BEHAVIOUR OF A CAPTIVE PAIR OF CLOUDED LEOPARDS (*NEOFELIS NEBULOSA)*: INTRODUCTION WITHOUT INJURY

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Abstract *Animal Welfare 1998, 7:* 57-76

The behaviour of a captive pair of clouded leopards was studied during a series of manipulations in order to devise a safe method of introduction for mating purposes. Manipulations consisted of allowing each individual unrestricted access to the other's outdoor enclosure, initially in the absence of the other individual, but culminating in joint access. Dominant activities involved sitting, lying, grooming, and adopting a low profile amongst the vegetation. The female tended to be more arboreal than the male, although both cats spent most of their time on the ground. The male marked various sites by foot-scrubbing (1-4% occurrence), which involved shuffling urine into the ground using his hind feet. This was less common in the female (< 1%). Male foot-scrubbing was most frequent on introduction nights, and in the female's enclosure. Both sexes exhibited cheek-marking behaviour, although it was more common in the male. The frequency of male cheek-marking increased in response to urine production by the female. Observations during introductions suggested that the male may assess the female's reproductive condition by stimulating her to urinate. The most marked changes in the behaviour occurred between control and introduction nights. The larger male took the initiative, and the female appeared extremely wary of his presence, striking out with her claws if he approached too closely. Although the individuals did not mate during the introductions, the method of gradual acquaintance through an experimentally induced overlap of 'home ranges' was effective, as the female was not injured even though the male had a history of aggression.

Keywords: *animal welfare, captive breeding, carnivore breeding behaviour, cheek-marking, clouded leopards, endangered species, foot-scrubbing*

Introduction

The clouded leopard (*Neofelis nebulosa*) is a medium-size felid that is native to Southeast Asia (Kitchener 1991), and rare enough to be classified as an endangered species (Humphrey & Bain 1990). It has been kept in various British zoos since 1854, but it has not been possible to establish a self-sustaining captive population (Richardson personal communication 1995). The purpose of this study, was to characterize the behaviour of clouded leopards in captivity to learn more about a species which is rare and elusive in the wild, and to use this information to improve the breeding success of captive individuals.

Between 1934 and 1994 the number of clouded leopards resident in the United Kingdom at any one time has been variable, ranging between 1 and 25 individuals (Hughes & O'Grady 1991; Richardson & Christie personal communication 1992). The current (1996) population for the UK comprises 18 animals (10 male, 8 female), of which seven (4 male, 3 female) were imported. Nine of the UK animals are over 10 years old and although they can breed at least until 12 years of age, the peak period for reproduction occurs between two and four years (Yamada & Durrant 1989). The UK captive population is thought to be in decline (Olney & Ellis 1991,1992; Richardson & Christie 1993; Rietkerk 1996).

The predominant problem encountered with the successful propagation of clouded leopards in the captive environment has been the introduction of unfamiliar adults for breeding purposes. Introductions have led to instances of males killing or severely injuring females (Seager & Demorest 1978; Theobald 1978; Penny 1984; Richardson 1985; Yamada & Durrant 1989; Law 1991; Mellen 1991). In the UK alone in the past 20 years, males have killed their prospective mate at five zoological establishments (Richardson personal communication 1993). As a result, a number of male clouded leopards that have killed females have been discarded as potential breeders.

Initial courtship and post-coital periods for all wild cat species in captivity can be dangerous for both sexes, and males and females of unknown compatibility should be introduced carefully before being housed together (Ashton & Jones 1980). One method put forward to avoid hazardous adult introductions in clouded leopards, is to establish potential mating pairs while the individuals are still immature (Yamada & Durrant 1989; Mellen 1991). A problem arises with this approach if suitable partners are unavailable at the right time to establish immature pairs. One alternative has been the maintenance of brother/sister couples (Richardson personal communication 1995). Inbreeding of captive stock is inadvisable as it promotes homozygosity which leads to genetic problems that can manifest themselves in a range of abnormalities (Seager & Demorest 1978). Furthermore, cats kept together from a very young age often lose interest in mating (Ashton & Jones 1980), although brief separation and subsequent reintroduction can stimulate renewed interest in breeding (Freeman 1980; Theobald 1978). These methods appeared to be inadvisable as most of the clouded leopards in the studbook (Hughes & O'Grady 1991) are old and many have never bred. The primary aim of this work was to devise a safe method of introducing unfamiliar adults for breeding purposes, to ultimately maximize the genetic potential of the captive population, without compromising the available gene pool. This method would need to reduce the likelihood of the male attacking the female.

Husbandry methods

Two captive management techniques have traditionally been employed for cats: either the pair is kept together continuously in the same enclosure, or the male is introduced only when the female is in oestrus. In the first case, the male is usually removed when cubs are expected (Fellner 1965; Weston 1991) although male clouded leopards have been left in with their cubs, with successful results (Geidel & Gensch 1976). The alternative is to remove the male after mating has taken place or oestrus has ended. It is generally believed that this second method is a more natural procedure, as cats are for the most part solitary by nature (Kitchener 1991). Success of the latter approach depends critically upon the detection of the onset of oestrus by animal managers.

The clouded leopard in its natural habitat

In order to achieve a more successful strategy for performing introductions of the clouded leopard, we considered what is known about the lifestyle of this species in the wild. It is distributed throughout Southeast Asia (Denis 1964; Dinerstein & Metha 1989) where it inhabits primary rainforest (Santiapillai & Ashby 1988). The dense habitat and secretive nature of this animal have made it difficult to study in the wild, despite significant efforts (Rabinowitz 1988).

Sightings of individuals in the wild have been sporadic (Gibson-Hill 1950; Guggisberg 1975; Lekagul & McNeely 1988; Davies 1990; Choudhury 1993; Griffith 1993) and it is not possible to draw definite conclusions from these as to their pair-bonding or courtship behaviour, although the evidence available suggests that clouded leopards may spend most of their time alone, possibly meeting up only for copulation.

Two forms of preliminary communication are possible for species that live in dense vegetation, primarily scent-marking and vocalization. Both of these methods are known to occur in other cat species that live in thick jungle (Rabinowitz & Nottingham 1986; Rabinowitz 1989; Hoogesteijn & Mondolfi 1992; Bailey 1993) and were thus investigated in this pair, although vocalizations did not occur frequently enough during the observation period to permit useful analysis.

A major function of zoos keeping rare species is to create appropriately realistic environments, so that the behaviour witnessed may be documented and assist in the conservation of the species both in captivity and in the wild, as well as in maximizing their reproductive output (Olney *et al* 1994). The objective during this study, was to provide a situation in captivity that would simulate, as closely as possible, the clouded leopards' natural environment in order to allow for a full expression of normal behaviour.

The aims of this study were to: i) provide an insight into the manner in which the male and female behave in captivity; ii) provide information on pre-copulatory mating behaviour; and iii) formulate an effective and safe method for introducing adult clouded leopards for mating in captivity with minimal risk of physical damage to the female.

Methods

Subjects

Two clouded leopards were involved in this part of the study, a 15-year-old male called Xiang who had been in the Glasgow Zoo for four years and a 12-year-old female known as Fua who had been in the Zoo for 10 years. Both cats were reported to be wild born.

Previous work detailing the reproductive parameters of clouded leopards in captivity revealed that 75 per cent of all litters were born to females between one and five years of age, and 63 per cent of the males had sired litters by the time they were four (Yamada & Durrant 1989). Reproductive success declined for males after the age of six years, although clouded leopards have been known to breed up to the age of 12 (Yamada & Durrant 1989).

The male clouded leopard in this study, Xiang, was reported to have attacked a female while at a previous collection and he was also known to be unusually aggressive towards humans. The female, Fua, had never accepted a mate although she was known to cycle regularly and had been introduced to at least two males. She was extremely friendly to keeping staff and it seemed likely that she had been reared from an early age by humans. This may have had adverse effects on her tendency to mate as hand-reared domestic cats exhibit a low rate of copulatory behaviour, and the highest rates of aggression (Mellen 1988). If we could achieve success with the most difficult cases of Xiang and Fua, the method would be of significant use for most clouded leopards in captivity.

Enclosure design

Xiang and Fua were housed next to each other in individual enclosures that formed part of the main cat house complex and contained a series of heated indoor denning areas connected to unheated outdoor runs. Adjacent indoor and outdoor areas were interconnected by sliding doors, which were essential for the purposes of this study as it meant that the cats could be given free access to the other's enclosure when required.

The outdoor enclosures were 9.1m long x 4.3m wide x 3.4m high with a network of logs and branches forming aerial walkways (Figure 1). Some of the thinner branches were suspended from the weldmesh roof on wire hawsers to allow them to swing as the cat walked over them. Outdoor enclosures contained vegetation with a layer of woodbark to provide a soft, self-sterilizing substratum (Chamove *et al* 1982). Heavy, green plastic netting was used to cover the roof of the enclosure thereby diffusing and lowering light levels to mimic the cover and intimacy of a forest canopy.

Observations

Observations were made over the winter months of 1990-1993, between December and March, as this is known to be the peak time for the occurrence of oestrus in captive clouded leopards (Yamada & Durrant 1989). The cats' behaviour was studied at night as they were generally relaxed in their captive situation without daytime distractions (eg visitors). Clouded leopards are thought to be mainly nocturnal in their natural environment (Rabinowitz 1988) and tend to be inactive during the day. Diffused light for observations in the outdoor enclosures was provided by a small flood lamp on the roof and two small red lamps in the back corners of the enclosures to light shadowy areas.

An interest in the environment was stimulated by using scatter feed techniques (Shepherdson *et al* 1993). This, and other forms of environmental enrichment, reduce the occurrence of stereotypic behaviour (Carlstead *et al* 1993) and it is important in captivity to preserve normal behaviour patterns as far as possible (Miller *et al* 1990; Shepherdson 1994).

During the winter daylight hours the cats had access to both outside runs and their heated dens, but they tended to be inactive except when hunting the small scatter feeds. These feeds were omitted when experimental introductions were planned, as the cats may have fought over food remnants (cf Mellen 1991). The main feed of chicken, rabbit or beef with vitamin supplement was provided in the isolated internal den area 2-3h prior to the observation period.

The first priority of the investigation was to characterize the typical behaviour of the male and female in their normal environment when each individual had free range to its own indoor and outdoor enclosures. To investigate the changes in behaviour that occur as the home range of the two sexes overlap, we devised a scheme which allowed each individual sole access to the other's enclosure. This situation allowed the intruder to mark or explore the alien enclosure and was subsequently reciprocated.

Observations were undertaken from a portable hide located adjacent to the outdoor enclosures, using instantaneous point samples (Martin & Bateson 1992) taken at intervals of 5min. The relatively protracted delay between point samples allowed the observer (GL) to collect data simultaneously for both the male and female. Twelve types of activity were recognised together with the category 'out of sight' (Table 1). Records were written on checksheets at the prompt of a bleeping stopwatch. On a typical night the observations extended over a 3h period, yielding 36 instantaneous point samples of behaviour. The number of scans for each of the 12 behavioural activities was then expressed as a percentage of the total observations for the night in question,

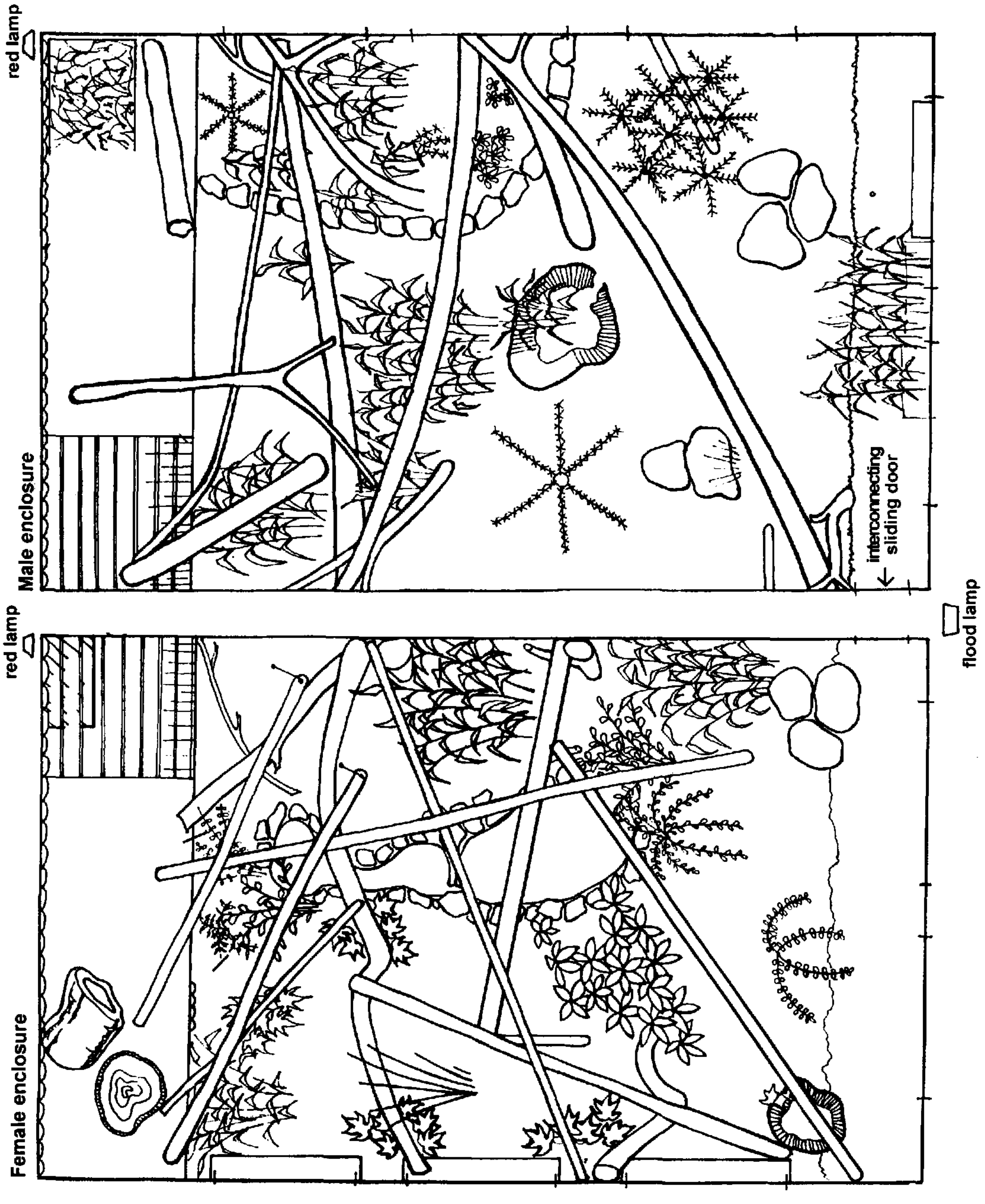

Figure 1 Plan view of the clouded leopard enclosures.

to facilitate comparability when the observation periods varied from the standard 3h. For example, one 15 December there were four records of branch walking by the male out of a total 36 observations, so the basic data for branch walking becomes 12 per cent (100 x 4/36) of the total activities.

Table 1 Description of the behaviour categories recognized for the clouded leopards in this study.

F/W - Floor walking	Moving over the ground or concrete ledge area, generally walking, but pacing and running was also included
L/A - Lying alert	Lying on the ground, or on a branch with eyes closed and with no noticeable body posture movements
A - Asleep	Lying on the ground, or on a branch with eyes closed and with no noticeable body posture movements
C/M - Cheek-marking	Actively rub cheek area on objects
S - Sitting	Sitting upright on the ground or on the concrete ledge at the back of the enclosure
B/S - Sitting on branch	Sitting on branch or suspended wooden shelf above the ground
U/S - Urine spray	Directed spray of urine, coinciding with a raised tail
F/M - Flehmen	Facial grimace, mouth agape, upper lip raised and mouth held slightly open for a few seconds
B/W - Branch walking	Moving across either the aerial walkway of branches or suspended wooden shelves
E - Eating	Chewing meat remains or plant material. Note that the main feeding period preceded the behavioural observations (see text)
F/S - Hind foot-scrubbing	Shuffling of hind feet back and forward over substratum after urinating (the latter not necessarily observed)
D - Defecate	Deposit faeces
O/S - Out of sight	Cat hidden from view. On most of these occasions the animal would have been stationary, but the actual behaviour could not be assumed without the introduction of bias

There were five treatments for each sex, the number of replicates varying from 9 to 45 (Tables 2 & 3). The results have been summarized by considering each separate activity (eg asleep) and calculating the average for each treatment (Table 2). Thus a result of 5.77 per cent sitting by the male on control nights (Table 2) indicates that on average, 6 per cent of the total male observations made on a control night (n = 45 control nights) involved sitting behaviour. This summarizes the total of 1620 observations (36x45) made on control nights.

Table 2 Summary of the behavioural activities of a male clouded leopard in captivity, given as the mean of the percentage of the total observations on a given night.

Behavioural activities	Control n = 45	Set-up n = 20	Response n = 9	Response & Set-up n = 12	Introduction n = 22
	Mean	Mean	Mean	Mean	Mean
Asleep	0.18	3.12	2.46	0	16.29
Laying alert	0.74	1.32	0	1.74	12.50
Groom	0.47	0.28	0.31	0	2.65
Sitting	5.77	2.56	4.63	4.63	17.61
Branch sitting	0.25	0	0	0.46	2.84
Branch walking	1.11	0.62	1.23	3.36	7.01
Floor walking	15.00	8.19	6.48	9.03	16.10
Eating	0.49	1.04	2.47	0.93	1.32
Urinating	0.40	0.42	0	0.23	0.19
Defecating	0.22	0.42	0.31	0	0.76
Cheek-marking	3.47	5.42	7.41	5.90	3.60
Flehmen	0.18	0.28	1.23	0.23	3.03
Foot-scrubbing	1.01	0.62	1.85	2.08	3.79
Out of sight	71.76	75.21	71.91	71.76	11.36

Table 3 Summary of the behavioural activities of a female clouded leopard in captivity, given as the mean of the percentage of the total observations on a given night.

Behavioural activities	Control n = 45	Set-up n = 10	Response n = 19	Response & Set-up n = 12	Introduction n = 22
	Mean	Mean	Mean	Mean	Mean
Asleep	1.67	3.89	1.83	4.17	3.41
Laying alert	2.22	1.94	6.36	2.77	3.60
Groom	2.16	2.43	0.58	3.93	0.76
Sitting	10.80	8.61	19.50	18.06	69.73
Branch sitting	7.99	10.28	8.29	7.18	14.58
Branch walking	4.26	8.33	3.36	4.28	1.51
Floor walking	27.27	28.89	23.92	16.20	5.30
Eating	0.59	2.50	0.95	0	0
Urinating	0.18	0.83	0.29	0.46	0
Defecating	0.25	0.28	0.36	0	0.36
Cheek-marking	1.29	2.50	2.78	1.16	0
Flehmen	0	0	0.29	0	0
Foot-scrubbing	0.12	0	0	0	0
Out of sight	40.98	29.72	31.78	41.43	0.57

Experimental manipulation of enclosure size

To simulate an overlap of the male and female home range, as might occur in the natural environment prior to courtship, the individuals were given access to the neighbouring enclosures, having first confined the neighbour in question to its inside denning area. The aim was to investigate changes in behaviour that arise as a result of access to a potential mate's home range, eg scent-marking behaviour, activity level. It was anticipated that this programme would provide a gradual escalation in the level of sexual interest, culminating in an introduction of the two animals when the female came into oestrus, to promote the chance of a successful mating episode. A control and three experimental treatments were devised to occupy four consecutive nights on a weekly basis over the winter months between December 1990 and March 1992.

On control nights the male and female had normal access to their own indoor and outdoor dens. These results provide a baseline behaviour, corresponding to activity in the male's and female's own home ranges. On set-up nights one cat had sole access to both its own and its neighbour's outside run, allowing it to scent-mark, defecate, urinate etc in either enclosure. The first control night in each set of four nights was followed by a set-up. Response & set-up nights occupied the third night during the week, and resembled response nights with respect to the fact that the second cat could respond to the scents and other cues provided by the first individual. However, as this cat had access to both enclosures as it responded, it was also setting-up the enclosures. The fourth night was a response night, with the first cat given access to its own enclosure to discover how it would respond to the presence of its neighbour on the previous night.

On control nights, data were collected directly after the cats had been released from their inside dens where they had been feeding. Following the observation period, the cats were left in their own enclosures with access to their inside dens until the next afternoon when they were once again fed in their indoor enclosures. Set-up and response & set-up nights followed the protocol outlined above for control nights, which meant that there was a period of up to 21h for the cat to 'set-up' the areas before the other individual was allowed access. After the last response night, the animals were given sole access to their own enclosures for at least a night and day before more control data were collected. The idealized sequence of experimental manipulations of enclosure size was occasionally frustrated for various practical reasons, but overall 22 female set-ups produced 21 male responses and 32 male set-ups produced 31 female responses.

Towards the end of winter 1991-1992, it was decided to allow the male access to both enclosures when the female was present. This course of action was taken even though the female had not displayed pronounced oestrus behaviour (but she had been restless and vocalizing). Observations on these nights followed standard protocol and this treatment is termed as an introduction night. On these nights, the sliding door between the outside enclosures was used (see Figure 1). Once an introduction night was planned, the female was let out first from her indoor den to settle after the interconnecting door had been opened. On release from his indoor den, the male invariably entered the female's enclosure and she always stayed in her own (n = 22/22). On introduction nights it was considered necessary to deny both cats access to their indoor dens, as any conflict in a confined area might have had fatal consequences. It was also considered important that the female's sense of security with her indoor area (as exclusively hers) must be maintained to allow her the confidence to rear cubs in the event of becoming pregnant.

To minimize the possibility of the male damaging the female, he was fed prior to the introduction to ensure that he was fully satiated and thus less likely to exhibit enthusiastic hunting behaviour. A further precaution involved the use of catnip (containing *trans*-nepetalactone), believed to minimize aggressive behaviour. The male clouded leopard reacted to the dried leaves of catnip by rolling, rubbing and generally displaying kitten-like behaviour in response to the scent. Prior to the first two introductions, catnip was added to both enclosures which may have had a calming effect on the male, although this is likely to have been transient, as it has been shown that the effects of catnip on domestic cats (*Felis catus*) are apparent for only about 10min (Morris 1986).

Data analysis

The scan sampling averages were compared for significant differences using the Mann-Whitney test (Zar 1996) based on the z distribution rather than 'U': (Statgraphics V6 Software, [Manugistics 1992]). Relationships between activities were examined by Pearson's correlation coefficient or simple linear regression (Zar 1996). Average body masses of the male and female were compared using the Student's t-test.

Results

A few behaviours were either practically impossible to identify, or rarely observed (eg lip-rubbing: female n = 3 and male, n = 2 scans, in 324h of observations). Sniffing provides an example of a behaviour which was difficult to identify, as it may occur without being apparent to the observer. Sniffing behaviour was recorded in seven scans for the female, although interestingly two of these sniffs were directed at the leaf of a plant the male had cheek-marked on the previous night. Male sniffing was observed slightly more often, on 17 occasions, but all outside formal observation periods. An escalated olfactory investigation was apparent as either lick-sniffing or flehmen for the male (eg flehmen n = 16, lick-sniffing n = 3).

On the control nights, the male was 'out of sight' an average of 72 per cent of the observations (Table 2), whereas the female was generally more active and hence more visible (out of sight = 41 per cent, Table 3, z = 5.27, $P < 0.01$). The tendency for the male to exhibit low-key, secretive behaviour (ie out of sight) was apparent throughout all the experimental situations (72-75% of the observations, Table 2) except for introduction nights, when he was 'out of sight' for only 11 per cent of the observations and significantly more visible than on the control nights (z = 6.20, $P < 0.01$).

The female appears to have been active during a higher percentage of the scans on set-up nights (30% out of sight) than on the control nights (41% out of sight) but this difference was not significant (z = 1.32, $P = 0.19$) even though she then had access to both outside runs, and her activities were slightly easier to observe. As with the male, the female was most visible on introduction nights (< 1% out of sight).

Sitting behaviour accounted for 6 per cent of the male and 11 per cent of the female observations on control nights (Tables 2 & 3), z = 3.29, $P < 0.01$). This frequency of sitting remained fairly constant over the different experimental situations, and the tendency for it to be more prevalent in the female was also maintained, although on introduction nights there was a significant rise above the control level for both the female (70%, z = 5.88, $P <$ 0.001) and the male (18%, z = 3.72, $P < 0.001$, Figures 2 & 3), as the female spent most of her time warily watching him. Sitting above the ground on branches occurred in less than 1 per cent of the male observations (excluding introduction nights), but accounted for between 7 and 15 per cent of the female's activities in the different experimental trials (Tables 2 & 3). This difference was significant for paired comparisons at the treatment level (z = 2.16, $P < 0.05$), suggesting that this female had a slightly greater tendency to be arboreal than the male.

The most frequent locomotory activity exhibited by the clouded leopards was 'floor walking' which, together with 'branch walking', reflected the extent to which the animals were moving about their enclosure. Floor walking occurred on every night for both sexes, ranging from 0 to 58 per cent of the total male observations on a given night and up to 73 per cent for the female. Although the percentage time spent floor walking appears to vary among experimental treatments, this was not significant, because of the extremely high nightly variability in this behaviour. For the male, the average frequency of floor walking ranged from 6 per cent on response nights through to 16 per cent on introduction nights (Table 2), while the female generally seemed to be more active, as her activity ranged between 16 and 29 per cent (Table 3). An exception occurred on introduction nights, when the female was significantly less mobile (5% floor walking) than on control nights (z = 5.17, $P < 0.001$). The male circled the female on these nights, while she tended to remain in one place until he came too close, and then she moved away.

Branch walking reflects the tendency for the animals to use the extensive aerial walkways of natural branches provided in the enclosures (Figure 1), accounting for about 1 per cent of the male's behaviour and 4 per cent of the female's on control nights. There was a significant increase in the frequency of branch walking by the female from control nights (4% total activities) to set-up nights (8% total activities, but up to a maximum of 19%; z = 2.02, $P < 0.05$), possibly reflecting a tendency for the female to explore more when given unchallenged access to the male's enclosure, although she showed only a marginal change in floor walking on these set-up nights.

Foot-scrubbing by the male on control nights accounted for about 1 per cent of his activities. This level rose significantly above the control level only on introduction nights (to 4%, z = 2.81, $P < 0.01$). On one of the introduction nights this behaviour accounted for 12 per cent of his total activities. Surprisingly however, foot-scrubbing occurred less often on set-up than control nights.

Both male and female clouded leopards engaged in cheek-marking behaviour, although the male did this significantly more frequently than the female across all treatments (Tables 2 & 3, z = 2.16, n = 5, $P < 0.05$). On control nights, 3 per cent of the male's activity involved cheek-marking and this rose to 7 per cent on response nights. By contrast, cheek-marking accounted for just over 1 per cent of the female's activity on control nights, rising to nearly 3 per cent on her response nights.

Urinating behaviour was identified in the absence of foot-scraping and categorized separately. Urine may contain hormonal breakdown products and, in the male, substances produced by the accessory reproductive glands (Wemmer & Scow 1977). It was therefore anticipated that urination behaviour and the response to it might have an important communication function between the sexes. Neither of the clouded leopards were observed to spray urine, although this is generally accepted as a widespread behaviour amongst the Felidae (Ewer 1973; Wemmer & Scow 1977; Mellen 1993). Wemmer and Scow (1977) cite evidence from Hemmer (1968) that male clouded leopards spray urine, but this has not been borne out by the individual in this study. All instances of urinating involved production of pool urine, but they were generally infrequent occurrences (< 1% Tables 2 & 3) for both sexes.

The female rarely exhibited the flehmen behaviour, this only being observed on her response nights and in few scans (< 1%, Table 3). By contrast, the male engaged in flehmen behaviour on a low proportion of the scans on control nights, but there was an increase through set-up and response nights to a peak of 3 per cent of the total scans on the introduction nights (no significant effects). Total flehmen responses by the male amounted to 180 scans, of which only 55 scans occurred in his enclosure and 125 scans in the female's area. The female produced a total of only 15 flehmen responses, but most of these were in her own area (ie only 3 in the male's enclosure).

Discussion

The out of sight category was a dominant feature of the study, which reflects the fact that the individual was concealed within the shadows of the planted areas, or resting in the inside den area. Both male and female had a tendency to select dark, shadowy areas to sit in, where they were often difficult, or impossible, to observe. The difficulty of viewing this species in a captive environment, explains the relative paucity of behavioural observations made in the field (Rabinowitz 1988).

It has been shown that cats in captivity tend to be inactive, spending large amounts of time out of sight or asleep (Hurni & Rossbach 1989; Shepherdson *et al* 1993), which probably accounts for much of our out of sight behaviour, as movement could easily be detected. Domestic cats can spend as much as 60 per cent of their time asleep (Hurni & Rossbach 1989) and lions (*Panthera leo*) are known to spend 20-21h a day indulging in inactive behaviours such as sleeping and sitting (Schaller 1973). Evidence suggests that various cat species reduce their home ranges in response to having a readily available food supply (Seidensticker *et al* 1973; Sunquist & Sunquist 1989) and for domestic cats, time that would have been spent hunting is replaced by sleep (Tabor 1983).

In the natural situation, most large cat species feed and rest after making a kill, during which time they slowly digest the food on which they have gorged themselves (Morris 1990). In captivity, if cats are well fed and housed, they seem content to sit and survey their surroundings, much as they do in the wild landscapes (Morris 1990). In consequence, the pronounced presence of low activity behaviours, such as out of sight, should be expected in a study of this kind. The percentage of scans recording sleeping and lying alert in all of the experimental trials was generally quite low for both the male and female (Tables 2 & 3), although it is possible that much of the out of sight category can be accounted for by this type of activity. Sleeping or lying alert each accounted for between 0.2 and 2 per cent of the activities on control nights. The only significant deviation from this level was found in the male on introduction nights (Figure 3), which is quite surprising as it suggests a lack of interest in the female. It is possible that the male's adopting a relaxed sleeping position may serve to calm the female, as this is likely to reflect non-aggressive intentions.

Throughout the trials both individuals preferred to sit on the ground, rather than on branches (Tables 2 & 3). Although branch sitting increased markedly during the introduction trials, there was also a concomitant increase in ground sitting at this time (Figures 2 & 3). On introduction nights, 15 per cent of the female's behaviour involved branch sitting (Figure 3), but this was not significantly more than in the other experimental trials, despite the fact that on some of these nights, she spent the whole period sitting on branches - presumably in order to avoid the male. The higher per cent time recorded for the male branch sitting on introduction nights (Figure 2) was due to him sitting near the female. The fact that the female performed very few behaviours other than sitting (Figure 3), on introduction nights suggests that she was under stress, as stressful conditions are known to suppress normal behaviour patterns in domestic cats (Konrad and Bagshaw 1970; Bradshaw 1992; McCune 1994).

It is surprising that the animals were not more active than normal when they had the opportunity to either explore their neighbour's enclosure (set-up nights) or to react to the recent presence of a conspecific, as neither sex significantly increased the percentage of time spent floor walking compared to control nights. There was, however, some suggestion that the female increased her percentage of time spent floor walking in response to more time spent floor walking by the male on his set-up and response and set-up nights (Figure 4, Pearson's $r = 0.39$, $P < 0.05$, n = 30).

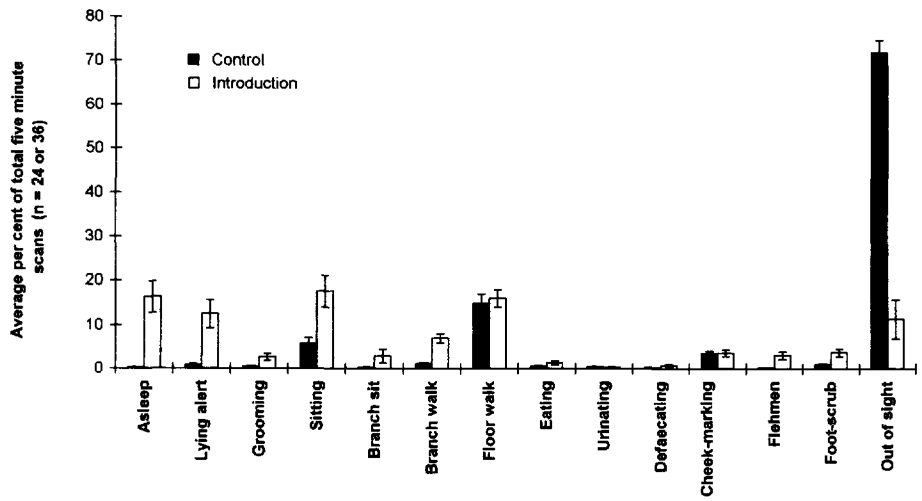

Figure 2 **Male clouded leopard activities on control and introduction nights. Behavioural scans are averaged over the number of observation periods in each treatment. Standard error bars are shown. The behavioural categories are given in Table 1.**

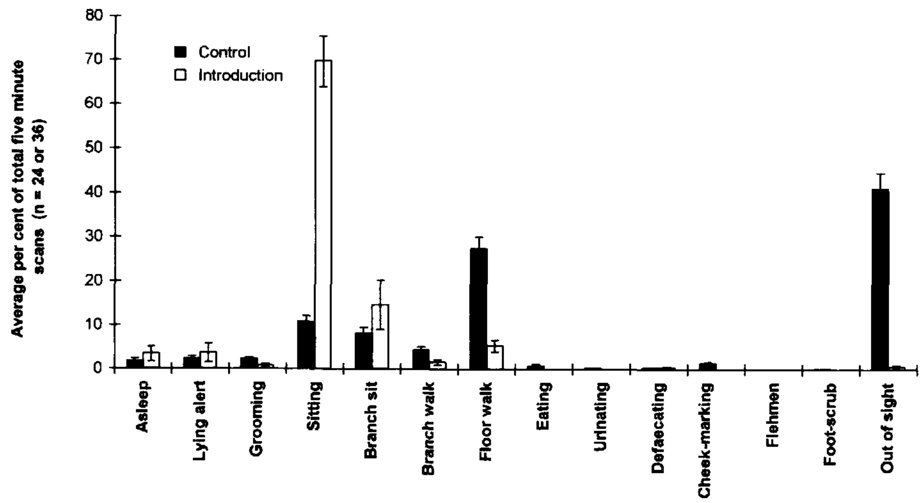

Figure 3 **Female clouded leopard activities on control and introduction nights. Behavioural scans are averaged over the number of observation periods in each treatment. Standard error bars are shown. The behavioural categories are given in Table 1.**

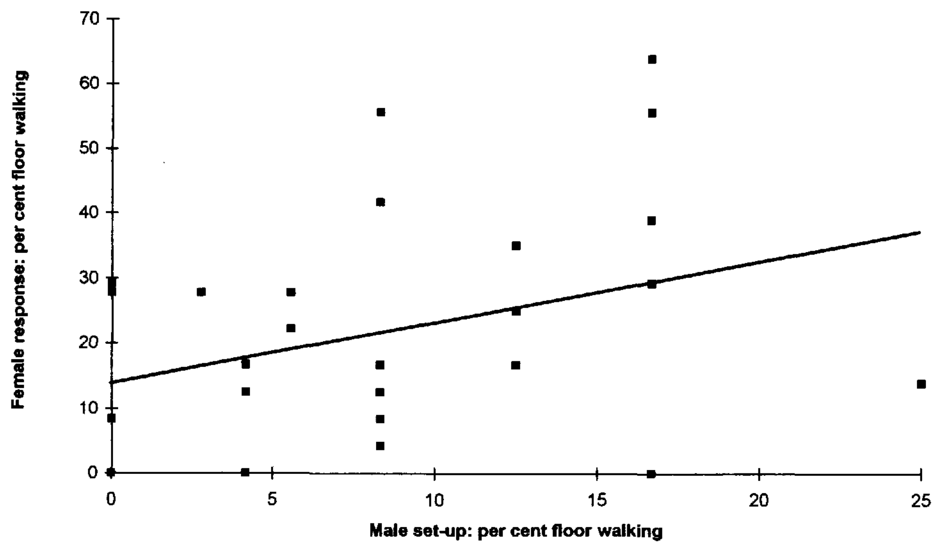

Figure 4 **Female floor walking relationship to male's activity during set-up treatments. Regression line: r^2 = 0.16, df = 30, $P < 0.05$.**

Both the male and female showed significant differences in branch walking behaviour on introduction nights in comparison with the control nights (Figures 2 & 3). The male increased his time spent branch walking (from 1 to 7%, $z = 2.33$, $P < 0.001$), such that it reached a maximum of 17 per cent of the total activities on one of the introduction nights. In contrast to this, branch walking by the female decreased by half on introduction nights (from 4 to 2%, $z = 2.32$, $P < 0.05$), which may have reflected her tendency to remain still in a safe position and watch the male, hence the concomitant increase in her branch sitting on introduction nights (Table 3). This feature of the female's behaviour on introduction nights is believed to be important in minimizing the possibility of her injury. Captive female clouded leopards are approximately 34 per cent lighter than the males (female mean weight = 13.71kg, n = 4; cf male mean weight = 20.93kg, n = 9; $t = 3.10$, $P < 0.01$) which probably makes them more agile compared to the males and is likely to provide them with a greater sense of security when moving in the branches. To assist this possibility, thin branches suspended on hawsers were provided on which the female could move with relative ease, but which severely challenged the male's sense of equilibrium.

Eating was recorded as a small proportion of activity for both males and females (Tables 2 & 3).There were 61 instances where the male was seen to chew bamboo (*Sinarundinaria nitida)*, but the function of this plant eating remains rather obscure.

Foot-scrubbing is a form of marking behaviour (Kitchener 1991; Bailey 1993), that often involves dribbling urine onto the substratum and then scrubbing with a shuffling motion of the hind feet, leaving an obvious scrape in the ground. It appears that foot-scrubbing is predominantly a male behaviour as far as the clouded leopards in this study are concerned (female < 1%, male 1–4%, Tables 2 & 3). It had been thought from field studies that clouded leopards did not leave scrapes or obvious faecal deposits along roads or trails (Davies & Payne 1982; Rabinowitz *et al* 1987), but this work suggests that marking in the form of scrapes does take place, at least in captivity. It is possible that the male's foot-scrubbing behaviour on introduction nights can be explained by his desire to mark the female's range as an indication of his presence/dominance to potential rivals. The presence of the female may be a direct stimulant in this respect. Thus, of the 55 recorded scans of foot-scrubbing by the male on introduction nights, 47 took place in the female's enclosure and always at the same two locations, either the wooden pallet on the back ledge of the enclosure (n = 37) or directly on the back ledge (n = 10) where the female tended to spend most of her time.

Cheek-marking involves the cat rubbing its face against objects and is thought to be a form of scent-marking behaviour (Rieger 1979; Feldman 1994) though surprisingly little research has been done on this topic. In general, both male and female members of the cat family cheek-mark to the same extent (Mellen 1993). When clouded leopards cheek-mark they are unique among members of the cat family as they hold their mouths wide agape. This gaping causes the masseter muscle to form a hard mass which is scrubbed along the surfaces to be marked. Cats are known to possess a number of skin (eccrine) glands which are thought to have a communicatory function. Cheeks and ears may produce odorous secretions, and the mutual flank-rubbing display performed by domestic cats suggests that this area may be equipped with scent-producing structures (Bradshaw 1992). Both sexes showed a similar pattern of changes in cheek-marking behaviour across the experimental trials: it increased from the control level to the set-up level and reached a maximum on response nights (response & set-up nights were intermediate) and declined again to approximately control levels on introduction nights (Figure 5).

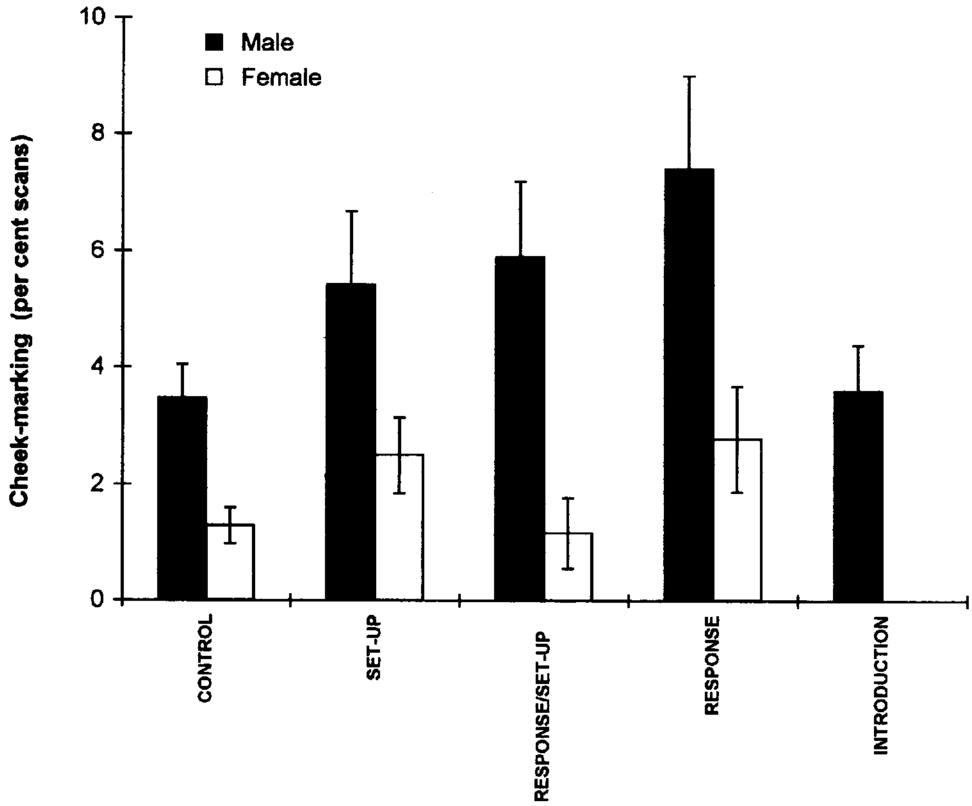

Figure 5 **Cheek-marking frequencies of male and female clouded leopards based on data from Tables 2 and 3. Standard error bars are shown.**

There was a significant positive relationship between the percentage time spent by the female urinating on set-up nights and the subsequent per cent of total scans by the male cheek-marking on the response nights (Figure 6, slope = 1.41, df = 20, $P < 0.05$, $r^2 = 0.21$). However, the male displayed cheek-marking on a significant number of scans, irrespective of this likely female stimulus (ie Figure 6: intercept = 5.6% of the total activities, t = 5.6, $P < 0.001$).

On introduction nights, the male was observed to approach the female, moving close enough to apparently stimulate her to urinate. Having achieved this, he then immediately ceased his pursuit, in favour of investigating her urine. The male was observed to sniff (n = 5) and sometimes 'lick-sniff' (n = 3) the urine-splashed area, his mouth partly open, head down, the tongue flicking in and out. A full flehmen response sometimes took place during these sequences (lick-sniff, n = 2, and sniffing, n = 3). After investigation, the male abruptly ended his 'interest' in the female and return to his own enclosure suggesting that some useful information had been obtained from the urine.

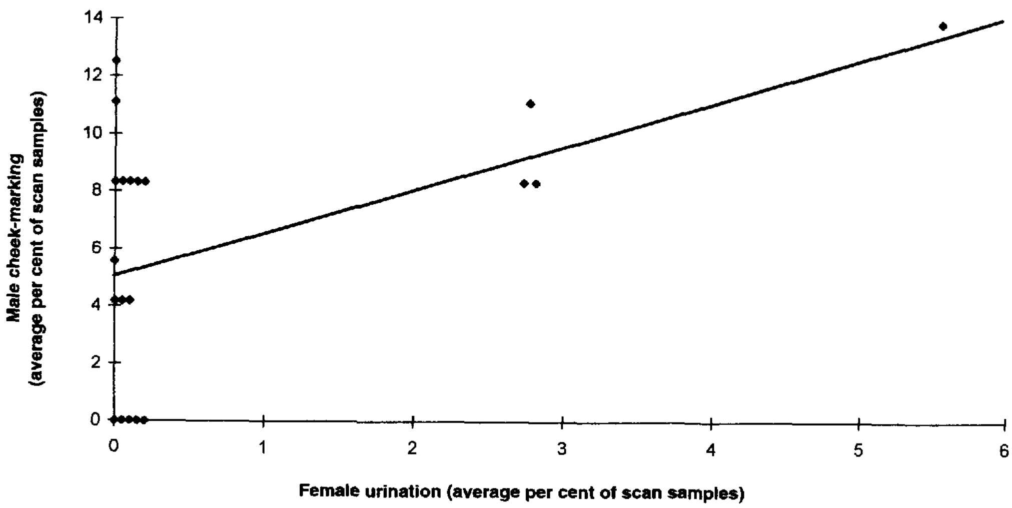

Figure 6 **Relationship between male clouded leopard cheek-marking and female urination. Regression line: $r^2 = 0.21$, df = 20, $P < 0.05$.**

Conclusions

The introduction of the clouded leopards at night, after the zoo had closed, took into account the sensitive nature of these nocturnal predators and encouraged an uninhibited display of their behaviour. During the 'active' nocturnal period, the normal (ie control) male and female behaviour in captivity was characterized by its secretive nature. It was considered important to provide the animals with a complex environment that provided places for them to hide.

Behavioural differences between the male and female in this study were not marked, although there was some suggestion that the female was slightly more active in moving around her enclosure. Both animals made use of an aerial array of branches, but showed a preference for walking on the ground. Contrary to expectation, urine-marking did not appear to be particularly significant before, or during, the predicted oestrous period. Both sexes cheek-marked at a fairly low intensity on a variety of materials, mostly wood, which should be available in the exhibit, while the female rarely foot-scrubbed or displayed the flehmen response. Dominant activities involved sitting, lying, grooming and adopting a low profile out of sight among the vegetation (Figures 2 & 3).

Changes in behaviour were apparent when the normally isolated male and female were allowed to come into contact (ie introduction nights). This took place after a series of trials during which each individual was given sole access to the other's outdoor enclosure. All interactions took place in the female's enclosure, as the male would move through immediately when given the opportunity. During the introduction phase, the male made all the approaches, while the female attempted avoidance, and would claw the male if he came too close. The inclusion of safe areas for the female to rest on and defend herself against the advances of the male were considered an important factor on introduction nights. At this time the male was not more active, but he was much more conspicuous. When introduced to the female, the total number of scans over which he was cheek-marking and foot-scrubbing increased, suggesting that these may be indirect initial methods of establishing communication links between the pair, although the female response to these was not apparent. When the two animals were in the same enclosure, the female was more visible, but less active than normal as she generally selected locations where she presumably could view the male and defend her position, rather than seeking seclusion. After introduction, the male initially approached the female, but when faced with continued repulsion he appeared content to sit and watch her, even to the extent of apparently sleeping.

Animal welfare implications

Although the behavioural characteristics recorded here may reflect the idiosyncrasies of these individuals, the methods outlined for the safe introduction of clouded leopards provide a useful strategy that should be considered when planning to introduce an unfamiliar pair for the first time. Application of this technique to other clouded leopards should yield behavioural data regarding the mechanisms which promote the development of courtship activity between initially incompatible predatory individuals. It has been shown here that the male takes the initiative in seeking out the female, and probably uses olfactory cues via the flehmen response to assess her state in the oestrous period. Relevant male behaviours included cheek-marking and foot-scrubbing, especially in the female enclosure, but her response to these was seldom overt. However, these interactions may be important in explaining the low level of aggression during the introduction periods.

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References

Ashton D G and Jones D M 1980 Veterinary aspects of the management of non-domestic cats. In: Barzdo J (ed) Management of Wild Cats in Captivity. *Proceedings of Symposium 4 of the Association of British Wild Animal Keepers* pp 12-22. Association of British Wild Animal Keepers: Bristol, UK

Bailey T N 1993 *The African Leopard, Ecology and Behaviour of a Solitary Felid.* Columbia University Press: New York, USA

Bradshaw J W S 1992 *The Behaviour of the Domestic Cat.* CAB International Publications: Wallingford, UK

Carlstead K, Brown J L and Seidensticker J 1993 Behavioural and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*). *Zoo Biology 12:* 321-331

Chamove A S, Anderson J R, Morgan-Jones S C and Jones S P 1982 Deep woodchip litter: hygiene, feeding and behavioural enhancement in eight primate species. *International Journal for the Study of Animal Problems 3:* 308-318

Choudhury A 1993 The clouded leopard in Assam. *Oryx 27:* 51-53

Davies A G and Payne J B 1982 *A Faunal Survey of Sabah.* World Wildlife Fund: Kuala Lumpur, Malaysia

Davies R G 1990 Sighting of a clouded leopard (*Neofelis nebulosa*) in a troop of pigtail macaques (*Macaca nemestrina*) in Khao Yai National park, Thailand. *Natural History Bulletin of the Siam Society 28:* 95-96

Denis A 1964 *Cats of the World.* Constable & Co Ltd: London, UK

Dinerstein E and Metha J N 1989 The Clouded leopard in Nepal. *Oryx 23:* 199-201

Ewer R F 1973 *The Carnivores.* Cornell University Press: New York, USA

Feldman H N 1994 Methods of scent marking in domestic cat. *Canadian Journal of Zoology 27:* 1093-1099

Fellner K 1965 Natural rearing of Clouded leopards (*Neofelis nebulosa*) at Dallas Zoo. *International Zoo Yearbook 5:* 111-113

Freeman H 1980 Snow leopard: a cooperative study between zoos. In: Blomqvist L (ed) *International Pedigree of Snow Leopards* (*Panthera uncia*) Volume 2 pp 127-136. Helsinki Zoo: Helsinki, Finland

Geidel B and Gensch W 1976 The rearing of Clouded leopards (*Neofelis nebulosa*) in the presence of the male. *International Zoo Yearbook 16:* 124-126

Gibson-Hill C A 1950 Notes on the Clouded leopard (*Neofelis nebulosa*). *Journal of the Bombay Natural History Society 49:* 543-546

Griffith M 1993 Ranging patterns and density of Sumatran tigers in Gunung Leuser National Park. In: Christie S (ed) *European Studbook for the Sumatran Tiger* (*Panthera tigris sumatrae) No 2* pp 14-27. Zoological Society of London: London, UK

Guggisberg C A W 1975 *Wild Cats of the World.* David & Charles: Newton Abbott, UK

Hemmer H 1968 Untersuchungen zur Stammesgeschichte der Pantherkatzen (Pantherinae). Teil 11 Studien zur Ethologie des Nebelparders *Neofelis nebulosa* (Griffith 1821) und des Irbis *Unica unica* (Schreber 1775). *Veroffentlichungen der Zoologischen Staatssammlang Munchen 12:* 155-242

Hoogesteijn R and Mondolfi E 1992 *The Jaguar.* Armitano: Caracas, Venezuela

Hughes D G and O'Grady R J P 1991 Clouded leopards. *UK Regional Studbook.* The Zoological Society of Glasgow & West of Scotland: Glasgow Zoo, Scotland, UK

Humphrey S R and Bain J R 1990 Endangered animals of Thailand. In: Arnett R H and Thomas M C (eds): *Flora and Fauna Handbook No 6* pp 349-352. Sandhill Crane Press Inc: Florida, USA

Hurni H and Rossbach W 1989 The laboratory cat. In: Poole T (ed) *Universities Federation for Animal Welfare (UFAW) Handbook on the Care & Management of Laboratory Animals, 6th edition* pp 476-492. Longman: London, UK

Kitchener A 1991 *The Natural History of the Wild Cats.* Christopher Helm: London, UK

Konrad K W and Bagshaw M 1970 Effects of novel stimuli on cats reared in a restricted environment. *Journal of Comparative and Physiological Psychology 70:* 157-164

Law G 1991 Clouded leopards. In: Partridge J (ed) *Management Guidelines for Exotic Cats* pp 77-81. Association of British Wild Animal Keepers: Bristol, UK

Lekagul B and McNeely J A 1988 *Mammals of Thailand,* pp 623-625. Saha Karn Bhaet Co: Bangkok, Thailand

Manugistics 1992. Statgraphics Version 6. Bitstream Inc: Cambridge, USA

Martin P and Bateson P 1992 *Measuring Behaviour: An Introductory Guide.* Cambridge Press: Cambridge, UK

McCune S 1994 Caged cats: avoiding problems and providing solutions. *Newsletter of the Companion Animal Behaviour Study Group 7:* 33-40

Mellen J D 1988 The effects of hand-raising on sexual behaviour of captive small Felids using domestic cats as a model. *American Association of Zoo Parks and Aquariums (AAZPA) Annual Proceedings* pp 253-259. Washington Park Zoo: Portland, USA

Mellen J D 1991 Little-known cats. In: Seidensticker J and Lumpkin S (eds) *Great Cats: Majestic Creatures of the Wild* pp 170-179. Merehurst Ltd: London, UK

Mellen J D 1993 A comparative analysis of scent-marking, social and reproductive behavior in 20 species of small cats *(Felis). American Zoology 33:* 151-166

Miller B, Biggins D, Wemmer C, Powell R and Thorne E T 1990 Development of survival skills in captive-raised Siberian polecats. *(Mustela eversmanni)* II: predator avoidance. *Journal of Ethology 8:* 95-104

Morris D 1986 *Catwatching, The Essential Guide to Cat Behaviour* pp 92-93. Jonathan Cape: London, UK

Morris D 1990 *Animal Watching, A Field Guide to Animal Behaviour.* Jonathan Cape: London, UK

Olney P J S and Ellis P (eds) 1991 *International Zoo Yearbook 31.* Zoological Society of London: London, UK

Olney P J S and Ellis P (eds) 1992 *International Zoo Yearbook 32.* Zoological Society of London: London, UK

Olney P J S, Mace G M and Feistner A T C 1994 *Creative Conservation, Interactive Management of Wild and Captive Animals.* Chapman & Hall: London, UK

Penny C 1984 *Rimau-dahan,* Tree tiger, Clouded leopard. *Zoonooz 57:* 11-13

Rabinowitz A 1988 The Clouded leopard in Taiwan. *Oryx 22:* 46-47

Rabinowitz A 1989 The density and behavior of large cats in a dry tropical forest mosaic in Huai Kha Khaeng wildlife sanctuary, Thailand. *Natural History Bulletin of the Siam Society 37:* 235-251

Rabinowitz A R and Nottingham B G 1986 Ecology and behaviour of the jaguar *(Panthera onca)* in Belize, Central America. *Journal of Zoology 210:* 145-159

Rabinowitz A, Andau P and Chai P P K 1987 The Clouded leopard in Borneo. *Oryx 21:* 107-111

Richardson D 1985 A Management Protocol for Breeding Clouded Leopards. Unpublished report 7pp. London Zoo: London, UK

Richardson D and Christie S 1993 *A Proposal for Electro-ejaculation, Semen Storage and Artificial Insemination for the UK Population of the Clouded Leopard.* Draft report 10pp. The Zoological Society of London: London, UK

Rieger I 1979 Scent rubbing in carnivores. *Carnivore 2:* 17-25

Rietkerk F 1996 A review of the 1994 European Endangered Species Breeding Programme Annual Reports. *International Zoo News 43:* 86

Santiapillai C and Ashby K R 1988 The Clouded leopard in Sumatra. *Oryx 22:* 44-45

Schaller G B 1973 *Serengeti a Kingdom of Predators.* Collins: London, UK

Seager S W J and Demorest C N 1978 Reproduction of captive wild carnivores. In: Fowler M E (ed) *Zoo and Wild Animal Medicine* pp 667-706. Morris Animal Foundation: Philadelphia, USA

Seidensticker J, Hornocker M G, Wiles W V and Messick J P 1973 Mountain lion social organization in the Idaho Primitive Area. *Wildlife Monographs 35:* 1-60

Shepherson D J, Carlstead K, Mellen J D and Seidensticker J 1993 The influence of food presentation on the behaviour of small cats in confined environments. *Zoo Biology 12:* 203-216

Shepherdson D 1994 The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In: Mace G, Olney P J and Feistner A (eds) *Creative Conservation: Interactive Management of Wild and Captive Animals* pp 167-175. Chapman & Hall: London, UK

Sunquist M E and Sunquist F C 1989 Ecological constraints on predation by large felids. In: Gittleman J L (ed) *Carnivore Behaviour, Ecology and Evolution* pp 283-301. Chapman & Hall: London, UK

Tabor R 1983 *The Wild Life of the Domestic Cat.* Arrow Books: London, UK

Theobald J 1978 Carnivores (Carnivora) Felidae. In: Fowler M E (ed) *Zoo and Wild Animal Medicine* pp 650-667. Morris Animal Foundation: Philadelphia, USA

Wemmer C and Scow K 1977 Communication in the felidae with emphasis on scent marking and contact patterns. In: Sebeok T A (ed) *How Animals Communicate* pp 749-766. Indiana University Press: Bloomington, USA

Weston M 1991 Some husbandry notes for Sumatran tigers and Persian leopards. In: Partridge J (ed) *Management Guidelines for Exotic Cats* pp 72-76. Association of British Wild Animal Keepers: Bristol, UK

Yamada J K and Durrant B S 1989 Reproductive parameters of Clouded leopards (*Neofelis nebulosa*). *Zoo Biology 8:* 223-231

Zar J H 1996 *Biostatistical analysis, 3rd edition.* Prentice Hall; Upper Saddle River, New Jersey, USA