Animal Conservation (2005) **8**, 223–237 © 2005 The Zoological Society of London. Printed in the United Kingdom doi:10.1017/S1367943005002301

A diagnosis for the Scottish wildcat (*Felis silvestris*): a tool for conservation action for a critically-endangered felid

Andrew C. Kitchener[1,2,†], Nobuyuki Yamaguchi[3], Jennifer M. Ward[1] and David W. Macdonald[3]

[1] Department of Natural Sciences, National Museums of Scotland, Chambers Street, Edinburgh, EH1 1JF, UK
[2] Institute of Geography, School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP, UK
[3] Wildlife Conservation Research Unit, Department of Zoology, South Parks Road, Oxford, OX1 3PS, UK

(Received 8 November 2004; accepted 1 March 2005)

Abstract

A recent estimate suggests that the Scottish wildcat may be critically endangered. Nevertheless, there is still no uncontroversial method for diagnosing the Scottish wildcat. We analysed morphological differences between wild-living cats in Scotland on the basis of 20 pelage characters, scoring from 1 (domestic cat) to 3 (wildcat), in combination with 40 skull parameters and intestinal length. A cluster analysis, based on Principal Components derived from the scores for pelage characters, showed that the wild-living cats fell into three main groups without any *a priori* classification. Each group corresponds well to the traditional characteristics of wildcats, hybrids and domestic cats, respectively, and the former two each show higher levels of morphological homogeneity compared with the third group. The three groups are most significantly differentiated by seven pelage characters: (1) extent of dorsal stripe, (2) shape of tail tip, (3) distinctness of tail bands, (4) presence/absence of broken stripes and (5) spots, on flanks and hindquarters, (6) shape and number of stripes on nape and (7) on the shoulders. Most Group-1 cats (75.6%, $n = 74$), but none of the other two groups, score more than 2 for all seven characters. All Group-3 cats ($n = 35$) and some Group-2 cats (19.2%, $n = 26$), but no Group-1 cats, scored 1 for one or more of the seven characters. We propose that Group-1, which is the furthest from the domestic cat in all criteria, should be used to define the Scottish wildcat. However, in practice, if a wild-living cat does not score 1 for any of the seven characters it should be treated as a wildcat in the field. These definitions provide a simple way of diagnosing a Scottish wildcat scientifically, as well as practically, which will effectively facilitate conservation action and the enforcement of protective legislation.

INTRODUCTION

The Scottish wildcat (*Felis silvestris grampia* Miller, 1907) is the only surviving indigenous wild felid in Britain. It is endangered and in the UK has full legal protection under Schedule 5 of the Wildlife and Countryside Act, 1981 (as amended in 1988), which is also required by the EU under Annex IV of the European Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora (Kitchener, 1998; Beaumont *et al*., 2001). Nevertheless, there has been considerable controversy in recent years concerning practical conservation of the Scottish wildcat, including enforcing protective legislation, largely due to whether it is possible reliably (and practically) to identify wildcats owing to extensive introgressive hybridisation with the domestic cat (*Felis catus* L., 1758: Nowell & Jackson, 1996; Balharry & Daniels, 1998; Kitchener, 1998). Meanwhile, it has been estimated that the current population of Scottish wildcats that is considered to be uninfluenced, or least influenced by introgression, could be as low as 400 individuals (Yamaguchi *et al*., 2004*b*). Based on this estimate, it is clear that the Scottish wildcat is critically endangered and that conservation action is required to restore it to viable population levels. Notwithstanding the considerable problems that need to be addressed in how to manage the conservation of the wildcat actively (Macdonald *et al*., 2004; Yamaguchi *et al*., 2004*a*), there is an urgent need for a reliable and practical diagnosis for the Scottish wildcat for both legal protection and conservation action.

Since hybridisation with the ubiquitous domestic cat is believed to have been occurring not only in Scotland but also worldwide for more than 200 years and, possibly, up to a few thousand years (Bewick, 1807; Hamilton, 1896; Roberts, 1951; Smithers, 1983; Harrison & Bates, 1991; Hubbard *et al*., 1992; Nowell & Jackson, 1996; Daniels *et al*., 2001), studies have been

[1]All correspondence to: Andrew C. Kitchener. National Museums of Scotland, Chambers Street, Edinburgh, EH1 1JF, UK. Tel: 0131-247-4240; Fax: 0131-220-4819; E-mail: a.kitchener@nms.ac.uk

carried out to try to distinguish 'pure' wildcats from feral domestic cats and their hybrids on the basis of various morphological characteristics including, for example, a shorter intestinal length (Schauenberg, 1977), a cranial index of less than 2.75 (Schauenberg, 1969), an index of purity based on scores for body and tail measurements and pelage characters (Suminski, 1962) and skull characters and measurements (Kratochvíl, 1973; French, Corbett & Easterbee, 1988). However, none of these characters can be examined in live animals and, hence, although undoubtedly important, they may have only limited application for identification in the field. Furthermore, since Scottish wildcats have been potentially sympatric with domestic cats since the Iron Age (up to *ca*. 3000 years ago; see Smith *et al*., 1994), there is the possibility that most, if not all, of the remaining population has been affected by introgression with domestic cats (Daniels *et al*., 1998; Kitchener, 1998). Therefore, attempting to develop a diagnosis for the Scottish wildcat by assuming the existence of 'pure' wildcats may be neither scientific nor practical without defining it properly (Daniels *et al*., 1998; Kitchener, 1998; Beaumont *et al*., 2001). Refining such a diagnosis is hampered by the absence of specimens from a pre-hybridisation Scottish wildcat population, although a comparison of specimens from a long time series (100 + years), or with those of other European populations which show different degrees of introgression, does provide ways of elucidating the key pelage characters that distinguish wildcats from domestic cats and their hybrids.

Based on morphological and genetic characteristics, without assuming the existence of 'pure' wildcats *a priori*, there seems to be two or more groups of wild-living cats in Scotland, which appear to form a morphological cline from the domestic cat at one end to wild-living cats at the other, which have many, if not all, of the characteristics traditionally associated with the wildcat, including a robust skull, low cranial index (i.e. greater cranial capacity) and short intestinal length (Daniels *et al*., 1998; Kitchener, 1998; Beaumont *et al*., 2001; Reig, Daniels & Macdonald, 2001; Yamaguchi *et al*., 2004*a*). Therefore, defining the Scottish wildcat based on the characteristics of the group of wild-living cats furthest from the domestic cat may be the best available option for the long-term conservation of the population (Daniels *et al*.,1998; Kitchener, 1998; Reig *et al*., 2001). The group furthest (morphologically and genetically) from the domestic cat appears to be characterised by the possession of the traditional pelage characters of the Scottish wildcat (Beaumont *et al*., 2001; Daniels *et al*., 2001; Macdonald *et al*., 2004; Yamaguchi *et al*., 2004*b*), suggesting the importance and usefulness of the pelage for conservation of the Scottish wildcat. However, there is still a need for a definition that has been scientifically tested, is practical in application and harmless when applied to live animals, in order to provide a reliable pelage-based identification for the Scottish wildcat in the field.

In this paper we investigate the correlations between pelage, skull and intestinal characters from the same individuals of a museum sample of wild-living cats from Scotland, which forms a time series of more than 100 years, in order to develop and test a reliable definition of the Scottish wildcat. On the basis of these results, we will propose a diagnosis for the Scottish wildcat based on pelage characters that can be used non-invasively in the field to assist conservation action, but which will also provide a reliable method for identification in order to help enforce protective legislation for this critically-endangered species.

MATERIALS AND METHODS

Specimens

The morphological investigation used 135 specimens of presumed wild-living cats from Scotland in the collections of the National Museums of Scotland, Edinburgh and the Natural History Museum, London. Most of these specimens (115) have predominantly striped-tabby coat patterns, 20 have sworl (i.e. blotched tabby) patterns and none possessed the 'typical' coat colour mutations seen in the domestic cat, such as ginger, white or tortoise-shell, except as a minor component of the overall pelage. Specimens were nominally classified either as being 'wildcat' ($n = 86$), 'hybrid' ($n = 24$) or 'domestic cat' ($n = 25$) based on their existing museum labels. These labels have been written over a 100-year period and it is impossible to know exactly on what basis the identifications were made, although they were probably determined using traditional wildcat and domestic cat pelage characteristics, but possibly without knowledge of the potential existence of widespread hybrids (e.g. Pocock, 1951; Smithers, 1983; Kitchener, 1998).

Recording morphological characteristics

All the scorings and measurements for pelage and skull were carried out by J. M. W. to eliminate errors between individual recorders. Intestinal measurements were carried out by Phil Howard. Twenty pelage characters were scored (1–3: Table 1 & Fig. 1) for each skin, based on characters suggested by previous authors as being useful for distinguishing wildcats from domestic cats (Pocock, 1951; Corbett, 1979; Easterbee, 1991; Kitchener, 1995). Character states were scored as either 1, 2 or 3 according to the range of morphological variation in a specific character. It should not be considered that we were defining the wildcat *a priori* using these 20 pelage characters – we did not know if they were actually able to discriminate any pelage-based groups among the wild-living cats in Scotland. However, for the sake of convenience, character states traditionally associated with domestic cats were each given a score of 1, those associated with wildcats scored 3 and intermediate states scored 2. Occasionally, specimens were given decimal scores (e.g. 1.5 or 2.5) and those scores were reclassified as 2 to avoid assigning any doubtful specimen to either end of the cline, unless clearly stated otherwise. A Total Pelage Score (TPS) was calculated for each pelt by

Table 1. Pelage characters and their character states with associated scores as numbered in Fig. 1

Character	Score		
	1	2	3
(1) White on chin	White extensive on muzzle	White on chin	Buff or off-white on chin
(2) Stripes on cheek	No dark stripes	Indistinct stripes	3 clear stripes (2 fused)
(3) Dark spots underside	Absent	Indistinct	Distinct
(4) White on paw	White extensive on paw	White tuft on paw	No white on paw
(5) White on flank	Present	–	Absent
(6) White on back	Present	–	Absent
(7) Extent of dorsal line	Absent/covers entire tail	Continues onto tail	Stops at base of tail
(8) Shape of tail tip	Tapered to a point	Intermediate	Blunt
(9) Colour of tail tip	Neither black nor dark	Dark	Black
(10) Distinctness of tail bands	Absent/joined by dorsal line	Indistinct or fused	Distinct
(11) Alignment of tail bands	Absent/not aligned	Disjointed	Aligned
(12)* Stripes on hind leg	< 4 or > 7 stripes	–	4–7 stripes
(13)* Bands encircling foreleg	< 2 or > 3 bands	–	2 or 3 bands
(14) Tabby coat patterns	Absent/not predominant	–	Predominant pattern
(15) Broken stripes on flanks & hindquarters	> 50% broken/no marking	25–50% broken	< 25% broken
(16)* Stripes on body	< 7 or > 11 unbroken stripes	–	7–11 unbroken stripes
(17) Spots on flanks & hindquarters	Many/no marking	Some	None
(18) Stripes on nape	Thin/no stripes	Intermediate	4 thick stripes
(19) Stripes on shoulder	Indistinct/no stripes	Intermediate	2 thick stripes
(20) Colour of the back of ear	Same colour as head	Weak ochre/reddish	Ochre/reddish

Asterisks indicate those characters that were excluded from the Principal Components Analysis (PCA) because of their categorical nature.

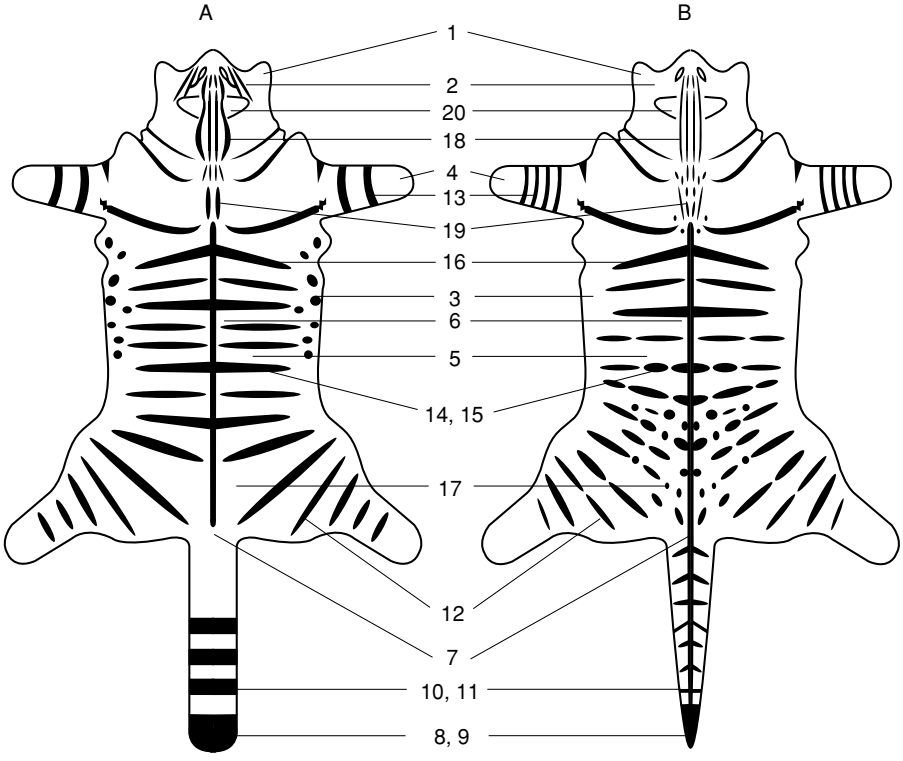

Fig. 1. Pelage characters and their character states for non-colour characters. All characters scored 3 each in A and all characters in B scored 1 each except character-14 (tabby pattern).

summing the scores for each character. Intestinal length was measured from the pyloric to anal sphincters by hanging the empty intestines from one end. The intestinal index (Schauenberg, 1977) was calculated by dividing intestinal length by head and body length, which was measured as a straight line between the tip of the nose and the base of the tail.

For adult and subadult skulls, when available, five skull characters were scored in a similar way to pelage characters, following Yamaguchi *et al*. (2004*a,b*), to give

a total skull score (TSS) for each skull. Cranial capacity, 37 skull measurements and five parameters derived from these were also recorded for each skull (Yamaguchi *et al*., 2004*a,b*).

Statistical analyses

All statistical analyses were carried out using the Statistica statistics package (Statsoft, Tulsa, USA). A Principal Components Analysis (PCA) was carried out based on the pelage characters, excluding three categorical characters (Table 1), using all cats together mainly to reduce the number of variables for the subsequent analyses by replacing them with the extracted Principal Components whose eigenvalues were greater than 1 (Tabachnick & Fidell, 2001). A cluster analysis was carried out using the standardised Principal Components (PCs) and summarised using UPGMA trees for each sex to investigate whether any grouping patterns exist within the Scottish wild-living cat population without any *a priori* classification. In any situation where there is introgressive hybridisation between two parent taxa, we might expect the wild-living cat population to include wildcats, domestic cats and various hybrids between them. Based on this theoretical assumption, we tried to interpret any clustering patterns in terms of the three main groups ('wildcats', 'domestic cats' and 'hybrids') unless such an interpretation would have been obviously impossible. Furthermore, in order to develop a practical method for classifying Scottish wild-living cats as either 'wildcats', 'hybrids' or 'domestic cats', for each variable statistically significant differences between the three groups (as identified by cluster analyses) were detected using Kruskal–Wallis tests or ANOVAs and between any two categories using Mann–Whitney *U*-tests or ANOVAs.

RESULTS

A PCA based on 17 pelage characters resulted in three PCs whose eigenvalues were greater than 1 (Table 2). A cluster analysis, based on these PCs, which were standardised for each sex, revealed that male wild-living cats in Scotland appeared to form six clusters and females formed four clusters without any *a priori* classification (Fig. 2). One group (cluster-1 for both sexes in Fig. 2) consisted almost exclusively of nominal 'wildcats'. Most cats belonging to cluster-2 for each sex were nominal 'wildcats' and 'hybrids', while those belonging to cluster-3 for each sex were 'hybrids' and 'domestic cats'. The rest of the tree (clusters-4, -5 & -6 for males and cluster-4 for females) contained almost exclusively 'domestic cats' (Fig. 2). On the basis of these clustering patterns, we categorised these wild-living cats into three groups: Group-1 (i.e. cluster-1 in Fig. 2), Group-2 (cluster-2) and Group-3 (the rest). These three groups were clearly separated on the basis of PCA and Group-1 and -2 cats (especially Group-1) showed greater homogeneity than did Group-3 cats based on the extracted PCs (Fig. 3).

Table 2. The results of a Principal Component Analysis based on 17 pelage variables in 135 cats

Principal Component	Eigenvalue	% explained	% cumulative
1	10.29	60.55	60.55
2	1.76	10.37	70.92
3	1.07	6.30	77.22

There was a significant difference in TPS based on the 20 pelage characters between the three groups of wild-living cats (d.f. = 2, $H = 105.79$, $P < 0.0001$: Fig. 4). Group-3 cats seemed to have two separate peaks in the total pelage score (Fig. 4), indicating that this might not be as coherent a group as the other two. Where data are available, it is clear that most cluster-3 cats have a cranial index of less than 2.75 (as do Groups-1 & -2), whereas all cluster-4 (also cluster-5 and cluster-6 for males) cats have a cranial index of greater than 2.75 (Fig. 5). Group-3 cats might consist of two subgroups: hybrids close to domestic cats and domestic cats. Thus, there are probably four groups in total: Group-1 includes wildcats, Group-2 is hybrids close to wildcats, New Group-3 is hybrids close to domestic cats and New Group-4 is domestic cats. Given that we are concerned only with distinguishing Group 1 (and possibly Group 2) cats from the rest, it is not necessary to distinguish between these two new Groups, which might result in unviable sample sizes. Also, notice that the overall level of branching based on Euclidean distances was less for females compared with that for the males, largely due to two males from cluster-6 (Fig. 2), which had white patches on their backs and were two of only three males with white on their flanks. This character was very rare in the sample and has influenced the level of branching concerning those individuals. No females had white patches on either back or flank (Fig. 1 and see Appendix 2). Therefore, it is likely that clusters 5 and 6 are artefacts of the inclusion of these three individual males in the sample.

Seven pelage characters showed the most highly significant differences between the three groups of wild-living cats for both sexes, i.e. extent of the dorsal line (character 7 in Table 1 & Fig. 1), shape of tail tip (character 8), distinctness of tail bands (character 10), broken stripes on flanks and hindquarters (character 15), spots on flanks and hindquarters (character 17), stripes on nape (character 18) and stripes on shoulder (character 19) (see Appendix 2). Only Group-1 cats (56 out of 74) had a score of greater than 2 for all these seven characters. Also, all Group-3 cats (35 out of 35) and some Group-2 cats (5 out of 26) had a score of 1 for any of these seven key characters. However, in terms of exclusion power, each of white on chin (character 1), stripes on cheek (character 2), dark spots on underside (character 3), white on flank (character 5), white on back (character 6), colour of tail tip (character 9), stripes on hind leg (character 12) and colour of the back of ear (character 20) were also useful in placing a cat into Group-3 (see Appendix 1).

Taking a closer look at the seven key pelage characters, we can see that some are more prone to change in Group-2 and Group-3 cats than in Group-1 cats (Fig. 6). For

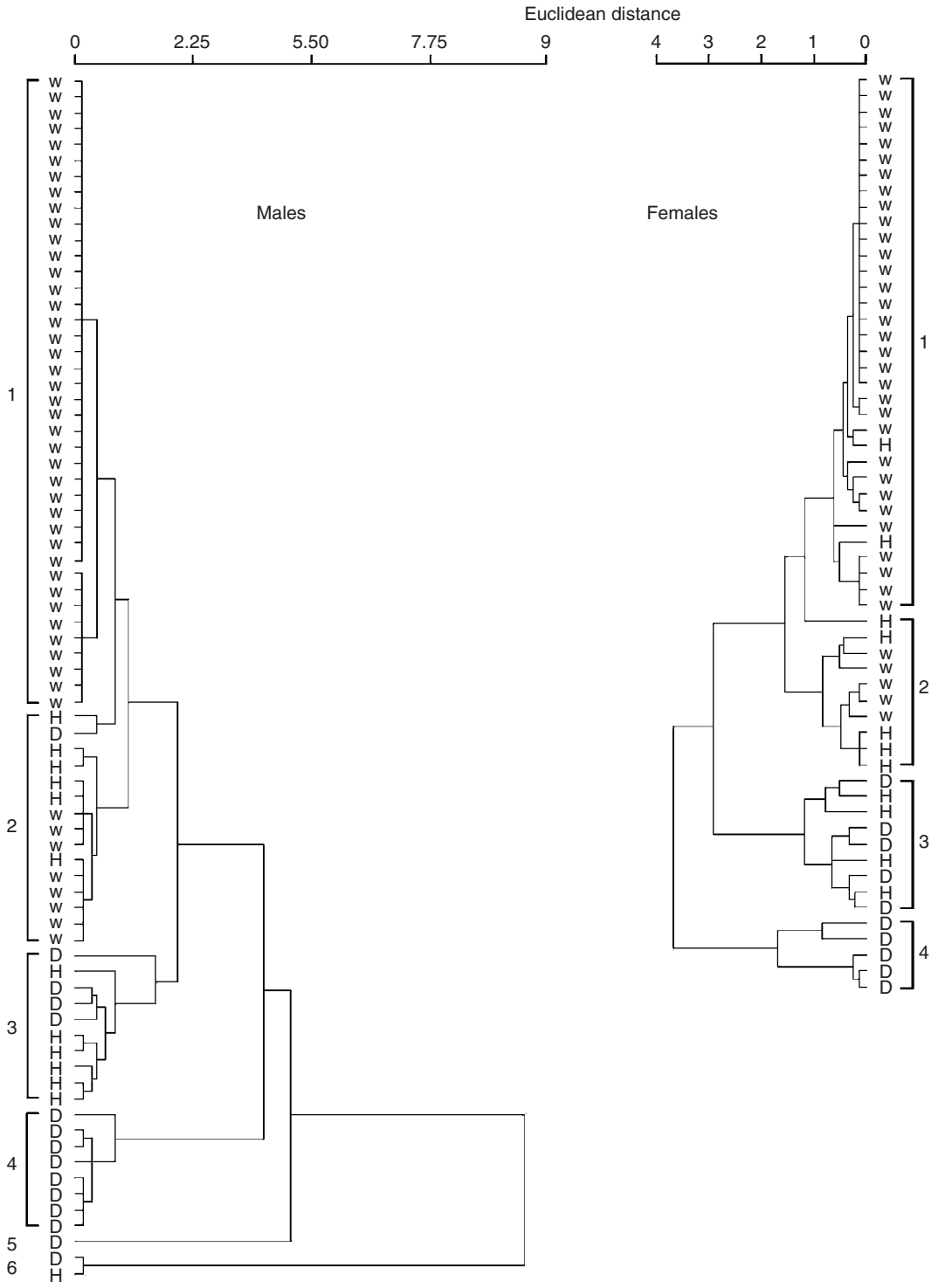

Fig. 2. Cluster analyses of individual skins of wild-living cats in Scotland. Trees were constructed using an UPGMA method from a similarity matrix of Euclidean distance based on the three principal components (PCs) for each pair of specimens. The PCs were standardised for males and females for the analyses. Cats were nominally classified as 'wild' (W), 'hybrid' (H) or 'domestic' (D) based on museum labels.

Group-1 cats some of the pelage characters always scored 3 (stripes on nape and stripes on shoulder), whereas others had a few intermediate-scoring characters (23% or less).

For each sex the three groups of wild-living cats showed statistically significant differences in TSSs, concerning shape of nasals, shape of parietal suture and development of the angular process of the mandible (see Appendix 2). However, there was no statistically significant difference in these variables between Group-1 and Group-2 cats for both sexes (Mann–Whitney *U*-tests: $P > 0.05$). For skull measurements, width of brain case, postorbital constriction, distance between infraorbital foramina, cranial volume and cranial index showed statistically significant differences between the three

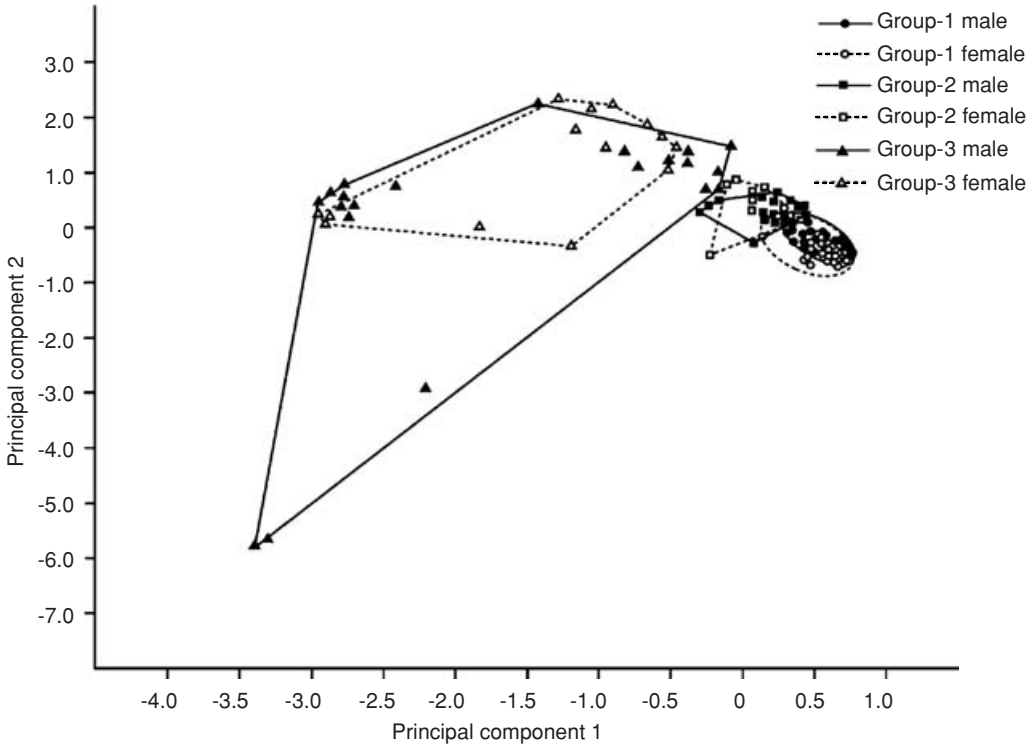

Fig. 3. A plot of the first two principal components for each of the free-ranging cats. PC1 accounted for 60.6% and PC2 for 10.4% of the variance based on the 17 pelage characters. The sample sizes are 40 (Group-1), 15 (Group-2) and 21 (Group-3) for males and 34 (Group-1), 10 (Group-2) and 14 (Group-3) for females.

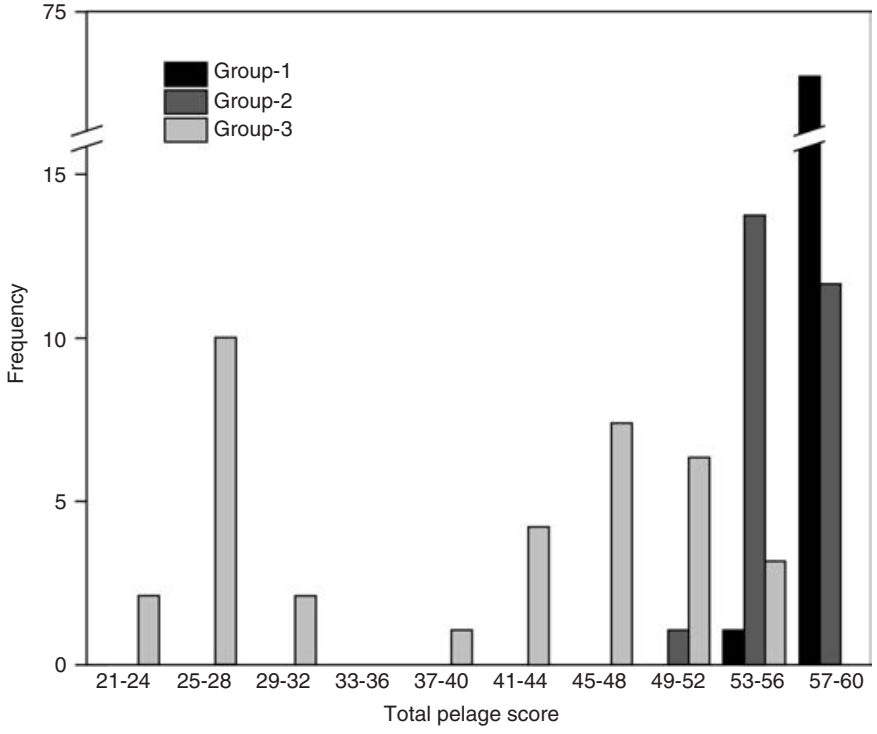

Fig. 4. Frequency distribution of the total pelage scores (TPSs) for each cat Group.

groups for each sex (see Appendix 3). Again, there was no statistically significant difference in any of these five variables between Group-1 and Group-2 cats for both sexes (ANOVA: $P > 0.05$). Also, there was a significant difference (d.f. $= 2$, $F = 9.56$, $P = 0.001$) in the gut index between these three groups (Fig. 7).

DISCUSSION

Concordance of characters

The results of the PCA and cluster analyses demonstrate that the nominal classification on museum labels appears to be well reflected in the clustering pattern derived

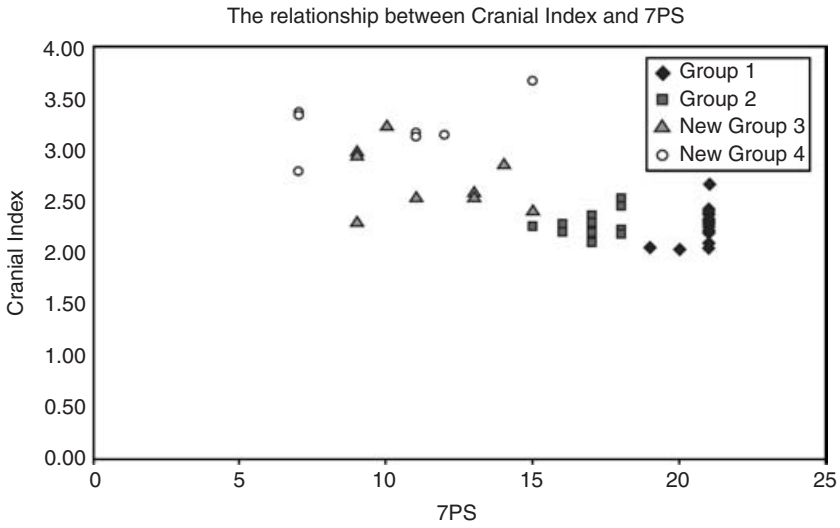

Fig. 5. The relationship between cranial index (CI) and 7PS for Scottish wild-living cats. All cluster-4/Group-3 cats have a CI of > 2.75 as expected for domestic cats, whereas most cluster-3/Group-3 cats have a CI < 2.75, suggesting that they are hybrids close to domestic cats; see the text for details.

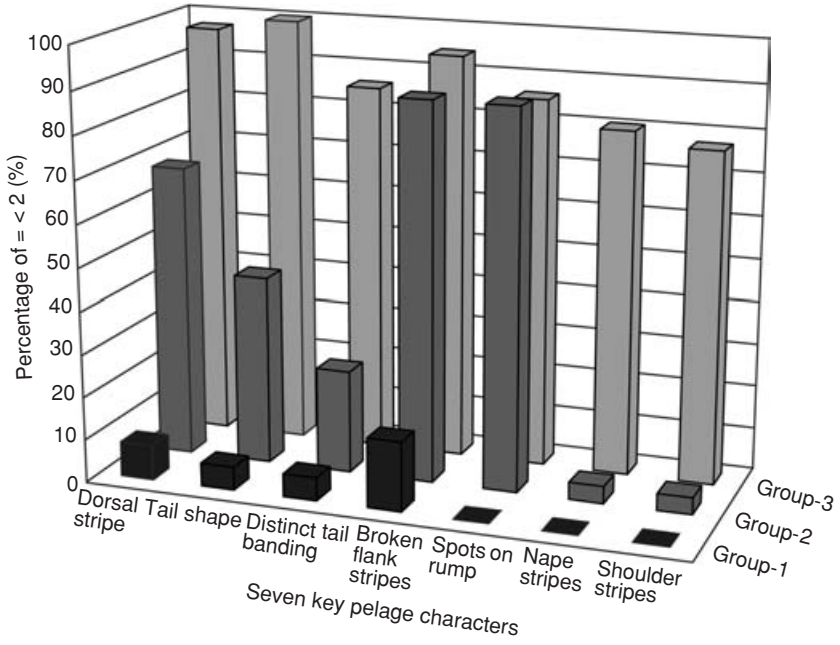

Fig. 6. The percentage of wild-living cats in Groups 1–3 with pelage scores of 2 or less for the seven key pelage characters.

from the three PCs based on 17 pelage characters. Of the three re-classified groups, Group-1 and -2 cats, especially the former, possess the morphological characteristics traditionally considered to be those of the Scottish wildcat (Pocock, 1951; Kitchener, 1998). Compared to Group-3 cats, these two groups, especially Group-1, have more homogeneous pelage characteristics, indicating that distinguishing these two groups from the rest of the wild-living cats in Scotland is relatively straightforward using these pelage characters. Given that these characters distinguish Group-1 cats collected over more than 100 years, during which levels of introgression may have varied, we can be more confident that these are probably diagnostic for the Scottish wildcat. The results show that there are good correlations between pelage characters and some non-pelage characters. The most obvious differences in non-pelage characters between the groups include cranial capacity, broadness of the skull, features related to the morphology of the parietal suture and mandible and length of intestine, but also TSS. Considering the smaller sample sizes for both skull and intestinal characters, these statistically significant differences, which are consistent in both sexes, may be regarded as strongly discriminating between the groups. However, based on these non-pelage characters, Group-1 and Group-2 cats do not appear to be distinguishable from each other. These two groups, in comparison to Group-3, possess both skull and intestinal characters associated with the group of wild-living cats

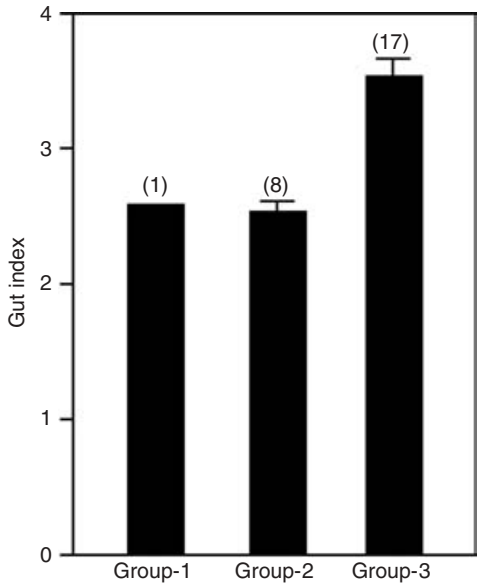

Fig. 7. Mean gut indices for the three cat groups. Males and females are pooled, owing to small sample sizes (*n*).

most distant from the domestic-cat morphological group reported by previous studies on the bases of skull and intestinal characters (French *et al*., 1988; Daniels *et al*., 1998; Reig *et al*., 2001). Therefore, as suggested by previous studies (e.g. Daniels *et al*., 1998, 2001; Beaumont *et al*., 2001), firstly the pelage-based groups do not perfectly match with groups based on other characteristics (and vice versa), secondly the pelage-based groups divide the non-domestic group of wild-living cats, as identified by other characters, further into smaller groups and thirdly the wild-living cats furthest from the domestic cat, based on pelage, qualify as the furthest from the domestic cat based on any other characteristics so far tested.

The apparent disparity between independent character sets may be explained in some individuals by the disruption of character concordance in F1 and F2 hybrids, where wild-type characters may mask some domestic cat characters. For example, Pitt (1921) found that F1 hybrids between a male polecat, *Mustela putorius*, and a female albino ferret, *M. furo*, had the typical dark pelage of polecats, but the typical skull morphology of ferrets. Backcrosses to either parent and F2 hybrids produced greater morphological variation. Therefore, individual cats with apparently disparate morphologies may represent F1 or similar progeny rather than being the result of prolonged introgression where parental characters may be melded to form a continuum.

There is no single pelage character that can distinguish any of the three groups clearly, but that is not unusual amongst closely related taxa and especially where a hybrid population exists. The domestic cats in this study were deliberately restricted to those with predominantly tabby markings as these would provide the greatest possibility of confusion with wildcats and their resultant hybrids. Most domestic cat colour mutants are readily distinguishable whilst distinguishing black hybrids (Kellas cats: Kitchener & Easterbee, 1992) from black domestics may be difficult in the field. Nevertheless, as far as the examined specimens are concerned, extent of dorsal line and shape of tail tip seem to be useful for separating Group-1 and Group-3 cats fairly accurately – this means that the tail tip can be used to distinguish a possible black Group-1 cat from a possible black Group-3 cat. Similarly, although to a lesser extent, distinctness of tail bands, stripes on nape and stripes on shoulder are useful for separating Group-1 and -2 cats from Group-3 cats. Also, a score of 1 for the following characters is recorded only in Group-3 cats, although this does not, alone, effectively discriminate any of the three groups: white on chin, stripes on cheek, dark spots on underside, white on flank, white on back, colour of tail tip, stripes on hind leg and colour of the back of the ear. Therefore, these characters may be useful in classifying a cat into Group-3. Most importantly, extent of the dorsal line and a combination of broken stripes and spots on the flanks and hindquarters, appear to be most useful in separating Group-1 from Group-2 cats.

Definition and diagnosis of the Scottish wildcat

Previous studies have highlighted how difficult it is to reach a scientifically defendable definition of the Scottish wildcat amongst the wild-living cats in Scotland (summarised in Macdonald *et al*., 2004). However, the results suggest that on the basis of the variation in the total scores for the seven key pelage characters (7PS), it becomes possible to define the wildcat more or less precisely, assuming Group-1 cats are those cats with little or no recent domestic-cat ancestry. The skin of the holotype of *Felis grampia* has a TPS of 60 and a 7PS of 21 (its skull has a TSS of 15), placing it firmly in Group 1 and confirming a strong positive association between this group and the classical phenotype of the Scottish wildcat. All but two Group-1 cats (97.3%) have a 7PS of 19 or greater. But there may be a morphological overlap in 7PSs if intermediate scores of 2 represent natural variation for some characters in the wildcat population. For example, the broken stripes on flanks and hindquarters had a relatively higher incidence (23%) in Group-1 cats, but in contrast to Group-2 and Group-3 cats, all Group-1 cats scored > 2 for spots on flanks and hindquarters. A possible consequence of a high degree of broken stripes is that they may fragment into distinct spots, which is what we see only in Group-2 and Group-3 cats (only 12% of Group-2 cats and 14% of Group-3 cats did not show this). However, the lower degree of broken stripes in Group-1 cats in the absence of spotting may actually represent the normal phenotypic variation in the Scottish wildcat rather than being attributable to introgression, and if this character is excluded, 86.5% of Group-1 cats have a score of > 2 for all of the remaining six characters.

Based on the results we propose that any cat that has a 7PS score of 19 or more for the seven key pelage characters with no scores of 1 should be regarded as a wildcat,

unless other data conflict with this. However, while this definition is clear and unequivocal for legal purposes, it may not be workable in the field and may exclude many cats that have a high proportion of wildcat characters (both morphological and genetic) that may usefully contribute to the restoration of the wildcat (Macdonald *et al*., 2004). If we include all cats that do not score 1 for any of the seven key pelage characters, this provides a relaxed definition for practical use in field identification. In other words any cat with a distinctly striped tabby coat pattern and a thick ringed tail with a black blunt tip (which never occurs in Group-3 cats: see Appendix 1) is effectively a wildcat and would include many of the cats that on closer inspection might fall in to Group-2, but which may contribute effectively to the 'wildcat' population. It may be necessary to confirm the preliminary identification by assessing the eight additional pelage characters (white on chin, stripes on cheek, dark spots on underside, white on flank, white on back, colour of tail tip, stripes on hind leg and colour of the back of the ear). A wildcat should not have a score of 1 for any of these characters. Needless to say, it is important to continue to improve our understanding of the morphology and genetics of the wildcat for a better diagnosis and to continue to monitor the contemporary population for evidence of greater or lesser concordance of independent character sets as evidence of changing degrees of introgression. However, as a first step, the 7PS would provide a relatively effective and easy-to-use diagnosis for the Scottish wildcat based on a non-invasive inspection of pelage characters.

Implications for conservation

The occurrences of some morphological characteristics (e.g. colour variation) found in wild-living cat populations at high frequencies are probably the result of introgressive hybridisation with the domestic cat (Yamaguchi *et al*., 2004*b*). However, at the individual level, possessing such characteristics may not necessarily be straightforward proof that the animal is a domestic cat – such characteristics may have always been present in wildcat populations although possibly in lower (or higher) frequencies compared to the current level. However, in Slovakia in a population considered to show very low levels of introgression with domestic cats, colour mutants represented only 1.2% of a sample of more than 300 wildcats (Sladek, 1976). Therefore, lack of protection for this very small proportion of the total population is probably acceptable if legal protection and conservation action can be made to be effective by using an accepted diagnosis for identification.

We suggest that it is necessary to tackle the conservation of the Scottish wildcat at the population level. Alarmingly, in this context, based on a sample collected from all over Scotland in the 1990s, only *ca*. 12% out of 187 wild-living cats possessed the classical wildcat pelage characteristics (= Group-1 cats) and as many as *ca*. 50% possessed the pelage characteristics similar to those of Group-3 cats, as identified by A. C. K. (Daniels *et al*., 1998). Harris *et al*. (1995) estimated that in the 1990s the population of Scottish wildcats was 3500. However, this figure should be interpreted such that the total population of wildcat is at a maximum of *ca*. 1800 (based on the relaxed definition), but it could be as low as 400, if based on the stricter definition, suggesting that the Scottish wildcat is critically endangered and needs immediate conservation attention. The most serious possible problem is that the other 1700 (or possibly 3100) wild-living cats, which show characteristics closer to the domestic cat and which are sympatric with these wildcats, are likely to continue hybridising with them under total legal protection. This concern is speculative at this stage as we have almost no knowledge of the process of introgression, its dynamics and the environmental and behavioural factors that may influence it. Therefore, further research, especially in genetics, is required urgently. However, we believe it is advisable to follow the precautionary principle to aid the conservation of the wildcat. As a fall-back position, a captive-breeding programme is being established under the auspices of the British and Irish Association of Zoos and Aquaria in order to establish a self-sustaining captive population of Group-1 wildcats, which could be used for future reintroductions or to reinforce existing populations; it would also allow researchers to study the morphology and genetics of the Scottish wildcat in relation to introgressive hybridisation by known and controlled matings with domestic cats and hybrids of known ancestry, morphology and genetics. However, in the first instance this may require some wildcats to be taken from the wild to establish a morphologically consistent population.

For existing wild populations, first of all, a non-invasive and continuing survey needs to be conducted to monitor the frequencies of occurrence of the wildcat, based on both the strict and relaxed diagnoses, in the Scottish wild-living cat population – our results suggest that practical identification would be feasible in the field based on some of the seven (and additional eight) key pelage characters. This would be backed up by an analysis of road kills from areas with differing levels of domestic cat populations, thereby affecting the expected proportions of hybrids and wildcats. Then, it would be desirable to remove probable non-wildcats (at least half of the total population in the 1990s) from the wild-living cat population in Scotland, although very few of them may be colour mutations of true wildcats. However, in practical terms, it will probably be desirable to explore this on a smaller scale to test the efficacy of this approach, involving a trial monitoring and control experiment on two estates; one where cats are removed as usual using non-discriminatory methods and the other where only non-wildcats are removed from the population. This must be associated with careful monitoring to assess changes in population characteristics, both morphological and genetic. Also, neutering and vaccination of pet cats should be encouraged or enforced in areas where wildcats occur. It is probable that simple protective legislation may not be enough to ensure the long-term survival of correlated characteristics associated with wildcats in Scotland, where levels of introgression

appear to be high, so that active intervention is urgently necessary if we are to retain an indigenous wildcat population.

Acknowledgements

We thank the Nigel Easterbee Memorial Fund, Glasgow Natural History Society, the Highland Distilleries Company and the University of Glasgow for financial support. We thank Mike Daniels and Carlos Driscoll for their useful comments on the manuscript. We also thank D. Hills and P. Jenkins (Natural History Museum, London) for their kind support and we are most grateful to P. Howard, A. Lothian and R. Pollitt for preparation of specimens.

REFERENCES

Balharry, D. & Daniels, M. J. (1998). Wild living cats in Scotland. *Scottish Natural Heritage Research, Survey and Monitoring Report*, No. 23. Perth and Edinburgh: Scottish Natural Heritage.

Beaumont, M., Barratt, E. M., Gottelli, D., Kitchener, A. C., Daniels, M. J., Pritchard, J. K. & Bruford, M. W. (2001). Genetic diversity and introgression in the Scottish wildcat. *Mol. Ecol.* **10**: 319–336.

Bewick, T. (1807). *A general history of quadrupeds*. Newcastle-upon-Tyne: Edward Walker.

Corbett L. K. (1979). *Feeding ecology and social organization of wildcats* ***(Felis silvestris)*** *and domestic cats* ***(Felis catus)*** *in Scotland*. Unpublished PhD thesis: University of Aberdeen.

Daniels, M. J., Balharry, D., Hirst, D., Kitchener, A. C. & Aspinall, R. J. (1998). Morphological and pelage characteristics of wild living cats in Scotland: implications for defining the 'wildcat'. *J. Zool., (Lond.)* **244**: 231–247.

Daniels, M. J., Beaumont, M. A., Johnson, P. J., Balharry, D., Macdonald, D. W. & Barratt, E. (2001). Ecology and genetics of wild-living cats in the north-east of Scotland and the implications for the conservation of the wildcat. *J. Appl. Ecol.* **38**: 146–161.

Easterbee, N. (1991). The wildcat *Felis silvestris*. In *The handbook of British mammals*: 431–437. 3rd edn. Corbett, G. B. & Harris, S. (eds). Oxford: Blackwell Scientific Publications.

French, D. D., Corbett, L. K. & Easterbee, N. (1988). Morphological discriminant functions of Scottish wildcats (*Felis silvestris*), domestic cats (*F. catus*) and their hybrids. *J. Zool., (Lond.)* **214**: 235–259.

Hamilton, E. (1896). *The wildcat in Europe.* London: Porter.

Harris, S., Morris, P., Wray, S. & Yalden, D. (1995). *A review of British mammals: population estimates and conservation status of British mammals other than cetaceans*. Peterborough: JNCC.

Harrison, D. L. & Bates, P. J. (1991). *The mammals of Arabia*. 2nd edition. Sevenoaks: Harrison Zoological Museum.

Heptner, V. G. & Sludskii, A. A. (1972). *Mammals of the Soviet Union volume II part 2 Carnivora (hyaenas and cats)*. Moscow: Vysshaya Shkola Publishers.

Hubbard, A. L., McOrist, S., Jones, T. W., Boids. R., Scott, R. & Easterbee, N. (1992). Is the survival of European wildcats *Felis silvestris* in Britain threatened by interbreeding with domestic cats? *Biol. Conserv*. **61**: 203–208.

Kitchener, A. C. (1995). *The wildcats*. London: The Mammal Society.

Kitchener, A. C. (1998). The Scottish wildcat – a cat with an identity crisis? *Brit. Wildl.* **9**: 232–242.

Kitchener, A. C. & Easterbee, N. (1992). The taxonomic status of black wild felids in Scotland. *J. Zool., Lond.* **227**: 342–346.

Kratochvíl, Z. (1973). Schädelkriterien der Wild- und Hauskatze (*Felis silvestris silvestris* Schreb. 1777 und *F.s.*f.*catus* L. 1758). *Acta Sc. Nat. Brno* **7**(10): 1–50.

Macdonald, D. W., Daniels, M. J., Driscoll, C., Kitchener, A. & Yamaguchi, N. (2004). *The Scottish wildcat: Analyses for conservation and an action plan*. Oxford: Wildlife Conservation Research Unit.

Miller. G. S. (1907). Some new European Insectivora and Carnivora. *Ann. Mag. Nat. Hist. 7th Ser.* **20**: 389–398.

Nowell, C. & Jackson, P. (1996). *Wild cats. Status survey and conservation plan plan*. Gland: IUCN.

Pierpaoli, M., Birò, Z. S., Herrmann, M., Hupe, K., Fernandes, M., Ragni, B., Szemethy, L. & Randi, E. (2003). Genetic distinction of wildcat (*Felis silvestris*) populations in Europe, and hybridisation with domestic cats in Hungary. *Mol. Ecol.* **12**: 2585–2598.

Pitt, F. (1921). Notes on the genetic behaviour of certain characters in the polecat, ferret and in polecat–ferret hybrids. *J. Genet.* **11**: 99–115.

Pocock, R. I. (1951). *Catalogue of the genus* Felis. London: British Museum.

Reig, S., Daniels, M. J. & Macdonald, D. W. (2001). Craniometric differentiation within wild-living cats in Scotland using 3D morphometrics. *J. Zool., (Lond.)* **253**: 121–132.

Roberts, A. (1951). *The mammals of South Africa*. South Africa: The Mammals of South Africa Book Fund.

Schauenberg, P. (1969). L'identification du chat forestier d'Europe *Felis s. silvestris* Schreber 1777 par une méthode ostéométrique. *Rev. Suisse Zool.* **76**: 433–441.

Schauenberg, P. (1977). Longeur de l'intestin du chat forestier *Felis silvestris* Schreber. *Mammalia* **41**: 357–360.

Sladek, J. (1976). Farbené anomálie v západokarpatskej populácii macky divej (*Felis silvestris* Schreber, 1777). *Lynx* **18**: 73–83.

Smith, C., Hodgson, G. W. I., Armitage, P. & Clutton-Brock, J. (1994). Animal bone report. In *Four millennia of Orkney prehistory*: 139–153. Smith, B. B. (Ed.). Monograph Series 9. Edinburgh: Society of Antiquaries of Scotland.

Smithers, R. H. N. (1983). *The mammals of the southern African subregion*. Pretoria: University of Pretoria Press.

Suminski, P. (1962). Les caractères de la forme pure du chat sauvage *Felis silvestris* Schreber. *Arch. Sci.* **15**: 277–296.

Tabachnick, B. G. & Fidell, L. S. (2001). *Using multivariate statistics fourth edition*. Boston: Allyn and Bacon.

Yamaguchi, N., Driscoll, C. A., Kitchener, A. C., Ward, J. M. & Macdonald, D. W. (2004*a*). Craniological differentiation amongst European wildcats (*Felis silvestris silvestris*), African wildcats (*F. s. lybica*) and Asian wildcats (*F. s. ornata*): implications for their evolution and conservation. *Biol. J. Linnean Soc.* **83**: 47–64.

Yamaguchi, N., Kitchener, A. C., Ward, J. M., Driscoll, C. A. & Macdonald, D. W. (2004*b*). Craniological differentiation amongst wild-living cats (*Felis silvestris*) in Britain and southern Africa: natural variation or the effects of hybridisation? *Anim. Conserv*.

APPENDIX 1. Differences in pelage characteristics between Group-1, Group-2 and Group-3 cats classified using cluster analyses based on three principal components extracted from 17 pelage variables

	Frequency, *H* and *P*										
	Group-1			Group-2			Group-3				
	Score			Score			Score				
Variables	1	2	3	1	2	3	1	2	3	*H*	*P*
White on chin											
Male	0	0	40	0	2	13	9	6	6	41.69	0.000
Female	0	2	32	0	1	9	4	3	7	14.85	0.001
Stripes on cheek											
Male	0	0	40	0	0	15	10	0	11	29.76	0.000
Female	0	0	34	0	0	10	3	0	11	9.77	0.008
Dark spots underside											
Male	0	0	40	0	0	15	11	0	10	33.24	0.000
Female	0	0	34	0	0	10	4	1	9	16.88	0.000
White on paw											
Male	0	0	40	0	3	12	11	1	9	29.79	0.000
Female	0	2	32	1	1	8	5	1	8	10.51	0.005
White on flank (scored either 1 or 3)											
Male	0	–	40	0	–	15	3	–	18	8.07	0.02
Female	0	–	34	0	–	10	0	–	14	–	–
White on back (scored either 1 or 3)											
Male	0	–	40	0	–	15	2	–	19	5.31	0.07
Female	0	–	34	0	–	10	0	–	14	–	–
Extent of dorsal line											
Male	0	4	36	1	10	4	14	6	1	51.16	0.000
Female	0	2	32	0	7	3	12	2	0	46.30	0.000
Shape of tail tip											
Male	0	2	38	0	5	10	14	7	0	58.42	0.000
Female	0	2	32	1	5	4	11	3	0	44.34	0.000
Colour of tail tip											
Male	0	1	39	0	2	13	6	2	13	14.94	0.001
Female	0	2	32	0	1	9	3	7	4	25.97	0.000
Distinctness of tail bands											
Male	0	3	37	1	1	13	14	2	5	38.23	0.000
Female	0	3	31	0	5	5	12	2	0	43.46	0.000

APPENDIX 1. Continued

	Frequency, *H* and *P*										
	Group-1			Group-2			Group-3				
	Score			Score			Score				
Variables	1	2	3	1	2	3	1	2	3	*H*	*P*
Alignment of tail bands											
Male	0	4	36	2	2	11	9	4	8	21.26	0.000
Female	0	3	31	0	4	6	4	5	5	17.49	0.000
Stripes on hind leg (scored either 1 or 3)											
Male	0	–	39	0	–	15	11	–	10	32.71	0.000
Female	0	–	34	0	–	10	4	–	10	13.27	0.001
Bands encircling foreleg (scored either 1 or 3)											
Male	1	–	38	0	–	15	12	–	9	29.26	0.000
Female	2	–	32	0	–	10	4	–	10	6.78	0.03
Tabby coat patterns (scored either 1 or 3)											
Male	0	–	40	1	–	14	12	–	9	34.05	0.000
Female	0	–	34	0	–	10	5	–	9	16.88	0.000
Broken stripes on flanks & hindquarters											
Male	0	11	29	0	13	2	13	8	0	49.72	0.000
Female	0	6	28	1	8	1	7	5	2	30.86	0.000
Stripes on body (scored either 1 or 3)											
Male	0	–	40	2	–	13	13	–	8	33.35	0.000
Female	0	–	34	0	–	10	9	–	5	32.90	0.000
Spots on flanks & hindquarters											
Male	0	2	38	2	11	2	18	2	1	62.01	0.000
Female	0	0	34	2	7	1	8	2	4	37.86	0.000
Stripes on nape											
Male	0	0	40	1	0	14	12	4	5	47.09	0.000
Female	0	0	34	0	0	10	10	2	2	46.39	0.000
Stripes on shoulder											
Male	0	0	40	0	2	13	14	2	5	46.76	0.000
Female	0	0	34	0	0	10	10	1	3	41.77	0.000
Colour of the back of ear											
Male	0	1	39	0	1	14	10	5	6	41.18	0.000
Female	0	0	34	0	0	10	6	2	6	28.54	0.000

Statistically significant differences between the three categories were detected using Kruskal–Wallis tests (d.f. = 2 for all tests).

APPENDIX 2. Differences in skull characteristic scores between Group-1, Group-2 and Group-3 cats classified using cluster analyses based on three principal components extracted from 17 pelage variables

	Frequency, H and P										
	Group-1			Group-2			Group-3				
	Score			Score			Score				
Variables	1	2	3	1	2	3	1	2	3	H	P
Nasal shape											
Male	2	6	6	0	3	3	5	1	2	6.07	0.05
Female	1	2	12	1	2	4	6	4	0	17.43	0.000
Nasal pit											
Male	0	6	8	0	2	4	2	3	3	3.51	0.17
Female	0	6	9	1	0	6	4	4	1	9.18	0.01
Parietal suture											
Male	0	0	16	0	3	3	3	4	1	19.08	0.000
Female	0	1	14	0	0	7	5	3	3	17.89	0.000
Nasal length											
Male	4	7	4	0	5	1	0	5	3	1.62	0.45
Female	1	7	7	0	2	5	2	4	3	2.99	0.22
Mandible (scored either 1 or 3)											
Male	0	–	14	0	–	6	3	–	4	9.29	0.01
Female	0	–	15	0	–	7	3	–	6	7.86	0.005
Total skull score (mean, range, sample size)											
Male	13.5, 12–15, 12			13.1, 12–15, 6			10.1, 8–13, 7			8.37	0.02
Female	13.9, 12–15, 15			13.9, 12–15, 7			9.4, 6–14, 7			10.78	0.005

Statistically significant differences were detected by Kruskal–Wallis tests (d.f. = 2 for all tests). Only adult and subadult data were included.

APPENDIX 3. Differences in skull characteristics between Group-1, Group-2 and Group-3 cats classified using cluster analyses based on three principal components extracted from 17 pelage variables

	Mean (mm) ± Standard Error (number examined)				
Variables	Group-1	Group-2	Group-3	F	P
Greatest length					
Male	99.47 ± 0.84 (12)	103.16 ± 0.78 (5)	97.46 ± 1.48 (8)	4.85	0.02
Female	92.37 ± 1.06 (9)	90.43 ± 1.44 (6)	89.54 ± 1.58 (8)	1.26	0.31
Condylobasal length					
Male	93.23 ± 1.02 (11)	94.37 ± 1.79 (6)	90.52 ± 1.31 (8)	2.08	0.15
Female	85.41 ± 0.59 (10)	84.98 ± 1.87 (7)	82.67 ± 1.59 (8)	1.25	0.31
Facial length					
Male	37.11 ± 0.61 (11)	37.89 ± 0.78 (6)	37.54 ± 0.76 (8)	0.30	0.74
Female	33.60 ± 0.64 (9)	34.99 ± 0.82 (7)	33.80 ± 0.64 (8)	1.10	0.35
Lateral snout					
Male	24.85 ± 0.44 (12)	24.97 ± 0.54 (6)	24.38 ± 0.47 (8)	0.37	0.70
Female	22.42 ± 0.26 (10)	22.60 ± 0.60 (7)	21.39 ± 0.56 (9)	1.90	0.17
Pm2–M1					
Male	22.21 ± 0.20 (11)	22.02 ± 0.21 (6)	22.37 ± 0.34 (8)	0.38	0.69
Female	20.83 ± 0.19 (9)	21.06 ± 0.24 (7)	20.11 ± 0.33 (10)	3.32	0.05
Pm2–Pm4					
Male	21.31 ± 0.23 (11)	21.36 ± 0.26 (6)	21.22 ± 0.28 (8)	0.06	0.94
Female	19.82 ± 0.19 (9)	20.24 ± 0.25 (7)	19.07 ± 0.31 (10)	5.13	0.01
Pm4 length					
Male	11.12 ± 0.13 (13)	11.24 ± 0.24 (6)	10.78 ± 0.22 (8)	1.48	0.25
Female	10.43 ± 0.11 (9)	10.43 ± 0.15 (7)	10.29 ± 0.25 (9)	0.20	0.82
Pm4 breadth					
Male	5.95 ± 0.07 (13)	6.04 ± 0.11 (6)	5.54 ± 0.21 (8)	3.73	0.04
Female	5.63 ± 0.07 (10)	5.44 ± 0.15 (7)	5.16 ± 0.21 (8)	2.65	0.09

APPENDIX 3. Continued

Variables	Mean (mm) ± Standard Error (number examined)			*F*	*P*
	Group-1	Group-2	Group-3		
Auditory bulla (anteroposterior)					
Male	20.78 ± 0.21 (13)	20.93 ± 0.40 (6)	20.66 ± 0.42 (8)	0.24	0.79
Female	19.47 ± 0.27 (9)	19.60 ± 0.30 (7)	19.47 ± 0.36 (9)	0.05	0.95
Mastoid breadth					
Male	44.99 ± 0.35 (12)	44.83 ± 0.48 (6)	43.64 ± 0.69 (8)	2.17	0.14
Female	42.20 ± 0.24 (10)	42.40 ± 0.75 (7)	40.66 ± 0.67 (9)	2.96	0.07
Occipoital condyles					
Male	25.02 ± 0.27 (12)	24.47 ± 0.25 (6)	23.32 ± 0.64 (7)	4.90	0.02
Female	23.25 ± 0.23 (10)	23.14 ± 0.30 (7)	22.30 ± 0.49 (9)	2.20	0.13
Foramen magnum					
Male	15.27 ± 0.19 (12)	15.04 ± 0.23 (6)	14.20 ± 0.08 (7)	5.99	0.008
Female	14.61 ± 0.20 (10)	14.49 ± 0.36 (7)	13.96 ± 0.29 (9)	1.67	0.21
Brain case					
Male	47.57 ± 0.41 (11)	47.23 ± 0.44 (6)	43.95 ± 0.68 (8)	14.69	0.000
Female	45.49 ± 0.29 (9)	45.71 ± 0.51 (6)	42.40 ± 0.77 (9)	10.52	0.001
Zygomatic breadth					
Male	71.59 ± 0.89 (13)	72.30 ± 1.27 (5)	68.73 ± 0.98 (8)	2.96	0.07
Female	65.70 ± 0.64 (10)	66.17 ± 1.75 (7)	63.70 ± 1.18 (9)	1.27	0.30
Frontal breadth					
Male	49.56 ± 0.68 (11)	51.34 ± 1.23 (6)	50.14 ± 0.55 (8)	1.21	0.32
Female	47.81 ± 0.75 (9)	49.24 ± 1.26 (7)	47.92 ± 1.33 (9)	0.45	0.64
Interorbital breadth					
Male	19.76 ± 0.43 (13)	19.84 ± 0.24 (6)	18.69 ± 0.41 (8)	2.07	0.15
Female	18.41 ± 0.41 (10)	18.57 ± 0.51 (7)	17.23 ± 0.61 (8)	2.01	0.16
Palatal breadth					
Male	41.36 ± 0.45 (13)	41.79 ± 0.60 (6)	40.13 ± 0.43 (8)	2.60	0.10
Female	38.58 ± 0.30 (10)	38.60 ± 0.74 (7)	37.14 ± 0.82 (9)	1.78	0.19
Rostrum breadth					
Male	24.43 ± 0.27 (13)	24.36 ± 0.51 (6)	23.44 ± 0.64 (8)	1.51	0.24
Female	22.02 ± 0.23 (10)	22.39 ± 0.49 (7)	21.26 ± 0.70 (9)	1.26	0.30
Postorbital constriction					
Male	34.20 ± 0.34 (11)	34.05 ± 0.70 (6)	31.65 ± 0.78 (8)	6.12	0.008
Female	33.84 ± 0.60 (10)	34.99 ± 0.70 (7)	32.26 ± 0.72 (9)	3.86	0.04
Between infraorbital foramena					
Male	29.74 ± 0.35 (12)	29.76 ± 0.60 (6)	27.38 ± 0.67 (8)	6.90	0.005
Female	27.12 ± 0.34 (10)	27.76 ± 0.73 (7)	25.30 ± 0.77 (8)	4.19	0.03
Minimum nasal					
Male	21.98 ± 0.64 (9)	22.97 ± 0.60 (6)	23.62 ± 0.45 (8)	2.27	0.13
Female	19.96 ± 0.51 (7)	21.72 ± 0.58 (7)	21.40 ± 0.53 (8)	2.89	0.08
Cranial suture					
Male	17.31 ± 1.18 (12)	13.04 ± 2.27 (6)	11.01 ± 1.68 (8)	4.75	0.02
Female	20.72 ± 0.85 (10)	21.01 ± 1.74 (7)	17.00 ± 1.28 (9)	3.24	0.06
Angular process (mandible)					
Male	66.38 ± 1.06 (11)	68.37 ± 1.63 (6)	63.89 ± 1.18 (7)	2.64	0.10
Female	60.73 ± 0.76 (8)	60.22 ± 1.35 (6)	59.40 ± 1.34 (8)	0.37	0.70
Coronoid process (mandible)					
Male	64.69 ± 0.60 (11)	66.06 ± 1.22 (6)	63.74 ± 1.50 (8)	1.03	0.38
Female	59.11 ± 0.71 (9)	60.15 ± 0.95 (6)	59.47 ± 1.04 (8)	0.31	0.74
Pm3–M1 (mandible)					
Male	21.27 ± 0.16 (11)	22.01 ± 0.41 (6)	20.25 ± 0.51 (7)	5.71	0.01
Female	19.92 ± 0.18 (9)	19.95 ± 0.28 (6)	19.21 ± 0.59 (8)	1.14	0.34
Ramus (mandible)					
Male	31.29 ± 0.60 (11)	31.71 ± 0.85 (6)	29.60 ± 0.51 (7)	2.58	0.10
Female	27.85 ± 0.27 (9)	26.99 ± 0.75 (6)	26.87 ± 0.72 (8)	0.93	0.41

APPENDIX 3. Continued

Variables	Mean (mm) ± Standard Error (number examined)			*F*	*P*
	Group-1	Group-2	Group-3		
WMC (mandible)					
Male	14.90 ± 0.21 (9)	15.34 ± 0.48 (6)	14.55 ± 0.41 (7)	1.15	0.34
Female	13.89 ± 0.27 (6)	13.54 ± 0.44 (6)	13.73 ± 0.28 (8)	0.25	0.78
Pm4 breadth (mandible)					
Male	3.16 ± 0.05 (10)	3.28 ± 0.08 (6)	3.08 ± 0.12 (7)	1.28	0.30
Female	3.02 ± 0.05 (9)	3.13 ± 0.05 (5)	2.83 ± 0.05 (8)	7.21	0.005
Cranial volume (ml)					
Male	44.53 ± 0.64 (10)	44.45 ± 0.69 (5)	33.28 ± 1.78 (8)	29.28	0.000
Female	40.73 ± 1.67 (4)	40.05 ± 1.15 (6)	30.70 ± 1.75 (10)	10.37	0.001
		Derived variables			
Cranial index					
Male	2.22 ± 0.039 (10)	2.32 ± 0.049 (5)	2.97 ± 0.122 (8)	26.89	0.000
Female	2.34 ± 0.116 (4)	2.27 ± 0.060 (6)	2.96 ± 0.170 (8)	7.19	0.006
I.O.F./snout					
Male	1.20 ± 0.014 (12)	1.19 ± 0.014 (6)	1.11 ± 0.018 (7)	8.83	0.002
Female	1.21 ± 0.013 (10)	1.23 ± 0.012 (7)	1.18 ± 0.025 (7)	1.52	0.24
Palatal/Pm2-M1					
Male	1.86 ± 0.020 (11)	1.90 ± 0.019 (6)	1.81 ± 0.042 (7)	2.29	0.13
Female	1.85 ± 0.022 (9)	1.83 ± 0.021 (7)	1.88 ± 0.028 (7)	0.95	0.40
POC/IOB					
Male	1.78 ± 0.043 (11)	1.72 ± 0.034 (6)	1.69 ± 0.042 (7)	1.10	0.35
Female	1.84 ± 0.037 (10)	1.89 ± 0.049 (7)	1.98 ± 0.045 (6)	2.55	0.10
CP/AP					
Male	0.98 ± 0.009 (11)	0.97 ± 0.008 (6)	1.00 ± 0.016 (7)	1.61	0.22
Female	0.97 ± 0.004 (8)	1.00 ± 0.009 (6)	1.00 ± 0.009 (8)	5.89	0.01

Statistically significant differences between three groups were detected by ANOVAs (d.f. = 2 for all tests). Only adult and subadult data were included. I.O.F, breadth between interorbital foramina; POC, postorbital constriction; IOB, interorbital breadth; AP, mandible length to angular process; CP, mandible length to coronoid process.