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Sexual dimorphism and sex identification in the South American culpeo fox, *Pseudalopex culpaeus* (Carnivora : Canidae)

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Abstract. Sexual dimorphism is analysed in skulls of the culpeo fox, *Pseudalopex culpaeus*, through multivariate and univariate approaches. The species shows a moderate level of sexual dimorphism with most cranial variables being, on average, 5% larger in males. Equations are obtained for inferring the sex of skulls of juvenile, subadult and adult culpeo foxes. The equations are based on a reduced set of variables obtained from stepwise discriminant analyses by age class on skull measurements. The discriminant power of all functions is estimated on the basis of a jackknife reclassification procedure. Correct classification is higher than 85% for both sexes, and is similar to, or higher than, the values reported for other foxes. The use of the discriminant function pooling subadult and adult skulls is recommended because it shows a high percentage of correct classification without the necessity of ascribing a collected skull to the subadult or adult age class before sex estimation. The equations provide an easy method to estimate the sex ratio of wild populations of this furbearer species using the abundant carcasses discarded throughout northwestern Patagonia as a result of the intense hunting of the species. The information on sex ratios will help in the study of population dynamics and when monitoring the harvest of culpeo foxes.

Introduction

Identification of sex and age is essential when harvesting or controlling wildlife (Caughley and Sinclair 1994). The proportion of juveniles and adults by sex can help evaluate trapping pressure, recruitment (Strickland *et al.* 1982), and population trends (Larson and Taber 1980). Sex identification is generally conducted on fresh material from primary sex characters (Larson and Taber 1980). Unfortunately, researchers often receive only skinned carcasses under varying degrees of decomposition, and often at great expense. In carnivore species, sex identification is usually based on osteological remains such as skulls (Flook and Rimmer 1965; Johnson *et al.* 1981; De Marinis *et al.* 1990), teeth (Gordon and Morejohn 1975; Dix and Strickland 1986), or pelt examination (Elder 1951).

The culpeo fox, *Pseudalopex culpaeus*, inhabits mountains and pampas along the Andean and Patagonian regions of South America from Colombia to southern Chile and Argentina (Ginsberg and Macdonald 1990; Novaro 1997). Across its range, the culpeo fox is found both in open and forested habitats, and is sometimes sympatric with other canids (Medel and Jaksic 1988; Ginsberg and Macdonald 1990). The culpeo fox, in contrast to other Argentinean furbearers such as felids and mustelids, is still under strong hunting pressure in Patagonia to reduce its predation on sheep (Bellati and von Thungen 1990) and for its fur, which is sold extensively in local and international markets (Mares and Ojeda 1984). As a result of these hunting activities, large numbers of skulls are discarded and piled up in distant sheep ranches, or found scattered across fields every year. Current management programs attempt to assess sustainability of its harvest (Novaro 1995), but this assessment needs information about the age structure and sex ratio of the culpeo populations.

Canids show sexual dimorphism to various degrees (Hildebrand 1952). Sexual dimorphism in culpeo foxes was first reported for external measurements (total, tail, hind foot, and ear lengths) from Neuquén Province, Argentina (Crespo and De Carlo 1963) and from 'Torres del Paine' National

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Park, Chile (Johnson and Franklin 1994). Novaro (1997) reported differences in average body weights (males: 11.02 kg, $n = 11$; females: 8.84 kg, $n = 11$) in Neuquén Province. Nevertheless, a detailed statistical evaluation of sexual dimorphism in the culpeo fox is lacking. In fact, sexual dimorphism was neither appraised in a recent morphology-based taxonomic revision of the group (Zunino *et al.* 1995), nor in a more general eco-morphological study on canids (Wayne *et al.* 1989). The goals of this study were to investigate sexual dimorphism in the skull morphology of the culpeo fox, and to develop a simple method for sex determination based on a few measurements of skulls collected in the field.

Material and Methods

This study was based on 77 female (42 juveniles, 18 subadults and 17 adults), and 93 male (54 juveniles, 15 subadults and 24 adults) skulls of the culpeo fox trapped from 1960 to 1963 in the Catan-Lil ranch (40°S, 71°W, 780 m above sea level), Neuquén Province, north-western Argentinean Patagonia. The skulls are deposited in the Museo Nacional de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina. The age of each specimen was determined by counting *cementum annuli* in thin sections of decalcified roots of the premolar teeth (Zapata *et al.* 1997). Skulls with permanent dentition and no *annuli* in their teeth were considered as juveniles; those with one *cementum annulum* as subadults, and those showing two or more *cementum annulli* as adults.

The following 16 standard cranial measurements were recorded by the senior author with a caliper to the nearest 0.01 mm: total length (TL), condylobasal length (COL), basilar length (BL), palatal length (PL), dental length (DL), postorbital breadth (POB), molar breadth on M^1 (MBU), zygomatic breadth (ZB), mastoid breadth (MAB), postorbital constriction (POC), condyle breadth (COB), P^4 length (P4L), mandible length (MAL), mandible height (MAH), M_1 length (M1L), and case height (CH). All measurements follow Wiig (1986), except for dental length (the distance from the incisor to the last molar in the maxilla), molar breadth (on M^1), and case height (Fernández Vicioso and López Rebollo 1994).

Data were first inspected for normality (PROC NORM of SAS). Missing values from incomplete skulls (8.78% of the original data) were estimated using the iterative EM (expectation maximisation) method of Little and Rubin (1987), which optimises the missing values as a set by stabilising the covariance matrix. All 16 variables were used to provide the most complete information about covariances. Differences at univariate level were tested by one-way ANOVAs, and significance levels were corrected for multiple comparisons for each subset of data. Overall differences between age classes, sexes, and their interaction, were tested by a two-way multivariate analysis of variance (MANOVA). Discriminant function analysis (DFA) was used to maximise differences between groups using the pooled covariance matrix. A linear combination of the more discriminant variables on the discriminant function (DF) was estimated by a stepwise discriminant analysis (to maximise at each step the mean Mahalanobis distance) for the subsets of juveniles, subadults, adults, and these two last age classes pooled. Discriminating power of the functions was tested by the option CROSSVALIDATE of PROC DISCRIM of SAS, which excludes each observation being reclassified from the data set used in the calculation of the DF (SAS 1987). All analyses were carried out using Matlab ver. 4.2c.1 (The Mathworks 1994) and SAS statistical package (SAS 1987). Copies of Matlab functions written for this study are available from the authors.

Results

Males showed consistently higher values for all measurements (except POC) and for both age classes (Appendices 1–3), having, on average, 5% larger skulls than females. The differences between sexes were all significant at the univariate level except for the mastoid breadth (MAB) and condyle breadth (COB) in subadults, which did not reach significance after the Bonferroni adjustment of the P level (Table 1). The post-orbital constriction (POC) was the most variable measurement in all age classes (Appendices 1–3), and is known to

Table 1. Sexual dimorphism in skull measurements at the univariate level

Results of one-way ANOVAs testing for differences between sexes in culpeo skull measurements by age classes. Asterisks indicate significant values after a sequential Bonferroni adjustment of significance levels to a table-wise $\alpha = 0.05$ value. Acronyms for variables are defined in Material and Methods

Variable	Juveniles			Subadults			Adults		
	F	*P*	d.f.	F	*P*	d.f.	F	*P*	d.f.
TL	36.3	<0.001*	1,86	21.8	<0.001*	1,30	33.2	<0.001*	1,34
COL	36.1	<0.001*	1,89	13.5	<0.001*	1,30	29.6	<0.001*	1,34
BL	21.4	<0.001*	1,91	16.1	<0.001*	1,29	23.9	<0.001*	1,34
PL	28.9	<0.001*	1,93	15.5	<0.001*	1,31	36.4	<0.001*	1,40
DL	45.9	<0.001*	1,86	8.3	0.007*	1,31	29.7	<0.001*	1,39
POB	21.7	<0.001*	1,91	34.0	<0.001*	1,32	17.7	<0.001*	1,37
MBU	35.1	<0.001*	1,92	29.6	<0.001*	1,32	14.8	<0.001*	1,40
ZB	14.7	<0.001*	1,81	15.9	<0.001*	1,32	19.5	<0.001*	1,36
MAB	32.1	<0.001*	1,95	6.5	0.016	1,32	35.0	<0.001*	1,40
POC	4.4	0.038	1,94	1.7	0.188	1,32	0.4	0.522	1,40
COB	35.2	<0.001*	1,96	5.4	0.027	1,32	22.2	<0.001*	1,40
P4L	29.7	<0.001*	1,89	11.4	<0.001*	1,32	10.6	0.002*	1,40
MAL	22.4	<0.001*	1,97	16.5	<0.001*	1,31	37.3	<0.001*	1,40
MAH	17.4	<0.001*	1,94	20.5	<0.001*	1,32	18.9	<0.001*	1,39
M1L	18.9	<0.001*	1,88	15.3	<0.001*	1,31	15.3	<0.001*	1,39
CH	18.5	<0.001*	1,88	0.7	0.410	1,31	16.9	<0.001*	1,39

decrease with age, particularly relative to other skull measurements (Wiig 1982). In our study, this variable was the only one to show a non-significant difference between sexes in all age classes (Table 1). The POC distance accounted also for most of the variation in exploratory multivariate analyses and was not considered in further analysis.

The MANOVA showed significant multivariate effects for sex ($F = 7.52$, d.f. = 15,152, $P < 0.001$), and age ($F = 6.41$, d.f. = 30,304, $P < 0.001$), but not for their interaction ($F = 1.11$, d.f. = 30,304, $P = 0.32$). The seven most discriminant variables for each function, and their coefficients, are listed in Table 2. All DFs were highly significant ($P < 0.001$). The percentages of correct classifications were above 85% for all discriminant functions and sexes. The highest values of the correct percentages were reached in the function for subadults and when data for subadults were combined with that for adults (Table 2).

Discussion

Both multivariate and univariate analyses clearly revealed significant sexual dimorphism in culpeo fox skulls. The dimorphism level found (5% on average) is similar to that of the red fox, *Vulpes vulpes* (Travaini and Delibes 1995), and can be considered to be 'small dimorphism' (Ralls 1976) among carnivores. Moderate sexual dimorphism is common among canids (Hildebrand 1952; Prestrud and Nilsen 1995). Nevertheless, this assertion may be based more on similar morphological patterns among the species studied than on a thorough knowledge of canids. Presumably, a small dimorphism level relates to monogamy, paternal care, and little competition for mates (Ralls 1976; Prestrud and Nilssen 1995).

The sex of any skull of the culpeo fox can be estimated by collecting skull measurements and solving the discriminant functions presented. In any of the equations a negative value will indicate that the skull is most probably that of a male. The sample used to obtain the discriminant functions can be considered unbiased given the wide array of capturing systems used in Patagonia, which include snares, traps, dog-chasing, poisoning and shooting (Novaro 1995). Nevertheless, patterns of sexual dimorphism could change as a result of the known morphological variation (mainly in body size and weight) in the species across its geographic range (Fuentes and Jaksic 1979; Jimenez *et al.* 1995). This potential problem should be addressed before our equations are applied to culpeo fox populations in other geographic areas.

All the discriminant functions achieve a level of correct classification similar to, or higher than, those obtained for other foxes (Hell *et al.* 1989), mustelids (Wiig 1986; de Marinis *et al.* 1990) or felids (du Toit *et al.* 1980; Wiig and Andersen 1986). The variables chosen in different linear combinations in the formation of the discriminant functions reflect the general cranial length, which seems to be the main difference in skull morphology between the sexes. The equations for both subadults and adults included other more trophically related variables such as the length of the teeth (first lower molar and carnassial). The variable common to all the equations is the condyle breadth (COB). This variable itself was able to classify correctly around 80% of the females, but was less useful in discriminating males. According to the variables selected in the discriminant functions, sexual dimorphism seems not to be related to any particular functional skull region in this species. The culpeo foxes differ in this characteristic from *Lynx lynx* (Wiig and Andersen 1986) and several mustelids (Wiig 1986), in which the trophic region of the skull is the major discriminant between sexes.

As would be expected, allometric relationships in the culpeo skulls changed differently with age between the sexes, the sexual dimorphism being greatest in the first year (subadults). Although juveniles of the culpeo fox can reach adult body size during their first seven months (Crespo and

Table 2. Coefficients and skull distances used in the linear discriminant functions for sex identification of the culpeo fox by age class

For any given skull, a negative value after solving the functions indicates the most probable sex to be male. Acronyms for the variables are defined in Material and Methods. The entry order in the function is shown from left to right. %F and %M show the percentages of correct classification for females and males, respectively, after a jackknife reclassification procedure (SAS 1987)

			Juveniles (%F = 85.7, %M = 85.7)				
Constant	*DL*	*COB*	*MAL*	*POB*	*PL*	*BL*	*COL*
56.844	−0.435	−0.789	0.357	0.555	0.430	0.560	−0.484
			Subadults (%F = 100.0, %M = 93.3)				
Constant	*POB*	*MBU*	*M1L*	*MAH*	*COB*	*MAB*	*MAL*
122.697	−2.342	−1.430	1.445	−2.779	−1.233	1.726	−0.629
			Adults (%F = 88.2, %M = 87.5)				
Constant	*TL*	*COB*	*BL*	*MBU*	*M1L*	*MAH*	*DL*
105.03	−1.175	−1.451	0.852	0.858	−1.452	0.401	−0.295
			Subadults + Adults (%F = 91.4, %M = 86.6)				
Constant	*TL*	*M1L*	*CH*	*POB*	*BL*	*P4L*	*COB*
68.352	−0.599	−2.087	0.522	−0.689	0.368	0.967	−0.351

De Carlo 1963), the pulp cavity of the teeth can be used to distinguish them by X-ray examination (Zapata *et al.* 1997). The basisphenoid–presphenoid suture seals up during the first year in culpeo foxes (Crespo and De Carlo 1963) and this character can be used easily in the field to distinguish subadults and adults from juveniles. Therefore, the use of the pooled equation for subadults and adults is recommended because it allows a high level of correct classifications without the necessity of ascribing a skull to the subadult or adult age class before estimation of sex.

The sex ratio in the culpeo foxes in north-western Patagonia has shifted in the last 30 years from 0.69 females per male (Crespo and De Carlo 1965) to 0.92 females per male (Novaro 1995). This trend towards a relatively larger proportion of females has also been found in other canids under high hunting pressure, such as the coyote, *Canis latrans* (Knowlton 1972), and is interpreted as a population mechanism to cope with a high mortality rate. The shift observed in the sex ratio of the culpeo fox could also indicate a severe hunting pressure on the culpeo population. The equations presented in this study will allow managers and researchers to monitor changes in the sex ratio of culpeo foxes and thus infer population responses of the culpeo population to hunting pressures.

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Appendix 1. Basic statistics for skull measurements of juvenile culpeo foxes, *Pseudalopex culpaeus*

Acronyms for variables are defined in Material and Methods. All measurements are in millimetres. c.v. = coefficient of variation

Distance	Females					Males				
	n	Mean	Min.	Max.	c.v.	*n*	Mean	Min.	Max.	c.v.
TL	39	157.4	131.6	169.4	5.2	48	167.6	151.0	178.0	4.5
COL	40	151.2	127.3	160.4	4.5	50	160.0	143.3	170.6	4.2
BL	39	140.6	116.5	149.1	5.3	53	148.2	124.7	159.5	5.4
PL	39	75.3	64.0	81.6	5.0	55	79.8	67.2	86.3	5.0
DL	36	77.9	69.8	82.8	3.7	51	82.3	74.7	87.1	3.6
POB	39	24.9	21.2	28.4	6.9	53	26.8	23.1	30.6	7.2
MBU	40	43.7	34.8	47.0	4.8	53	46.1	41.6	50.1	4.1
ZB	35	78.0	67.7	88.6	7.1	47	83.0	70.5	93.3	7.1
MAB	42	51.9	47.1	55.7	3.9	54	54.4	48.7	59.2	4.1
POC	41	25.5	22.4	28.5	6.5	54	26.4	21.2	31.3	8.5
COB	42	28.4	25.9	31.5	3.5	55	29.7	27.6	32.7	4.0
P4L	37	15.1	13.6	16.4	4.0	53	15.9	14.3	17.5	4.9
MAL	42	115.4	96.4	124.7	6.1	56	122.3	99.0	133.2	6.0
MAH	41	40.2	33.7	44.3	7.4	54	42.9	35.2	49.4	7.5
M1L	37	16.0	14.6	16.9	3.4	52	16.6	13.4	18.1	4.9
CH	42	51.7	49.2	57.7	3.3	51	53.4	50.6	58.7	3.5

Appendix 2. Basic statistics for skull measurements for subadult culpeo foxes, *Pseudalopex culpaeus*

Acronyms for variables are defined in Material and Methods. All measurements are in millimetres. c.v. = coefficient of variation

Variable	Females					Males				
	n	Mean	Min.	Max.	c.v.	*n*	Mean	Min.	Max.	c.v.
TL	18	168.2	159.8	176.7	3.2	13	178.3	164.9	188.4	3.7
COL	18	160.6	154.2	169.1	3.3	13	168.2	156.0	175.5	3.8
BL	17	150.2	143.7	158.4	3.3	13	158.2	147.0	165.0	3.7
PL	17	80.3	75.6	84.3	3.2	15	84.1	78.0	87.9	3.4
DL	17	82.1	78.3	86.4	3.3	15	85.1	79.3	90.3	3.7
POB	18	27.3	25.8	30.1	3.7	15	29.8	27.6	32.1	4.8
MBU	18	45.6	43.1	48.6	2.7	15	48.1	45.1	50.9	2.8
ZB	18	87.5	82.3	95.3	4.0	15	93.3	83.7	101.5	5.2
MAB	18	54.1	51.3	57.4	3.5	15	56.2	51.3	61.2	4.6
POC	18	26.4	23.5	28.9	5.5	15	26.4	22.6	30.5	7.5
COB	18	28.9	27.2	30.7	3.6	15	30.1	26.5	32.4	5.9
P4L	18	15.3	14.5	16.6	4.0	14	16.2	14.7	17.5	4.5
MAL	18	124.0	117.4	131.8	3.4	15	130.5	121.3	137.3	3.9
MAH	18	43.3	40.0	47.8	5.1	15	46.9	42.6	50.5	4.9
M1L	18	16.3	15.2	17.5	3.4	14	17.0	16.0	17.8	3.3
CH	18	53.9	50.3	56.4	3.5	14	54.5	51.0	57.8	3.8

Appendix 3. Basic statistics for skull measurements for adult culpeo foxes, *Pseudalopex culpaeus*

Acronyms for variables are defined in Material and Methods. All measurements are in millimetres. c.v. = coefficient of variation

Variable	Females					Males				
	n	Mean	Min.	Max.	c.v.	*n*	Mean	Min.	Max.	c.v.
TL	17	168.7	156.5	177.6	3.4	18	179.8	169.3	191.7	3.1
COL	17	161.2	150.3	172.1	3.5	18	170.8	163.6	181.3	4.8
BL	17	151.3	140.9	161.4	3.8	18	159.8	151.7	170.1	2.8
PL	17	80.5	77.2	85.5	3.1	24	85.2	79.0	90.7	2.8
DL	16	81.6	77.6	86.9	3.1	24	86.3	81.2	92.0	3.2
POB	15	28.0	23.4	31.2	6.2	23	30.5	27.0	33.7	5.8
MBG	17	46.2	40.1	51.0	5.3	24	49.2	45.9	52.4	3.7
ZB	15	89.5	75.2	98.2	6.2	22	96.5	87.4	103.2	4.3
MAB	17	54.4	49.6	57.9	3.5	24	57.8	54.8	61.0	3.1
POC	17	25.7	22.8	30.1	6.7	24	26.1	21.0	29.6	8.3
COB	17	29.0	26.7	32.8	4.7	24	30.9	28.5	33.0	3.6
P4L	17	15.4	14.0	16.9	4.8	24	16.1	14.6	17.3	4.0
MAL	17	124.7	112.0	135.7	4.3	24	133.5	126.1	142.3	2.9
MAH	17	43.7	40.1	48.4	5.1	23	47.6	42.3	56.2	6.6
M1L	17	16.1	14.9	17.0	3.7	23	16.9	15.3	17.7	3.7
CH	17	53.3	48.8	56.8	3.7	22	56.2	52.3	60.4	4.1

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