Journal of Applied Ecology 2001
38, 146–161

Ecology and genetics of wild-living cats in the north-east of Scotland and the implications for the conservation of the wildcat

MIKE J. DANIELS*§, MARK A. BEAUMONT†, PAUL J. JOHNSON*, DAVID BALHARRY‡, DAVID W. MACDONALD* and ELIZABETH BARRATT†

**Wildlife Conservation Research Unit, University of Oxford, Department of Zoology, South Parks Road, Oxford OX1 3PS, UK; †Institute of Zoology, Zoological Society of London, Regents Park, London NW1 4RY, UK; and ‡The Croft, Tomich, Strathglass, Inverness-shire IV4 7LY, UK*

Summary

1. The wildcat is considered to be threatened by interbreeding with the domestic cat. As a result of interbreeding the definition of a wildcat in Scotland is contentious. Many authors consider pelage characteristics to be diagnostic, yet few data exist on sympatric cats with different pelages.
2. A study of 31 wild-living cats was conducted from 1995 to 1997 in an area associated with wildcats. Seventy-four per cent of cats caught had striped tabby pelages while 26% had other (non-tabby) phenotypes.
3. On the basis of data from eight nuclear DNA microsatellite loci there was no strong evidence of two groups, and tabby and non-tabby cats did not depart significantly from Hardy–Weinberg equilibrium.
4. There were significant differences in gene frequencies and genotypes between the two pelage types. Non-tabby cats were also significantly more similar to domestic cats than tabby cats, although still noticeably differentiated from them.
5. There were potential parent–offspring and sibling–sibling relationships between and within tabby and non-tabby cats, suggesting recent interbreeding. On average, however, non-tabby cats were genetically less related to each other than tabby cats.
6. Radio-tracking revealed that non-tabby adult females had significantly larger home ranges than tabby adult females. However, for all other aspects of home range size, social organization, activity patterns and habitat use there were no significant differences between cats of different pelage type.
7. The implications of these results are that traditional approaches for attempting to distinguish wild animals in the face of interbreeding with their domestic forms are neither accurate nor effective. Instead, conservation should focus on mechanisms for dealing with groups of animals below the species level.
8. Specifically for the wildcat in Scotland, conservation should focus on protection by area. If domestic cat controls were conducted within specified areas then the potential threat posed by interbreeding would be reduced.

Key-words: conservation below species level, pelage variation, relatedness, tabby.

Journal of Applied Ecology (2001) **38**, 146–161

Introduction

One of the main threats to the wildcat *Felis silvestris* Schreber world-wide is considered to be hybridization with the domestic cat *Felis catus* L. (Nowell & Jackson 1996). Recent morphological and genetic studies have highlighted the difficulties in defining a wildcat in Scotland because of long-term interbreeding with domestic cats. (Balharry, Daniels & Barratt 1997; Daniels *et al*. 1998). It has been suggested that there may be no exclusive genetic or morphological criteria that define a wildcat in what is essentially a

§Present address and correspondence: Dr M.J. Daniels, Department of Veterinary Clinical Sciences, University of Sydney, PMB3, Camden, NSW 2570, Australia.

'cline' of wild-living cats, ranging from domestic cats, through feral cats to wildcats (Daniels *et al.* 1998).

Yet previous authors have maintained that a wildcat can be defined on the basis of having a particular pelage type (Corbett 1979; French, Corbett & Easterbee 1988; Kitchener 1991). Corbett (1979) described this pelage (here called tabby) as: 'The typical and fairly consistent coat colour seen in wildcats is tabby grey or yellowish brown with about 8–11 dark body stripes (sometimes broken on the underside), about 4–7 strong black leg bands (often incomplete), and up to five black rings encircling the tail', while Easterbee (1991) described wildcats as being 'similar to domestic "tabby" cats but typically larger and more robust' and having 'seven to 11 dark body stripes and no substantial areas of white (e.g. on paws) or ginger markings'.

However, Kitchener & Easterbee (1992) reported the presence of black felids living wild in Scotland. Daniels *et al.* (1998) found that 32% of a sample of 187 wild-living cats from throughout the north of Scotland had non-tabby pelages, and even those with a tabby pelage showed significant variation in the numbers of body, limb and tail stripes. Similarly, variation has been reported among putative wildcats in Germany (Piechoki 1990), and in the Swiss Jura, Dötterer & Bernhart (1996) described five (26%) of a sample of 19 cats caught as 'non-wild coloured'.

Most previous authors have considered the presence of a non-tabby pelage to be a result of the introduction of domestic coat colour genes into the wild population through interbreeding (Corbett 1979; French, Corbett & Easterbee 1988; Easterbee 1991; Kitchener 1991; Kitchener & Easterbee 1992). Equally however, it could be hypothesized that cats of non-tabby pelage may be feral domestic cats or merely the result of naturally occurring mutations within the wild population. Naturally occurring phenotypic variation has been reported within populations of at least 20 other felid species (Robinson 1978).

To date neither the ecology, morphology nor genetics of sympatric tabby and non-tabby cats has been described or the relationship between the two assessed. We report here on the results of a 2-year study of wild-living cats caught in the north-east of Scotland. Specifically we asked the following questions.

1. How do the morphologies of tabby and non-tabby cats relate to previously published criteria on the definition of a wildcat?

2. How are tabby and non-tabby cats related to each other and to other wild-living cats in Scotland?

3. Do tabby and non-tabby cats exhibit significant differences in their home range size, activity patterns and habitat use?

4. What are the implications for interbreeding between wild and domestic forms in general and specifically for the conservation of the wildcat in Scotland?

Materials and methods

STUDY AREA

The study was conducted in the Angus Glens (56°51′ N and 2°59′ E) in the north-east of Scotland, between March 1995 and April 1997. The area has a relatively low human population density (< 1 person km^{-2}), high altitude (for the UK; up to 650 m) and consists of three parallel glens at the southern edge of the Grampian mountains. The glens contain landcover types 'rough and improved grassland', interspersed with 'mixed woodland' and 'coniferous plantations', which are surrounded by 'heather moorland' and large 'coniferous plantations' as defined by MLURI (1993). These habitat types are similar to those described as suitable for wildcats by Easterbee, Hepburn & Jefferies (1991) and the area is within the distribution of wildcats given by these authors. The area is also associated with specimens classed as wildcats held in Dundee Museum (series NH73–76) and is situated 30 km south-west of a previous study site for wildcats in Scotland (Corbett 1979).

TRAPPING

Live trapping was carried out throughout the study area, usually for periods of 1 month, intermittently between March 1995 and January 1997, using between 10 and 50 traps simultaneously (Racoon and Bobcat traps, Tomahawk Live Trap Co., Tomahawk, WI). During trapping periods, traps were baited at least weekly with fresh rabbit and checked daily.

Captured cats were immobilized via intramuscular injection with 20 mg kg^{-1} ketamine hydrochloride (Vetalar, Parke, Davis and Company, Pontypool, UK) in combination with 1 mg kg^{-1} xylazine (Rompun, Bayer UK Ltd, Bury St Edmunds, UK), to enable fitting of radio-collars, recording of ages, sexes, weights, body measurements, photographs and the collection of up to 10 ml whole blood for extraction of DNA. Whole blood samples were frozen immediately at –20 °C.

Radio-collars consisted of transmitters with internal loop aerials coated in waterproof resin. Transmitters were attached to soft leather watch straps that were fastened around the cat's neck, then secured with Superglue. For juvenile cats, collars were left several centimetres looser to allow for growth. The total collar weight was 40 g, constituting between 0·6% and 2·3% of the body weight of cats at capture.

CLASSIFICATION OF CATS: AGE CLASS, PELAGE AND MORPHOLOGY

The age class of cats at capture was estimated on the basis of body weight and dentition. For females, cats were classed as adult if they had full adult dentition and their weight was > 2·5 kg, and for males, if they had full adult dentition and were > 3·5 kg. Otherwise

cats were classed as juvenile (following Jones & Coman 1982).

Cats' pelages were assessed from dorsal, lateral and ventral photographs in terms of the description of a wildcat by Corbett (1979 and see above) and in relation to the presence of phenotypes associated with 'mutant' alleles found in domestic cats (after Robinson 1977). Cats that matched Corbett's (1979) description (i.e. striped tabbies) were classed as tabby, all other cats (including blotched tabbies and those expressing mutant alleles) were classified as non-tabby.

For the purpose of comparing study animals with previous definitions, cats were classified according to three other published criteria, where data were available, i.e. for a subsample of nine cat mortalities subsequently recovered: (i) cranial index – length of skull (mm)/cranial capacity (mm^3), Schauenberg (1969); (ii) intestine index – length of the small intestine (cm)/body length (cm), Schauenberg (1977); and (iii) morphological grouping – following the discrimination function used by Daniels *et al*. (1998) based on intestine length and limb bone size.

MOLECULAR ANALYSES

Total DNA was isolated using a standard proteinase K lysis and an organic solvent purification method as described in Sambrook, Fritsch & Maniatis (1989). Briefly, 1–2 ml of blood was digested overnight with proteinase K at 50 °C. DNA was then extracted by treatment with phenol, phenol/chloroform/isoamyl alcohol (25 : 24 : 1) and chloroform/isoamyl alcohol (24 : 1). Precipitation was achieved by the addition of 1/10 volume 3 M sodium acetate and two volumes of absolute ethanol. The DNA was washed in 70% ethanol before being resuspended in sterile distilled water.

Eight microsatellite loci, originally isolated in domestic cats, were used to screen the above samples (Fca8, Fca23, Fca43, Fca45, Fca77, Fca90, Fca96, Fca126; Menotti-Raymond & O'Brien 1995). Detection of microsatellite alleles in genomic DNA was achieved by end-labelling one primer of the pair using γ-ATP^{32} (Amersham Life Science Ltd, Little Chalfont, UK) and T4 polynucleotide kinase [New England Biolabs (UK) Ltd, Hitchin, UK] at 37 °C for 1 h, and performing 30 cycles of polymerase chain reaction (PCR) amplification in a 10-µl reaction volume containing 100–200 ng of genomic DNA, 1·5 pmoles of each primer, 100 µM of each dNTP, 1·5–2·5 mM $MgCl_2$, 16 mM $(NH_4)_2SO_4$, 67 mM Tris–HCl (pH 8·8 at 25 °C), 0·01% Tween-20, 1 µl DMSO (100%) and 0·4 unit of Taq. Cycling was carried out in a Hybaid thermal cycler as follows: 94 °C for 3 min; [94 °C for 1 min; 55/56 °C for 1 min 30 seconds; 72 °C for 1 min]; 72 °C for 10 min. Two microlitres of each product was then mixed with 2 µl of formamide loading dye (Amersham) and heated to 95 °C before being loaded onto a 6% sequencing gel (Sequagel™, National Diagnostics, Hull, UK). An M13 control sequencing reaction (USB Sequenase kit, Amersham) was run adjacent to the samples to provide an absolute size marker for the microsatellite alleles. Further samples of known allele size were used as additional size standards. Gels were dried down and exposed overnight at –70 °C (Ciofi *et al*. 1998).

RADIO-TRACKING

Radio-collared animals were tracked using a radio receiver and a hand-held directional four element Yagi aerial (Mariner Radar, Bridleway, UK). Initial tracking suggested that cats were active throughout the 24-h period. Consequently cats were tracked continuously (i.e. radio locations every 10 min) for 4-h periods, rotating randomly between periods and cats. Where possible, cats were tracked for six periods per month, i.e. to cover 24 h for each cat in a month. In addition, extra radio locations were recorded on all animals whenever possible (i.e. while checking traps or on the way to another focal animal) to supplement data available for home range estimation.

For each radio location, grid cell, habitat, altitude, activity and weather information were recorded. Locations were recorded directly as 100 × 100-m grid cells on 1 : 25 000 scale Ordnance Survey (OS) maps. The habitat at each radio location was recorded as one of five habitat types: pasture, heather moorland, clear-felled woodland, woodland and stream edge. Altitude was recorded in metres from the OS maps. Precipitation, wind speed, cloud cover and moonlight were recorded in three qualitative classes: 0 if none or absent, 1 if moderate and 2 if strong. Activity was recorded as active if a fluctuation in signal strength (due to changing obstructions and reflections in the path of the transmitter to the receiver) were recorded. If no fluctuation was observed then the radio location was recorded as inactive.

DATA ANALYSIS

Gene frequencies and Hardy–Weinberg equilibrium

The genotypes of 31 individuals, scored at the eight loci (Appendix 1), were added to a database of 301 domestic and wild-living Scottish cats previously analysed (Beaumont *et al.* 2001). The data were split into tabby and non-tabby cats. Differences in gene frequencies between the two groups were tested using the program GENEPOP (Raymond & Rousset 1995). The program creates contingency tables for each locus containing frequency counts of alleles. The gene frequencies in the two groups were then compared using Fisher's exact test. A similar analysis was performed using the genotypes of individuals. Overall *P*-values were calculated across loci using Fisher's method of combining probabilities. The genotype frequencies for each locus using all cats were also tested for deviations from random-mating (Hardy–Weinberg) proportions, also carried out using Genepop (Raymond & Rousset 1995).

Ordinations and density estimation for molecular data

Pairwise allele-sharing distances (Bowcock *et al*. 1994) were calculated between all pairs of alleles for the 31 cats as described in Beaumont *et al*. (2001). These were then ordinated using standard principal coordinates analysis (PCA). The density-fitting procedure of Kooperberg & Stone (1991) was used to estimate the shape of the distribution of scores on the first axis from the ordination. This estimates the log-density with splines and is fully automatic. It places a number of spline knots evenly over the range of the data and then successively deletes individual knots (without changing their placement) to minimize $-2L + \log(n)(n_k - 1)$, where L is the maximum log-likelihood for a given number of knots, n_k, and n is the sample size. This corresponds to the Bayesian information criterion of Schwarz (1978) for comparing nested sets of models.

Relatedness

In order to infer the nature of the relationships between pairs of cats, likelihood ratio tests were performed to compare the probability of obtaining the pair of multilocus genotypes of two individuals under one hypothesis vs. the probability under another hypothesis. Significance was assessed using parametric bootstrapping (i.e. comparing the observed likelihood ratio with the distribution obtained from simulating pairs of individuals under the null hypothesis). This was carried out using the program KINSHIP 1.2 (http://gsoft.smu.edu/GSoft.html; Queller & Goodnight 1989).

In order to calculate these probabilities, baseline gene frequencies of unrelated individuals were needed, so the sample of 230 wild-living cats described in Beaumont *et al*. (2001) was used. We tested for parent–offspring (po), sibling (sib) and half-sibling (hsib) relationships. Although many other relationships are equally plausible and indistinguishable, especially at the hsib level, these three were indicative of the degree of relatedness of pairs of individuals. In order to see if particular relationships could be identified unambiguously, the following sets of significance tests on the 465 possible pairwise comparisons were carried out: po vs. unrelated; sib vs. unrelated; hsib vs. unrelated; po vs. sib; sib vs. po; po vs. hsib; hsib vs. po; sib vs. hsib; hsib vs. sib. The 0·01 level of significance was used to give some protection against type I error. The expected number of false rejections of the null model was then around 5 in each set of tests, but using a lower critical P-value greatly increased the proportion of type II errors (the program KINSHIP 1.2 also estimates the proportion of type II errors for each level of significance used by simulating pairs of individuals according to the hypothesized degree of relationship).

The average pairwise relatedness among categories of cats was estimated using the program RELATEDNESS 5.0.5 (http://gsoft.smu.edu/GSoft.html; Queller & Goodnight 1989) with the same baseline gene frequencies as above. The mean relatedness was estimated for adults and juveniles and also for tabby and non-tabby cats. Standard errors for these estimates were constructed by jack-knifing over the eight loci, and t-tests based on these were used to assess whether there were differences in mean pairwise relatedness between the categories.

Home ranges

Radio-tracking data were analysed using WILDTRAK (Todd 1993). One-hundred per cent minimum convex polygons (MCP) were calculated for each cat for which at least 30 radio locations separated by an hour were available, but using all radio locations for that month. The reason for this approach was that, for half of the cats tracked, the minimum time interval when radio locations could be considered independent was not reached (Swihart & Slade 1985). Instead an estimate of biological independence based on the maximum time taken for moving animals to cross their total range was calculated – 1 h – using the 'movements' module available in WILDTRAK (Todd 1993). By this method the mean number of radio locations used per cat per month was 171 ± 45 ($n = 78$ months). Most ranges did reach an asymptote when plotted against cumulative radio locations but there were continual shifts in home range such that, although monthly range size was fairly constant, the 'lifetime' range continued to increase (Daniels 1997). Seasonal ranges were calculated by combining monthly data for spring (1 March–31 May), summer (1 June–31 August), autumn (1 September–30 November) and winter (1 December–28/29 February).

Overlap and fidelity were estimated for the monthly and seasonal home ranges calculated. 'Home range overlap' was defined as the percentage of shared MCP (Todd 1993) between any two cats whose ranges coincided. 'Home range fidelity' was defined as the percentage of overlap in consecutive monthly or seasonal home ranges for the same individual.

Habitat use

Seasonal habitat use was analysed for all cats for which at least 100 radio locations were available in a season, following the compositional methods described by Aebischer, Roberston & Kenward (1993) using SAS (SAS 1989) code written by one of us. Woodland (the most available and most used habitat type) was used as the denominator in the calculation of log-ratios, and for differences in log-ratios between utilized and available habitat. The differences in log-ratios calculated for woodland (here termed 'preferences') were compared between groups of cats to test for differences in habitat use.

Habitat availability 'within ranges' was estimated for seasonal MCP by overlaying the ranges of animals over the OS maps and recording the numbers of 1-ha squares for each landcover type present. Habitat

availability 'within study area' was estimated from LCS88 data (MLURI 1993) for a 20 × 30-km area surrounding the ranges of all cats that were radio-tracked. Data for the number of hectares within this area, for LCS88 landcover types equivalent to the habitat types used here, were computed using the Countryside Information System Gb 5.23a (Barr *et al*. 1993). Data were combined to produce estimates of percentage availability for the five habitat types described.

Activity

Radio locations were classed as day or night using periods derived monthly following Corbett (1979) for a study site at a similar latitude. Day periods were thus defined as between sunrise plus 1 h and sunset minus 1 h, i.e. at their extremes day radio locations were between 10.00 hours and 15.00 hours for December and 05.00 hours and 21.00 hours for June. Activity patterns were investigated by fitting simple models (using SAS PROC GLM; SAS 1989) to a dependent variable defined as the proportion of active radio locations. These proportions were calculated for each individual cat for each combination of the levels of the independent variable of interest (season, day/night, altitude, wind, precipitation and moonlight) and square-root arcsine transformed. The identity of the cat was included in these models as a blocking factor, and cats for which data were sparse (fewer than 100 radio locations) were excluded. Because the variables included in these models were non-orthogonal, sequential sums of squares were used to form *F*-ratios, and attention was given as to how the order of inclusion in the model affected conclusions about individual effects.

Results

AGE, SEX, PELAGE AND MORPHOLOGY OF CAPTURED CATS

A total of 8500 trap nights resulted in 31 captures (and 24 recaptures). At date of first capture, six out of 18 (33%) females and nine out of 14 (64%) males caught were adult. While the majority had striped tabby pelages (*sensu* Corbett 1979), 10/31 (26%) were non-tabby, of which five were black and three had phenotypes suggesting the presence of other mutant alleles, for example long hair (Table 1 and Fig. 1). Within the tabby-marked cats there was considerable variation in the pattern and boldness of stripes and markings. Even within individuals there were notable differences between seasons, with cats recaptured in the summer having less bold markings than those caught in the winter. Between individuals there was also variation in the amount of white on the ventral side of the body. Most cats had a small spot of white on the throat and the groin, but this was more extensive in some individuals (most notably F15) than others. This is consistent with Robinson (1977), who described the possibility of the partial dominance of S, or the presence of another 'low grade' spotting gene, responsible for variation in the area of white observed in these body regions.

For the small subsample of recovered mortalities, 60% (3/5) were classed as wildcats on the basis of skull size (Schauenberg 1969), 63% (5/8) on the basis of intestine length (Schauenberg 1977) and 67% (4/6) as Group 1 cats on the basis of intestine length and bone size (Daniels *et al*. 1998) (Table 1).

MOLECULAR ANALYSIS

Gene frequencies and Hardy–Weinberg equilibrium

Basic data on the genetic diversity of the cats studied are presented in Appendix 2. There was no evidence of departure from Hardy–Weinberg equilibrium when results from all loci were combined using Fisher's method (*P*-value = 0·12). However, there were significant differences in gene frequencies ($P = 0{\cdot}004$) and genotype frequencies ($P = 0{\cdot}022$) between tabby and non-tabby cats (as defined above).

Ordinations and density estimation

The results of the ordinations of the cats are shown in Fig. 2, where the density of the scores of cats on the first axis of the PCA is plotted. Also plotted are the positions of individual cats both in this study and in the study described in Beaumont *et al*. (2001). The cats were divided into different groups as described in the figure caption. Individual cats grouped by the discriminant function of Daniels *et al*. (1998) were also grouped by traditional criteria as described in Beaumont *et al*. (2001) (i.e. they formed a subset). All other individuals were uniquely categorized in the figure. The domestic (house) cat sample ($n = 74$) was a mixture of individuals obtained from veterinary surgeries in Kirriemuir, York and Surrey (all UK). Analyses showed that the gene frequencies were very similar among these three domestic cat groups, and also the distributions of the three groups on the first axis of the ordination were indistinguishable.

A likelihood ratio test between a unimodal and bimodal density gave $\chi^2 = 34{\cdot}8$ with 2 d.f. ($P < 0{\cdot}001$). The distribution of scores among the tabby and non-tabby cats was significantly different (Kruskal–Wallis rank sum test: $\chi^2 = 9{\cdot}7$, d.f. = 1, $P = 0{\cdot}002$), which was in accord with the results from the gene frequency analysis (see below). The overall pattern was very similar to that found by Beaumont *et al*. (2001), with non-tabby cats more similar to house cats than to those with tabby markings, yet still noticeably differentiated from them.

Relatedness

Using the likelihood ratio tests, six categories of relationships were identified (Table 1): sib, hsib, po or sib, po or hsib, sib or hsib, po or sib or hsib. No po relationships

Journal of Applied Ecology, **38**, 146–161

Table 1. Classification of 31 cats on the basis of pelage and morphological characteristics. Statistically significant ($P < 0{\cdot}01$) genetic relationships between cats are presented: sib, sibling; po, parent–offspring; hsib, half-sibling; Total number of relationships. See text for details

Code*	Age†	Pelage‡	Cranial index§	Intestine index**	Group††	sib	hsib	po/sib	po/hsib	sib/hsib	po/sib/hsib	Total
F1	A	B [aa]	–	–	–					F5	M7, M9, M10, M13, F11, F12, F13	8
F2	J	B [aa]	*n*(2·90)	**W**(2·32)	2(0·44)					M1	F3	2
F3	A	T	–	–	–						M1, F13	2
F4	J	T	–	–	–				M4	F10	M2, M7, M9, M10, F5, F9, F12, F13, F18	11
F5	J	T	–	–	–					M2, M9, F1, F12	M7, M10, F4, F6, F18	9
F6	A	T	**W**(2·34)	*n*(3·47)	**1**(– 0·03)					F11	F5, F16, F18	4
F7	A	T	–	–	–						M13, F8, F10, F15	4
F8	A	B [aa]	–	–	–						F7, F13	2
F9	J	T	–	*n* (3·56)	–	M4				M10, F11, F17	M3, M5, M9, M13, F4, F12	10
F10	J	T	–	–	–					M9, F4, F12	M7, F7, F13	6
F11	J	B [aa]	–	–	–	M5				M9, F6, F9, F16, F18	M4, M8, M10, M13, F1	11
F12	J	T	–	–						M1, M6, M9, F5, F10, F15, F16, F18	M4, F1, F4, F9	12
F13	A	T	–	–	–						M1, M2, M3, M7, M9, F1, F3, F4, F8, F10	10
F14	J	TW [S,ll]	–	–								0
F15	J	**T** [S]	–	–	–				M6	F12, F16, F18	F7	5
F16	J	T	–	–	–			F18		M4, M6, M8, F11, F12, F15	F6	8
F17	J	T	–	–	–					M4, M10, F9	M5	4
F18	J	T	**W**(2·35)	**W**(3·11)	2(20·78)		M1	F16		M4, M6, M10, F11, F12, F15	F4, F5, F6	11
M1	A	T	–	**W**(2·61)	–		F18			F2, F12	F3, F13	5
M2	A	T	**W**(2·64)	–	**1**(– 0·63)	M9				F5	M7, F4, F13	5
M3	A	T	–	–	–						M4, M9, F13	3
M4	J	T	–	–	–	F9			F4	M8, M9, M10, F16, F17, F18	M5, M13, F11, F12	12
M5	J	T	–	*n*(3·64)	–	F11					M4, M8, M9, M10, M13, F9, F17	8
M6	A	B [aa]	–	–	–				F15	F12, F16, F18		4
M7	J	T	–	–	–						M2, M9, F1, F4, F5, F10, F13	7
M8	A	T	–	–	–					M4, F16	M5, F11	4
M9	J	T	–	**W**(2·84)	**1**(– 2·59)	M2				M4, M12, F5, F10, F1, F12	M5, M7, M13, F1, F4, F9, F13	14
M10	A	T	–	–	–					M4, F9, F17, F18	M5, M13, F1, F4, F5, F11	10
M12	A	BW [aa,s]	*n*(2·91)	**W**(2·51)	**1**(– 3·19)					M9	M13	2
M13	A	T	–	–	–						M4, M5, M9, M10, M12, F1, F7, F9, F11	9
M14	A	TS [t^b]	–	–	–							0

*F, female; M, male.
†A, adult; J, juvenile.
‡T, tabby, B, black; BW, black and white; TS, tabby sworl; TW, tabby and white; inferred mutant alleles in square brackets.
§'Wildcat' if index is < 2·75 (Schauenberg 1969).
**'Wildcat' if index is between 2·040 and 3·173 (Schauenberg 1977).
††Group 1 if 'standardized intestine length –0·86 (mean standardized bone measurement) +0·004' is negative, group 2 if positive (Daniels *et al*. 1998).

Fig. 1. Pelage patterns of a subsample of captured wild-living cats from the north-east of Scotland. Cats are anaesthetized to have radio-collars fitted. F = female; M = male. All cats are adults except F14 and M4, which are juveniles. F3, F7, M1, M2 and M4 exhibit 'tabby' pelages, F8, F14 and M12 'non-tabby'.

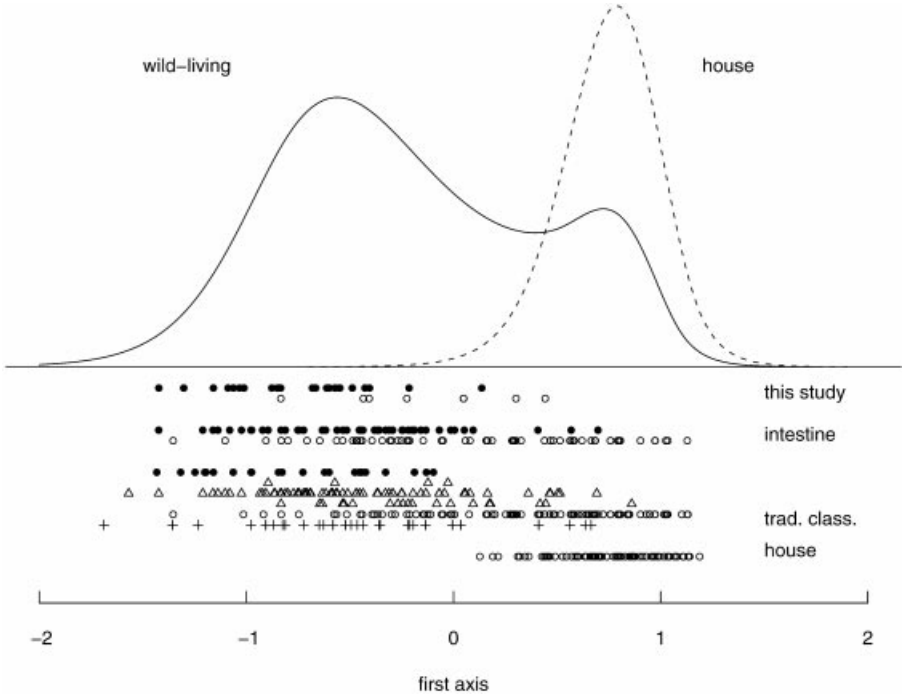

Fig. 2. Estimated density curves for the score of individual cats along the first axis of a principal component analysis of allele sharing differences. Curves are shown for wild-living cats combined with data from Beaumont *et al*. (2001). Density for house cats has been scaled by a factor of 0·5 to fit the plot. Scores of individual cats are plotted beneath density curves: Cats in this study are illustrated as tabby (black circles) and non-tabby (white circles); cats from Daniels *et al*. (1998), here labelled 'intestine', as group 1 (black circles) and group 2 (white circles); cats based on traditional criteria after Beaumont *et al*. (2001) with wildcats (black circles), hybrids (white triangles), domestics (white circles) and unclassified (crosses). House cats (white circles) after Beaumont *et al*. (2001).

could be unambiguously identified. A relationship was included in the table if at least one of the likelihood ratios for sib, hsib or po vs. unrelated was significant at the 0·01 level. The simulation tests for the rate of type II errors gave the following rates: po, 0·75%; sib, 19·4%; hsib, 71·2%. This indicated that with these eight loci there was reasonable power for detecting relationships at the po and sib level but the ability to detect hsib was weak.

Six categories of relationships are listed (Table 1) because for many of the cats a number of different relationships was equally plausible. For example, the null hypothesis that two cats are unrelated could be rejected in favour of an alternative hypothesis that they are sibs but not against the hypothesis that they are hsibs. Thus the results of comparing different hypotheses was used to place relationships into the different categories. For example, for relationships placed into the sib category, both tests of sib vs. hsib and sib vs. po were significant at the 0·01 level. Relationships were put into the po/sib/hsib category if none of the three postulated types of relationship was identified as significantly less likely in both tests against the others (for example, the possibility of a sib relationship would only be excluded if both the tests of po vs. sib and hsib vs. sib were significant). Table 1 therefore identifies the most likely relationships among cats purely from genetics, irrespective of age or other information. Behavioural and age data narrowed the range of likely relationships (see Table 2, discussed later).

One cat, M14, possessed an allele of length 101 at locus Fca90 that was not found in any of the 234 wild-living cats used to provide a baseline (it was present at a frequency of 0·027 in the sample of 74 house cats taken from the three locations in the UK). Because of this, it had a relatedness of zero to all other cats. M14 also possessed a number of alleles not observed in the current sample (although present in the baseline sample), and no significant relationships were found between M14 and any other cats in additional tests using only seven loci or using the gene frequencies observed in the 31 cats described here as a baseline.

Of the 465 pairwise comparisons, 101 were included in Table 1 using the criterion given above. It can be seen from the table that most relationships could not be distinguished from each other. Only three sib and one hsib relationship could be identified unambiguously. The large number of po exclusions enabled many sib/hsib relationships to be distinguished from po relationships. Some individuals showed the possibility of a large number of relationships (for example M9 showed evidence of relationships to 13 other individuals). There was a tendency for juveniles to have the highest number of relationships, whereas the non-tabby cats tended to have the fewest. For example, the two cats that showed no evidence of relationships to any other individuals, M14 and F14, were both non-tabby. The non-tabby cats F1 and F11 were clear exceptions to this, however, and had similar numbers of relationships as the other

Table 2. Genetic evidence for relationships between cats suggested by field observations. Proposed parents and siblings excluded on genetic evidence are shown struck out. The inferred degree of relationship (see Table 1) for statistically significant pairs ($P < 0{\cdot}01$) in bold are shown in superscript (psh: po/sib/hsib; sh: sib/hsib; ps: po/sib; s: sib). Non-tabby cats are in italics

Juvenile	Potential fathers	Potential mothers	Potential siblings
M4	~~M2~~ ~~*M6*~~		**M5**^{psh} M7 **F9**^{s} ***F11***^{psh}
M5	~~M2~~ ~~*M6*~~		**M4**^{psh} M7 **F9**^{psh} ***F11***^{s}
M7	**M2**^{psh} ~~*M6*~~		M4 M5 F9 *F11*
M9	~~M10~~	***F1***^{psh} ~~F3~~ **F13**^{psh}	F2 **F4**^{psh} **F10**^{sh} **F12**^{psh}
F2	~~M10~~	~~*F1*~~ **F3**^{psh} ~~F13~~	M9 F4 F10 F12
F4	**M10**^{psh}	~~*F1*~~ ~~F3~~ **F13**^{psh}	**M9**^{psh} F2 **F10**^{sh} **F12**^{psh}
F5	~~M2~~ ~~*M6*~~	**F6**^{psh}	
F9	~~M2~~ ~~*M6*~~		**M4**^{s} **M5**^{psh} M7 ***F11***^{sh}
F10	~~M10~~	~~*F1*~~ ~~F3~~ **F13**^{psh}	**M9**^{sh} F2 **F4**^{sh} **F12**^{sh}
F11	~~M2~~ ~~*M6*~~		**M4**^{psh} **M5**^{s} M7 **F9**^{sh}
F12	~~M10~~	***F1***^{psh} ~~F3~~ ~~F13~~	**M9**^{sh} F2 **F4**^{psh} **F10**^{sh}
F14	~~M1~~ ~~M3~~	~~F7~~ ~~F8~~	F15
F15	~~M1~~ ~~M3~~	**F7**^{psh} ~~F8~~	F14
F16	~~*M12*~~ ~~M13~~ ~~*M14*~~		F17 **F18**^{ps}
F17	~~*M12*~~ ~~M13~~ ~~*M14*~~		F16 F18
F18	~~*M12*~~ ~~M13~~ ~~*M14*~~		**F16**^{ps} F17

cats. In addition, of all the comparisons among the non-tabby cats, only F1 and F11 show a significant po/sib/hsib relationship.

From trapping and radio-tracking observations, a number of possible relationships on the basis of range overlap were identified, as shown in Table 2. Juveniles of similar age occupying the same area were identified as potential siblings, while adults occupying the same area as juveniles were identified as potential parents. Most of these potential po relationships were excluded by the genetic data (shown struck out in Table 2), and all the inclusions were identified as significant by the likelihood ratio tests. The genotyping was repeated twice for the whole sample and a third time if there was variation. Female cats appeared to have a greater chance of being genetically identified as parents than male cats.

It can be seen that the non-tabby cat F1 was supported genetically and observationally as the mother of tabby cat F12 and possibly tabby cat M9 (another potential mother was F13, which showed a po/sib/hsib relationship with F1). The other non-tabby cat showing a large number of relationships, F11, could be identified genetically and observationally as a full sib of the tabby cat M5. The genetic data also suggested a po/sib/hsib relationship between F11 and F1 (Table 1) but there was no observational evidence to support such a relationship. The non-tabby cats M6, M12, M14 and F8 were identified observationally as potential parents or siblings, but none of the putative relationships was supported genetically.

The mean relatedness within different age and pelage categories of cats is presented in Table 3. It should be noted that relatedness can be viewed as a measure of the mean correlation between individuals in their gene frequencies and can be negative as well as positive (Queller & Goodnight 1989). Overall, the mean relatedness of non-tabby cats to tabby cats was $0{\cdot}156 \pm 0{\cdot}036$, and the mean relatedness of juveniles to adults was $0{\cdot}161 \pm 0{\cdot}032$. Because the estimates were based on pairwise comparisons it was not possible to carry out a 2-way ANOVA with the data. The mean relatedness of juvenile non-tabbies was significantly lower than that of juvenile tabbies ($t = 3{\cdot}19$, d.f. = 14, $P < 0{\cdot}01$) and the relatedness of all non-tabbies was significantly lower than that of all tabbies ($t = 2{\cdot}48$, d.f. = 14, $P < 0{\cdot}05$). However, non-tabby cats were not less related to tabby cats than tabby cats were to each other.

Table 3. Mean and standard errors of relatedness between cats grouped on the basis of age and pelage type

	Adult	Juvenile	All cats
Tabby	$0{\cdot}183 \pm 0{\cdot}060$	$0{\cdot}356 \pm 0{\cdot}091$	$0{\cdot}260 \pm 0{\cdot}067$
Non-tabby	$0{\cdot}064 \pm 0{\cdot}099$	$-0{\cdot}061 \pm 0{\cdot}094$	$0{\cdot}037 \pm 0{\cdot}060$
All cats	$0{\cdot}128 \pm 0{\cdot}052$	$0{\cdot}270 \pm 0{\cdot}084$	$0{\cdot}185 \pm 0{\cdot}042$

ECOLOGY OF CATS TRACKED

Home ranges

Thirty-one cats were followed for an average of 5 months (range 1–21) and a total of 22 831 radio locations was collected. Insufficient data were collected from two cats (F12 and M14) to analyse further. There were no significant differences in median home range area between tabby males (419 ha) and non-tabby males (588 ha: $U = 39$, $P = 0{\cdot}82$, Mann–Whitney U-test). Non-tabby adult females had significantly larger median home ranges (197 ha) than those of tabby adult females (102 ha: $U = 35$, $P < 0{\cdot}01$) but these were still in the same order of magnitude and significantly smaller than those of all adult males (459 ha) or non-tabby adult males (588 ha: $U = 74$, $P < 0{\cdot}01$).

Table 4. Summary of ecological data for wild-living cats in the north-east of Scotland. Median values for ecological characteristics of radio-tracked cats for which sufficient radio locations were available for analyses (see text for details)

Sex + age	Monthly 100% MCP (ha) all year	% of active radio locations all year	% fidelity all year	Preference indices for woodland (spring)	Altitude of home ranges (m) spring
Adult males	459	56	63	0·55	352
Adult females	177	61	67	0·09	347
Juvenile males	159	47	38	0·14	311
Juvenile females	63	53	59	0·17	332

From these results it appeared that there was little difference between cats of tabby and non-tabby pelage. Hence, below, cats are considered together to summarize the results. Adult males had significantly larger median ranges (459 ha) than those of all other sex and age classes (Table 4). Adult female median ranges were significantly larger than juvenile females ($U = 178$, $P < 0{\cdot}01$, Mann–Whitney U-test) but not juvenile males ($U = 74$, $P = 0{\cdot}45$). Juvenile males ranges were significantly larger than juvenile females ($U = 63{\cdot}5$, $P < 0{\cdot}04$). There were no significant differences between median home range size for cats between seasons, but differences in consecutive seasonal home range fidelity were highly significant ($P < 0{\cdot}01$, Kruskal–Wallis test), with adult females the most faithful to their ranges over time and juvenile males the least (Table 4).

Adult males shared a relatively small percentage of their range with adjacent cats (*c.* 20–30%). Adult female ranges overlapped only slightly with each other (*c.* 10%) but shared more of their ranges with one adult male (*c.* 70%) and juvenile females (36%). Similarly, juveniles (both males and females) had little overlap with each other but shared *c.* 70% of their ranges with adult males or females. However, even though ranges of collared animals overlapped, they were seldom found together, suggesting that where any shared range use occurred it was mostly in terms of area rather than time.

All cats were essentially solitary. 'Interactions' between cats were defined as occurring when two or more radio-collared cats were recorded together in the same 100×100-m square. Interactions occurred on only 54 occasions, totalling 518 out of the 22 831 radio locations collected (2%). The majority of all interactions (88%) were between males and females and 79% occurred in spring and winter, significantly more than would be expected by chance ($\chi^2_{15} = 39{\cdot}2$, $P < 0{\cdot}01$). Out of 90 observations, cats were seen alone on 88 occasions, the exceptions being when an adult female was observed with two kittens. Twelve observations of non-collared cats were also made (although it is likely that some of these individuals were subsequently collared) and all were alone.

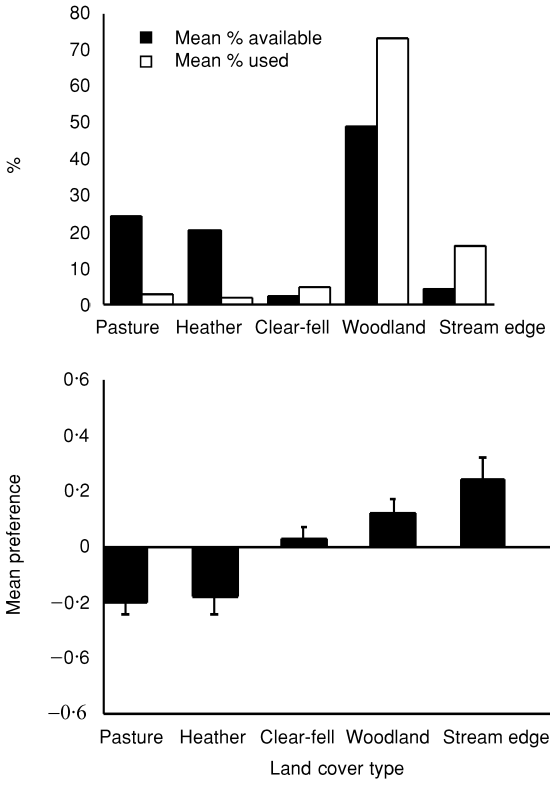

Fig. 3. Mean availability and utilization and preference indices (±1 SE) for five landcover types associated with the home ranges of 17 wild-living cats in the north-east of Scotland in spring (combined for 1995, 1996 and 1997).

Habitat use

Most data were available for 17 cats in spring. These showed that, on average, cats significantly preferred stream edge and woodland habitat types and avoided pasture and heather moorland within their ranges ($P < 0{\cdot}0001$; Fig. 3). Cats used clear-fell approximately in proportion to its availability. The results were similar for habitat selection in relation to the whole study area (as opposed to 'within range'), except that cats showed a stronger preference for stream edge habitat and a stronger aversion to heather moorland ($P < 0{\cdot}0001$).

There was no significant difference in woodland use between sexes and between adults and juveniles, and there was no significant difference between cats of different pelage types (all $P > 0{\cdot}01$; Table 4). Cats were located at a range of altitude medians between 320 m and 383 m. There were also no significant differences in median altitude between cats of different sex, age or pelage (all $P > 0{\cdot}05$; Table 4).

Table 5. Significance levels from general linear models on the effects of environmental and biological variables on cat activity

Variable	*F* numerator, denominator	*P*
Cat individual	28,820	0·0001
Time of day (day/night)	1,820	0·0001
Time of day × season	3,320	0·0001
Season	3,820	0·10
Wind	1,820	0·0001
Altitude	1,820	0·26
Precipitation	1,820	0·66
Moon	2,294	0·03
Sex	1,25	0·03
Age	1,25	0·19
Pelage	1,25	0·64

Activity

There was strong evidence that the effect of time of day on activity varied with season (Table 5). Stratifying the data into day and night, and into season separately, suggested that cats were significantly more active during the night in all seasons. During the day, the highest activity levels were observed in a declining rank order from autumn, summer, winter to the lowest in spring.

Of the weather variables, only wind appeared to influence activity: there was very strong evidence that cats were less active in windy conditions (Table 5). In a separate model including only night radio locations, there was evidence that the phase of the moon influenced the activity of both sexes. Cats were significantly less active under conditions of low moonlight. Overall, female cats were consistently more active than males (Table 4) but there was no evidence that cats of different ages or pelage types exhibited different levels of activity.

Discussion

THE MORPHOLOGY, GENETICS AND ECOLOGY OF WILD-LIVING CATS

This study aimed to investigate the relationship between sympatric tabby and non-tabby cats. The data described here were collected in an area where wildcats were considered to occur (Easterbee, Hepburn & Jefferies 1991). In general the cats displayed morphological characteristics associated with wildcats, although their pelages were more varied than traditionally described (Corbett 1979; Kitchener & Easterbee 1992), with the frequency of non-tabby pelages (26%) similar to that reported for Scotland as a whole (Daniels *et al*. 1998) and for wildcats caught in Switzerland (Dötterer & Bernhart 1996).

In terms of genetics, there was no strong evidence of two groups, despite significant differences in gene frequencies and genotypes between tabby and non-tabby groups. Most wild-living cats were clearly differentiated genetically from domestic cats, yet those with non-tabby markings tended to be more similar to domestic cats than were those with tabby markings.

The relatively high mean relatedness among the cats (Table 3) is perhaps not surprising, given the evidence from behavioural observations of a relatively stable resident population. It also follows from the fact that we have used a previous genetic database to provide the baseline gene frequencies (Beaumont *et al.* 2001). The pairwise Weir & Cockerham theta between the two populations is 0·032. This estimates Fst, the probability that two genes share a common ancestor within the population, averaged over both populations, relative to a common baseline gene frequency (Weir 1996). As the observed gene frequency in one of the populations is used to provide the baseline in this analysis of relatedness, this corresponds to an estimate of Fst of 0·064 in the study population and an Fst of 0 in the reference population (Beaumont *et al.* 2001). If the sample gene frequencies had been used instead, then the average relatedness would by definition have been 0. However, it is biologically more realistic to use the large sample baseline because it more closely reflects the gene frequencies of unrelated individuals immigrating into the area.

Both tabby and non-tabby cats showed levels of relatedness to members of each others' groups (especially the black cats F1, F2 and F11) that were statistically significant. At a group level, though, the non-tabby cats caught here appeared to be less related to each other than were tabby cats. This suggested that the pattern of recent ancestry of the non-tabby cats was, on average, different from that of the tabby cats. A plausible explanation is that the recent ancestors of the non-tabby cats, or some individuals themselves (for example M14), are independent immigrants into the population. This was supported to some extent by radio-tracking data for M14, who appeared to be itinerant (and indeed was not located within the study area for a sufficient period of time to be included in any of the ecological analyses). On the other hand, non-tabby cats (for example F1) were significantly related to tabby cats and appeared to be resident, showing similar patterns of social organization, range use and activity.

With the exception of adult females, there were no significant differences in social organization, home range, habitat use or activity patterns between tabby and non-tabby cats. In general, cats exhibited a pattern of intrasexual territoriality displayed by other asocial felids (Kleiman & Eisenberg 1973; Wrangham & Rubenstein 1986; Caro 1989; Ferreras *et al*. 1997; Stander *et al*. 1997), including wildcats (Corbett 1979; Stahl, Artois & Aubert 1988). In other words, they did not demonstrate the complex society described for farm cats by Kerby & Macdonald (1988), yet their behaviour (and that of wildcats described from previously studies) was also broadly consistent with that described for feral cats living independently of people

(Corbett 1979; Jones & Coman 1982; Fitzgerald & Karl 1986; Langham & Porter 1991; Langham 1992).

In terms of home range, the data from the group of cats presented here also conform to previous studies on wildcats (for example median home ranges here of 459 ha for males and 177 ha for females, compared with mean ranges of 573 ha and 184 ha for males and females, respectively, in France; Stahl, Artois & Aubert 1988) and to those of feral cats (620 ha for males and 170 ha for females in Australia; Jones & Coman 1982). The same is also true with regard to habitat use and activity patterns [see Corbett (1979) and Artois (1985) for wildcats, and Jones & Coman (1982), Fitzgerald & Karl (1986), Langham & Porter (1991) and Langham (1992) for feral cats].

In conclusion, the ecology of the cats described in this study overlaps with that reported for both wildcats and feral cats in Scotland and other parts of the world. Equally, while there were some significant differences in the ecology and genetics of tabby and non-tabby cats, there was also considerable overlap. Both these points raise important questions about the origins of wild-living cats in Scotland and the conservation of the wildcat.

THE ORIGINS OF TABBY AND NON-TABBY CATS

The coexistence and relatedness of tabby and non-tabby cats, combined with the conclusion that despite gene frequency differences there was no exclusive differences between them, raises several hypotheses as to the origins of the population of cats caught and tracked in this study. First, non-tabby cats may simply represent phenotypic variation in the wild population. While previous studies have attempted to define wildcats on the basis of their pelage, excluding non-tabby cats (Kitchener & Easterbee 1992; Ragni & Possenti 1996), black cats provide a telling illustration of the difficulty in defining an animal purely on its pelage.

Melanism is the most common morph among wild mammals (Robinson 1970) and black variants have been reported in at least 20 other felid species (Robinson 1978), for example the golden cat *Felis temminckii* (Martyr 1997). Indeed, Daniels *et al*. (1998) reported 17% of a sample of wild-living cats from Scotland as black, and similarly 16% of the cats caught here had a black phenotype. It is possible, therefore, that the mutant alleles responsible for the variation in pelage described here are at least in part a result of natural variation.

Variation within populations of other wild felid species has been widely reported, including the serval *Felis serval* where a 'servaline' phenotype is recognized as the result of a mutation at the tabby locus (Kitchener 1991). van Aarde & van Dyk (1986) also describe the occurrence of a mutation at the tabby locus (analogous to t^{b-} as found in M14; Table 1) that is responsible for the 'blotched' coat pattern found in 'King cheetahs' *Acinonyx jubatus*, at one time described as a separate species. Caro & Durant (1991) describe variation within tail banding of cheetahs that they attribute to both genetic and environmental (uterine) effects. Within the Iberian lynx *Lynx pardinus*, sufficient variation in the size, pattern and distribution of spots may merit the distinction of three pelage types (Beltran & Delibes 1993).

A second possibility for the origin of these wild-living cats is that they are feral domestic cats. Studies of feral domestic cats in regions of Australia with low human density (< 1 person km^{-2}) have reported comparable proportions of striped tabbies to that described here. For example, 83% of cats in national parks in New South Wales and 62% in Victoria (Jones & Horton 1984) were tabbies, as were 74% of cats in subantarctic Macquarie Island (Brothers, Sikra & Copson 1985). In contrast, Clark (1975, 1976) reported much lower percentages of tabby cats in an urban area of Scotland (Glasgow) ranging from 16% to 33%. In Australia, only 29% of feral cats in two populated rural areas (i.e. > 1 person km^{-2}) had a striped tabby phenotype, although the frequency was 93% in another population. Generally, domestic cats and feral cats in urban situations had higher frequencies of mutant alleles (for example aa) than those reported in Table 1 (Clark 1975, 1976; Jones & Horton 1984; Brothers, Sikra & Copson 1985).

Consequently, in terms of their pelage as well as their social organization (as outlined above), the cats trapped and tracked here could well be a feral population. However, the third hypothesis is that the population here (and indeed cats throughout Scotland; Daniels *et al*. 1998) represent the product of long-term interbreeding between wild and domestic or feral domestic cats.

Instances of interbreeding have been anecdotally documented (reviewed in Daniels *et al*. 1998) but largely stem from records in captivity. However, Robinson (1976) claims 'Hybrids between the domestic cat and European wildcat have been obtained repeatedly' and that the potential for intraspecific breeding in the Felidae is generally high because of the high level of similarity in karyotype. Todd (1978) notes that 'direct evidence of interbreeding and interfertility is largely anecdotal but no doubt valid'.

Potentially at least, the possibilities for interbreeding have been present since the domestic cat arrived in Britain. Feral or domestic cats occur throughout areas thought to be occupied by the wild form and relatively few domestic cats in rural areas are neutered (for example between 6% and 30% of females; Clark 1976). Certainly there was potential in our study population for contact between radio-collared cats and domestic cats associated with farms.

However, as described above, interbreeding is usually deduced from the presence of non-wild type pelages in wild-living cats (French, Corbett & Easterbee 1988). That variation has not been widely reported in

'wildcats' before may therefore reflect a human perception that cats exhibiting these phenotypes are 'hybrids'. Equally, however, the presence of mutant alleles, to date described only in domestic cats (for example long hair, ll, F14; Table 1), may indicate that interbreeding has taken place.

RECOMMENDATIONS REGARDING FUTURE CONSERVATION OF THE WILDCAT

The results indicate that there are problems with regards the 'traditional' pelage-based definition for the wildcat for conservation and legal protection (Balharry, Daniels & Barratt 1997; Daniels *et al*. 1998). First, the concept of the type specimen may have been misused. Rather than expecting animals to fall within a range of variation from which the type specimen was drawn (Dadd 1970), in the case of putative wildcats, animals have been expected to conform very closely to it. Secondly, tabby pelages may be selected for and become more frequent in truly feral populations (Darwin 1868; Jones & Horton 1984; Brothers, Sikra & Copson 1985), possibly as an adaptation towards crypsis for hunting. Thirdly, the type specimen for wildcat was collected when the native wildcat and introduced domestic cat had already been in sympatry for 2000 years. Consequently, the population from which it came (and the specimen itself) may have been interbred.

The genetic data presented here do not include any samples pre-dating the arrival of the domestic cat. Consequently the relationship between contemporary populations and the ancestral wildcat remains unclear. Furthermore, the relationship between putative wildcats in Scotland and those found in other countries has yet to be elucidated.

However, it appears that, in Scotland at least, instead of conforming to a tight physical definition, current knowledge points to a morphological cline among wild-living cats in Scotland (Daniels *et al*. 1998). Cats at one end of the cline appear to be characterized by large bone and skull size, short intestine length (Daniels *et al*. 1998) and, from this study, specific gene frequencies and a 'solitary' social system. The probability of finding cats of this type appears be related to specific environmental correlates, such as the suitability of land for forestry, and consequently to specific geographical areas (Daniels *et al*. 1998) or altitudes (Beaumont *et al.* 2001). No morphological, behavioural or genetic characteristics have been identified that are exclusive to one group of cats and hence lend themselves as criteria for a discrete definition. Instead, wildcat conservation needs to address the challenges of managing a population below the species level.

Increasingly, the traditional view of the species [as defined by Mayr's (1942) 'reproductively isolated' concept] as the only unit for conservation is being challenged. O'Brien & Mayr (1991) confirmed the usefulness of differentiation at this level but also argued that for conservation purposes subspecies could be recognized as having a unique geographical range, habitat or natural history. For example, currently in the United States the Endangered Species Act defines and allows for the conservation of 'distinct population segments' for groups taxonomically below the subspecies level (Pennock & Dimmick 1997).

One approach to the conservation of the wildcat would be to define areas for conservation action on the basis of current data indicating where the greatest morphological, ecological and genetic divergence from domestic cats occurs. The hypothesis is that, within these areas, if further interbreeding and persecution are minimized, cats will remain or continue to adapt to the environment and at the same time have less contact with domestic cats. The map produced by Daniels *et al*. (1998) demonstrates one possible approach for defining such areas.

Within defined areas, measures encouraging responsible cat ownership could be promoted. These could range from banning the keeping of domestic cats to encouraging or imposing neutering. Where feral cats threaten indigenous wildlife, eradication programmes have been undertaken, for example in South Africa's subantarctic Marion Island (van Aarde *et al*. 1996), or mainland Australia (Risbey, Calver & Short 1997). In parts of Australia, where indigenous wildlife is threatened, local government has been encouraged to introduce 'curfews' requiring owners to confine cats between certain hours (Paton 1993). In South Africa, Stuart & Stuart (1991) advocate neutering programmes, limiting the number of cats per household and licensing, as measures for protecting both the wildcat and indigenous wildlife.

It is clear that around the world mechanisms exist as potential models for domestic cat control. It is likely that by controlling domestic cats in specified areas, the potential threat posed by interbreeding to the wild population would be reduced. There is a need for wide-ranging debate and consultation on the usefulness of domestic cat control in specific areas, to aid the future conservation of the wildcat in Scotland.

Acknowledgements

Trapping was carried out under licence from Scottish Natural Heritage (SRA:02:96/(R)SRA:02:96) and anaesthesia and blood sampling under Home Office Licence (PIL 60/4400). We are most grateful to Forest Enterprise Tay District, Airlie Estate, Balnaboth Estate, North of Scotland Water Authority and Glen Prosen Sporting Ltd for permission and access to land, and to Scottish Natural Heritage for the use of their traps and equipment. Special thanks are also given to staff of the above organizations for all of their help and in particular to Willie Walker, David Laird, Alex Boath, Dave Eddon and Colin Lanyon. Shaila Rao, Danielle Kreb and Ben Fairgrieve helped with trapping and tracking. We thank Dada Gotttelli for help in

running and scoring microsatellite gels, and Mike Bruford and Rob Hammond for helpful advice with genetics. The work was funded through grants from Tusk Force, J & B Care For The Rare, Care for the Wild, People's Trust for Endangered Species and vehicles kindly supplied by Asia and Kia motors, without which the project would not have been possible. Shaila Rao, Ben Fairgrieve, Mairi Cooper, Hans Kruuk, Pall Hersteinsonn, Tim Caro, Andrew Kitchener and four anonymous referees provided helpful comments on earlier versions of the manuscript.

References

van Aarde, R.J. & van Dyk, D.A. (1986) Inheritance of the king coat colour pattern in cheetahs *Acinonyx jubatus*. *Journal of Zoology*, **209**, 573–578.

van Aarde, R., Ferreira, S., Wassenaar, T. & Erasmus, D.G. (1996) With the cats away the mice may play. *South African Journal of Science*, **92**, 21–22.

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993) Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, **74** (5), 1313–1325.

Artois, M. (1985) Utilisation de l'espace et du temps chez le renard (*Vulpes vulpes*) et le chat forestier (*Felis silvestris*) en Lorraine. *Gibier Faune Sauvage*, **3**, 33–57.

Balharry, D., Daniels, M.J. & Barratt, E.M. (1997) Wildcats: can genetics help in their conservation? *The Role of Genetics in Conserving Small Populations* (eds T.E. Tew, T.J. Crawford, J. Spencer, D. Steven, M.B. Usher & J. Warren), pp. 102–111, Joint Nature Conservancy Council, Peterborough, UK.

Barr, C.J., Bunce, R.G.H., Clarke, R.T., Fuller, R.M., Furse, M.T., Gillespie, M.K., Groom, G.B., Hallam, C.J., Hornung, M., Howard, D.C. & Ness, M.J. (1993) *Countryside Survey 1990*. Department of the Environment, Eastcote, UK.

Beaumont, M., Barratt, E.M., Gotelli, D., Kitchener, A.C., Daniels, M.J., Pritchard, J.K. & Bruford, M.W. (2001) Genetic diversity and introgression in the Scottish wildcat. *Molecular Ecology*, in press.

Beltran, J.F. & Delibes, M. (1993) Physical characteristics of Iberian lynxes (*Lynx pardinus*) from Donana, southwestern Spain. *Journal of Mammalogy*, **74**, 852–862.

Bowcock, A.M., Ruiz-Linares, A., Tomfohrde, J., Minch, E., Kidd, J.R. & Cavalli-Sforza, L.L. (1994) High resolution of human evolutionary trees with Spolymorphic microsatellites. *Nature*, **368**, 455–457.

Brothers, N.P., Sikra, I.J. & Copson, G.R. (1985) Biology of the feral cat, *Felis catus* (L.), on Macquarie Island. *Australian Wildlife Research*, **12**, 425–436.

Caro, T.M. (1989) Determinants of asociality in felids. *Comparative Socioecology. The Behavioural Ecology of Humans and Other Mammals* (eds V. Standen & R.A. Foley), pp. 41–74, Blackwell Scientific Publications, Oxford, UK.

Caro, T.M. & Durant, S.M. (1991) Use of quantitative analyses of pelage characteristics to reveal family resemblances in genetically monomorphic cheetahs. *Journal of Heredity*, **82**, 8–14.

Ciofi, C., Funk, S.M., Coote, T., Cheesman, D.J., Hammond, R.L., Saccheri, I.J. & Bruford, M.W. (1998) Genotyping with microsatellite markers. *Molecular Tools for Screening Biodiversity* (eds A. Karp, P.G. Isaac & D.S. Ingram) Chapman & Hall, London, UK.

Clark, J.M. (1975) The effects of selection and human preference on coat colour gene frequencies in urban cats. *Heredity*, **35**, 195–210.

Clark, J.M. (1976) Variation in coat colour gene frequencies and selection in the cats of Scotland. *Genetica*, **46**, 401–412.

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

Dadd, M.N. (1970) Overlap of variation in British and European mammal populations. *Symposium of the Zoological Society (London)*, **26**, 117–125.

Daniels, M.J. (1997) *The biology and conservation of the wildcat in Scotland*. PhD Thesis. University of Oxford, Oxford, UK.

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'. *Journal of Zoology*, **244**, 231–247.

Darwin, C. (1868) *The Variation of Animals and Plants under Domestication*. Vols I and II, John Murray, London, UK.

Dötterer, M. & Bernhart, F. (1996) The occurrence of wildcats in the southern Swiss Jura Mountains. *Acta Theriologica*, **41**, 205–209.

Easterbee, N. (1991) The wildcat. *The Handbook of British Mammals* (eds G. Corbet & S. Harris), pp. 431–437, Blackwell Scientific Publications, Oxford, UK.

Easterbee, N., Hepburn, L.V. & Jefferies, D.J. (1991) *Survey of the Status and Distribution of the Wildcat in Scotland, 1983–1987*. Nature Conservancy Council for Scotland, Edinburgh, UK.

Ferreras, P., Beltrán, J.F., Aldama, J.J. & Delibes, M. (1997) Spatial organization and land tenure system of the endangered Iberian lynx (*Lynx pardinus*). *Journal of Zoology*, **243**, 163–189.

Fitzgerald, B.M. & Karl, B.J. (1986) Home range of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Ecology*, **9**, 71–80.

French, D., Corbett, L.K. & Easterbee, N. (1988) Morphological discriminants of Scottish wildcats (*Felis silvestris*), domestic cats (*F. catus*) and their hybrids. *Journal of Zoology*, **161**, 75–123.

Jones, E. & Coman, B.J. (1982) Ecology of the feral cat, *Felis catus* (L.), in south-eastern Australia. III. Home ranges and population ecology in semiarid north-west Victoria. *Australian Wildlife Research*, **9**, 409–420.

Jones, E. & Horton, B.J. (1984) Gene frequencies and body weights of feral cats, *Felis catus* (L.), from five Australian localities and from Macquarie Island. *Australian Journal of Zoology*, **32**, 231–237.

Kerby, G. & Macdonald, D.W. (1988) Cat society and the consequences of colony size. *The Domestic Cat: the Biology for its Behaviour* (eds D.C. Turner & P. Bateson), pp. 67–81, Cambridge University Press, Cambridge, UK.

Kitchener, A.C. (1991) *The Natural History of the Wild Cats*, Croom-Helm, London, UK.

Kitchener, A.C. & Easterbee, N. (1992) The taxonomic status of black wild felids in Scotland. *Journal of Zoology*, **277**, 342–346.

Kleiman, D.G. & Eisenberg, J.F. (1973) Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour*, **21**, 637–659.

Kooperberg, C. & Stone, C.J. (1991) A study of logspline density estimation. *Computational Statistics and Data Analysis*, **12**, 327–347.

Langham, N.P.E. & Porter, R.E.R. (1991) Feral cats (*Felis catus* L.) on New Zealand farmland. I. Home range. *Wildlife Research*, **18**, 741–760.

Langham, N.P.E. (1992) Feral cats (*Felis catus* L.) on New Zealand farmland. II. Seasonal activity. *Wildlife Research*, **19**, 707–720.

Martyr, D. (1997) Important findings by FFI team in Kerinci Seblat, Sumatra, Indonesia. *Oryx*, **31**, 80–82.

Mayr, E. (1942) *Systematics and the Origin of Species*, Columbia University Press, New York, NY.

Menotti-Raymond, M.A. & O'Brien, S.J. (1995) Evolutionary consequences of ten microsatellite loci in four species of felidae. *Journal of Heredity*, **86**, 319–322.

MLURI (1993) *The Land Cover of Scotland 1988*. Macaulay Land Use Research Institute, Aberdeen, UK.

Nowell, K. & Jackson, P. (1996) *The Wild Cats: Status Survey and Conservation Action Plan*. International Union for Nature Conservation/Cat Specialist Group, Gland, Switzerland.

O'Brien, S.J. & Mayr, E. (1991) Bureaucratic mischief: recognizing endangered species and subspecies. *Science*, **251**, 1187–1188.

Paton, D.C. (1993) The impact of domestic and feral cats on wildlife. *Cat Management Workshop Proceedings*, pp. 5–15, Queensland Department of Environment and Heritage, Brisbane, Australia.

Pennock, D.S. & Dimmick, W.W. (1997) Critique of the evolutionarily significant unit as a definition for 'distinct population segments' under the US Endangered Species Act. *Conservation Biology*, **11**, 611–619.

Piechoki, R. (1990) *Die Wildkatze*, A. Ziemsen-Verlag, Wittenberg Lutherstadt, Germany.

Queller, D.C. & Goodnight, K.F. (1989) Estimating relatedness using genetic markers. *Evolution*, **43**, 258–275.

Ragni, B. & Possenti, M. (1996) Variability of coat-colour and markings system in *Felis silvestris. Italian Journal of Zoology*, **63**, 285–292.

Raymond, M. & Rousset, F. (1995) Genepop (Version 1.2): population genetics software for exact tests of ecumenicism. *Journal of Heredity*, **86**, 248–249.

Risbey, D.A., Claver, M. & Short, J. (1997) Control of feral cats for nature conservation. I. Field tests for four baiting methods. *Wildlife Research*, **24**, 319–326.

Robinson, R. (1970) Homologous mutants in mammalian coat colour variation. *Symposium of the Zoological Society (London)*, **26**, 251–269.

Robinson, R. (1976) Homologous genetic variation in the *Felidae*. *Genetica*, **46**, 1–31.

Robinson, R. (1977) *Genetics for Cat Breeders*, 2nd edn, Pergamon Press, Oxford, UK.

Robinson, R. (1978) Homologous coat color variation. *Carnivore*, **1**, 68–71.

Sambrook, J., Fritsch, E.F. & Maniatis, T. (1989) *Molecular Cloning: A Laboratory Manual*, 2nd edn, Cold Spring Harbour Laboratory Press, Cold Spring Harbour, NY.

SAS (1989) *SAS/STAT User's Guide, Version 6*, 4th edn, SAS Institute Inc., Cary, NC.

Schauenberg, P. (1969) L'identification du chat forestier d'Europe *Felis silvestris* Schreber, 1777 par une methode osteomertrique. *Revue Suisse Zoologie*, **76**, 433–441.

Schauenberg, P. (1977) Longuer de l'intestin du chat forstier d'Europe *Felis s.silvestris* Schreber, 1777. *Mammalia*, **41**, 357–360.

Schwarz, G. (1978) Estimating the dimension of a model. *Annals of Statistics*, **6**, 461–464.

Stahl, P., Artois, M. & Aubert, M.F.A. (1988) Organisation spatiale et déplacements des chats forestiers adultes (*Felis silvestris*, Schreber, 1777) en Lorraine. *Revue Ecole de Terre et Vie*, **43**, 113–132.

Stander, P.E., Haden, P.J., Kaqece, /./. & Ghau, //. (1997) The ecology of asociality in Namibian leopards. *Journal of Zoology, London*, **242**, 343–364.

Stuart, C. & Stuart, T. (1991) The feral cat problem in southern Africa. Time to stop pussyfooting? *African Wildlife*, **45**, 13–15.

Swihart, R.K. & Slade, N.A. (1985) Testing for independence of observations in animal movements. *Ecology*, **66**, 1176–1184.

Todd, I. (1993) *Wildtrak. Non-parametric Home Range Analysis for the Macintosh*. Department of Zoology, University of Oxford, Oxford, UK.

Todd, N.B. (1978) An ecological behavioural genetic model for the domestication of the domestic cat. *Carnivore*, **1**, 52–60.

Weir, B.S. (1996) *Genetic Data Analysis*, 2nd edn, Sinauer Associates, Massachusetts, USA.

Wrangham, R.W. & Rubenstein, D.I. (1986) Social evolution in birds and mammals. *Ecological Aspects of Social Evolution: Birds and Mammals* (eds D.I. Rubenstein & R.W. Wrangham), pp. 452–470, Princetown University Press, Princetown, USA.

Received 1 October 1999; revision received 24 July 2000

Appendix 1

Microsatellite genotypes of the 31 cats. Names of loci are given in the first row. Missing values are denoted by –1.

	Fca 8		Fca 23		Fca 43		Fca 45		Fca 77		Fca 90		Fca 96		Fca 126	
M1	123	123	134	134	120	124	144	158	148	150	109	113	210	224	136	144
M2	121	121	132	134	120	128	158	158	144	144	107	109	210	210	142	142
M3	123	139	132	134	118	120	152	158	144	144	105	109	210	210	140	148
M4	123	139	134	148	120	134	152	158	144	148	109	113	210	224	138	148
M5	123	145	134	150	–1	–1	152	158	144	148	–1	–1	210	224	138	140
M6	121	137	132	132	–1	–1	151	152	144	144	–1	–1	210	224	136	142
M7	121	123	132	134	120	122	156	158	144	148	107	109	210	224	–1	–1
M8	139	145	148	150	120	134	157	158	144	144	109	113	210	210	140	142
M9	121	123	132	134	120	120	158	158	–1	–1	107	109	210	210	138	138
M10	121	123	134	146	120	120	152	158	144	150	109	111	212	224	138	148
M12	121	123	–1	–1	120	120	144	144	150	152	107	109	210	212	138	142
M13	123	123	134	146	120	122	–1	–1	148	150	109	111	210	224	138	140
M14	123	123	134	144	122	128	150	156	146	148	101	113	210	210	144	150
F1	123	137	132	146	120	122	157	158	144	148	107	109	210	224	138	142
F2	123	123	–1	–1	120	124	152	158	150	152	109	113	212	224	142	142
F3	123	123	134	134	120	120	154	158	144	150	113	113	210	212	–1	–1
F4	121	139	134	134	120	120	158	158	144	144	109	109	210	224	138	142
F5	121	121	132	134	120	122	158	158	144	148	109	109	212	224	138	142
F6	121	135	134	148	120	120	150	158	144	148	–1	–1	212	224	140	142
F7	123	137	134	134	120	120	152	158	150	150	107	111	210	224	140	140
F8	123	137	132	134	120	128	152	154	144	150	107	107	210	210	140	144
F9	123	139	134	150	120	120	152	158	144	148	109	109	210	210	138	148
F10	121	137	132	134	120	120	158	158	–1	–1	109	111	210	224	140	144
F11	123	145	146	148	120	120	152	158	144	148	109	113	210	224	138	140
F12	137	139	132	134	120	128	158	158	144	148	109	109	210	224	136	138
F13	121	123	132	134	–1	–1	154	158	144	148	–1	–1	210	210	–1	–1
F14	139	141	134	146	122	128	150	160	144	144	109	115	210	210	140	140
F15	137	141	132	134	–1	–1	152	156	144	150	–1	–1	212	224	136	140
F16	121	121	148	150	120	120	152	158	144	144	109	109	212	224	136	140
F17	123	123	132	150	120	134	152	152	144	148	109	111	212	224	138	144
F18	121	121	134	148	120	120	152	158	144	144	109	109	212	224	136	142

Appendix 2

Heterozygosity for baseline population (Beaumont *et al.* 2001) and study population for the eight alleles studied.

	Baseline population		Study population	
Allele range	Heterozygosity	Number	Heterozygosity	Number
115–147	0·814	11	0·745	7
132–154	0·722	12	0·711	6
118–134	0·650	9	0·514	6
144–163	0·901	16	0·704	9
134–156	0·689	12	0·636	5
91–117	0·833	11	0·665	7
184–230	0·749	10	0·613	3
136–152	0·760	9	0·818	7