

# SEXUAL DIMORPHISM IN CRANIAL SIZE AND SHAPE AMONG RED FOXES *VULPES VULPES* FROM NORTH-EAST IRELAND

John M. Lynch

## ABSTRACT

Sexual dimorphism in cranial form was investigated for a sample of 204 adult red foxes *Vulpes vulpes* from north-east Ireland. Using a combination of principal component analysis and discriminant function analysis, size variation and allometry was found to account for 65.29% of the between-sex variation. The crania of male foxes were larger, more elongate and had a relatively narrower post-orbital constriction than those of the female of the species. A set of discriminant functions allowed sexing of unsexed material with over 86% accuracy. Discriminant functions derived from English and Welsh fox populations were found to sex Irish foxes with 78.4% and 85.8% accuracy, thus indicating that discriminant functions may not be entirely population-specific. These findings were discussed in the light of other studies of dimorphism in the species and on the 'adaptive' nature of such shape variation in carnivores.

## INTRODUCTION

The red fox *Vulpes vulpes* L. is one of the six members of the mammalian order Carnivora that occur in Ireland. Whilst the species has a widespread distribution throughout most of the northern hemisphere (Harris and Loyd 1991), British and Irish populations were formerly ascribed to the subspecies *V. v. crucigera* Bechstein 1789, which was said to be slightly smaller than the nominate form while having widely spaced premolars (Miller 1912). Continuity of range in the species is such that it is doubtful whether any discrete subspecies can be recognised (Corbet 1978). In common with most mammalian species that occur in Ireland, we know little about morphological or genetic variation amongst red foxes within the island, nor indeed about variation between Irish and other European populations. However, recent studies have provided information on four of the other carnivore species. There is substantial morphological variation between British, Irish and European populations of the American mink *Mustela vison* (Lynch and Hayden 1995), the otter *Lutra lutra* (Lynch, Conroy *et al.* 1996), the badger *Meles meles* (Lynch, O'Corry-Crowe *et al.* 1993) and stoat *Mustela erminea* (Lynch, in press). This current study examines sexual dimorphism in the cranium of the fox.

Most of our knowledge about the ecology and biology of the red fox in Ireland comes from the studies of Fairley (1969; 1970). Fairley and Bruton (1984) examined craniometric variation in a sample of 253 crania collected in the late 1960s and

held in the collections of the Ulster Museum. They discovered significant differences between skulls from Antrim and Down and that north-eastern Irish foxes had longer skulls than those of their counterparts in southern England. In addition, they demonstrated that, for all dimensions examined (except width of the post-orbital constriction), the mean for males exceeded that for females.

Fairley and Bruton (1984) utilised standard univariate statistical techniques to examine dimorphism. Morphometric variation is unlikely to be due to adaptation of a few characters to a single environmental variable; it is more likely to be a multidimensional process involving the adaptation of many characters to a variety of interdependent environmental factors. Thus a correct understanding of such variation will be derived from a multivariate perspective (Gould and Johnston 1972), and so we ought to strive to examine the patterns of variance and covariance among characters using multivariate statistics. While there has been some debate as to the relative suitability of univariate and multivariate methodology (Corruccini 1987; Willig *et al.* 1986), it has been generally realised that multivariate methods offer many advantages to the researcher (Lynch and O'Sullivan 1993). The use of discriminant functions (Neff and Marcus 1980) to sex unknown specimens appears to be one of the more popular multivariate techniques, although there is some debate as to the applicability of discriminant functions to populations beyond those from which they are derived (Calgano 1981; Wood and Lynch, in press).

J.M. Lynch, Mammal Research Group, Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland. Present address: Interdisciplinary Humanities Program, Arizona State University, Tempe, AZ 85287-0302, USA.

Received 24 April 1995. Read 11 December 1995. Published 14 June 1996.

In the present paper discriminant function and principal component analyses are used to describe the differences in cranial size and shape that occur between male and female foxes from north-east Ireland. A mathematical function is presented which allows sex determination for material of unknown sex, and these results are discussed in the light of previous studies of sexual dimorphism within this species.

#### MATERIAL AND METHODS

This study is based on the crania of 210 foxes in the collections of the Ulster Museum (Belfast) that were previously studied by Fairley and Bruton (1984). Raw data were lodged in the museum's archives by J.S. Fairley and, as will be detailed below, a total of 204 specimens formed the database for the results presented herein. All specimens originated from either Antrim (88 males and 87 females), Down (15 males and 13 females) or Tyrone (one male), and all were considered adult by Fairley and Bruton (1984).

A maximum of eleven standard craniometric measurements were available for each specimen. These are detailed in Southern 1964 and Fairley and Bruton 1984: greatest length (GL), condylobasal length (CL), occipitonasal length (OL), palatal length (PA), mastoid width (MA), zygomatic width (ZW), width of the post-orbital constriction (PO), width of the occipital condyles (OC), length of the maxillary tooth row (TR), height of the braincase (BH), and length of the mandible (LM). Some specimens (87; 41.4%) were damaged in such a manner as not to allow one or more of these measurements to be taken. Fifty-one specimens were missing one measurement and 36 two or more, while most (206 out of 210) specimens had the measurements CL, PA, PO and

OC. As multivariate procedures require data with no missing values, stepwise multiple regression was utilised to estimate the missing data. This form of estimation has previously been used in morphometric studies (e.g. Reig 1992) without serious problems, such as leading to inaccurate estimation of sample means and covariances. Regression equations were developed to predict missing values of the variables based on subsets of the four variables present in most specimens. The full details of these regressions are presented in Table 1. It should be noted that no attempt was made to predict missing values based on values that were previously estimated using regression. The absolute value of mean residuals varied between 0.0mm and 0.05mm for measurements that were taken to an accuracy of 0.1mm. Thus these estimations are unlikely to greatly affect the multivariate results presented here.

Sexual dimorphism was investigated using a combination of multiple group principal component analysis (MGPCA; Thorpe 1988) and discriminant function analysis. Full details of these methods are given in Lynch and O'Sullivan 1993, and only a brief summary is given below. Data were pooled by sex and log-transformed. A principal component analysis of the pooled within-group covariance matrix resulted in principal components, the first of which can often (as here) be said to represent within-group size variation. The subsequent ten components can then be said to represent size-independent shape variation. These components can be interpreted by examining the signs and magnitudes of the component coefficients (Table 2), and non-significant coefficients were detected using asymptotic procedures (see Lynch and O'Sullivan 1993). Univariate ANOVAs were carried out on the principal components to detect variation between the sexes. ANOVA *P*-

**Table 1—Details of the stepwise multiple regressions utilised to estimate missing values. All regressions were significant at  $P < 0.0001$ . Abbreviations for measurements are given in the text. 'R' is the multiple correlation coefficient. 'Intercept' is the intercept for the equation to predict the dependent. 'CL', 'PA', 'PO' and 'OC' are regression coefficients ('—' indicates that the variable was not selected by the stepwise procedure).**

Dependent	R	F	df	Intercept	Regression coefficient				Mean residual	SD of residual
					CL	PA	PO	OC		
GL	0.954	592.93	3, 176	+0.635	+0.919	+0.247	-0.219	—	-0.0006	0.2001
ON	0.943	1513.27	1, 188	-0.241	+0.953	—	—	—	-0.0010	0.2011
MA	0.742	111.78	2, 183	+1.312	+0.212	—	—	+0.213	+0.0000	0.1298
ZY	0.773	256.51	1, 173	+1.632	+0.454	—	—	—	+0.0005	0.2200
TR	0.867	330.77	2, 176	+0.643	+0.268	+0.422	—	—	+0.0013	0.1509
HB	0.590	104.49	1, 196	+2.541	+0.169	—	—	—	-0.0009	0.1387
LM	0.951	1846.36	1, 195	-0.274	+0.792	—	—	—	-0.0049	0.1603

values were adjusted for multiple comparisons using the Bonferroni procedure, such that a  $P$  less than 0.0045 was required for statistical significance. Finally, the components were entered into a discriminant function analysis which aimed to examine the ability of cranial size and shape to differentiate the sexes. As the results of multivariate analyses of this nature are often dependent on the number of observations (in this case 204) and the number of variables (11), Wilks's  $\Lambda$  statistics (a measure of the degree of separation between the two groups, which decreases with increased separation) were calculated for 10,000 randomisations of the dataset (i.e. specimens were assigned a sex randomly, and a discriminant analysis run on this artificial dataset). If the difference between the sexes is truly not an artifact of the data, the Wilks's  $\Lambda$  statistic for the real dataset should be less than the 10,000 values from the randomised datasets. Randomisations were carried out using the MULTIVAR program (Cavalcanti 1995), while all other statistical analyses were carried out using version 6.01 of SPSS for Windows.

## RESULTS

Although six (PCs 1, 2, 3, 4, 7 and 8) of the eleven derived principal components contributed to variation between the sexes, only three (PCs 1, 2 and 7) retained significance following Bonferroni adjustment (Tables 2 and 3). The first principal component had positive coefficients of similar magnitude for all measurements except width of the post-orbital constriction (PO). This exception aside, the first principal component can be said to describe size variation and that shape variation that

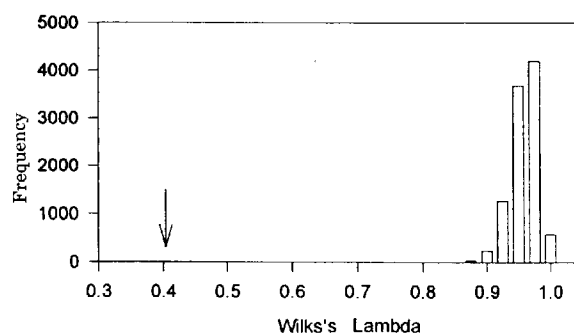


Fig. 1—Histogram of Wilks's  $\Lambda$  values obtained from 10,000 randomisations of the dataset. The arrow marks the  $\Lambda$  value obtained for the 'real' data. This value is less than all other values obtained, thus indicating that the results obtained in this analysis are not an artifact of the high dimensionality ( $204 \times 11$ ) of the dataset.

can be attributed to scaling (allometric shape). This component accounted for 48.9% of the variation within and 65.3% of the variation between the sexes. Male foxes had larger skulls than females (having greater values of PC1; Table 3), and a narrower post-orbital constriction (high values for PC2; Table 3) than those of the female of the species. PC7 was a measure of decreasing skull length for overall skull size and was greatest in females (Table 3). Male foxes thus have relatively large, elongate skulls with narrow post-orbital areas.

As might be expected, when all eleven principal components are entered into a discriminant function analysis, a significant separation results (Wilks's  $\Lambda = 0.445$ ;  $F = 21.76$ ;  $df = 11$  and  $192$ ;  $P < 0.0001$ ). This separation was more significant than the 10,000 others derived from randomised analyses ( $P < 0.0001$ ; Fig. 1). The Mahalanobis

Table 2—Coefficients for the derived multiple group principal components (PC); 'ns' indicates a non-significant coefficient; '%WV' and '%BV' are the percentage of within- and between-sex variation accounted for by a given principal component.

PC	1	2	3	4	5	6	7	8	9	10	11
GL	+0.33	ns	-0.13	ns	ns	ns	-0.34	ns	ns	ns	ns
CL	+0.34	ns	ns	ns	ns	ns	-0.19	ns	ns	ns	ns
OL	+0.34	ns	-0.10	ns	ns	ns	-0.50	ns	+0.53	-0.53	ns
PA	+0.34	ns	-0.20	-0.34	ns	ns	ns	+0.68	ns	ns	ns
MA	+0.27	ns	ns	ns	-0.58	+0.64	ns	ns	ns	ns	ns
ZY	+0.29	ns	ns	+0.57	ns	-0.58	ns	ns	ns	ns	ns
PO	ns	-0.97	ns	ns	ns	ns	ns	ns	ns	ns	ns
OC	+0.29	ns	+0.89	ns	ns	ns	ns	ns	ns	ns	ns
TR	+0.34	ns	-0.20	-0.28	ns	ns	ns	-0.64	ns	ns	ns
HB	+0.18	ns	ns	ns	+0.75	+0.33	ns	ns	ns	ns	ns
LM	+0.36	ns	-0.12	ns	ns	ns	ns	ns	-0.75	ns	ns
%WV	48.94	23.63	9.12	5.69	4.54	2.43	2.02	1.67	1.06	0.48	0.44
%BV	65.29	13.84	2.91	2.49	0.53	0.89	10.28	1.82	0.38	0.29	1.28

distance (difference between the mean discriminant score for each sex) was 4.939 standard deviation units. This distance decreased to 1.714 units when an analogous analysis was carried out using all principal components except the first. Thus, removal of size resulted in the sexes being less readily separated, though the separation remained highly significant (Wilks's  $\Lambda = 0.698$ ;  $F = 8.35$ ;  $df = 10$  and  $193$ ;  $P < 0.0001$ ; Fig. 2). This reduced separation is clearly seen if the derived discriminant functions are utilised to reclassify the specimens. The function which included size allocated 84.8% of the specimens correctly, while the 'size-out' function correctly allocated 75.4%.

As an aid to the future examination of unsexed specimens, a discriminant function can be developed from the raw data (in centimetres). Step-wise linear discriminant function analysis was utilised to choose that subset of the eleven variables that best separated the sexes (i.e. minimised the Wilks's  $\Lambda$  statistic). The function contrasted two measurements, such that

$$D = 2.114[GL] - 1.874[PO] - 27.478,$$

with a  $D$ -value greater than zero indicating a male, and less than zero a female (Wilks's  $\Lambda = 0.472$ ;  $P < 0.0001$ ). This function clearly shows the increased greatest skull length of the male versus the increased width of the post-orbital constriction of the female. As such, it primarily reflects the separation achieved by the first two within-group principal components. The functions allowed 86.0% of the female and 87.5% of the male foxes to be correctly sexed, thus giving a theoretical accuracy of, on average, 86.8%.

### DISCUSSION

This study has described the pattern of variation in skull shape and size between male and

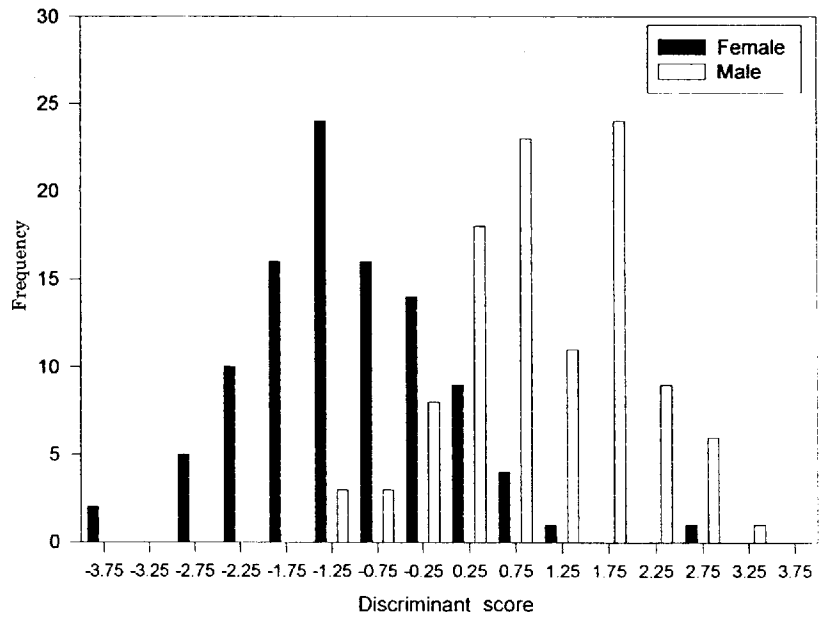


Fig. 2—Separation between male and female red foxes on the basis of a discriminant function derived from ten within-group principal components (the first component removed).

female foxes from the north-eastern region of Ireland. Size variation and allometric scaling were found to account for 65.3% of the between-sex variation. Male foxes were found to have relatively large, elongate skulls with narrow post-orbital areas. Derived discriminant functions allowed between 73% and 87% of specimens to be correctly reallocated to their sex.

A number of previous studies have examined sexual dimorphism within fox populations. Churcher (1960) used zygomatic width, total length and mastoid width to sex 113 specimens with 89.3% accuracy. Frajford (1993) used a discriminant function of eight cranial measurements to classify

Table 3—Summary statistics for the eleven principal components derived from the dataset. 'F' and 'P' refer to the significance of differences between the male and female groups. 'P' values marked 'NS' were non-significant.

PC	Male mean	Male SD	Female mean	Female SD	F	P
1	2.9133	0.0367	2.8458	0.0385	164.41	0.0001
2	0.0630	0.0267	0.0416	0.0254	34.85	0.0001
3	-0.4377	0.0193	-0.0431	0.0121	7.32	NS
4	-0.2251	0.0130	-0.2228	0.0122	6.28	NS
5	0.0395	0.0133	0.0378	0.0092	1.33	NS
6	0.1144	0.0092	0.1125	0.0074	2.25	NS
7	-0.2736	0.0083	-0.2682	0.0069	25.89	0.0001
8	0.0314	0.0074	0.0293	0.0064	4.58	NS
9	-0.0666	0.0052	-0.0658	0.0059	0.95	NS
10	0.1595	0.0038	0.1590	0.0036	0.72	NS
11	0.0147	0.0037	0.0156	0.0034	3.22	NS

116 Norwegian red foxes with an accuracy of 73%, while Huson and Page (1979) provide discriminant functions for both Welsh and English fox populations. The Welsh function reclassified specimens with an accuracy of 88% ( $n = 379$ ) and was derived using four measurements (zygomatic width, greatest length, condylobasal length and palatal length). The English function (which used greatest length and palatal length) achieved 80% accuracy ( $n = 192$ ). If these various functions are used to reclassify the Irish material, 78.4% and 85.8% accuracy are achieved with the English and Welsh functions respectively. Thus, while it would appear that although the measurements selected by various analyses differ, their ability to sex specimens would appear to be similar (c. 80–90%) when used on the dataset from which they are derived. Indeed, within the British Isles at least, functions derived for one population (either Welsh or English) would appear to have some utility in sexing material from another (Irish) population. Thus it would appear that, even allowing for between-population size differences (as occur between larger Irish and smaller English foxes; Fairley and Bruton 1984), population-independent discriminant functions exist which allow sexing of cranial material with reasonable accuracy. Ongoing research aims to examine variation in patterns of sexual dimorphism within British, Irish and other European populations of the red fox.

The evolution of dimorphism in body size, shape and ornamentation has fascinated evolutionary biologists for many years. Both sexual selection (Darwin 1871; Andersson 1994) and avoidance of competition (Selander 1966; Shine 1989) have been seen as agents promoting dimorphism in body size (and shape). While the effects of sexual selection pervade many of the aspects of an animal's biology (Møller 1994), examples of size-independent difference in trophic structure offer strong evidence for the importance of ecological factors (see Shine 1989 for review). As with many other carnivores (e.g. otter, Lynch and O'Sullivan 1993; mink, Lynch and Hayden 1995; wolverine *Gulo gulo*, Wiig 1989), male foxes are relatively narrow in the inter-orbital region and thus have the potential for stronger bite forces which could allow handling of relatively larger prey (Wiig 1986; Lynch and O'Sullivan 1993). While there is abundant evidence for niche separation between the sexes of mustelids (Dayan and Simberloff 1994), current evidence does not indicate any such separation between male and female foxes (and indeed, between the sexes of other canids). If relative narrowing of the inter-orbital region allows niche (dietary) separation beyond that brought about by gross size differences, the trait may indeed be considered an adaptation. However, it may be more correct to say that this narrowing is not an adaptation *per se*, but an epiphenomenon which,

once present, would allow such niche separation. The trait is thus an exaptation (a trait that has not resulted from selection for its current use; Gould and Vrba 1982). More importantly, the two general hypotheses (sexual selection and niche separation) must not be seen as in some way competing but as working in tandem, producing the final phenotype (Lynch and O'Sullivan 1993). As Mayr (1982) notes, 'too often . . . evolutionary factors or processes are presented as alternatives when in reality they occur simultaneously'.

As with previous studies of morphological variation among Irish carnivores, it is obvious that we know too little about the behaviour, ecology and population genetics of mammalian species within the island. The importance of islands as 'natural experiments' has been recognised by many authors. With its impoverished fauna (Corbet and Harris 1991) and unique biogeographic history (Sleeman *et al.* 1986; Costello and Kelly 1993), Ireland is in a singular position within Europe to test many important evolutionary hypotheses, and collaborative research between Irish and other European biologists must form an important part of future studies.

#### ACKNOWLEDGEMENTS

It is my great pleasure to thank James Fairley (University College Galway) for making available the data from his original study. Mauro J. Cavalcanti (Universidade Santa Ursula, Rio de Janeiro, Brazil) kindly provided help with his MULTIVAR program. This study was conducted while in receipt of funding from EOLAS and the Mammal Society of Britain and Ireland.

#### REFERENCES

- Andersson, M. 1994 *Sexual selection*. Princeton University Press.
- Calgano, J.M. 1981 On the applicability of sexing human skeletal material by discriminant function analysis. *Journal of Human Evolution* **10**, 189–98.
- Cavalcanti, M.J. 1995 *MULTIVAR—Comparison of multivariate samples with randomization tests*. MSDOS software. Departamento de Biologia Geral, Universidade Santa Ursula, Rua Fernando Ferrari, 75, Botafogo, 22231-040, Rio de Janeiro, Brazil.
- Churcher, C.S. 1960 Cranial variation in the North American red fox. *Journal of Mammalogy* **41**, 349–60.
- Corbet, G.B. 1978 *The mammals of the Palaearctic region: a taxonomic review*. London. British Museum (Natural History).
- Corbet, G.B. and Harris, S. (eds) 1991 *The hand-*

- book of British mammals (3rd edn). Oxford. Blackwell Scientific Publications.
- Corruccini, R.S. 1987 Univariate versus multivariate morphometric variation: an alternative viewpoint. *Systematic Zoology* **36**, 396–7.
- Costello, M.J. and Kelly, K.S. (eds) 1993 *Biogeography of Ireland: past, present and future*. Dublin. Irish Biogeographical Society.
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London. Murray.
- Dayan, T. and Simberloff, D. 1994 Character displacement, sexual size dimorphism, and morphological variation among the mustelids of the British Isles. *Ecology* **75**, 1063–73.
- Fairley, J.S. 1969 Tagging studies of the red fox (*Vulpes vulpes* (L.)) in north-east Ireland. *Journal of Zoology, London* **159**, 527–32.
- Fairley, J.S. 1970 The food, production, form, growth and development of the fox *Vulpes vulpes* (L.) in north-east Ireland. *Proceedings of the Royal Irish Academy* **69B**, 103–37.
- Fairley, J.S. and Bruton, T. 1984 Some observations on a collection of fox skulls from north-east Ireland. *Irish Naturalists' Journal* **21**, 349–51.
- Frafjord, K. 1993 Sexual size dimorphism in the skull of the Norwegian red fox *Vulpes vulpes* L. *Fauna Norvegica, Series A* **14**, 59–60.
- Gould, S.J. and Johnston, R.F. 1972 Geographic variation. *Annual Review of Ecology and Systematics* **3**, 457–98.
- Gould, S.J. and Vrba, E.S. 1982 Exaptation—a missing term in the science of form. *Palaobiology* **8**, 4–15.
- Harris, S. and Loyd, H.G. 1991 Fox. In G.B. Corbet and S. Harris (eds), *The handbook of British mammals* (3rd edn), 351–67. Oxford. Blackwell Scientific Publications.
- Huson, L.W. and Page, R.J.C. 1979 A comparison of fox skulls from Wales and south-east England. *Journal of Zoology, London* **187**, 465–70.
- Lynch, J.M. (in press) Postglacial colonisation of Ireland by mustelids, with particular reference to the badger (*Meles meles* L.). *Journal of Biogeography* **23** (1).
- Lynch, J.M. and Hayden, T.J. 1995 Genetic influences on cranial form: variation among ranch and feral American mink *Mustela vison* (Mammalia: Mustelidae). *Biological Journal of the Linnean Society* **55**, 293–307.
- Lynch, J.M. and O'Sullivan, W.M. 1993 Cranial form and sexual dimorphism in the Irish otter *Lutra lutra* L. *Biology and Environment: Proceedings of the Royal Irish Academy* **93B**, 97–105.
- Lynch, J.M., Conroy, J.W.H., Kitchener, A.C., Jefferies, D.J. and Hayden, T.J. 1996 Variation in cranial form and sexual dimorphism among five European populations of the otter *Lutra lutra* (L.). *Journal of Zoology, London* **238**, 81–96.
- Lynch, J.M., O'Corry-Crowe, G., Cheeseman, C.L., Harris, S., Duke, E.J. and Hayden, T.J. 1993 Morphometric and genetic variation among badger populations. In T.J. Hayden (ed.), *The badger*, 94–107. Dublin. Royal Irish Academy.
- Mayr, E. 1982 *The growth of biological thought*. Cambridge. Belknap Press of Harvard University Press.
- Miller, G.S. 1912 *Catalogue of the mammals of western Europe exclusive of Russia in the collection of the British Museum*. London. British Museum.
- Møller, A.P. 1994 *Sexual selection and the barn swallow*. Oxford University Press.
- Neff, N.A. and Marcus, L.F. 1980 *A survey of multivariate methods for systematics*. New York. American Museum of Natural History (privately published).
- Reig, S. 1992 Geographic variation in pine marten (*Martes martes*) and beech marten (*M. foina*) in Europe. *Journal of Mammalogy* **73**, 744–69.
- Selander, R.K. 1966 Sexual dimorphism and differential niche utilisation in birds. *Condor* **68**, 113–51.
- Shine, R. 1989 Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* **64**, 419–61.
- Sleeman, D.P., Devoy, R.J. and Woodman, P.C. (eds) 1986 *Proceedings of the Postglacial Colonisation Conference*. Dublin. Irish Biogeographical Society.
- Southern, H.N. (ed.) 1964 *The handbook of British mammals* (1st edn). Oxford. Blackwell.
- Thorpe, R.S. 1988 Multiple group principal component analysis and population differentiation. *Journal of Zoology, London* **216**, 37–40.
- Wiig, Ø. 1986 Sexual dimorphism in the skull of minks *Mustela vison*, badgers *Meles meles*, and otters *Lutra lutra*. *Zoological Journal of the Linnean Society* **87**, 163–79.
- Wiig, Ø. 1989 Craniometric variation in Norwegian wolverines *Gulo gulo* L. *Zoological Journal of the Linnean Society* **95**, 177–204.
- Willig, M.R., Owen, R.D. and Colbert, R.L. 1986 Assessment of morphometric variation in natural populations: the inadequacy of the univariate approach. *Systematic Zoology* **35**, 195–203.
- Wood, C.G. and Lynch, J.M. (in press) Sexual dimorphism in the craniofacial skeleton of modern humans. In L.F. Marcus, M. Corti, A. Loy, D. Slice and G.J.P. Naylor (eds), *Advances in morphometrics. Proceedings of the 1993 NATO Advanced Study Institute*. New York. Plenum Press.