diet would also have greater bite force. Adult females had greater estimated bite force than juveniles (both sexes), but consumed less sheep carrion. The dietary separation for adult females is therefore not directly due to bite force constraints, since if juveniles are capable of eating a largely carrion diet, then adult females (with greater bite force than juveniles) should also be able to process sheep meat. This difference between animal cohorts therefore suggests that prey availability influences adult female diet, probably supporting the conclusion that adult female foxes have smaller foraging ranges than males through monopolization of the richest patches (Henry, Poulle & Roeder, 2005). Viranta & Kauhala (2011) found craniodental changes in female, but not male, red foxes before and after the arrival of the invasive, omnivorous, raccoon dog (*Nyctereutes procyonoides*) in Finland; the changes in females suggest that the new competitor species drove female red foxes towards a higher degree of carnivory.

This is mirrored by a study from rural Poland (Kidawa & Kowalczyk, 2011), which found that adult male foxes and juveniles had wider food niche breadths (and had a high degree of overlap) than did adult females. Female red foxes could, therefore, be more susceptible to inter and intraspecific competition than males.

Highly specialized species need particular skull morphologies to capture, kill and process their food. Segura (2013) described the ontogenetic changes over the first year in the skull of the culpeo, and identified that most changes were associated with increased ability to capture, kill and process a highly carnivorous diet (Eisenberg & Redford, 1992). Other specialists, such as bone-crushing spotted hyenas (La Croix *et al.*, 2011) show similar marked ontogenetic changes in skull morphology due to their diet, and juveniles are at a distinct disadvantage compared to adults in their ability to process food. The ontogenetic changes in skull morphometry we recorded indicate that the skulls of red foxes similarly change over time towards a form that is more conducive of a high carnivory diet, with relatively larger jaws and more robust crania. Juveniles have the same adult dentition as the adults but weaker estimated bite force. Despite their weaker bite forces, however, juvenile males and females ate a similar carnivorous diet to adult males, with a large proportion of their stomach contents made up of sheep carrion. The lower estimated bite force for juveniles therefore did not limit their ability to eat a carnivorous diet comparable to that of adult males.

Adult male and both male and female juvenile foxes ate 60–64% carrion by volume, but juveniles showed significantly worse body condition compared with adults. Scavenging by foxes is well known in Australia and elsewhere, with the substantial meal in a large carcass representing an easy supply of nutrients for minimal energy expenditure (e.g. Cagnacci, Lovari & Meriggi, 2003; Saunders *et al.*, 2004; Fleming *et al.*, 2016). McIntosh (1963) reported sheep carrion made up 36% of fox diet by volume in a 2-year study in the Australian Capital Territory, and suggested that foxes scavenged from necessity, not preference. The high incidence of sheep carrion in our samples contrasts with the importance of rabbits (*Oryctolagus cuniculus*) in fox diets for most semi-arid and agricultural regions of eastern Australia (Coman, 1973; Croft & Hone, 1978; Lugton, 1993; Saunders *et al.*, 2004). In semi-arid western New South Wales, Catling (1988) found that fox predation on rabbits was heavy during the rabbit breeding season, but shifted to different prey, including carrion, at other times. Although there was a low incidence of rabbits in our diet samples, the Red Card programme also culls rabbits, and their data suggest reasonable availability of rabbits across south-west Western Australia at the time of the cull (RCRF 2016).

Conclusions

Most studies examining skull morphology make inferences about the respective diets of animals, but do not simultaneously measure both in the same animals. Studies based on stomach contents might sex individuals, but very rarely (if ever) age the animals examined. In addition, most diet analyses are based on scat material where it is impossible to age animals and sexing animals is probably only possible through molecular techniques. To the best of our knowledge, this is the first paper where skull morphology of red foxes has been compared directly to the diet of the same individuals.

Our diet data were a snapshot in time, since the stomach contents represent what the foxes had eaten immediately before they were shot. These foxes were also captured across a reasonably wide geographic range and therefore could have had different food availability. Despite these caveats, we found a strong pattern of dietary separation between sexes and ages. The generalist and eclectic diet of red foxes and their lack of specialization are doubtless the main contributors to their position as the most successful canid in the world (Macdonald & Reynolds, 2004) and their marked success in agricultural (Cavallini & Volpi, 1996), natural (Risbey, Calver & Short, 1999; Saunders *et al.*, 2010) and urban (Bateman & Fleming, 2012) landscapes.

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Author contributions

JLF-H performed the cranial morphology analyses; HMC performed the diet analyses; SJD coordinated the data collection; NMW, PJA, MCC, PWB and PAF conceived and designed the experiment; JLF-H, HMC, MCC and PAF analysed the data; NMW, PWB and PAF wrote the paper; other authors provided editorial advice.

Conflict of interest

The authors declare that they have no conflict of interest.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Geographic locations from which foxes were sampled – all sites were within the Intensive Landuse Zone (ILZ; the agricultural ‘wheatbelt’) and represent four Interim Biogeographical Regions of Australia (IBRA) botanical zones.

Table S1. Description of cranial measurements taken on red fox skulls. These measurements represent components of the skull previously interpreted to have functional meaning in terms of food acquisition and processing (Ewer, 1973; Radinsky, 1981; Ansorge, 1994). The coefficient of variation (CV; %) was calculated from three sequential measurements of the same 10 skulls.