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Feral cats: their role in the population dynamics of *Felis catus*

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Abstract

The so-called domestic cat occupies a unique position within the truly domestic animals since it freely interbreeds with feral populations, and there is considerable gene flow in both directions. This is possible because the likelihood of an individual cat forming a relationship with people is strongly affected by its experiences during the socialisation period (3–8 weeks of age), although this does not preclude differences between owned and feral populations in the relative frequencies of alleles which affect social behaviour towards humans. We suggest a hitherto unconsidered reason why a separate domesticated population of cats (apart from pedigree breeds) has not yet emerged: the unusual and stringent nutrient requirements of the cat may historically have militated against successful breeding on a completely human-provided diet, and led to the retention of the ability to achieve a nutritionally complete diet by scavenging and/or hunting. More recently, the widespread availability of nutritionally complete manufactured foods and veterinary care in western countries appears to be leading towards a rapid change in the population dynamics and population genetics of both owned and feral cats.

Keywords: Domestication; Feral populations; Population dynamics; Cat

1. Introduction

The domestic cat *Felis (silvestris) catus* is now the most numerous companion animal in the US and many parts of Europe (Anon., 1995). It is usually considered to have much in common with the domestic dog *Canis (lupus) familiaris*; for example,

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both are classified as ''small animals'' by veterinarians, and from a biological perspective, both species are members of the Order Carnivora. However, the cat has at least two characteristics which tend to distinguish it from other domesticated animals. First, its ancestral species *F. silvestris* is thought to be exclusively asocial when adult (discussed in Bradshaw, 1992); second, almost all its owned populations are sympatric with and interbreed freely with feral populations, with mate choice decided by the cat rather than by man. Such interbreeding does occasionally occur for other domestic species in rural environments in the West (e.g., feral horses in the USA; McKnight, 1964) and in urban environments in non-Western countries (e.g., pariah dogs in India; Fox, 1978), but it is unusual in urban environments in the West, suggesting that the interface between *F. catus* and *Homo sapiens* may be qualitatively different from that for other companion animals. Our aim in this paper is to explore the past, present, and future importance of feral populations within *F. catus* as a whole.

2. Populations

Currently, the only populations of cats which can be unambiguously classified as domesticated are the various pedigree breeds, such as Persians and Siamese. Over the past century or so, and to some extent for much longer (Kratochvíl and Kratochvíl, 1976), these have been maintained as isolated populations, largely breeding only with members of their own breed, and subject to strong artificial selection. Matings between pedigree and other cats are usually accidental and their progeny usually become part of the general pet population. Genes are therefore occasionally transferred out of, but rarely into, the pedigree populations. Some breeds have physical characteristics which would be maladaptive for a free-ranging lifestyle, such as the shortened jaw and long coat of the Persian (Exotic) breeds, and therefore while their genes may be successfully transferred into the pet population, they are unlikely to persist if transferred into feral populations. This, coupled with the human intervention in breeding, means that pedigree cats can be regarded as a set of, more or less, isolated populations which have little or no connection to feral cats, and we will not consider them further.

Terms such as ''feral cat'', ''wild domestic cat'' and ''farm cat'' are often used interchangeably, yet free-ranging (i.e., unowned) cats can have varying degrees of association with man (Table 1), and this needs to be taken into account when considering their population dynamics. If the term ''wildcat'' is reserved for the ancestral species *F. silvestris* and other small felids, the term ''pseudo-wild'' may be appropriate for populations of cats, for example, those on uninhabited islands, which are entirely independent of man and are ecologically equivalent to any other generalist carnivore (Fitzgerald, 1988). Strictly speaking, these are the truly feral cats, since they are descended from domestic animals but no longer depend upon man, but the term ''feral'', when applied to cats, usually refers to individuals or populations whose relationship with man can best be described as partially commensal. They are usually capable of shifting between hunting, and scavenging around sources of food provided either deliberately or accidentally by man (Table 1). While many feral cats are wary of humans themselves, some may be classified as generally friendly towards people, while

Table 1
Populations of *F. silvestris catus*, defined according to their degree of dependence upon humans. Feeding by people may be specific (i.e., provided on an individual basis), general (i.e., provided at a location but not specifically to any one individual), accidental (e.g., garbage dumps) or none (i.e., a cat that subsists mainly or entirely by hunting). Shelter may be provided specifically (i.e., owned cats that spend much of their time in and near their owner's dwelling), accidentally (e.g., farm buildings) or not at all (i.e., cats living at some distance from human habitation, e.g., occupying unused burrows of other species). Socialised cats display affiliative behaviour towards at least some people

Population	Food	Shelter	Socialised
Pedigree	Specific	Specific	Yes
Pet	Specific	Specific	Yes
Semi-feral	General	Accidental	Yes
Feral	Accidental/general	Accidental	No
Pseudo-wild	None/accidental	None	No

not maintaining regular contact with any one individual person (i.e., they would not be considered to be ''owned''). In countries such as the UK, most such cats are rapidly assimilated into the owned (''pet'') population, often via the agency of rescue charities, but in southern Europe, for example, they exist alongside, if somewhat indistinct from, cats that ''belong'' to a single household. The important characteristic that separates them from feral cats is their behaviour towards people, hence, they have been separately classified as ''semi-feral'' in Table 1.

3. Early experience and sociability to man

The extent to which an individual cat can take advantage of food and shelter provided by man may depend upon the extent of its fear reaction towards people in general; the most fearful cats are likely to be put at a disadvantage by being more readily disturbed from resting places and sources of food than cats which are at least tolerant of human proximity. This fear reaction is influenced by both genetic and developmental components (McCune, 1995), but is most notably inhibited by exposure to people during the primary socialisation period (3–8 weeks of age) (Karsh and Turner, 1988; McCune et al., 1995). Kittens which have little or no contact with humans until they are 2-months-old are likely to remain fearful of people for life unless remedially socialised (Bradshaw and Cook, 1997) This is a time-consuming process which seems unlikely to occur accidentally, although anecdote supports the occasional gradual habituation of unsocialised adult cats towards people, and, conversely, abandoned pet cats becoming wary of people. Suitability for the feral state may therefore be subject to some cultural inheritance, since unsocialised mothers, or mothers which have become feral through aversive experiences of humans, are more likely than human-friendly mothers to den in inaccessible places. However, even the kittens of human-unfriendly mothers have the potential to be socialised if discovered early enough in life, and conversely, the kittens of human-friendly mothers may accidentally avoid socialisation and become feral. This flexibility means that within the pet, semi-feral and feral populations (Table 1), the offspring of one cat

have the potential to move to the adjacent population (i.e., pet to semi-feral, semi-feral to feral, and vice versa), and, with more concerted human intervention or, conversely, neglect, even between feral and pet. The ability of cats to adopt a range of social strategies, from solitary territoriality to a substantial degree of sociality, both intra-specifically (Liberg and Sandell, 1988) and towards humans and other domestic species (Karsh and Turner, 1988), is an important factor in maintaining interchange between these various populations. The offspring of ferals may in turn become pseudo-wild (Table 1) by the acquisition of hunting skills, which are also culturally transmitted (Caro, 1980). However, they may not be able to compete effectively with other small carnivores unless these are absent (e.g., on oceanic islands, in Australasia) and so may only make a local contribution to the overall population.

Non-pedigree cats (otherwise known as ''mongrels'' or ''moggies'') therefore show a considerable degree of behavioural and ecological flexibility, and are capable of moving from being fully dependent on man, through commensalism, to independence, all within a few generations. The cat is therefore a very widespread companion animal on the one hand, but also an animal which has retained the ability to live at least semi-independently of man.

4. Factors sustaining feral populations

There are several possible explanations for this apparent paradox. One is simply that a rather small number of generations (perhaps 4000) has elapsed since the initial domestication by the Egyptians (Clutton-Brock, 1993), and this has simply not been enough to eliminate the ''wild'' characteristics and create a self-contained pet population, with the obvious exception of the pedigree breeds. Within Christian societies during the first half of this millennium, the cat was persecuted as a symbol of paganism and witchcraft (Serpell, 1988). Under these circumstances, the feral population may conceivably have been at an advantage in terms of reproductive success, and therefore, the self-contained pet population may actually only date back for about 300 generations. Certainly, the more ancient pedigree breeds appear to be of Middle-Eastern (Angora) and Far-Eastern origin (Siamese) (Kratochvíl and Kratochvíl, 1976), away from the influence of Christianity, which may therefore have been a factor militating against complete domestication in Western Europe.

Another explanation is that until recently, even pet cats performed their original function as predators for the control of rodents in human habitations (Clutton-Brock, 1987), and therefore needed to retain the ability to hunt. If the same individuals were also able to deliver the properties of companionship and low maintenance required by cat owners today (Selby and Rhoades, 1981), and therefore presumably historically, there might be no pressure for separate pest-controlling and companion populations to form. Terrier dogs and, to a lesser extent, ferrets, have fulfilled similar roles, but do not interbreed significantly with feral populations; this may be because populations of feral dogs or mustelids are unlikely to be tolerated near to human habitations because they pose a risk to livestock, children or even adults.

A third explanation, which appears not to have been explored in the literature, is that until recently, the nutritional peculiarities of the domestic cat (Table 2) have selected in favour of the retention of both the ability to hunt, and also the ability to scavenge selectively according to nutritional need. The Felidae are obligate carnivores, unlike the Canidae, which are omnivores, and have lost the ability to synthesise certain key nutrients that can only be found in a carnivorous diet. These include niacin, vitamin A, arachidonic acid, and taurine (MacDonald et al., 1984). Now that these idiosyncrasies are fully understood, it is possible to manufacture nutritionally complete cat foods, but historically, it is likely that home-made diets would have been nutritionally incomplete, particularly when animal products were scarce or expensive (e.g., in winter) and largely retained for human consumption. For example, diets deficient in arachidonic acid, which is virtually absent from plants, inhibit oestrus in the cat and lead to reduced resistance to respiratory infections in kittens (reviewed by MacDonald et al., 1984). Dogs can be kept and will breed on a vegetarian diet; it is very difficult to achieve this for cats (Legrand-Defrétin, 1994).

Since the widespread availability of a nutritionally complete cat food is a very recent event on an evolutionary time-scale, both hunting behaviour and the ability to scavenge selectively based upon nutritional need should still be widespread among non-pedigree cats, since both of these adaptations would have made a significant contribution to reproductive success in their recent evolutionary history. Many pet cats do indeed hunt, even when they should have no nutritional need to do so (Turner and Meister, 1988). Mongrel cats possess a variety of mechanisms for diet selection based upon nutritional content, including learned aversions to toxic or nutritionally unbalanced foods (Bradshaw et al., 1996), avoidance of abundant but potentially incomplete foods via preferences for rare foods (Church et al., 1996), and probably also learned preferences for foods containing key nutrients such as thiamine (J.W.S. Bradshaw and B.A. Baker, unpublished data).

Because these traits are present in present-day pet cats where they have no obvious function, they must presumably have been adaptive in the (evolutionarily) recent past. This provides evidence to support the hypothesis that since until recently man did not have the knowledge or resources to provide large numbers of cats with a balanced diet year-round, non-pedigree cats have retained two capabilities:

(i) to hunt for food which matches the exacting nutritional requirements inherited from their wild ancestors,

Table 2
Nutritional peculiarities of the domestic cat

High protein requirement: cat 12%, kitten 18% (cf. adult dog 4%, puppy 12%)
Requires arginine at every meal, to restart urea cycle
Needs large amounts of sulphur-containing amino acids (cysteine, methionine, taurine)
Requires arachidonic acid as precursor for prostaglandins
Poor digestion of lactose
Unable to synthesise vitamin A from carotene
High requirement for niacin and thiamine

(ii) to be nutritionally selective when exploiting sources of food provided accidentally, haphazardly or even deliberately by man.

Cats with neither of these abilities would have produced fewer and weaker offspring than those that did not. These abilities would have been important for all cat populations, whether socialised or not, thereby facilitating movement of individuals, and interbreeding, between all the populations in Table 1.

We therefore propose that three factors have acted in combination to ensure that the cat has retained the ability to switch between commensalism and symbiosis with man: (i) the probability that diets provided by man were unlikely to meet its nutritional requirements, until these became known; (ii) the small number of generations that has elapsed since domestication began, and (iii) the historical dual role of the cat as pest controller and companion.

5. Reproductive success — current constraints

Humans influence cat populations in a number of ways. Feral cats have been subjected to control regimes in areas where they pose a severe threat to native fauna, e.g., on Marion Island in the southern Indian Ocean (Bloomer and Bester, 1991), and in Western Australia (Risbey et al., 1997). Neuter and return strategies have been used in Britain to control feral cats (Neville and Remfry, 1984), and in the US (Zaunbrecher and Smith, 1993). In Australia, 94% of adult pet cats had been neutered in 1994, leading to a reduction in the pet population of 10% between 1993 and 1994 (Anon., 1994). Surveys carried out in the US revealed neutering rates of 79.8% (Patronek et al., 1997). However, the popularity of cats has increased in Britain and the US, where they now outnumber dogs (Patronek and Rowan, 1995); one likely reason for this trend is that cats need relatively little attention on a day-to-day basis, and thus make suitable pets for households where all the human members are absent during the day.

Over the past half-century, the advent of both manufactured foods and widely available veterinary care have altered some of the factors which determine reproductive success in each of the types of populations of cats (see Table 3). Pedigree cats are subject to artificial selection for the traits of appearance and temperament, resulting in, for example, the recent appearance of such breeds as the hairless Sphynx, and the placid

Table 3
Probable constraints on reproductive success in the populations of *F. silvestris catus* defined in Table 1. Breeding may be controlled (i.e., mate choice and frequency of breeding determined largely by the human owner), suppressed (by neutering) but without control of mate choice, or uncontrolled

Population	Breeding	Mate choice	Reproductive success
Pedigree	Controlled	Human	Appearance, temperament
Pet	Suppressed	Cat	Avoiding neutering
Semi-feral	Uncontrolled/ suppressed	Cat	Resistance to disease, nutrition, avoiding transfer to pet status
Feral	Uncontrolled	Cat	Resistance to disease, nutrition
Pseudo-wild	Uncontrolled	Cat	Hunting ability, resistance to disease

Ragdoll. Pseudo-wild and feral populations are likely to be subject to the same selection pressures as wild carnivores, such as resistance to disease, ability to obtain adequate nutrition, and mate choice. The increasingly widespread practice in the UK of ''rescuing'' feral kittens, and sterilising both male and female feral cats (Universities Federation for Animal Welfare, 1995) may be selecting for traits of ''wildness'' in some feral populations. For example, trap-shy cats are unlikely to be caught for sterilisation; queens that are fearful of man are likely to move their litters to inaccessible places if disturbed by people. While these traits are undoubtedly affected by the developmental history of the individual cat, they also have an additive genetic component (Karsh and Turner, 1988; McCune, 1995) which can therefore be selected for. As a result, feral cats may be becoming progressively less amenable to socialisation in areas where ''rescue'' is widespread. Populations in areas other than North America, Western Europe and Australasia are likely to be under different selection pressures, such as wholesale culling, but these have not been extensively documented. The progressive ''westernisation'' of some of these areas, and specifically, the adoption of western attitudes to animals, may result in the future in a convergence with the population pressures currently experienced in, for example, the UK.

6. Effects of neutering on population dynamics of owned cats (case study)

Recently, neutering of domestic cats has been encouraged by veterinary surgeons and rescue organisations as a means of population control for both the pet and feral populations. This is likely to have profound effects on cat population dynamics (and population genetics). In an attempt to quantify this, we have carried out population studies, by means of door-to-door surveys in Southampton and the surrounding area. The aims were to quantify levels of neutering, and investigate the recent reproductive status of the cat population.

The most comprehensive of these surveys was carried out in a 50 ha area in the Shirley area of Southampton (UK). Householders were interviewed from 949 (80.8%) of the 1175 residences in the area. This revealed a population of 315 cats, of which 21 were pedigrees (and were excluded from further analysis) and 294 were mongrels. Overall neutering rates were very high: 96.8% of adult males and 98.7% of adult females were neutered. The oldest cats in the survey had been born 18 years previously, so it was possible to examine trends in neutering over this time period. However, many females were allowed to reproduce before being neutered, so a more informative analysis came from relating lifetime fecundity (mediated by neutering) to year of birth. Mean lifetime fecundity could be calculated for each cohort where all the females had ultimately been neutered. The regression (Fig. 1) shows a dramatic decline in the mean number of litters born per female, from over 0.6 in 1978 to 0.12 in 1991–1992. With a measured median litter size of 4, 0.5 litters/female are needed to keep the population size constant; increasing neutering has meant that the cats in the Shirley survey area fell below this level of fecundity in the early 1980s. In 1994, owned cats in the area could only produce sufficient kittens to maintain the population at approximately 25% of its present level.

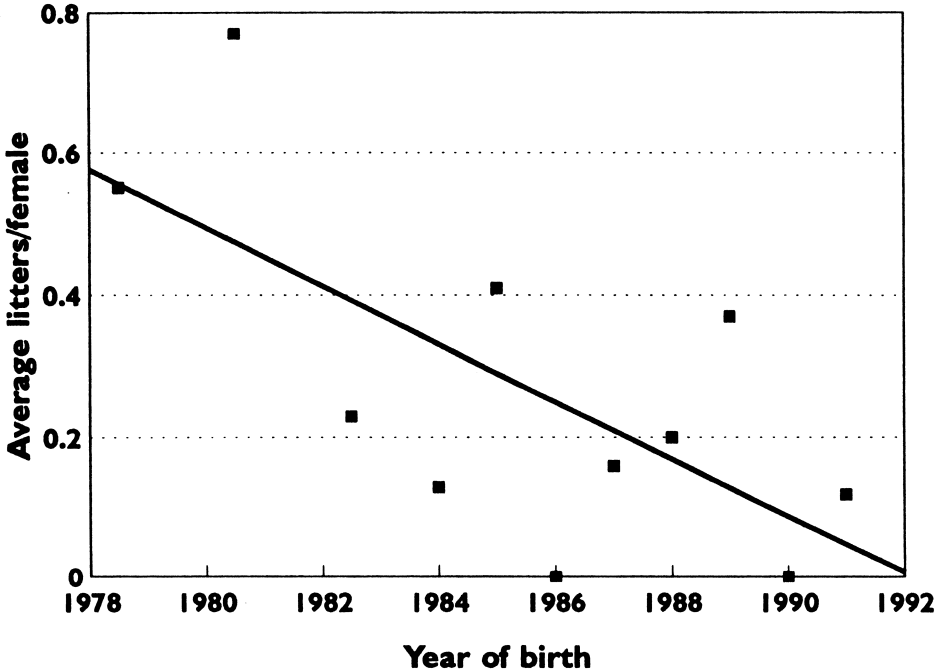

Fig. 1. Mean lifetime fecundity in litters per female, from a survey of a 50-ha urban area in Southampton, UK. Data for 1978–1979, 1980–1981 and 1982–1983 have been pooled. Slope $= -0.43$, $R = 0.68 \pm 0.19$, $P = 0.02$.

Analysis of the age structure of the population did not, however, indicate that it was in decline. This is explained by the fact that 72% of cats under 4-years-old had been brought into area by humans, or adopted as ''strays'', rather than having been born in households in the study area. Interestingly, only 1/3 of kittens born in the area recently were the offspring of these immigrant females. This is because immigrant cats have a higher chance of being neutered at an early age, which can be partially attributed to rescue organisations, which ensure that all the cats that pass through their hands are neutered. These organisations are increasingly important in mediating the transfer of cats into the Shirley area, providing 20% of the total population at present.

The continued immigration of cats into the Shirley area indicated that neutering rates might be lower elsewhere. Additional, less comprehensive population surveys showed that demographically different areas had different neutering rates. One affluent suburban area had virtually no breeding cats, with over 70% of cats being obtained from shelters. However, other areas within Southampton contained enough entire cats to sustain local population levels. Reproduction was often heavily skewed, with a small number of entire females producing large numbers of offspring. However, the prospects for survival, if not for reproduction, for kittens born under the current neutering regime are likely to be higher than they were when neutering rates were lower, due both to

improved veterinary care and the fact that homes can usually be found for the reduced number of kittens born. There was evidence of semi-feral cats being adopted by householders, such as one case where a cat had given birth to eight litters in a garden over the last 4 years. These were all subsequently taken in by a rescue organisation and homed.

The breeding output of males is much harder to quantify than that of females. Entire domestic males lived at an estimated density of 1 per 11 ha in the Shirley area. Although a radio telemetry study (Horsfield, 1998) has shown that males do have home ranges of this size in an urban environment, it is possible that the high rate of neutering among domestic males gives a relative advantage to feral males, the density of which is difficult to quantify, in breeding with the remaining domestic females.

7. Conclusions

Cats which belong to specific breeds are the only domestic cats which fit all the criteria for full domestication, i.e., permanent isolation from the wild species, and human control of breeding, territory and food supply (Clutton-Brock, 1992). All other ''domestic'' cats are only partially domesticated by this definition, and many have relationship with man which would more accurately be described as commensal. The reasons for the lack of separation between the house-dwelling and other populations are probably complex, but certainly, the small number of generations (c. 4000) that has elapsed since the species' original association with man may have contributed, i.e., there may be limits to the rate at which artificial selection on this or indeed any species can act, predicting that domestication is likely to be completed sometime in the foreseeable future.

We have suggested that one factor which has impeded the domestication of the cat has been its unusual and stringent nutritional requirements, which are not straightforward to satisfy apart from by the provision of fresh meat. Since historically, meat that was surplus to human requirements was not widely available on a year-round basis, reproductive success would have, until recently, been higher in cats which either retained the ability to obtain prey through hunting, and/or the ability to scavenge selectively from food provided both deliberately and accidentally by man. The advent of nutritionally balanced commercial cat foods has largely removed this selection pressure in many western countries, and this, coupled with the change in the primary role of the cat from pest-controller to companion, may eventually lead to a reduction in both abilities in the pet population.

A second recent development which is likely to have profound implications for the population dynamics of the domestic cat in western countries is the widespread availability of surgical sterilisation of both males and females. Neutering levels in some parts of the world are already high enough to prohibit self-replacement of owned populations, while demand for pet cats has been increasing. This is likely to result in an increased reproductive success for unowned animals, although those of their offspring which become pets are almost certain to be sterilised before producing offspring of their own.

It would be surprising if such rapid changes in selection pressures and population dynamics had not led to changes in population genetics. Little attention seems to have been paid to the effects on behavioural traits of widespread neutering in the pet population. However, Clark (1975) demonstrated that human preferences for light coat colours (e.g., orange, dilute, white spotting) had not led to selection in favour of these alleles, simply because the cats carrying them were likely to be neutered before reproducing. It is therefore possible that neutering is also altering the relative frequencies of alleles which influence socialisation to man, since cats which form close relationships with people may be more likely to be neutered than those which do not. We have also suggested that neutering of feral colonies may further select against traits which enhance tractability. This may eventually lead to feral populations that produce kittens which are less suitable for socialisation towards people than at present, and the demand for pet cats, if sustained, may therefore result in an increase in the wholly domesticated pedigree population.

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