

Increased carnivory in Finnish red fox females — adaptation to a new competitor?

Suvi Viranta¹ & Kaarina Kauhala²

¹ Department of Biomedicine/Anatomy, P.O. Box 63, FI-00014 University of Helsinki, Finland (e-mail: suvi.viranta-kovanen@helsinki.fi)

² Finnish Game and Fisheries Research Institute, Itäinen Pitkätatu 3 A, FI-20520 Turku, Finland (e-mail: kaarina.kauhala@rktl.fi)

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Carnivore teeth, especially the carnassials, are subjects to selection in the presence of dietary competition. We compared several craniodental characters in the Finnish foxes before and after arrival of an invasive species, the raccoon dog. The female foxes displayed increased adaptation to carnivory, whereas we found no significant change in the male foxes after the arrival of the raccoon dog. We suggest that the presence of a new competitor may be driving the Finnish female foxes towards more carnivorous diet.

Introduction

Brown and Wilson (1956) launching the theory of character displacement suggested that where two similar species of animals are sympatric, their ecological, morphological or behavioral differences are accentuated. Competition for or partitioning of resources may not only result in interspecific divergence, but may be intraspecific occurring between sexes of the same species (Slatkin 1984, Shine 1989). Numerous studies in various taxa have exposed character displacement. In mammalian carnivores the dentition especially has confirmed the rule (Davies *et al.* 2007).

Several craniodental characters correlate with the diet in the carnivores. Skull shape and proportions reflect the bite, as well as the size and shape of the muscles of mastication (Van Valkenburgh 1990). Dietary adaptations are reflected by prominence of the appropriate teeth and their dimensions and/or number and shape of cusps.

The heterodont dentitions of carnivores have both slicing and grinding functions. Carnivores with a tendency toward more omnivorous diet typically have emphasis on the grinding molars, whereas more hypercarnivorous taxa have long blade-like lower carnassial trigonids and strong premolars good for meat slicing (Van Valkenburgh 1989). Although original works were done on larger carnivores, Friscia *et al.* (2007) showed similar trends in smaller carnivores including foxes.

Members of the family Canidae maintain the unique carnivore heterodonty. The carnassials are of special importance in their dietary adaptations (*see* Dayan *et al.* 1989). The trigonid length and breadth of the lower carnassial vary between species according to diet, but show little intraspecific variation (Meiri *et al.* 2005a). The canid canines, on the contrary, tend to have considerable intraspecific variation in size and shape and have weak correlation with dietary adaptations (Meiri *et al.* 2005a, 2005b).

The red fox (*Vulpes vulpes*) is very adaptable, inhabiting in its Holarctic range many different environments from tundra and northern taiga to agricultural areas, deserts and even large cities (Baker & Harris 2004, Holmala & Kauhala 2009). Significant size variation between different fox populations has been found (Larivière & Pasitschniak 1996). Regional differences have been correlated with sympatric species, climatic factors such as humidity, and latitude. Also morphological variation and variation in the degree of sexual dimorphism has been reported and correlated with differences in contemporary fauna or other environmental factors. Similar to canids in general, Dayan *et al.* (1992) showed that the morphology of fox carnassial and postcarnassial dentition is ecologically significant and related to food processing and hunting. Intense competition may increase sexual dimorphism in the fox carnassial pair and upper first molar: e.g. Szuma (2008a) found that species sympatric with other fox species have pronounced sexual dimorphism in these teeth.

The raccoon dog (*Nyctereutes procyonoides*) arrived in Finland from introductions made in the former Soviet Union (Lavrov 1971). The population spread from southeast, started to increase rapidly in southern and central Finland in the early 1970s and is now established in the whole country except northern Lapland (Helle & Kauhala 1991). Both the red fox and raccoon dog are adaptable, omnivorous and opportunistic canids (Larivière & Pasitschniak-Arts 1996, Ward & Wurster-Hill 1990, Sutor *et al.* 2010). Ecologies of the two now sympatric species in Finland have been studied to some detail (Kauhala 1993, Kauhala *et al.* 2006, Holmala & Kauhala 2009). Results showed that foxes and raccoon dogs partly share their home ranges and food resources but the fox is more carnivorous of the two. There were no clear indications of competitive exclusion (Kauhala *et al.* 1998), although the fact that an experimental raccoon dog removal coincided with a temporary increase in the red fox population, indicates possible interaction (Kauhala 2004).

Here, we study dental and cranial morphometrics of a native canid species in Finland, the red fox, before and after the arrival of a potential canid competitor, the raccoon dog. Our study is

unique studying short term temporal changes in a native species during an invasion of an alien species. For the southern Finland red foxes, we hypothesized three changes to have taken place as a result of the arrival of the raccoon dog:

1. Size increase. We predict that competition with a smaller and less carnivorous species will lead to a larger size of the red fox, when foxes shift to more carnivorous diet and select larger prey.
2. Morphological changes in the craniodental characters. We predict that the tendency toward hypercarnivory will lead to expression of more carnivorous traits in the dentition and will have the greatest effect on the carnassials and the cranial characters related to the muscles of mastication.
3. Increase in sexual dimorphism. We predict that increased competition will lead to prey partition between sexes and will result in increased dimorphism in the species.

We also studied the Lappish population. Our hypothesis predicted that the Lappish foxes were larger than those from southern Finland: body size tends to be positive correlated with latitude (Bergmann's rule, as cited in Mayr 1970).

Material and methods

Material

Skulls in the collections of the Finnish Museum of Natural History and those collected for the Finnish Game and Fisheries Research Institute were used in the present study. Only skulls of adult foxes (≥ 1 yr) were used. In total, there were 151 skulls (80 males and 71 females) from different localities of Finland. Skulls had been collected between 1885 and 2005. They came from two different geographic areas: Lapland and southern Finland (Fig. 1).

Methods

Nine cranial and 11 dental measurements were taken to the nearest 0.1 mm using a sliding cali-

per. Due to *pre* or *post mortem* damage to bone or teeth it was not possible to take all the measurements from all the specimens. Measurements were taken by both authors. We did blind tests and found a good correlation between our measuring techniques.

Dental measurements taken were:

C_1L, C_1W : the lower canine mesio-distal length and labio-lingual width at the base of the crown.

M_1L, M_1W : mesio-distal length at the base of the crown and the greatest labio-lingual width of the lower carnassials.

$M_1\text{trig}$: the mesio-distal length of the lower carnassial trigonid (formed by the three anterior cusps; protoconid, paraconid and metaconid).

M_2L : the mesio-distal length of the second lower molar.

C^1L, C^1W : the upper canine mesio-distal length and labio-lingual width at the base of the crown.

M^1L, M^1W : the mesio-distal length and the labio-lingual width at the base of the crown of the first upper molar.

Cranial measurements taken:

ZW: the widest point of the skull measured from the zygomatic arch to the other.

RB: rostral breadth measured between the lateral alveolar margins.

IC: interorbital constriction, the minimum distance between the two orbits.

PB: postorbital projection measurement between the posterior margins of the medial orbital walls.

PC: postorbital constriction or the narrowing between orbits and the braincase.

OCB: distance measured between the lateral margins of the occipital condyles.

ML: maximum mandibular length measured from the angular process to the mesial base of the lower incisors.

MW: minimum width of the mandibular ramus.

PL: profile length or the maximum length of the skull.

Individuals were coded for their spa-

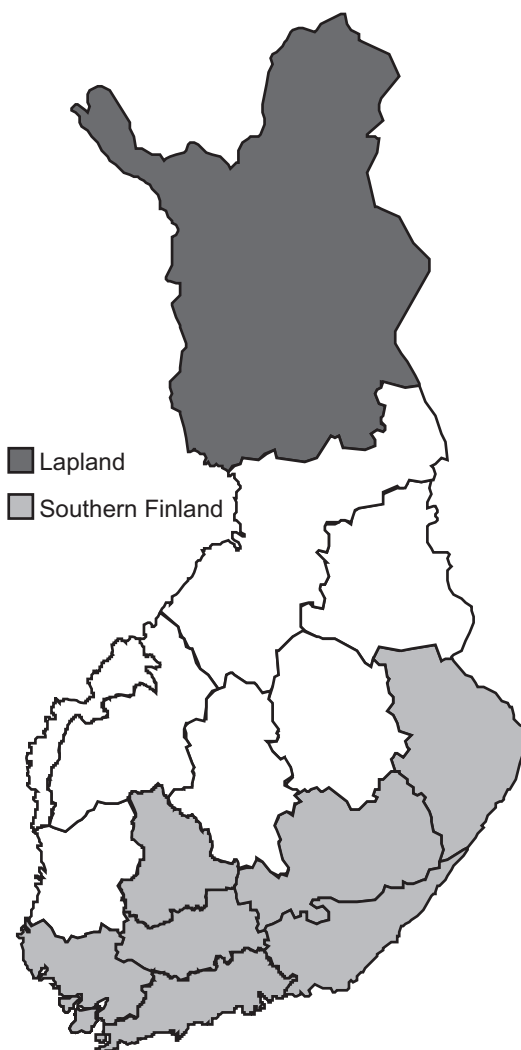


Fig. 1. Map of Finland showing the study areas.

tial occurrence, temporal occurrence and sex (Table 1). The spatial occurrence was coded as the locality (either from Lapland or southern Finland). For the temporal occurrence, animals which lived before 1970 were considered to belong to the pre-raccoon-dog population and the ones that were killed after 1970 were considered to belong to the post-raccoon-dog population. The year 1970 was chosen as a cut point, because prior to 1970 the raccoon dog population was scarce in Finland but increased rapidly thereafter (Helle & Kauhala 1991).

In addition to the absolute measurements, relative measurements were used to study any

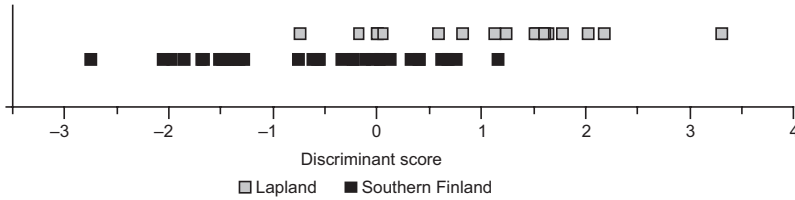


Fig. 2. Classification of the red foxes to Lappish and southern Finnish populations. Classification was done using the classical discriminant analysis with the cranial measurements of fox skulls as predictors. Canonical discriminant scores for each original skull are given.

possible morphological changes. For the relative dental measurements, the absolute measurements were divided by the lower carnassial length (M_1L) and, for the relative skull measurements, the absolute measurements were divided by OCB. As an index of the overall size we used PL.

We ran statistical tests using the commercial package of SYSTAT (ver. 12) and tested normality of the data distribution using a Kolmogorov-Smirnov one-sample test. We tested for differences in the morphology or size of skulls and teeth between the different groups and also differences in the sexual dimorphism in time or space using the *t*-test, paired *t*-test and the classical discriminant analysis (with jackknifed classification).

Results

Lappish red fox skulls were significantly larger than those from southern Finland. Mean skull length (PL) was 155.2 mm in Lapland and 147.9 mm in southern Finland ($t_{128} = 4.11, p < 0.001$).

Table 1. Numbers of fox skulls from which cranial and dental measurements were taken for southern and Lappish populations.

	Pre-raccoon-dog period		Post-raccoon-dog period		Total
	Females	Males	Females	Males	
Cranial measurements					
Southern	14	19	39	41	113
Lappish	8	10	–	–	18
Dental measurements					
Southern	14	18	49	52	133
Lappish	8	10	–	–	18

Also the discriminant analysis with cranial measurements as predictors classified well the skulls as belonging to Lappish or southern populations (79% correctly classified, Wilk's $\lambda = 0.76, F_{9,107} = 3.8, p < 0.001$; Fig. 2). Because of this and the fact that all the Lappish skulls were from the pre-raccoon-dog period, we decided to omit the Lappish material from the further testing. Because the male skulls were significantly longer than the female skulls (Table 2), we did all tests separately for males and females.

Change in cranial and dental measurements

There was no apparent skull-size change in the foxes after the arrival of the raccoon dog. In females, the mean skull length (PL) changed from 142.1 mm to 144.7 mm, but this was not significant (Table 3). However, the difference in skull length between sexes has decreased from 10 mm to 6.2 mm.

The discriminant analysis did not reveal any difference in the fox cranial morphology between the populations before and after the arrival of the raccoon dog (females: Wilk's $\lambda = 0.85, F = 0.70, df = 9, 36, p = 0.699$, males: Wilk's $\lambda = 0.79, F_{9,44} = 1.30, p = 0.262$; Fig. 3). Only RB ja IC increased among females (Table 3). Analyses of the relative measurements yielded similar results (females: Wilk's $\lambda = 0.86, F_{8,37} = 0.78, p = 0.626$, males: Wilk's $\lambda = 0.81, F_{8,45} = 1.37, p = 0.237$). However, 76% of the female skulls were correctly classified by the discriminant analysis on the basis of dental characters as belonging to pre- or post-raccoon-dog population (Wilk's $\lambda = 0.43, F_{10,31} = 4.1, p = 0.001$; Fig 3). C_1W, M_1 trigonid, M_2L and $M'W$, were larger in females

after the raccoon dog arrival (Table 4). The discriminant analysis could not classify the male skulls correctly (Wilk's $\lambda = 0.68$, $F_{10,33} = 1.6$, $p = 0.165$). The classification of the female skulls on the basis of relative dental measurements was significant (Wilk's $\lambda = 0.47$, $F_{9,32} = 4.1$, $p = 0.002$). Again, the discriminant analysis failed to classify the male skulls correctly (Wilk's $\lambda = 0.70$, $F_{9,34} = 1.6$, $p = 0.144$). Of the relative measurements, M_1 trigonid, M_2L , C^1L and M^1W of females were larger in the post-raccoon-dog

population (Table 5). In the males, only the relative measurement of the trigonid had increased.

Sexual dimorphism

Sexual dimorphism was evident in the fox population from southern Finland (Table 2). The discriminant analysis with cranial measurements as predictors classified 77% of the skulls correctly according to sex (Wilk's $\lambda = 0.54$, $F_{10,89} = 7.7$,

Table 2. Finnish red fox cranial data from the pre- and post-raccoon-dog periods by sex. Number of specimens and the mean with SD of each measurement is given. A degree of sexual dimorphism (SP index) was calculated as a relation between the male measurement mean and the respective female measurement mean. Significance of the differences between the female and male measurements was tested using Student's *t*-test.

		<i>n</i>	Mean (mm)	SD	SP index	<i>t</i>	df	<i>p</i>
Pre-raccoon-dog period								
PL	Female	14	142.1	5.79	1.07	-5.25	31	< 0.001
	Male	19	152.1	5.09				
ZW	Female	14	76.0	3.15	1.03	-2.04	31	0.050
	Male	19	78.4	3.46				
RB	Female	14	23.1	1.52	1.08	-3.7	31	0.001
	Male	19	24.9	1.27				
IC	Female	14	26.7	2.57	1.08	-3.01	31	0.005
	Male	19	28.9	1.50				
PB	Female	14	35.5	3.15	1.05	-1.48	31	0.150
	Male	19	37.1	3.33				
PC	Female	14	23.4	1.26	0.98	0.72	31	0.478
	Male	19	22.9	1.91				
OCB	Female	14	25.7	1.09	1.04	-3.39	31	0.002
	Male	19	26.7	0.62				
ML	Female	14	103.4	7.72	1.07	-3.52	31	0.001
	Male	19	110.7	4.13				
MW	Female	14	14.9	1.04	1.11	-5.01	31	< 0.001
	Male	19	16.5	0.85				
Post-raccoon-dog period								
PL	Female	38	144.7	5.39	1.04	-4.85	77	< 0.001
	Male	41	150.9	5.89				
ZW	Female	36	76.5	2.74	1.05	-4.65	70	< 0.001
	Male	36	80.0	3.53				
RB	Female	39	23.9	1.01	1.04	-3.33	77	0.001
	Male	40	24.8	1.34				
IC	Female	38	28.0	1.59	1.05	-3.23	77	0.002
	Male	41	29.3	1.88				
PB	Female	37	36.5	2.99	1.04	-2.25	75	0.027
	Male	40	38.0	2.66				
PC	Female	38	23.1	1.76	0.99	0.88	77	0.381
	Male	41	22.7	1.64				
OCB	Female	37	25.9	0.93	1.04	-4.27	73	< 0.001
	Male	38	26.8	1.06				
ML	Female	38	106.2	4.56	1.04	-3.67	77	< 0.001
	Male	41	110.2	5.12				
MW	Female	39	15.3	0.81	1.07	-5.1	78	< 0.001
	Male	41	16.3	0.95				

$p < 0.001$). Sexual dimorphism was evident both before and after the raccoon dog arrival (before: 76% correct, Wilk's $\lambda = 0.27$, $F_{9,23} = 6.8$, $p < 0.001$; after: 75% correct, Wilk's $\lambda = 0.59$, $F_{9,57} = 4.5$, $p < 0.001$). The discriminant analysis with dental measurements as predictors also revealed sexual dimorphism in the fox populations both before and after the raccoon dog arrival (before: 70% correct, Wilk's $\lambda = 0.39$, $F_{10,19} = 3.0$, $p = 0.019$, after: 75% correct, Wilk's $\lambda = 0.53$, $F_{10,45} = 4.1$, $p = 0.001$).

Throughout the data, most of the cranial and dental measurements were significantly larger in males than in females (Tables 2 and 6). Of the individual cranial measurements, all but the postorbital constriction (PC) were significantly larger in males (and PB in pre raccoon dog population). Of the dental measurements, all but M_1W , M_2L and $C'L$ in pre raccoon dog population, and both postcarnassial teeth (M^1L and M_2L) in post raccoon dog population were significantly larger in males (Table 6).

Table 3. Differences in the cranial measurements between pre- and post-raccoon-dog populations of Finnish foxes. The mean and SD of each measurement is given along with the results of Student's *t*-test.

		<i>n</i>	Mean (mm)	SD	<i>t</i>	df	<i>p</i>
Females							
PL	pre	14	142.1	5.79	-1.48	50	0.145
	post	38	144.7	5.39			
ZW	pre	14	76.0	3.15	-0.52	48	0.607
	post	36	76.5	2.74			
RB	pre	14	23.1	1.52	-2.28	51	0.027
	post	39	23.9	1.01			
IC	pre	14	26.7	2.57	-2.21	50	0.032
	post	38	28.0	1.59			
PB	pre	14	35.5	3.15	-1.14	49	0.261
	post	37	36.5	2.99			
PC	pre	14	23.4	1.26	0.58	50	0.564
	post	38	23.1	1.76			
OCB	pre	14	25.7	1.09	-0.61	49	0.548
	post	37	25.9	0.93			
ML	pre	14	103.4	7.72	-0.61	49	0.548
	post	38	106.2	4.56			
MW	pre	14	14.9	1.04	-1.7	51	0.095
	post	39	15.3	0.81			
Males							
PL	pre	19	152.1	5.09	0.79	58	0.433
	post	41	150.9	5.89			
ZW	pre	19	78.4	3.46	-1.54	53	0.130
	post	36	80.0	3.53			
RB	pre	19	24.9	1.27	0.31	57	0.758
	post	40	24.8	1.34			
IC	pre	19	28.9	1.5	-0.83	58	0.412
	post	41	29.3	1.88			
PB	pre	19	37.1	3.33	-1.04	57	0.302
	post	40	38.0	2.66			
PC	pre	19	22.9	1.91	0.45	58	0.658
	post	41	22.7	1.64			
OCB	pre	19	26.7	0.62	-0.56	55	0.578
	post	38	26.8	1.06			
ML	pre	19	110.7	4.13	0.34	58	0.733
	post	41	110.2	5.12			
MW	pre	19	16.5	0.85	0.71	58	0.481
	post	41	16.3	0.95			

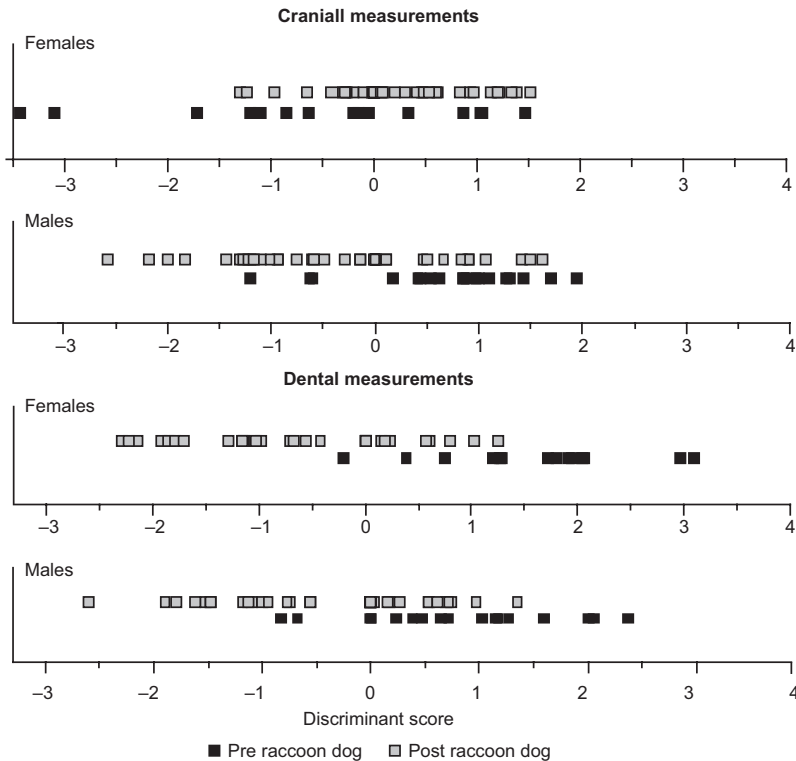


Fig. 3. Classification of the red foxes to pre- and post-raccoon-dog populations. Classification was done using the classical discriminant analysis with cranial and dental measurements of fox skulls as predictors. Canonical discriminant scores for each original skull are given. Females and males were analysed separately.

A paired *t*-test on the sexual dimorphism indices suggested a small difference toward decreased dimorphism (for cranial measurements $t_8 = 2.23$, $p = 0.056$; for dental measurements $t_9 = 2.39$, $p = 0.040$). In the dental material, the mean SP index was 1.067 and 1.038 for the pre- and post-raccoon-dog populations, respectively. In the cranial material, the mean SP index was 1.057 and 1.040 for the pre- and post-raccoon-dog populations, respectively. Except for ZW and PC, the SP index decreased for all other individual skull measurements. In the dental characters, the SP index decreased in all measurements except for M_1W and C^1L .

Discussion

Change in size

We predicted larger sizes for the Lappish foxes.

Our results were in accordance with the prediction and with Bergmann's rule showing that the Lappish skulls were larger than those from southern Finland. Szuma (2008b) also found the largest Holarctic foxes (as measured from total skull length and lower carnassial length) from Scandinavia. Finnish foxes were not included in her study, but our results showed that their medians were very close to those of the largest foxes from northern Eurasia. Against our prediction, we did not record any significant skull size change in the red fox in southern Finland from pre- and post-raccoon-dog populations (Table 3).

Morphological change

We predicted that competition with a more omnivorous carnivore would lead to more hypercarnivorous traits in the dentition and cranial characters in the red fox. Indeed, our data indicated pro-

nounced hypercarnivory with enlarged trigonid and increased rostral width after the arrival of raccoon dogs. The changes were more marked in females than in males (Table 4). The rostral width showed no increase in males (Table 3).

Yom-Tov *et al.* (2003) showed that many dental and cranial characters of the Danish foxes increased in size during the 20th century although the total skull length show no change,

indicating the change in morphotype not in the overall size. The authors attributed the change to wider dietary range due to increased commensalism with humans. Ecological studies have indicated a similar trend towards commensalism with humans in the behavior of the Finnish foxes (Lappalainen & Vuorisalo 1996), but this is not relevant to our study which included skulls of foxes collected mainly from rural areas.

Table 4. Differences in the dental measurements between pre- and post-raccoon-dog populations of Finnish foxes. The mean and SD of each measurement is given along with the results of Student's *t*-test.

		<i>n</i>	Mean (mm)	SD	<i>t</i>	df	<i>p</i>
Females							
C ₁ L	pre	14	7.0	0.84	0.53	42	0.602
	post	30	6.9	0.65			
C ₁ W	pre	14	4.4	0.45	-2.06	42	0.046
	post	30	4.7	0.33			
M ₁ L	pre	14	15.4	0.88	-1.24	61	0.221
	post	49	15.7	0.73			
M ₁ W	pre	14	6.3	0.62	0.87	61	0.386
	post	49	6.2	0.33			
M ₁ trig	pre	14	10.6	0.56	-2.53	61	0.014
	post	49	11.0	0.59			
M ₂ L	pre	14	6.9	0.53	-3.31	61	0.003
	post	49	7.4	0.53			
C ['] L	pre	14	7.0	0.51	1.97	40	0.056
	post	28	6.7	0.53			
C ['] W	pre	14	4.4	0.32	0	40	1.000
	post	28	4.4	0.29			
M ['] L	pre	14	9.8	0.65	-1.31	61	0.196
	post	49	10.0	0.48			
M ['] W	pre	14	11.1	0.78	-3.24	61	0.002
	post	49	11.7	0.56			
Males							
C ₁ L	pre	18	7.7	0.7	2.04	47	0.047
	post	31	7.4	0.57			
C ₁ W	pre	18	5.0	0.4	1.45	47	0.155
	post	31	4.9	0.3			
M ₁ L	pre	18	16.4	0.86	0.34	68	0.734
	post	52	16.3	0.93			
M ₁ W	pre	18	6.5	0.31	-0.22	68	0.824
	post	52	6.5	0.3			
M ₁ trig	pre	18	11.2	0.67	-1.46	68	0.149
	post	52	11.6	0.91			
M ₂ L	pre	16	7.2	0.53	-1.83	66	0.072
	post	52	7.5	0.49			
C ['] L	pre	18	7.2	0.34	1.19	44	0.240
	post	28	7.0	0.52			
C ['] W	pre	18	4.7	0.34	0.48	44	0.637
	post	28	4.7	0.33			
M ['] L	pre	18	10.4	0.62	1.3	67	0.191
	post	51	10.2	0.42			
M ['] W	pre	18	12.2	0.53	0.03	67	0.980
	post	51	12.1	0.77			

Sexual dimorphism

We predicted increased sexual dimorphism due to competition between the raccoon dog and the red fox. Similar to earlier studies (Dayan *et al.* 1992, Szuma 2008a), we found existing sexual dimorphism in most of the studied characters. Interestingly, sexual dimorphism — especially in teeth size — decreased in the population co-existing with the raccoon dog (Table 2). We suggest that increased competition with raccoon

dogs resulted in increased dental size in females, but not in males leading to lesser degree of dimorphism. Perhaps the diet of smaller female foxes overlapped more with the diet of raccoon dogs than did the diet of larger male foxes.

We also found that the change in sexual dimorphism was greater in some characters than others (Table 2). In the pre-raccoon-dog population, fox canines showed higher degree of sexual dimorphism than found for the red fox in earlier studies (Szuma 2008a), but in the post-raccoon-dog pop-

Table 5. Differences in the relative dental measurements between pre- and post-raccoon-dog populations of Finnish foxes. The relative measurements were obtained by dividing the actual measurements by M_1L . The mean and SD of each measurement is given along with the results of Student's *t*-test.

		<i>n</i>	Mean (mm)	SD	<i>t</i>	df	<i>p</i>
Females							
C ₁ L	pre	14	0.46	0.05	1.28	42	0.206
	post	30	0.44	0.04			
C ₁ W	pre	14	0.29	0.03	-1.20	42	0.237
	post	30	0.3	0.02			
M ₁ W	pre	14	0.41	0.04	1.93	61	0.059
	post	49	0.4	0.02			
M ₁ trig	pre	14	0.69	0.04	-1.74	61	0.014
	post	49	0.7	0.03			
M ₂ L	pre	14	0.45	0.04	-2.49	61	0.015
	post	49	0.47	0.02			
C ['] L	pre	14	0.46	0.03	3.16	40	0.003
	post	28	0.43	0.03			
C ['] W	pre	14	0.28	0.02	0.8	40	0.429
	post	28	0.28	0.02			
M ['] L	pre	14	0.64	0.04	-0.17	61	0.869
	post	49	0.64	0.03			
M ['] W	pre	14	0.72	0.05	-2.29	61	0.025
	post	49	0.75	0.03			
Males							
C ₁ L	pre	18	0.47	0.04	0.99	47	0.328
	post	31	0.45	0.06			
C ₁ W	pre	18	0.31	0.02	0.48	47	0.631
	post	31	0.3	0.03			
M ₁ W	pre	18	0.4	0.02	-0.57	68	0.570
	post	52	0.4	0.02			
M ₁ trig	pre	18	0.69	0.03	-2.87	68	0.005
	post	52	0.71	0.03			
M ₂ L	pre	16	0.45	0.03	-1.34	66	0.186
	post	52	0.46	0.05			
C ['] L	pre	18	0.44	0.02	0.29	44	0.776
	post	28	0.44	0.05			
C ['] W	pre	18	0.29	0.02	-0.22	44	0.831
	post	28	0.29	0.03			
M ['] L	pre	18	0.63	0.03	0.54	67	0.592
	post	51	0.63	0.04			
M ['] W	pre	18	0.75	0.04	-0.03	67	0.800
	post	51	0.75	0.06			

ulation dimorphism dropped to the average level of the Palearctic region. Earlier studies (Szuma 2007) showed the highest sexual dimorphism in fox canines in England where foxes are not highly dimorphic in other traits such as the carnassials. They are the only canid species on the island, but occur at high densities. English foxes often are city dwellers that tend to form social groups

(Harris & Baker 2001). It is difficult to address the cause of the decreased sexual dimorphism of canines without any ecological data of the possible change in social behaviour in Finnish fox.

The sexual dimorphism of the lower carnassials has been shown to correlate with sympatry of the red fox with other *Vulpes* species (Szuma 2008a). In our study, sympatry with the raccoon

Table 6. Finnish red fox dental data for the pre- and post-raccoon-dog populations by sex. Number of specimens and the mean with SD of each measurement is given. The degree of sexual dimorphism (SP index) was calculated as a relation between the male measurement mean and the respective female measurement mean. Significance of the difference between the female and male measurements was tested using Student's *t*-test.

		<i>n</i>	Mean (mm)	SD	SP index	<i>t</i>	df	<i>p</i>
Pre-raccoon-dog period								
C ₁ L	Female	14	7.0	0.84	1.10	-2.6	30	0.014
	Male	18	7.7	0.7				
C ₁ W	Female	14	4.4	0.44	1.13	-3.83	30	0.001
	Male	18	5.0	0.4				
M ₁ L	Female	14	15.4	0.88	1.06	-3.05	30	0.005
	Male	18	16.3	0.86				
M ₁ W	Female	14	6.3	0.62	1.03	-0.97	30	0.340
	Male	18	6.5	0.31				
M ₁ trig	Female	14	10.6	0.56	1.06	-2.88	30	0.007
	Male	18	11.2	0.67				
M ₂ L	Female	14	6.9	0.53	1.03	-1.52	28	0.140
	Male	16	7.2	0.53				
C'L	Female	14	7.0	0.51	1.03	-1.19	30	0.242
	Male	18	7.2	0.34				
C'W	Female	14	4.4	0.29	1.07	-3.4	30	0.002
	Male	18	4.7	0.34				
M'L	Female	14	9.8	0.65	1.06	-2.35	30	0.026
	Male	18	10.4	0.62				
M'W	Female	14	11.1	0.78	1.10	-4.41	30	< 0.001
	Male	18	12.2	0.53				
Post-raccoon-dog period								
C ₁ L	Female	30	6.9	0.65	1.07	-2.9	59	0.005
	Male	31	7.4	0.57				
C ₁ W	Female	30	4.7	0.33	1.04	-2.28	59	0.026
	Male	31	4.9	0.31				
M ₁ L	Female	49	15.7	0.73	1.03	-3.44	99	0.001
	Male	52	16.3	0.93				
M ₁ W	Female	49	6.2	0.33	1.05	-4.67	99	< 0.001
	Male	52	6.5	0.3				
M ₁ trig	Female	49	11.0	0.59	1.05	-3.54	99	0.001
	Male	52	11.6	0.91				
M ₂ L	Female	49	7.4	0.53	1.01	-0.55	99	0.586
	Male	52	7.5	0.49				
C'L	Female	28	6.7	0.54	1.04	-2.52	54	0.015
	Male	28	7.0	0.52				
C'W	Female	28	4.4	0.32	1.07	-3.9	54	< 0.001
	Male	28	4.7	0.33				
M'L	Female	49	10.0	0.48	1.02	-1.67	98	0.098
	Male	51	10.2	0.42				
M'W	Female	49	11.7	0.56	1.03	-3.1	98	0.003
	Male	51	12.1	0.77				

dog in Finland had an opposite effect, i.e. size dimorphism decreased in the fox (Table 2). The most significant discriminating factor in Szuma's study was dimorphism increase in the M_1 length. Again our results contradicted those of Szuma's as the sympatry with the raccoon dog resulted in dimorphism decrease in the M_1 length in the red fox.

Conclusions

Competition for food resources between vixens and raccoon dogs may be heavier than competition between male foxes and raccoon dogs. It is possible that the diet of female foxes has been closer to that of raccoon dogs whereas, even before the arrival of the raccoon dog, fox males had been more carnivorous and hunted larger prey than raccoon dogs were capable of catching. During the breeding season, both parents hunt larger prey for the pups but consume smaller prey themselves (Lindström 1994). The breeding season is a time of intense competition and selection. The absolute increase in size of female teeth and trigonid may be a requirement for acquiring enough food for pups.

Finnish foxes may be specializing on larger prey such as hares (*Lepus* sp.) and the young of roe deer (*Capreolus capreolus*) (Jarnemo & Liberg 2005). If the foxes' survival or survival of pups were enhanced by better adaptations to predation on larger prey, then the ones with more carnivorous bite would be favored by natural selection.

In the light of previous dietary studies and our observations on morphology, we conclude that the Finnish red foxes (but mainly the vixens) are becoming more hypercarnivorous. This is possibly a response to the arrival of a new carnivore. However, changes in the prey composition or other environmental changes cannot be ruled out, and may contribute or be completely responsible for the change.

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References

- Baker, P. J. & Harris, S. 2004: Red foxes. The behavioural ecology of red foxes in urban Bristol. — In: Macdonald, D. W. & Sillero-Zubiri, C. (eds.), *Biology and conservation of wild canids*: 207–216. Oxford University Press, Oxford.
- Brown, W. L. Jr. & Wilson, E. O. 1956: Character displacement. — *Systematic Zoology* 5: 49–64.
- Davies, T. J., Meiri, S., Barraclough, T. G. & Gittleman, J. 2007: Species co-existence and character divergence across carnivores. — *Ecology Letters* 10: 146–152.
- Dayan, T. D., Tchernov, E., Yom-Tov, Y. & Simberloff, E. 1989: Ecological character displacement in Saharo-Arabian foxes: outfoxing the Bergmann's rule. — *Oikos* 55: 363–372.
- Dayan, T. D., Simberloff, E., Tchernov, E. & Yom-Tov, Y. 1992: Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. — *Biological Journal of Linnean Society* 45: 315–331.
- Frischia, A. R., Van Valkenburgh, B. & Bicevicius, A. R. 2007: An ecomorphological analysis of extant small carnivores. — *Journal Zoology, London* 272: 82–100.
- Harris, S. & Baker, P. 2001: *Urban foxes*. — Whittet Books, Suffolk, UK.
- Helle, E. & Kauhala, K. 1991: Distribution history and present status of the raccoon dog in Finland. — *Holarctic Ecology* 14: 278–286.
- Holmala, K. & Kauhala, K. 2009: Habitat use of medium-sized carnivores in southeast Finland — key habitats for rabies spread? — *Annales Zoologici Fennici* 46: 233–246.
- Jarnemo, A. & Liberg, O. 2005: Red fox removal and roe deer fawn survival: a 14-year study. — *The Journal of Wildlife Management* 69: 1090–1098.
- Kauhala, K. 1993: Growth, size, and fat reserves of the raccoon dog in Finland. — *Acta Theriologica* 38: 139–150.
- Kauhala, K. 2004: Removal of medium-sized predators and the breeding success of ducks in Finland. — *Folia Zoologica* 53: 367–378.
- Kauhala, K., Holmala, K., Lammers, W. & Schregel, J. 2006: Home ranges and densities of medium-sized carnivores in south-east Finland, with special reference to rabies spread. — *Acta Theriologica* 51: 1–13.
- Kauhala, K., Laukkanen, P. & von Rége, I. 1998: Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. — *Ecography* 21: 457–463.
- Larivière, S. & Pasitschniak-Arts, M. 1996: *Vulpes vulpes*. — *Mammalian Species* 537: 1–11.
- Lavrov N. P. [Лавров Н. П.] 1971: [Results of raccoon dog introductions in different parts of the Soviet Union]. — *Trudy Kafedry Biologii MGZPI* 29: 101–160. [In Russian].

- Lappalainen, M. & Vuorisalo, T. 1996: *Kaikenkarvaiset kaupunkilaiset*. — TS-Yhtymä, Turku.
- Lindström, E. 1994: Large prey for small cubs — on crucial resources of the boreal red fox population. — *Ecography* 17: 17–22
- Macdonald, D. 1987: *Running with the fox*. — Unwin Hyman, London.
- Mayr, E. 1970: *Populations, species and evolution: An abridgement of animal species evolution*. — Harvard University Press, Cambridge.
- Meiri, S., Dayan, T. & Simberloff, D. 2005a: Variability and sexual dimorphism in carnivores: testing the niche variation hypothesis. — *Ecology* 1432–1440.
- Meiri, S., Dayan, T. & Simberloff, D. 2005b: Variability and correlations in carnivore crania and dentition. — *Functional Ecology* 19: 337–343.
- Shine, R. 1989: Ecological causes for sexual dimorphism: a review of evidence. — *Quarterly Review of Biology* 64: 419–461.
- Slatkin, M. 1984: Ecological cause of sexual dimorphism. — *Evolution* 38: 622–630.
- Sutor, A., Kauhala, K. & Ansorge, H. 2010: Diet of the raccoon dog — a canid with an opportunistic foraging strategy. — *Acta Theriologica* 55: 165–176.
- Szuma, E. 2007: Geography of dental polymorphism in the red fox and its evolutionary implications. — *Biological Journal of Linnean Society* 90: 61–84.
- Szuma, E. 2008a: Geography of sexual dimorphism in the tooth size of the red fox *Vulpes vulpes* (Mammalia, Carnivora). — *Journal of Zoological Systematic and Evolutionary Research* 46: 73–81
- Szuma, E. 2008b: Evolutionary and climatic factors affecting tooth size in the red fox *Vulpes vulpes* in the Holarctic. — *Acta Theriologica* 53: 289–332.
- Van Valkenburgh, B. 1989: Carnivore dental adaptations and diet: a study of trophic diversity withing guilds. — In: Gittleman, J. L. (ed.), *Carnivore behaviour, ecology, and evolution* vol. 1: 410–436. Chapman & Hall, London.
- Van Valkenburgh, B. 1990: Skeletal and dental predictors of body mass in carnivores. — In: Damuth, J. & MacFadden, B. J. (eds.), *Body size in mammalian paleobiology: estimation and paleobiological implications*: 181–207. Cambridge University Press.
- Ward, O. G. & Wurster-Hill, D. H. 1990: *Nyctereutes procyonides*. — *Mammalian Species* 358: 1–5.
- Yom-Tov, Y., Yom-Tov, S. & Baagøe, H. 2003: Increase of the skull size in the red fox (*Vulpes vulpes*) and Eurasian badger (*Meles meles*) in Denmark during the twentieth century: an effect of improved diet? — *Evolutionary Ecology Research* 5: 1037–1048.