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Proximate factors in the control of sandbathing in the chinchilla (*Chinchilla laniger*)

Barber, Nigel, Ph.D.

City University of New York, 1989

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PROXIMATE FACTORS IN THE CONTROL OF SANDBATHING IN THE CHINCHILLA (CHINCHILLA LANIGER)

by

NIGEL BARBER

A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

1989

This manuscript has been read and accepted for the Graduate Faculty in Psychology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

PROXIMATE FACTORS IN THE CONTROL OF SANDBATHING BEHAVIOR IN THE CHINCHILLA (CHINCHILLA LANIGER)

by

Nigel Barber

Adviser: Professor Robert L. Thompson

Sandbathing behavior of rodents adapted to arid environments is recognized as one component of a functional class known as care of the body surface (COBS) although its precise biological significance is poorly understood. COBS exhibits considerable motivational complexity, the most striking aspect of which is its reliance on other behavioral systems including temporal dependence (e.g., postprandial grooming) and motivational subordination (displacement activity, disinhibition). Nevertheless, causal models have emphasized the role of cutaneous stimuli.

When sandbathers are deprived of a suitable particulate substrate, their fur becomes matted and greasy in appearance. The number of sandbathing contacts with the substrate following termination of deprivation tends to increase with increasing length of the deprivation period. The lipid-regulation hypothesis explains this relationship by imputing a causal role to the cutaneous sensory inputs associated with greasy fur in relation to sandbathing.

Sixteen chinchillas served in each of four experiments (repeated measures) designed to test predictions derived from the lipid

regulation hypothesis:

1. Sandbathing frequency will increase with deprivation of the opportunity to sandbathe. (The number of sandbathing rolls, together with three measures of attraction to sand, were measured during a 10-min test following zero, one, or five days of sand deprivation).

2. Lipid removal from fur will reduce sandbathing frequency. (Experimental subjects were tested at a sand-deprivation level of 25 days one day after shampooing).

3. Addition of lipid to the fur will increase sandbathing frequency. (Mineral oil was added to the fur one day before tests conducted at a sand-deprivation level of one day).

4. Sandbathing will reduce the lipid content of the fur. (Lipids were extracted from fur samples taken after 25 days of sand deprivation, after 24 hrs access to sand, and after shampooing, in that order).

All of these predictions were supported except the second. Since this constitutes the most critical test of the causal hypothesis, the lipid-regulation hypothesis was rejected as an explanation for deprivation effects on sandbathing. Intense peripheral stimulation such as that provided by experimental lipid treatment seems to evoke a quite general mammalian response of using the substrate as an aid in COBS. Endogenous pelage lipids probably do not produce this effect. A variety of sensory factors may affect sandbathing frequency but the effect of deprivation on sandbathing frequency is not easy to explain in terms of any of them. Sandbathing frequency appears to be importantly influenced by a central mechanism.

ACKNOWLEDGMENTS

This dissertation research could not have been planned, carried out or written up without the help of many people. Some were implicated for professional reasons. Some were talked into it. Others had it thrust upon them. A fourth category consists of those who volunteered. This is a separate grouping but it overlaps with all of the above.

Perhaps I should begin with the members of my Supervisory Committee each of whom has played a special role in my intellectual development at Hunter. Gerald Turkewitz first provided me with the background in developmental psychology which whetted my interest in the fascinating enigma of animal play behavior. I expect that this problem will continue to exercise my curiosity for many years to come and would like to take the opportunity of thanking Gerald for his support and assistance in that project as well as the present one.

Howard Topoff has done more than anyone else to foster my interest in the evolution of behavior. This interest was a major reason for joining the Biopsychology Program in 1986 and it influences the form in which the dissertation is presented. Howard has always been strongly supportive but at the same time intellectually challenging and stimulating.

Rounding out this trinity is my adviser, Robert Thompson, who has suffered more with the research than anyone apart from myself. Although this may have served to magnify my own character flaws (abrupt, sassy, too damn independent!) our dealings have been overwhelmingly positive, harmonious and constructive. Robert's most important single contribution has been his unusual objectivity and skepticism (said to be a golden quality in science!). I am particularly grateful for the energy and enthusiasm which he devoted to editing the manuscript at a time when he was surrounded by so many other pressing responsibilities. I continue to be amazed by his intellectual openness, breadth of interests, and capacity to be absorbed by new problems. Robert has cast a watchful eye over so many aspects of my development and welfare at Hunter that I can only say: IOU RLT!

Peter Moller and Robert Landsman deserve a special word of thanks for assistance in purchasing and transporting glassware - exertions beyond the call of any possible duty for which I am deeply appreciative. Tom Cox, now succeeded by Su Boatright, deputized for Robert Thompson in lab supervision for a year. I would like to thank them both for the many kinds of practical assistance, moral support, and advice, without which it is difficult (or impossible?) to get through graduate school.

Irene Woerner and Ellen Breheny in the Biopsychology Office have displayed remarkable fortitude in coming to terms with the tangled skein of my administrative history for which I am beholden. I would also like to thank the Psychology Department personnel, particularly Miriam Gallindez who was unfailingly kind and helpful. The staff of the Hunter College Library were made busier by my presence and I am especially grateful to the Interlibrary Loan section, namely, Jean-Jacques Strayer, Grace Sanders, and Joseph Semenovich who were much put upon by my requests and left no stone (or page!) unturned to locate the material.

My experiments involved shattering the serenity of at least three other laboratories and I want to commiserate with my victims and benefactors in this. The Biology Department graciously consented to my use of the Graduate Lab for a year. For this I am obliged to Marcia Brody and to Peter Lipke who generously acceded to my many subsequent requests. Phil Pedersen and Brian Herbert helped me out with the nuts-and-bolts of the operation and I want to thank them for their interest and understanding.

Vicky Luine very kindly put laboratory space and equipment at my disposal at a critical juncture in the research and thereby proved a friend in need. Gordon Barr also granted the use of equipment and Myra Joyce provided technical advice.

There is also the person who interfaced with a computer to come up with the finished manuscript but has asked to remain anonymous. How kinky!

Finally, there is my mother. I feel that whatever strivings I may have towards excellence in academic life, or anything else, must be largely attributable to her influence.

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CHAPTER 1

Care of the Body Surface

Care of the body surface (COBS) is a broad functional category of behavior which has been studied in a wide variety of vertebrates and invertebrates. Sometimes the functional significance of the term "care" may appear quite obvious as in the removal of ectoparasites or the dressing of wounds. On other occasions COBS may arise independently of such stimuli, exhibiting routine or habit-like characteristics or emerging "inappropriately" in situations of motivational conflict (a number of examples are described in Chapter 5). Such observations suggest that COBS has in some sense a low motivational priority, i.e., that it is an activity which may emerge in the absence of pressing or useful alternatives (Goodwin, 1956). However, as the behavior continues to receive serious scientific attention (following earlier neglect in favor of more apparently important behavior), this impression may have to be revised. In one well-studied species, the Mongolian gerbil, autogrooming has been shown to have important, but unexpected, thermoregulatory consequences. In addition, it mediates social facilitation of arousal, affects social status and mating success - all these consequences being mediated by the distribution of exudate from the Harderian gland (Thiessen, 1977).

While COBS movements may thus have far-reaching social or nonsocial biological effects, which may be poorly understood in many species, this behavioral category can be defined in terms of stimulus context, topography, and immediate consequences. COBS refers to behavior in which an animal touches its body surface either with part of its own body or with some other object or substance with the consequence that these movements serve to clean the integument of dirt, to dress wounds, to remove parasites, to rearrange hairs, feathers or other integumentary appendages, or to distribute various secretions (e.g., saliva, apocrine secretion, uropygial oil, Harderian lipid) around the skin and its appendages (Borchelt, 1980; Eisenberg, 1981).

COBS can be divided into three types:

1. Autogrooming in which the same individual is both the actor and the recipient of grooming.

2. Allogrooming in which actor and recipient are different individuals of the same species. This is particularly well developed in primates and appears to have consequences for bond-formation and the appeasement of aggression, e.g., chimpanzees (Simpson, 1974).

3. Symbiotic COBS. Actor and recipient belong to different species. Well-known examples include the anting behavior of birds (Kelso & Nice, 1963) and removal of ectoparasites, scarred tissue and fungal infections from larger fish by small cleaner wrasse (Potts, 1973).

Autogrooming has been described for a wide variety of animals (Grier, 1984) including flies (Dawkins & Dawkins, 1976), praying mantis (Zack, 1978), quail (Borchelt, 1975), marsupials (Eisenberg & Golani, 1977), and a large number of other mammals. A surprisingly complex relationship may exist between skin secretions and COBS. For example, the uropygial secretions (or preen waxes) of birds are spread through the feathers via behavior known as oiling. This consists of mandibulation of the uropygial gland followed by preening of oil onto the feathers. Although its function is poorly understood, preen wax may serve an antibacterial or antifungal role and may contain substances which act as chemical signals in interspecific communication (Jacob & Ziswiler, 1982; but see Appendix 1). Not only do birds rely on a behavioral mechanism for distributing this important secretion, but their COBS repertory includes a separate complex behavioral system, known as dustbathing, which appears to remove excess preen wax from the feathers (Borchelt & Duncan, 1974).

Mammals are the only vertebrates with hair. Their lipid-secreting sebaceous glands are fairly evenly distributed about the hirsute surfaces of the body. Found in close association with hair follicles, they open into the hair-sebaceous gland canals (Sololov, 1982). The distribution of lipid around the mammalian integument is thus accomplished by physiological means so that there is no requirement for behavior analogous to oiling in birds. One interesting exception is the Mongolian gerbil which distributes Harderian lipid around the fur by means of autogrooming (Thiessen, 1977; Thiessen & Kittrell, 1980).

Mammalian autogrooming can be subdivided into (1) face washing, (2) body grooming, (3) scratching, (4) sandbathing (Borchelt, 1980; Eisenberg, 1981). In face washing, the forepaws are moistened with saliva and rubbed over the head region. In addition to cleaning the fur, this behavior impregnates it with saliva (and perhaps with Harderian exudate) which may be an important source of chemical information for conspecifics (Eisenberg, 1981; Thiessen, 1977).

Face washing frequently precedes body grooming. In body grooming, the fur is washed with the tongue and rearrangement of the hairs is accomplished by means of the teeth which act as a comb (Eisenberg, 1981).

Scratching movements of the hind limbs are directed behind the ears, over the shoulders and head, and to other parts of the body. These stereotyped movements typically conclude an autogrooming bout (Eisenberg, 1981).

Sandbathing

Use of the substrate as an aid in COBS occurs in many species when the fur becomes wet. Contact with dry soil speeds up the drying process. Motor patterns used in contacting the substrate are of three major types:

1. The animal produces a writhing movement while lying on its back, side, or ventrum.

2. The trunk musculature is extended and then flexed while the ventral surface contacts the substrate.

3. The animal rotates (rolls) partially or completely around its long axis (Eisenberg, 1963a, 1981).

These behaviors may be organized into a predictable pattern known as sandbathing. Sandbathing has evolved convergently in many mammalian species inhabiting a desert environment. It is most common among rodents and desert-adapted marsupials (Eisenberg, 1981).

Species inhabiting nondesert environments may exhibit structurally similar behaviors which are normally termed "dustbathing" or "wallowing" and are believed to play a role in chemical communication. Examples of dustbathers include chimpmunks, ground squirrels, flying squirrels, deermice (Eisenberg, 1963a), the mountain zebra (Penzhorn, 1984) and the mountain hare (Flux, 1970). Wallowing is typical of Rhinocerotidae and Suidae (Byers, 1984). As these examples show, apparent odor marking of a particulate substrate is a very widespread mammalian activity. A form of "dustbathing" may even occur in aquatic forms such as the elephant seal which exhibits a "sandflipping" behavior although this is understood to be thermoregulatory in nature (Heath & Schusterman, 1975).

Odorous substances deposited on the substrate may also elicit rolling or wallowing movements which have the consequence of anointing the active individual with the odor. According to Kleiman (1974), neonatal <u>Pediolagus</u> (see Appendix 2 for common names) roll in adult urine deposits and the scent which is acquired in this way promotes social tolerance by adult males. Sandbathing movements thus fulfil a role which in <u>Octodontomys</u>, <u>Cuniculus</u>, and <u>Myoprocta</u> is accomplished through active urination by males over young. In addition, in several hystricomorph genera (<u>Octodon</u>, <u>Octodontomys</u>, <u>Pediolagus</u>, <u>Microcavia</u>), "localized sites become saturated with urine and anal gland secretions, and are used preferentially for sandbathing. This ensures that members of the same group share the same scent" (Kleiman, 1974, p. 181). Self-anointing with urine and other odors is common among primates. The cebus monkey, for example, washes itself by urinating into a cupped hand (Jolly, 1985). However, the substrate is rarely, or never, used as an intermediary in the anointing process.

Odorous deposits on the substrate may also elicit wallowing movements in animals which do not dustbathe as part of their COBS repertory. This behavior may be distressing to dog owners since rolling behavior is elicited by substances such as decayed flesh, dung, and rotting garbage. Lemon rind, perfume, and tobacco were found to produce a similar response in the laboratory. Morris (1987a) suggests that wild canids may anoint themselves with the droppings of a prey animal either as a form of olfactory camouflage to be used during hunting or as a means of inciting pack members to hunt the prey species whose scent has been acquired. Current information seems inadequate to evaluate these ideas.

A similar response is elicited in felids by the catnip plant (Nepeta cataria) and also by valerian (Valeriana officinales). According to one interpretation the aromatic oil of the catnip plant mimics a felid reproductive pheromone and this view is supported by the fact that estrus cats engage in rolling behavior similar to that elicited by catnip. However, the catnip response occurs in males as well as females and is unaffected by spaying or castration. The odor may have drug-like effects explicable in terms of brain receptor populations but otherwise devoid of biological significance (Morris, 1987b; Todd, 1963).

Species exhibiting the highly organized and stereotyped pattern of true sandbathing experience increased greasiness and matting of the fur if deprived of access to a suitable sand substrate. This does not happen in the case of nonsandbathing species (Eisenberg, 1963a) and it reflects the phenomenon of increased sebaceous gland production by small desert-adapted mammals (Quay, 1965). Examples of genera in which sandbathing has been described are presented in Table 1. This compilation has no pretension to completeness and includes only those species whose sandbathing behavior has been a major focus of the study cited. No doubt a thorough review of the literature on mammals adapted to desert, or arid, conditions would uncover many incidental references to sandbathing. In addition, Eisenberg (1967) states that "it should be understood that sandbathing is not confined to desert rodents alone, but that the frequency of occurrence and stimuli necessary to elicit the pattern are characteristic of desert-adapted species" (p. 14).

The production of large amounts of skin lipid (sebum) by desert-adapted rodents is believed to prevent evaporative water loss from the skin (Quay, 1965). However, this view is controversial. In reviewing the topic, Hadley (1985) states:

> Although such lipids spread on the surface would likely have some effect on the diffusion of water, sebum itself probably contributes little to the major integumental water barrier. Kligman (1963) noted that it would require at least 10 times the normal amount of sebum on the skin surface before the effect on permeability would be noticeable, and at this thickness the sebum would tend to flow into valleys, minimizing its

Table 1. Distribution of Sandbathing Among Mammals

Genus	Common Name	Reference
Sminthopsis	Dunnart	Ewer, 1968
Dasyuroides	Marsupial mouse	Eisenberg & Golani, 1977
Antechinus	Marsupial rat	Eisenberg & Golani, 1977
Dipodomys	Kangaroo rat	Borchelt, Griswold, & Branchek, 1976
Perognathus	Pocket mouse	Eisenberg, 1963a
Microdipodops	Kangaroo mouse	Eisenberg, 1963a
Chinchilla	Chinchilla	Stern & Merari, 1969
Octodon	Degus	Wilson & Kleiman, 1974
Octodontomys	Choz-choz	Wilson & Kleiman, 1974
Dolichotis	Mara	Wilson & Kleiman, 1974
Neotoma	Desert woodrat	Fleming & Tambosso, 1980
Salpingotus	Pygmy jerboa	Rogovin, 1979
Jaculus	Desert jerboa	Eisenberg, 1967
Allactaga	Five-toed jerboa	Eisenberg, 1967
Gerbillus	Northern pygmy gerbil	Eisenberg, 1967
Meriones	Gerbil	Tortora, Eyer & Overmann, 1974
Tatera	Large naked-soled gerbil	Eisenberg, 1967
Pachyuromys	Fat-tailed gerbil	Eisenberg, 1967

effectiveness. (p. 138)

The functions of skin lipids can thus be considered something of a biological riddle. Apart from waterproofing it has been proposed that they have a thermoregulatory role, keep the skin soft and pliable, lubricate the fur, prevent the hairs from becoming brittle, prevent the entry of pathogens, produce an antibacterial or antifungal effect, and play a role in communication (Hadley, 1985; Jacob & Ziswiler, 1982; Kligman, 1963; Pendergrass & Thiessen, 1981; Sokolov, 1962). Only communication and thermoregulation are considered in any detail in the body of this thesis. However, the topic receives a fuller treatment in Appendix 1.

Not only is there strong skepticism concerning the water barrier function of sebum but there is empirical evidence that lipid accumulation in the fur may actually increase evaporative water loss. In Mongolian gerbils that were prevented from sandbathing, matting of the pelage resulted in exposure of the skin. Animals with bare patches of skin suffered an increased rate of water loss (Harriman & Thiessen, 1983; Thiessen & Pendergrass, 1985).

Sandbathing is believed to have a primary role of cleaning excess lipid from the fur and this view is based on three simple observations:

1. Sand-deprived animals may become visibly greasy (Eisenberg, 1963a).

2. Upon exposure to sand, greasy animals exhibit an increased frequency of sandbathing relative to those with constant access to

sand. This is referred to as a deprivation effect (Borchelt, Griswold, & Branchek, 1976; Stern & Merari, 1969; Tortora, Eyer, & Overmann, 1974).

3. Exposure to sand has been reported to produce a light and fluffy appearance of the fur similar to the effect of shampooing (Griswold, Borchelt, Branchek, & Bensko, 1977) or to cause a measurable reduction in fur lipids (Thiessen & Pendergrass, 1985).

In addition to its role of regulating pelage lipids, sandbathing may also serve to deposit odorous substances on the substrate which are involved in intraspecific communication. Both bannertail and Merriam's kangaroo rats are reported to concentrate their sandbathing at loci previously used for the same purpose by conspecifics (Eisenberg, 1975; Laine & Griswold, 1976; Randall, 1981a, 1982). The same is true for <u>Gerbillus nanus</u>. All three species exhibit social intolerance. More sociable species may not share sandbathing loci (Eisenberg, 1963b, 1967).

Kangaroo rats possess a specialized sebaceous dorsal gland which is believed to be the origin of a signal substance . Information communicated by a sandbathing deposit includes species, gender, and perhaps reproductive status of the depositor (Randall, 1981a). The precise biological significance of olfactory communication at sandbathing loci is unknown and the same is true of many other forms of scent marking (Doty, 1980; Johnson, 1973).

Lipids in the fur probably increase thermal insulation thereby increasing the capacity to withstand cold stress (Pendergrass & Thiessen, 1981; Randall, 1981b; Thiessen & Kittrell, 1980). However, this idea has not received sufficient empirical investigation. The only hard evidence in its favor is the demonstration by Thiessen & Kittrell (1980) that gerbil lipid significantly increases the insulative capacity of silk. It is difficult to generalize from this result to fur on a living animal.

Excess lipid tends to mat the pelage. This would reduce the size of the envelope of air trapped in the fur, thereby reducing its insulation (see Birkebak, 1966; Hammel, 1955; Scholander, Hock, Walters, Johnson, & Irving, 1950; Scholander, Walters, Hock, & Irving, 1950). Sandbathing can correct this problem by removing excess lipid and fluffing up the fur (Borchelt et al., 1976).

Pendergrass & Thiessen (1983) found, however, that the Mongolian gerbil sandbathes frequently at 30 °C but very little at 5 °C. Lipid accumulation in this species darkens the fur leading to increased absorption of solar radiation whereas sandbathing lightens coat color and increases the reflectance of the fur.

Sandbathing may thus affect water and thermal homeostasis as well as having a communicatory role. It should be emphasized that these ideas are little more than working hypotheses at present. The research reported here concerns the sandbathing behavior of the chinchilla. While most authorities agree that sandbathing in the chinchilla serves to care for the pelage (e.g., Bowen & Jenkins, 1969; Glickman, 1973; Weir, 1976) no more precise function has been proposed (see Chapter 4). The experiments were conducted to investigate immediate rather than evolutionary causation and focus upon the possible effect of lipid levels in the fur on sandbathing frequency.

CHAPTER 2

Sandbathing from an Ethological Perspective

According to received ethological wisdom a complete picture of animal behavior can be assembled only by due consideration of four central issues, "the four whys of ethology" (Hinde, 1982; Tinbergen, 1963). The four questions refer to evolutionary origin, ontogeny, adaptive function, and proximate cause. Proximate cause is the focus of this thesis. While ethologists normally endeavor to analyse the four questions separately, this is not always the case. For example, knowledge about ontogeny has been applied to immediate causal analysis. Thus, the development of fear responses in ducklings coincides with the end of the critical period for imprinting and this information was used to support a classical conditioning account of the imprinting mechanism (Hoffman, 1978).

Phylogenetic History

When did the behavior emerge in evolutionary history and how has it changed in the course of evolutionary time? Since behavior leaves few fossils this question is normally addressed by a comparison of living species using the assumption that shared behavior elements can be traced to branch points in the phylogenetic tree. Eisenberg (1963a) conducted a comparative analysis of sandbathing in the five living genera of heteromyid rodents.

All genera exhibited the perineal drag, a conservative (i.e., early-evolved) rodent marking pattern which is often produced upon wakening and leaving the nest or burrow. This consists of depressing the anal-genital areas against the substrate and walking forward. This would serve to mark the nest or burrow region with secretions from glands in the anal and genital areas or with drops of urine. Specialized anal scent glands in heteromyids were not mentioned by Eisenberg (1963a), or by Sokolov (1982), however, although Perognathus does have a caudal gland which is absent in the other genera (Quay, 1965). In Heteromys and Liomys, this primitive marking pattern is elaborated, apparently by the inclusion of movements normally associated with stretching. This ritualized extension and flexion of the body is referred to as a ventrum rub. Heteromys never rub the side of the body against the substrate and although this movement is occasionally seen in Liomys, it is not combined with ventral rubbing. Eisenberg concluded that the sandbathing of these genera serves the function of spreading scent and is not used to dress the pelage.

Whereas Heteromys and Liomys inhabit moist regions, the other three heteromyid genera, Perognathus, Microdipodops, and Dipodomys can be considered as, in varying degrees, specialists for arid conditions with Dipodomys as an extreme example of a desert-adapted rodent (Eisenberg, 1975). The desert-adapted species tend to develop a matted greasy pelage if denied access to sand suitable for dressing the fur. This never happens in the case of species belonging to Liomys or Heteromys (Eisenberg, 1963a). Sandbathing as a constituent in COBS frequently involves the integration of ventral rubs with side rubs into a complex pattern. "True" (p. 18) sandbathing thus incorporates scent-marking movements and may retain its ancestral scent-marking function as well as the derived COBS role.

The family chinchillidae contains three genera, Lagostomus (the plains viscacha), Lagidium (the mountain viscacha), and Chinchilla. Like Chinchilla, Lagidium is specialized for an arid mountain habitat (Eisenberg, 1981; Pearson, 1948, 1959). Since information is available only concerning the sandbathing movements of the chinchilla, although all three genera are said to dustbathe (Nowak & Paradiso, 1983), no comparative analysis is possible at present. However, it is unlikely that sandbathing in Chinchilla evolved from scent-marking movements since none of the sandbathing movements involves vigorous application of the perineal region to the substrate. Those regions of the body which do make contact do not appear to have identifiable scent glands although specialized odor-secreting glands in the anal region have been described (Sokolov, 1982).

Developmental History

Little information is available concerning the development of sandbathing behavior. Chinchillas are highly precocial, like most other hystricomorphs and are fully furred at birth (Eisenberg, 1981). Whether sandbathing can be elicited on the day of birth is not known. However, of a pair of male twins which I tested beginning at 7 days, one produced the normal adult sandbathing pattern on the first day whereas the other failed to do so until 22 days. Sandbathing may thus emerge at the age of one week or earlier in the chinchilla kit. Anyone wishing to study the development of sandbathing in the chinchilla or another species will find useful experimental paradigms in Borchelt and Overmann (1974) used in connection with work on dustbathing in quail. Age, and duration of exposure to the relevant substrate was carefully controlled in this work. In general, dustbathing in birds tends to increase with increasing age (reviewed in Borchelt, Eyer, & McHenry, 1973).

Eisenberg (1963b) reported that heteromyids are altricial at birth but develop comparatively rapidly with adult-type locomotion being present at 14-19 days. He suggested that sandbathing emerges early but is annoyingly vague on the point:

> Sandbathing seems to develop spontaneously, but because rubbing the side and stretching have been practiced by the young animal before it begins actually to sandbathe, it is difficult to establish absolute times of onset. (p. 74)

Ewer (1968) stated that the marsupial Sminthopsis which emerges from its nest three weeks after leaving the pouch is "able to perform all the normal toilet patterns and frequently indulge[s] in the characteristic sand rolling" (p. 243).

Wilson and Kleiman (1974) presented information about the development of sandbathing in three species of caviomorph rodents - all with precocial young. The choz-choz and the degus both begin to eat solid food on the second or third day after birth but sandbathing does not emerge until the second week. The salt-desert cavy sandbathes "within a few minutes of birth" (p. 344). According to Kleiman (1974), this allows for the acquisition of male and group odors from urination sites which may be important in eliciting social tolerance towards the neonate.

Function

The small literature on sandbathing offers conflicting views on its function which is hardly surprising given the possibility that its adaptive consequences may be different for different species. Stern and Merari (1969) stated that "while the sand bathing behavior of the chinchilla serves no apparent biological need it reacts to deprivation in a manner comparable to behaviors known to serve a need, e.g., eating and drinking" (p. 115). The key word in this quotation is "apparent" since the authors do not want to perpetuate the view that sandbathing has no biological significance - a perilous position since it is founded on ignorance.

Eisenberg (1963a) suggested that sandbathing in heteromyid rodents combines an ancestral scent-marking function with a more recent pelage-cleaning adaptation. Borchelt et al. (1976) were more circumspect and put sandbathing within the context of a general COBS model:

> Face-washing, grooming, scratching and sandbathing presumably function to clean the pelage or remove ectoparasites from the animal's body surface or both. (p. 347)

It is not clear whether removal of ectoparasites was attributed to sandbathing per se. This is alleged to be unimportant in the chinchilla since its fur is so fine that it is said to defeat common ectoparasites such as the flea (Perry, 1981). However, finely-furred species of Peru inhabiting a range formerly occupied by chinchillas, e.g. the chinchilla rat, do harbor ectoparasites such as fleas, mites and chiggers (Pearson, 1959) and Mohlis (1978) found that wild chinchillas themselves harbor fleas and lice.

The reason that Borchelt et al. (1976) combined sandbathing with face-washing, grooming, and scratching is presumably because the response classes occur in close temporal association. This is not normally true of the chinchilla however since prolonged autogrooming is rarely seen within the context of a 10 min sandbathing test (personal observation). Chinchillas also groom less than other rodents in an open-field test-setting (Glickman & Hartz, 1964).

Since the scent-marking function of sandbathing (Randall, 1981a) can be achieved without true sandbathing movements (Eisenberg, 1963a), it is necessary to invoke some other consequences in order to account for the evolution of sandbathing behavior. Sandbathing has evolved convergently in desert-adapted rodents which exhibit copious sebaceous secretion. If deprived of access to sand, such rodents develop a greasy, matted appearance of the fur while access to sand produces a noticeable improvement in its condition and apparently reduces lipid level (Borchelt et al., 1976).

One of the most useful approaches to behavioral function is the analysis of immediate consequences (Hinde, 1975). Since sandbathing appears to clean the pelage through removal of excess lipid, thereby separating matted hairs, care of the pelage is assumed to be one of its primary functions (Borchelt et al., 1976; Eisenberg, 1963a; Quay, 1965). This interpretation raises two questions which have not been discussed in the literature:

1. Why is lipid secretion not controlled at an optimal level in the same way as other bodily secretions, notably hormones? The immediate cause appears to lie in the absence of any sort of feedback mechanism by which accumulation of lipid could be used to shut off sebum production. Sebum production does not appear to be influenced by any afferent signal and the rate of secretion for an individual of a given age and sex is understood to be constant (Ebling 1967, 1974; Ebling & Skinner, 1967; Kligman, 1963). However, the question remains as to why this constant rate of production is excessive in mammals occupying desert or semi-desert habitats. It has been proposed that a high rate of lipid production is secondary to increased density of the fur in desert-adapted rodents (Sokolov, 1962) but this does not explain why lipid production is in excess of any apparent need (see Appendix 1 for discussion of the function of skin lipids).

2. Assuming that lipid secretion, even excessive lipid secretion, is somehow adaptive, why are conservative mammalian autogrooming movements not used to clean the fur? The implication is that conservative COBS is inadequate to remove lipid from the fur. This view is supported by the observation that sand-deprived sandbathing rodents do become greasy-looking (Borchelt et al., 1976; Eisenberg, 1963a).

Another issue raised by the view that sandbathing serves primarily to remove excess lipid from the fur relates to the advantage associated with cleaning the fur of lipid. Why, in other words, is the lipid stated to be excessive?

Skin lipids are believed to prevent evaporative water loss (Quay, 1965). In addition, lipid in the fur increases thermal insulation thereby facilitating thermoregulation in cold environments (Perdergrass & Thiessen, 1981; Randall, 1981b; Thiessen & Kittrell, 1980). Both functions could be compromised if lipid level in the fur is high enough to cause appreciable matting. This would tend to reduce the size of the envelope of air entrapped in the fur which reduces its insulative value (Hammel, 1955). In addition, matting of the fur tends to expose the skin which would increase evaporative water loss. Harriman and Thiessen (1983) found that Mongolian gerbils which are prevented from sandbathing lose body water more rapidly than sandbathing animals.

Before accepting these adaptive rationales in their entirety, a cautionary word is in order. Does sandbathing really reduce lipid levels in the fur? Most of the evidence in favor of this view is anecdotal, taking the form that sand-deprived animals appear greasy while their appearance is improved following a sandbathing bout or access to sand (e.g. Borchelt et al. 1976; Eisenberg, 1963a). There is little hard data on the point. The one study which has looked at the effect of living on a sand substrate on pelage lipids does not provide strong support for the lipid-reduction view. Thiessen & Perdergrass (1985) measured the change in pelage lipids of Mongolian gerbils following prolonged exposure to sand. They found that 8 days of sandbathing produced no reduction in pelage lipids while 16 days on a sand substrate did produce a significant reduction in lipids. This result tends to contradict nonquantitative observations that fur lipids of kangaroo rats (Dipodomys merriami) decrease within a single sandbathing bout (Borchelt et al., 1976). The discrepancy may be due to the fact that gerbils have an additional source of pelage lipid - the Harderian gland - which is readily mobilized through autogrooming. Harderianectomy in the gerbil produces a loss of pelage lipids that is approximately 10 times as great as the effect in mice, rats, or hamsters (Thiessen & Kittrell, 1980).

Proximate Cause

Sandbathing is a motivated behavior in the sense that increased levels of sand deprivation produce an increased frequency of sandbathing behavior. This was found to be true of chinchillas (Roche & Thompson, 1987; Stern & Merari, 1969), Mongolian gerbils (Tortora, Eyer, & Overmann, 1974), and kangaroo rats (Dipodomys merriami, Borchelt et al., 1976). The key question to be asked in connection with this effect is whether the increased tendency to sandbathe is mediated by sensory cues such as those arising from the increased greasiness of the fur, or whether a central mechanism is primarily involved. Many examples of such central mechanisms are provided in the ethological literature under rubrics such as "spontaneity", "action-specific energy" and "vacuum behavior" (reviewed in Eibl-Eibesfeldt, 1970). Implicit in these notions is the view that deprivation of the opportunity to engage in some species-typical response leads to an increased readiness to engage in the response independent of deprivation-induced changes in sensory inputs. This approach has also been applied to the investigation and interpretation of instrumental learning (Allison & Timberlake, 1975; Premack, 1962; Timberlake, 1984). Since the question of proximate causation is the main theme of this thesis, it is taken up in detail in Chapter 3.

CHAPTER 3

Proximate Causes of Sandbathing

1. Peripheral Factors

Although the issues of ultimate and proximate causation of behavior are better discussed separately so as to avoid confusing one with the other, this is not always done and COBS is a case in point. Discussions in the literature have often assumed that the cues eliciting COBS are directly connected to its function and have not always avoided scrambling the two levels of explanation (see below).

Another important distinction concerns the separation of afferent and efferent influences on behavior. In practice, as Tinbergen (1951) clearly recognized, both factors are normally implicated:

> Behavior is reaction in so far as it is, to a certain extent, dependent on external stimulation. It is spontaneous in so far as it is also dependent on internal causal factors, or motivational factors responsible for the activation of an urge or drive. (p. 15)

In referring to peripheral factors, I mean reaction to sensory stimulation. There is a confusing superfluity of terms each making essentially the same distinction and some of these are presented in Table 2.

Grooming behavior of various kinds is most often conceived as a

Table 2.

Terms Used in Distinguishing Between Two Major Proximate Causal Factors in Behavior

Peripheral	Central
Afferent	Efferent
Reactive	Spontaneous
Stimulation	Motivation, Disinhibition
Response	Drive
Elicited	Emitted
Stimulus-induced	Deprivation-induced
Sensory Feedback	Motor Program

response to some noxious cutaneous irritant. COBS both removes the source of stimulation and prevents possible biological harm, so what could be more natural than to identify eliciting stimulus with biological function? Ewer (1968) believes that in the marsupial Sminthopsis grooming is normally elicited in this way but there are many instances of grooming in homiotherms when a behavioral episode can be elicited independently of peripheral input (see Chapter 5).

Borchelt, Hoffman, Hurrell, and McCarthy (1979) make an explicit connection between evolutionary and proximate cause when they state that "Two hypotheses have been proposed for the function and control [my emphasis] of dustbathing in birds." (p. 134). Not only was dustbathing (correctly) believed to reduce the number of feather mites in infested birds but the presence of the mites was (incorrectly) considered necessary to elicit dustbathing.

The second function-and-control hypothesis focuses upon uropygial lipid deposited on the feathers through oiling behavior. This "lipid-regulation hypothesis" (p. 134) proposes that dustbathing is elicited by accumulation of uropygial secretion in the feathers and has the adaptive consequence of cleaning away the excess lipid. The hypothesis is supported by correlational evidence that depriving bobwhite quail of dust increases both feather lipids and the frequency of dustbathing once the particulate substrate is made available (Borchelt, Eyer, & McHenry, 1973). However, a direct test of the control part of the hypothesis which involved lipid reduction via removal of the uropygial gland found that lipid level had no effect on dustbathing behavior (Borchelt et al., 1979).

The reason for dwelling on the causation of dustbathing in birds is that the lipid-regulation hypothesis has been taken directly from the ornithological literature and applied to sandbathing in mammals - specifically kangaroo rats (Dipodomys). This appropriation can be understood in terms of similarity in presumed stimulus (lipid accumulation in skin appendages), consequence (lipid removal), and response topography (contacting a particulate substrate with the integument and its excresences). A striking difference which has not been emphasized is that while birds of many (but not all) species (Bolliger & Varga, 1961) control the level and distribution of feather lipids through the application of preen waxes derived from the uropygial gland, via oiling behavior, the level and distribution of mammalian hair lipids is controlled largely by physiological parameters such as the size, site, and activity of sebaceous glands. A notable exception here is the Mongolian gerbil which can produce a rapid change in pelage lipids when it spreads Harderian exudates throughout the fur by means of autogrooming movements (Thiessen & Pendergrass, 1985). Dustbathing in quail is tightly coupled to oiling behavior in the sense that its frequency is limited by the frequency of oiling (Borchelt et al., 1979). No such relationship has been described for the gerbil.

The lipid-regulation hypothesis was tested by Griswold et al. (1977). Either lanolin or water (control) was applied to the left or right side or to the ventrum of kangaroo rats (Dipodomys merriami). Subjects treated with lanolin increased the frequency of sandbathing acts directed to the treated body surface while animals treated with water did not. This was interpreted as support for the lipid regulation hypothesis.

There is good reason to question this conclusion. First, lipid was not manipulated <u>at normal physiological levels</u> so that the experimental findings might not explain normal behavior. In addition, lanolin is solid at room temperature so that the experimentally-applied wax (which was first heated to (38 °C) would tend to harden on the fur. As such, it might be expected to provide a stimulus modelling some hard object snagged in the fur rather than increased greasiness. This notion is supported by the persistence of sandbathing and grooming during the whole 10 min of the test while sandbathing normally satiates in 3 min, even after a deprivation period as long as 10 days (See Borchelt, Griswold, & Branchek, 1976).

The receptor population involved in monitoring greasiness of the pelage does not appear to have been discussed in the literature. However, this is not a problem for the lipid-regulation hypothesis. One of the most plausible accounts of the evolution of hair sees it as derivative of sensory structures (Ling, 1970). In addition to its protective and insulative role, mammalian hair retains a sensory function. Specialized tylotrich follicles (which are similar in structure and function to the vibrissa follicle) are distributed at intervals of 3 to 5 mm around the skin of the rat and chinchilla and are present in other mammals (Straile, 1960). Since increased greasiness leads to matting of the fur, it could plausibly alter the input from neural networks associated with the tylotrich follicle via altered deflection of the fur. Another possibility is that a greasy mammal may experience reduced insulative capacity of the fur leading to an altered state in cutaneous thermoreceptors.

2. Hormonal Factors

The frequency of scent-marking behavior in many species is affected by sex hormones (reviewed in Johnson, 1973). Androgens produce a peripheral effect by increasing the size and hence the secretory capacity of scent glands. Thus, Quay (1953) found that the dorsal gland of two Dipodomys species showed a cycle of secretory activity which was correlated with the breeding cycle. Castration of male Merriam's kangaroo rats causes involution of the specialized sebaceous gland in the dorsum but does not produce a reduction in the frequency of sandbathing (Lepri & Randall, 1983).

Although increased sebum production may generate peripheral stimulus conditions capable of enhancing scent-marking frequency, this is not the only possibility. Androgens are known to have a central effect on marking behavior and Thiessen and Yahr (1970) identified the hypothalamus as the site of androgenic action in the case of the Mongolian gerbil. They also report that removal of the ventral scent gland has no effect on marking frequency. It should be noted that although the gerbil exhibits sandbathing behavior (Tortora, Eyer, & Overmann, 1974), its marking behavior is directed towards low-lying objects, rather than to a particulate substrate (Thiessen, Blum, & Lindzey, 1969; Thiessen, Friend, & Lindzey, 1968) and can be clearly distinguished (Tortora et al., 1974), marking and sandbathing in Dipodomys merrami (and in microps) are topographically identical (Randall, 1981b). The desert woodrat (Neotoma, lepida

lepida) appears to resemble the gerbil in both ventral marking and sandrolling topography. Marking behavior of this species is controlled by androgens but sandrolling is not. Females roll more than males and estrogenic control has been demonstrated (Fleming & Tambosso, 1980). Randall (1986) reports a lack of gonadal control of sandbathing in Dipodomys spectabilis (bannertail kangaroo rat).

Central Factors

A clear indication of central control of sandbathing frequency has yet to be reported although there is considerable evidence that other COBS activities are emitted independently of tactual sensory input or feedback. An example of the first sort is provided by Baillie and Morrison's (1963) demonstration that postprandial grooming in the rat may follow intragastric delivery of food indicating that movements are not stimulated by food debris attached to the orofacial region. An extreme example of the second sort is the persistence of species-typical autogrooming patterns in mice whose forelimbs were amputated at birth (Fentress, 1973a). (For other examples, see Chapter 5.) Behavioral demonstration of central control of sandbathing could be accomplished by showing that sandbathing frequency increases with deprivation of the opportunity to perform the behavior even when relevant peripheral inputs remain constant. As already described, lipid level in the fur has been proposed as one source of appropriate information controlling sandbathing. If lipid level were held constant while deprivation level varied and was shown to affect sandbathing frequency, then a case could be made for primarily central control of sandbathing frequency. Such experiments have not been carried out. Even if the above result were produced, the behavior would not be emitted in the absence of appropriate contextual determinants. Preliminary work on the chinchilla in this laboratory suggests that the texture of the substrate is one important influence since coarse sea sand may fail to elicit sandbathing in a suitably sand-deprived animal. However, it appears that this form of control may be overridden by other strong contextual cues since an animal that is accustomed to sandbathing on being placed in a particular container may produce a number of sandbathing spins when the container is presented completely empty of sand.

CHAPTER 4

The Chinchilla and its Sandbathing Behavior

Taxonomy

The rodent family Chinchillidae contains three living genera and a total of six species. Lagostomus consists of a single species, Lagostomus maximus (the plains viscacha). Lagidium (the mountain viscachas) have been divided into three species based on size, color, and locality (see Rowlands, 1974). The third genus, Chinchilla, is normally divided into two species, C. laniger (the more familiar chinchilla which is farmed for its fur) and C. brevicaudata (the short-tailed chinchilla). While this division has been disputed, it appears to be firmly supported by information concerning the infertility of (male) hybrids (Grau, 1974). A good discussion of the taxonomic controversy surrounding Chinchilla is provided by Mohlis (1978).

Ecology

While certain behavioral similarities, such as colonial living in burrows or rock cavities, unite all three genera, a broad distinction can be made on the basis of ecological niche. Lagostomus is a plains-dwelling creature while both Lagidium and Chinchilla are adapted to rocky montane conditions and their "natural habitat" is stated to be the rather barren areas of the Andes at elevations of 3,000 to 5,000 m (Nowak & Paradiso, 1983). That chinchillids can exist and breed at such elevations certainly tells us something about the selection pressures shaping their behavior and physiology.

Eisenberg (1981) compares their niche to that of Ochotonidae (pikas of Asia and North America) which typically inhabit alpine slopes. Nevertheless, the wild chinchillas (Chinchilla laniger) studied by Mohlis (1978) occupied a region whose maximum elevation was 1,700 m and reports by early observers suggest that chinchillas at one time survived right down to sea level (e.g., Bidlingmaier, 1937). Distribution maps for the two species of chinchilla are provided in Mares and Ojeda (1982) and in Grau (1974). Both confine C. laniger mainly to Chile but the more recent publication places them in the extreme north of the country while Grau places their range entirely south of 28° latitude. Mohlis (1978) provides a distribution map which substantially agrees with that of Grau (1974).

High altitude, per se, does not appear to be a critical necessity for reproductive success. What is necessary is the existence of rockpiles having an abundance of narrow crevices in which the chinchilla can elude its many predators including foxes, felids, grison, and hawks. Mohlis (1978) reports that chinchillas were found only on rocky slopes with an inclination from 18 to 40 degrees. "The substrate is usually a combination of sandy soil, fine gravel, and talus, with rockiness ranging from 30 to 100%" (p. 25).

Chinchillas are probably better characterized as rock-dwelling rather than as high altitude specialists, although the presence of abundant talus slopes in the high Andes have probably acted as a safe haven allowing the species to survive in the wild despite extinction at lower elevations due to over-hunting. Many forms of behavioral and morphological convergence have recently been identified in rock-dwelling animals (Mares & Lacher, 1987). These include: herbivory, padding of the feet with nail reduction, the presence of a specialized grooming claw or analogous structure, use of rocks as lookout posts, and the giving of alarm calls. Both Chinchilla and Lagidium share most or all of these features of the typical rock-dweller and Lagidium also exhibits the tendency to climb trees (see photo in Nowak & Paradiso, 1983). However, neither conforms to the system of social organization based on harem polygyny which has arisen among many rock-dwelling mammals - apparently because suitable rock habitat is a resource which can be controlled by a single male. Both chinchillas and mountain viscachas live in colonies which are composed of distinct reproductive units based on mated pairs (Grau, 1974; Kleiman, 1974; Mares & Lacher, 1987; Mohlis, 1978; Nowak & Paradiso, 1983; Osgood, 1943; Pearson, 1948).

Other important parameters of the chinchilla habitat reported by Mohlis (1978) include rainfall and temperature. Annual precipitation averaged 161 mm during the 3 years of the study and was distinctly seasonal falling only between the months of May and August. Chinchillas are largely nocturnal so that they experience the lowest daily temperatures which range from approximately -2 °C to 15 °C throughout the year. Average daily maximum temperatures remain quite close to 30 °C for much of the year. A substantial daily fluctuation in temperature would thus appear to be the norm. Temperature within the rocks would fluctuate much less. This means that the chinchilla, due to its nocturnality occupies a low-temperature niche while mountain viscachas occupying similar terrain experience a more temperature climate by virtue of their diurnality (Pearson, 1948).

The key to the ability of the chinchilla to withstand low temperatures in its barren and windswept montane habitat (Osgood, 1943; Pearson, 1948; Perry, 1981) is in its extremely fine fur. The number of wool hairs per guard hair has an average value of 50-60 (Lyne, 1965; Wilcox, 1950) compared to a reported value of "a dozen or so hairs per tuft" in the mountain viscacha whose fur has little commercial value (MacClintock, 1966). The thickness of the fine wool hairs is variously reported as 5-11 micrometers (Wilcox, 1950) and 13-17 microns (Sokolov, 1982) while the guard hairs range from 12-15 microns (Wilcox, 1950) and 50-59 micrometers (Sokolov, 1982). Density of the hair is 250/mm^2 compared with 310/mm^2 for <u>Gerbillus nanus</u> and 167/mm^2 for <u>Dipodomys merriami</u> (Sokolov, 1982). The importance of fur density (as opposed to thickness, see Hammel, 1955) as an adaptation to cold is underscored by Sokolov's (1962) finding that in several rodent species the fur is much thinner in summer than in winter.

<u>Social Behavior</u>

A brief description of chinchilla social behavior is relevant to the study of sandbathing because odor deposits at sandbathing loci apparently have a communicatory role in some species. Evidence for this role in <u>Meriones</u>, in various heteromyids, and in <u>Degus</u> has already been presented.

Wild female chinchilla are heavier than males, (442 ± 34 g SD vs. 423 ± 31 g, Mohlis, 1978). They are also more aggressive although aggressiveness declines during the post-partum estrus when mating occurs (Weir, 1966). The sex ratio is highly skewed in favor of males (119 males per 100 females, Weir 1976). While Grau (1974) maintains that chinchillas are monogamous, this has been disputed (Mohlis, 1978). However, trapping data does suggest male-female bonding although this is apparently less stable over time than the bonds between females and their offspring, particularly female offspring (Mohlis, 1978).

Whatever the reality of the chinchilla mating system, adult males follow the hystriocomorph pattern of unusually high tolerance towards young and it is reported that they sit with offspring and may be protective of them (Kleiman, 1974). Colonies consist of several breeding pairs with their offspring (Grau, 1974; MacClintock, 1966; Mohlis, 1978; Weir, 1970) and it appears that dens may be defended against conspecifics since a male which sought refuge in nearby rocks upon release from a trap was attacked by residents and died from its wounds shortly afterwards (Mohlis, 1978).

Sandbathing

All three chinchillid genera are said to engage in dustbathing behavior (Nowak & Paradiso, 1983) but only the sandbathing behavior of the chinchilla appears to have been described in the scientific literature published in English. This consists of a sequence having three major components:

1. The paw phase in which the front paws execute rapid digging movements that throw loose substrate beneath the ventrum.

2. The cheek phase in which either or both of the cheeks or the vibrissae touch the substrate briefly.

3. The rolling phase in which the chinchilla throws itself on its lateral or dorsal surface, writhes, and returns to its feet either by retracing its rotational course or by completing a 360° revolution. The direction of the roll is typically the same as that of the last cheek rub. Ventrum rubs are rarely seen. The phases usually occur in the above sequence but order is not invariant and the pattern may be incomplete. Sandbathing may be followed by vigorous shaking of the entire body (Eisenberg, 1963a; Stern & Merari, 1969). It should be noted, however, that fine-grained quantitative analysis of sandbathing components has not been performed.

An immediate consequence of sandbathing in the case of the chinchilla which has been deprived of sand for long enough for the fur to become noticeably greasy and matted is an apparent reduction in fur lipids. Following 24 hrs access to sand, the fur appears light and fluffy and the effect is analogous to shampooing.

Sandbathing distributes fine particles of sand throughout the pelage and these may remain in the fur for some time following removal of the sand box. However, it is likely that much of the sand that contacts the fur is removed by simple gravitation, by ordinary locomotion, or by body-shaking.

If lipid in the fur adheres to the sand particles, it can be drawn off when the sand is removed. (As Eisenberg, 1981, notes, the same method is used by many mammals in drying their fur.) This principle has also been used in the clothing industry. A fine clay, known as fuller's earth, absorbs oil and grease and is useful in scouring textiles (Linton, 1973). Fuller's earth is an effective substrate for eliciting sandbathing in the chinchilla (Glickman, 1973; Stern & Merari, 1969) and preliminary observations in this laboratory indicate that a sea sand, a much coarser material, is less effective in this regard. The same dependence upon substrate texture was noted by Benson and Schein (1965) and by Borchelt and Overmann (1974) in connection with work on dustbathing in two species of quail (Japanese and bobwhite).

Some hypothetical functions of sandbathing have already been outlined and it seems likely that the behavior does serve to care for the skin in chinchillas whether this takes the form of cleaning and rearranging the pelage or of removing ectoparasites (perhaps by interfering with their respiration, by dessicating them, or by scraping them from the skin, see Borchelt et al., 1979). To the extent that sandbathing fluffs up the fur and thereby increases its insulative capacity (Hammel, 1955) a thermoregulatory role might be suspected. However, this hypothesis would predict an increased frequency of sandbathing at low temperatures while the known temperature dependence of sandbathing in the Mongolian gerbil is in the opposite direction and this has been explained in terms of the effect of sandbathing on fur color - it lightens it - in this species. A lighter pelage has an increased solar reflectance (Pendergrass & Thiessen, 1983). The chinchilla is nocturnal and chromatic effects on reflectance are probably irrelevant. Since lipid level in the fur may be positively related to insulation (Thiessen & Kittrell, 1980), the effect of altering temperature on sandbathing frequency in the chinchilla would be an intriguing experiment which offers the possibility of deciding between two reasonable but contradictory hypotheses. One predicts decreased sandbathing in the cold so as to conserve insulating lipids. The other predicts increased sandbathing which would have the effect of fluffing up the fur thereby increasing the volume of entrapped insulating air.

Whether sandbathing plays a role in preventing evaporative water loss in the chinchilla is doubtful because this species is not an extreme specialist for arid conditions. Chinchilla colonies typically do not have access to water holes (Mohlis, 1978) but drinking water is said to be obtained from the course grasses and herbs on which the chinchilla feeds (Perry, 1981). In captivity, drinking may be rather copious and Fried (1986) measured a mean daily intake of approximately 83 ± 24 ml/kg SD for six chinchillas.

This contrasts with the kangaroo rat (Dipodomys spectabilis) which can subsist on a completely dry diet through the use of metabolically-derived water. This meager water supply is defended by an extreme concentration of the urine together with respiratory adaptations which minimize moisture loss in the breath (Schmidt-Nielsen, 1964).

Whether sandbathing fulfills a communicatory role in chinchillas must be regarded as an open question. My own attempt to replicate, using chinchillas, Randall's (1981a) experiment on olfactory communication by kangaroo rats at sandbathing loci produced negative results. However, there are many social and physiological differences between Chinchilla and Dipodomus which mean that Randall's design may well be inappropriate.

In the first place, chinchillas do not seem to have a specialized skin gland analogous to the dorsal sebaceous gland of the kangaroo rat (Quay, 1955). The only such glands are located in the anal region (Sokolov, 1982) and chinchillas do not appear to have a marking movement associated with the anal glands.

Second, chinchillas are colonial (Mohlis, 1978) while kangaroo rats are solitary (Lepri and Randall, 1983, Randall, 1982). It has been suggested that for solitary species deposition of scent at sandbathing loci increases familiarity between neighboring individuals. This could have the important result of reducing intraspecific aggression so that mating is possible when the animals encounter each other (Fleming & Tambosso, 1980; Randall, 1982).

Among group-living animals, there is no need for a specific process of familiarization between mates - this might be expected to result from mere proximity. In such cases, sandbathing may have a role in the acquisition of colony odors as suggested by Kleiman (1974) for infant degus. The aggression directed by chinchillas against an intruding conspecific (Mohlis, 1978) suggests that the colony may be defended against unfamiliar individuals. Safe havens in the rock are believed to be a limiting resource for both Lagidium (Pearson, 1948) and Chinchilla (Mohlis, 1978). Most rock-dwelling specialists do, in fact, defend their refuges against conspecifics (Mares & Lacher, 1987).

CHAPTER 5

Sandbathing as a Behavioral System with Complex Determinants

COBS has functional (Borchelt, 1980) and structural similarities across taxa as widely separated as birds and mammals (Lorenz, 1958). Lorenz interprets the awkward wing-lowering of birds when they preen the head feathers, which resembles the head-scratching movement of mammals, as derived from a common tetrapod reptilian ancestor. Whether such similarities are homologous or convergent is often difficult to say but the assumption that COBS of homeothermic vertebrates reflects some shared mechanisms appears reasonable.

Cutaneous irritants (dirt, parasites, lipid accumulation) have been mentioned as possible stimuli eliciting COBS but even a superficial review of the literature cannot avoid the impression that grooming may occur independently of skin stimulation. A number of observations support this conclusion:

1. Fentress (1973b) observed that grooming in voles may increase in frequency under fear-eliciting conditions.

2. Autogrooming is socially facilitated in the Mongolian gerbil (Thiessen, 1977).

3. Removal of the lipid-producing uropygial gland in birds does not reduce their dustbathing behavior (Borchelt, 1980).

4. If a rat is prevented from grooming itself by means of an Elizabethan collar, it will direct grooming behavior towards the pelage of a conspecific, even though such allogrooming is atypical of adult-adult encounters (Raino & Carr, 1986).

5. "Sandbathing" in the chinchilla can be produced in the absence of sand (Roche, unpublished data) suggesting that the behavior may be controlled by a context (being placed in the test chamber) rather than by cutaneous stimulation associated with the substrate.

6. Preening behavior of the herring gull may emerge as a result of conflicting behavioral tendencies. For example, if the bird is incubating and a weak escape tendency is provoked by a distant predator, there is an apparent disinhibition of preening (Alcock, 1975). According to Randall (1982, and personal communication) kangaroo rats may sandbathe soon after release from the trap suggesting that the tendency to escape from the trap site may be in conflict with the tendency to return to the adjacent burrow producing a disinhibition of sandbathing. For a review of such "displacement" grooming, see Zeigler (1964).

7. In general, the grooming behavior of many mammals seems to occur as part of a daily routine independent of dirt or matting in the coat or the presence of parasites (Bunnell, 1973).

8. Grooming may follow intragastric delivery of food in rats (Baillie & Morrison, 1963). This rules out the commonsense explanation that post-prandial grooming is elicited by food particles adhering to the orofacial region, and suggests that there is a sequential dependency between feeding-related processes and COBS.

9. Bolles (1960) reported that grooming in the rat is sequentially dependent on several other behavioral systems:

> Grooming is a form of activity that occurs after other kinds of directed behavior have occurred. According to this hypothesis, some type of grooming may be expected after an animal has eaten, drunk, manipulated novel objects, or been frightened. It is not proposed that all grooming occurs under these conditions; grooming also occurs when animals prepare for sleep, or are bitten by fleas. (p. 310)

According to Barnett (1975) brushing of the vibrissae occurs in the rat following interruption of exploration, coitus, or attack. Tinbergen (1952) similarly lists several examples of grooming as a response to frustration: scratching the fur in chimpanzee and orangutan; headscratching, nailbiting and rearrangement of hair in humans. He also describes precopulatory preening and bathing in various bird species.

10. Fentress (1983) describes postural facilitation of grooming in young mice:

> Golani and I demonstrated this by setting infant mice up into a posture commonly used by adults when grooming. Finding themselves thusly situated, the animals frequently commence to groom (that is, make the rhythmic forelimb movements we are calling, for convenience, grooming). And if they slow down or doze off, they can be made to "groom" again merely by pinching the tail lightly! (p. 32)

11. Grooming movement sequences in mice may survive deafferentation of the forelimbs and even persist in the complete absence of peripheral input caused by forelimb-amputation at birth. Thus, rhythmical tongue extension, which normally serves to moisten the forelimbs, maintains its synchrony with movement of the leg stumps even though these cannot extend to the face (Fentress, 1973a).

Considering the above examples, it is possible to conclude that COBS in general and sandbathing in particular may have complex determinants which can be analyzed in terms of distinct initiating, maintaining and terminating factors. Experimental methodology deals with such complex problems through independent manipulation of single variables. Investigation typically focuses on factors considered to account for much of the variance in the behavior.

The lipid-regulation hypothesis has been advanced as an explanation for the correlation between sandbathing frequency and sand deprivation level in kangaroo rats (Griswold et al., 1977) although some problems were encountered in the interpretation by these authors of their experimental results. Could a similar mechanism control sandbathing frequency in the chinchilla?

Testing the Lipid-Regulation Hypothesis

The lipid-regulation hypothesis (LRH) begins with the observation that deprivation of access to a suitable particulate substrate leads to two consequences. First, lipid level of the integumentary appendages is increased. Second, the frequency of sandbathing movements is increased once access to the particulate substrate is provided. The second consequence is explained in terms of the first.

From this perspective the IRH can be seen as an explanation for the effect of sand-deprivation on sandbathing frequency. As noted in Chapter 2, sandbathing frequency is reported to increase with deprivation level for a number of rodent species, including the chinchilla (Stern & Merari, 1969). An unfortunate aspect of the Stern and Merari design was their failure to gain control over the sand-deprivation level. This point is illustrated by the presence of order effects in the data. In addition, these authors do not present a baseline measure at 0 days deprivation against which the effects of sand-deprivation can be assessed. An experiment was therefore run which measured baseline sandbathing and which was designed to deal with the problem of order effects (Experiment 1). It does this by providing continuous 24 hrs access to sand between deprivation periods and through partial counterbalancing. In the Stern and Merari (1969) experiment, access to sand was received only during the 10 min tests.

The IRH yields three testable predictions:

1. Addition of lipid to the fur will increase sandbathing frequency. This prediction was tested by Griswold et al. (1977) using kangaroo rats. Their results supported the IRH but interpretation of the experiment is complicated by two problems. First, as noted above, it can be questioned whether the experimentally applied lanolin is an appropriate model for natural accumulation of skin lipids. Second, according to Eisenberg (1981), wetting of the fur may lead to bodily contact with the substrate (as

an aid to drying) even in species which do not normally sandbathe. This again suggests that the experimental stimulus, which is suddenly applied, may be unrelated to the stimuli normally controlling sandbathing. It should be noted that the inclusion of a water control does not answer this objection since a similar cleaning reflex may be elicited in each case, the only difference being that water is rapidly removed while lanolin is not. One solution to this problem is to allow time to elapse between application of the experimental lipid and behavioral testing thereby allowing any rapid-acting reflex response to the treatment to become fatigued. However, this is not an entirely satisfactory approach because reflex body-wiping may simply fail to be elicited in the absence of an appropriate substrate. This experiment was nonetheless carried out in the interests of a comprehensive interpretation of factors eliciting sandbathing (Experiment 3).

2. Removal of fur lipids should result in a decrease in sandbathing frequency. Loss of all lipids removable by sandbathing should result in little or no sandbathing behavior. This prediction would appear to offer a more promising opportunity for testing the LRH since lipid levels can be manipulated within normal upper physiological limits. It does not appear to have been adopted in any previous investigation of sandbathing. Experiment 2 examines the effect of shampooing on sandbathing frequency.

3. Lipid level in the fur increases with sand deprivation and decreases as a function of exposure to sand. This prediction is supported by mainly anecdotal evidence. The one quantitative test

(of the second element of the prediction) found that 8-16 days of living on a sandy substrate are necessary before pelage lipids are reduced in the Mongolian gerbil (Thiessen & Pendergrass, 1985). The gerbil may be anomalous in this respect due to the copiousness of its Harderian secretions. The first element in the prediction is consistent with data derived from quail in which feather lipids increase with dust deprivation (Borchelt & Duncan, 1974). Once again, the oiling behavior of birds can be used to question the relevance of this work to most mammals. An experiment was therefore carried out with the objective of measuring the effect of exposure to sand on lipid levels in chinchilla fur (Experiment 4).

CHAPTER 6

General Aspects of Design and Procedure

(Experiments 1-4)

As previously discussed, the lipid-regulation hypothesis predicts a positive correlation between sandbathing frequency, as a function of deprivation, and lipid content of the fur. Frequency refers to the number of sandbathing acts in which the substrate is contacted by the fur (rubs, rolls, etc.). Test procedures typically measure changes in sandbathing frequency within a bout but it is important to realize that the frequency of bouts may also be responsive to deprivation. No previous study has measured both sandbathing frequency and lipid level of fur in the same subjects in any species. The reason for this is that measurement of lipid levels may be intrusive with respect to the behavioral measure (Borchelt et al., 1976).

Lipid measurement commonly involves the close clipping of fur samples, and the creation of exposed patches of skin might be expected to interfere with sandbathing behavior. The same objection could be raised against other possible extraction procedures (e.g., dipping the whole animal in solvent) and at present there does not appear to be a genuinely noninvasive technique for reliable measurement of fur lipids (Nicolaides & Kellum, 1965).

This problem can be overcome by completing the behavioral tests first and taking fur samples in a subsequent experiment which replicates the sand deprivation conditions of the behavioral experiments. This method is indirect and the separation of behavioral and lipid measures in time is a possible source of confounding. Nevertheless, this strategy was adopted as offering the best promise for elucidating the relationship between lipid in the fur and sandbathing frequency.

The same subjects were used in all four experiments. A repeated measures design was chosen as a convenient method of removing between-subject variability which can be substantial with respect to both sandbathing frequency and pelage lipid level (the main dependent variables of the experiments). Order effects were dealt with in two different ways. First, shampooing was used with the objective of restoring a constant baseline initial condition of the pelage. This assumption is supported by pilot data derived from three subjects, each shampooed four times. Mean lipid level following the first shampoo (53 mg lipid/g fur) was virtually the same as that following the fourth (55 mg lipid/g fur). Second, partial counterbalancing was used to distribute the effects of the order in which a particular treatment was received. For this purpose, subjects were divided into two groups (A and B) each group containing 4 males and 4 females. Groups were matched according to sandbathing frequency in preliminary tests.

Subjects

Eight male and eight female chinchillas were tested in each of the four experiments. With one exception, the same subjects were used for each experiment: A female subject died of unknown causes following the conclusion of the first experiment and was replaced for subsequent experiments by a suitably prepared female (see below). Fourteen of the subjects ranged from 9-37 months of age at the beginning of the experiments (M = 22 ± 11 months SD). Ages of the other three animals were unknown due to inadequate record keeping but they were at least three years old. Average weight was 446 ± 64 g SD, males, and 512 ± 58 g, females. Eight of the the subjects were experimentally naive. The others had served in pilot studies (height preference, operant level running). All were raised in the Hunter College colony and derive from stock acquired from Brown University. Housing was in individual cages (46 x 46 x 34 cm). Lighting was regulated at 12L : 12D and the light cycle began at 0730 hours. Testing started at 0800. Temperature was controlled at 21 °C (± 2 °C SD). Food (Purina Chin Chow, Ralston Purina Co, St. Louis, MO) and water were available ad lib. Subjects were provided with pine gnawing blocks.

Apparatus

Behavioral testing was carried out in the home cage using 16 glass aquaria (each 30 cm long x 15 cm wide x 20 cm deep) fitted with 3 mm transparent plexiglass lids which served as sand containers. The purpose of the lids was to prevent undue dispersion of sand about the colony room during sandbathing activity. Access to the sand was via a 100 mm diameter circular hole in the lid. Each subject was assigned its individual test container so as to rule out social odor-mediated effects on sandbathing frequency which have been reported for sandbathing loci in kangaroo rats (Eisenberg, 1963b, 1967, 1975; Laine & Griswold, 1976; Randall, 1981a) and in desert woodrats (Fleming & Tambosso, 1980). Effects of human odor deposits were minimized by wearing disposable plastic gloves whenever the test chambers were handled.

Preliminary testing

Experimental subjects were selected from an initial subject pool of 21 on the basis of sandbathing performance in preliminary tests. Habituation to the individual sand containers was via three sessions of 24 hrs continuous access in the home cage separated by three and two days respectively. Following habituation, access to sand was allowed only during the 5-min preliminary tests. The intersand access interval varied from 1-4 days. The purpose of these preliminary tests was to establish prompt and reliable entry into the sand chamber and emission of sandbathing behavior upon introduction of the container into the home cage. The criterion for selection as a subject in the experiments was the production of at least one sandbathing roll per test in 10 consecutive tests. This criterion was reached by all 16 subjects within 25 tests. The final seven tests were received at an intersand interval of 24 hrs and the last five of these tests were used to assess the reliability of individual measures of the number of sandbathing rolls. Two of the five tests were chosen by random selection without replacement for each subject. The correlation coefficient was calculated as $\underline{r}(14) = .92$, $\underline{p} < .001$. This implies that test-retest reliability in sandbathing rolls of individual subjects was 85% ($\underline{r}^2 = .85$). This value compares favorably with estimated reliabilities of dustbathing components in quail the maximum value of which was $\underline{r}(16) = .83$ ($\underline{r}^2$

= .69, Borchelt, 1975).

Behavioral Test

Behavioral tests were initiated by placing the test chamber in the home cage. The duration of the test was 10 min. Failure to enter the test container within 10 min resulted in a recorded sandbathing frequency of zero and a latency score of 600 s. Sandbathing rolls and other behaviors were recorded in 1 min intervals using a simple checklist. Also recorded were visits to sand (occasions on which the subject entered the sand box). Grooming behavior (i.e., oral contact with the fur) was recorded on a One-Zero basis in Experiment 3. This sampling technique is not suitable for a quantitative analysis of behavior (Altmann, 1974; Martin & Bateson, 1986) but can be used where the sole objective is to establish whether, and in which intervals a behavior occurs, i.e., where there is no intention to convert the data to frequencies or durations (see Altmann, 1974). The latency to sand, i.e., time elapsed between placement of the container and the subject touching the sand (1 L of ground Attapulgus clay, 50/80 RVM, Engelhard Minerals and Chemicals), was recorded to the nearest second using a digital watch. Time spent in the sand was cumulated using a micro-timer (Dimco-Gray) operated by a hand switch.

The door of the cage was opened 20 s before the beginning of the test. When 10 s had elapsed the test container was slowly moved into the cage and held well clear of the cage floor for a further ten seconds. When the container was placed horizontal on the cage floor the test began. The cage door was then quickly but gently closed and the subject was observed through the (19 mm) mesh.

Shampooing

Subjects were shampooed both as a means of producing a standard initial condition of the fur with respect to lipid content (Experiment 1, 2, 4) and also as an experimental manipulation of pelage lipid (Experiment 2, 4). Johnson's Baby Shampoo has been used for such purposes in a number of other studies (Lepri & Randall, 1983; Randall, 1981b; Thiessen & Kittrell, 1980; Thiessen & Pendergrass, 1985) and was also used here - its choice determined by the desire to avoid skin irritation.

During shampooing, subjects were held, by the neck, in a restraint device. All of the fur, apart from that of the head, was thoroughly soaked under running warm (35 ± 1 °C SD) tapwater. Following an application of Johnson's Baby Shampoo, (approx. 8 ml), the subject's fur was massaged for 1 min and then rinsed. This procedure was repeated twice for a total of three applications of shampoo. Following the final rinse, the subject was returned to its cage and allowed to dry. This took approximately 2 hrs. Control washing with water alone was intended to leave fur lipids intact (see Thiessen & Kittrell, 1980). This consisted of soaking the subject thoroughly under warm tapwater (approx. 30 sec). More prolonged water washing and manipulation of the fur were avoided because of the possibility that lipids might be removed as a result.

CHAPTER 7

Experiment 1: Effect of Sand Deprivation Level on Sandbathing Frequency

The main purpose of the first experiment was to look at the relationship between sand deprivation period (0, 1, or 5 days) and sandbathing frequency. The effect of sand deprivation on the frequency of sandbathing rolls ("spins") was previously investigated by Stern and Merari (1969, reproduced as Appendix 3). Three females and one male chinchilla served as subjects in this experiment. Four deprivation periods were used (1, 3, 5, 7 days) and all subjects were tested four times at each deprivation level (16 tests) such that each deprivation period both preceded and followed every other deprivation period exactly once.

While Stern and Merari (1969) found that the number of sandbathing rolls by chinchillas does increase as a function of intersand interval, interpretation of this finding is complicated by two aspects of the design. The first was failure to include a control condition in which subjects were tested at a deprivation level of zero. The second arises from the fact that access to sand was received only within the 10 min tests. Although a sandbathing bout may conclude within this time, an ad lib level of sandbathing is not reached. This point can be deduced from the existence of strong order effects in the data. For example, the number of rolls produced by an intersand interval of 7 days which happened to follow a previous intersand interval of 1 day was less than the number of rolls produced by an intersand interval of 1 day which happened to follow a previous intersand interval of 5 or 7 days. In analyzing Stern and Merari's (1969) data, I have found that the sum of present and previous intersand interval produces a much better predictor of sandbathing frequency ($\underline{r}$ = .85) than does present intersand interval alone ($\underline{r}$ = .61). The same is true for the sum of the three most recent intersand intervals ($\underline{r}$ = .78).

This cumulative effect of successive intersand intervals is an interesting finding since it suggests a complex motivational system which can be compared with that controlling feeding. The point of the analogy is that both behaviors appear to be organized on more than one time scale. While a sandbathing bout (or a meal) may terminate within a 10 min test, knowledge about such short-term satiation does not permit more longterm predictions to be made. Thus, a rat that is reduced to 70% of its body weight and then provided with ad lib. food will not continue to eat until the deficit in body tissue is made good. Instead, it will respond by an increase in meal frequency and perhaps in meal size until body weight has been restored to its defended level (Le Magnen, 1971). The apparent existence of a similar effect of deprivation on the temporal patterning of sandbathing raises the issue of whether some physiological parameter analogous to body weight (e.g., lipid level in the fur) is defended by sandbathing.

Interesting as the Stern and Merari (1969) order effects are, it is desirable to avoid them in the interest of a more precise specification of the independent variable (deprivation of sand).

Subjects were given 24 hrs continuous access to sand in the home cage prior to each deprivation period with the intention of establishing an ad lib level of sandbathing. In addition, partial counterbalancing was used to distribute, and to enable visualization of, order effects. Finally, a baseline measure was taken (i.e., 0 days deprivation) both before and after the experimental manipulations so as to assess the possibility of a spurious deprivation effect based on order.

Method

Procedure

The design of the experiment is presented in Table 3. Groups were matched for sandbathing frequency and each contained four males and four females (see Chapter 6). Group A received its deprivations in the order 0, 1, 5, 0 days while Group B received them in the order 0, 5, 1, 0. Deprivation periods were initiated by shampooing (to produce a standard initial condition of the pelage and ended in a 10 min behavioral test (described in Chapter 6). Control measures differed in this respect since subjects were shampooed the day before testing so as to minimize the possible confounding effects of shampooing on the test day on sandbathing frequency. The shampooing procedure is described in Chapter 6.

Access to sand in the home cage was provided by placing individual test chambers for approximately 24 hrs. After such continuous access, the sand was sieved in order to remove fecal pellets. If the lids became soiled, these were removed and washed in warm tapwater. Disposable plastic gloves were worn when handling the

Table 3

Design of Experiment 1

	Manipulations	
Day/s	Group A (N = 8)	Group B (N = 8)
1	Shampoo	Shampoo
1-2	Sand[a]	Sand
2	Test (D = 0)[b]	Test (D = 0)
2-3	Sand	Sand
3	Shampoo	Shampoo
3-4	Mesh[c]	
3-8		Mesh
4	Test (D = 1)	
4-5	Sand	
5	Shampoo	
5-10	Mesh	
8		Test (D = 5)
8-9		Sand
9		Shampoo
9-10		Mesh
10	Test (D = 5)	Test (D = 1),
	Shampoo	Shampoo
10-11	Sand	Sand
11	Test (D = 0)	Test (D = 0)

[a] Continuous access to sand in home cage. [b] Zero days sand deprivation. [c] Access to mesh substrate (i.e., cage floor) only.

test containers so as to minimize the potentially confounding effects of human odor deposits.

Results

Comparison of baseline measures (sand deprivation level = 0 days) for each of the four dependent variables, using the Wilcoxon test (Siegel, 1956) found that there was no significant difference between the first and the second tests (days 2 and 11, Table 3). The mean of the two values was thus used in subsequent analysis. Comparison of Group A and Group B means at deprivation levels of five and one days revealed no significant difference for any of the variables so the data were pooled. Between-group comparisons were made using the Wilcoxon test (see Table 4).

Further analysis of results was by means of two-factor ANOVA with one repeated-measures factor (deprivation) and one between-subjects factor (sex, see Winer, 1962, p. 302). Before conducting the ANOVA, data were screened for homogeneity of variance across deprivation conditions using the Cochran $\underline{C}$ statistic (Winer, 1962). The homogeneity assumption was violated by both rolls and latency measures ($\underline{p} < .01$) and the tendency for variance to increase with the mean is apparent in Figure 1. A log transformation corrected this problem ($\underline{p} > .05$) and also reduced the $\underline{C}$ value associated with the visits measure. Time spent in sand satisfied the homogeneity assumption without transformation and log transformation actually created unequal variance ($\underline{p} < .01$) so this variable was analyzed without transformation while the other three were log-transformed. Contrasts between treatment means were conducted by the

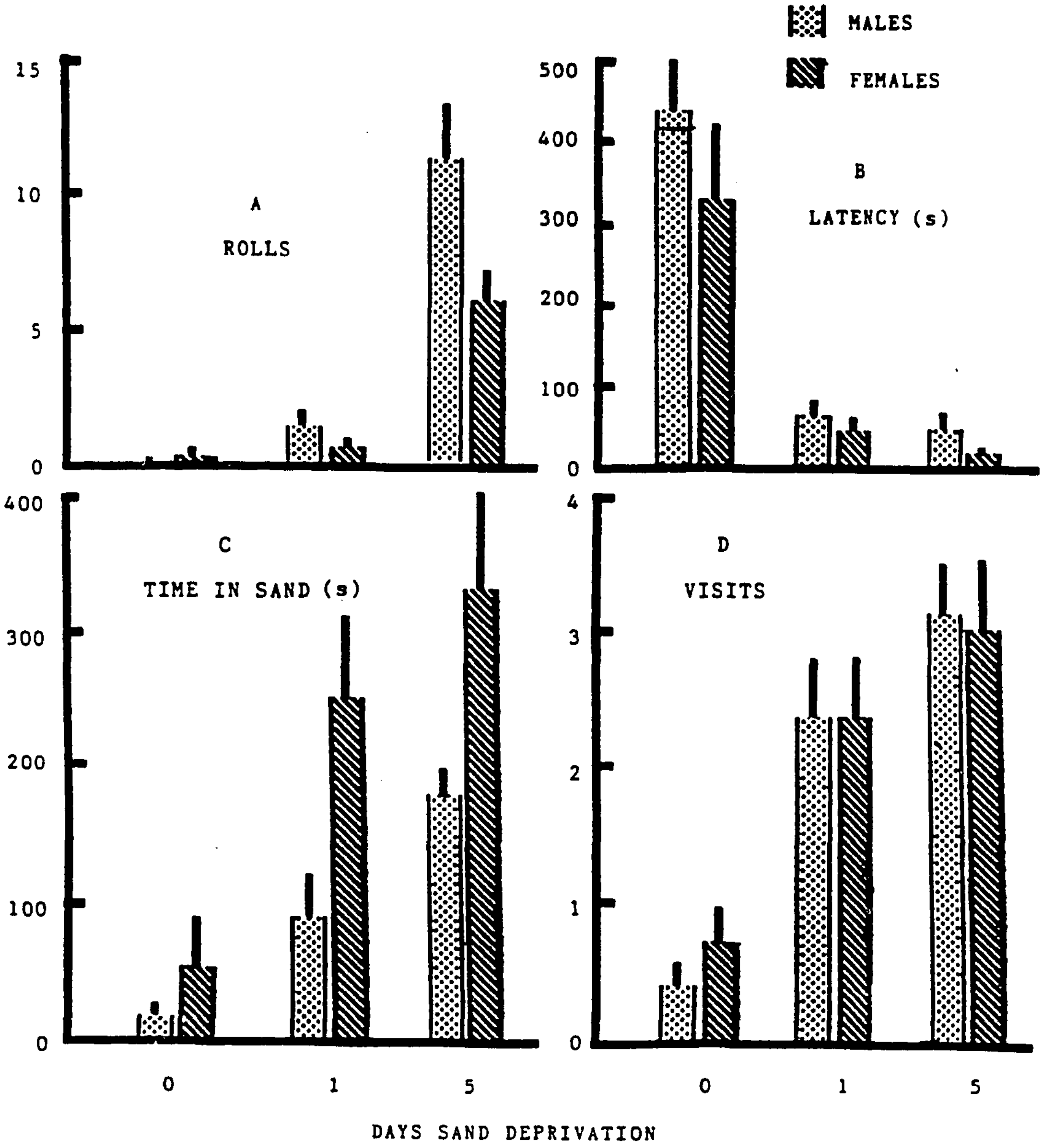

Figure 1. Effects of sand deprivation on sandbathing frequency (rolls) and other measures of attraction to sand (N = 8 males, 8 females). Columns represent means (+ SE). See text for explanation.

Table 4

Tests for Order Effects by Comparison of Group Means

Dependent variable	D[a]	Means Group A	Means Group B	Wilcoxon T (df)[b]	p
Sandbathing rolls	1	1.1	1.0	(8) 17.5	> .05
	5	7.6	9.6	(8) 13	> .05
Latency (s)	1	54	53	(8) 16	> .05
	5	34	30	(8) 16.5	> .05
Time in sand (s)	1	143	190	(8) 16	> .05
	5	223	293	(8) 8	> .05
Visits to sand	1	3.0	2.3	(7) 4	> .05
	5	3.3	2.9	(6) 7.5	> .05

[a] Sand deprivation level in days. [b] Degrees of freedom associated with the Wilcoxon test, i.e., the number of pairs of matched scores which were not tied.

method of Newman-Keuls using a 95% confidence level (Winer 1962, see Appendix 4).

Results of the first experiment are presented in Figure 1 and the significant effects are summarized in Table 5 (see Appendix 4 for ANOVA tables). All four dependent measures were affected by deprivation but only time in sand yielded a significant sex effect.

The number of sandbathing rolls increased with deprivation level, $\underline{F}(2,28) = 104.11$, $\underline{p} < .001$. Chinchillas sandbathed significantly more at five days of deprivation than at one day and significantly more at one day than in the baseline condition. There was no significant sex difference although it can be seen that males sandbathed considerably more than females at the higher deprivation level ($\underline{M} = 11.0$ vs. 6.3 rolls, Figure 1A). There was no sex X deprivation interaction. In the preliminary tests, a similar tendency for males to sandbathe more than females was present. Analysis of mean sandbathing rolls produced by each subject in the final ten preliminary tests revealed a significant sex difference, Mann-Whitney $\underline{U} = 4$, $\underline{p} < .01$ ($\underline{M} = 13.1$ vs. 4.9 rolls). The number of sandbathing rolls produced at five days of deprivation was not correlated either with age or weight of the subjects and the same was true for preliminary data.

Latency to contact with sand from the beginning of a test decreased with deprivation level, $\underline{F}(2,28) = 82.78$, $\underline{p} < .001$. Latency at one day of deprivation was significantly shorter than baseline latency and significantly longer than latency at five days of deprivation (Figure 1B).

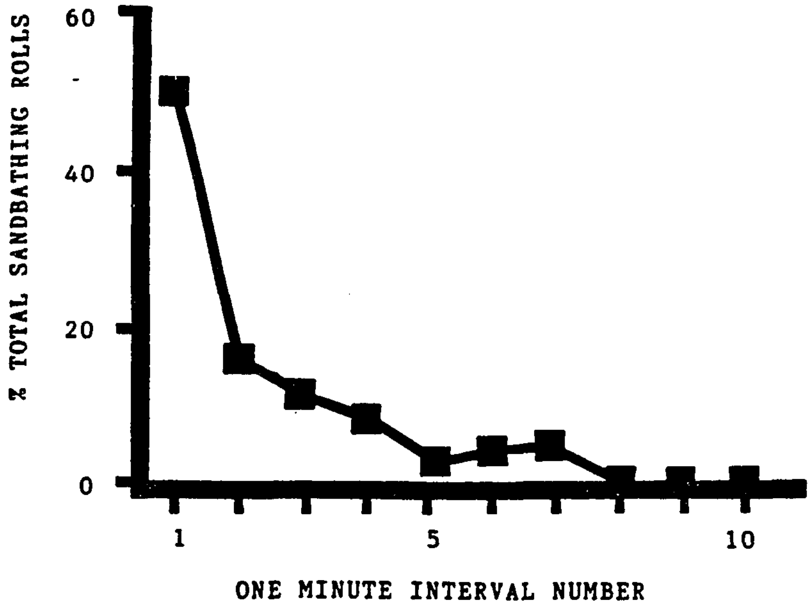

Figure 2. Satiation curve of sandbathing within a 10 min test at a deprivation level of five days ($\underline{N}$ = 16).

Table 5

Summary of Results of Experiment 1 (Means ± SD)

Dependent variable	Sand Deprivation Level (days) 0	1	5	Deprivation effects
Sandbathing[a] rolls	0.1 ± 0.3	1.1 ± 1.3	8.6 ± 5.0	0 < 1 < 5
Latency (s)[a]	380 ± 223	54 ± 48	32 ± 36	0 > 1 > 5
Time in sand (s)	37 ± 80	167 ± 193[b]	259 ± 158[b]	0 < 1 < 5
Visits to sand[a]	0.5 ± 0.6	2.4 ± 1.2	3.1 ± 1.2	0 < 1, 5

[a] No sex effect. [b] Females > males.

Time spent in sand increased with deprivation level, $\underline{F}(2,28) = 25.50$, $\underline{p} < .001$. This was also a systematic effect. Females spent longer in the sand than males at all deprivation levels and the sex difference was significant, $\underline{F}(1,14) = 5.84$, $\underline{p} < .05$ (Figure 1C).

The number of visits to sand increased with deprivation, $\underline{F}(2,28) = 43.87$, $\underline{p} < .001$. The sand container was entered significantly more often under each experimental condition than in baseline but the difference between visits at one and five days of deprivation was not significant (Figure 1D).

Sandbathing rolls tended to occur early in the test (see Figure 2). During the first one-minute segment 41% of rolls occurred at a deprivation level of one day (not shown) and 52% of rolls occurred at a deprivation level of five days. The first half of the 10 min test accounted for 82% of rolls at a deprivation of one day and 88% of rolls at a deprivation level of five days. Deprivation level did not significantly affect the number of individuals producing some rolls in the second half of the test ($\chi^2(1) = 1.13$, $\underline{p} > .05$, McNemar test).

Sand deprivation produced effects on all behavioral measures. If these changes were associated with a change in sandbathing motivation, then a statistical relationship between sandbathing rolls and the other measures would be predicted. This possibility was tested by computing a correlation matrix for the four dependent variables using data collected at a deprivation level of five days. None of the six correlation coefficients was statistically significant ($\underline{p} > .05$, joint confidence level, see Appendix 5).

Discussion

Experiment 1 supports the findings of Stern and Merari (1969) and Roche and Thompson (1987) that sandbathing frequency increases with deprivation level, and this finding can be interpreted as evidence that deprivation increases the size of a sandbathing bout (i.e., number of rolls). Effects of deprivation on bout frequency remain to be investigated. The plasticity of bout size in sandbathing contrasts with the relative inertness of meal size (in rats) subjected to various levels of food deprivation. For this species, and behavior system, compensation following deprivation is largely by means of an alteration in bout frequency (Le Magnen, 1971).

Differences from Stern and Merari (1969)

The results exhibit three striking differences from Stern and Merari's (1969) investigation of the effect of sand deprivation level on sandbathing frequency in the chinchilla. The first is the absence of order effects in the present study. This indicates that 24 hrs of continuous access to sand does indeed reduce sand deprivation level to its minimal value while 10-min access to sand is ineffective in this respect. Yet, sandbathing behavior appears to satiate completely within the 10-min test (Figure 2). This apparent contradiction can be resolved if sandbathing is organized into bouts analogous to the organization of feeding behavior into meals. A 10-min test allows a single sandbathing bout to be concluded, whereas, during 24 hrs of continuous access, several bouts may occur. As a result, sandbathing motivation would be reduced to a lower level than it is following a single bout.

The second striking difference between the present results and those of Stern and Merari (1969) is the lower frequency of sand rolling recorded in the present study. It should be noted that Stern and Merari employ the term "spins" but I use "rolls" since this is a more correct designation of the sandbathing movements which is used by other authors for other species, e.g., Ewer (1968, dunnart), Fleming and Tambosso (1980, desert woodrat), Tortora et al., (1974, gerbil).

The lower level of sandbathing in the present study can be largely attributed to the manner in which the deprivation manipulation was applied. This explanation is supported by the preliminary data in which subjects were treated rather as Stern and Merari (1969) treated their experimental subjects, i.e., only brief periods (5 min) access to sand. During the later part of the preliminary period, access to sand was given daily. Under these conditions, my subjects produced a mean of approximately 9 rolls compared to 12 rolls for the Stern and Merari subjects (1 male, 3 female) in a 10 min test at a "deprivation level" of one day following a previous deprivation of one day. If an adjustment were made for the different lengths of the tests, (based on the distribution of sandbathing in the 10 min tests) then my subjects would have produced approximately 11 rolls. Since these subjects only produced an average of about one roll at one day of deprivation in the experiment, it can be inferred that 24 hrs of continuous access to sand may reduce the effect of a "present deprivation", to use Stern and Merari's terminology, by a factor of about ten.

The third major difference was the failure of the present study to reproduce Stern & Merari's result of increasing proportion of rolls in the first half of the test with increasing deprivation level. This difference can be interpreted in terms of a different history of access to sand. My subjects received 25 preliminary sessions of 5 min access to sand and always concentrated more of their sandbathing in the first half of the experimental tests than Stern and Merari's subjects did at any deprivation level. It is also possible that chinchillas exhibit substantial individual differences in their distribution of sandbathing rolls throughout a 10 min test just as they differ markedly in overall sandbathing frequency.

In discussing the factors responsible for differences between the present data and those of Stern and Merari, I neglected to mention one important potential source of variation. My subjects were shampooed and would thus be expected to have lower pelage lipid levels. The second experiment investigates the effect of pelage lipid on sandbathing frequency.

Independence of Measures

The fact that the four dependent variables were statistically independent (i.e., not correlated) suggests that the deprivation manipulation may affect a number of distinct motivational systems. Chinchillas are among the most active of rodents in an open field test and the slowness with which they adapt to a novel setting gives them a behavioral profile which is more characteristic of wild than of domesticated species (Glickman & Hartz, 1964). The number of visits to sand can be viewed as an index of exploratory activity directed to the test chamber since this has an exterior as well as an interior surface so that exploration would involve an alternation between those two sources of relatively novel sensory input. Substrate preference, as such, does not appear to have been an important factor influencing effects of deprivation on amount of time spent on sand since, on average, subjects never spent more than half of test duration in the test chamber. Time spent in sand may thus be attributable to specific activities in the behavioral repertory. Sandbathing and exploration are two activities which increase with deprivation period (Fowler, 1965; Stern & Merari, 1969) so these must be at least partly responsible for the increasing time spent in sand as a function of deprivation.

Sex Differences

Females spent more time in sand although they sandbathed less than males. The reason for the time difference is not altogether clear but two possibilities can be mentioned. The first is the fact that a single female did show a preference for the sand substrate (or the test chamber) in the sense that she spent all of the test time (minus latency) in the sand container on one of the baseline sessions and on the two experimental sessions. This would have biased the result for females as a whole. Secondly, four different females were observed to engage in extended digging activity which resembled burrowing. This behavior was not seen in males. It tended to follow the conclusion of sandbathing rolls. It is interesting that chinchillas exhibit nail reduction, are poor burrowers and normally do not inhabit burrows of their own construction (Mares & Lacher, 1987; Mohlis, 1978).

CHAPTER 8

Experiment 2: Effect of Lipid Removal, by Shampooing, on Sandbathing Frequency

Experiment 1 supported Stern and Merari's (1969) main finding that sandbathing frequency in the chinchilla increases as a function of sand deprivation level. Sandbathing apparently serves to reduce pelage lipid. During sand deprivation, pelage lipid is evidently increased since the fur becomes visibly greasy. This increased lipid level in the fur is correlated with increased frequency of sandbathing once a suitable substrate is made available. The lipid-regulation hypothesis explains the correlation by making a causal inference: sandbathing is controlled by pelage lipid so that a high lipid level produces frequent sandbathing (Borchelt et al., 1973, 1976; Eisenberg, 1963a; Griswold et al., 1977).

Correlation between lipid level and sandbathing frequency can be interpreted in other ways. For example, it is possible that the tendency to sandbathe is increased by deprivation of the opportunity to engage in the behavior acting in some way upon unspecified neural substrates independently of cutaneous sensory inputs. The behavior regulation approach to instrumental performance has developed a concept of behavioral set-points which tend to be defended against experimentally-induced constraints. Although controversial, the set-point concept receives empirical support from data showing that free baseline levels of a given response may be both reliable and recoverable. The level of a particular set point is affected by environmental incentives as well as the physiological state of the organism (see Allison & Timberlake, 1975; Timberlake, 1984). It is worth noting that many contextual cues (e.g., substrate texture, substrate odors, season, time of day, ongoing activity, social factors, presence of fear-evoking stimuli) may conceivably influence sandbathing in the chinchilla. While these would not be expected to vary directly with sand deprivation level, the possibility of complex interaction between contextual factors and either central or cutaneous influences cannot be ruled out.

The lipid-regulation hypothesis views greasiness of the fur as a necessary stimulus to produce sandbathing behavior under normal conditions. It thus predicts that reduction of pelage lipids (such as that produced by shampooing) should lead to a corresponding reduction in sandbathing frequency (see Borchelt et al., 1979; Griswold et al., 1977). If shampooing is capable of removing all of, or more than, the lipid which can be removed by sandbathing, then sandbathing frequency following shampooing should fall to zero. If shampooing were less effective than sandbathing with respect to lipid removal, then sandbathing frequency would merely be reduced.

A less stringent prediction could be formulated by assuming that effects of deprivation and fur lipids are additive. In this case, shampooing would still be predicted to decrease sandbathing frequency, but never to zero.

Method

Procedure

Each subject was tested twice at a sand-deprivation level of 25 days. This period was chosen because pilot work suggested that lipid

Table 6

Sequence of Manipulations in Experiment 2

	Manipulations	
Day/s	Group A (N = 8)	Group B (N = 8)
1-2	Sand[a]	Sand
2	Shampoo[b]	Shampoo
2-27	Mesh[c]	Mesh
26	Shampoo	Water wash control[b]
27	Behavioral test[b]	Behavioral test
27-28	Sand	Sand
28	Shampoo	Shampoo
28-53	Mesh	Mesh
52	Water wash control	Shampoo
53	Behavioral test	Behavioral test

Note: Day 1 corresponds to day 10 of Experiment 1.

[a] Continuous access to sand, for 24 hrs in test container, in home cage. [b] See Chapter 6 for description of procedure. [c] Access to mesh substrate (floor of cage) only.

level of the fur reaches a plateau within this time following shampooing. One of the tests was received 24 hrs following shampooing (the experimental manipulation), the other 24 hrs following water wash (the control). The experiment was initiated by shampooing, to produce a uniform initial condition of the fur. The sequence of manipulations is presented in Table 6. It can be seen that the effect of order in which experimental and control treatments was received was partially counterbalanced since Group A received the experimental manipulation first while Group B received the control treatment first. (Details of subjects, test apparatus, behavioral test procedure, shampooing and control procedures are presented in Chapter 6.) Deprivation periods were begun following 24 hrs continuous access to sand in the home cage ("sand" in Table 5).

Results

Group A and Group B results (Shampoo: A, day 27 vs. B day 53; Water: B day 27 vs. A day 53) were compared using Wilcoxon tests to assess whether the order in which treatments were received had an effect on the number of sandbathing rolls produced in the behavioral tests. No significant difference was found either for the shampooing manipulation or for the water wash control: $\underline{T}(8) = 9$, $\underline{p} > .05$; and $\underline{T}(8) = 14$, $\underline{p} > .05$, respectively. Data for the two groups were pooled in subsequent analysis.

The difference between rolls produced in the test following shampooing ($\underline{M} = 16.9 \pm 11.2$ SD) was compared with rolls following the water wash control ($\underline{M} = 17.0 \pm 9.2$) using the Wilcoxon test. It did not reach significance ($\underline{T}(16) = 67$, $\underline{p} > .05$, one-tailed). There was

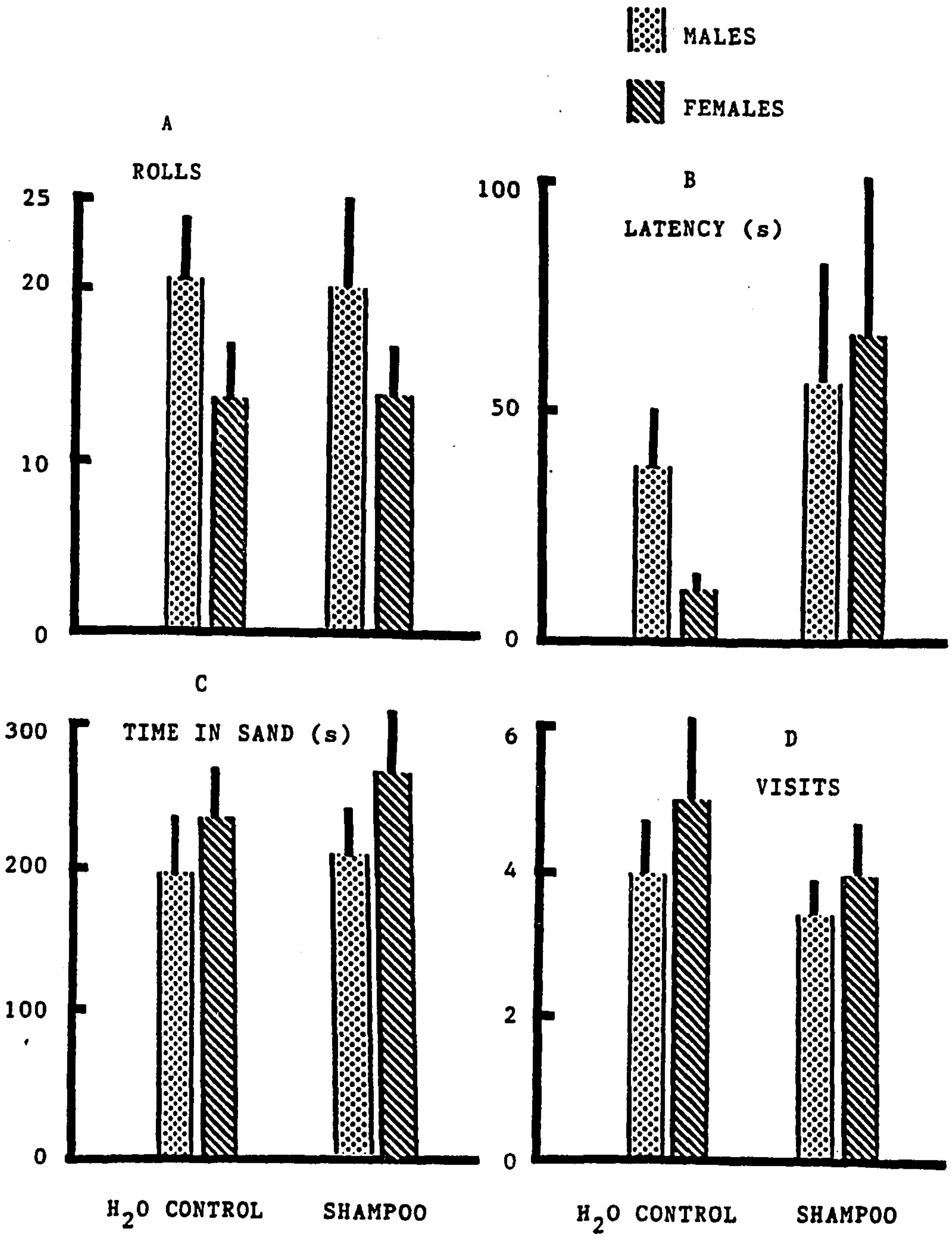

Figure 3. Effect of shampooing on sandbathing rolls and other measures of attraction to sand. Subjects (N = 8 males, 8 females) tested at 25 days sand deprivation. (Means + SE).

no sex difference in sandbathing frequency for either experimental or control condition: Mann-Whitney $\underline{U} = 21.5$, $\underline{p} > .05$; and $\underline{U} = 17$, $\underline{p} > .05$ respectively (see Figure 3).

Latency to sand was longer for the experimental than for the control condition (61 s vs. 23 s, $\underline{T}(16) = 24$, $\underline{p} < .05$). Neither time spent in sand nor number of visits to sand differed significantly between experimental and control conditions: $\underline{T}(16) = 38$, $\underline{p} > .05$, and $\underline{T}(12) = 20.5$, $\underline{p} > .05$, respectively. There was no significant sex difference in any of these dependent variables (see Figure 3).

Correlation matrices were computed for the four dependent variables for both control and experimental treatments. There was no significant intercorrelation (see Appendix 5).

Rolls data for the experimental condition were used to compare sandbathing frequency at a deprivation level of 25 days ($\underline{M} = 16.9$) with results obtained at a deprivation level of 5 days in Experiment 1 ($\underline{M} = 8.8$). This difference was highly significant ($\underline{T}(14) = 7.50$, $p < .01$). Analysis of rolls by one-minute intervals is presented in Figure 4 which is based on control data. Comparison with Figure 2 which describes the distribution of sandbathing at five days' sand deprivation (Experiment 1), reveals that it is essentially the same curve.

Discussion

If, as might reasonably be supposed, shampooing removes lipid from the fur, then reduction in fur lipid did not produce a corresponding decrease in sandbathing frequency as predicted by the lipid-regulation hypothesis. If lipid level in the fur were the only

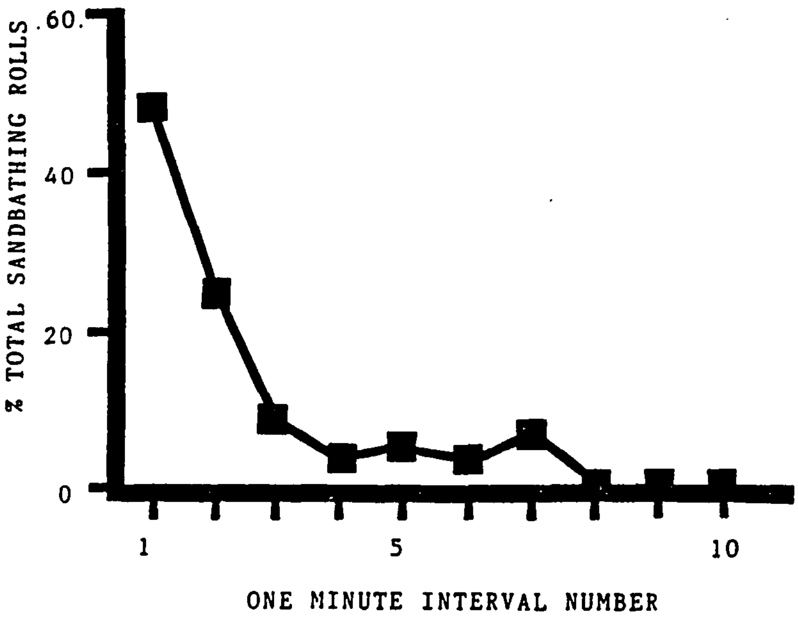

Figure 4. Satiation curve of sandbathing during a 10 min test at a sand deprivation level of 25 days. Control data, see text for explanation (N = 16).

determinant of sandbathing frequency, then the number of sandbathing rolls produced five days after shampooing (Experiment 1) would be greater than the number of rolls in the present experimental condition, where testing took place one day after shampooing. However, this was not the case. The higher deprivation level of the present experiment (25 days) produced almost twice as much sandbathing despite removal of lipid by shampooing as was produced by a five-day deprivation during which lipid was allowed to accumulate in the fur in Experiment 1.

If lipid level in the fur were the sole determinant of sandbathing frequency, then shampooing would be expected to reduce sandbathing frequency virtually to zero. This clearly did not happen. If however, lipid level in the fur was only one of several factors influencing sandbathing frequency, then shampooing would be predicted to reduce the frequency of sandbathing. The lack of a significant difference between experimental and control data can be considered as evidence of the independence of fur lipid level and sandbathing frequency. The results can thus be interpreted as a direct falsification of the lipid-regulation hypothesis. Sandbathing frequency increased as a direct function of sand deprivation level but was independent of fur lipid. However, it could be argued that shampooing produced a skin irritation which counteracted the effect of lipid removal. This possibility appears to be ruled out by the very low levels of sandbathing produced one day after shampooing in Experiment 1.

While shampooing did not affect sandbathing frequency (or the number of visits to sand, or time spent in sand) it had the somewhat surprising effect of increasing the latency to sand. This rather weak ($\underline{p} < .05$ for $\underline{N} = 16$) effect, if not attributable to Type 1 error, is perhaps explicable in terms of greater wariness produced by shampooing compared to the briefer control treatment of soaking with water. This difference is a flaw in the design which was chosen in preference to the risk of removing fur lipid by prolonged water washing (but see Thiessen & Kittrell, 1985). If shampooing was indeed more stressful than the control treatment, then a suppression of sandbathing would be predicted. This would have magnified the difference between control and experimental conditions. The fact that no difference was found suggests that this design problem did not influence the outcome.

Failure to find a sex difference in sandbathing reinforces the impression, produced by Experiment 1 results, that the greater frequency of sandbathing by males is not a robust phenomenon. On the one hand, there is considerable overlap between the sexes. On the other, there is substantial variability between individuals. Long deprivation periods may also have the effect of increasing the unfamiliarity of the test situation and thereby constituting a source of error. When subjects received daily access to sand during the preliminary tests, sex differences were highly reliable (see p. 60).

Figure 4 shows that the distribution of sandbathing by one-minute intervals at a deprivation level of 25 days is essentially the same as the distribution of sandbathing across the ten segments of the test at a deprivation level of five days (Experiment 1) which is presented in Figure 2. Deprivation thus appears to have little effect on the length of a sandbathing bout but increases the overall number of rolls without altering the temporal course of satiation.

CHAPTER 9

Experiment 3: Effect of Adding Oil to the Fur on Sandbathing Frequency

Many reservations have been expressed concerning the application of exogenous lipid as an attempt to model the natural accumulation of lipid in the fur. These can be summarized as follows:

1. Tactile sensation not appropriately modelled.

2. The exogenous substance does not respond to sandbathing in the same way as pelage lipid does.

3. The time course is different since the accumulation of natural lipid is gradual while experimental application is sudden.

The skeptical reader might be tempted to ask why these deviations of the model from natural conditions are so important if it is, after all, successful in evoking sandbathing behavior in the treated subjects (as was the case in the Griswold et al., 1977, study using lanolin). In fact, there is a very fundamental distinction which can be drawn between stimuli which are sufficient to produce a given behavior and those which are necessary. Results of Experiment 2 show that sandbathing can be produced in the chinchilla in the absence of a greasy pelage. Stimuli associated with a high lipid level are thus not necessary to produce sandbathing behavior. Experiment 3 investigates whether such stimuli are sufficient to produce sandbathing in subjects tested at a low level of sand deprivation (one day).

There are two main reasons why the design of Griswold et al., (1977), could not be replicated with the chinchilla subjects. First, the topography of sandbathing differs between chinchillas and kangaroo rats (Dipodomys merriami). A key difference is that the chinchilla does not dress the left and right side and the ventral fur in three distinct directed movements. While the sandbathing roll is necessarily initiated at one side, it may have similar consequences for the fur of the other side in the event of a 360° rotation. Preliminary tests using unilateral application of exogenous substances (water, mineral oil, lanolin) failed to produce a reliable lateral directionality of rolling.

Second, lanolin, which is solid at room temperature, causes severe damage to the fur. The chinchilla cannot remove it either by sandbathing or by grooming. The treated fur was eventually pulled out. [The same may be true of the kangaroo rats of Griswold et al., (1977) whose attentions to the treated fur persisted throughout a 10 min test even though sandbathing normally satiates within approximately 3 min, (Borchelt et al., 1976).]

Mineral oil was chosen as a more effective model of the fur lipid - even though it is not a naturally-occurring substance - for a number of reasons:

1. It does not result in damage to the fur.
2. It cannot be removed from the fur except by sandbathing.
3. It is nontoxic (Kolattukudy, 1976) and virtually odorless.
4. Sandbathing of oil-treated subjects appears normal in structure.

Table 7

Design of Experiment 3

	Manipulations	
Day/s	Group A (N = 8)	Group B (N = 8)
1-10	Mesh[a]	Mesh
	(for lipid recovery)	
10-13	Sand[b]	Sand
13	Oil treatment	Water control
13-14	Mesh	Mesh
14	Behavioral test[c]	Behavioral test
14-17	Sand	Sand
17	Water control	Oil treatment
17-18	Mesh	Mesh
18	Behavioral test	Behavioral test

Note: Day 1 begins the day following day 53 in Experiment 2.

[a] Access to mesh substrate (cage floor) only. [b] Continuous access to sand in test container in home cage. [c] Test procedure is described in Chapter 6.

Method

Procedure

The design of Experiment 3 is presented in Table 7. (Details of subjects, apparatus, behavioral measures are presented in Chapter 6). Either mineral oil or water (the control) was added to the fur one day before running a behavioral test. The time lapse was intended both to minimize the effect of handling on behavioral measures and also to study the effect of continuously high lipid level in the fur rather than that of an application immediately before the test. Each subject served as its own control and the partial counterbalancing procedure was exactly the same as in Experiment 2.

Ten days were allowed at the beginning of the experiment so that a natural recovery of lipids following final shampooing in Experiment 2 could take place. Subjects were allowed three days of continuous access to sand ("sand" in Table 7) before treatments so that initial condition of the pelage might be uniformly clean (see Randall, 1981). (Shampooing was avoided in this experiment since it would tend to neutralize the effect of adding oil.)

During application of the exogenous substance (mineral oil, water) subjects were held in a restraint device. The liquid (5 ml) was applied at various sites around the fur using a syringe (without needle). The fur was then massaged thoroughly (using disposable plastic gloves) so as to achieve a fairly even distribution throughout the pelage - with the exception of the head region which was not treated so as to avoid causing any irritation to the eyes.

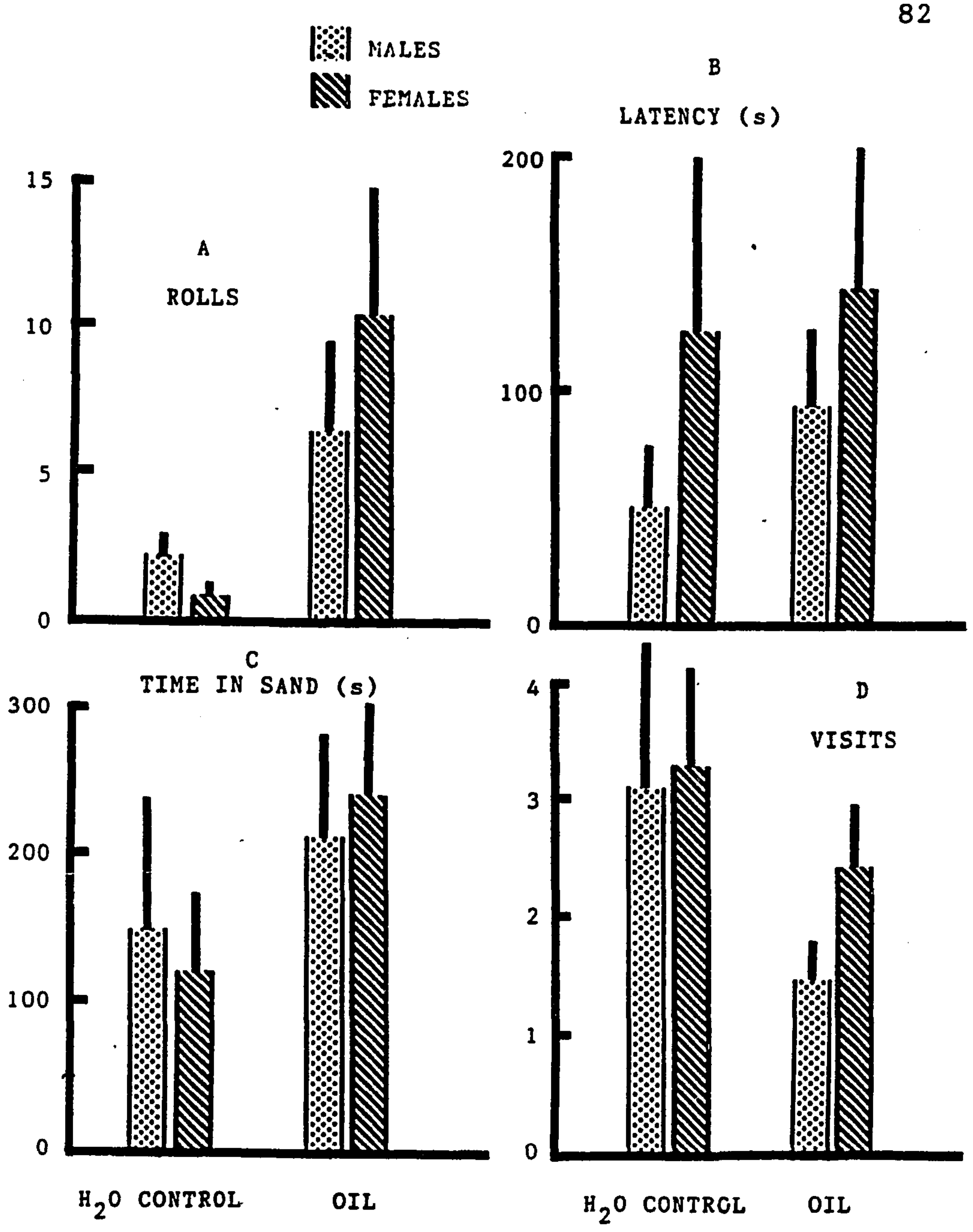

Figure 5. Effect of oil treatment on sandbathing rolls and three measures of attraction to sand (*N* = 8 males, 8 females). Columns represent means (+ SE).

The quantity of oil used was far in excess of that which could accumulate from sebaceous secretion (see Chapter 10).

In addition to the standard behavioral measures, body grooming, defined as oral contact with the fur, was recorded on the basis of occurrence or nonoccurrence by 1 min segments.

Results

Comparison of Group A and Group B mean sandbathing rolls using the correlated Wilcoxon test revealed that the order in which oil treatment or control was received had no effect on the main outcome measure, i.e., rolls: $\underline{T}(7) = 14$, $\underline{p} > .05$; and $\underline{T}(4) = 2.5$, $\underline{p} > .05$, respectively. Subsequent analysis combined data from the two groups.

Results of the experiment are presented in Figure 5 and in Table 8. It can be seen that oil treatment increased the number of sandbathing rolls. The effect of the experimental manipulation was rather unreliable however and was produced by only 10 of the 16 subjects (5 male, 5 female). Although numerically substantial, (mean rolls increased from 1.44 to 8.31), the effect was statistically weak ($\underline{T}(12) = 8.5$, $\underline{p} < .05$)

Oil treatment produced a significant decrease in the number of visits to sand relative to the control ($\underline{T}(13) = 15$, $\underline{p} < .05$) but had no effect on either latency or time spent in sand. Oil-treated subjects engaged in grooming much more often than controls (11 experimental vs. 0 control tests, McNemar test, $\chi^2(1) = 9.09$, $\underline{p} < .01$). Grooming was observed in more males (8) than in females (3, Fisher exact $\underline{p} = .01$). There was no sex difference in any of the

Table 8

Summary of Results of Experiment 3 (means ± SD, N = 16)

Dependent variable	Control	Experimental	p[a]
Sandbathing rolls	1.4 ± 1.5	8.3 ± 10.7	<.05
Latency(s)	88 ± 153	118 ± 136	>.05
Time in sand(s)	137 ± 169	227 ± 183	>.05
Visits to sand	3.2 ± 2.9	1.9 ± 1.2	<.05
Subjects exhibiting body grooming	0	11	<.01[b]

[a] Wilcoxon signed-ranks (T) test. [b] McNemar test (see Siegel, 1956).

other dependent measures (Mann-Whitney tests). Dependent measures were not significantly intercorrelated (Appendix 5).

Oil treatment also affected the distribution of sandbathing with 20% of rolls occurring in the second half of the test compared with 0% for controls. This tendency to persevere was significantly different from the control ($\chi^2(1) = 5.14$, $p < .05$, McNemar Test). Oil treatment did not affect the frequency of expression of sandbathing in the first half of the test ($\chi^2(1) = 1.00$, $p > .05$, McNemar Test).

Discussion

The main finding of Experiment 3 was that application of an oily substance to the pelage may indeed increase the amount of sandbathing which is engaged in by a chinchilla. This result echoes that of Griswold et al. (1977) with respect to kangaroo rats. Application of lanolin also produced a perseveration of sandbathing throughout the 10 min test in that study. A similar effect is seen in the greater proportion of rolls produced by chinchillas in the second half of the test for experimental (20%) compared to control procedure (0%). However, this result may be an artifact related to the very low frequency of sandbathing for controls and can be put in context by comparison with the results of Experiment 1 where 18% and 12% of rolls occurred in the second half of the test for subjects tested at one and five days of sand deprivation, respectively.

A somewhat perplexing aspect of the results is the unreliability of the effect of oil application on sandbathing. The most obvious explanation would be that since the oil had been applied approximately 24 hrs before testing, the subject had succeeded in cleaning itself by other means, e.g., by grooming. A number of observations suggest that this interpretation is incorrect:

1. The experimental subjects appeared much the same as they did following oil application, i.e., fur appeared dark, greasy, matted and flattened against the body in patches.

2. Persistent body grooming was observed in 11 of the 16 experimental tests but never in control tests.

3. A lower frequency of visits to the sand chamber by subjects in the experimental tests indicates that their behavior was altered by application of oil. This lower level of movement suggests increased wariness (sensitization, freezing, disorientation, inhibition of movement due to aversive cutaneous feedback).

Another possible explanation for the unreliability of oil-induced sandbathing concerns competing activity. Perhaps subjects failed to sandbathe because they were engaged in grooming, for example. However, there was no evidence for such an interpretation in the data. Subjects failing to sandbathe did not necessarily groom and subjects sandbathing frequently were just as likely to groom as were those with fewer sandbathing rolls. In addition, there was no clear temporal pattern in the relationship between sandbathing and grooming: grooming occurred before, during, and after sandbathing.

Although chinchillas were apparently unable to remove the oil by grooming during the 24 hrs following application, three days of continuous access to sand removed all visible traces of the oil and the effectiveness of exposure to sand in cleaning the fur is supported by the absence of order effects in the data. It thus appears that the oil was eventually removed by sandbathing. Another possibility is that, with time, the subjects managed to remove the oil by grooming. The issue of whether sandbathing does remove pelage lipid is investigated in Experiment 4. To summarize, it appears that oil in the fur can be removed only by sandbathing, but this has not been definitely established. Yet, when oily subjects were presented with sand in the test session, four of them did not sandbathe at all and two others failed to sandbathe more than in the control condition. The main finding that an unnaturally high level of lipid in the fur can increase sandbathing frequency is clear enough. The weakness and unreliability of the effect are difficult to explain. The experiment supports one of the predictions of the lipid-regulation hypothesis but supports it in an equivocal way. Lipid in the fur is a sufficient stimulus to produce sandbathing behavior but it can be questioned if endogenous lipids could ever accumulate to a degree sufficient to evoke sandbathing in chinchillas with continuous access to sand. The result also needs to be interpreted in the light of observations that the substrate may be used to aid cleaning or drying of the fur by mammals which do not normally sandbathe (Eisenberg, 1981).

CHAPTER 10

Experiment 4: Effect of Sandbathing on Pelage Lipid

Much that is written about the function and control of sandbathing makes the assumption that sebaceous lipid is removed from the fur. This point of view is supported by observational evidence to the effect that the fur of a sand-deprived animal may appear cleaner, lighter in color, and fluffier in texture following exposure to sand, e.g., Borchelt et al., (1976). As previously noted, the existence of a mechanism by which sand could remove lipid is supported by the fact that Fuller's earth (a finely ground clay effective in evoking sandbathing responses of chinchillas) is used commercially to remove grease from textiles (Linton, 1973).

Although there is evidence that deprivation of a particulate substrate may lead to elevated lipid levels in the feathers of quail (Borchelt & Duncan, 1974), there is little firm evidence that sandbathing removes lipid from mammalian fur. The one study which has looked at the effect of living on a sand substrate on pelage lipids does not provide overwhelming evidence in favor of the view that a single sandbathing bout may clean the fur of "excess" lipid. Thiessen and Kittrell (1985) measured the change in pelage lipids of Mongolian gerbils following prolonged exposure to sand. They found that it takes 8-16 days of living on a sand substrate before there is a significant reduction in pelage lipids. Gerbils were exposed either to a sand substrate or to a wire mesh substrate suspended above (and out of reach of) sand. Fur lipids were measured after 2, 8, or 16 days. At 2 days, there was no difference between sand-exposed and non sand-exposed animals. At 8 days, fur lipids were elevated in the mesh-substrate group but were unchanged in sandliving gerbils. At 16 days, fur lipids of the sand-exposed animals had decreased significantly to 66% of their level at 2 days. The fact that pelage lipids in the mesh-substrate group were elevated (approx. 20%) suggests that pre-experimental housing on pine shavings may have resulted in appreciable absorption of fur lipid.

This appears to be inconsistent with nonquantitative observations that fur lipids of kangaroo rats (<u>Dipodomys merriami</u>) decrease during a single sandbathing bout (Borchelt et al., 1976). The discrepancy may be due to the fact that gerbils have an additional source of pelage lipid - in the Harderian gland - which is readily mobilized through autogrooming. Harderianectomy in the gerbil produces a loss of pelage lipids that is approximately 10 times as great as the effect in mice, rats, or hamsters (Thiessen & Kittrell, 1980). At present, there is no information about the role of Harderian lipid in the chinchilla.

Sebaceous glands secrete continuously and the rate of lipid production is generally constant although it can be influenced by plasma concentration of sex hormones. Testosterone increases the rate of sebaceous secretion via its trophic action on sebaceous glands so that sebum production tends to be elevated in males (Ebling, 1967; Ebling & Skinner, 1967; Hadley, 1985; Kligman, 1963; Quay, 1953; Sokolov, 1982; Spearman, 1973).

In Experiment 4, subjects were initially shampooed and lipid level in the fur was measured after 25 days of access to a mesh substrate only. Limited pilot data suggested that lipid level in the fur reached a maximum value at around this time presumably because lipid loss to the environment was sufficient to balance the rate of sebaceous secretion (see Kligman, 1963). Fur lipids were subsequently measured following 24 hrs access to sand so that the amount of lipid removed by sandbathing could be assessed. A final lipid measure was taken following shampooing. This allowed investigation of the effectiveness of shampooing in removing fur lipids and also provided a convenient benchmark against which the effect of sandbathing could be assessed.

Method

Procedure

The design of Experiment 4 is presented in Table 9. Experiment 4 used a mixed design since an across-groups comparison was conducted in order to test whether the control water treatment (Experiments 2, 3) really had no effect on pelage lipid.

Shampooing method was the same as for the other experiments. Access to sand was for 24 hrs in the home cage. Three fur samples were taken for each subject - one following 25 days of sand deprivation, one following access to sand and one following shampooing, in that order. The second fur sample was taken a minimum of 30 min following removal of the sand container. This allowed some of the sand in the fur to be removed by shaking, locomotion, or simple gravitation.

Table 9.

Design of Experiment 4

	Manipulations	
Day/s	Group A	Group B
1	Shampoo	Shampoo
1-26	Mesh[a]	Mesh
25	Water control	-
26	Fur sample	Fur sample
26-27	Sand[b]	Sand
27	Fur sample, shampoo	Fur sample, shampoo
28	Fur sample	Fur sample

[a] Access to mesh substrate (i.e. floor of cage) only.

[b] Continuous access to sand, in test container, in home cage.

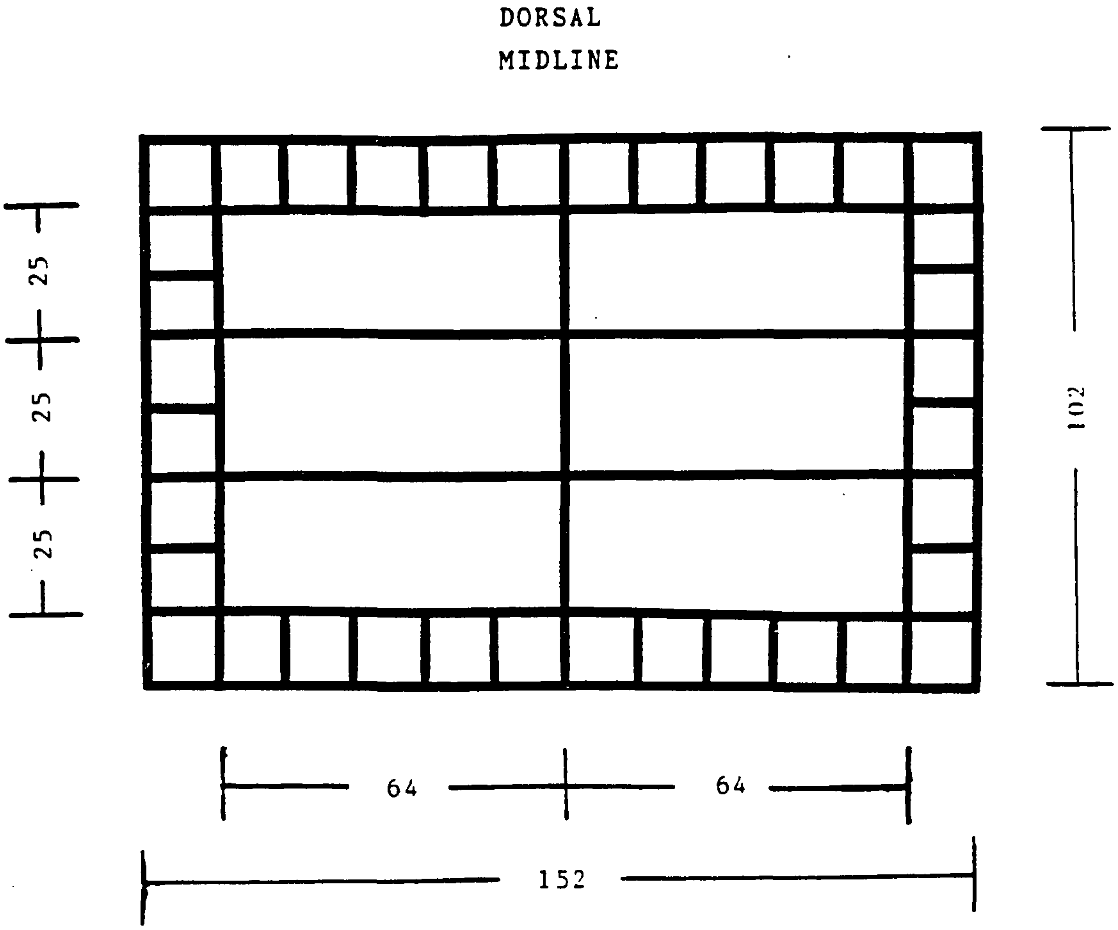

Figure 6. Wire guide used in fur sampling shown before bending. See text for full explanation. All dimensions in mm.

Fur sampling. Fur was taken from subjects' dorsal and lateral aspects excluding the neck and flank regions. This area of the fur is uniform in appearance and can be clipped close to the skin with a low risk of causing abrasions or minor cuts. Fur was taken from one of three standard rectangles (64 mm x 25 mm) on each side of the animal for each sample (see Figure 6). Fur cut from the left (relative to the dorsal midline) was combined with fur cut from the right so as to increase sample bulk and thereby minimize error in the lipid assay to be described. Sampling areas of the left and right were arranged such that the long side of the rectangles was at right angles to the dorsal midline. The rectangles were continuous with each other so as to form a larger rectangle 76 mm (measured along the spine) x 127 mm. Choice of sampling area was counterbalanced between the three experimental conditions to ensure that any systematic rostral-caudal variation in lipid content of fur could not produce a bias in the results.

Clipping positions were standardized by means of a guide constructed from 12.7 mm square wire mesh Rectangles corresponding to the sampling areas were cut from the wire grid and the cut ends filed clean (see Figure 6). The guide was then molded to fit over the animals' torso with boundary wires close to the skin.

Subjects were caught by the tail and placed in a restraint device which held them by the neck, taking care to avoid manual contact with the sampling region. Hind legs and tail were held in the left hand while the sample was taken. The guide was fitted using the vertical surface of the restraint device as a reference point.

Fur was clipped to within approximately 2 mm of the skin with a hair shears. The shears was used to convey the cut fur directly to a small circular collecting tray. From there, it was transferred to 100 ml clean glass bottles for storage prior to extraction of the lipid. (Bottles and other glassware used in the experiment were cleaned using laboratory glass detergent, Sparkleen, rinsed in distilled water and allowed to drain dry.) All samples were weighed to within .0001 g on a Sartorius model 1601 scales.

Lipid extraction. Fur is a surprisingly difficult material from which to effect a complete extraction of lipids. Ebling and Skinner (1967) could only remove about 50% of the lipids in rat hair on the first (ether) extraction, for example, and found that five extractions were required before the yield fell below 5%. My pilot data on chinchilla fur suggested a similar extraction profile. By contrast, Bligh and Dyer (1959) succeeded in removing about 94% of the lipid from fish meal samples on their first (chloroform/methanol) extraction. I have found that soaking chinchilla fur in the solvent overnight produces a yield of approximately 80% of extractable lipids on the first extraction.

Many of the choices made in designing an appropriate lipid-extraction procedure are essentially arbitrary since there is a scarcity of data concerning their effects. Defense of any particular procedure is thus largely heuristic: other researchers did this and it produced acceptable results. Although Ebling and Skinner (1967) found it necessary to use five extractions for complete removal of ether-extractable lipids, behaviorally-oriented researchers have rinsed fur samples just twice in all procedures for which sufficient information is available (Lepri & Randall, 1983; Pendergrass & Thiessen, 1983; Randall 1981b; Thiessen & Pendergrass, 1983). This saves time, avoids the use of large quantities of solvent, and produces reliable results especially when a garlic press (or other such device) is used to express as much solvent as possible from the fur (Pendergrass & Thiessen, 1983; Thiessen & Pendergrass, 1985).

The behaviorally-oriented researchers above have also differed from Ebling and Skinner (1967) in the procedure used to evaporate the solvent. The latter used a hot plate to hasten evaporation of the ether. Two factors may contribute to the unpopularity of this technique - its potential as a fire hazard and the fact that modern electronic weighing apparatus can be rendered inaccurate by a substantial temperature gradient between the apparatus itself and the vessel being weighed. Whatever the reason, placement of the extract-containing solvent beneath an evaporation hood has been the method of choice and this simpler procedure is used in the present study. Evaporation hoods are equipped with a fan which maintains an upward flow of air. This would normally be expected to prevent the settling of minute dust particles in the extract-containing vessels. In the present study, the fan was turned on the day before the extraction was carried out which would minimize the possibility of larger particles within the hood being dislodged during the evaporation period and falling into the open vessels (beakers). No other extraction procedure mentions precautions of this sort suggesting that it is not a serious problem.

Most previous methods of extracting lipid from animal hair have used diethyl ether as the solvent. However, Nicolaides and Kellum (1965) recommend chloroform/methanol (2/1, V/V) as the solvent of choice for complete removal of polar lipids.

Chloroform/methanol is represented by Bligh and Dyer (1959) as a suitable system for extracting most biological lipids and Christie (1973) states:

> It now appears to be generally agreed that a mixture of chloroform and methanol in the ratio of 2:1 (V/V) will extract lipid more exhaustively from animal, plant or bacterial tissues than most other simple solvent systems. The more common simple and complex lipids can be readily extracted with this mixture and indeed the only important exceptions are the polyphosphoinositides of brain where it may be necessary to add acid...or inorganic salts...to the solvents to obtain quantitative yields. (p. 33)

Chloroform/methanol (2/1, V/V) was therefore used to extract lipid from the chinchilla fur samples. Following the extraction procedure, non-lipids were removed by shaking the extract-containing solvents with one third of their combined volume of .88% potassium chloride solution in distilled water (W/W). When the resulting mixture is allowed to settle two phases form. The upper phase contains most of the water together with methanol and water-soluble materials. The lower phase contains virtually all of the chloroform together with the purified lipid (See Bligh & Dyer, 1959; Christie, 1973). Steps in the extraction procedure are listed below:

1. 20 ml of 2/1 chloroform/methanol (V/V, both 99.9% pure, residue after evaporation .0002%, 2 parts/million respectively) was added to the fur in its glass sample bottle. The bottle was sealed with an airtight (wax-free) lid, shaken to ensure that all of the fur was saturated in solvent and allowed to stand overnight.

2. Solvent was poured off the sample and filtered using Whatman #2 filter paper, into a tared 150 ml beaker. (Disposable plastic gloves were worn to prevent contamination of the beaker or filter paper by contact with human skin). The fur was then shaken into a garlic press and squeezed until no further solvent could be removed.

3. Fur was replaced in the sample bottle through manipulation with a glass rod and a further 20 ml of solvent was added.

4. Fur was agitated for approximately 2 min using the glass rod.

5. Step 2 was repeated using the same beaker.

6. Fur was replaced in sample bottle and placed under an evaporation hood to dry (48 hrs).

7. To the filtrate was added one third of its volume of .88% potassium chloride (.0005% insoluble) in distilled water.

8. The mixture was placed in a separatory funnel, shaken thoroughly and allowed to settle. Two phases formed.

9. The lower phase (containing chloroform and dissolved lipid) was drained into the tared beaker, care being taken to ensure that none of the upper phase (containing methanol, water and water-soluble material) was included.

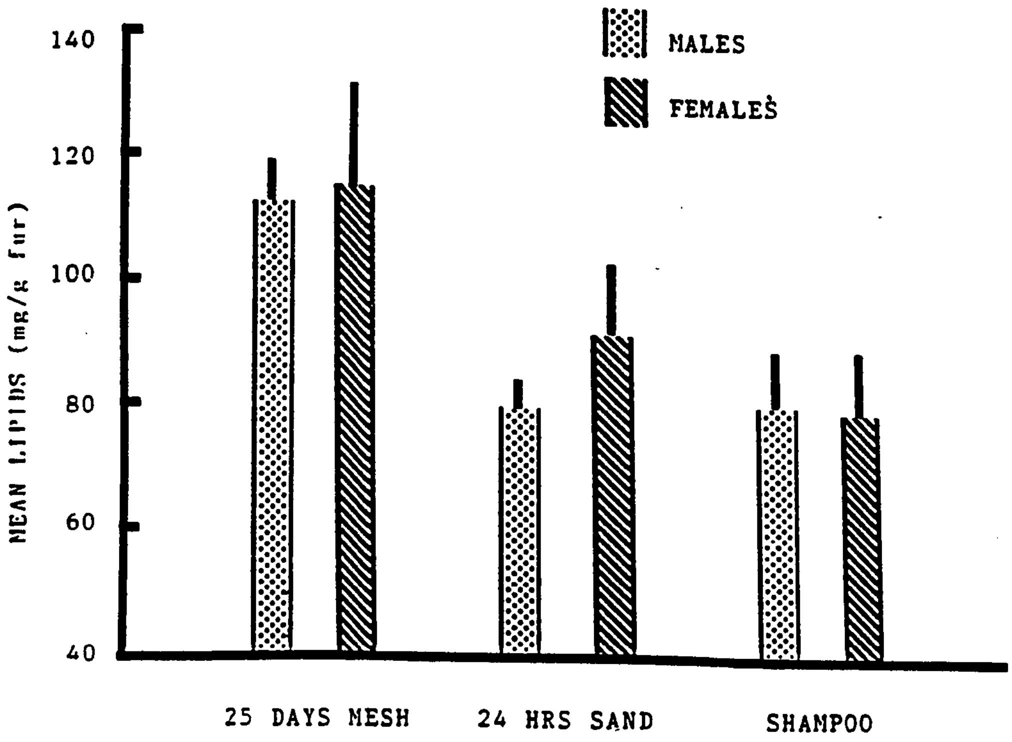

Figure 7. Change of pelage lipids with successive manipulations. Vertical bars indicate 1 SE.

10. The beaker was placed under an evaporation hood for 48 hrs.

11. Fur samples were reweighed. They were found to be approximately 12% below their initial weight and were assumed to be completely dry. This second weight was used to calculate the lipid/fur ratio.

12. Beakers containing lipid extract were reweighed. They were then packed in their delivery carton to prevent contamination by dust. After five days another weighing was carried out. The mean weight loss during the five-day interval was 0.3 ± 0.2 mg (SE). It was assumed that constant weight had been reached and the second weight was used to calculate the weight of extracted lipid. Results were expressed as a ratio of mg lipid/g fur.

Results

Group A subjects received the control water wash while Group B did not. Assessment of the effect of this treatment on pelage lipids was made by comparison of lipid levels in the initial fur sample. Group A lipid ($\underline{M}$ = 109.8 mg/g fur) did not differ significantly from that of Group B ($\underline{M}$ = 119.6 mg/g fur, Wilcoxon $\underline{T}(8) = 14$, $\underline{p} > .05$). Data for the groups were combined in subsequent analysis.

Data were found to satisfy the assumption of homogeneity of variance (Cochran $\underline{C}(15,3) = .47$, $\underline{p} > .05$) and further analysis was by means of two-factor repeated-measures ANOVA with sex as a between-subjects factor. Post hoc contrasts were by the method of Newman-Keuls and used a 95% confidence level (Winer, 1962).

The effect of experimental condition on pelage lipid was highly significant, $\underline{F}(2,28) = 24.19$, $\underline{p} < .001$. Fur lipid following 25 days on mesh was significantly higher than that following sand exposure or shampooing. However, the latter two conditions did not differ significantly from each other (see Figure 7). There was no sex difference in lipid and no interaction between sex and experimental condition (see Appendix 4). From Figure 7, it can be seen that the results of the second and third test for males and the third test for females converge at a value of approximately 80 mg/g fur suggesting a floor effect for lipid removal by sandbathing or shampooing.

Mean weight of fur samples was .49 ± .14 g SD before extraction and .43 ± .11 g after extraction. Sample size was correlated with lipid score to investigate whether this variable was a systematic source of error. It was not ($\underline{r}(46) = -.05$, $\underline{p} > .05$). The coincidence of mean lipid values for males in the second and third test (Figure 7) means that data can be interpreted as replicate measurements and used to estimate the test-retest reliability of the extraction procedure. Correlational analysis produced a coefficient of determination ($\underline{r}^2$) of .82. Error thus accounts for 18% of the variance in scores.

Analysis of constituents of fur samples broken down by experimental condition and expressed as percentages of initial fur weight is presented in Table 10. It can be seen that lipid accounts for approximately 10% of sample weight following prolonged deprivation of sand but falls to approximately 7% after 24 hrs of access to sand. "Loss" was derived by subtraction and is comprised of fragments of fur lost in the filtration process together with dust, sand, or non chloroform-soluble materials washed out of the fur during the extraction process. The greater value of "loss" in the second condition (24 hrs sand) suggests that fur samples contained more foreign materials for this condition. The difference probably represents sand particles trapped in the fur following sandbathing.

Discussion

Access to sand was effective in reducing fur lipids of chinchillas which were previously deprived of sand for 25 days. This is the first quantitative demonstration that short-term exposure to sand can remove lipid from the fur. Presumably, sandbathing was responsible for the effect.

The shampooing procedure resulted in a total cumulative lipid removal (along with sandbathing) of only about 30% of the initial fur lipid and it is interesting that Ebling and Skinner (1967) produced a similar result (31%) for rats using sodium lauryl sulphate as the detergent. Thiessen and Pendergrass (1985) succeeded in removing approximately 60% of total extractable lipids by shampooing Mongolian gerbils with Johnson's Baby Shampoo. The greater effectiveness of the shampoo in that study compared with the present experiment can be accounted for in a number of ways:

1. Approximately half of the lipid in <u>Meriones unguiculatus</u> fur may be of Harderian origin (Thiessen & Pendergrass, 1985). It is distributed about the fur via admixture with saliva during autogrooming and might thus be readily removed by experimental shampooing - particularly if it is deposited on top of sebaceous lipid.

2. Thiessen and Pendergrass combed and towelled their subjects

Table 10

Constituents of Fur Samples by Weight

Experimental condition	Final fur weight (%)[a]	Lipid (%)[b]	Loss (%)[c]	Initial fur weight (%)
25 days mesh	86.11	10.02	3.87	100.00
24 hrs sand	85.68	7.37	6.95	100.00
Shampoo	89.52	7.23	3.25	100.00

[a] Weight of fur following extraction procedure expressed as a percentage of initial sample weight. [b] Extracted lipid as a percentage of initial fur weight. [c] Percentage of initial fur weight unaccounted for. Includes fur fragments and other solids retained in the filter as well as non chloroform-soluble material removed from the fur extract in the washing process.

following shampooing which may have effected a mechanical removal of lipid.

3. The (ether) extraction procedure used to estimate total lipids may not have been completely effective. This would tend to produce an overestimation of the effectiveness of shampooing. In fact, there is such divergence in the lipid extraction procedures which have been used that no comparison can be made between studies with any confidence.

In male rats, less than 2% of a fur sample is lipid (by weight, Ebling & Skinner, 1967). In the chinchilla, if post-sandbathing data are used as the best indicator of normal condition, over 7% of a fur sample is accountable as lipid. This is not an exceptionally high value in terms of nonrodents since sheep wool may be up to 16% sebum although this ranges downward to 2% for coarse-wooled breeds (Truter, 1956).

High lipid level in the fur of desert-adapted rodents is apparently related to its fineness and Sokolov (1962) found that sebaceous glands were largest in species with a dense pelage. He attributed this to increased requirement for lubrication of the hairs (see Appendix 1).

The finding that sandbathing may be a highly effective method of cleaning lipid from the fur is consistent with one prediction of the lipid-regulation hypothesis. However, this consequence accrues to 24 hrs access to sand. The question of whether a single sandbathing bout can have a measurable effect on fur lipids has not been investigated so it is not possible to state whether alteration in fur lipids could in principle, be used as a feedback loop to control the duration or intensity of a sandbathing bout. There was no relationship between the lipid level of subjects' fur following 25 days of sand deprivation and the number of rolls produced at a deprivation level of 25 days in Experiment 2 (control data, $r = .36$, $p > .05$)

Perhaps the most surprising result of Experiment 4 was the fact that so much of the lipid could be retained in fur following shampooing. On the one hand, this suggests that the extraction procedure was highly effective. It also indicates that hair may be in Kligman's (1963) words "a sebum trap" (p. 307). Hair cuticle consists of concentric circles of projecting scales whose structure has been compared with that of a pine cone (Bruner & Coman, 1974). It is possible that the scales trap sebum on their inner surfaces. For illustrations of the cuticular structure of a broad sample of mammalian hair, including chinchilla, see Hausman (1920).

CHAPTER 11

Conclusions

The lipid-regulation hypothesis was encountered as an amalgamation of functional and causal ideas. If sandbathing cleans excess lipid from the fur (its functional aspect) then the hypothesis predicts that lipid in the fur which is in excess of a theoretical set point will evoke sandbathing. When lipid has been reduced, by sandbathing, to its appropriate level, the match between sensory inputs and set point produces a termination of the behavior. This is a highly parsimonious account of sandbathing which attempts to place it within the motivational context of other COBS activities. For example, if an animal is attacked by a parasite it may feel cutaneous irritation or pain. Grooming activity occurs and by removing the parasite, the host animal reduces the intensity of the disagreeable stimulus which allows grooming to stop. This is a reasonable account of some forms of grooming which is intuitively valid for anyone who has relieved a skin irritation by scratching but it is far from being a satisfactory framework within which the causation of all forms of COBS, or all instances of any form, can be interpreted (Chapter 5).

All of the major predictions of the lipid-regulation hypothesis have been tested in the experiments reported here so that its usefulness as an explanatory model can be assessed. It is convenient to separate this evaluation into its functional and causal aspects.

Lipid-Regulation as a Functional System

The central question to be asked here is whether sandbathing is suitable for, or capable of removing lipid from chinchilla fur. Experiment 4 clearly provides affirmative answers. Sandbathing can remove pelage lipid and its effectiveness can be compared favorably with that of shampoo detergents. However, it must be acknowledged that this lipid removal occurred after 25 days of sand deprivation. Under natural conditions such extended deprivations are unlikely to occur although there are occasions when the substrate may be covered by snow for several days (Pearson, 1948). Substantial lipid accumulations would not occur so that the biological importance of lipid removal can be questioned. In short, it can be stated that sandbathing may have the consequence of maintaining pelage lipid at a low level. Whether this is its only, or primary function remains to be determined.

Lipid-Regulation as a Control System

Establishing experimental control over a behavior does not automatically lead to comprehensive predictions about the conditions under which it will occur. The addition of lipid to the fur evokes sandbathing in kangaroo rats (Griswold et al., 1977) and in chinchillas (Experiment 3). Artificially-applied lipid is therefore sufficient to elicit sandbathing.

While failure to elicit sandbathing could have been taken as a falsification of the lipid-regulation hypothesis, the positive finding does not constitute unequivocal support since it provides no information about whether stimulation associated with high lipid level of the fur is necessary to produce sandbathing. Experiment 2 showed that lipid removal had no effect on sandbathing frequency and therefore nullified the causal hypothesis of the lipid-regulation model, namely that stimuli associated with high lipid level are, under normal circumstances, necessary to produce sandbathing and therefore control its frequency.

Although superficially contradictory, results of Experiments 2 and 3 can be easily reconciled. Wetting or addition of a sticky substance to the pelage may elicit use of the substrate as an aid in COBS of species which are not normally considered to be sandbathers (Eisenberg, 1981). Lipid addition to the fur evidently produces a similar response in sandbathing species although this draws upon their sandbathing repertory.

The real issue in relation to the causal portion of the lipid-regulation model is whether natural changes in lipid level can produce stimulus changes which are intense enough to initiate, maintain, or terminate the behavior. Experiment 2 shows quite clearly that lipid reduction by shampooing (a change of a larger magnitude than would be predicted for naturalistic conditions) had no effect on sandbathing frequency. It is therefore concluded that stimuli associated with endogenous lipid level of the fur cannot be the factor which controls variation in sandbathing frequency as a function of deprivation. The lipid regulation hypothesis is therefore falsified in its central prediction at least so far as the chinchilla is concerned.

This conclusion is not unprecedented and actually mirrors the findings concerning dustbathing in quail. Since lipid level in the feathers increases as a function of dust deprivation period, it seems that dustbathing regulates feather lipids (Borchelt & Duncan, 1974). However, the prediction that dustbathing frequency is controlled by lipid level of the feathers was not borne out. Removal of the preen gland, a major source of lipid, was found to have no effect on dustbathing frequency. Addition of small quantities (25-175 mg) of lipid to the feathers also failed to increase dustbathing frequency. However, spraying with large quantities of water (20-25 ml) produced an increased frequency of oiling behavior which in turn increased dustbathing frequency (Borchelt et al., 1979). For the quail, as for the chinchilla, dustbathing frequency is not normally regulated by peripheral feedback related to lipid level in the integumentary appendages. However, an intense peripheral stimulus is capable of affecting (albeit indirectly) the frequency of dustbathing.

The resolution of the apparent contradiction between the results of Experiments 2 and 3 offered above assumes that oiliness is not a necessary attribute of the sort of exogenous stimulation which can produce sandbathing at low sand-deprivation levels. In other words, any foreign substance might be as effective if applied in sufficient quantity. This idea could be tested by comparing the effectiveness of water with that of oil in eliciting sandbathing. Preliminary work indicates that if a subject is sprayed immediately before testing, water is a more effective substance in eliciting sandbathing.

Deprivation Level as a Determinant of Sandbathing Frequency

If lipid level in the fur does not determine sandbathing frequency, then what does? Experiments 1 and 2 show that sand-deprivation level is an important determinant of sandbathing frequency and that the effect of deprivation is independent of lipid accumulation. By comparing experimental and preliminary data it can be seen that duration of access to the sand has an interactive relationship with intersand interval in determining the effectiveness of the deprivation manipulation. This suggests that the chinchilla somehow monitors the amount of sandbathing it has engaged in, compares this with some baseline level and emits the behavior with a frequency which reflects cumulative deficits stretching back over several days, or even weeks (see Stern & Merari, 1969).

Sandbathing can be interpreted as a motivated behavior analogous to the motivation of feeding. Amount eaten is just as important an index of food deprivation as is time since the last meal. Sandbathing is evidently organized into bouts. The amount of sandbathing per bout is more responsive to deprivation than is the amount eaten in a meal (by rats, see Le Magnen, 1971). However, the length of a sandbathing bout is not influenced markedly by deprivation: sandbathing rolls simply occur more rapidly at a high deprivation level (Figures 2, 4).

Motivation of sandbathing operates on two time scales - one corresponding to the length of a bout, the other stretching over several bouts, even where these are separated by several days as in the Stern & Merari (1969) study. This suggests that some sort of steady state is being defended. Lipid level in the fur was proposed as being the defended parameter. While sandbathing may keep lipid at some low baseline level, it has been concluded that peripheral stimulation from fur lipid is not the basis on which the behavior is regulated. The possibility of other peripheral changes with deprivation of sand cannot be ruled out, but it is hard to see what these could be. Sandbathing frequency is apparently regulated spontaneously at some baseline frequency just as other behaviors appear to be (e.g., Premack, 1962). This leads to the prediction that it could be used as a reinforcer (see Allison & Timberlake, 1975; Timberlake, 1984).

When deprived of sand, chinchillas will learn a variety of instrumental responses if access to a sand substrate is made contingent upon these responses. Access to sand has been used to reinforce lever pressing, pole pushing and running in an alley (Barber, 1987; Roche & Thompson, 1987). However, Glickman (1973) reported that chinchillas did not learn to run a maze for access to sand although he gave no details of the method.

If the activity of sandbathing is reinforcing, then it could also be controlled by noninstrumental contingencies. Chinchillas which are accustomed to sandbathing on being placed in a particular container will continue to do so if the amount of sand is gradually reduced until none is left (Roche, unpublished data) or even if the container is presented empty without any fading process (personal observation). This suggests that the incentive value of the behavior may consist more in its execution than in any sensory feedback attributable to a suitable particulate substrate. However, there is not, at present, sufficient data to exclude from sandbathing the hedonic connotation sometimes attributed to autogrooming movements by terming them "comfort movements". Lipid reduction does not appear to be related to sandbathing motivation but this is only one of many sensory variables potentially affecting the initiation, maintenance, and termination of sandbathing in the chinchilla. Some of these are amenable to experimental analysis.

Sensory Factors in the Control of Sandbathing.

1. Texture discrimination. Sandbathing rolls are normally initiated by a "cheek rub" (Stern & Merari, 1969) but it is not clear whether the cheek always contacts the substrate or whether stimulation of the vibrissae is important. Chinchillas may be capable of a rather fine discrimination between different substrates since preliminary data from this laboratory indicates that subjects may fail to roll in a sea sand which is coarser than Fuller's earth. Presumably a cheek rub provides information which can be used in assessing the suitability of the substrate. Information may also be derived from the soles of the feet. Juvenile chinchillas may exhibit sandbathing rolls in the home cage in the absence of a sand substrate following oral contact with the fur of the mother who has recently returned from sandbathing. This suggests that rolling is a reflex response to stimulation of facial skin by fine sand particles. Topical skin anesthesis might be used to test this hypothesis.

2. Olfactory cues. Olfactory communication appears to play an important role in the sandbathing behavior of hystricomorph rodents (Kleiman, 1974). Communal sandbathing sites may have a role in familiarizing an individual with the odors of other colony members. Kleiman states that sandbathing in several species takes place at urination sites. This means that the sandbather would anoint itself

with the odors of other colony members with the probable effect of inhibiting intragroup aggression. (A similar interchange probably facilitates mating in solitary animals - see Daly, 1977; Fleming & Tambosso, 1980; Randall, 1981a, 1982). Rogovin (1979) distinguishes between mark-related and "comfort" sandbathing in the three-toed jerboa and Steiner (1974) makes a similar point for ground squirrels. The same distinction is made between species by Eisenberg (1963). Investigation of mark-elicited sandbathing in the chinchilla might begin by experimental treatment of sand with conspecific urine or with a water control to investigate whether the frequency or locus of sandbathing can be manipulated in this way. If so, then olfactory cues would clearly be important in eliciting or maintaining sandbathing.

3. Temperature. Temperature dependence of sandbathing has been demonstrated for the Mongolian gerbil (Pendergrass & Thiessen, 1983) which increases its sandbathing frequency in a warm compared to a cold experimental setting. Since many activities may be reduced at low temperatures, it is difficult to be confident that diminished sandbathing frequency constitutes a specific thermoregulatory response (see Pendergrass & Thiessen, 1981, 1983; Thiessen & Harriman, 1982; Thiessen & Kittrell, 1980). The chinchilla might provide an interesting comparative counterpoint since it is a nocturnal animal adapted to a cold habitat while the gerbil is diurnal and may have to withstand intense solar radiation.

4. The effect of foreign materials adhering to the fur. Experiment 3 results are consistent with the finding of Griswold et

al., (1977) that adding lipid to the fur of kangaroo rats increased the number of sandbathing acts directed to the treated surface. However, in Experiment 3, the lipid was added to subjects' fur 24 hrs before testing. Would treatment immediately before the test have a stronger effect? What would be the effect of applying water immediately before the test? What if the manipulations were performed at a higher sand deprivation level? Would experimental matting of the fur stimulate sandbathing?

5. Direct stimulation of the skin. Various forms of cutaneous irritant might be tested to establish whether sandbathing could be produced without appreciable alteration of the condition of the fur. Potential sources of stimulation include the following:

1. Live parasites. It will be recalled that dustbathing in birds was originally conceived of as a defense against ectoparasites (see Borchelt, 1980).

2. Punctate stimuli modelling the consequences of being bitten.

3. "Itching powder" modelling the movement of ectoparasites.

4. Mild pain stimulation delivered by means of a forceps used to pinch the skin or by plucking strands of fur. Tail-pinching was used by Fentress (1983) to evoke posturally-facilitated grooming in young mice. Although this procedure has been used to potentiate a great variety of behavioral responses in rats - including feeding, licking of food, or other objects, gnawing, digging, sexual behavior, maternal behavior, and operant responding for electrical brain stimulation - it does not induce grooming (O'Brien, Chesire, & Teitelbaum, 1985; Szechtman, 1980).

6. Receptor Populations of the Skin and Sandbathing. Cutaneous stimulation may play two roles in sandbathing - discrimination of appropriate substrate and as eliciting stimulus. These may sometimes be difficult to separate. Investigation of such sensory influences on sandbathing can be furthered by a consideration of the receptor types which may be implicated.

As previously discussed (p. 27), deflection of fur is detected by tylotrich follicles which could register matting and disorder of the pelage. Similar, but more sensitive, receptors transduce bending of the vibrissae (Straile, 1960). It is possible that the chinchilla can assess fineness of the substrate in terms of resistance encountered by the tips of the vibrissae as the face is moved relative to the substrate in a cheek-rub. Another possibility is that texture is sensed in terms of pressure changes to skin on the soles of the feet or in the orofacial region. Texture discrimination probably involves integration of inputs from several types of mechanoreceptor.

A finely-textured substrate will tend to produce less vibration to the feet than a coarse or solid one causing diminished stimulation of the Pacinian corpuscles. Single grains of sand moving relative to the skin probably stimulate rapidly-adapting Meissner corpuscles. These are present only in hairless skin and cheek rubs may excite Meissner corpuscles in bare skin around the mouth. Slowly-adapting mechanorecptors are probably less important in fine texture discrimination since information about the fineness of a particulate or a textured surface tends to be lost in the absence of movement.

However, Merkel receptors do respond to indentation of skin.

Since sandbathing is temperature-dependent in the gerbil, (as discussed above) thermal receptors in the skin may influence expression of the behavior. To the extent that wetting of skin stimulates cold receptors, these may mediate the general mammalian pattern of using the substrate as an aid in drying the fur.

Finally, if sandbathing can be elicited by parasites, then several types of pain receptors may be involved. Most important of these would be mechanical nociceptors (pain receptors) which are activated most effectively by sharp objects such as the piercing mouthparts of external parasites. Movement of parasites would stimulate the hair receptors as well as unmyelinated fibers responsible for itch sensations.

APPENDIX 1

The Functions of Sebum and Other Surface Lipids

The issue of function is central to the science of biology but theoretical and methodological problems encountered in its investigation are often formidable. Strictly speaking, function refers to the consequences of a trait which enhance the reproductive success of its possessor. In practice it may be difficult or impossible to perform the sort of empirical study which measures the fitness effect of a particular trait so that the term function can only be used in a "weak" sense referring to beneficial consequences of a trait (Hinde, 1975). The weak meaning is intended here.

Whether lipid secreted by the sebaceous glands does produce beneficial consequences is by no means obvious. In the human case, the skin disease acne is caused by overactive sebaceous glands while young children, whose glands are inactive, suffer no apparent dysfunction attributable to lack of sebum. In fact, the skin of children is said to have superior cosmetic properties as a result (Kligman, 1963).

Human acne may not be of crucial importance in discussing such a widespread vertebrate phenomenon as skin glands which produce lipid. However, a clear case can be made in favor of the view that sebum production entails a biological cost. This implies the existence of complementary benefits. Otherwise, sebaceous glands would have been removed by natural selection.

Lipid is an energy-dense substance. Energy is essential for growth and reproduction and can thus be considered a limiting property of biological systems such as organisms, populations, and ecosystems. Each individual organism must satisfy its energy requirements or perish - either literally through starvation or metaphorically through failure to transmit any of its genetic complement to future generations. As the organism goes about the task of satisfying its energy requirements it will encounter fluctuations both in its needs and in the supply of available food sources. At certain points in time these vicissitudes will combine to generate energetic crunches or situations in which requirements cannot be met. At such times disaster may be avoided by a number of energy-saving adaptations (see King & Murphy, 1985). However, lipid production by sebaceous glands may continue (albeit at a reduced rate) during severe food shortage.

This claim is supported by experiments on domestic sheep subjected to an 80% reduction in food intake. Under these conditions the rate of wool production is reduced to approximately one third of its normal level. The proportion of lipid in the fur tends to increase (Truter, 1956) as fiber production shrinks. Sebum production may contribute to energetic shortfall and so involve a definite biological cost which implies the existence of countervailing biological advantage. Rats and humans respond to starvation by a change in sebum composition which results from suppression of fatty acid synthesis (Downing, 1976).

What the advantage of sebum production might be is a question which has provoked a great deal of speculation and some empirical work - much of it devoted to two species, humans and sheep. This allows a convenient separation of hypotheses into hair-related and surface functions. A second distinction, orthogonal to the first, can be made between suggested physical or mechanical versus chemical effects of sebum (Table A).

Hair-or-Feather-Related Functions

Sebaceous glands can be considered appendages of the hair follicle. Kligman (1963) argues on the basis of anatomical association that the function of sebum must be hair-related rather than skin-surface-related. In humans, hair is vestigial so "the sebaceous gland is out of work. It is a living fossil with a past but no future." (p. 308). It follows that "human sebum seems to be useless." (p. 318). Before discussing Kligman's dismissal of the many proposed functions of human sebum (see Table A under "Surface") it is worth looking at the functions which he sees as important in connection with hair:

> In feathered and furred animals sebum seeps out on the hair shaft coating it with fat. Hair is a sebum trap. The fat protects the hair against overwetting and maceration. It also adds sleekness to the coat and insulates against temperature change. A fat-coated hair floats; defatted hair promptly sinks. A striking demonstration of this is afforded by the hapless ducks which were unable to stay afloat when the feather fats were removed by soaping, or when detergents were added to the water. A convincing illustration of the importance of lipid

Table A

Suggested Functions for Surface Lipids

	Hair-or-feather-related	Surface
Physical or mechanical	Keeps hair/feathers dry Excludes dirt Prevents maceration Increases flexibility/ elasticity Prevents matting Lubricates Protects from solar radiation Flotation Insulation	Prevents water loss Preserves skin moisture Keeps skin flexible Prevents absorption of toxins
Chemical	Communication (about species, sex, reproductive status, colony membership, individual identity, etc.)	Antibacterial Antimyocotic Vitamin D synthesis

> in conditioning hair is given in Hou's (1928) experiments on the preen gland, which secretes the lipids in birds. When the gland of ducks was extirpated the plumage deteriorated, becoming soiled, dull and rough. In cold water, the body temperature fell more rapidly. (pp. 307-8)

This quotation raises a number of points which can be elucidated in view of current information. First a word about the "hapless ducks". Kligman seems to misinterpret an experiment by Rutschke (1960, cited in Jacob & Ziswiler, 1982). Addition of detergent to water does allow increased penetration of the feathers but this is not related to the fat content of the plumage but is caused by decreased surface tension of the water. Rutschke found that the feathers of ducks retain their waterproof characteristics when defatted by solvent treatment. The physical properties of feathers are the basis of their water repellence (see Jacob & Ziswiler, 1982).

There is some confusion in the above passage about the mechanisms of lipid distribution in birds. The uropygial secretion (preen wax) does not "seep" over feathers but is actively spread via oiling behavior. However, the uropygial gland is not the only source of surface lipid in birds. Cells with sebaceous secretion may be widely distributed around the skin of species such as bobwhite and Japanese quail, guineafowl, albatross, and pigeon (Borchelt et al., 1979; Jacob & Ziswiler, 1982).

The fact that extirpation of the uropygial gland of ducks does lead to a progressive deterioration in the appearance of the feathers, which become rough and loose their sleekness, suggests that preen wax plays a role in care of the body surface. It has been suggested that preen wax makes feather keratin more flexible thereby facilitating the maintenance of correct arrangement in the fine structural elements of the plumage (Jacob & Ziswiler, 1982). As to Kligman's (1963) claim that preen wax affects thermal insulation, I have not succeeded in locating the Hou (1928) paper on which it is based and have not encountered any other evidence of the same sort. However, it has been suggested that mammalian sebum increases thermal insulation of fur. Thiessen and Pendergrass (1985) sought to test this hypothesis by coating pieces of silk with various amounts of gerbil lipid. They found that such treatment does indeed reduce the cooling effect of an air current. It is difficult to generalize from this result to fur on live animals. However, these authors also showed that gerbils whose hair fats were reduced by shampooing exhibited greater reduction of body temperature in response to cold exposure. Why sebum should increase fur insulation is not altogether clear. Hair is an extremely effective insulator whose thermal conductivity is lower than that of fats and waxes (Hadley, 1985). Lipid could perhaps reduce convective heat loss by causing adjacent fibers to adhere to each other thereby promoting a more effective entrapment of air. There are no data in support of this idea. However, air entrapment appears to be far more important for insulation than is the thermal conductivity of the insulating material (Sokolov, 1982). Air may be very effectively held in the fur of aquatic mammals. This is at least partly attributable to the structure of the guard hairs which may be flattened and bent at the tips as in the case of the duckbill platypus (see Hausman, 1930, for illustration). Some aquatic mammals also have numerous large sebaceous glands for which a waterproofing function has been suggested, e.g., seals (Montagna & Harrison, 1957).

Kligman's remaining claims about the functions of sebum refer to its protective role with respect to individual hairs, i.e., that it prevents wetting and maceration (or splitting). Such issues have been discussed and investigated by textile scientists and the hypothesized protective role of sebum can be extended to include defense against weathering (principally by ultraviolet solar radiation). However, none of these hypotheses receives overwhelming support.

While wool wax may provide some slight protection against ultraviolet photolysis, the wax film is probably too thin to have any practical impact. In summarizing the results of many intricate experiments bearing on possible protective actions of sheep sebum, Truter (1956) concludes that "the biological function of wool wax is obscure" (p. 29) and goes on to suggest, on the basis of the observation that wool production and wax production covary that wax could be "a possible means of removing waste products from the fibre biosynthesis" (p. 29). This notion appears to ignore the fact that the site from which hair grows (the matrix cells of the hair bulb) is anatomically distinct from the cells producing sebum (Parakkal & Alexander, 1972). It might also be asked why no "waste products" are generated in the production of other structures (horn, nail) composed largely of keratin fibers.

A further piece of evidence concerning the correlation between fur production and lipid production is advanced by Sokolov (1962) who found that the size of sebaceous glands and hence presumably the rate of lipid secretion was related to density of fur in desert-adapted rodents. Sokolov explains this correlation by proposing that sebum serves to lubricate the fur. He does not indicate why lubrication is necessary. Sokolov (1982) believes that high sebum production by subterranean mammals protects them from abrasion against their tunnels.

Hadley (1985) states that sebum "is believed to help keep hair from becoming dry and brittle" (p. 138). He does not cite any evidence in support of this view. Sokolov (1982) also states that sebum maintains elasticity of the hair. Truter (1956) considers a related hypothesis - that sheep wax prevents the wool from felting, i.e., becoming tangled and matted. He dismisses this idea, however, on the basis that scoured and unscoured wool shipped from New Zealand to England did not differ in processing characteristics. Instead of preventing matting, large quantities of lipid in the fur may actually cause it (Thiessen & Kittrell, 1980). Ideas about maintaining pliability of the fur and preventing maceration or splitting are commonplaces of the literature which have not, it seems, received empirical investigation.

Surface Functions

Perhaps the most obvious hypothesis concerning the role of sebaceous lipid on the skin surface is that it forms a hydrophobic barrier which protects water balance by preventing transpiration from the surface of the skin. Thus, Quay (1965) assumes that the high rates of sebum production exhibited by desert-adapted rodents prevent water loss and many other authors share this view. The same functional tautology encountered in relation to waterproofing of hair and feathers recurs here: the skin already has an effective water barrier in the stratum corneum, the outer layer of hardened cells (Downing, 1976; Hadley, 1985; Kligman, 1963; Nicolaides, 1963, 1974; Scheuplin & Blank, 1971). It is true, however, that the water-barrier function of the skin is not perfect. Harriman and Thiessen (1983) found, for example, that changes in pelage condition of gerbils as a result of sandbathing altered the amount of water lost through the skin. Fur may thus have an important role in complementing the barrier function of the epidermis and the same idea has been raised in connection with sebum.

However, treatment of excised patches of human skin with solvents did not increase water permeability except where the period of exposure to the solvent was long enough to cause tissue degradation. Conversely, addition of sebum to skin samples did not produce an appreciable reduction in the transpiration of water until the sebum level was increased to about ten times that normally found even in oily areas of the skin (Kligman, 1963). Sebum therefore plays little or no role in water-barrier function of human skin.

Not all sebaceous glands open into hair-sebaceous gland canals. Some open onto the skin surface. According to Sokolov (1982):

> In man such glands are found on the eyelids (Meribomian glands),

> the mucous membrane of the cheeks, and the pigmented surface of the lips, the nipples and the preputrum (Tyson's glands). Other mammals have gigantic sebaceous glands which open on the skin surface in the anal and circumanal regions. (p. 21)

Omitted from this list are the glands of the outer ear which produce wax, a form of sebum. Unlike the pilosebaceous glands, these are apparently very active in children.

Moisturizing and emollient properties of sebum (its proposed cosmetic functions) are also discussed by Kligman, the former in exhaustive detail. He concludes that sebum does not form an emulsion with sweat or in any way retain moisture in the skin. While sebum may have a smoothing (emollient) effect on the skin due to penetration of the spaces between cells in the outer layers of the stratum corneum, this effect is dismissed as "merely cosmetic" (p. 318).

Chemical Functions

Antibacterial and antifungal roles have been proposed for sebum but these ideas do not receive empirical support. The putative antibacterial action was originally held to reside in the mild acidity of surface lipid leading to the use of the term "acid mantle". However, in vitro studies showed that both resident and transient bacteria may thrive at the pH range of skin. Sebum may be a food source for some species and it probably protects them from dessication (Kligman, 1963).

The observation that ringworm is so rare in adults was explained by suggesting that postpubertal sebum contained a greater proportion of free fatty acids which enhances its antifungal action. However, ringworm fungi were found to grow just as well when exposed to adult as to juvenile sebum. Another early misconception was the notion that 7-dehydrocholesterol, the precursor of vitamin D, is a constituent of sebum. In fact, it is produced by the epidermis and not by sebaceous glands (Kligman, 1963). Before leaving this topic, it should be noted that free fatty acids do have well established antibacterial and antimyocotic effects (Jacob & Ziswiler, 1982) but Kligman (1963) emphasizes that such effects are only found for the high concentrations used in in vitro demonstrations.

Communication

The evidence in favor of communication by sandbathing rodents at shared sandbathing loci has already been outlined. Urine and sebaceous glands are the principal source of the signal odors in this context. Sebaceous glands have been modified as specialized odor-producing glands used in a variety of other contexts by a large number of vertebrate species (see Adams, 1980; Brown & McDonald, 1985; Muller-Schwarze & Silverstein, 1982).

Since birds may have a well developed sense of smell (Jones & Gentle, 1985), uropygial secretion may have a communicatory role for them also. In one early experiment, removal of the uropygial gland from female ducks led to maltreatment by conspecifics. Goslings were also found to be capable of discriminating the odor of their mother's uropygial secretion (Jacob & Ziswiler, 1982).

Such a communicatory role is interesting but it is unlikely that the ancestral function of sebum was related to communication. A more plausible interpretation is that sebaceous glands do have (or did have) some physiological function and that the communicatory role is derived.

Biological Consequences of Sebaceous Lipid Production

A number of possibly beneficial consequences of sebum production have been discussed. Many of these suggested functions were previously dismissed in Kligman's (1963) review but live on in the scientific literature. The notion that sebum is functionally related to hair is eminently reasonable given their anatomical association and should serve as the starting point for any future investigation. Sebum production is correlated with hair production in two ways:

1. Secretion rate proceeds in a fairly constant proportion with the growth rate of hair.

2. More finely furred animals (e.g., desert rodents, sheep) have larger, more active sebaceous glands. Fur density is positively correlated with humidity of the environment and wind speed (Sokolov, 1982) and can thus be regarded as an adaptation to conditions which promote chilling. Dense fur is presumably more effective as an insulator because of its enhanced capacity to prevent convective heat loss. It retains an envelope of inert air which has been warmed by the body and prevents the entry of cold air. Does lipid in the fur promote a more effective entrapment of air (e.g., by causing adjacent hairs to adhere slightly)?

The role played by sebum in preventing structural deterioration of hair deserves further empirical investigation. Is defatted hair really more brittle, more likely to split or become tangled? Is it less elastic and flexible? If the functions of sebum remain obscure, this is at least partly due to insufficient information about such basic questions.

APPENDIX 2

Key to Common Name of Animals Referred to by Scientific Name

Scientific name	Common name
Allactaga	Five-toed jerboas
Antechinus	Marsupial rats
Chinchilla laniger	Chinchilla
Chinchilla brevicaudata	Short-tailed chinchilla
Cuniculus	Pacas
Dasyuroides	Marsupial mouse
Dipodomys merriami	Merriam's kangaroo rat
Dipodomys microps	Chisel-toothed kangaroo rat
Dipodomys spectabilis	Bannertail kangaroo rat
Dolichotis	Patagonian cavies
Gerbillus nanus	Field gerbil
Heteromys	Forest spiny pocket mice
Jaculus	Desert jerboas
Lagidium	Mountain viscachas
Lagostomus	Plains viscacha
Liomys	Spiny pocket mice
Meriones unguiculatus	Mongolian gerbil
Microcavia	Mountain cavies
Microdipodops	Kangaroo mice
Myoprocta	Acouchis

Neotoma lepida lepida	Desert woodrat
Octodon	Degus
Octodontomys	Choz-choz
Pachyuromys	Fat-tailed gerbils
Pediolagus	See Dolichotis
Perognathus	Pocket mice
Salpingotus	Pygmy jerboas
Sminthopsis	Dunnarts
Tatera	Large naked-soled gerbils

APPENDIX 3

The bathing behavior of the chinchilla: Effects of deprivation[1]

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Four chinchilla were deprived of the sand in which they rub their fur by spinning. With increased levels of deprivation the number of spins increased and the time course of the spins was altered.

When presented with a box containing sufficient sand, a chinchilla *(Chinchilla lanigera)* will rub its fur in the sand by rotating around its longitudinal axis. The sand spinning behavior of the chinchilla can be divided into three phases. The first, or paw phase, is characterized by the chinchilla thrusting its front paws forward and with one or more rapid strokes drawing surface sand back towards its body. The second, or cheek phase, is characterized by the chinchilla rubbing either or both of its cheeks in the sand. The final, or spin phase, is characterized by the chinchilla partially or completely rotating around its longitudinal axis typically in the direction of its last "cheek-rub," e.g., if the chinchilla has just rubbed its right cheek in the sand, its spin (if any) will be in a clockwise direction. These three phases usually (but not necessarily) appear in the sequence outlined above.

The present study examines the effects of various periods of sand deprivation on the spinning behavior of the chinchilla.

SUBJECTS

There were four Ss, three females and one male. At the start of the experiment the females were approximately 270 days of age while the male was approximately 120 days old. Each S was housed in an individual cage with food and water available ad lib throughout the experiment. Ss were on a reversed 12-h-on/12-h-off light cycle. All testing was conducted 1-2 h prior to the dark period.

PROCEDURE AND DESIGN

All tests lasted 10 min. E placed a clear plastic sandbox (14 x 14 x 4 in.) containing approximately 2 in. of rock dust in S's home cage and recorded S's behavior. In order to examine the effects of previous as well as present deprivation, Ss were given two periods of deprivation separated by one 10-min test. For example, in Cell 1 (Table 1) the animals were initially deprived of the sand for three days, given access to the sandbox for 10 min, and then deprived of the sand for an additional seven days. The cell numbers refer to the sequence of deprivation periods for all animals.

RESULTS AND DISCUSSION

There does not appear to be any relation between days of sand deprivation and paw movements or between days of deprivation and cheek-rubs. Whether one looks at the absolute number of these movements or the ratio of the movements to spins one finds no systematic trend.

With regard to spins there are two major trends. First, as the level of deprivation was increased, the number of spins increased (Fig. 1). An analysis of variance performed on tests reveals an F ratio of 4.06, df = 3/48 ($p < .025$) for present deprivation and an F ratio of 2.36, df = 3/48 ($p < .06$) for previous deprivation. Secondly, as the level of deprivation was increased the percentage of spins occurring during the first half of the test increased (Table 2; $\chi^2 = 23.27$, df = 3, $p < .001$). Therefore, while the levels of sand deprivation employed in this study do not affect the number of paw movements or cheek-rubs, they do affect the number of spins and their time course. In conclusion, it is noteworthy that while the sand bathing behavior of the chinchilla serves no apparent biological need it reacts to deprivation in a manner comparable to behaviors known to serve a need, e.g., eating and drinking.

Table 1
Design of the Experiment. See Text for Explanation.

Previous Deprivation (Days)	Present Deprivation (Days)			
	1	3	5	7
1	3	9	11	4
3	10	16	6	1
5	8	15	7	12
7	2	5	14	13

Table 2
Percentage of Spins Occurring During each Half of the Test.

Days of Deprivation	Minutes 1-5	Minutes 6-10
1	57	43
3	52	48
5	73	27
7	80	20

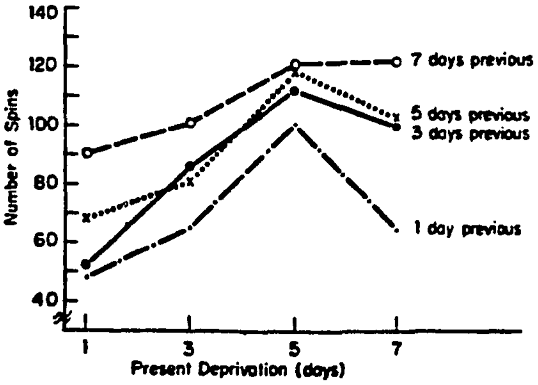

Fig. 1. Total number of spins for all Ss as a function of deprivation.

NOTE

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APPENDIX 4

ANOVA: Data Screening and Results (Experiments 1, 4)

Table A

Experiment 1. Cochran Tests for Homogeneity of Variance on Linear and Log-transformed ($Y_i^1 = \log_{10}(Y_i + 1)$) data

Variable	Linear data		Log-transformed data	
	C^a	p	C^2	p
Rolls	.93	$< .01$	.48	$> .05$
Latency	.93	$< .01$	.42	$> .05$
Visits	.45	$> .05$	.41	$> .05$
Time in sand	.46	$> .05$	.69	$< .01$

[a] For 15 degrees of freedom with three levels of deprivation ($k = 3$).

Table B

ANOVA Tables for Experiment 1 (Rolls, Latency, Time in Sand, Visits) and Experiment 4 (Lipid Levels in Fur)

Source	SS	df	MS	*F*	*p*
			Rolls[a]		
Sex	.132	1	.132	2.55	> .05[b]
Subjects within groups	.724	14	.052		
Deprivation	6.886	2	3.443	104.11	< .001
Sex x dep.[c]	.133	2	.067	2.03	> .05[d]
Dep. x subjects within groups	.926	28	.033		
			Latency[a]		
Sex	1.04	1	1.04	1.39	> .05
Subjects within groups	10.45	14	.75		
Deprivation	13.59	2	6.80	82.78	< .001
Sex x dep.	.11	2	.06	.75	> .05
Dep. x subjects within groups	2.80	28			

Table B (contd.)

Source	SS	df	MS	*F*	*p*
			Time in sand		
Sex	168,509	1	168,509	5.84	< .05
Subjects within groups	403,613	14	28,830		
Deprivation	397,962	2	198,981	25.50	< .001
Sex x dep.	33,752	2	16,876	2.16	> .05
Dep. x subjects within groups	218,511	28	7,804		
			Visits to sand[a]		
Sex	.005	1	.005	.15	> .05
Subjects within groups	.466	14	.033		
Deprivation	1.858	2	.929	43.87	< .001
Sex x dep.	.018	2	.009	.43	> .05
Dep. x subjects within groups	.593	28	.021		

Table B (contd.)

Source	SS	df	MS	*F*	*p*
			Lipid levels in fur		
Sex	238	1	238	.14	> .05
Subjects within groups	24,077	14	1,720		
Treatments	10,784	2	5,392	24.19	< .001
Sex x dep treatments	532	2	266	1.19	> .05
Treatments x subjects within groups	6,241	28	233		

[a] Log-transformed variables. [b] Critical value of $F_{.05}(1,14) = 4.61$. [c] Dep. = deprivation. [d] Critical value of $F_{.05}(2,28) = 3.35$.

Table C

Tests on Differences Between Treatment Means by Newman-Keuls Method

Rolls

Deprivation (days)	0		1		5	(5-0)
Ordered means[a]	.04		.24		.93	
Differences		.20*		.69*		.89*
Sb = .045[b]		r = 2[c]		r = 2		r = 3
q.95(r,28)[d]		2.90		2.90		3.50
Sbq.95(r,28)[e]		.13		.13		.16

Latency

Deprivation (days)	0		1		5	(0-5)
Ordered means[a]	2.45		1.47		1.21	
Differences		.98*		.26*		1.24*
Sb = .071		r = 2		r = 2		r = 3
q.95(r,28)		2.90		2.90		3.50
Sbq.95(r,28)		.21		.21		.25

Table C (contd.)

Time in sand

Deprivation (days)	0		1		5	(5-0)
Ordered means[a]	36.6		167.3		258.6	
Differences		130.7*		91.3*		222.0*
Sb = 22.1		r = 2		r = 2		r = 3
q.95(r,28)		2.90		2.90		3.50
Sbq.95(r,28)		61.1		64.1		77.4

Visits to sand

Deprivation (days)	0		1		5	(5-0)
Ordered means[a]	.16		.52		.61	
Differences		36*		.09		.45*
Sb = .036		r = 2		r = 2		r = 3
q.95(r,28)		2.90		2.90		3.50
Sbq.95(r,28)		.10		.10		.13

Table C (contd.)

	Time in sand					
Treatments	Mesh		Sand		Shampoo	(Sand-Shampoo)
Ordered means	114.7		86.0		80.1	
Differences		28.7*		5.9		34.6*
Sb = 3.73		r = 2		r = 2		r = 3
q.95(r,28)		2.90		2.90		3.50
Sbq.95(r,28)		10.8		10.8		13.1

[a]Log-transformed data. [b]Standard error of the mean for all observations at a given level of the within-subject factor (see Winer, 1962, p. 309). [c]Number of steps apart of means in the ordered sequence plus one. [d]Studentized range statistic. [e]Critical differences between means. Compare with "Differences" row to establish significance of contrasts.

*p < .05, multiple confidence level.

APPENDIX 5

Pearson Correlation Matrices for Dependent Variables in Experiments 1-3

Table A

Experiment 1. Data Collected at a Sand Deprivation Level of Five Days (N = 16)

	Rolls	Latency	Time in Sand
Latency	.29		
Time in sand	-.50	-.22	
Visits	.05	-.25	-.30

Note Critical *r* ($p < .05$, joint confidence level) = .65

Table B

Experiment 2. Data Collected at a Sand Deprivation Level of 25 Days Following Either (Experimental) Shampooing or (Control) Water Wash. (N = 16, Both Conditions).

	Rolls	Latency	Time in sand
		Experimental Tests	
Latency	−.35		
Time in sand	.41	.10	
Visits	.23	−.43	.45
		Control Tests	
Latency	.06		
Time in sand	.39	−.17	
Visits	.09	−.21	.31

Note Critical *r* ($p < .05$, joint confidence level) = .65

Table C

Experiment 3. Data Collected at a Sand Deprivation Level of One Day Following Either (Experimental) Oil or (Control) Water Treatment (N = 16, Both Conditions).

	Rolls	Latency	Time in Sand
		Experimental Tests	
Latency	-.50		
Time in sand	.47	-.46	
Visits	.64	-.40	.45
		Control Tests	
Latency	-.23		
Time in sand	-.41	-.35	
Visits	-.24	-.33	.34

Note Critical *r* ($p < .05$, joint confidence level) = .65.

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