Applied Animal Behaviour Science 68 (2000) 131–140
www.elsevier.com/locate/applanim
APPLIED ANIMAL BEHAVIOUR SCIENCE

The organization and control of grooming in cats

Robert A. Eckstein, Benjamin L. Hart *

Department of Anatomy, Physiology and Cell Biology School of Veterinary Medicine, University of California, Davis, CA 95616, USA

Accepted 5 January 2000

Abstract

Grooming in small felids has received little attention compared with grooming in rodents, bovids and primates where grooming is also common. This study set out to describe the general pattern, time budget and degree of cephalocaudal sequencing of self-oral grooming in the domestic cat. In 11 cats confined for the purposes of videotaping, sleeping and resting accounted for 50% of the time budget. Oral grooming, 91% of which was to multiple body regions, accounted for 4% of the overall time budget or 8% of non-sleeping/resting time. Scratch grooming, always directed to single regions, occupied about 1/50 of the time of oral grooming. There was a moderate and significant cephalocaudal trend to grooming. An increased likelihood for oral grooming to follow periods of sleep or rest was indicated by a significant negative correlation between sleep/rest duration and latency to the subsequent grooming bout. The effect of enforced deprivation of grooming on the subsequent occurrence of grooming was explored by the 3-day application of Elizabethian collars, which prevented oral grooming or control collars that did not prevent grooming. In the 12 h immediately after removal of the Elizabethian collars, oral grooming increased by 67% and scratch grooming by 200% compared with the grooming rate after removal of control collars. By the second 12 h, the apparent catch-up effect of grooming had disappeared. The occurrence of cephalocaudally-directed, multiple-region oral grooming and deprivation-enhanced grooming would appear to represent aspects of a central control mechanism for the organization and regulation of grooming.

Keywords: Grooming behaviour; Fleas; Cats

* Corresponding author.
E-mail address: blhart@ucdavis.edu (B.L. Hart).

PII: S0168-1591(00)00094-0

1. Introduction

Grooming is a frequently occurring and commonly studied behavior of rodents, bovids and non-human primates. Another taxonomic group known for frequent grooming is small felids, including domestic cats. However, little descriptive information is available about the time budget, pattern and determinants of grooming in cats. Among the non-primate species, two distinct patterns of oral grooming have been recognized. One pattern, characteristic of bovids, involves delivering a bout of grooming episodes with the tongue or lower incisors to just one area of the body. The grooming bout is followed by non-grooming behavior before another bout is delivered to a different region. The second pattern involves delivering a bout of grooming episodes to multiple areas and is exemplified in rodents and small felids. Both rodents and cats engage in paw licking and face washing as well as licking the pelage. Cats typically draw the cornified papillae of the tongue over the surface of the pelage repeatedly in bouts of licking episodes. In rodents, grooming follows a cephalocaudal pattern in which the bout of grooming progresses more or less in a caudal direction to one or more additional regions (Richmond and Sachs, 1980). The degree to which cats also exhibit a cephalocaudal trend in delivery of grooming episodes is not known and was one of the questions explored in the present study.

One of the important functions of grooming is the removal of ectoparasites (Hart 1990, 1997). We have shown elsewhere that temporary prevention of grooming in cats living in a flea-infested environment can allow adult flea numbers to increase to at least twice the level of that of cats in which grooming is freely allowed (Eckstein and Hart, 2000). Other functions as well have been attributed to grooming, namely removal of dirt and stale oil, maintaining insulating capacity of the pelage and temperature control.

A particular interest of the current study was exploring evidence for the type of physiological control of grooming with reference to two models. One is the reactive or stimulus-driven model in which grooming occurs in response to cutaneous or peripheral irritation such as from an ectoparasite bite. The second model is programmed grooming in which most bouts of grooming are periodically activated by a central generator independent of peripheral stimulation (Hart et al., 1992). It is possible to distinguish between these two models because they lead to different predictions. The occurrence of vigorous grooming of rats in ectoparasite-free environments has led authorities on rodent behavior to conclude that internal factors are more important than peripheral factors in controlling grooming (Barnett, 1963; Ewer, 1967). Extensive studies on antelope grooming, including body size comparisons, the effect of gender status, habitat constraints and levels of ectoparasite exposure, are all consistent with the programmed grooming model as opposed to the stimulus-driven model (reviewed in Hart, 1997).

The predominant form of grooming in cats, characterized by stroking the tongue through the pelage over multiple regions in one bout is not the type of grooming that would be expected to occur in response to cutaneous itch at a point source. Our previous study on the effects of grooming in control of fleas was consistent with programmed grooming in the sense that the presence of fleas increased grooming but the grooming was still primarily directed to multiple regions rather than single regions as one would predict for stimulus-driven grooming (Eckstein and Hart, 2000). Programmed grooming would be adaptive by inducing periodic grooming bouts for care of the pelage, as well as for removal of ectoparasites before they bite and consume blood or inject pathogens.

In the present study, we explore predictions from the programmed grooming model within the context of examining the time budget for grooming in cats. The occurrence of a cephalocaudal trend within multiple-region grooming bouts would suggest that grooming is governed by a central mechanism as opposed to random delivery of grooming episodes, guided by cutaneous stimuli. The programmed grooming model would also predict that when a cat engages in sleep or rest where no grooming occurs, the period following sleep should include temporarily increased grooming. Such ‘‘catch-up grooming’’ would also be expected to follow a period in which grooming was physically prevented. A similar catch-up effect in endogenously regulated behavior following enforced deprivation has been reported for REM sleep (Lucas, 1975) and dustbathing in birds (Borchelt et al., 1973; Vestergaard 1982). Because grooming is important in ectoparasite control, deprivation-induced grooming enhancement could be adaptive in nature. Cessation of grooming from injury or illness would likely be followed by a build up of ectoparasite numbers and temporarily increased grooming would reduce ectoparasites. In Experiment 2, we examined the effects of grooming deprivation on subsequent grooming rates compared with non-deprived grooming rates. This experiment was conducted in an ectoparasite-free environment to avoid the complication of ectoparasites.

2. Experiment 1: time budget and organization of grooming

2.1. Methods

2.1.1. Subjects and design

Eleven domestic cats (*Felis domestica*; five spayed females, six neutered males, age range: 1–6 years) from an ectoparasite-free breeding colony at the University of California, Davis served as subjects. The cats were maintained indoors in one four-cat group and one eight-cat group. Because videotaping was used to record behaviour for detailed analysis, it was necessary for each cat to be placed alone in an observation cage ($61 \times 96 \times 127$ cm high) equipped with a shelf, food, water and litter. The subjects were in visual, auditory, and olfactory contact with the other cats of the colony. The subject's behaviour was recorded on a time-lapse videotaping system, between 0600 and 1800 h on 2 consecutive days following an initial 12-h habituation period. The colony room was on a 12-h light–dark cycle with lights on at 0600. The subjects were all healthy and showed no signs of ectoparasitism. The videotape of one of the 12 cats available proved unsatisfactory, limiting the number of subjects to 11.

2.1.2. Analysis of videotapes

Scoring of behaviour was based on an ethogram of mutually exclusive behavioural categories appropriate to a solitary-caged cat (Table 1). The duration of time spent in each behavioural category was recorded in sequence. The category of ‘‘sleep/rest’’ included what appeared to be unconscious sleep as well as conscious, but quiet rest in

Table 1
Ethogram of mutually exclusive behavioural categories

Category	Description
General activity	Sitting (usually attending to environmental stimuli) or mobile (exploring, playing), while not engaged in another specific behaviour
Sleep/rest	In recumbence with minimal head and limb movements. Movement to re-position was included as continuous rest
Oral groom	Stroking the tongue through the skin or hair, or applying saliva to the head with the front limbs after licking them (face washing)
Scratch groom	Scratching the body with the hind claws
Eat	Eating from the food bowl and subsequent chewing
Drink	Drinking from the water bowl
Eliminate	Urination and defection, including subsequent raking of the litter box

sternal recumbency. Because it was not always possible to distinguish between sleep and rest, these two behavioural states were treated as one category. In either case, the animal was in a posture in which very limited grooming, if any, was possible. The category of ‘‘general activity’’ included moving about the cage and sitting where grooming could easily occur.

Grooming was noted as either oral or scratch grooming, and the anatomical area(s) groomed were recorded. Each oral grooming bout was categorized as being directed to multiple regions or a single region. A grooming bout was considered terminated when a non-grooming activity occurred (e.g., eating, eliminating, rest), or if more than 60 s elapsed without a licking episode. Cats were seen sometimes to deliver several licks, pause for a few seconds without engaging in any other identifiable behaviour, and then continue licking; this was not considered a new grooming bout. However, in order to improve recording accuracy of cumulative grooming time within prolonged grooming bouts, separate start and stop times were entered if more than 5 s of non-grooming followed a grooming episode within a grooming bout. These separate entries were then summated to derive the duration of the bout. For oral grooming, no distinction was made between incisor nibbling or tongue-stroking when grooming was directed to a single region. Oral grooming bouts directed to multiple regions were always of the tongue-stroking type. The anatomical regions for oral grooming were: head (face washing), neck and chest, sides and back, abdomen, hindlegs, anogenital area and tail. These regions were grouped into four progressively caudal zones for analysis of cephalocaudal progression (Table 2). For scratch grooming, the anatomical regions were chin (including head rostral to the ears), ear and neck. In preliminary trials, a greater than 90% inter-observer reliability was established for the two individuals scoring the videotapes.

2.1.3. Statistical analysis

The time budget analysis was derived from data pooled from all cats, and tabulated as a percentage of total observation time. Because each subject was observed for the same amount of time, data from each individual animal contributed equally to the data set.

The cephalocaudal analysis was inherently at risk for pseudoreplication because some subjects engaged in more grooming sequences than others. It would not be valid to treat

Table 2
Anatomical areas of grooming

Zone	Region	Anatomical details
Oral grooming		
1	Face (Wash)	Front paws and legs; head
1	Neck/Chest	The frontal plane including the chest and shoulders
2	Sides/Back	The sides and back, caudal to the shoulders and cranial to the tail, groomed by lateral neck flexion
2	Abdomen	The ventral area caudal to the shoulders and cranial to the tail, groomed by ventral neck flexion
3	Hindleg	Hindlegs and feet
3	Anogenital	The genital, anal and perianal areas and proximal third of the ventral tail
4	Tail	Distal 2/3 of the tail
Scratch grooming		
	Chin	The head rostral to the ears, including the chin
	Ear	The head caudal to and including the ears
	Neck	Caudal to the head and cranial to the shoulders

each observed sequence as an independent data point, nor would it be reasonable to limit the analysis to only one sequence per subject and leave most data unutilized. The statistical approach chosen was first to conduct a Spearman test for a correlation between the rank of each zone groomed and its location in the sequence for each multiple-site grooming bout for each subject. In the absence of a cephalocaudal trend, the Spearman correlation would not differ from zero; a positive and significant deviation would support a cephalocaudal pattern. The Wilcoxon signed-rank test was conducted on these correlation results to test for significant deviations from zero. Statistical significance for these Wilcoxon tests was set at 0.05.

A second analysis was to examine the relationship between the duration of sleeping or resting (when grooming was necessarily limited) and the latency to oral grooming subsequent to a period of sleep/rest. This relationship was examined by a Spearman rank correlation between the duration of sleep/rest and latency to the next bout of oral grooming with significance set at 0.05.

2.2. Results

Rounded to whole numbers (except when $< 1\%$) sleep/rest accounted for 50% of the time budget. Oral and scratch grooming accounted for 4% and 0.1%, respectively of the full-time budget, but of non-sleeping/resting time (when grooming was possible), oral and scratch grooming accounted for 8% and 0.2% respectively. The other categories were: general activity 43%, elimination 0.4% and eating and drinking 3%. The region receiving the most oral grooming was the head in the form of face washing (31%), followed by the hindleg licking (21%), sides–back (13%), neck–chest (11%), anogenital (10%), abdomen (9%) and tail (5%).

Grooming of multiple areas accounted for a group mean of 91% of grooming bouts; the remainder being directed to single regions. Of bouts delivered to multiple areas there

Table 3
Individual Spearman rank correlation coefficients for cephalocaudal sequencing of oral grooming bouts

Subject	Coefficient
1	0.21
2	0.71
3	0.22
4	0.15
5	0.16
6	0.43
7	0.08
8	0.40
9	−0.04
10	0.25
11	0.46

was a cephalocaudal trend. The mean Spearman correlation coefficient of all subjects for cephalocaudal sequencing of oral grooming was 0.21, which was significant at $p < 0.01$. Although there was considerable individual variation in the correlation coefficients among subjects, all but one of the subjects had a positive correlation coefficient (Table 3).

The Spearman correlation test of sleep/rest duration and latency to the next oral grooming bout revealed a negative and significant correlation ($r = -0.167$, $p < 0.05$). Among the 11 subjects, eight had negative coefficients, two positive coefficients and one a coefficient of 0.

3. Experiment 2: effects of grooming deprivation

Experiment 1 provided an indication that cats have an increased tendency to perform oral grooming following a period of sleep/rest. To acquire more definitive information about whether a deprivation of grooming leads to a compensatory enhancement, this experiment involved 3 days of enforced deprivation of grooming. To preclude the possibility that ectoparasites might accumulate and stimulate grooming, this experiment was conducted with cats in ectoparasite-free environments.

3.1. Methods

3.1.1. Subjects

Nine cats kept as household pets by veterinary students were recruited (five neutered males, four spayed females, ages 1–8 years). All subjects were indoor cats from households with no history of ectoparasite infestation. Additionally, subjects were examined with a flea comb at the start of the study to confirm the absence of flea infestation.

3.1.2. Experimental design

In a repeated measures design, each subject served as its own control. For 3 days, each cat wore either an Elizabethan collar (E-collar, of the type used in veterinary practice to control excessive licking) that prevented oral grooming and scratch grooming of the head (scratch grooming could still occur caudal to the collar), or a control collar, 1.0 cm wide, that did not prevent grooming. The collared cats were allowed to move about freely in the home and preliminary observations revealed the E-collar did not affect eating, sleeping or resting behaviour. When the collars were removed 3 days later, the subjects were immediately placed in an observation cage ($61 \times 96 \times 127$ cm high) in the home and videotaped continuously for the next 24 h. The procedure was then repeated for each subject with the alternative collar. Four of the nine subjects wore the control collar first, and five wore the E-collar first.

3.1.3. Analysis

The 24-h time-lapse videotapes were analyzed for all grooming activity including frequency and duration of oral and scratch grooming bouts. As in Experiment 1, each oral grooming bout was categorized as being directed to multiple regions or a single region. A grooming bout was considered terminated when a non-grooming activity occurred (e.g., eating, eliminating, rest), or if more than 60 s elapsed without a licking episode. As in Experiment 1, separate start and stop times were entered if more than 5 s of non-grooming followed a grooming episode within a grooming bout. The observer of the videotape did not know whether the cat had been wearing the E-collar or the control collar prior to being placed in the observation cage.

Because preliminary observations suggested that the difference in grooming rates following removal of E-collar would occur within the first few hours after collar removal, the 24-h observation period was divided into two 12-h periods to derive an estimate of the duration of the grooming enhancement. The non-parametric Wilcoxon signed rank test was used to test for statistical significance with the level of significance set at 0.05. A one-tailed test was used because the prediction was that grooming would increase following restraint of grooming.

3.2. Results

In the initial 12 h following removal of the E-collar, cats orally groomed a mean of 67% more than when they had been wearing the control collar (the increase was significant, $p < 0.05$). In the second 12 h, there was not a significant difference between the two conditions (Fig. 1). Also there was more than a twofold increase in time spent in scratch grooming in the first 12 h following removal of the E-collars compared with removal of the control collars ($p < 0.01$), and again there was no difference during the second 12 h (Fig. 1). The enhancement of oral grooming in the first 12 h was due to an increase in both bout frequency and bout duration (neither of which alone reached significance). There was no significant change in the proportion of grooming distributed to multiple vs. single regions. Grooming of multiple regions was a mean of 92% in the control situation and 96% following E-collar removal. Both scratch grooming bout

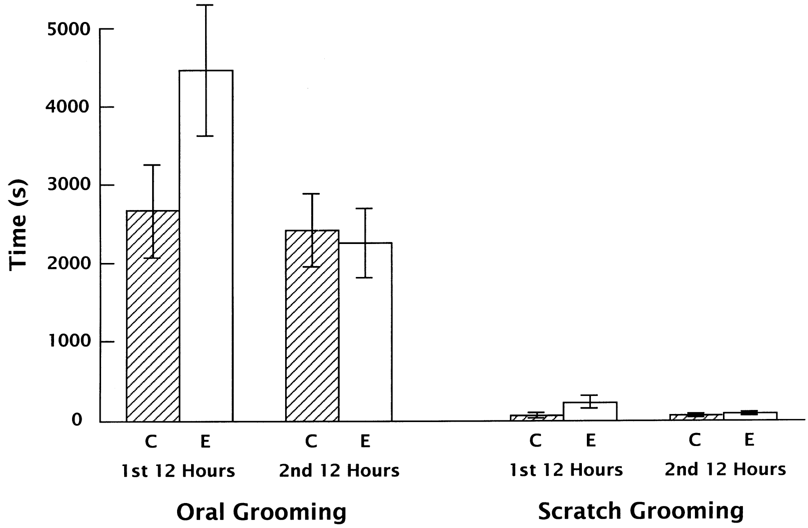

Fig. 1. Mean (±SEM) time spent in oral and scratch grooming following removal of control collars (C) or E-collars (E) for the first and second 12-h periods immediately after collar removal. The difference between the control and E-collar condition was significant for oral and scratch grooming for the first 12 h but not the second 12 h.

frequency and bout duration were significantly increased in the first 12 h following E-collar removal ($p < 0.05$).

4. Discussion

To our knowledge, this is the first report of a time budget estimate of behavioral activities for domestic cats in loose confinement. Accounting for 50% was the category of combined sleep and rest with general activity representing 43%. Oral grooming, accounting for 4%, occupied about the same proportion of the total time budget as eating and drinking. Scratch grooming accounted for only 0.1%. However, of non-sleeping/resting time, where grooming was physically possible, oral grooming accounted for 8% of the budget. The proportion of time spent in grooming is similar to the 6% reported for normal cats in home cages by Swenson and Randall (1977) based on an 8-h sampling period (0900–1700 h).

Oral grooming was directed most often to the head in the form of face-washing. The next most frequently groomed areas, in rank order, were hindlegs, side–back, neck–chest, anogenital region, abdomen and tail. Scratch grooming was directed most often to the chin, followed by the ear and neck and all scratch grooming was to single regions. More than 90% of oral grooming bouts were dedicated to multiple-body regions and there was a moderate and significant cephalocaudal trend (mean correlation coefficient = 0.21) in the oral grooming of multiple regions. The degree of cephalocaudal sequencing within multiple-region grooming bouts varied considerably among subjects with four subjects having a correlation coefficient of 0.40 or greater.

The predominance of multiple-area grooming, with a cephalocaudal trend, is consistent with the model of centrally controlled, programmed grooming, rather than stimulus-driven grooming, as the underlying basis of oral grooming in cats. As argued by Swenson and Randall (1977), if grooming was merely a response to peripheral stimuli one would not expect grooming bouts to sequence from one area to another.

The results of the experiment on temporary deprivation of grooming by E-collars are also consistent with the programmed grooming model. Periods of sleep and recumbent rest constitute a form of naturally occurring short-term grooming deprivation because the cat is either unconscious or drowsy and in a posture where grooming is not likely. The significant negative correlation between sleep/rest duration and latency to a subsequent oral grooming bout points to an enhancement of grooming following a prolonged period of non-grooming. This deprivation-induced enhancement of grooming was explored more fully in Experiment 2 where E-collars were used to prevent grooming for 3 days. Following removal of the E-collars, there was an increase of about 70% in oral grooming in the first 12 h compared with grooming rate after removal of control collars which did not restrict grooming. The increase in oral grooming came about by an increase in both the frequency and the duration of bouts. The enhancement effect had disappeared by the second 12 h. The proportional distribution of grooming bouts to multiple and single regions did not differ between the control and deprivation-induced conditions. Scratch grooming was also significantly increased in the first 12 h.

The deprivation-induced enhancement of grooming could reflect a catch-up aspect of a programmed grooming generator as discussed in the Introduction. This would be an adaptive response in nature, because grooming is effective in removing ectoparasites (Eckstein and Hart, 2000), and when grooming is suppressed, one would expect ectoparasites to increase in number. The enhancement of grooming would be effective in removing the excess ectoparasites even if they do not markedly increase peripheral stimulation.

Other than a transient enhancement of programmed grooming, the alternative mechanism that might lead to increased grooming following deprivation would be an increase in cutaneous stimulation. In nature, this could occur with a build-up of ectoparasites. However, the cats of Experiment 2 were maintained in ectoparasite-free environments. Theoretically, grooming deprivation could lead to some enhanced cutaneous itching even without ectoparasites. As alluded to above, the predominant pattern of oral grooming, that of stroking the tongue over the pelage in bouts directed to multiple regions, is not the type of grooming one would expect if there was itching at a point source. Also, the cats were free to rub body areas against objects in the environment to relieve local itching. Thus, the most likely explanation for the enhancement of oral grooming is that an endogenous generator recognizes a deficit when grooming is prevented, and programmed grooming is temporarily accelerated. The increase in scratch grooming that is directed to single areas may have reflected an increase in itching, especially where the collar rested on the neck.

The control of most grooming activity in cats by central or internal factors, rather than peripheral stimulation, is supported by experimental work on the interaction of several subcortical brain areas in controlling oral grooming. Both pontile and tectal lesions resulted in a reduction in grooming time (Swenson and Randall, 1977). The primary behavioral deficit in the cats was a failure of grooming bouts to progress from the body area initially groomed to a subsequent body area. These physiological findings reinforce the conclusions from the behavioral results of the present study that oral grooming in domestic cats is primarily organized and controlled by a central or internal generator rather than by peripheral or cutaneous stimulation.

References

Barnett, S.A., 1963. The Rat: A Study in Behaviour. Aldine Press, Chicago.

Borchelt, P.L., Eyer, J., McHenry, D.S. Jr., 1973. Dustbathing in Bobwhite quail (*Colinus virginianus)* as a function of dust deprivation. Behav. Biol. 8, 109–114.

Eckstein, R.A., Hart, B.L., 2000. Grooming and control of fleas in cats. Appl. Anim. Behav. Sci. 68 (2) 141–150.

Ewer, R.F., 1967. The behaviour of the African giant rat (*Cricetomys gambianus* Waterhouse). Z. Tierpsychol. 24, 6–79.

Hart, B.L., 1990. Behavioral adaptations to pathogens and parasites: five strategies. Neurosci. Biobehav. Rev. 14, 273–294.

Hart, B.L., 1997. Effects of hormones on behavioral defenses against parasites. In: Beckage, N.C. (Ed.), Parasites and Pathogens: Their Interplay with Host Hormones and Behavior. Chapman and Hall, NY, pp. 210–230.

Hart, B.L., Hart, L.A., Mooring, M.S., Olubayo, R., 1992. Biological basis of grooming behaviour in antelope: the body-size, vigilance and habitat principles. Anim. Behav. 44, 615–631.

Lucas, E.A., 1975. Effects of five to seven days of sleep deprivation produced by electrical stimulation of the midbrain reticular formation. Exp. Neurol. 49, 554–568.

Richmond, G., Sachs, B.D., 1980. Grooming in Norway rats: the development and adult expression of a complex motor pattern. Behaviour 75, 82–95.

Swenson, R.M., Randall, W., 1977. Grooming behavior in cats with pontile lesions and cats with tectal lesions. J. Comp. Physiol. Psychol. 91, 313–326.

Vestergaard, K., 1982. Dust bathing in the domestic fowl-diurnal rhythm and dust deprivation. Appl. Anim. Ethol. 8, 487–495.