

## THE BEHAVIOUR OF DOCKYARD CATS: INTERACTIONS OF ADULT MALES

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### ABSTRACT

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A study was conducted on the feral cats living in Portsmouth Naval dockyard, an enclosed site with an area of less than 100 ha, supporting a population of about 200 adult cats. Data were collected by direct observation, and individuals were recognized primarily by coat pattern. The behaviour of mature tom-cats was observed with respect to females and to other mature males. Most toms visited several groups of females, but the frequency with which a particular group was visited varied between toms. Some toms spent most of their time with one group, adopting a role similar to that of a "pride lion". The courtship and mating behaviour observed in the dockyard conformed with that recorded for laboratory cats. However, females in oestrus were not heard to call, but toms which were apparently seeking oestrus females emitted a characteristic cry. Up to 6 toms were observed in attendance on unreceptive oestrus females. Sexual behaviour was observed in most months, with peaks in the spring and autumn. Most of the aggressive interactions observed between toms and females were initiated by unreceptive females during courtship. Male aggression towards females was rare. Amicable behaviour was shown, and was more frequently initiated by females than by toms. Females appeared to interact amicably more frequently with toms with which they were familiar. No amicable behaviour between mature toms was observed. Interactions were characterised by aggression, tolerance or avoidance. Agonistic encounters were mainly ritualised, and few fights were observed. It is possible that a dominance hierarchy existed between toms, formed by fights when young toms first became sexually mature.

### INTRODUCTION

The domestic cat (*Felis catus* L.) has always been considered to be a solitary animal, and this idea has been supported in the limited scientific literature on the subject (Baron et al., 1957; Kiley-Worthington, 1976). It is only in recent years that evidence has been accumulating to show that cats have the ability to exist in social groups (Fagen, 1978; Macdonald and Apps,

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1978; Dards, 1979), the degree of sociability depending on the quality of the habitat and, related to this, the population density.

There have been relatively few studies of feral or free-living cats, and Fitzgerald and Karl (1979) have given a review of the relevant published work, excluding that of Laundré (1977). Portsmouth dockyard provided an ideal opportunity to study feral cats living at high densities. (The term "feral" is used, as defined by the R.S.P.C.A., as an animal that is "not domiciled with man".)

The object of the study was to determine the status of the cat population in Portsmouth dockyard, in order to supply scientific data in the emotive debate concerning whether or not the animals were pests and should be eradicated. This information was also required in order to determine policy should rabies enter the country. Thus, the study was primarily an ecological one, and the methods of data collection (see below) were dictated by this consideration. However, as social behaviour was considered an integral part of the study, behavioural data were recorded in as much detail as this framework allowed. Although this information is not as complete or as well-structured as could be desired, it was felt that it should be presented, in view of the lack of any other study dealing with large numbers of cats.

The present paper confines its scope to a consideration of the behaviour of the adult male cats of Portsmouth dockyard, and their interactions with females and with other adult males. It is hoped that this information will provide some insight into the social structure of the cat, an animal which is usually only known as an artificially isolated individual in a domestic situation. These data should make possible comparisons with other felids and with cats in other habitats, in addition to providing some of the information required before methods of population control of feral cats are considered. The structure of the social groups, and the interactions of immature males and kittens, will be considered elsewhere.

The dockyard, which is effectively enclosed, has a land area of less than 100 ha, and supports a population of about 300 cats. Food appears to be plentiful, much of it provided by some of the 10 000 people who work in the dockyard (Dards, 1981). Home ranges (by the minimum area convex polygon) averaged 8.4 ha for toms, and 0.8 ha for females. Although the ranges of toms were found to overlap apparently freely, those of the females were largely divided into a number of discrete groups, within which ranges overlapped almost completely, and included a shared core area (as defined by Kaufmann, 1962) in which the cats were most frequently seen (Dards, 1978).

## METHODS

The study was carried out in Portsmouth dockyard from October 1975 until June 1979. Data were recorded by direct observation, using, primarily, coat pattern for identification of individuals. Most data were obtained by

"patrolling" a set route around the dockyard, which covered all areas without going over the same ground twice. Most of these patrols were conducted during evenings and weekend afternoons, when the cats appeared to be more active. This was later confirmed by round-the-clock observations on limited numbers of cats (Dards, 1979). The patrolled-watch results given in this paper are derived from those of October 1975 to December 1977, covering a total of 545 h.

Cats could be sexed by observation of the testes, pregnancy, production of kittens or lactation, or mating. It was also possible to distinguish mature toms from females or young toms on the basis of facial features, build and behaviour. The ages of cats which were already adult when the study commenced could not be ascertained, but the ages of cats that were born during the study, or shortly before it commenced, could be determined.

For the purposes of this study, cats over a year old were considered to be adults. The division between juveniles and adults was rather arbitrary, since the age at sexual maturity varies between sexes and between individuals of the same sex (Kling et al., 1969; Scott, 1970). Females were capable of breeding when less than a year old, but did not always do so, and none bred when still classed as juveniles. Toms would be expected to be mature at about a year old. Those which did not show any of the secondary sexual characteristics after this age were referred to as "immature adult males". This term appears contradictory, but it was not known whether the immaturity was physiological or behavioural. Maturity in toms less than a year old was not observed. In this paper, the discussion of behaviour is confined to toms which were sexually mature.

Behavioural interactions which were observed during the patrolled watches were always recorded. These provided a useful background to the types of behaviour displayed by a large number of cats of differing social status and location. However, active interactions between cats were seen relatively infrequently during the patrolled watches, since cats spend much of their time resting. A more detailed picture was given by the "long watch" studies. Although it proved impossible to keep adult toms under observation without disturbing their behaviour, female cats proved much easier to observe, mainly because they were more sedentary, and little active following was required. It was possible to observe a whole group, so that although all the interactions of particular toms could not be observed, all their interactions with the group under study were recorded.

During the long watches, the behaviour of the members of 2 groups was recorded continuously, in a series of shifts which covered all times of the day and night. Observations were conducted using a parked car as a base, although it was often necessary to leave this in order to keep the cats in view. The cats soon became accustomed to the presence of the observer, who was usually ignored. Details of behavioural interactions were recorded on tape, using a pocket dictaphone.

The 2 groups studied were Group C (5 adult females) and Group W (4

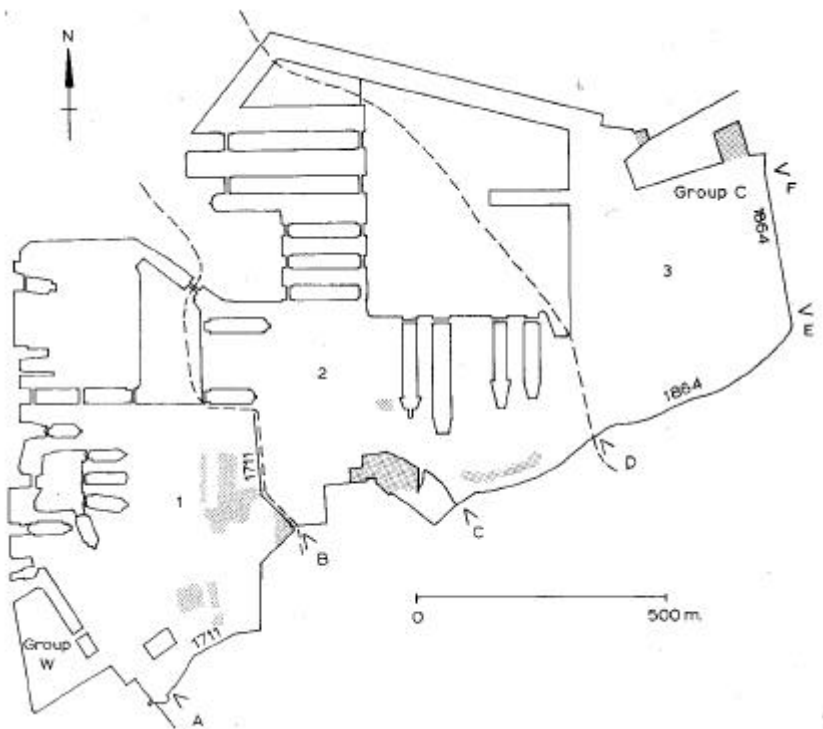


Fig. 1. Map of Portsmouth dockyard, showing the division into three areas, the dates of the walls, the gates (A-F), and the main areas of vegetation (stippled) and location of Groups C and W.

adult females), whose locations are shown in Fig. 1. Group W was first studied in the summer of 1977, and the first long watch lasted for 19 h. It became apparent that there was no advantage in observing the group for very long periods; since most of the females in a group could be found in the area quite quickly. As a result, most of the subsequent watches were of only about 4 h duration. In December 1977, observations were conducted on both Group W and Group C. These groups were each watched for two 24-h cycles, in 6-h shifts, from 3 to 20 December (except for 2 h on Group W, which were missed due to illness).

## RESULTS

### *Interactions between males and females*

#### *Toms and groups*

There was considerable variation in range size between mature males, extremes of 0.8 ha and 24.0 ha (by the minimum area method) being recorded, with a relatively even distribution of range sizes between these extremes

(Dards, 1978). Thus, although most mature males ranged over the areas of several groups of females (where they utilised the food supplies), there was variation in the amount of time they spent in the area of any particular group. This meant that the females of a group encountered some toms more often than others.

In cases where the home range was small, a mature male usually spent most of his time with one group of females, with which he interacted extensively (as was the case with 275, described below). Other toms visited several groups, therefore spending relatively little time with each, and ranging over as much as half the dockyard. Although this difference in behaviour existed, there was no distinct division into two or more types, but rather a range in behaviour types between the two extremes.

To illustrate the type of distribution observed, Fig. 2 shows the ranges of toms in the east half of the dockyard, compared with those of females. (The method of analysis and source of data are given in Dards, 1978.)

Males which had grown up within a group usually emigrated or disappeared when they were between 1 and 2 years old, and it was rare for a tom to maintain contact with his family group after he was sexually mature (Dards, 1979).

#### *Courtship and mating*

Observations of courtship and mating among the dockyard cats conformed, in general, with the descriptions given for captive cats and house-cats (Fox, 1975; Leyhausen, 1973).

One feature of interest in the dockyard cats' behaviour was the apparent absence of "calling" by oestrus females, which has been recorded for house-cats (Beadle, 1977), and presumably attracts the attention of males. Its absence in the dockyard may be due to the very high density of entire males. Toms, however, were frequently observed and heard giving a "prau" call. This is a short cry, relatively high-pitched, with a rapid rise in frequency, and is emitted repeatedly. This may be related to the call which Leyhausen (1965) describes as being used to call out young males to fight. However, in the dockyard, this cry appeared to be used when seeking oestrus females. For example, it was used when toms were seeking females, early in oestrus, which had hidden after an initial encounter. On one occasion, a tom was observed to trot off giving this cry after giving the flehmen (gaping) response to a puddle of urine, presumed to be from an oestrus female. (The flehmen response of cats to urine has been described by Verberne, 1970.) The "prau" cry can also be heard in town streets. It has a surprisingly long carrying distance, and can often be heard when the calling tom is out of sight.

During the patrolled watches, the most frequently observed aspect of courtship and mating was the attendance of toms on females in early oestrus, which were sexually interesting to the toms but not yet ready to mate. This type of waiting behaviour by the tom was evident from his close attention to the female, and the fact that he would follow her if she walked away, and chase her if she was disturbed and fled.

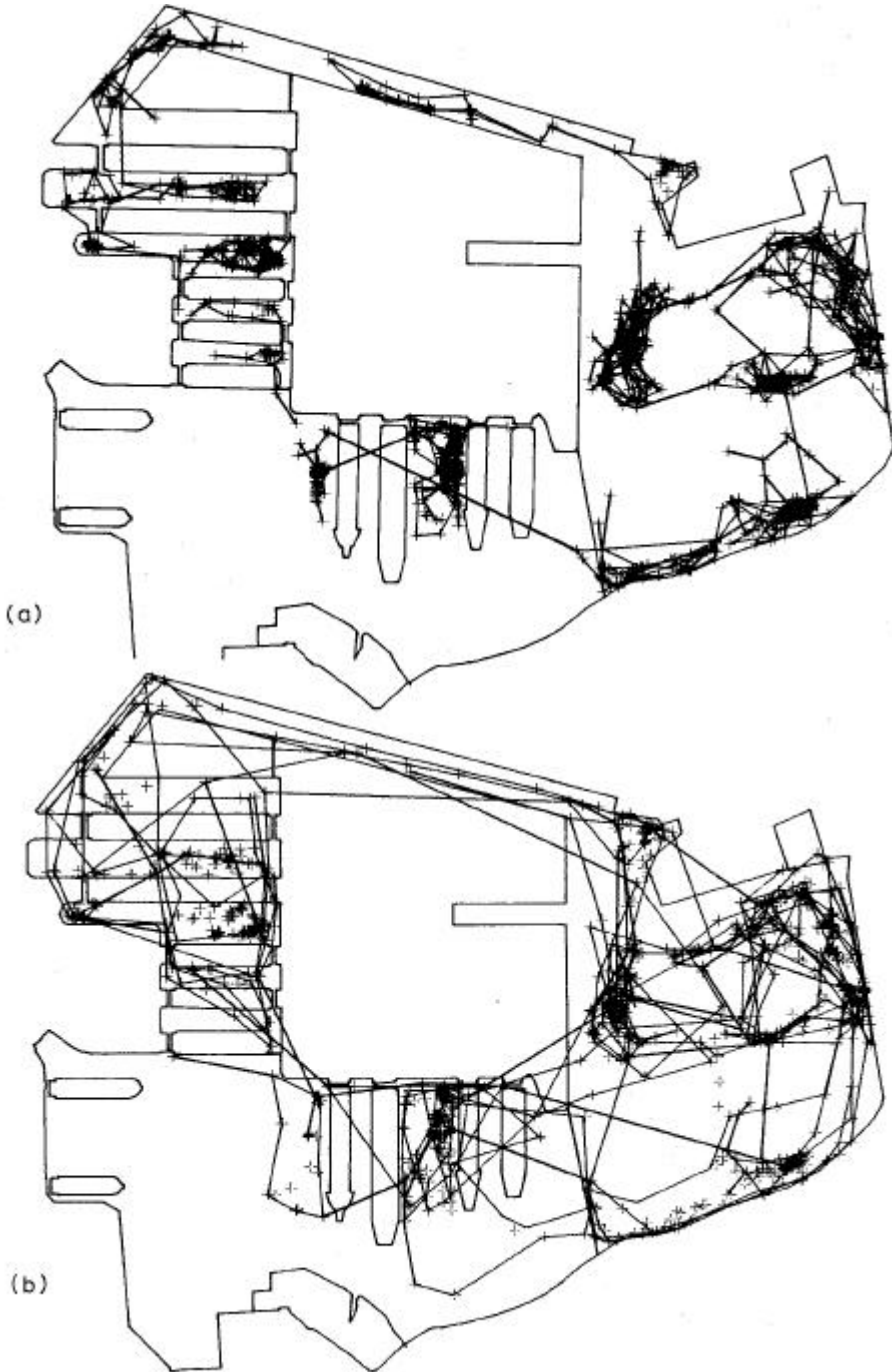


Fig. 2. Range plots (restricted range method, Dards, 1978) for cats living in the east half of the dockyard. (a) 67 females, with a total of 2529 sightings, showing group ranges. (b) 28 toms, with a total of 1101 sightings, showing the overlap of ranges.

Early in oestrus, the female is not receptive to the male, and usually rebuffs him if he approaches (Scott, 1970). However, this was not always the case. In one group, a 13-month-old female approached and greeted a tom (numbered 275) who associated closely with the group. 275 attempted to mount and mate with her, although she did not exhibit lordosis and tried to stand up. 275 continued his unsuccessful attempts for at least 5 min. The atypical lack of aggression from this obviously unreceptive female may have been due to the unusually close association between 275 and the females of this group, combined with the young female's inexperience.

A female in oestrus may attract many toms (Fig. 3), up to 6 being seen in attendance on 1 female. The distribution of observations of different sized groups of these males is shown in Fig. 4, for the period from October 1975 to December 1977, which consisted of 93 observations. Mounting or mating were recorded 30 times during this period. No fighting was observed among these waiting males. It is not known whether the females mated with only 1 tom, or with several.

Few females came into oestrus from late September to early January, and the onset of oestrous cycling in January and February produced an increase in courtship behaviour and mating. The calling of the toms was heard frequently at this time of year. However, sexual behaviour was observed in most months. The distributions of observations of males in attendance on

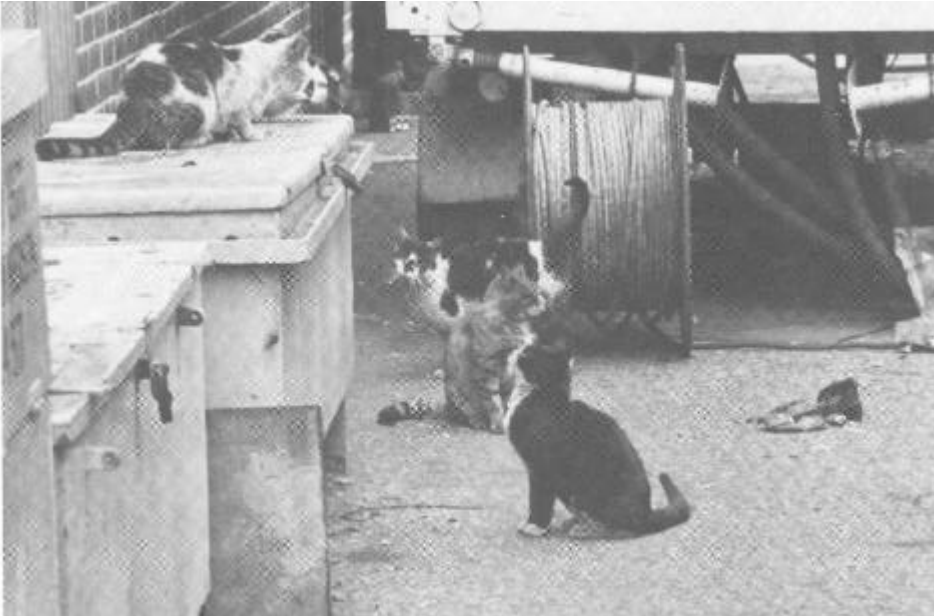


Fig. 3. An oestrus female (upper left, facing the camera) surrounded by toms. A fifth tom is present, but concealed from view by the box on which the female sits. (Note that this female had a permanently folded left ear.)

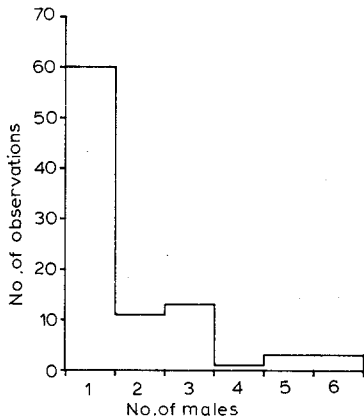


Fig. 4. The distribution of observations of different sized groups of males in attendance on oestrus females, for 93 observations during the patrolled watches (October 1975-December 1977).

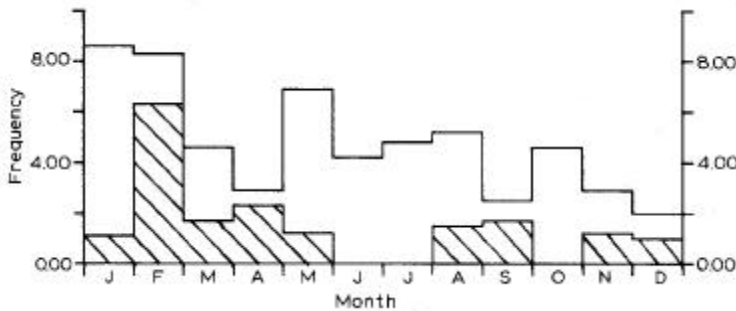


Fig. 5. The distribution of observations of males in attendance on oestrus females (open), and mounting and mating (shaded) through the year. (Patrolled watch observations for October 1975-December 1977; the frequency is corrected to allow for the different number of areas visited each month, as described in the text.)

females, and mounting and mating, through the year are shown in Fig. 5. (These values are corrected to allow for the different numbers of patrolled watches in each month. This was achieved by dividing the number of observations per month by a correction factor, which was the number of areas visited that month divided by the minimum number of areas visited in a month. Observations and numbers of areas visited per month were summed across different years.)

*Agonistic behaviour*

During all the patrolled watch observations of cats in the dockyard, only 3 cases of a tom behaving aggressively towards a female were recorded. One was merely a slap while feeding, another was a slap back at a female who had slapped, and the third was when a tom (275) fluffed up and yowled at a juvenile female who had entered the group area from a neighbouring area.



(This juvenile appeared very ill, and was not seen again after this incident.)

Females, however, were frequently observed to behave aggressively towards toms, although much of this occurred when toms approached unreceptive early-oestrus females, as described in the previous section.

The incidence of observations of female aggression and threat behaviour towards mature toms during the patrolled watches (October 1975 to December 1977) are summarised in Table I. Slaps and hisses are low-intensity aggression. Wails or yowls and "fluff" (pilo-erection) are defensive threats. The 2 occasions on which "fluff" was recorded were when a female met a tom unexpectedly, and this behaviour probably reflects a "startled" state. The one case of a female attacking a tom was when a group of cats were being fed. A tom sniffed a kitten as it went past, and the mother slapped and bit him, giving a quiet cry. The tom cowered, and the mother attacked again, yowling and lashing her tail. The tom cowered with his head in a corner, and the mother sniffed the base of his tail and then ignored him.

The frequency of female aggression and threat behaviour towards toms during both the patrolled and long watches is summarised in Table II. It can be seen that this behaviour was relatively uncommon during the long watches. This may be partly due to the dates of these observations, which were not during the peaks of the breeding season, aggression associated with courtship therefore being infrequent. In addition, the Group W females' interactions with mature toms were only with toms with which they were very familiar, since they spent much of their time in the group area, and other toms were rarely seen there.

TABLE I

The incidence of observations of female aggression and threat behaviour towards toms, during the patrolled watches of October 1975 to December 1977 (545 h). "Situation" is based on the location or behaviour of the male relative to females, together with kittens or food

Situation	Fight	Slap	Slap + hiss	Hiss	Wail/yowl	"Fluff"	Chase/stalk	Total
♂ followed or chased ♀	-	5	2	1	1	-	-	9
♂ approached ♀	-	2	1	3	1	-	-	7
By kittens	-	-	-	-	1	-	2	3
By kittens and food	1	-	-	-	-	-	1	2
By food	-	2	-	-	1	-	-	3
♂ and ♀ met	-	-	-	-	1	2	-	3
Total	1	9	3	4	5	2	3	27

TABLE II

The incidence of observations of female aggression and threat behaviour towards mature toms (patrolled and long watch data)

Group	Period	Hours	No. of observations
	Patrolled watches, Oct. 1975-Dec.1977	545	27
W	26. 5.77	19	2
W	22. 6.77-7.7.77	37	2
W	13.12.77-20.12.77	48	0
C	3.12.77-11.12.77	48	2

The 4 cases of aggression or threat towards a mature male in Group W were all directed at 275, but were very mild. On one occasion, 275 approached one of the females (305) and her kittens, and she lashed her tail at him and he backed away. On another occasion, he approached the hole in which 305's kittens were located. 305 ran over and miaowed at him, and he moved away, while 305 looked down the hole. Once 328, a "pet" cat who was not a group member, ran up to 275 and he ran away. The fourth occasion involved 275 chasing a young male, 348, who was approaching sexual maturity. The females often chased after the toms when this occurred, but seemed excited rather than aggressive. However, on this occasion one of the females chased up to 275 and slapped him.

It should be stressed that these interactions were with a tom towards whom the females more frequently exhibited amicable behaviour (see below). The interactions with mature males in Group C, however, differed from the above situation. One tom (13) spent most of his time with the group, and no aggression towards him was observed. The aggression and threat from the females was directed at 2 toms which were relatively infrequent visitors. One of these fled from the author past a female, who mewed and then wailed quietly at the tom. Another tom met with a female at the corner of a building. He blocked her escape route, and she was mewing at him. However, the tom left when an immature male arrived.

Other forms of agonistic behaviour were noted in addition to those recorded in Table II. One of these was an intense stare at a feeding cat. In Group W, a female (280) took some food from a skip (a large refuse container) and fed. A tom (279) approached closer and closer, twitching the end of his tail. He dragged the food away a little, and the two cats fed uneasily together, before 280 retreated a little way. She tried to pull the food towards her with one forepaw, then just sat and stared at 279, before finally leaving. The "food-stare" was observed 4 times in Group C, twice by more than one female towards 45, a tom who was a relatively infrequent visitor, and he ignored them. The other 2 observations were of stares directed at 13. On one occasion, he ignored them. The other time, however, involved a

series of changes of possession of a piece of food, between 13 and a female (18). Each fed for a period while the other stared, then stopped feeding and stared while the other fed. It is assumed that the "food-stare" is intended to intimidate the feeding cat into leaving the food.

The other form of behaviour recorded was "nervous" behaviour of one cat (Fig. 6), in the absence of threat from another cat. In Group W, a young female watched 279 rather nervously when he looked at her. In Group C, females 3 times fled from 45, and once from 70 (another visitor) when they approached.

One case of mature male aggression towards females was observed during the long watches, in Group C, when 13 appeared to lunge at 18 while they were feeding.

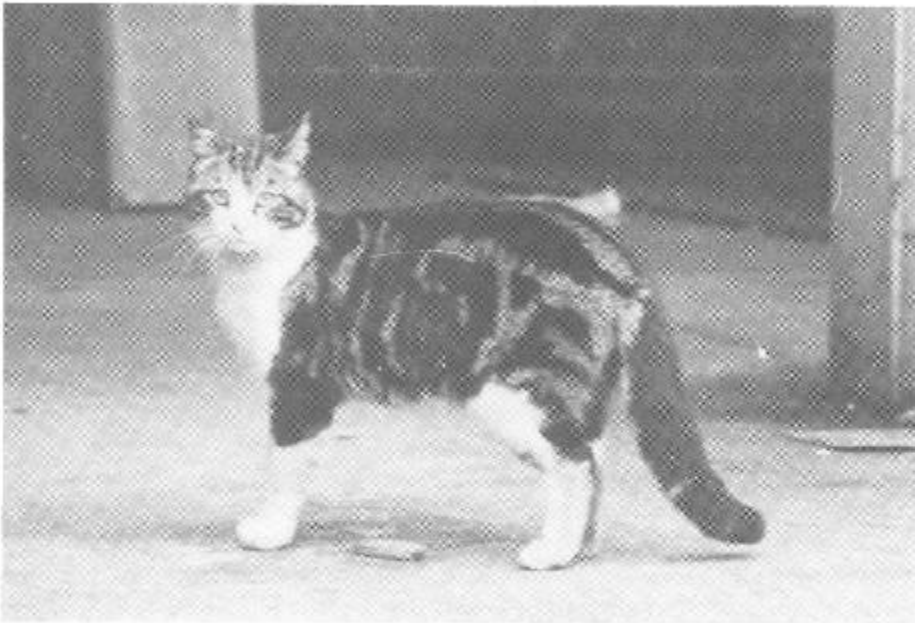


Fig. 6. An adult male showing the characteristic "nervous" expression, with the ears turned but not flattened, and the eyes wide open. Note also the slight pilo-erection. This posture was associated with avoidance behaviour (and in this case induced by the cat being persistently followed by the author with a camera).

#### *Amicable behaviour*

Amicable behaviour, consisting of allogrooming and "greeting" behaviour, was observed between females and mature males, and was of the same form as that observed between females. Greeting behaviour is shown when 2 or more cats meet or pass, and consists of 3 main components. These may be described as "tail-up", "sniff-noses" and "head-rub", usually occurring in this sequence if all are displayed.

The tail-up posture is the lowest intensity, and most commonly observed,

component of greeting. A cat normally holds its tail at an angle of about  $45^\circ$  below the horizontal, but when greeting another cat the tail is raised. This may merely be an acknowledging lifting of the tail to the horizontal as 2 cats pass, or may involve the tail being carried straight up, sometimes with a slight curl in the end.

In the sniff-noses component, the 2 cats appear to touch their noses together. A sniff may sometimes be directed at another part of the second cat's body, usually from a little distance away.

The most extreme form of greeting is head-rubbing (which is also observed in lions; Schaller, 1972). This involves 2 cats rubbing their cheeks or foreheads against each other, either from face to face or side by side. The headrub may be continued along the length of the body. A cat may persistently rub round the body of another cat which does not respond.

In some interactions between mature toms and females, it was difficult to distinguish between true greeting and low-intensity sexual behaviour. For example, a sniff from a male could sometimes have been an investigation of the sexual condition of the female. A female which followed and rubbed round a tom could have been displaying courtship behaviour, especially when this was associated with rolling by the female.

During the patrolled watches, amicable behaviour between mature toms and females was observed 42 times. Of these, 6 encounters may have been checks by a male, a sniff being directed at the female's body but not at her face, and these are excluded. Six encounters which may have been female courtship are included since they reflect an amicable relationship between the female and the tom. The interactions are summarised in Table III. It can be seen that females greeted males more than twice as often as males greeted females, and that female-initiated greeting tended to be of a higher intensity. Males often did not respond to females' greetings.

During the long watches, the females' interactions with mature males in Group W were mainly with 275, and these are summarised in Table IV. It can be seen that 275 received many more greetings than he initiated. On one occasion during the summer watches, 4 of the 5 adult females of the group were rubbing round him at one time. In addition to greetings, one female

TABLE III

A summary of the amicable interactions between toms and females, observed during the patrolled watches (for October 1975 to December 1977)

Interaction	Type of greeting			Total
	Tail-up	Sniff noses	Head-rub	
Mature male to female	-	10	1	11
Female to mature male	2	6	14	25

TABLE IV

The frequency of interactions initiated and received by 275, a mature male of Group W, with the females of the group

Female	Date 26.5.77 (19 h)		Period 22.6.77-7.7.77 (37 h)		Period 3.12.77-11.12.77 (48 h)	
	Initiated	Received	Initiated	Received	Initiated	Received
293	-	5	-	2	*	*
347	-	7	1	2	*	*
280	-	3	-	-	1	2
305	2	4	-	2	-	-
396	*	*	-	7	-	-
527	*	*	*	*	-	4

\*Denotes that this female was not alive, or was still a kitten, during this period of observation.

(293) was observed licking 275 on 3 occasions, and 275 once licked a juvenile female. He sniffed at females twice.

The only other mature male observed in Group W's area during the long watches was 279 (who died in November 1977). He was seen less frequently with the females than was 275, and they usually ignored him, or watched him. However, he was twice greeted by young females.

Only 2 greetings between females and mature males were observed in Group C during the long watches. In one, a female (23) greeted 13, the "resident" tom. On the other occasion, 45 (a visitor) raised his tail as he passed an immature male, but this may have been directed at 23, who was nearby.

#### *Interactions between mature males*

Amicable behaviour between mature males was never observed in the dockyard. Behaviour between these cats consisted of agonistic encounters, avoidance or tolerance.

Agonistic encounters observed generally consisted of ritualized threat postures and vocalisations. No fights as violent as one observed between 2 females were seen. However, serious fights obviously did sometimes occur, since some toms had torn ears, and on 2 occasions cats were observed with a raw patch on the throat, which may have been a wound received during a fight.

The posture and vocalisations of an aggressive tom consist of an upright posture (the cat appearing taller than normal), with the legs straight, and the cat moves with a stiff-legged gait, very slowly. The hindquarters appear higher than the shoulders, and this is emphasised by an arch in the tail, near its base. The hair is erected slightly on the body, and more so on the tail,

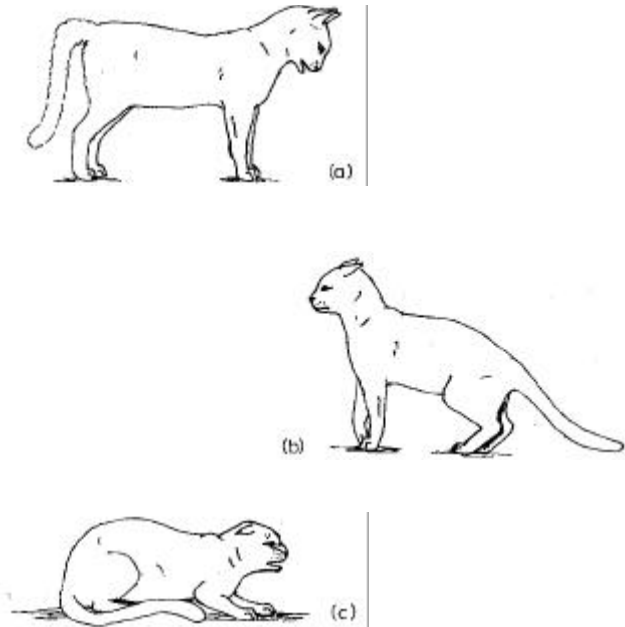


Fig. 7. Examples of agonistic behaviour. (a) Aggressive threat, which is accompanied by yowling and "chomping" with the lower jaw. (b) Elements of defensive threat appear in response to a stronger aggressive threat. (c) "Submission", with elements of defensive threat. (True passive submission was not observed.)

which is lashed from side to side. The head is held relatively high, with the nose pointing downwards, and the lower jaw is moved in a rhythmic "chomping" motion, accompanied by low wails. These start quietly, but during the encounter can increase in volume to a loud yowling. (The postures described in this section are illustrated in Fig. 7.)

In "submissive" behaviour, the cat crouches, either half-sitting, or flattened against the ground. The head is drawn back and held low, but the ears are laid back, which indicates defensive threat, and the cat may spit or wail.

Defensive threat elements can also be seen associated with offensive threat. The arched-back posture appears to be more defensive than the high hindquarters posture, although a cat was observed to advance on another tom with his back arched, but otherwise showing offensive threat. Increased pilo-erection appears to show an increased proportion of defence in the threat, although aggressive cats usually show some degree of pilo-erection, even when the other cat appears submissive. Full defensive threat as described by Leyhausen (1973), with the tail vertical and "bottle-brushed", was never observed in the dockyard.

One other component of agonistic behaviour was observed. This was the aversion of the head during an encounter, rather than both cats looking at

one another. The head is averted at right angles to the other cat. This may indicate a defensive component in the threat (a direct stare being an offensive threat, with head-aversion exposing the throat), although it was usually associated with an otherwise offensive display. Sometimes both cats stood with heads averted, and sometimes a cat averted its head while nose-down and "chomping".

Agonistic encounters between toms tended to end in both cats reducing the level of threat slightly, and one cat moving very slowly away. The stiffness and slowness of the retreat depended on the level of offensive threat still being shown by the other cat. In some cases, the cat which walked away appeared to have been the more aggressive one, and it was not always obvious which cat had "won" an encounter.

Observations of agonistic behaviour between mature toms during the parolled watches are summarised in Table V. In only 5 cases did an interaction result in one tom striking another. The most interesting "fight" was between a Manx tom (41) and another tom (84) who frequented the same area (the core area of a group of females). 84 met 41, and yowling was heard. 41 was lying down, yowling, and 84 was standing, lashing his tail, and also starting to yowl, building up to a screech. 41 had his head low and pulled back, and his ears flattened, while 84 was "chomping". As 41 backed away, 84 advanced, still yowling. 41 screeched and jumped back, and 84 continued to advance. 41 fled under some wooden trays, and when 84 still advanced he gave a loud yowl and hid. The two cats peered round the wood at each other (ignored by the female resting on top of the pile), and then 84 started striking at 41 in his hiding place with one forepaw. This apparently hit 41, who cried out with each blow. 84 eventually backed out, shook himself, washed and then left. Thus 41's extremely non-aggressive response failed to deter 84 from striking him.

Of the other 4 interactions in which blows were struck, one consisted of a tom slapping at another tom which persistently approached him. Once a young tom (13) met another male (35) further south than his usual range, and the toms struck at each other with their forepaws, while yowling. This may have been the first time these cats had met. On another occasion, a tom came across another tom which was rolling. This cat fled, and the first cat chased him, caught up with him and pinned him down. The cat managed to work free and fled. The final interaction involved one tom pawing and hissing at another while several toms were round a female. This behaviour was rare, cats in this situation usually behaving very peaceably towards each other, unless they were disturbed and one cat fled too close to another.

Fighting among toms seems to be most common when young toms first emigrate from their natal areas. One "fight" was observed (in 1978) when a young male which had just left his natal group in the east of the dockyard was attacked by a resident in the centre of the dockyard. This young tom eventually settled down in the north-east of the yard. Other young toms observed in new areas were sometimes noted to have scratched noses.

TABLE V

A summary of the observations of agonistic behaviour between mature males, during the patrolled watches (for October 1975 to December 1977)

Initiation	Reaction												Total	
	Attack/strike	Submit	Threaten	Stiffen and leave	Threaten and flee	Flee	Avoid	Leave	Chase	Threaten and follow	Stare	Watch		No marked response
Attack/strike	1	1	1	-	-	-	-	-	-	-	-	-	-	3
Threaten	-	5	16	2	3	3	1	3	-	-	-	-	2	35
Threaten (distant)	-	-	-	-	-	-	-	-	-	-	-	-	1	1
Threaten and skirt	-	-	-	-	-	-	-	-	-	-	-	-	2*	2
Threaten and leave	-	-	-	-	-	-	-	-	-	1	-	-	4	5
Threaten and flee	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Defensive threat	-	-	-	-	-	-	-	-	-	-	1	-	5	6
Follow	1	-	-	-	-	-	-	1	-	-	1*	-	3	6
Approach	-	-	-	-	-	2*	-	-	-	-	-	-	1	3
Stalk	-	-	-	-	-	-	-	-	-	-	-	-	3	3
Stare	-	-	-	-	-	-	-	-	-	-	5	-	6	11
Watch	-	-	-	-	-	-	3	-	-	-	-	2	1	6
Flee	1*	-	-	-	-	-	-	-	1	1	-	-	-	3
Normal behaviour	-	-	-	-	-	-	1	2	-	-	-	-	-	3
Total	3	6	17	2	4	5	5	6	1	2	7	2	28	88

\*Two initiation-reactions in one encounter. Note that, for most initiation behaviours, different responses may be elicited on different occasions.

It appears that a tom which is relatively "resident" in an area may be driven away by another tom. This appeared to have happened to 45, who originally spent much of his time with one group (Group F). A new tom (78) appeared there, and shortly afterwards it was noted that 45 did not visit Group F, and that his ears were very torn. Curiously, 78 later left Group F and moved to another area, while a young tom which appeared to have grown up in the group (43) grew larger and stockier, and seemed to take over the role of "resident" tom. (Physical maturation of toms was not usually observed in animals that did not emigrate; Dards, 1979.)

Interactions of any sort between mature males were observed infrequently during the long watches. For Group W, interactions were observed between



275 and 279 during the summer watches. (279 was dead by December.) These 2 toms were only seen in view of each other on 6 occasions. On 2 of these, they were some distance apart and ignored each other, and once they were watching each other, but not simultaneously. Once they were observed lying about 1 m apart, both appearing very tense. It is possible that there was an oestrus female (328) close by. A little later they were both under a but watching 328, and ignoring each other. The only sign of active aggression was when 275 followed 279, walking slightly faster to catch up. 279 turned round and saw 275 when he was about 2 m away. They yowled at each other very quietly, lashing their tails. First 275 and then 279 sat down. After a few minutes, 275 left with a stiff, slow walk. It may be of relevance to the lack of interaction between these 2 toms, which lived in the same area, that both were unusually large cats.

In Group C, only 3 encounters between mature toms were recorded. Once 13 was close to 45, while both watched a female who was probably in oestrus, and the toms ignored each other. Once 13 watched 45 feed. The only agonistic encounter was when 41 (the Manx tom) approached the group's core area, where 13 and the females were. 13 crouched down, with his head held very low. 41 went up to one of the females, and then appeared to notice the other cats around him. He sat down when he saw 13, and later left.

## DISCUSSION

Until recently, it was considered that the lion was the only social felid. It is interesting to note that, like lions (Schaller, 1972; Rudnai, 1973; Bertram, 1975), the dockyard cats have a social unit which consists of a group of related females and their offspring (Dards, 1979). They differ from lions, however, in the relationship between the males and the female groups. Schaller (1972) considered his pride lions to be loosely linked to the pride lionesses, since they did not interact extensively with them, and could be replaced by new pride lions every few years. He therefore excluded them when considering group structure. Although some dockyard toms adopted a role which was equivalent to that of a pride lion, most were even more loosely attached to the females.

The relationship between females and mature toms is interesting. Although females' aggression towards toms is much more frequent than towards other females, most of this aggression is in the context of courtship, at food, or when a tom approaches the female's kittens. Within this, there is a range of variation in the degree of tolerance or amicable behaviour shown towards toms, which appears to depend on how familiar the tom is to the female. Some preferences between individuals may also be present. It is interesting that the females tend to initiate more, and more intense, amicable interactions than do toms, and the reason for this is not clear. The opposite was true of the farm cats studied by Laundré (1977), although this was

mainly due to 2 toms in his study, one of which appeared to be young.

It is puzzling that the reactions of females towards strange toms sometimes appeared to be fearful, since male aggression towards females was very rare, and only mild. It is possible that this behaviour is related to reports of infanticide by strange males, but in these cases female aggression rather than timidity has been observed (D.W. Macdonald, 1980, personal communication).

The relationships between mature toms are notable for their lack of amicable behaviour. This is perhaps surprising, in view of the cooperative pairs or groups of males which are found in lions. This cooperation among lions has been shown to be advantageous to them in maintaining control over a pride of females (Bertram, 1978). Its lack in the dockyard toms may be due to the absence of close association with one particular female group. Conversely, the toms' distribution over several groups may be due to their inability to maintain control over one group, because of the lack of cooperation between toms. This latter argument is supported by the behaviour of 275 towards Group W. This exceptionally large tom did maintain almost exclusive control over one group, and seldom visited other areas. However, there is also evidence that residence with only one group may not be favourable. The groups of cats in the dockyard tend to be smaller than lion prides, and therefore offer a resident tom only limited opportunities for mating. This must be balanced against the tendency of females to behave more amicably towards familiar toms. It seems likely that a female will be more likely to mate with a tom which is familiar to her than one which is not. This means that the toms' behaviour must strike a balance between visiting as many females as possible, and spending sufficient time with each female for her to accept him readily, to maximise his mating opportunities.

In addition to becoming familiar with females in other areas, the tom must also be able to cope with encounters with other males. Although no direct evidence of a dominance hierarchy among the males was found, since encounters between toms were observed infrequently, it is likely that such a hierarchy is present. This is supported by the lack of aggression between toms waiting by an oestrus female, when fighting would be expected unless a rank order had already been established. Such a rank order would probably be determined by fights when the cats first met. Evidence for this theory is provided by observations of aggression when young toms enter new areas, and the scratches which are often observed on the faces of these animals.

Once a hierarchy is established, aggression can be minimised by avoidance or submissive behaviour. In the dockyard cats, avoidance of other toms appears to be the method used. Leyhausen (1973) suggested that cats do not have a submissive display, although Fox (1975) interpreted the crouched posture as a passive submissive display. However, this was not observed in the dockyard without some elements of defensive threat. From this posture, the cat can roll on to its back and rake its adversary with its claws. The fact that the crouched posture does not always inhibit aggression is shown by the

attack on 41 by 84. Given the opportunity, toms usually avoid potentially aggressive cats, and the crouched posture is seen only when an aggressive tom approaches without warning. Avoidance of more aggressive toms (which are assumed to be higher in the hierarchy) is probably aided by scent marking. In view of the infrequency with which mature toms were observed in close proximity to each other despite their overlapping ranges, it is possible that the toms practice the "time-sharing" range-use suggested by Leyhausen (1965).

Observations of tolerance between toms (such as 275 and 279) are probably due to the cats possessing nearly equal strength and rank. It is also possible that males which are tolerant of each other are related. These animals would be more familiar to each other, and the genetic pressure for competition would also be less. This appears to be the case in the cooperative groups of lions, and may be another reason why this cooperation is absent in dockyard cats. Due to the usually smaller size of groups, and the higher mortality, it is relatively uncommon for adult immature toms of the same age to be found in one group. In cases where this did occur, the toms emigrated at different times, except in one case, where it appeared that 2 brothers left at the same time and moved into the same area.

The flexibility of mammalian social systems has recently come under consideration, and the social structure of the dockyard cats, with its parallels with that of lions, is especially revealing in view of the fact that this is an animal which has always been considered to be solitary. It is evident that the domestic cat is capable of a much more complex social structure than has previously been thought, and that this also extends to the adult males, which at first sight appear to be independent of it.

Although the behaviour of individual cats was not studied in great detail, the study of the large dockyard population, with its separate groups, provides an indication of the range of variation in behaviour. This information is not available from recent studies which involve only a few cats, and which may be strongly influenced by individual differences (Laundré, 1977; Macdonald and Apps, 1978).

The information on the behaviour of mature toms is of special interest in view of the current discussion on methods of controlling feral cat populations. The dockyard population was very stable, and there was some evidence of social factors among females influencing breeding success (Dards, 1979). Although the toms did not appear to play a part in population regulation in this stable situation, their role could be dramatically altered in a population subject to human control methods, such as culling or neutering. The variation in ranging-behaviour suggests that there would always be new toms available to move into an area where the original cats had been removed, and the observations of many toms in attendance on oestrus females suggests that neutering policies are unlikely to be successful unless attention is focussed on the females. More detailed studies of the social structure and behaviour of groups of cats are still required, to supplement the broader picture provided by the dockyard study, before we know sufficient about the

social behaviour of cats to enable us to manipulate their populations.

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