These data clearly establish an SD locus, but the question remains whether or not the SD antigens of cattle are controlled by a single gene or several closely linked genes as is true of most other mammalian species whose MHS are well defined. In our studies of families we found that about 10 percent of the "haplotypes" carried more than one specificity. We do not know if these represent the products of closely linked genes in a haplotype or simply cross-reactions of our oligospecific typing serums. However, segregation data on antigen 4 suggest that it is controlled by a linked locus. Also, we have 15 additional antiserums which detect specificities that do not appear to be associated with any of the 11 groups reported here.

Whereas previous studies (*5*) have described some lymphocyte antigens of cattle, the present report, along with the one on LD loci (*2*), makes it possible to add cattle to the list of mammalian species in which an MHS has been described (*1*). Our data on transplantation strongly suggest that the SD antigens described here play an important role in histocompatibility. Reciprocal skin grafts between three cows with identical SD antigens survived for 19 days, while all those between each of these cows and another with different SD antigens were rejected within this same period. In addition, the LD loci of these cows did not appear to influence the fate of these grafts at least within the 19 days of observation.

Unfortunately, we do not have enough data to clearly demonstrate linkage between the *BoLA-A* and the LD loci. However, in at least two sire families they behaved as if linked (*1, 6*).

BEATRIZ AMORENA
W. H. STONE

Laboratory of Genetics,
University of Wisconsin–Madison,
Madison 53706

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4. Even by gene counting it was not always possible to determine if an individual was homozygous for an allele or heterozygous for a null allele (for example, *3/3* or *3/null*). In these cases, an estimate of the two classes was obtained using the formula $P_i^2/P_i^2 + 2\, p_i q_0$, where p_i was a preliminary estimate for the frequency of the *i*th allele and q_0 a preliminary estimate for the frequency of the null allele. Since this adjustment involved only a few animals, the effect on the gene frequency values was negligible.
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7. We thank K. McLaughlin for obtaining the blood samples, P. Jelen, J. Bader, and J. Meyer for technical assistance, and F. Bianchini, M. Curie-Cohen, and W. Usinger for help in analyzing the data and critically reading the manuscript. This work was supported in part by PHS grant AI 03204, and in part by funds provided in the cooperative agreement with the Science and Education Administration of the U.S. Department of Agriculture (12-14-3001-758), and by the College of Agricultural and Life Sciences, University of Wisconsin–Madison.

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Loss of Hippocampal Theta Rhythm Results in Spatial Memory Deficit in the Rat

Abstract. *Rats learned, using distal room cues, to run to a goal on an elevated, circular track starting from any position on the track. The goal was one of eight equidistant, recessed cups set around the track, the goal cup being distinguished from the others solely by its position in the room. After learning, electrolytic lesions were made in the medial septal nucleus eliminating hippocampal theta rhythm in some animals but not in others. Rats without theta rhythm were no longer able to perform the spatial task, whereas rats with undisturbed theta rhythm retrained normal performance. Although rats without theta rhythm could not find their way directly to the goal, they recognized its location when they came upon it by chance. This type of spatial deficit appears similar to that shown by hippocampally lesioned patient H.M. Subsequent tests demonstrated that rats deprived of theta rhythm before training could nevertheless learn the task.*

Hippocampal damage in humans results in a pervasive amnesia for ongoing events as well as a deficit in spatial orientation (*1, 2*). Two types of findings in rats suggest that the hippocampus may be closely associated with the processing of spatial information in this species. First, correlations have been reported between the firing of hippocampal neurons and the position or orientation of animals in space (*3*). Second, lesions of the hippocampus or associated structures have been found to result in deficits in spatial learning (*4*) and memory (*5*). If, as implied by these last studies, the ability of rats to acquire and use spatial information is dependent on normal hippocampal function, then it is possible that disruption of hippocampal theta rhythm might result in deficits in the performance of spatial tasks, since (i) theta rhythm invariably accompanies exploratory behavior in the rat (*6*), and (ii) theta rhythm is associated with intracellular potential changes which should be capable of modifying the excitability of hippocampal neurons (*7*) and might be presumed to play a role in normal hippocampal function. To investigate this possibility, behavioral tests were undertaken in which rats were trained in a spatial task and the effect of medial septal lesions just sufficient in extent to eliminate theta rhythm was determined.

Rats were trained on a circular maze (*4*) consisting of a circular track 2.4 m in diameter with a track width of 30.5 cm. The track was elevated 60.6 cm above floor level and had attached side walls 8.9 cm high. From any position on the track, the animal was afforded a full view of the testing room, which contained diverse landmarks (Fig. 1A). Spaced equidistantly around the track and set into its surface were eight cups, each 5.1 cm in diameter, to which water could be delivered from a remote source or from which water could be withdrawn by tubes connected to the bottoms of the cups. Each cup was equipped with a photocell detector which signaled remotely when an animal poked its nose into the cup to a depth of more than 2.5 cm for 2 seconds or longer. Each animal was maintained with free access to food and water and, on the day prior to training, was allowed to explore the maze for four sessions, each 10 minutes long. Thereafter, the animal had free access to food but was partially water-deprived. Water was available only for brief periods on the maze and for a 15-minute period in the animal's home cage each day when tests were complete. For each rat, eight trials spaced 20 minutes apart were carried out each day during the hours of 9 a.m. to 1 p.m. In each trial, the rat was released at a random position on the track, facing alternately in successive trials either toward the center of the maze or outward. The animal was given water when it activated the photoelectric detector at a designated goal cup by poking its head into it. The animal was then allowed to drink for 10 seconds and the water was withdrawn, completing the run. Alternatively, the trial was terminated if the goal cup was not activated within 5 minutes of release. The goal cup was distinguished from the others only by its con-

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stant position with respect to the landmarks in the room. Between trials the maze was rotated so that a new cup assumed the goal location in the room and became the cup to which water was delivered in the next trial. Between trials, the track was cleaned and all cups were wiped dry to eliminate possible intramaze cues.

Untrained animals typically proceeded around the maze from the starting point, poking into various cups and receiving water when they chanced upon the goal cup. With training, animals learned to run from the starting point to the goal cup and to activate the photoelectric detector in the goal cup without activating any other. A rat was considered to have learned the spatial task when, within the eight trials of a given day, it met this criterion for three successive trials and, in addition, passed what was termed a retention test. This was a fourth successive trial in which the animal was required to activate the goal cup detector according to the previous criterion. However, in this instance water was not delivered immediately. Rats typically either remained at the goal location, continuing to poke into and circle the cup, in which case they were given water after 10 seconds, or they proceeded to an adjacent cup or some distance further around the maze only to look around and run directly back and poke into the goal cup, at which time water was delivered. To pass the retention test, animals had to engage in one of these behaviors. By means of a shaping procedure, rats reached training criterion within approximately 4 days of training and remembered the task for a period of at least 2 weeks (*8*).

Experimental rats were anesthetized with pentobarbital, and a lesioning electrode was positioned in the medial septal nucleus (*9*). In addition, bilateral recording electrodes were placed in the hippocampus to monitor hippocampal slow-wave activity (*10, 11*). Several days after surgery, recordings were made from the hippocampal electrodes during four behavioral states: slow-wave sleep, the still-alert condition, and the two states during which theta rhythm occurs in the rat (*6, 12*), rapid eye movement (REM) sleep and voluntary movement. Animals were retained for further experimentation only if both the dentate gyrus and CA$_1$ components of theta rhythm could be clearly detected (*10*) and the amplitude of the dentate gyrus component was greater than 500 μV. These rats were then trained on the circular maze as described above. After the behavioral trials on the third training day, recordings were made during each of the four behavioral states again, to verify the stability of the signals. The learning criterion was reached for each rat on either the fourth or fifth day of training and a medial septal lesion was made 2 hours after the training was complete. Theta rhythm during voluntary movement was monitored directly before lesioning and for 1 hour afterward. Recordings during all four behavioral states were also made 1 day after lesioning and on every third day thereafter until the experimental procedure for each rat was complete.

Twenty-one rats received medial septal lesions. In six of these rats, theta rhythm from both the dentate gyrus and the CA$_1$ generators was eliminated. Recordings from a typical animal in this class are shown in Fig. 1B. On the left are recordings in the four behavioral states taken on the third day of training from an electrode in the dentate gyrus. On the right are recordings from the same electrode on the day after the lesion was made. During voluntary movement and REM sleep, normally occurring theta rhythm was replaced by a low-amplitude, irregular signal (traces 1 and 2). A similar signal appeared during the still-alert state (trace 3). Recordings taken during slow-wave sleep (trace 4) were qualitatively unchanged. In those animals, recordings obtained after placement of the lesions remained stable throughout the course of the behavioral tests that followed.

In seven rats, although abnormal activity was recorded immediately after the

Table 1. The number of trials required for the initial training of six rats in which theta rhythm was later eliminated (experimental); seven rats with theta rhythm undisturbed (control); for the retraining of the experimental group; and for seven more untrained rats with theta rhythm eliminated before training. The mean time required to complete an individual successful trial in each group was: experimental, 16.7 seconds; control, 20.7 seconds; retrained experimental, 21.4 seconds; untrained, 18.2 seconds; S.E., standard error.

Group	Cue-assisted training		Total to criterion	
	Trials to criterion (mean ± S.E.)	Days to criterion*	Trials to criterion (mean ± S.E.)	Days to criterion*
Experimental	23.0 ± 2.4	2.9	37.0 ± 5.4	4.6
Control	19.8 ± 4.3	2.5	36.4 ± 4.4	4.5
Retrained experimental	16.0 ± 4.6	2.0	29.0 ± 6.7	3.6
Untrained	32.0 ± 4.6	4.0	49.1 ± 5.9	6.1

*Equivalent number of days to reach criterion (eight trials per day).

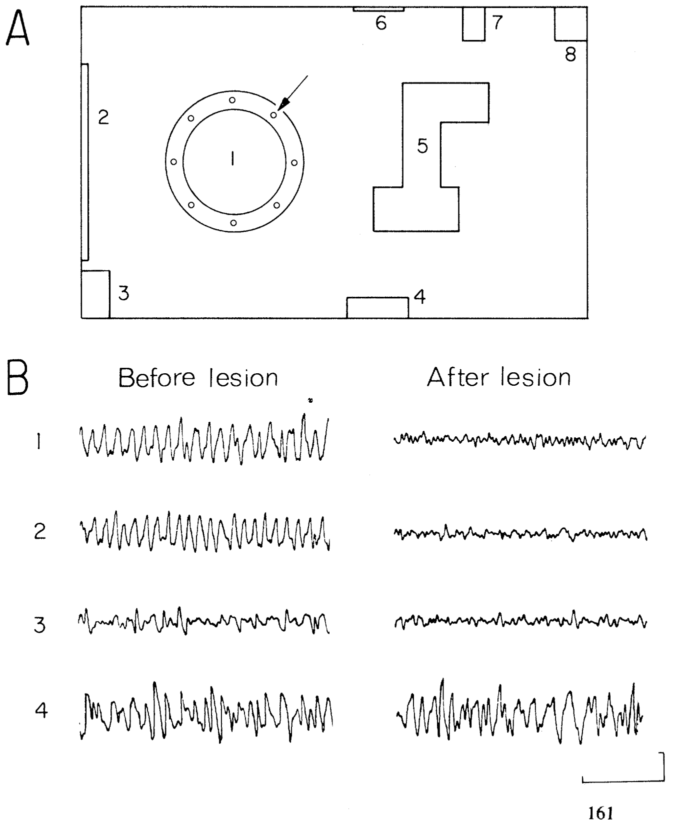

Fig. 1. (A) Plan view of the testing room (5.5 by 9.1 m). Contents: 1, circular maze; 2, elevated ventilating duct; 3, table; 4, animal cages; 5, test console; 6, door; 7, sink; 8, cabinet. Overhead fluorescent lights provide 330 lumen/m^2 of illumination at the level of the maze. (B) Recordings obtained during 1, voluntary movement; 2, REM sleep; 3, still-alert; and 4, slow-wave sleep. The recordings before and after a medial septal lesion was made which eliminated theta rhythm were from the same electrode. Time and voltage calibration: 1 second and 500 μV.

lesion was made, recordings of theta rhythm on the next day and subsequently were substantially unchanged (*13*) in both amplitude and frequency compared to recordings obtained before the lesion. Judged qualitatively, recordings taken during the still-alert condition and slow-wave sleep also remained unchanged.

The six rats with theta rhythm eliminated were used as the experimental animals in the subsequent behavioral tests and the seven rats with theta rhythm undisturbed were used as controls. Eight rats in which the effect of the lesions was ambiguous (*14*) were not used. In no case did an animal display the hyperexcitability seen with larger lesions (*15*). Subsequent histological examination showed that in the experimental animals all lesions destroyed a major part of the medial septal nucleus bilaterally, whereas in the control group destruction of this nucleus was less extensive (*16*). Figure 2 shows a typical lesion in an experimental (left) and a control (right) animal.

Table 1 shows that the number of trials required for the initial training of the experimental and the control groups was almost identical. For each group a normal series of trials was performed on the day after lesioning. Each animal in the control group met the criterion of passing three successive trials and a retention test on this day. No animal in the experimental group reached criterion. The animals without theta rhythm were active on the track but they poked into wrong cups before reaching the goal cup (*17*). There were occasional successful trials, generally when the random drop point was adjacent to the goal cup, but no two successive trials were successful. All animals were then returned to their home cages and retested 1 week later. The results were the same. All control animals met criterion on the day they were retested but none of the experimental animals did. Although the experimental animals were presumably not able to use room cues to find the goal cup, they gave some indication that they recognized the goal location when they arrived at it (*18*).

We attempted to retrain the rats without theta rhythm using the original shaping procedure. This was accomplished, the average number of trials to retrain being somewhat less than the original training time, although not significantly so ($P > .05$) (Table 1). In a retest 1 week later, all animals met criterion within the first eight trials.

Because previous training of the rats without theta rhythm may have enabled them to relearn the task, tests were performed with seven new animals in which theta rhythm was eliminated before training by means of the lesioning procedure described previously. These animals also learned the task, taking somewhat longer to reach criterion (Table 1) than the experimental or control groups, or the group of normal animals trained in preliminary tests (*8*). The increase in training time was largely in the cue-assisted phase and was not significant ($P > .05$) with respect to any of the groups. All animals were tested again 1 week later and reached criterion within the first eight trials.

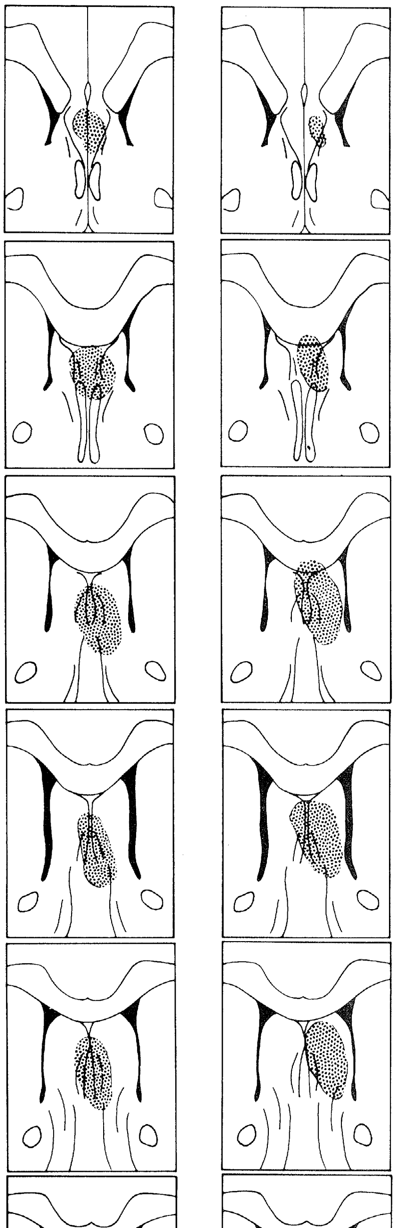

Fig. 2. Coronal histological sections showing (stippled) typical lesion which eliminated theta rhythm (left) and lesion which was ineffective (right). From top to bottom the sections proceed rostrocaudally and correspond to levels A9410 to A7470 in the atlas of König and Klippel (*20*). Lower right section: *LS*, lateral septum; *MS*, medial septum, *AC*, anterior commissure.

The loss of hippocampal theta rhythm (*19*) apparently results in a spatial memory deficit in the rat. This finding is consistent with the suggestion made earlier that the elimination of theta rhythm might impair hippocampal function and thus result in a spatial deficit, in this case a deficit in memory. Spatial memory deficits have been observed after hippocampal lesions (*5*). The spatial memory deficit seen here appears to resemble that of patient H.M. who was reported (*2*) not able to find his way within the general area in which he lived but able to regain his bearings within the immediate vicinity of his house. This suggests the possibility that certain aspects of the way in which the hippocampus processes spatial information may be similar in rat and man. However, the similarity may not extend to the theta rhythm, which has not yet been shown to be present in the primate hippocampus. It has also been shown here that rats without theta rhythm can learn the task used in this experiment. Presumably, such animals find alternative means of learning. The ability of rats with hippocampal damage to find such alternative means when given repeated trials may explain in part the difficulty that has been encountered in establishing a rodent model for the human hippocampal syndrome.

JONATHAN WINSON
Rockefeller University, New York 10021

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8. Adult male Sprague-Dawley rats weighing 275 to 350 g were used in this experiment. During initial training, the goal location was marked by a cue. For each trial, a black card (7.6 by 12.7 cm) was fastened to the white inner surface of the outer side wall of the track in front of the goal cup. The cue was eliminated once an animal passed three successive trials in 1 day (proceeding to the goal cup without activating any other) and training was then continued until the learning criterion was achieved. To determine the ability of normal animals to learn and remember the task, eight rats were trained to criterion, held in their home cages for a period of 2 weeks, and then retested. The mean number of trials to learn the task was 31.4 (3.9 days), of

which the first 15.6 trials (2 days) were spent in cue-assisted training. On the day of testing after the 2-week holding period, all animals met criterion, passing four consecutive trials, the last of which was a retention test. The mean time to complete a successful trial was 19.8 seconds.

9. In this experiment, medial septal lesions were used to eliminate theta rhythm. Cells of the medial septal nucleus are known to project to the hippocampus [G. Raisman, *Brain* **89**, 317 (1966); S. Mosko, G. Lynch, C. W. Cotman, *J. Comp. Neurol.* **152**, 163 (1973); L. W. Swanson and W. M. Cowan, in *The Septal Nuclei*, J. DeFrance, Ed. (Plenum, New York, 1976), p. 37] and medial septal lesions can abolish theta rhythm [C. Mayer and C. Stumpf, *Arch. Exp. Pathol. Pharmakol.* **234**, 490 (1958)]. The lesioning electrode was a No. 00 stainless steel insect pin coated with Epoxylite insulating lacquer and cleared of insulation for a distance of 400 μm from the tip. The animal was positioned in a stereotaxic device so that skull flat plane (passing through bregma and lambda and parallel to the interaural line) was level, and the electrode was implanted 1 mm anterior to bregma and 6.3 mm below the surface of the skull. The electrode was implanted 1 mm to the left of the midline to avoid the superior sagittal sinus and was inclined in the frontal plane toward the midline at an angle of 15° from the vertical so as to position its tip in the midline area. Lesions were made by passing 2 mA of current to the lesioning electrode from an anal ground for 8 seconds (septal electrode negative). These lesioning parameters were chosen to be marginally effective in eliminating theta rhythm.
10. Details of electrode construction, implantation, and recording were as in J. Winson, *Electroencephalogr. Clin. Neurophysiol.* **36**, 241 (1974); and (*11*).
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13. From the recordings taken on the third day of testing, six samples of theta rhythm constituting approximately 10 cycles each were selected during voluntary movement, and six samples were selected during REM sleep. For each behavior, the average amplitude and the average frequency of the theta rhythm were determined from the totality of these samples, by measurements taken directly from the polygraph records (*10*). The criterion used for selecting a control animal was that, within each behavior, the average amplitudes and frequencies after placement of lesions did not differ from the prelesion values by more than 15 percent.
14. In these rats, lesions resulted either in a stable, intermediate condition in which theta rhythm was diminished in amplitude but not eliminated, or a condition in which the amplitudes were initially attenuated but recovered to some extent over a period of several days to 2 weeks.
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16. All lesions were rostral to the decussation of the anterior commissure. Lesions in the experimental animals had in common the bilateral destruction of the major part of the medial septal nucleus anterior to the decussation. Damage to the lateral septum was in almost all cases confined to the medial half of the lateral septal nucleus (partes dorsalis, intermedialis, and ventralis) where it was generally bilateral. In two animals there was unilateral destruction extending to the lateral aspects of the lateral septal nucleus (intermedialis and ventralis). Lesions in the control animals were generally slightly displaced from the midline. Damage to the medial septal nucleus either was unilateral or, when bilateral, was restricted to the more anterior parts of the nucleus. In all cases there was unilateral destruction of both medial and lateral portions of the lateral septal nucleus (dorsalis, intermedialis, and ventralis) and, in some instances, bilateral damage to the more medial portion of this nucleus.
17. There was no apparent pattern in the behavior of four of the animals. Two poked in every cup around the track, a behavior previously noted in rats with fornical lesions tested on a similar maze (*4*).
18. On the seventh trial of the tests performed on the day after the lesions, as well as on the seventh trial of the tests 1 week later, water was withheld when the rat, after poking in a number of other cups, finally poked in the goal cup. In contrast to their behavior at nongoal cups where rats activated the photoelectric detector and then moved on, when animals arrived at the goal cup, in some instances they in effect passed a retention test. They either did not move away from the goal cup, in which case they were given water after 10 seconds, or they moved to an adjacent cup and immediately returned to poke again in the goal cup and were given water. Five of the six rats displayed this behavior, one rat on the trial performed on the day after lesioning, two rats on the trial given 1 week later, and two rats on both occasions.
19. The destruction of pathways which originate in or pass through the medial septum, other than those responsible for generating theta rhythm, may also contribute to the deficit. Among the fibers which traverse the medial septal area are serotonergic [L. C. A. Conrad, C. M. Leonard, D. W. Pfaff, *J. Comp. Neurol.* **156**, 179 (1974)] and noradrenergic [L. W. Swanson and B. K. Hartman, *J. Comp. Neurol.* **163**, 467 (1975); B. E. Jones and R. Y. Moore, *Brain Res.* **127**, 23 (1977)] fibers which provide part of the monoamine innervation of the hippocampus.
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21. Supported by a grant from the Harry F. Guggenheim Foundation. I thank J. Caguiat for technical assistance.

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Sex Ratio and Local Resource Competition in a Prosimian Primate

Abstract. Competition between female kin for local limiting resources may explain a male-biased secondary sex ratio in the prosimian *Galago crassicaudatus*. Data demonstrating the skewed sex ratio, a brief summary of field observations on the species, and a simple mathematical statement of the hypothesis are presented. Local resource competition may influence sex ratio in other mammals.

The African galagos comprise a family (Galagidae) of nocturnal, arboreal prosimian primates. I report a secondary sex ratio skewed toward males in the largest-sized species, *Galago crassicaudatus*, and possibly also in some of its congeners. The results of a worldwide survey of museum collections (*1*), a survey of births in captivity, and a 1½-year field study all demonstrate a preponderance of males. The inequality is present at birth and is neither the result of nor compensated for by differential death of sexes after birth. This inequality is not satisfactorily explained by existing hypotheses on high sex ratios. Rather, I suggest that it results from a social structure which produces sibling and mother-offspring competition for limiting resources that involves only one sex (in this case, female).

Evidence for a high sex ratio in *G. crassicaudatus* is presented in Tables 1 to 3. In all cases, samples were analyzed by the chi square goodness-of-fit test, discounting "unknowns" from the analysis.

Collections from worldwide museums comprise the museum data (Table 1). Specimens were classified as to subspecies in accord with Hill (*2*) and tabulated as "♂," "♀," or "?" (no record present with the specimen). It is clear that, where sample size is sufficient, numbers of individual subspecies are often significantly skewed toward males, never toward females, and that the overall museum count is significantly male-biased.

Obviously, there may be sampling error problems: either sex may be more conspicuous, trappable, or desirable as a trophy. However, personal experience with trapping, retrapping, and observing this galago species suggests that females are at least as trap-prone and conspicuous as males (*3, 4*); indeed, older adult males are hardest to trap and quickest to flee. The slight sex difference (*5*) is hardly discernible in the field and unlikely to influence the nocturnal hunter, who locates animals by light reflecting from the tapeta of their eyes. Thus, I propose that the data do accurately approximate the sex ratio of subadult and adult galagos.

Records of captive births (Table 2) demonstrate a significant preponderance of males born. Questionnaires were sent to institutions known to be breeding *G. crassicaudatus* or reporting births in the *International Zoo Yearbook*. Some of the latter stated that they had no breeding galagos at present (1976) and, since it was often impossible to tell whether an institution reported the same data in the questionnaire that it had presented in the *International Zoo Yearbook*, yearbook birth reports (1970 to 1974) are given separately (Table 2). The number of unknowns includes animals on which sex determination was simply not made and dead infants that were partially consumed before they were found. In testing the captive birth data, I found no evidence for differential death before maturity (*6*). Thus, I suggest that the museum data represents the secondary sex ratio in those populations sampled.

Finally, my 1.5-year field study of a population of *G. crassicaudatus umbrosus* in North Transvaal, South Africa, yielded both birth data and a total population ratio for June 1977 (Table 3). All animals on the site plus those in immediately adjacent bush were trapped, their sex was recorded, and they were individually marked. Where I had not observed the mother at or soon after parturition, I assumed that multiparous females had