antigen to the salivary glands may contribute to the level of salivary antibody (*14*).

The occasional adverse reactions that accompany parenteral immunization may be circumvented by oral administration of antigen. This point is important in relation to prevention of dental caries in human beings. In previous studies, effective anticaries immunity was provided through immunization routes that are unlikely to be suitable for human use.

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References and Notes

1. H. W. Scherp, *Science* **173**, 1199 (1971); P. H. Keyes, *J. Am. Dent. Assoc.* **76**, 1357 (1969); W. J. Loesche, J. Rowan, L. H. Straffon, P. J. Loos, *Infect. Immunol.* **11**, 1252 (1975).
2. *Symposium on the Immunological Aspects of Dental Caries*, R. Genco, W. Bowen, T. Lehner, Eds., *J. Dent. Res.* **55**, C206 (1976), special issue; W. Bowen, R. Genco, T. O'Brien, Eds., *Immunologic Aspects of Dental Caries: Selection of Immunogens for a Caries Vaccine and Cross Reactivity of Antisera to Oral Microorganisms with Mammalian Tissues* (Government Printing Office, Washington, D.C., in press).
3. J. F. Heremans, in *The Antigens*, M. Sela, Ed. (Academic Press, New York, 1974), vol. 2, pp. 365–522.
4. B. Guggenheim, R. Mühlemann, B. Regolati, R. Schmid, in *Dental Plaque*, W. D. McHugh, Ed. (Thomson, London, 1970), pp. 287–296; J. M. Tanzer, G. J. Hageage, R. H. Larson, *Arch. Oral Biol.* **18**, 1425 (1973).
5. R. T. Evans, F. G. Emmings, R. J. Genco, *Infect. Immunol.* **12**, 293 (1975).
6. M. A. Taubman and D. J. Smith, *ibid.* **9**, 1079 (1974); J. R. McGhee, S. M. Michalek, J. Webb, J. M. Navia, A. F. R. Rahman, D. W. Legler, *J. Immunol.* **114**, 300 (1975).
7. P. C. Montgomery, J. Cohn, E. T. Lally, in *The Immunoglobulin A System*, J. Mestecky and A. R. Lawton, Eds. (Plenum, New York, 1974), pp. 453–462; R. M. Goldblum, S. Ahlstedt, B. Carlsson, L. Å. Hanson, U. Jodal, G. Lidin-Janson, Å. Sohl-Akerlund, *Nature (London)* **257**, 797 (1975).
8. Adult germfree rat dams were maintained in Trexler plastic isolators. Rat pups were weaned at 20 days of age, transferred to experimental isolators, and provided purified caries-promoting diet [S. M. Michalek, J. R. McGhee, J. M. Navia, *Infect. Immunol.* **12**, 69 (1975)].
9. S. M. Michalek, T. Shiota, T. Ikeda, J. M. Navia, J. R. McGhee, *Proc. Soc. Exp. Biol. Med.* **150**, 498 (1975).
10. P. H. Keyes, *J. Dent. Res.* **37**, 1088 (1958).
11. Immunoglobulin levels were determined by radial immunodiffusion as previously described [J. R. McGhee, S. M. Michalek, V. K. Ghanta, *Immunochemistry* **12**, 817 (1975)]. Agglutinin antibody levels were determined by the microtitration technique as described [McGhee *et al.* (*6*)].
12. J. R. McGhee, S. M. Michalek, V. K. Ghanta, *Immunochemistry* **12**, 817 (1975).
13. Fresh tissues were frozen in liquid nitrogen and processed as described [F. W. Kraus and J. Mestecky, *Arch. Oral Biol.* **16**, 781 (1971)]. Fluorescein isothiocyanate–labeled goat antiserums to mouse μ, α, and γ chains (Meloy Laboratories) were applied to various sections. These antiserums were previously found to cross-react with the corresponding rat immunoglobulins. Sections were examined with a fluorescence microscope equipped with a vertical illuminator according to Ploem (Orthoplan, Leitz, Germany).
14. J. M. Crawford, M. A. Taubman, D. J. Smith, *Science* **190**, 1206 (1975); F. G. Emmings, R. T. Evans, R. J. Genco, *Infect. Immunol.* **12**, 281 (1975).
15. S. M. Michalek, J. R. McGhee, V. K. Ghanta, *J. Reticuloendothel. Soc.* **16**, 213 (1974).
16. After centrifugation and precipitation of casein [J. Mestecky, R. Kulhavy, F. W. Kraus, *J. Immunol.* **108**, 738 (1972)] the samples were chromatographed on a Sephadex G-200 column (1.6 by 100 cm) equilibrated in 1 percent ammonium bicarbonate buffer, *p*H 7.0. The distribution of immunoglobulin classes in fractions was determined by precipitation as described by McGhee *et al.* (*12*).
17. S. W. Craig and J. J. Cebra, *J. Exp. Med.* **134**, 188 (1971); J. G. Hall and M. E. Smith, *Nature (London)* **226**, 262 (1970); A. R. Moore and J. G. Hall, *ibid.* **239**, 161 (1972); D. Guygrand, C. Griscelli, P. Vassalli, *Eur. J. Immunol.* **4**, 435 (1974); M. D. Cooper, P. W. Kincade, D. P. Bockman, A. R. Lawton, in *The Immunoglobulin A System*, J. Mestecky and A. R. Lawton, Eds. (Plenum, New York, 1974), pp. 13–22; A. F. Williams and J. L. Gowans, *J. Exp. Med.* **141**, 335 (1975).
18. Supported by NIH grants DE 04217, DE 02670, and AI 10854. We thank Drs. M. D. Cooper, H. M. Fullmer, and F. W. Kraus for criticisms of this report; R. Kulhavy for excellent assistance; and C. A. Sims and J. Morris for editorial advice.

28 January 1976; revised 6 April 1976

Lekking Behavior in Kafue Lechwe

Abstract. *The Kafue lechwe (*Kobus leche kafuensis*) exhibits lekking behavior in which a number of males occupy small territories clustered together in discrete areas where females go for mating. Similar behavior in antelope is known only in the Uganda kob (*Kobus kob thomasi*). Lechwe lekking occurs only during a main rutting season although some breeding occurs throughout the year.*

Three subspecies of the lechwe antelope, *Kobus leche* Gray, are recognized in the Central African Republic of Zambia (*1*). The Kafue lechwe, *Kobus leche kafuensis* Haltenorth, exhibit territorial behavior on leks during their main rutting season. Although many African antelopes are territorial when they breed (*2*) and some features of lekking have been observed in the lechwe and other members of the genus *Kobus* (*3*), full-scale lekking has been reported only in the congeneric Uganda kob *Kobus kob thomasi*, which breeds on leks throughout the year (*4*).

The characteristic features of lekking behavior are known principally from a few species of ground-living birds (*5*). While satisfying the defining attributes of territorial behavior, that is, attachment to a limited area which is defended against conspecifics, lekking includes several additional features. A lek is a circumscribed area, often the same from year to year, in which a few adult males occupy a cluster of small, adjacent territories used solely for mating. The male occupants spend much of their time engaging in ritualized displays, regardless of whether females are present. Displays are enhanced by eye-catching morphological features usually found in males of lekking species (for example, vivid plumage). Females enter a lek to mate and choose a male for the purpose. The social status of males on a lek is unequal and it is usual to observe most or all females on a lek with a single male on a "prime" territory. Only a small percentage of adult males occupy a few scattered leks and, of these, only a small percentage do most of the breeding. It is likely that these features of lekking, in combination with its seasonality, explain why reports of lechwe behavior in the past have been contradictory with regard to the question of whether lechwe are aggressive or territorial (*3*, *6*).

The estimated population of Kafue lechwe in 1974 was about 110,000. It is centered on Lochinvar and Blue Lagoon National Parks, two small game reserves with a combined area of about 840 km^2 that are located on nearly opposite sides of the Kafue River, which drains central Zambia. Much of the park area falls within the Kafue Flats, a floodplain of the river located at about 15.5°S and 27° to 28°E. When possible, lechwe are usually found on the open floodplain and are often found grazing in or near water (*3*, *6*). Much smaller herds of zebra and wildebeest share the open plains with the lechwe. All natural predators were eliminated from the area years ago, and poaching has been the only major threat although hydroelectric development poses a major problem in the future (*7*). This report is based on ten field trips to Lochinvar at approximately 2-week intervals between August 1974 and February 1975, the first stage of an ongoing project.

The life of the lechwe is marked by seasonal fluctuations related to a marked annual flooding cycle on the Flats. Zambia has a single rainy season from about November until March, with a peak in December and January. There is a corresponding rise and fall in the water level on the Flats; the peak flood occurs from about April through June. This forces the lechwe herds into an annual cycle of movements and changes in population density related to the availability of grazing (*6*). Although mating and parturition occur to some extent throughout the year, there is a higher frequency of sexual activity and enlarged testes from mid-November until mid-February (*6*).

Because the flood begins to rise with the onset of the rains, the male and female herds are already migrating from the lower-lying areas when the peak of the rutting season occurs in December and January. This is the only time that lekking was observed.

The spatial distribution of territorial males and sexually active females was consistent with lekking. Within nearly circular areas about ½ km in diameter, usually between 50 and 100 adult males were found on successive days. They were spaced about 15 m apart in the center and further apart on the edges (Fig. 1). Four such areas were found at widely separated locations, all on elevated or exposed areas adjacent to permanent water. When females were within these areas, usually between 10 and 20 were tightly clustered around one or two males, evidence of the unequal status among occupants. Adjacent to the leks were large mixed herds composed of both sexes and all ages, with some tendency for clusters to form of the same sex and age.

Territorial behaviors exhibited by the lekking males were typical of leks in birds (*5*) and markedly similar to those of the kob (*4*). Territoriality was inferred from the attachment, displays, and defense directed to the small areas occupied by the males. Attachment was shown by the presence of the same males on the same patches of ground over successive hours or days and by spatial limitations when interacting with other lechwe. Chases of one male by another often ended when the pursuer drew up sharply and displayed, with head held high, feet prancing, tail wagging, and head shaking. The same was also seen when a female entered a male's territory. He typically ran up to and around the female, trying to prevent her escape without physical contact. If she left the territory, the male's chase ended abruptly in a display, thus allowing the next male to take over, and so on in relay until the female either chose to remain within a male's territory or left the lek. Males entering a lek were often chased successively in the same manner as if the lek occupants were an elite "corporate body" defending the lek as a unit.

Displays were exhibited most of the time by occupying males. The males rarely grazed, but instead stood in an exaggerated pose with head held high, legs prancing, tail wagging vigorously, and the penis often erect (Fig. 1). In lechwe, displaying is enhanced by features present only in the larger adult male—lyrate horns averaging 72 cm along the front curve (*1*) and solid black markings on the fore- and hind legs, with the foreleg patches extending up to conspicuous shoulder markings (Fig. 1). Another frequent display made use of a behavior common in many ungulates (*8*), that is, tearing at the ground with the horns. The head is swung vigorously from side to side, causing tufts of grass to be flung high into the air and often draped on the horns and neck.

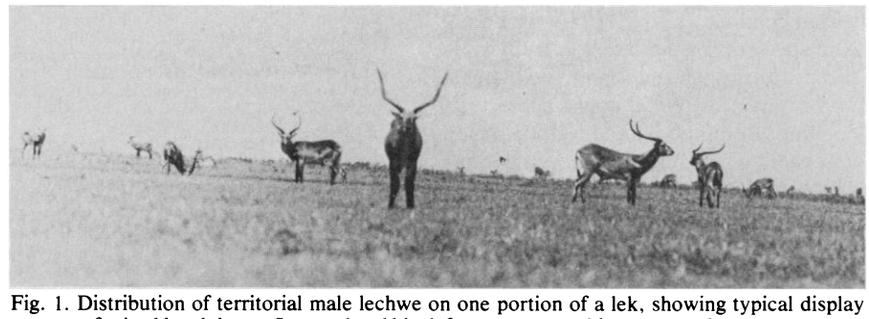

Fig. 1. Distribution of territorial male lechwe on one portion of a lek, showing typical display posture of raised head, horns flattened and black forequarter markings exposed.

Defense of a territory against neighboring occupants was highly ritualized, with threats and chases far more frequent than physical contact. Lechwe leks were notable for the almost continual occurrence of male to male interactions between territorial occupants, conveying an atmosphere that was highly charged and unstable. The movement of a male or female almost anywhere was likely to set off a chain reaction of chases and fights. Chases were more frequent. Of 184 recorded male to male interactions on leks, 140 were threat walks or chases without face-to-face confrontation. Typically, the pursuer trotted "deliberately" toward the pursued male with head low, ears back, and horns flattened until the latter either left or was chased from the area. The pursuer followed for a few meters and then pulled up abruptly in a head-up display with vigorous head shaking.

In 41 face-to-face confrontations, boundary defense against neighboring males was accomplished with a set of ritualized threat behaviors executed in near-perfect synchrony with little or no actual fighting. If the animals faced off more than about 2 to 3 m apart, they would lower their heads to the ground in face-to-face ground tearing or agonistic grazing, sometimes alternating between the two. If they approached to within about 1 or 2 m of each other, the heads of the two contestants would rise with their muzzles kept pointing at each other as their heads were swung from side to side. This could lead to a still closer approach in which they dropped abruptly into the typical fighting posture of antelope: heads down, horns vertical, noses pointing to the ground, with the body angled forward and the rear legs braced for butting and pushing. The head up and head down positions could alternate rapidly as the contestants approached and withdrew in rapid alternation, never making horn contact. If actual contact occurred, the animals would simultaneously make rapid thrusts with horns vertical so that their horns clashed only briefly, after which they quickly separated, their heads rising together. The total time spent in clashing was small, with most of the contest being spent in alternating approach and withdrawal and in lengthy intervals of ground tearing and grazing if the contestants moved apart. Such nonviolent contests could be prolonged; of those observed, ten lasted for 5 or more minutes and one for more than 20 minutes. The confrontation ended when one contestant turned and walked off, usually to an adjacent territory.

Three observed fights were more intense and were notable for little or no preliminary ritual and for lengthy periods of continuous contact. The combatants rushed into combat from some distance apart, the heads lowering immediately and the horns clashing violently. The horns were first tested against each other in vertical position with rapid thrusts. Then the horns were interlocked in horizontal position for extended periods and the fight consisted mostly of pushing and shoving, the combatants twisting and turning until sometimes their bodies were parallel or one animal was forced to the ground. Such fights had a single encounter, with the loser abruptly breaking contact and running off a long way and the victor pursuing and then displaying. We interpret such intense fighting as an attempt on the part of an intruder to contest a territory with the present occupant.

Understanding of the socioecological significance of lekking is furthered by the highly similar habitats of the Kafue lechwe and Uganda kob and the many similarities in their lekking behaviors. Both species live in high concentrations

within confined areas. Each is the dominant species within its habitat. Both habitats feature open grassland, permanent water, and low-lying areas subject to flooding. Both kob (*9*) and lechwe prefer to locate leks on high or exposed ground which is dry but adjacent to water. At Lochinvar, few sites fit all these requirements, a circumstance appropriate for the development of a type of territoriality in which numbers of territories are compressed together on a few suitable locations. A related finding is that lekking was never observed outside the main rutting season, when the frequency of mating was lower. Apparently, a necessary condition for lekking is a large number of adult males simultaneously rutting.

The ecology of the Kafue Flats may also be responsible for some unique features in the lekking behavior of lechwe. There are variations in flood levels from year to year and gradually rising flood levels during each lekking season. Two leks seen at the start of the season were empty a month later; a fourth lek was not seen until midway during the main rutting season when most lechwe had migrated off the floodplain. Reproduction seems to be organized around a succession of temporary leks as the lechwe migrate to higher ground. This could explain the almost continual chasing and fighting. On new leks, territories can only be marked by means of behavioral displays. There are no conspicuous areas of cropped grass, bare ground, or excrement to denote territorial areas. This should contribute to a more unstable situation in which neighbors are more likely to wander into each other's territory, precipitating territorial conflict.

It has been suggested that seasonal territoriality in antelope can be usefully subdivided into three stages corresponding to successive periods when territories are established, maintained, and dissolved (*2*). Aggression is supposedly most frequent and intense during the initial stage as contestants vie for possession, establish boundaries, and expel competitors. Lechwe lekking may be an example of a system that is perpetually in the early stages of territoriality.

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References and Notes

1. W. F. H. Ansell, *Puku Occas. Pap. Dep. Wildl. Fish. Natl. Parks No. 2* (1964), p. 10; *ibid. No. 5* (1969), p. 1.
2. F. R. Walther, *Zool. Afr.* **7**, 303 (1972).
3. A. de Vos and R. J. Dowsett, *Mammalia* **30**, 30 (1966); P. C. Lent, *East Afr. Wildl. J.* **7**, 147 (1969).
4. H. K. Buechner, *Science* **133**, 698 (1961); *Proc. 16th Int. Congr. Zool.* **3**, 59 (1963); _____ and R. Schloeth, *Z. Tierpsychol.* **22**, 209 (1965); H. K. Buechner, J. A. Morrison, W. Leuthold, in *Comparative Biology of Reproduction in Mammals*, I. W. Rowlands, Ed. (Academic Press, New York, 1966), pp. 69- → H. K. Buechner and H. D. Roth, *Am. Zool.* **14**, 145 (1974); W. Leuthold, *Behaviour* **27**, 214 (1966).
5. V. C. Wynne-Edwards, *Animal Dispersion in Relation to Social Behaviour* (Oliver & Boyd, London, 1962), chap. 11.
6. J. A. Sayer and L. P. van Lavieren, *East Afr. Wildl. J.* **13**, 9 (1975); B. L. Mitchell and J. M. C. Uys, *Oryx J. Fauna Preserv. Soc.* **6**, 171 (1961); W. L. Robinette and G. F. T. Child, *Puku Occas. Pap. Dep. Wildl. Fish. Natl. Parks No. 2* (1964), p. 84.
7. A hydroelectric project under construction on the Kafue River is scheduled for completion in 1978. This includes dams up- and downriver from the lechwe habitat and could alter the ecology of the area by reducing the extent and increasing the duration of the annual flooding cycle. This, in turn, would reduce the amount of grass available for forage. Thus the lekking patterns described here may be affected by reduction in population density and by interference with the annual migrations across lekking areas. The future of the Kafue lechwe is therefore uncertain.
8. A. F. Fraser, *Reproductive Behavior in Ungulates* (Academic Press, New York, 1968).
9. H. K. Buechner, in *The Behavior of Ungulates and Its Relation to Management*, V. Geist and F. Walther, Eds. (Paper No. 49, International Union for Conservation of Nature and Natural Resources, Morges, Switzerland, 1974).
10. I thank the Kafue Basin Research Program of the University of Zambia and the Fauna Preservation Society of the Zoological Society of London for continuing financial support and the Zambia Electricity Supply Corporation for donation of a land rover to the Kafue Basin Research Program. The Department of Wildlife and National Parks of the Ministry of Lands and Natural Resources gave permission for the study to be carried out at Lochinvar Park. My children, Ben and Ruth, and my student, S. P. T. Nyandiya, provided many observations contained in this report. The first draft was written while I was a visiting research fellow of the Laboratory of Experimental Psychology, University of Sussex, Falmer, Brighton, England.

25 November 1975; revised 30 March 1976

Evaluation of Transcendental Meditation as a Method of Reducing Stress

Abstract. *Transcendental meditation is said to induce in its practitioners an altered state of consciousness resulting in relief of stress, an increased sense of awareness, and a sense of well-being. Release of catecholamines has been associated widely with stress and lends itself to quantitation. Plasma epinephrine and norephinephrine, as well as lactate, were measured in 12 volunteers before, during, and after meditation. Values were compared with those obtained from controls matched for sex and age who rested instead of meditating. Essentially the same results were obtained for the two groups, which suggests that meditation does not induce a unique metabolic state but is seen biochemically as a resting state.*

Among the physiological and biochemical changes that accompany stress are increased concentrations of catecholamine in the blood (*1*). Exposing rats to brief, but repeated, stressful situations permanently raises concentrations of catecholamine in urine (*2*). Although some degree of stress appears to be essential for the success of both a society (*3*) and the individual (*4*), our society has become concerned with relieving stress. Some 900,000 persons in the United States (*5*) are reported to practice transcendental meditation (TM), a technique said to produce relief from stress, increased awareness and productivity, and a state of well-being.

Physiological changes characteristic of rapidly induced, wakeful hypometabolic states have been described during the practice of TM. These include changes in electrodermal activity (*6*), electroencephalographic waves (*7*), oxygen consumption, carbon dioxide elimination (*7, 8*), respiratory rate (*7, 8*), blood pressure, (*7*), and heart rate (*7*). Biochemical measurements reported to be altered during TM include blood *p*H and lactate concentrations (*7*). In most of these studies the meditating subjects served as their own controls.

Our investigation was undertaken to determine whether the relief from stress apparently achieved by practitioners of TM is translated biochemically in terms of plasma catecholamine or plasma lactate concentrations. (The latter can reflect alterations in availability of oxygen to tissues.)

Twelve volunteers, six males and six females, from the Students International Meditation Society served as subjects for the study. All 12 had received standardized instruction in TM. Nine were trained by the Society and were qualified as teachers by Maharishi Mahesh Yogi, the originator of the technique.

The selection of the meditators was essentially random. The only conditions placed on their acceptability were (i) that they had been active meditators for at least 12 months, (ii) that they were not routine users of drugs, and (iii) that, to the best of their knowledge, they were free of any acute or chronic disabilities. Their ages ranged from 21 to 50 years with a median of 25. All members of the group were Caucasian. Nine volunteers from the research unit who were unfamiliar with the technique of TM were chosen to approximate the age and sex distribution of the experimental group.

A spacious, pleasant, quiet room equipped with arm chair and hospital bed