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Abstract: Of the 37 or so wild species of cats in the world most are regarded as solitary, secretive, non-social mammals. However, at least two species, the lion and the domestic cat, may show high degrees of sociality, and others, such as tigers, cheetahs and lynxes, may form social groups in certain situations. This paper explores the ecological and environmental constraints on cat sociality by focussing on the spectrum of social group size displayed by lions and domestic cats in different parts of their distributions. It also looks in detail at how cats communicate with each other, mainly through scent marks. Perhaps the majority of cat species are not solitary after all, but have instead a dispersed and flexible social system which allows them to exploit efficiently the environmental and ecological opportunities wherever they are found. Instead the term "solitary" should probably be reserved for the hunting strategy of most cats and other carnivores.

All the best
Adrian

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ARE CATS REALLY SOLITARY?[1]

by

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ABSTRACT

Of the 37 or so wild species of cats in the world most are regarded as solitary, secretive, non-social mammals. However, at least two species, the lion and the domestic cat, may show high degrees of sociality, and others, such as tigers, cheetahs and lynxes, may form social groups in certain situations.

This paper explores the ecological and environmental constraints on cat sociality by focussing on the spectrum of social group size displayed by lions and domestic cats in different parts of their distributions. It also looks in detail at how cats communicate with each other, mainly through scent marks.

Perhaps the majority of cat species are not solitary after all, but have instead a dispersed and flexible social system which allows them to exploit efficiently the environmental and ecological opportunities wherever they are found. Instead the term "solitary" should probably be reserved for the hunting strategy of most cats and other carnivores.

1. Introduction

There are approximately 37 species of wild cats in the world today, most of which (up to 95%) are regarded as having a solitary social system, but two species may live in social groups of varying composition i.e. the lion, *Panthera leo*, and the cheetah, *Acinonyx jubatus* (Kitchener, 1991; Nowell & Jackson, 1996). The domestic cat, *Felis catus*, may also live in social groups, often at very high population densities, which is in contrast to its ancestor, the African wildcat, *Felis (silvestris) lybica* (Turner & Bateson, 1988). In this paper, I want to explore the social systems of cats and to try and discover the key factors, which allow some species to live together, but which apparently force most to live apart. In doing this I want to see if it is really justified to regard most cat species as solitary.

2. Solitary cats

Most cat species defend home ranges, which are large enough to include all those areas

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in which a cat finds sufficient prey, resting places, water, shelter and dens for rearing young during the course of the year, even when the abundance of prey may be at its lowest in any particular year. The extent and intensity of usage of home ranges is usually studied by radiotracking, whereby the home range is mostly defined as the minimum convex polygon which encloses 95% of the radio fixes made during the study period.

There are two main patterns of home range use, depending on the degree of overlap between the home ranges of animals of the same sex. In the Royal Chitwan National Park in Nepal the tiger shows a non-overlapping pattern, in which females defend home ranges from each other and males defend home ranges from each other (Sunquist, 1981). However, male ranges completely overlap those of two to three females. In the Cockscomb River basin in Belize jaguars, *Panthera onca*, show a high degree of overlap (up to 80%) between the home ranges of males (Rabinowitz & Nottingham, 1986). These two patterns probably depend on the density and clumping of prey and/or females (Liberg & Sandell, 1988). Where prey is clumped in particular areas, female cats will show a high degree of overlap of their home ranges so that they can all get an opportunity to exploit this resource. In the case of the Belizean jaguars, their most frequently caught prey is so abundant in small areas, that they may only occupy a small proportion (ca. 8%) of their total annual home range at any one time (Rabinowitz & Nottingham, 1986). Male home ranges are much larger than females', because they try to encompass as many female ranges as possible in order to maximise their mating opportunities and hence reproductive success. Male ranges tend to overlap where female ranges are clumped, but also overlap when female population densities are low, so that the opportunities for mating are limited, even though females may be evenly distributed. Conversely, where prey is evenly spread through an area, female ranges are exclusive, but male ranges are only exclusive from those of other males if females live at high population density (Liberg & Sandell, 1988).

Home range use does not require that every part of the area is used, but it includes those areas for hunting, rest etc. linked by well-used trails, which the cats use to travel between them. Some cats use their home ranges very intensively all year round. For example, ocelots, *Leopardus pardalis*, in Peru cover all areas of their home range every two days (Emmons, 1988), but pumas, *Puma concolor*, in the Idaho Primitive Area of the USA occupy high ground during the summer months and follow their prey (deer) to lower ground during the winter, where snow fall does not impede their movement or feeding so much (Seidensticker et al., 1973). In general, the size of home ranges is broadly related to body size. For example, female ocelots in Peru occupy up to 2.5 km^2, female bobcats, *Lynx rufus*, in South Carolina up to 22 km^2 and female pumas in California up to 119 km^2 (Kitchener, 1991). However, it is also related to the availability of prey. For example, home range size in Canada lynxes, *Lynx canadensis*, varies from 30 to more than 700 km^2 partly in relation to snowshoe hare, *Lepus americanus*, population cycles, but also other factors including suitable cover and conditions for hunting (Kitchener, 1991).

Although regarded as solitary, all cats show some degree of sociality. In fact these cats should be more properly regarded as solitary hunters and in most species the following social groups are seen: Male and female in oestrus, female and her young, and dispersing siblings (Kitchener, 1999). The female and young grouping is the most enduring

and may last up to three years in big cats such as lions and tigers (Schaller, 1967; 1972). However, for most of the time the 'solitary' cats probably rarely meet, except for territorial disputes or mating. Even so-called solitary cats may show more sociality than we realise; Schaller (1967) saw groups of jungle cats, *Felis chaus*, coming together in the breeding season, but the reason for this was uncertain.

The aim of the social system of solitary cats is to maximise the lifetime reproductive success of males and females, but in different ways. By defending as large an area as exclusively as possible, a male achieves matings with several females within his home range with little competition. This polygynous mating system is typical of many mammals. A female may mate with more than one male (promiscuity), which it has been suggested may increase the genetic diversity of her young, because more than one male may fertilise her eggs (Darie & Boersma, 1984). It has been suggested that this may promote the survival of at least some young in areas where there are changing environmental conditions. However, it seems to me that a female may encourage multiple matings with different males in order to convince all the males in her area that they have fathered the young. In this way, male infanticide of the young should be minimised. Infanticide is widely regarded as a male reproductive strategy, which destroys the reproductive output of a rival male and brings the female into oestrus for mating with the new male faster than if he waited for her current young to disperse. Infanticide has been recorded in ocelots, tigers, pumas, Canada lynxes and leopards, *Panthera pardus* (Emmons, 1988, Smith et al., 1988, Kitchener, 1991, Bailey, 1993).

3. The social cats

A few cat species show a high degree of sociality. Lions are the most familiar social species, which in the Serengeti National Park of Tanzania and in many other parts of their distribution live in fission-fusion groups called prides, which consist of 2-20 (usually) related females and their cubs in a shared home range, which is defended cooperatively against other prides (Schaller, 1972; Bertram, 1975b; Nowell & Jackson, 1996). A group of up to seven (usually) related males, called a coalition, defends the pride from other coalitions (Bygott et al., 1979; Nowell & Jackson, 1996). Larger coalitions retain exclusive mating rights with a pride for longer or may defend two prides, thereby promoting the formation of coalitions (Bygott et al., 1979). Prides show a number of cooperative behaviours, e.g. they suckle and defend each others' cubs in crèches, they synchronise oestrus so that cubs tend to be of similar age, and they hunt together and share prey (Schaller, 1972; Bertram, 1975a; 1983).

Related domestic cat females have also been observed living in groups or prides in some areas. For example, in Portsmouth Dockyard the cats have probably been isolated from other domestic cats for 200 years (Dards, 1981). The female lives in groups of 2-7, where young are reared cooperatively just like lion cubs. However, the males do not live in coalitions, but move singly between prides for mating.

Cheetah males and females show very different social groupings (Caro, 1994). Females are solitary and range over huge areas (800 km^2), but males live in smaller home ranges in groups of 2-3 (Caro & Collins, 1987a). These males tend to be brothers from the same litter. It is still not clear why males defend these home ranges. They tend to occur in areas where prey density is high, so that females in oestrus attracted to the area

Pride of female lions and their cubs in the Serengeti National Park of Tanzania. Photo: Sim Broekhuizen.

would be mated by at least one of the coalition males (Durant et al., 1988). It has also been noted that coalition males tend to be in better health than solitary males, so that it is probable that coalition males may live longer and hence achieve a higher lifetime reproductive success (Caro & Collins, 1987a,b).

Tigers have been recorded showing some degree of sociality. Groups including males, females and cubs have been seen in Ranthambhore National Park (Thapar, 1986), and males have also been seen sharing kills with females and cubs, and playing with subadult cubs, in the Royal Chitwan National Park (Tyabji, 1991, 1998).

Why do these cats live in groups together, while the majority of species are 'solitary'? It is most likely that in part the degree of sociality is related to the density and availability of food. For example, Canada lynx females and their young move through woodland in single file, but when hunting they fan out and move in the same direction, so that any snowshoe hare flushed by one lynx are likely to be caught by another (Parker et al., 1983). In fact hunting success increases and interkill distances decrease with increasing hunting group size (Parker et al., 1983). Individuals of both Cana-dian and Eurasian lynxes, *L. lynx*, may lie in ambush while a conspecific drives prey towards them (Haglund, 1966; Barash, 1971). This hunting strategy is very similar to the cooperative hunting shown by lions in the Serengeti (Schaller, 1972). This suggests that lynxes would benefit from living in groups all the time, but the cycles and other variations in populations of their prey probably prevent stable social groups forming.

Domestic cat prides seem most likely to develop in areas where there is a huge clumped supply of food. The highest domestic cat population density (2,350 km^2) has been recorded in a fishing village in Japan where fish processing waste is able to support these huge numbers (Izawa & Ono, 1986). Abundance and clumping of food probably also affects the social grouping of lions to some extent; high population densities of large ungulates allow lions to live in large groups by hunting cooperatively

and sharing kills, which are too big to be consumed by an individual. However, this is not the key factor in all situations. In the Serengeti Schaller (1972) found that although lion prides may comprise up to 12 females and their cubs, the optimum hunting group size for maximum hunting success and intake of food is two. A recent and more extensive study in the Serengeti by Packer et al. (1990) has confirmed Schaller's observations and shows that optimum hunting group size is two or six. Therefore, there is a disparity between pride group size and hunting group size, and yet it is evident that lions could not live together in large groups unless they have access to an abundance of large prey. However, these observations may only be typical for the Serengeti. In the Etosha National Park in Namibia Stander (1992) has observed lions hunting cooperatively and singly. Lions hunting alone had a very low hunting success (2.3%), so that cooperative hunting is probably unavoidable. Moreover, hunting success increased broadly linearly with hunting group size in Kalahari lions (Stander & Albon, 1993).

There are several other suggestions as to why lions live in such large groups. These are all broadly defined as being based on kin selection, whereby groups of related individuals can increase their own reproductive fitness by promoting the survival of close relatives, with whom they share varying proportions of their own genes through common inheritance (Bertram, 1976). Therefore, shared rearing and defence of cubs promotes the survival of a particular female's own cubs genes as well as those found in her nephews and nieces etc. In the Serengeti lions may lose their kills to spotted hyaenas, *Crocuta crocuta,* or to other, particularly male, lions. When sharing a kill within a pride, even though an individual may not get as much food as if she were to hunt on her own, kin selection dictates that it would be better to share the food with closely related conspecifics than other species. Packer et al. (1990) suggested that the formation of crèches by females allows hunting females to hunt in optimum group sizes with the assurance that their own cubs are cared for and defended. It should also be noted that there might be negative consequences of dispersal from prides. Although, lionesses may disperse from prides, they usually stay within their natal pride (Pusey & Packer, 1987). Dispersing females may suffer delayed breeding if they eventually return to their pride, and higher mortality and little or no breeding success if they remain nomadic (Pusey & Packer, 1987).

Therefore, even though abundant large prey probably provide the preconditions for sociality in lions, other factors which promote reproductive fitness such as kin selection through shared suckling and defence of cubs and sharing of prey are probably vital for pride survival in the Serengeti at least. Whether these factors are as important elsewhere in the lion's distributional range remains to be seen. For example, in the Kalahari Desert of Botswana, lions live in prides of up to about six females and their young for only part of the year during the rainy season (Leyhausen, 1988). During the dry season prey is so scarce that prides break down and the lions are 'solitary'. In the more arid regions of the Kalahari lions are said to live in monogamous pairs in the vicinity of waterholes or oases (Eloff, 1973).

4. A spectrum of sociality

In some ways the Serengeti lions display an extreme of social behaviour which is not seen elsewhere. Leyhausen (1988) reviewed lion social groups throughout Africa and

Asia, where known. Although there was a tendency for lions to live in prides, in arid regions (e.g. Namibia), lions occurred in groups of one male and one female, and there is anecdotal evidence to support similar small group sizes in North Africa and the Cape, where the lion is now extinct. Domestic cats show a similar flexibility in their social organisation, ranging from the prides observed in Portsmouth Dockyard to typical solitary non-overlapping home ranges on the Monach islands in the Western Isles of Scotland (Dards, 1981; Corbett, 1979).

This spectrum of sociality in lions and domestic cats is clearly related to availability and distribution of prey or food. In areas where there is low prey density or low food availability, these social species behave like 'solitary cats. However, other factors may be important (see above) in actually determining whether social groups are formed or not. For example, despite access to similar prey, cheetah females in the Serengeti remain 'solitary' and nomadic, because their cubs are particularly vulnerable to predation, even though males in the same area form coalitions. There are also limits on population density independent of abundance of food. In a study of feral domestic cats in Brooklyn, New York, Calhoon & Haspel (1989) found that acces to shelter limited population density in one area where food from refuse was far in excess of what could be consumed by the cats.

Given this flexibility in social systems within single felid species, is it fair to regard other felid species as solitary? Perhaps all species could live in more permanent social groups if ecological conditions allowed. After all the stable home range systems and successful breeding displayed by all so-called solitary species show that individuals must interact all the time or else there would be social anarchy with high degrees of agonistic encounters, unstable and disrupted home ranges and high levels of infanticide. These characteristics have not been discovered in field studies of so-called solitary cats (Kitchener, 1991; Nowell & Jackson, 1996).

5. Another look at 'solitary' cats

The stable home range systems shown by 'solitary' cats requires communication between neighbouring individuals, if they are to be maintained. Sociable cats communicate at short range using facial and body postures, and vocal communication. For example, lions display 17 different visual signals as well as contact patterns and vocalisations (Schaller, 1972). 'Solitary' cats also communicate in this way (Wemmer & Scow, 1977), but as we have seen earlier they rarely meet, so that other longer range methods are required, which do not require the sender of the message to be present. The most important method of communication for indicating home range tenure is scent marking. Cats are covered in glands, some of which (e.g. on cheeks, root of tail) can be used to communicate at short range e.g. cheek and head rubbing when cats greet (Macdonald, 1985). However, the secretions of all glands can be used for leaving scent marks on inanimate objects to communicate with conspecifics. Secretions from the interdigital glands between the toes are spread on to scratching posts to provide a powerful visual and olfactory signal. Urine is sprayed on tree trunks at a height that is convenient for other curious noses to sniff. Faeces or scats are deposited on prominent objects with or without secretions from anal glands and anal sacs by trails. Urine and/or faeces may also be deposited in scrapes made by scraping the hind feet

on the ground. All felid scent marks are visually conspicuous so that strange cats see them more easily.

Scent marks may vary in their longevity. Urine and cheek gland secretions may last for only a few days and require constant reinforcement, but scrapes, scats and scratching posts may survive for several weeks, although their effectiveness may diminish over time. Cats may even try to extend the life of their scent marks. For example, tigers spray urine on the underside of leaning trees to shelter their scent marks from rainfall (Smith et al., 1988).

Scent marking conveys a variety of information according to their chemical composition, position, frequency etc. Therefore, they are able to convey a wide range of information to conspecifics including the identity of the home range holder, sex, breeding condition and age of the individual that has left them. For example, hormonal products in the urine of oestrus females is detected by males using the vomeronasal organ in the roofs of their mouths, which results in a characteristic grimace or flehmen response (Estes, 1972). Scent marks have also been shown to have been used in border disputes between tigers, where the density and frequency of deposition of scats increased in contentious areas (Smith et al., 1988).

Scent marking in many mammals is thought to work by means of scent matching. This scenario was first developed from observation of bovids by Gosling (1982), but appears to apply equally well to felids (Kitchener, 1991). Scent matching involves linking the scent from scent marks to the cat making them. Therefore, cats often rub their cheeks against urine sprays or transfer urine to their hind legs during scraping. Also, strongly scented objects within the home range (e.g. a rotting carcass), elicit scent rubbing (Rieger, 1979) which transfers this strong scent to the home range owner. Scent marks are not distributed only at the border of the home range, but also along trails and particularly at intersections of trails within the home range where they are most likely to be encountered (e.g. Iberian lynx, *Lynx pardinus*; Robinson & Delibes, 1988). When a cat enters a new area, it will encounter strange scent marks and from these learn the individual scent of the home range owner. Therefore, when the cat encounters another cat within the strange territory, it will be able to identify the cat as the home range owner by matching the scent of the scent marks with the scent of the other cat. In this way it can decide whether to retreat or repel the strange cat. Therefore, far from being antisocial and unaware of their neighbours, cats have an extensive knowledge of each other through scent marks. They may even form temporary associations; dispersing female cats (e.g. domestic cats, tigers) will often share part of the home range of their mother (50-80% in domestic cats in Japan; Izawa & Ono, 1986). This temporary alliance may assist the long term survival of the female kitten and help the mother with home range defence (Kitchener, 1999).

Social cats use the same kinds of scent marks, although they share a common home range. Frequent greetings between sociable cats involving head, cheek and tail base rubbing presumably mixes sebaceous secretions, so that there is probably some form of group scent, although this has not been confirmed. Lions differ from other cats in not using faeces to mark their home range (Schaller, 1972). Presumably, there are so many scats produced in the home range, that they convey no useful information. Instead lions roar together, which not only locates and reinforces bonds between pride members, but also advertises the continuing presence of a pride in the home range to neighbouring prides (Estes, 1991).

Table 1. A comparison of the dispersed social system of so-called solitary cats (tiger) and the sociable system of some lion populations.

	Lion	Tiger
1. Home range	Shared discrete interpride	Discrete intrasexual shared intersexual
2. Territorial markers	Urine sprays scrapes scratching posts Roaring	Urine sprays scrapes scratching posts Scats
3. Communication marking	Vocal Postures Scent marking Contact patterns Group scent?	(Vocal) (Postures) Scent marking Contact patterns
4. Mating system	Polygynous Promiscuous	Polygynous Promiscuous
5. Suckling & defence of cubs	Shared	Solitary
6. Hunting	Cooperative (solitary in some populations)	Solitary (cooperative in some tiger and a few other spp.)
7. Food sharing	Yes	Occasional

A pattern is beginning to emerge of only subtle differences in the social systems of so-called solitary and sociable cats (Table 1). It would seem that if there is a sufficient high density and clumped prey base, social groups may form in a variety of cat species, although other factors (e.g. competition with and defence from other predators/scavengers, communal care of young) may be important in creating more cohesive and enduring social groups. Far from being isolated, antisocial species with mainly agonistic interactions with neighbouring cats, so-called solitary felids appear instead to have a dispersed social system, which promotes territorial stability through scent marking, so that most social encounters are positive interactions involving mating and rearing of young. This dispersed sociality promotes increased probabilities of reproductive success for both males and females; a male's home range usually encompasses more than one female range, where he tries to monopolise matings through territorial defence, whereas females may mate with more than one male (and may encourage competition between males) in order to minimise the risks of infanticide through uncertain paternity.

At the other end of the spectrum at least two felid species may form social groups of females and their young, which defend common home ranges and display a variety of cooperative behaviours. Perhaps the time has come to restrict the term 'solitary' to the hunting strategy of most cat (and indeed carnivore) species, and regard all cats as being social, although ranging from dispersed social systems of most cats to the sociable groups of some lions and domestic cats?

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SAMENVATTING

Zijn katten echt solitair?

Van de ongeveer 37 soorten recente katachtigen worden de meeste als solitair, niet-sociaal levend beschouwd. Er zijn echter een paar soorten die sociaal levende groepen vormen; naast de huiskat *Felis catus* en de leeuw *Panthera leo* zijn dat, zij het in mindere mate, ook de tijger *P. tigris*, de cheetah *Acinonyx jubatus* en de lynx *Lynx lynx*. Het sociale systeem van huiskatten en leeuwen kan sterk variëren, al naar gelang de beschikbaarheid en de ruimtelijke verdeling van het voedsel c.q. de prooidieren. Ook zaken als gemeenschappelijke verdediging van jongen en het vergroten van de overlevingskansen van jongen van verwanten ('kin selection') spelen een rol.

Het feit dat alle katachtigen territoriaal leven en communiceren met hun buren door middel van geurmerken of geluid, geeft aan dat geen van hen antisociaal leeft, maar dat de zogenaamde solitaire soorten eerder in een'verspreid sociaal systeem' leven. De hypothese wordt ontwikkeld dat in principe het sociale systeem van alle katachtigen tot op zekere hoogte variabel is, maar dat bij veel soorten de variatie niet tot uiting komt doordat het ecosysteem waarin ze voorkomen dit niet toelaat. Het begrip 'solitair' zou dan voor de katachtigen beperkt moeten worden tot het alleen jagen op prooi.

(S. Broekhuizen)