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Body size of the red fox *Vulpes vulpes* in Spain: the effect of agriculture

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The body size of animals is affected by several factors, including ambient temperature and food availability. Ambient temperature is often negatively related to body size (Bergmann's rule) whereas an improved diet, especially during growth, has a positive effect. Animals commensal with man commonly exploit additional food sources (e.g. garbage dumps), thereby increasing their food supply. Using museum material, we studied morphological variation in skull size (and thus body size) among Spanish red foxes. Four measurements were taken of each skull and were related to the habitat from which the foxes were collected (agricultural and non-agricultural), and to latitude as a proxy for ambient temperature. The skull size of foxes collected in agricultural areas during the late 20th Century was significantly larger than that of those from non-agricultural areas, and was negatively related to latitude, thus contradicting Bergmann's rule. We suggest that increased food availability from animal husbandry is the cause for the observed increase in skull size (and thus body size).

ADDITIONAL KEYWORDS: animal husbandry – Bergmann's rule – commensal animals – food availability.

INTRODUCTION

It is an accepted fact that nutrition has a strong effect on body size of animals, particularly during the growth period (Geist, 1987). Conditions experienced during early development affect growth and ultimately body size, as well as a range of related properties, including metabolism, survival, and reproductive performance, in many birds and mammals (Henry & Ulijaszek, 1996; Lindstrom, 1999). This is demonstrated by the observations that, during the last two centuries, body height and weight in human populations have both increased significantly, predominantly in European and European origin populations as well as in Japan (Ulijaszek, Jonhston & Preece, 1998). The prime determinants of this trend are considered to be improved nutrition and the availability of public health services (Ulijaszek *et al.*, 1998). Similar phenomena have been observed in animals. For example, red foxes (*Vulpes vulpes*) and Eurasian badgers (*Meles meles*) in Denmark and several species of commensal carnivores in Israel have increased in size during the 20th Century, apparently due to increased food availability due to human activity (Yom-Tov, 2003; Yom-Tov, Yom-Tov & Baagøe, 2003). A similar trend was observed in harbour porpoises (*Phocoena phocoena*), where body length of calves increased and females reached maturity earlier, apparently due to increased prey availability (Read & Gaskin, 1990).

Bergmann's rule predicts 'In warm blooded animals, races from warm regions are smaller than races from cold regions' (Mayr, 1970). Global mean surface temperatures have increased by 0.6 °C from the late 19th century onwards (IPCC, 1995). Recently, it has been claimed that global warming has affected body size in several species of passerine birds (Yom-Tov, 2001) and rodents in south-west USA (Smith, Browning & Shepherd, 1998) and Japan (Yom-Tov & Yom-Tov, 2004).

Mass change in mammals can occur rather rapidly, as reported for animals introduced into new environments. For example, rats (*Rattus rattus* and *Rattus*

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norwegicus) and house mice (*Mus musculus*) that were introduced into various Pacific islands adapted their body size to their new conditions within a few decades (Yom-Tov, Yom-Tov & Moller, 1999), as did the brush-tail possum (*Trichosurus vulpecula*) that was introduced from Australia into New Zealand (Yom-Tov, Green & Coleman, 1986).

The red fox is widely distributed in Spain. Various Spanish populations show great variability in size but, to our knowledge, there is no report of a geographical trend, such as the one predicted by Bergmann's rule (Gortazar, 2002). Foxes feed on a great variety of food items, including invertebrates, fruit, reptiles, birds, and small mammals (during the breeding season in Spain they prefer rabbits, *Oryctolagus cuniculus*). In the agricultural region of Castile and near human settlements, they are commensal with man, eating carcasses of domestic ungulates, offal, garbage, and road kill (Reig, Cuesta & Palacios, 1985; Gortazar, 2002).

Spain is a large country (approximately 0.5 million km^2) inhabited by approximately 40 million people. It has extensive agriculture both for domestic consumption and export. Its animal husbandry includes pigs, cattle, sheep, goats, chicken, and turkeys, many of which are processed in large factories. Until 2000, animal residue was readily available for commensal carnivores near farms and factories alike, thus providing them with easily accessible, protein-rich food. Similar to other commensal carnivores, the red fox in Spain exploits domestic ungulates both by eating carrion and predating upon young animals (Gortazar, 2002).

The aim of the present study was to test the prediction that red foxes living in agricultural areas are larger than those living elsewhere.

MATERIAL AND METHODS

Skulls of 267 red foxes were measured at the Museum of Natural History, Madrid, Spain (Appendix). The specimens selected were adults with data on latitude, longitude, and year of collection. All specimens, apart from one, were collected between 1969 and 1986. Skulls of young specimens (open sutures between the bones of the skulls or with milk teeth) were not measured. For each skull, we noted from the museum catalogue its sex (if recorded), locality, and date of collection. Using digital calipers, four measurements were taken from each skull to an accuracy of 0.01 mm: greatest length (GTL), zygomatic breadth (ZB), interorbital constriction (IO), and the length of the largest upper cheek teeth: the shearing upper premolar (carnassial, M1). In mammals, GTL and ZB are closely associated with body weight and length.

Each specimen was categorized according to the mean latitude of the province from which it was collected. In addition, using 1 : 250 000 scale maps that provide information on types of natural vegetation (forests, etc.) and agriculture, each specimen was allocated to one of two groups: agricultural and non-agricultural areas. Agricultural areas are the municipalities where approximately more than 50% of their area is declared as crop production or other kind of agriculture. In these areas, there are farms devoted also to stock husbandry (with extensive animal husbandry such as pigs, poultry, sheep, or cattle), and the wastes are available for foxes (or used to be when the foxes were collected). Non-agriculture areas are mainly forest and mountain areas, where the number of farms is much lower than in agricultural areas.

It should be noted that, until 2000, offal and other residues of meat production were often simply discarded in such a way that they became available to foxes and other commensal carnivores.

We used principal component analysis to combine the information in three of the morphological measurements (GTL, ZB, and IO) into a single variable and used the first principal component (PC1) score for comparing skull size of individuals from agricultural and non-agricultural areas. This is because these three skull parameters are related to each other and their combination provides a better estimate of skull size than does a single parameter.

We tested the effect of agriculture on body size by using residual PC1 after correcting this parameter for latitude to account for the possible effect of Bergmann's rule.

There were 80 specimens whose sex was known. The proportion of males was 69% (22 males, ten females) and 65% (31 males, 17 females) among specimens in agricultural and non-agricultural regions, respectively, indicating that there was no difference in the proportion of males between the two habitats.

RESULTS

PC1 clumped the three skull measurements (GTL, ZB and IO) into one variable. Eigenvalue was 2.322, and the proportion of variance explained by PC1 was 77.4%. There were negative relationships between PC1 and all four skull parameters and latitude, significant for PC1, GTL, ZB, and M1, and almost significant for IO (PC1: $F_{1,262} = 25.584$, $r^2 = 0.089$, $P < 0.0001$; GTL: $F_{1,265} = 38.112$, $r^2 = 0.126$, $P < 0.0001$; ZB: $F_{1,264} = 28.025$, $r^2 = 0.096$, $P < 0.0001$; IO: $F_{1,263} = 3.585$, $r^2 = 0.013$, $P = 0.0594$; M1: $F_{1,265} = 12.286$, $r^2 = 0.044$, $P = 0.0005$).

There were no significant relationships between year of collection and any of the four skull parameters or PC1 (PC1: $P = 0.2731$; GTL: $P = 0.1913$; ZB: $P = 0.4986$; IO: $P = 0.0594$; M1: $P = 0.8459$).

There was no difference in the latitudinal range of foxes between agricultural and non-agricultural areas

Table 1. Results of two-way analysis of variance on the first principal component (PC1) calculated from three skull parameters (length, zygomatic breadth, interorbital constriction) and corrected for latitude, on foxes whose sex was known

	d.f.	Mean square	*F*	*P*
Sex	1	13.476	21.222	< 0.0001
Agriculture	1	2.936	4.624	0.0348
Sex × Agriculture	1	1.126	1.773	0.1871
Residual	75	47.624		

d.f., degrees of freedom.

(for agricultural and non-agricultural areas, mean ± SD: 41.46 ± 1.12°N and 40.95 ± 2.19°N, respectively; t = –1.671, $P = 0.0959$).

To account for the possibility that the two sexes used the agricultural and non-agricultural areas differently, we ran a two-way analysis of variance (ANOVA) on the first principal component (PC1), calculated from three skull parameters (GTL, ZB, and IO) and corrected for latitude, on those specimens whose sex was known (Table 1). PC1 was significantly affected by sex ($P < 0.0001$), as well as by agriculture ($P = 0.0348$), but there was no interaction between sex and agriculture ($P = 0.1871$). These results indicate that skull size is related to sex (i.e. males being larger) and habitat (i.e. animals from agricultural areas are larger), but there was no differential use of the two habitats by the two sexes. Hence, in the next stage of the analysis, we used the whole sample, thus increasing it from 80 to 267 individuals. In this stage, we omitted gender and ran a one-way ANOVA on the residuals of PC1 (corrected for mean provincial latitude) and found that PC1 was significantly larger in agricultural areas than in non-agricultural ones ($F_{1,261} = 5.814$, $P = 0.0166$) (Fig. 1), indicating that foxes from agricultural areas are larger than others.

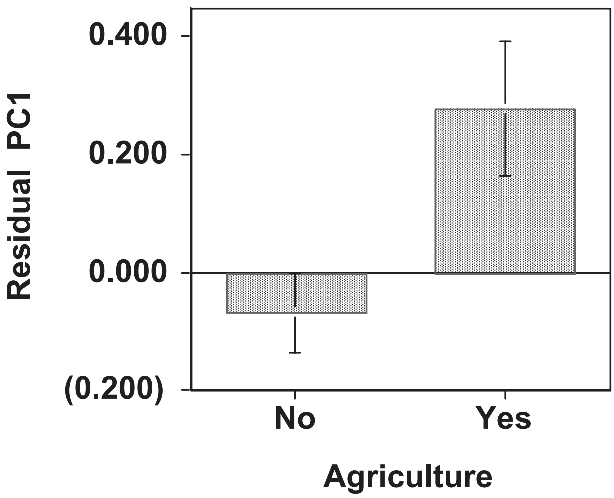

Figure 1. Comparison of residual PC1 (corrected for mean provincial latitude) of red foxes from agricultural and non-agricultural areas, means ± standard errors; $F_{1,261} = 5.814$, $P = 0.0166$. Yes, agricultural areas; No, non-agricultural areas.

DISCUSSION

The results of the present study show that foxes inhabiting agricultural areas are larger than those living elsewhere. Gortazar, Traban & Delibres (2000) have shown that, in two different regions in Spain, foxes living in high-productive habitat were larger than those in low-productive habitat. Similar results have been reported for this species in Denmark (Yom-Tov, Yom-Tov & Baagøe, 2003) and other commensal carnivores in Israel (Yom-Tov, 2003). The above studies attributed the larger body size to increased food availability, and we suggest that the same factor affected the body size of Spanish foxes. Hilderbrand *et al*. (1999) have demonstrated that the proportion of salmon in the diet of brown bears in North America explains most of the variance in female body mass, thus giving further support to the belief that food quantity and quality determines body size. These results provide support for the hypothesis that food quality and quantity strongly affect body size of animals, particularly for omnivorous species. Individuals whose diet comprises of a larger proportion of animals tend to be larger than those consuming less protein-rich diet (Hilderbrand *et al*., 1999).

Increased food availability also affects other parameters, such as population density and breeding success. The population density of red foxes in Spain is determined by the availability of resources (Gortazar, 2002). Gortázar (1997) studied fox densities in Aragon (north-eastern Spain), and found that in an extensive, irrigated, agricultural area fox density was 2.5 foxes km^{-2} whereas, in a steppe area, it was only 0.8 foxes km^{-2}. Similar results were found in the Galilee, Israel, where fox density near poultry farms was significantly higher and females raised approximately two-fold more offspring than foxes in other areas (Amit Dolev, pers. comm.). Yom-Tov, Ashkenazi & Viner (1995) have shown that golden jackals (*Canis aureus*) in the Golan Heights maintain a very high population density due to availability of carcasses of poultry and domestic ungulates. Hence, increased protein-rich food availability has an important effect on not only on body size of foxes and other commensal carnivores, but also on other parameters of their biology.

We do not know when the observed trend of increasing body size started. Our sample covers a time span of only 17 years, and this relatively brief period is too short to pinpoint the origin of the trend.

Spain joined the European Union in 1985 and, according to EU regulations, carcasses and garbage should not be available to wild animals, but these regulations were not enforced in Spain until 2000. In November 2000, the first case of 'mad cow' disease was detected in Spain and, subsequently, these regulations started to be enforced seriously. We predict that when these regulations are enforced, the food availability for foxes will decrease to some extent and the trend of increasing body size will slow down, as a major food resource will be eliminated (whereas predation on domestic stock will continue).

Latitudinal and annual trend

It is interesting to note that skull size of the studied red foxes was negatively related to latitude, thus contradicting Bergmann's rule. Latitude explains only 4.4–12.6% of the variation in skull size, depending on the parameter, and this may be due to the small latitudinal range of Spain (approximately 7°). This reversed trend (to the prediction of Bergmann's rule) is similar to the situation found for wood mice (*Apodemus sylvaticus*) in Europe in general and in Spain (Alcantara, 1991). Alcantara (1991) attributed this trend to interspecific competition from the congeneric yellow-necked mouse (*Apodemus flavicollis*). Interspecific competition is unlikely to explain the observed size trend in red foxes. The only other member of the canid guild in Spain is the wolf (*Canis lupus*). It inhabits only the north-west quarter of Spain and even there it is scarce and patchily distributed (Blanco, Reig & Cuesta, 1992), and wolves generally consume larger prey than foxes. At present, we cannot offer any explanation for this trend in body size of the foxes in Spain.

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APPENDIX

MUSEUM NUMBER (MUSEUM OF NATURAL HISTORY, MADRID, SPAIN) OF ALL RED FOXES MEASURED IN THE STUDY

Museum numbers				
16832	16930	17053	17244	17369
16833	16932	17055	17245	17415
16834	16933	17056	17247	17429
16836	16934	17058	17248	17430
16839	16935	17062	17249	17437
16840	16938	17064	17250	17440
16843	16939	17065	17252	17443
16844	16950	17097	17253	17444
16845	16953	17105	17255	17445
16846	16954	17106	17258	17447
16847	16956	17109	17259	17448
16848	16957	17116	17260	17451
16849	16958	17118	17261	17455
16851	16960	17119	17262	17461
16852	16962	17125	17263	17462
16853	16963	17127	17265	17465
16854	16977	17129	17266	17472
16855	16978	17130	17268	17476
16859	16988	17131	17269	17477
16861	16989	17132	17270	17480
16863	16990	17135	17272	17481
16866	16992	17140	17273	17482
16867	16993	17141	17275	17486
16870	16995	17142	17277	17489
16871	16997	17151	17279	17494
16872	16998	17157	17280	17495
16874	17000	17176	17281	17502
16876	17001	17196	17285	17503
16880	17002	17201	17286	17506
16881	17003	17203	17288	17509
16882	17005	17207	17289	17513
16883	17008	17210	17292	17514
16884	17009	17211	17294	17517
16885	17011	17213	17297	17531
16886	17013	17216	17298	17544
16888	17014	17217	17300	17573
16894	17020	17218	17302	17575
16902	17024	17219	17304	17592
16903	17025	17220	17305	17593
16905	17029	17221	17308	17608
16906	17030	17223	17312	17612
16908	17034	17225	17327	17613
16911	17035	17226	17335	17615
16912	17036	17227	17339	17616
16913	17039	17231	17344	21473
16914	17043	17232	17347	21475
16919	17044	17233	17349	21476
16921	17045	17234	17350	21477
16922	17047	17235	17352	21478
16923	17048	17237	17355	21488
16924	17049	17238	17360	
16925	17050	17239	17362	
16927	17051	17240	17363	
16928	17052	17242	17367	