lateral deviations. The main effect of repeated trials, which was the day-4 to day-8 improvement effect, was significant at $P < .0005$ [the analysis of variance F ratio for 1 and 9 degrees of freedom (df) = 80.89]. The effects of base orientation and the interaction between base orientation and repeated trials were not significantly different, although, of course, the direction of the errors was opposite for base-right and base-left subjects.

A total of 14 chicks responded at day 8 when first wearing control hoods containing 0° clear plates (the 11 chicks mentioned above, plus three which failed to respond at day 4 and hence could not be included in the earlier analysis). No subject returned to 0 mm average pecking displacement. All but two of the 14 responded in the direction opposite to their initial displacement (negative aftereffect). The average negative aftereffect was 1.285 mm in the optically predicted directions. These results are significant at $P < .005$ [$t = 3.38$, 13 df (one-tailed test)] when compared to the hypothetical no effect predicted by Hess (*2*).

The existence of the negative aftereffect is in direct opposition to the concept that visual direction relationships in domestic fowl cannot be modified through experience. It would appear that it is the significant negative aftereffect rather than adaptation which is the more important finding. The pecking response of the chick requires that he make a directional choice at a distance with little or no opportunity for in-flight correction of aim. The test of negative aftereffect used in this experiment closely approximates the blind pointing or reaching without visual feedback measures of human (*8*) and higher primate (*9*) adaptation to lateral optical displacement, and thus these results can be used as a second and perhaps more useful index of comparative adaptation capacity.

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Androgen Control of Territorial Marking in the Mongolian Gerbil

Abstract. *Gerbils mark objects with the secretion of a midventral sebaceous gland. Both the behavior and the gland integrity are under androgen control, as indicated by castration and replacement with testosterone propionate. The integrity of the gland seems less important for marking than an influence on the central nervous system, although the gland can be used as an external measure of androgen levels. It is possible that the secretion acts as a pheromone to signal territorial possession.*

The Mongolian gerbil (*Meriones unguiculatus*) is rapidly becoming a significant target for biological research (*1*). Members of this species (order Rodentia; family Cricetidae) weigh about 70 to 90 g as adults, are highly exploratory and tractable, and require no water other than that derived as a metabolic by-product. Recently, we have described for the gerbil an abdominal skimming response that we interpret as territorial marking (*2*). In brief, both males and females rub a ventral sebaceous gland over low-lying objects, leaving a sebum that is oily to the touch and musky in smell. The response is highly discrete, involving rapid approach to an object, sniffing of the object, mounting it and then pressing the ventral sebaceous gland against its surface, and finally a forward dismount. Males mark objects about twice as frequently as females, corresponding in a rough way to the sex difference in the size of the sebaceous gland. When a male enters a territory already masked by the sebum from another animal its marking frequency is reduced (*2*). In a well-developed male the gland is a midventral, orange, fusiform pad approximately 3 cm long, 0.7 cm wide, and 0.2 cm thick. Its histology has been described and, in the male, its integrity is dependent on the gonads (*3*). Generally the gland is enfolded by ventral body hairs but can be detected by the orange stain from the sebum or exposed by clipping or shaving the surrounding hair (*4*). This report on the male emphasizes the effects of castration and testosterone therapy on the marking behavior and the morphology of the ventral sebaceous gland.

Marking behavior and activity were assessed in an area (1 m²) on a wooden floor marked off into 16 squares of equal size. A roughened Plexiglas peg, 2.6 cm long, 1.2 cm wide, and 0.7 cm high, was permanently positioned at each of the nine lined intersections. The field was surrounded by gray wooden walls 47 cm high, each of which held one 15-watt light bulb shielded at the top and focused into the interior of the field.

Sixty male Mongolian gerbils, obtained from Tumblebrook Farms in New York and approximately 80 days old, began the experiment. Each animal was given one 5-minute trial in the field every 3rd day until six trials were complete. A trial consisted of placing the gerbil in the middle of the field and recording the number of peg marks and

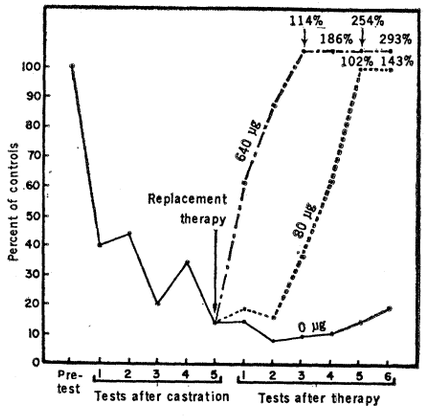

Fig. 1. Effects of castration and testosterone propionate therapy on territorial marking.

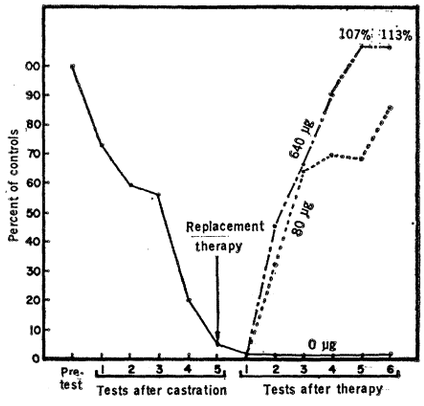

Fig. 2. Effects of castration and testosterone propionate therapy on size of the ventral gland.

line crossings made during a 5-minute period. A mark was recorded whenever an animal skimmed a peg and flattened its abdomen over the surface. Three measures of gland size were taken during this pretest period by shaving the ventral area and measuring the sebaceous gland. All gland measurements are expressed, in centimeters, as length times width. After each trial the apparatus was thoroughly cleaned with a 70-percent solution of alcohol. Testing was carried out in midafternoon.

Only those animals ($N = 24$) reaching a criterion of five or more marks during the 5-minute test were retrained for further study. Three-fourths of these were castrated on the day following the last test, and one-fourth were sham-operated; 1 week later behavioral testing was resumed. Each animal was tested every 3rd day until marking in the castrates approached zero. To minimize handling and trauma, gland measurements were taken after every other test.

When marking approached zero in the castrates, three groups were formed of six animals each whose mean precastration marking scores were identical and matched the mean of six sham-operated controls. One castrate group received 80 μg of testosterone propionate during the next phase of the experiment, another received 640 μg of the hormone, and the third received the vehicle substance only (safflower oil). The sham-operated group also received injections of safflower oil. The hormone and vehicle or the vehicle alone was injected subcutaneously every 3rd day for 24 days in volumes of 0.1 ml. Behavioral testing and gland measurement every 3rd day resumed 1 week after the first injection.

Figures 1 and 2 show the effects of castration and replacement therapy on marking and on gland size, respectively. Variations of castrate and hormone replacement groups are expressed as the percentage of values of sham-operated controls. Average daily marking score and gland size for control gerbils were 11.0 $\pm$ 0.72 marks and 1.33 $\pm$ 0.13 cm, respectively. Thus, both marking and gland integrity are androgen-dependent. The extreme differences in formation of glands between intact and castrate gerbils are seen in Fig. 3.

Several points deserve emphasis. First, there is a strong correlation between marking and gland size, both with the percentage of changes of the two variables ($r = .78$; df = 18; $P < .01$) and absolute changes ($r = .64$; df = 18; $P < .01$). Moreover, markings before and after tests are significantly related ($r = .46$; df = 18; $P = .05$), but pretest and post-test gland size are not. It is obvious that both the decline in marking after castration and the recovery of marking after large doses of testosterone propionate are more sensitive to the hormonal state than gland morphology is. This would suggest that ordinarily marking level and gland morphology are dependent upon systemic titers of androgen, but that a loss or gain of hormone at some central locus is the instrumental factor in the regulation of the behavior, and this appears to be independent of the integrity of the marking gland per se.

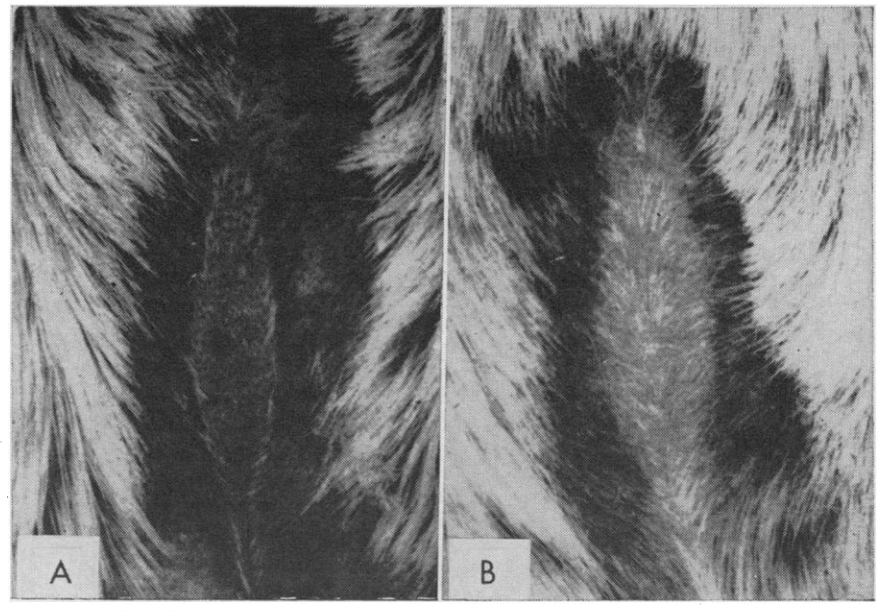

Fig. 3. Gland characteristics in intact (A) and castrate (B) gerbil.

Second (and this too bears on the point that marking behavior is centrally controlled), replacement therapy with 640 μg of testosterone propionate results in "supermarkers" (control versus 640-μg group on last test, $P < .05$). Terminal gland size, on the other hand, did not increase over control levels. It should also be noted that some castrates continue to mark at low levels despite the complete absence of a ventral gland and that other gerbils that never mark have well-developed glands.

Third, activity measures, as indicated by line crossings during the 5-minute period, did not correlate significantly with marking or hormone dosage. One cannot, therefore, attribute marking frequency to general exploration. On the basis of our data it seems probable that the primary means of territorial signaling by the gerbil is through the use of an odorous pheromone spread on objects by the ventral sebaceous gland and sensed by conspecifics.

The similarities between this androgen-controlled behavior and sex behavior, another androgen-controlled behavior, in the male rat are striking (*5*). Aggression, although not as thoroughly studied as sex behavior, is also androgen-mediated in some rodent forms (*6*). It is possible that sex behavior and aggression in the gerbil are under similar control. If this assumption proves correct, we would have an interesting situation in which one hormone, androgen, controls three important dimensions of species survival—intraspecies competition, territorial formation and signaling, and reproductive competence. A high titer of androgen in the blood would qualify an individual for all responses necessary to pass its genes on to the next generation.

One last comment should be made about the importance of the sebaceous marking gland as a biological assay tissue. Within limits the morphology of the gland accurately reflects the activity of the gonads. For the study of hormone-dependent behaviors a readily measured external referent is a distinct advantage. In this regard the ventral marking gland of the gerbil may take its place beside other biological indices of hormone activity, such as the cock comb, the pigeon crop sac, rodent mammary glands, and the vaginal cycle of several species.

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20 February 1968

Barking, Dominance, and Territoriality in Male Sea Lions

Abstract. *Experiments in which male sea lions* (Zalophus californianus) *were removed and reintroduced into a social group demonstrate that barking by larger males restricts movement and barking by other smaller males. Barking and aggression were primarily directed toward animals of most nearly equal size. Two 6-year-olds seeking to establish and maintain territorial status used aggressive tactics similar to those observed in breeding males in the field.*

Aggressive behavior in vertebrate social groups is controlled by social structure, territoriality, and vocal signaling (*1*). Field observations made during the breeding season of several species of pinnipeds suggest that breeding males signal and defend territorial possessions primarily by means of a highly stereotyped series of vocalizations (*2*). Vocal signaling is thought to reduce actual fighting during the establishment and maintenance of territories.

Underwater sounds (barks, clicks, bangs, buzzes, and growls) produced by the sea lion (*Zalophus californianus*) are apparently a function of its social and investigatory responsiveness (*3*). Barking by individual males appears specifically related to the group social structure and territoriality (*4*). Manipulation of the social structure should therefore change the amount of barking by individual male sea lions in the group. On this hypothesis, a series of experiments was conducted in which group composition was modified by removing and reintroducing individual animals and recording the frequency of barking and attack by 10-second intervals on a time-ruled check sheet.

All experiments were conducted in two outdoor rectangular compounds enclosed and separated from each other by a cyclone wire fence. Compound 1 (where the animals were usually housed) contained a pool and a long concrete slide; there was a graded rocky slope running along one side of both compounds. The fence separating the two compounds had three gates. Six male *Zalophus,* living together for at least 3 months, and a seventh animal (G), introduced during the last experimental sessions, were observed from above the rocky slope (Table 1). All but one (S) of the sea lions were fed before the sessions which usually took place between 1300 and 1900 hours. On all but one occasion, sea lions were removed from compound 1, placed in compound 2, and reintroduced one at a time. Observations and recordings usually began approximately 30 seconds after an animal's removal or return. Living with the sea lions were three other species of pinnipeds: two young elephant seals (*Mirounga angustirostris*; one yearling and one 2-year-old), two adult harbor seals (*Phoca vitulina*), and two yearling Stellar sea lions (*Eumetopias jubata*).

During the first experiment, the most mature animal (M), which was removed and reintroduced, barked the most; when M was removed to compound 2, the next largest sea lion (W) barked the most. Further experiments substantiated this trend (Fig. 1). In another series of experiments, to determine the frequency of barking by individuals in both compounds, we removed sea lions M, W, and P (in that sequence) and then returned each one in reverse order (Fig. 2). In general, these results are similar to those previously obtained. The wire fence served as a signal to younger animals that barking and other aggressive displays by M could not be followed up by physical attack. The amount of individual barking always depended on the nature of the group's dominance structure.

The relation between barking and dominance is shown by the analysis of attack-withdrawal scores (Table 1), which represents the total number of 10-second intervals in which one sea lion was in the process of attacking another during the entire series of experiments. The most mature sea lion attacked, on a discriminative basis, usually the next largest sea lion in the group. Less mature animals never attacked larger individuals; the more mature sea lions rarely attacked the two smallest individuals.

Removal or reintroduction of a dominant or alpha animal dramatically affected the behavior of the (beta) individual next in line in the social hierarchy. A dominant sea lion usually maintained a position in the pool, either swimming around the perimeter or holding a quadrupedal stance at the shallow edge while producing a rather continuous series of barks. The beta animal was usually positioned at or near the top of the rocky slope. This spatial relationship between alpha and beta animals was stereotyped: when the beta animal moved from the top of the rocky slope he was usually attacked and pursued by the alpha animal until the beta individual resumed its former position. Usually, when it returned to compound 1, a dominant individual immediately set up a barking pattern and locomoted directly to the pool, while the beta animal immediately fell silent and

Table 1. Attack-withdrawal scores and characteristics of the male sea lions (*Zalophus californianus*) in the social group.

Age (yr)	Wt (kg)	Attacking animal	Withdrawing animal						
			G	M	W	P	K	S	T
5–6	136	G	–	8	1	0	0	0	0
5–6	153	M	0	–	42	1	0	0	0
3	68	W	0	0	–	104	54	6	4
3	58	P	0	0	0	–	6	3	1
2	50	K	0	0	0	0	–	10	1
2	40	S	0	0	0	0	0	–	2
2	38	T	0	0	0	0	0	2	–