

GENOTYPIC CORRELATES OF BODY AND ADRENAL WEIGHT IN A  
POPULATION OF FERAL CATS FELIS CATUS.

R.J. van Aarde  
Mammal Research Institute  
University of Pretoria  
Pretoria 0002, South Africa

B. Blumenberg  
Faculty of Sciences  
Lesley College  
29 Everett St.  
Cambridge, Mass. 02238 U.S.A.

**Abstract:** *Body and adrenal weight in a population of feral cats, Felis catus, inhabiting Marion Island was studied. Body weight is high, characteristic of feral populations and provides a demonstration of sexual dimorphism. A significant allometric relationship between body and adrenal weight is indicated. There is an influence of the S allele upon adrenal weight that appears to differ between agouti and nonagouti genomes. Keeler's predictions for the relationship between body weight, coat color and domesticated behavior do not appear to apply to Felis. In general, body weight and adrenal weight decrease as phenotypes become progressively darker. This relationship is congruent with speculation about the behavioral adaptation called forth by the urban habitat. Although feral for approximately 24 generations, the genotypic correlates of body and adrenal weight in the Marion Island population reflect the "urban" history of the founder population.*

#### INTRODUCTION

Anatomical and physiological changes associated with domestication have been documented for a number of species, particularly farm animals (Ucko and Dimbleby 1969). Less distinctive are the changes that presumably occurred within early domesticated forms of *Canis* and *Felis*, two genera whose association with man is now fostered primarily for aesthetic and emotional reasons (Baldwin 1975; Clutton-Brock 1977; Todd 1978).

Free-ranging populations of *Felis catus* are now distributed worldwide and in many regions such populations are, in part, fostered by a cultural priority given to the pet relationship (Fagen, 1978; Todd, 1977a, 1978). Feral populations of *F. catus* living independently of any influence of man became established on several islands, including some in the sub-Antarctic (van Aarde, 1978).

Population densities in the urban habitat colonized by cats are high and may approach 20% of the human population in a given area (Todd 1977b). Density dependent correlations for the frequencies of the coat colour mutants nonagouti (*a*) and blotched tabby (*t<sup>b</sup>*) have been identified in the United Kingdom/Eire region of northwest Europe (Blumenberg and Lloyd In press). The advantages accruing to individuals possessing the dark phenotype characteristic of the urban environment have provoked speculation (Clark 1976; Todd 1978). This paper represents a first attempt to find relationships between certain anatomical parameters (body and adrenal weights) and those mutant alleles that confer a dark phenotype upon individuals; and to speculate upon the possible adaptive significance of such relationships.

The Marion Island cat population represents the descendants of a tiny urban founder population (van Aarde and Robinson, In press) that was abruptly exposed to a relaxation of urban selective pressures,

while concomitantly forced to adapt to the requirements of a sub-Antarctic environment (van Aarde 1978. In press). In assessing measurable correlates of anatomical, physiological or behavioral parameters, the domestic origins of the founding population as well as the challenges presented by the Marion Island environment, must be taken into account.

#### METHODS

Information on body weights, adrenal weights and coat colour mutants were obtained for 160 individuals collected between December 1974 and April 1978. Cats were killed using a 410 gauge shotgun, or trapped and then killed with Euthabarb (Goldfields Veterinary Medical Supplies) for humane euthanasia. Mutant alleles controlling coat colour and pattern were scored as described by van Aarde and Robinson (In press) and adrenals were weighed using an H8 Metler electric balance.

Phenotypic classes were compared using Student's t test which shows particular robustness to departures from normality in data distribution. The test is, therefore, quite conservative when demonstrating significant differences between means computed from small samples (Simpson, Roe and Lewontin 1960).

#### RESULTS AND DISCUSSION

Coefficients of kurtosis and skewness and the fourth moment indicate that adrenal weight is normally distributed. However, a normal distribution in body weight is questionable, an observation that is not surprising considering the sensitivity of this parameter to season and food resource availability.

The phenotypic counts and mutant allele frequencies characterizing the present sub-sample are given in Table 1. The genetic profile differs from that reported for the total study group (n=839) discussed by van Aarde and Robinson (In press). However, only p(S) shows a significant difference ( $\chi^2 = 4.57$ ) between the two groups. The difference may well be accounted for by the difficulty in detecting low grades of piebald spotting in individuals observed at a distance through binoculars. Such a procedure was employed for 656 of the cats pre-

viously scored (van Aarde and Robinson, In press). The population does not exhibit the genetic profile believed characteristic of long term feral populations; i.e. low frequencies of all common mutant alleles except, perhaps,  $t^b$  (Dartnall, 1975).

Table 1 Autosomal mutant alleles, phenotypes observed and allele frequencies\* in the studied sub-sample of the Marion Island cat population.

Mutant phenotype		Number observed	Allele frequencies
Non-agouti	$a^+ \underline{aa}$	26 134	$q(a)=0,915 \pm 0,016$
Blotched tabby	$t^+ \underline{t^b t^b}$	11 12	$q(t^b)=0,722 \pm 0,072$
Dilute	$d^+ \underline{dd}$	156 4	$q(d)=0,158 \pm 0,039$
Longhair	$l^+ \underline{ll}$	159 1	$q(l)=0,079 \pm 0,039$
Piebald spotting**	$S \underline{s^+ s^+}$	64 96	$q(S)=0,225 \pm 0,025$

\*Allele frequencies and standard errors determined by well established procedures (see van Aarde and Robinson, In press).

\*\*An alternative p(S) may be calculated assuming the S4-7 individuals to be homozygous at the S locus and all other piebald spotted individuals to be heterozygous (Dreux 1975). Such a procedure yields a p(S) of 0,209 which does not change the significance of the difference vis a vis the data of van Aarde and Robinson, In press).

The genotypic constitution of the small 1949 founder population and second introduction is well known (van Aarde and Robinson, In press) and the founder effect predominates on Marion Island. The individuals in the founder population may be considered representative of animals drawn from typical urban or free-ranging groups.

Sexual dimorphism in body weight is apparent from the data in Table 2, males

being significantly heavier than females ( $p < 0.001$ ). The pregnant female subgroup differs from the nonpregnant subgroup ( $p < 0.001$ ) and the lactating subgroup ( $p < 0.01$ ). Sexual dimorphism with respect to adrenal weight is less clear. Adrenal weights of males and females do not differ significantly. However, male adrenal weight does differ significantly from that of the pregnant female subgroup ( $0.02 > p > 0.01$ ). Within the female population, differences in adrenal weight exist between the entire group and the pregnant subgroup ( $0.02 > p > 0.01$ ); between the nonpregnant subgroup and both the pregnant and lactating subgroups ( $p < 0.001$  and  $0.02 > p > 0.01$  respectively). Latimer (1939) found adrenal weights in the cat very similar to these with the mean for males slightly higher than that for females; the difference was statistically nonsignificant. Northrup and Van Liere (1960) present adrenal weight: body weight ratios (but not the raw adrenal weight data) for a domestic cat sample that are in excess of those shown in Table 2. They claim that their data support a conclusion of sexual dimorphism. Considering the problems inherent in the statistical comparison of ratios (Dodson 1978), this conclusion may have been premature. In order to eliminate sex as a variable influencing either body or adrenal weight, the investigation of genotypic correlates of body and adrenal weight in this study was conducted on the male and female samples separately.

Contrary to the statement of Larson (1978), a good allometric relationship between adrenal and body weight is obtainable for the cat and may be here demonstrated for both the male and female samples (Table 3). Latimer (1939) reports a linear regression for male adrenal weight upon body weight and a nonlinear relationship for female adrenal weight upon body weight with significant correlation coefficients for both equations ( $p < 0.001$ ). Northrup and Van Liere (1960) state that adrenal weight in cats does not adhere to the allometric relationship with respect to body weight. Stahl (1965) reports a highly significant allometric relationship between adrenal weight and body weight over the entire spectrum of non-primate animals.

Table 2: Mean body and adrenal weights by sex and female reproductive classes at Marion Island.

Group	Sample size n	Body weight (kg)	CV	Adrenal weight/body weight ( $\times 10^4$ )
Population	160	3.28 $\pm$ 0,984	30	1.16
Males	106	3.49 $\pm$ 1,040	29	1.09
Females	54	2.86 $\pm$ 0,675	24	1.35
nonpregnant	36	2.65 $\pm$ 0,691	26	1.30
pregnant	18	3.29 $\pm$ 0,330	10	1.44
lactating $\times\times$	7	2.92 $\pm$ 0,270	9	1.65

$\times$ No significant difference in adrenal weight between LHS and RHS, therefore mean organ weight per individual has been used throughout. This observation allows the few single adrenal weights to be considered mean values for the purpose of keeping the data base as large as possible.

$\times\times$ Includes individuals at the end of lactation.

Table 3: Scaling of adrenal weight (AW) to body weight (BW).

Males:  $AW = 0.102BW^{1,023}$   $r = 0.809$

$P < 0.001$  (df = 104)

Females:  $AW = 0.147BW^{0,886}$   $r = 0.683$

$p < 0.001$  (df = 52)

Table 4: Body weight and adrenal weight against coat colour phenotype classes for the male component of the Marion Island cat population.

Phenotype	n	Body weight (kg)	Adrenal weight (gr)	Adrenal/body weight ratio x 10 <sup>4</sup>
a <sup>+</sup> _	18	3.58±0,832	0.417±0,179	1.16
a <sup>+</sup> _s <sup>+</sup> s <sup>+</sup>	11	3.41±0,774	0.456±0,198	1.34
a <sup>+</sup> _s_	7	3.85±0,850	0.356±0,122	0.92
a <sup>+</sup> _t <sup>+</sup> _	8	4.06±0,561	0.432±0,171	1.06
a <sup>+</sup> _t <sup>+</sup> _s <sup>+</sup> s	4	3.85±0,269	0.481±0,218	1.25
a <sup>+</sup> _t <sup>+</sup> _s_	4	4.28±0,683	0.383±0,078	0.89
a <sup>+</sup> _t <sup>b</sup> t <sup>b</sup>	7	3.24±0,774	0.437±0,203	1.35
a <sup>+</sup> _t <sup>b</sup> t <sup>b</sup> s <sup>+</sup> s <sup>+</sup>	5	3.24±0,742	0.514±0,169	1.59
a <sup>+</sup> _t <sup>b</sup> t <sup>b</sup> s_	2	3.25±0,850	0.243±0,138	0.75
aa	88	3.47±1,080	0.372±0,149	1.07
aa s <sup>+</sup> s <sup>+</sup>	48	3.21±1,170	0.333±0,150	1.04
aa s_	40	3.79±0,863	0.419±0,172	1.11
aa t <sup>+</sup> _s_	2	3.75±0,250	0.447±0,177	1.19
aa s3-7	3	4.10±0,408	0.461±0,137	1.12
aa dd	2	3.40±1,200	0.232±0,032	0.68

Table 5: Body weight and adrenal weight against coat colour phenotype classes for the female component of the Marion Island cat population.

Phenotype	n	Body weight (kg)	Adrenal weight (gr)	Adrenal weight/Body weight x 10 <sup>4</sup>
a <sup>+</sup> _	8	2.64±0,654	0.304±0,081	1.15
a <sup>+</sup> _s <sup>+</sup> s <sup>+</sup>	7	2.53±0,627	0.300±0,086	1.19
a <sup>+</sup> _s_	1	3.40	0.334	0.98
a <sup>+</sup> _t <sup>b</sup> t <sup>b</sup>	5	2.72±0,611	0.315±0,060	1.16
a <sup>+</sup> _t <sup>b</sup> t <sup>b</sup> s <sup>+</sup> s <sup>+</sup>	4	2.55±0,568	0.311±0,066	1.22
a <sup>+</sup> _t <sup>b</sup> t <sup>b</sup> s_	1	3.40	0.334	0.98
aa	46	2.90±0,672	0.402±0,135	1.39
aa s <sup>+</sup> s <sup>+</sup>	30	2.94±0,505	0.387±0,112	1.32
aa t <sup>+</sup> _s <sup>+</sup> s <sup>+</sup>	1	3.30	0.508	1.54
aa s_	16	2.83±0,901	0.429±0,166	1.52

Tables 4 and 5 present mean body and mean adrenal weights for each phenotypic class for males and females separately. Several phenotypic classes exhibit statistically significant sexual dimorphism in body weight: all nonagouti (aa --), nonagouti with piebald spotting (aa S<sub>-</sub>); all agouti (a<sup>+</sup>--); and agouti with no piebald spotting (a<sup>+</sup> s<sup>+</sup>s<sup>+</sup>). In striped tabby males (t<sup>+</sup>), body weight is significantly higher than in blotched tabby (t<sup>b</sup>t<sup>b</sup>) males (0.05 > p < 0.02). In nonagouti females, body weight is almost significantly lower than that of agouti females as judged in nonpiebald spotted animals (0.1 > p < 0.05). The male data appear to demonstrate a positive effect of the S allele (piebald spotting) upon body weight. A significant difference in body weight between the aa s<sup>+</sup>s<sup>+</sup> and aa S<sub>-</sub> classes exists. Considering that 37 out of 40 male piebald nonagoutis (aa S<sub>-</sub>) are S1-3, this observation most likely indicates the effect of a single S allele (Dreux 1975). Dreux's work indicates that some, or all, of the three S4-7 individuals are homozygous for the S allele. They, therefore, should have a higher mean body weight than that describing the entire male aa S<sub>-</sub> class. This proves to be true (4.1 kg vrs. 3.8 kg), although the difference is statistically nonsignificant. The tiny sample size of the S4-7 group precludes further exploration of this observation.

Sexual dimorphism in adrenal weight is suggested, but not established, by a comparison of males and females in the a<sup>+</sup> s<sup>+</sup>s<sup>+</sup> and t<sup>b</sup>t<sup>b</sup> s<sup>+</sup>s<sup>+</sup> classes (both p's 0.1 >> 0.05). In nonpiebald (s<sup>+</sup>s<sup>+</sup>) males, adrenal weight of nonagouti individuals is lower than that of agouti animals (both p's 0.05 >> 0.02). In nonpiebald agouti (a<sup>+</sup> s<sup>+</sup>s<sup>+</sup>) males, adrenal weight of striped tabbies (t<sup>+</sup>) is lower than that of blotched tabbies (t<sup>b</sup>t<sup>b</sup>) but the difference is nonsignificant. In nonpiebald females, adrenal weight differences approach significance only when the entire nonagouti and agouti classes are compared (0.1 > p > 0.05). For females, data do not exist that would allow for the assessment of differences in adrenal weight between striped and blotched tabby phenotypes within either agouti or nonagouti genomes (see Table 5).

There appears to be an effect of the S

allele upon adrenal weight which is different in agouti and nonagouti genomes. The adrenal weight of a<sup>+</sup> s<sup>+</sup>s<sup>+</sup> is higher than that of a<sup>+</sup> S<sub>-</sub> in males, although the difference is nonsignificant. Furthermore, in males, the adrenal weight of aa s<sup>+</sup>s<sup>+</sup> individuals is lower than that of aa S<sub>-</sub> individuals, this difference being significant (0.01 > p > 0.001). Considering that the absolute magnitude of the difference between the nonagouti classes is less than that seen between the agouti classes, the nonsignificance of the former comparison is no doubt heavily influenced by the small sample sizes.

In a series of papers, Keeler (1947, 1970, 1975) suggests correlations between body weight, adrenal weight, behavior and coat colour genes in the Norway rat (*Rattus norvegicus*) and the red fox (*Vulpes vulpes vulva*). Rats homozygous for two or three coat colour genes show tame (i.e. "domesticated") behavior towards humans and smaller adrenal weights when compared to the wild type (Keeler 1947). The three loci involved are hooded, black and albino. Only albino has an homologous locus in the cat genome (Searle, 1975). It is unclear whether the mutant Keeler terms black is an allele at the agouti locus or at the dominant black locus (E).

In the red fox, Keeler (1970, 1975) reports correlations between tameness, increasing body weight, decreasing adrenal weight and the progressive addition of coat colour mutant alleles to the genome. Evidence also exists for altered adrenal biochemistry in the domesticated colour phases of foxes (Belyaev and Trut 1975; Keeler 1970, 1975). It should be pointed out that Keeler's designations of significant differences are "soft". His body and adrenal weight data have not been subjected to the t test and are not presented in a form that would allow others to do so. His study involved the additive effects of mutant alleles at four loci: black, blue, chocolate and white. In informal communications and unpublished manuscripts, cat researchers have frequently discussed the participation of the black locus in this situation because Keeler refers to the mutant allele at this locus as nonagouti. However, serious doubt exists whether this locus is homologous to the agouti locus

in the cat. Robinson (1975) believes Keeler's nonagouti mutant to be an allele of the R gene.

Keeler's correlations are not with a progressive darkening of the pelage. He never attempted to establish an index of relative darkening via photometric readings of reflected light from the pelage or through the application of a numerical phenotypic measure derived from allele frequencies such as the coefficient of darkness (Blumenberg and Todd, 1978). It is, therefore, unclear whether or not the domesticated colour phases of the red fox are darker than the wild type. Keeler's correlations are with the progressive addition to the genome of mutant alleles affecting coat colour that are rare or nonexistent in wild fox populations. If these results were applicable to *Felis*, one should observe (1) an increase in body weight and a decrease in adrenal weight when agouti phenotypes are compared to nonagouti; and (2) an increase in body weight and a decrease in adrenal weight as mutant alleles affecting coat colour are successively added to the genome. The Marion Island population is by no means ideal for testing Keeler's hypothesis because of the small sample sizes of the agouti phenotypes. This is, however, the only data that exist in a form appropriate for this discussion and thereby provide some preliminary observations.

The predicted distinction between agouti and blackish phenotypes can be tested by comparing  $a^+_s s^+s^+$  and  $aa s^+s^+$  classes, thereby controlling for the effects of the S allele. In males, body weight of  $a^+_s s^+s^+$  individuals is higher than body weight of  $aa s^+s^+$  individuals but in females the reverse is seen. Both observations are statistically nonsignificant. The predicted decrease in adrenal weight when  $a^+_s s^+s^+$  individuals are compared to  $aa s^+s^+$  animals is seen in females, but the reverse relationship is observed in males. The difference between the male phenotypes is statistically significant. In summary, Keeler's predictions for the differences in body and adrenal weight that should be discernible between agouti and blackish (non-agouti?) phenotypes have not been confirmed by these data.

Table 6 demonstrates that the effects

upon body and adrenal weight of progressive additions of mutant colour alleles to the *Felis* genome do not follow the pattern reported for the red fox with the exception of an increase in body weight seen when a third mutant allele is added to the genome (males only).

In spite of the lack of agreement between Keeler's results on *Vulpus* and this analysis, it seems quite plausible that coat colour mutants in *Felis* must have pleiotropic effects upon physiology and behavior so as to facilitate adjustment to, and exploitation of, the urban niche as Clark (1975, 1976) and Todd (1978) have suggested. Pleiotropic effects on morphology have been demonstrated for a series of alleles at the agouti locus in the house mouse *Mus musculus* (Leamy and Sustaric 1978). The association of high frequencies of the mutants nonagouti and blotched tabby, which confer darker phenotypes than alternative alleles at their loci, with dense urban populations of Europe and the New World has been firmly established (Blumenberg and Lloyd 1980; Clark 1975, 1976; Todd 1977a, 1978; Todd, Garrad and Blumenberg 1979).

As Todd (1963, 1978) implies, one might logically speculate that a small dark cat with reduced adrenals is best adapted to cope with the behavioral stress presented by the dense populations of the urban environment. Adding to the density dependent selective pressures (contrary to their conspecifics) that would foster and emphasize such a morphology, might be the selection of such phenotypes by man because of their "tameness"; i.e. domesticated behavior. Such thoughts lead to a prediction of decreasing body and adrenal weight as one proceeds through the phenotypic sequence striped tabby to blotched tabby to nonagouti; i.e. progressive darkening of the pelage. The male data in Table 7 indicate the larger body and adrenal weights of  $t^+$  individuals when compared to  $aa$  animals; the larger body weight of  $t^+$  vrs.  $t^{btb}$ ; and the larger adrenal weight of  $t^{btb}$  when compared to  $aa$ . Only the body weight difference between striped ( $t^+$ ) and blotched ( $t^{btb}$ ) tabby is statistically significant (male data). The effect of the S allele should be spread equally among all phenotypic classes and thus be of little influence. There are only three S4-7 individuals and therefore the "lightening"

Table 6: Hypothetical trend in body weight (BW) and adrenal weight (AW) according to the Keeler hypothesis, where body weight would increase and adrenal weight would decrease as the number of mutant alleles in the genome increases.

Body Weight	$t^+_{-}s^+s^+$ > $t^+_{-}s_{-}$		$t^{btb}_{s^+s^+}$ > $t^{btb}_{s_{-}}$	
			and $aa\ s^+s^+$	and $aa\ s_{-}$
Number of mutant alleles	<u>0 or 1</u>	<u>1 or 2</u>	<u>2</u>	<u>3</u>
n (males)	4	4	53	42
BW (kg) (males)	3.85	4.28	3.21	3.76
n (females)	-	-	34	17
BW (kg) (females)	-	-	2.89	2.86

Adrenal Weight	$t^+_{-}s^+s^+ < t^+_{-}s_{-}$		$t^{btb}_{s^+s^+} < t^{btb}_{s_{-}}$	
			and $aa\ s^+s^+$	and $aa\ s_{-}$
Number of mutant alleles	<u>0 or 1</u>	<u>1 or 2</u>	<u>2</u>	<u>3</u>
n (males)	4	4	53	42
AW (gr) (males)	0.481	0.383	0.350	0.411
n (females)	-	-	34	17
AW (gr) (females)	-	-	0.378	0.423

Table 7: The Domestication Hypothesis according to which body weight (BW) and adrenal weight (AW) decreases with a progressive darkening of the pelage.

Body Weight	$t^+$	$t^{btb}$	$aa$
n (males)	8	7	88
BW (kg) (males)	4.06	3.24	3.47
n (females)	-	5	46
BW (kg) (females)	-	2.72	2.90
Adrenal Weight			
n (males)	8	7	88
AW (gr) (males)	0.432	0.437	0.372
n (females)	-	5	46
AW (gr) (females)	-	0.315	0.402

effect upon these phenotypes of high grades of piebald spotting is of no concern. Considering the very small sample sizes for the tabby phenotypes, the fit of these comparisons to the prediction for a domesticated anatomy is gratifying. An expansion of this study to one using a large urban population that could provide significant numbers of tabby animals would be of great interest. In terms of the agouti, tabby and piebald spotting loci, these results suggest that the phenotype best adapted to the urban environment would be nonagouti-blotched tabby-nonpiebald ( $aa\ t^{bt}b_s^+s^+$ ). This phenotype is found in large numbers in the dense urban populations of Europe and New World cities (Blumenberg and Lloyd, In press; Clark 1975, 1976). Unfortunately, this phenotype is not represented in the Marion Island data, and the prediction of lower body and adrenal weight in contrast to other phenotypes carrying alternative alleles at these loci cannot be tested. Garten (1976) reports a correlation between aggressive behavior and heterozygosity (at the biochemical level) in oldfield mice *Peromyscus polionotus*. It would be interesting to rank aggressiveness in *F. catus* for individuals heterozygous and homozygous for mutant alleles at the agouti and tabby loci.

Approximately 24 generations have passed during which selective pressures characteristic of the domesticated habitat were abruptly removed and replaced by those exerted by a volcanic tundra biome. Nonetheless, the Marion Island cat population still shows genotypic correlates of body and adrenal weight that may reflect the urban history of the founder population lineage.

#### ACKNOWLEDGEMENTS

Information presented in this paper forms part of a full scale ecological investigation on the cat population at Marion Island, which has been carried out under the auspices of the Mammal Research Institute of University of Pretoria. We wish to thank the Director, Prof. J.D. Skinner for his support and interest. Logistical and financial support was provided by the South African Department of Transport on advice of the South African Committee for Antarctic Research (SASCAR). Prof. N.B. Todd is acknowledged for help-

ful advice provided during the preparation of the manuscript.

#### LITERATURE CITED

- Baldwin, J. A. 1975. Notes and speculations on the domestication of the cat in Egypt. *Anthropos* 70: 428 - 448.
- Belyaev, D.K. and L.N. Trut. 1975. Some genetic and endocrine effects of selection for domestication in silver foxes. In: *The Wild Canids: Their Systematics, Behavioural Ecology and Evolution*. M. W. Fox (Ed.) Van Nostrand Reinhold Co., New York.
- Blumenberg, B. and A.T. Lloyd In Press. Mutant allele frequencies in the domestic cat: a preliminary discussion of selection with particular reference to the United Kingdom and Eire. *Genetica*.
- Blumenberg, B. and N.B. Todd 1978. Calculation of the phenotype frequency of sex-linked orange and the coefficient of darkness (*F. catus*). *Carniv. Genet. Newsl.* 3: 180-183.
- 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.
- Clutton-Brock, J. 1977. Man-made dogs. *Science* 197: 1340-1342.
- Dartnall, J.A. 1975. Gene frequencies of feral domestic cats in Tasmania. *Carniv. Genet. Newsl.* 2: 248-250.
- Dodson, P. 1978. On the use of ratios in growth studies. *Syst. Zool.* 27: 67-71.
- Dreux, Ph. 1975. Génétique de population des domestiques de Marseille (Bouches-du-Rhône, France). *Ann. Genet. Sel. anim.* 7: 23-33.
- Fagen, R.M. 1978. Domestic cat gene frequencies in Chiangmi and Bangkok, Thailand. *Proc. First. Int. Conf. Domestic Cat Pop. Genet. Ecol. Carniv. Genet. Newsl.* 3: 346-349.
- Garten, Jr., C.T. 1976. Relationships between aggressive behaviour and genic heterozygosity in the Oldfield Mouse. *Peromyscus polionotus*, *Evolution* 30: 59-72.
- Keeler, C.E. 1947. Modification of brain and endocrine glands as an explanation



- of altered behaviour trends in coat character mutant strains of the Norway rat. *J. Tenn. Acad. Sci.* 22: 202-209.
- Keeler, C.E. et al. 1970. Melanin, adrenalin and the legacy of fear. *J. Hered.* 61: 81-88.
- Keeler, C.E. 1975. Genetics of behaviour variations in colour phases of the Red Fox. In: N.W. Fox (Ed.). *The Wild Canids: Their Systematics, Behavioral Ecology and Evolution*. Van Nostrand Reinhold Co., New York.
- Larson, S.G. 1978. Scaling of organ weights in *Macaca artoides*. *Am. J. Phys. Anthropos* 49: 95 - 102.
- Latimer, H.B. 1939. The weights of the hypophysis, thyroid and suprarenals in the adult cat. *Growth* 3: 435-445.
- Leamy, L. and S.S. Sustarsic 1978. A morphometric discriminant analysis of agouti phenotypes in C57BL/6 house mice. *Syst. Zool.* 27: 49-60.
- Robinson, R. 1975. The Red Fox, *Vulpes vulpes*. In: R.C. King (Ed.), *Handbook of Genetics*, Vol. 4. Plenum Press, New York.
- Searle, A.G. 1975. Distribution and probable homologies of some genes determining coat colour in mammals. In: R.C. King (Ed.), *Handbook of Genetics*, Vol 4 Plenum Press, New York.
- Simpson, G.G., Roe, A. and R.C. Lewontin 1960. *Quantitative Zoology*. (revised ed.) Harcourt, Brace and World, New York.
- Stahl, W.R. 1965. Organ weights of primates and other mammals. *Science* 150: 1039-1042.
- Todd, N.B. 1963. Behaviour and genetics of the domestic cat. *Cornell Vet.* 53: 99-107.
- Todd, N.B. 1977a. Cats and commerce. *Sci. Am.* 237: 100-107.
- Todd, N.B. 1977b. The dynamics of owned domestic cat populations. *Carniv. Genet. Newsl.* 3: 100-104.
- Todd, N.B. 1978. An ecological, behavioural genetic model for the domestication of the cat. *Carnivore* 1: 52-60.
- Todd, N.B., L.S. Garrad and B. Blumenberg 1979. Mutant allele frequencies in domestic cats of the Isle of Man. *Proc. First Int. Conf. Domestic Cat Pop. Genet. Ecol. Carniv. Genet. Newsl.* 3: 388-407.
- Van Aarde, R.J. 1978. Reproduction and population ecology in the feral house cat, *Felis catus*, on Marion Island. *Proc. First. Int. Conf. Domestic Cat Pop. Genet. Ecol. Carniv. Genet. Newsl.* 3: 288-316.
- Van Aarde, R. J. In press. Distribution and density of the feral house cat, *Felis catus* at Marion Island. *S. Afr. J. Antarc. Res.*
- Van Aarde, R.J. and T.J. Robinson. In press. Gene frequencies in a feral population of *Felis catus*. *J. Hered.*
- Ucko, P.J. and G.W. Dimbleby. 1969. *The Domestication and Exploitation of Plants and Animals*. Aldine Pub. Co., Chicago.

#### ADDENDUM

To end of first paragraph under Methods: Such specimens were obtained as part of an overall program of ecological/ physiological/ behavioral studies designed to assess the impact of the cat population on the local avifauna and to suggest the best approach for preserving native bird species.