

Fig. 2. Percentage of subjects, on the first trial of the second task, making response which was correct in original learning.

than during relearning [ratio of variance (F) = 105.72, degrees of freedom (df) = 1 and 60, P < .001] (3). (ii) The linear, quadratic, cubic, and quartic components of the relearning function were significant (P < .005, except that P < .05 for the quadratic component). The significant linear component indicated a general tendency for fewer errors to be made in relearning with increasing length of the retention interval, while the significance of the other components of the relearning curve reflected the relatively large number of errors made in relearning after the 2day retention interval. For reversal learning, a significant linear component of the curve (P < .005) revealed a general tendency to become more difficult as the retention interval lengthened. Thus, while relearning becomes easier with time, reversal learning becomes more difficult. Moreover, significant cubic and quartic components of the reversal learning curve (P <.05) reflected the fact that, as an exception to the general increase in difficulty with time, reversal learning was relatively easy after a cold 2-day retention interval. Therefore it seems reasonable to conclude that the reminiscence effect is a memory-related phenomenon and that it does not appear to be related to nonspecific factors such as amount of motivation.

The data also indicate the possibility that more than one stage of memory may exist in *Tenebrio* adults. Consolidation of memory trace in the adult *Tenebrio* beetle may involve at least two memory storage systems, a theory consistent with increasing evidence of

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similar systems in higher animals (4). After the beetle has been in the cold for 2 days, the trace is in the process of being transferred from one system to the other; and, if the animal is warmed or tested (or both) during this critical transfer period, the trace is lost. In fact, the loss of memory on day 2 appears to be complete. (i) The animals on day 2 made a mean of 4.62 errors in relearning, a figure that compares closely with the mean of 4.78 errors made by all the animals in original learning. (ii) The difference in retention between these animals and those with other retention intervals was present on the first trial of the second task (Fig. 2). (iii) The poor retention of the 2-day group was not confined to the first day of relearning, as it might be if some temporary difficulty were involved. The 2-day group made significantly more errors on their 2nd day of relearning than the 3-day group made on their 1st day (t = 2.75, df = 14, P < .02), despite the fact that the 2-day group had had practice for an additional day. Thus the warming of the beetle on day 2 causes apparently total forgetting. In the development of the memory, day 2 may represent a critical period during which the engram is sensitive to temperature manipulation; this period may represent engram transfer to another memory stage.

The nearly perfect retention of the cold beetles on day 5 suggests that the cold may act to protect the memory. The failure to find reminiscence with larvae (I) suggests that whatever mechanism was protected in our study either does not exist in the larvae or has a different temporal course. Finally, we wish to emphasize the simple techniques involved in performing these experiments and the possible use of this preparation in discerning the electrophysiological and biochemical substrates of memory.

THOMAS M. ALLOWAY ARYEH ROUTTENBERG

Department of Psychology, Northwestern University, Evanston, Illinois 60201

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 That our findings were the result of trail
- 2. That our findings were the result of trail pheromones seems unlikely because (i) each animal would be required to distinguish between his own trail and that of 39 other animals, and (ii) it would be necessary to assume that on day 2 there was a reduced pheromone sensitivity which recovered on day 3.

- 3. Half the subjects in each experimental group were run in each of two independent replications. In the analysis of variance and trend, these replications were considered as a variable orthogonal to the experimental variables. Thus the error term for the *F*-tests has 60 df, instead of 70 df which would otherwise be the case. There was no statistical significance to replications either as a main effect or as an interaction with the other variables.
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- 5. Supported by PHS contract MH11991-02 to A.R., to whom requests for reprints should be directed.

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Squirrel Monkey Reproduction: The "Fatted" Male Phenomenon and Seasonal Spermatogenesis

Abstract. Records of reproduction in a Miami colony of squirrel monkeys living in a seminatural state and of monkeys in the field indicate that the male undergoes an annual testis cycle. The spermatogenic phase is associated with the seasonal acquisition of a secondary sexual characteristic which we have termed the "fatted" condition. Body weights, measurements of subcutaneous fat, and testicular histology studied over a 12-month period further establish this cycle. Climatological analyses suggest that this cycle is associated with the precipitation cycles of the respective environments.

Field studies indicate that many nonhuman primates are seasonally reproductive. Lancaster and Lee (1) discuss cyclic reproduction in Old World primates; however, descriptions of such periodicity in New World primates is almost totally lacking. Carpenter (2) did not report seasonal reproduction in either the howler monkey (Alouatta palliata) or the red spider monkey (Ateles geoffrey). However, discrete mating and birth seasons have been observed in a colony of squirrel monkeys (Saimiri sciureus) living in a seminatural environment at Monkey Jungle, Miami, Florida (3). The concept of reproduction cycles in male simian primates is even more recent. A seasonal spermatogenic cycle has been described in the rhesus monkey (Macaca mulatta) on Cayo Santiago (4). We have studied the reproduction cycle in the male squirrel monkey, especially the seasonal acquisition and loss of a secondary sexual characteristic which we have termed the "fatted" state, its relationship to the seasonal spermato-

	Aug.Sept.Oct. Nov. Dec. Jan. Feb. Mar. Apr. May Jun. Jul. Aug. Sept.
1960-1961	First birth Feb. 24 8-10 Viable livebirths
1961-1962	Apr. 21 15± Viable
1962—1963	May 10 15± Viable
1963-1964	June 30
1964-1965	June 18 25± Viable
1965-1966	June 12

* Total of 37 Squirrel Monkeys introduced, 140⁴ and 239 on Aug. 16, 1960, less 6 animals that died.

🛲 mating season.

birth season: high portion indicates birth peak, when most of the births occur.

Fig. 1. Six-year record of reproduction in the Monkey Jungle colony of squirrel monkeys, illustrating seasonal reproduction and its shift from the Iquitos to the local cycle.

genic cycle, and the association of these conditions with observed mating activity and recorded births.

The colony of squirrel monkeys at Monkey Jungle is composed of the type that originated from Iquitos, Peru, and was described by MacLean (5) as "Roman." The Florida environment is a 4-acre tract of subtropical jungle in a subtropical climate which permits year-round outdoor living. The monkeys are provisioned but are otherwise not managed or provided for. They are essentially self-regulated and do not react to human observers (6).

A complete record has been kept of reproduction in the Monkey Jungle colony since its introduction in August 1960 (Fig. 1). All births were confined to very discrete periods each year. However, the birth season shifted from winter (February and March) to summer (June, July, and August) over a period of 3 years.

Since 1964, the birth period has stabilized and has occurred at the same time each year. The discreteness of this period is demonstrated by the fact that, of the more than 100 births recorded over the 6-year period, even while the cycle was changing, not one was out of phase. Since 1963, females born in the colony have been maturing and entering the maternal population each year, but they have always given birth in phase with the older adults.

During the mating season (mid-December through March) the fully adult socially mature males have an appearance different from that at other times of the year. There is a characteristic heaviness and an increased fluffiness of pelage, particularly about the upper torso, shoulders, and arms (Fig. 2A), which is gradually lost during April and completely lost by May. It does not appear again until late December (Fig. 2B). This "fatted" appearance has been observed over a 3-year period in the Miami environment.

Approximately 270 hours of behavioral observations were conducted from June 1966 through June 1967, so that periods of mating behavior, the appearance of "fatted" and "nonfatted" males, and periods when females deliver their young could be accurately determined. As adult males began developing the "fatted" condition during late November and December, a marked increase in social interactions by the males was recorded. During December, a dominance hierarchy was established among the then "fatted" males. We determined dominance positions by quantitatively recording the roles assumed by participating males in the highly ritualized penile display interactions. Sexual approaches and copulations were observed throughout the period when the males were "fatted", and mating activity was confined to this period (December through March).

During the birth season (June, July, and August) and into the lactating season, the aggressive, volatile, vocal nature of the "fatted" male gives way to the much more retiring, passive behavior of the "nonfatted" male, which loses not only the masculine appearance but also the masculine behavior. Males become virtually rejected neuters during this period of the year when the maternal group dominates the social activity of the colony.

Because this pattern of reproduction was so clearly established locally, we thought a similar periodicity might be found in the Iquitos environment which would be 6 months out of phase as a result of the previously mentioned local shift in the reproductive cycle.

The reproductive cycle and the position of the "fatted" males in the cycle were determined for the Iquitos environment by surveys, at approximately 30-day intervals, of fresh shipments of Saimiri arriving at compounds of local importers. Careful estimates were made of the presence and percentages of adult females, "fatted" and "nonfatted" males, pregnant females, aborted fetuses, and clinging infants. This sample included approximately 3500 animals distributed over a 13month period from July 1966 through July 1967. Time in transit from jungle to Miami is so short that a fairly accurate chronology of the Saimiri reproductive cycle could be determined for comparison with that found in the local environment.

Approximately 30 "fatted" males were observed in two shipments totaling some 300 animals which arrived during July 1966. No survey samples were taken in August or September. Among 2800 animals surveyed from November through May, no "fatted" males were observed, although fully adult but "nonfatted" males were recorded in every shipment. In June 1967, several partially "fatted" males were observed among 200 animals, and in July a shipment of 150 animals contained 12 fully "fatted" males.

Noticeably pregnant animals were not found until December; aborted fetuses and newborn infants were found in January. Clinging infants 2 to 3 months old were seen in March; however, none were observed in two shipments arriving in February, perhaps because this is a critical stage in the infants' development. During the remainder of the year, April through July, juveniles were seen which appeared to be of an age consistent with a winter birth season.

The indication of a cyclical production of androgen as expressed in changes in behavior, morphology, and actual mating activity led us to investigate the existence of a spermatogenic cycle and to try to define quantitatively the morphological changes taking place during the cycle. We thought that obtaining testis samples from animals in the local environment might jeopardize the behavioral studies being conducted, and we felt that more significant information would be obtained if the spermatogenic cycle was determined in the natural environment. Consequently, all but one of the 16 testis samples were taken from newly imported animals during our 13-month survey. Samples were secured from animals arriving during August, November, December, February, March, April, May, and July. A sample was taken from one "nonfatted" male of the Monkey Jungle colony, which helped to verify the existence of the cycle locally. Its structure was consistent with the displacement of the cycle by 6 months.

Test animals were anesthetized, and

their maturity was confirmed with roentgenograms. The animals were then weighed, and standard anthropometric measurements were recorded. Tissue samples were obtained from cross sections of whole testicles fixed in Bouin's solution and stained with hematoxylin and eosin.

The seasonal testis cycle may be divided into the spermatogenic phase in the "fatted" males during mating season (Fig. 2A) and the inactive phase in the "nonfatted" males (Fig. 2B), with intermediate stages of regression and development between the two extremes. In the spermatogenic phase, active spermatogenesis is evident in nearly all seminiferous tubules (Fig. 2C). The structure of the tubule wall is well defined, and the wall abounds with germ cells in all stages of spermatogenesis. Abundant spermatozoa are embedded in the Sertoli cell cytoplasm at the borders of the lumina. During the



Fig. 2. (A) Colony male (January 1967) in the fully "fatted" state. Note the heaviness about the shoulders and upper arms. (B) Same animal (July 1967) in the "nonfatted" state. For comparison note the relationship of head size to shoulder area in the two conditions. (C) Sample of testis with maximum spermatogenic activity taken from a "fatted" Iquitos male arriving in August 1966. (D) Testis sample with maximum regression taken from a "nonfatted" Iquitos male arriving in February 1967. Tubule walls essentially consist of a basal layer of spermatogonia and Sertoli cells; the greatly enlarged lumina are virtually clear of cells.

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Iquitos regression phase (November through January) the structure of the walls becomes poorly defined; masses of cells detach from the walls and clog the lumina, which appear greatly enlarged. During advanced regression in February (Fig. 2D), the detached cells apparently slough off, leaving greatly enlarged lumina virtually clear of cells. The tubule diameter is somewhat smaller, and the wall structure is essentially reduced to the basal layer of Sertoli cells and spermatogonia with little indication of mitotic activity.

Samples taken from March through June illustrated increasing redevelopment. Mitotic activity was in evidence, and the tubule walls became increasingly thicker, first with primary spermatocytes, then with secondary spermatocytes, and finally with spermatids. Samples taken in June contained a few tubules with mature spermatozoa, but many had almost closed tubules largely filled with cells at earlier stages of spermatogenesis. The first fully producing sample of 1967 was obtained in July along with the recording of the first fully "fatted" males since the previous July. All nonspermatogenic samples showed evidence of prior spermatogenesis; the lumina of the epididymis and vas deferens contained masses of mature sperm cells, possibly remnants from the preceding mating season.

The average weight of "fatted" males was 800 g; that of the "nonfatted" males was 715 g. The average thickness of skinfolds in the "fatted" males was 4.0 mm; that of the "nonfatted" males was 1.2 mm. All other parameters demonstrated what we considered to be only normal individual variations not related to the two conditions.

The sample included nine "fatted" and ten "nonfatted" animals. Although the sample was small and a perfect distribution was not possible, the evidence of a cyclical spermatogenesis associated with the "fatted" condition is clear.

Since the reproductive cycle might be correlated with some meteorological factor, we analyzed the respective climates of the Iquitos and local environments. We compared the major climatological factors (light-dark cycles, precipitation, and temperature) of the two environments by months (7) (Fig. 3). Light-dark cycles have long been associated with biological triggering mechanisms, but the maximum deviation in



• hrs. of daylight, precipitation and temp. for the Amazon. Ins. of daylight, precipitation and temp. for Miami. hand birth seasons. mating seasons

Fig. 3. Climatological comparison of the Western Amazon Basin with the local Miami environment, showing in both environments the correlations of birth season with periods of maximum rainfall and of mating seasons with periods of minimum rainfall.

the cycle for Iquitos is only \pm 11 minutes, and it is difficult to seriously consider this as a triggering or controlling factor.

The precipitation cycles in the two environments occur 6 months out of phase. In both environments the mating seasons occur during the dry periods, whereas the birth seasons occur during the rainy ones. Thorington (8) reports that a birth season occurs during February, March, and April in San Martin, Colombia, which is 4° north of the equator and in the same, though greatly attenuated, light-dark cycle as Miami. However, the rainy season for the area is March, April, and May. Again the correlation is evident. There was no apparent relationship between the temperature cycles of the two environments and reproduction.

Mating seasons occur in the valleys of the precipitation curves for all three environments reported. There must be present in the early dry season some factor that causes hormone production to begin. Two possible ones are (i) the wavelength quality of solar radiation as influenced by atmospheric moisture, and (ii) a nutritional factor possibly associated with the forest flowering sequence, which in turn is usually associated with nonvegetative phases during dry periods.

More and more primates are being described as seasonally reproductive and, although ours, we believe, is the first report of such a phenomenon in a New World primate, others may also exhibit some form of seasonal reproduction. What may be unique in the Saimiri is the extent to which this sexual periodicity influences the whole animal, causing in the males significant physiological, morphological, and behavioral changes that have not been observed in the Old World primates reported to date.

Our findings suggest that mating phases of both sexes must be in synchrony before reproduction can occur. Reproduction asynchrony may result from random pairings of animals in various stages of the shift in the cycle from feral environment to the laboratory environment. These factors, which probably have not been considered by investigators attempting to establish breeding groups, may be associated with the history of poor reproduction among squirrel monkeys in laboratories. Groups composed of animals simultaneously imported during the feral mating season, or in which permanent membership has been maintained over several years, would probably be in reproductive synchrony.

FRANK V. DU MOND

Monkey Jungle, Inc.,

Miami, Florida 33170

THOMAS C. HUTCHINSON Department of Obstetrics and Gynecology, University of Miami School of Medicine, Miami, Florida 33152

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Behavior Development in the Dog: An Interspecific Analysis

Abstract. Young dogs were maintained in isolation from other dogs and under varying degrees of exposure to an alien species (mature rabbits). Parametric observations indicate that an interspecific social attachment develops during the initial hours of cohabitation. The later social interaction patterns of the dogs were influenced, but not irrevocably fixed, by the early cross-specific rearing experience.

Immature animals that have been isolated from their own kind and reared with another species generally demonstrate a strong affinity for the "alien" animals (1). Despite the relevance of this curious phenomenon for the processes of species-identification and attachment behavior, it has been infrequently studied under laboratory conditions (2). Virtually no information is available with respect to the timecourse of the process in mammals, or the extent to which the effects of early exposure to an alien species are enduring. To obtain parametric data on these issues, we reared young canines under various conditions of interaction with mature lagomorphs. We found that interspecific attachments develop with great rapidity in young dogs, an outcome which is in accord with the stimulus pattern theory of mammalian attachment behavior (2)

In our first experiment, 30 purebred dogs from the Jackson Laboratory were placed at 29 \pm 2 days of age in individual compartments (1.2 by 0.8 by 1.2 m high) enclosed on four sides by opaque walls and open at the top. The rearing conditions permitted neither physical nor visual contact with other dogs. Ten animals were assigned to each of three conditions: (i) interaction, in which a dog was permitted continuous physical contact with a rabbit cohabitant; (ii) noninteraction, in which a dog and rabbit were separated by a double wire fence (2.5 by 5.1 cm interstices) down the midline of the compartment, which permitted visual and olfactory stimulation but no physical contact; and (iii) isolation, in which a dog was reared alone. The rearing conditions were comparable for all conditions save the varying degree of contact permitted with the alien cohabitant. Five pure breeds of dogs were used: basenjis (N = 7), beagles (N =4), cocker spaniels (N = 2), Shetland

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