the small amount which is adsorbed on the surface of montmorillonite clay particles, although it may be available to the plants, is not enough to cause significant inhibition to the plants. This is in agreement with desorption studies which showed that when the herbicides paraquat and diquat were adsorbed on montmorillonite clay, only 5 percent was removed by four extractions with $1M$ $BaCl_2$. When the herbicides were adsorbed on kaolinite clay, however, approximately 80 to 85 percent was removed with the same extraction solutions. This surface-adsorbed paraquat appears to be available to the plant roots. It was also found that one of the organic cations could exchange for the other (*1*), if the clay was first saturated to its cation exchange capacity with one of the cations. Below the cation exchange capacity, however, both of the organic cations were completely adsorbed in exchange for inorganic cations on the clay surfaces. Paraquat, which has been found by x-ray analysis (*1*) to be adsorbed in the interlayer spaces of the montmorillonite clay, is apparently held so tightly or in such a manner that the compound is not available to the cucumber roots. The small amount of paraquat adsorbed on the exterior surfaces of montmorillonite clay is probably available to the plant roots (*4*). The paraquat, which is adsorbed to the exterior surfaces of the kaolinite clay particles, slowly becomes available to the cucumber roots, probably through ion exchange.

The nonavailability, or slow availability, to plants of this cationic herbicide from clay minerals is not of grave concern at present, since this material is applied in amounts from 1 to 2 pounds (2 to 4 kg) per acre. For instance, assuming that none of the paraquat adsorbed on montmorillonite clay is available to plant roots, it would take approximately 2250 pounds of paraquat to saturate the cation exchange capacity of the 6-inch plow layer of a soil which contains 1 percent montmorillonite clay; and this would assume no degradation of the herbicides by microorganisms. It must be determined whether or not this herbicide, when adsorbed in the interlayer spacings of montmorillonite-type clay minerals, is degradable by microorganisms. Preliminary studies utilizing isotope-labeled diquat and paraquat indicate that when these compounds are adsorbed in the interlayer spacings of montmorillonite clay, the amount of degradation by soil microorganisms is very small. These compounds are readily degraded by microorganisms, however, when they are adsorbed on kaolinite clay (*4*).

Another facet of the adsorption of these organic cationic herbicides by soil clays is the effect they have on the water- and nutrient-holding capacity of the clays. Since these compounds are very strongly adsorbed, they no doubt displace water or nutrient elements in the clay minerals. Such displacement could have a beneficial or a deleterious effect on the production potential of a particular soil.

These studies demonstrate the necessity of employing several detection methods when measuring the persistence of herbicides in the soil. Bioassay plants are very useful in detecting the toxicity of herbicides to plants and do indicate the plant-available herbicide present. The amount of paraquat removed from the two clays by extraction with $1M$ $BaCl_2$ has been shown to be related to the amount of the herbicide that was available to cucumber plants, and this may be useful if one is interested in predicting the herbicide in the soil which is available to plant roots. It may be of interest, however, to determine not only the plant-available herbicides in the soil, but also the total amount which is present. Since neither the $1M$ $BaCl_2$ extractions, nor the plant bioassays were able to detect paraquat which was adsorbed in the interlayer spacing of the montmorillonite clay, a stronger extracting solution would be needed to determine the total amount of paraquat in a soil containing this clay mineral.

JEROME B. WEBER
DONALD C. SCOTT
Crop Science Department, North Carolina State University, Raleigh

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5. Paper No. 2130 of our journal series.

7 March 1966

Tree Shrews: Unique Reproductive Mechanism of Systematic Importance

Abstract. Tupaia *offspring are maintained in a separate nest constructed by the male parent and are suckled by the female only once every 48 hours. The young are nevertheless able to maintain a constant external body temperature of 37°C.*

The tree shrews (family Tupaiidae) are widely regarded as the most primitive members of the order Primates (lemurs, monkeys, apes, and man) and have often been described as a "missing link" relating Primates to Insectivora stock. For this very reason, the tree shrews have been considered as suitable objects for medical research, although hopes in this direction have foundered due to poor breeding successes, the overall laboratory average having been estimated at 20 percent (1).

Opinion is divided over the exact systematic position of the Tupaiidae, although most workers believe that tree shrews are intermediate between the Insectivora and Primates. Primitive features have led some workers (*2*) to place the tree shrews with the Insectivora; some advanced features have led others to include tree shrews with the Primates (*3*). There are also resemblances to Marsupialia and features reminiscent of Rodentia and Lagomorpha. General features of reproduction and the unique breeding mechanism described in this report support much recent evidence that any relationship of the Tupaiidae to the Primates is very tenuous.

Although much work has been carried out on the tree shrew (*4, 5*), a number of important features of the reproductive behavior have remained obscure. Our animals (*Tupaia* sp.) were kept in pairs in cages much larger than has been usual (8 rather than 1 m^3) and were provided with excess food including fresh milk, meat, insects, fresh fruit, and vitamin additives. Suit-

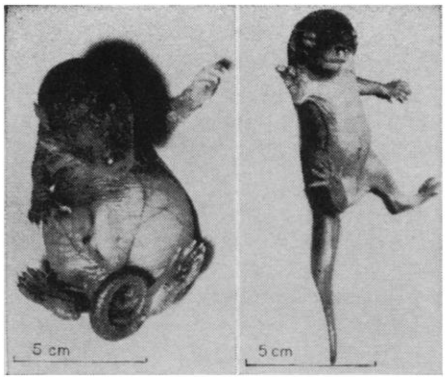

Fig. 1. (Left) One-day-old young with stomach distended with milk; (right) 10-day-old young showing stomach virtually empty just prior to suckling.

able nest material and a minimum of four nest boxes were provided. Reports that tree shrews carry food remains and other litter into the nest box, either as food for the young or as genuine nest material (*4*) stem from the fact that no suitable nest material was provided. If dried beech leaves are provided, the nest is constructed entirely with leaves. Dry, inedible matter is preferred.

The young are maintained in a separate ("maternal") nest built entirely by the male, a fact unique among mammals. From 1 to 5 days before the female is due to give birth, the male carries up to 400 leaves into formerly unoccupied nest boxes, usually concentrating upon one box. The bulk of the male's nest-building activity is typically restricted to one evening. When the main nest is complete, the male does not normally enter the nest box again before the young are weaned and leave the nest (at 4 weeks of age).

The female *Tupaia* gives birth to the young in the main nest. The litter usually contains two young in all tree shrews, although one or three offspring sometimes occur. Laboratory births can occur at any time of the day or night. In the course of 1 to 2 hours, the female gives birth, disposes of the embryonic membranes and umbilical cord, and suckles the young until the stomachs are fully distended (Fig. 1). The female then leaves the nest box. At this stage, the young weigh approximately 15 g, of which roughly 6 g represents milk. Thereafter, the young are usually suckled only once every 48 hours (*6*). Apart from the visits of the female every 2 days to suckle the young, this maternal nest is not normally entered by either parent. The parents sleep together in another, usually specific, nestbox. When the female suckles the young, she remains only 4 to 10 minutes in the nest. After suckling, the female rapidly leaves the nest box, runs some distance away and licks the mammary area extensively.

The young maintain a constant body temperature (37° ± 1°C, at laboratory temperature 25°C). They can be removed from the nest between suckling visits without apparent disturbance of the parents' behavior, and measurements of temperature and growth can be carried out (Fig. 2).

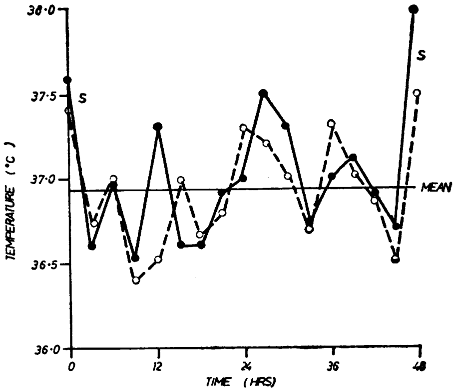

Fig. 2. Variation in external body temperature of two littermates in one 48-hour period between suckling visits (day 1 to 3). *S,* suckling visit.

There are a number of special adaptations in the behavior of the young. Since the mother only spends approximately 5 minutes with the young at each visit, during which time she provides from 10 to 20 g of milk, the young must be capable of extremely rapid suckling. There is no time for the mother to groom the young, and they apparently groom themselves, since the full "self-washing" patterns are present from birth. The young appear to burrow up to meet the mother when she arrives, suckle until she leaves the nest, and then burrow back beneath the leaves. Under the leaves, the young maintain a constant body temperature from the 1st day of birth quite independently.

The offspring of *Tupaia* emit an explosive snort after mechanical disturbance (or optical disturbance, when the eyes have opened after day 20) and thrust out with all four limbs. The leaves are rustled as a result, and the net effect is quite startling. This reaction probably represents an antipredator device. The explosive snort of the young *Tupaia* shows a smooth development into the explosive aggressive vocalization given by the adult in intraspecific fights and is still given, as in juveniles, when adults are disturbed in the nest. Of the seven typical vocalizations which can be identified in the adult, only the explosive snort occurs in the nest phase, whilst all other vocalizations appear within a few days after the young leave the nest. A similar vocalization seems to be present in all species of tree shrews.

The young *Tupaia* has no audible distress call, and no reaction can be identified in the parents when the young are disturbed. The parents do not exhibit carrying or retrieving behavior. Most Primates carry the young clasped on the fur, whilst some lemurs and many primitive, plantigrade mammals carry the young in the mouth. In short, parental behavior of *Tupaia* during the nest phase is limited to provision of milk by the female.

Juvenile tree shrews (*Tupaia*) increase in weight very rapidly. The young increase from 15 to 80 g in the 4-week nest phase (Fig. 3) and have achieved adult body size and weight (200 g) by 3 months of age. Sexual maturity is achieved at least by the age of 4 months. Thus, the speed of general maturation provides a sharp contrast to all Primates.

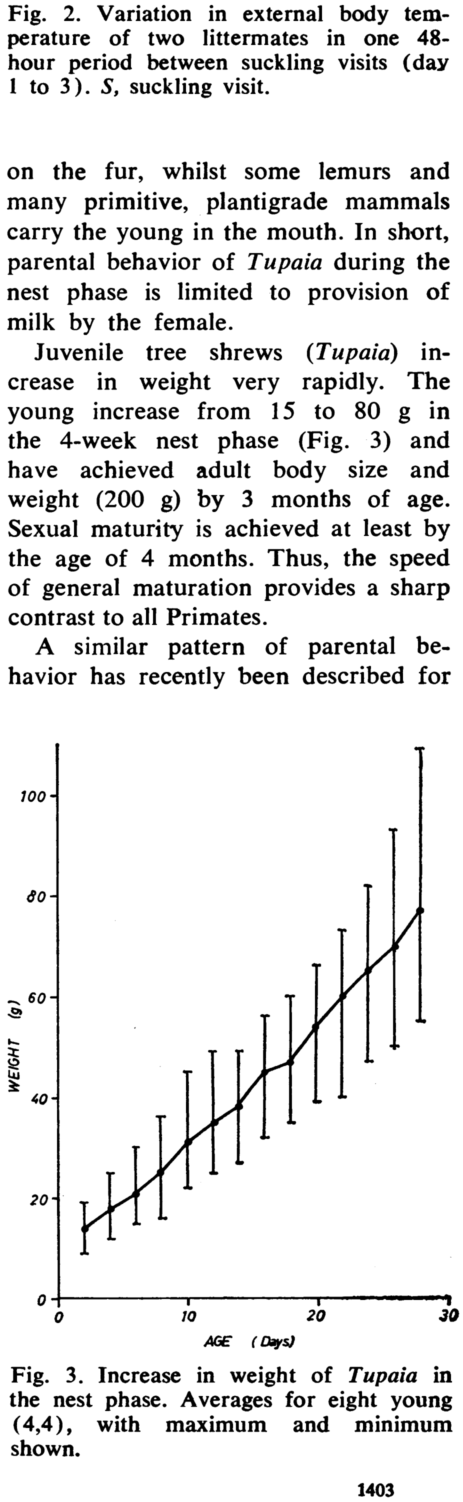

Fig. 3. Increase in weight of *Tupaia* in the nest phase. Averages for eight young (4,4), with maximum and minimum shown.

A similar pattern of parental behavior has recently been described for the rabbit (*7*), where the long interval between suckling visits of the female apparently functions to reduce predation.

In the tree shrews, a number of similarities to Primates can now be explained as convergent. The long intersuckling interval places an upper limit on the number of young, and the number of mammary glands is consequently reduced. In the Primates, on the other hand, the number of young (and of mammary glands in the female) has been reduced as a specific adaptation deriving from a greatly increased pregnancy period (60 to 65 days in the tiny *Microcebus*; 3 months or more in all other Primates). The interbirth interval of 45 days in *Tupaia* (*4*, *6*, *8*) is shorter than the pregnancy period of all Primates.

The reproductive anatomy of *Tupaia* is very different from that of all living Primates. Whereas the urethra and the vagina open separately to the exterior in all Primates (probably in connection with the advanced age of the young at birth), the urethra of *Tupaia* opens into the vagina at some distance from the common clitoric duct (as in Lagomorpha and other primitive placentals). The female *Tupaia* lacks the os clitoridis typical of basic Primates. In male tree shrews, the testes are anterior to the penis (as in Marsupialia and Lagomorpha) and not posterior as in Primates. Male tree shrews lack the os penis typical of male Primates.

Renewed studies of the pyramidal tracts (*9*), the tympanic region of the skull (*10*), the innervation of the skin (*11*), optical junctions in the brain (*12*), and of the supposed Tupaioid fossil *Anagale* (*13*) show that there are considerable differences between tree shrews and Primates. Detailed consideration of all evidence now available (*6*) indicates that the tree shrews are best classified as a separate order of mammals (Tupaioidea), as suggested by Straus (*14*) and that they show significant similarities to the Marsupialia.

R. D. MARTIN
Max-Planck-Institut für
Verhaltensphysiologie, Seewiesen
und Erling-Andechs, Germany

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* Present address: Max-Planck-Institut für Verhaltensphysiologie, 8131 Seewiesen, Germany.

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Heart Rate: Changes during Conditioned Suppression in Rats

Abstract. *Heart rate of rats was recorded in the Estes-Skinner conditioned emotional response situation. Response to the conditioned stimulus was a decrease in rate. The change in heart rate was conditioned more slowly than suppression of bar-pressing; it was of shorter duration and was more variable than suppression.*

Since a number of responses are conditioned at the same time in classical conditioning, the following question arises. To what extent are the classically conditioned responses (CR's) affected differently, and to what extent are they affected similarly by the same classical conditioning procedure? There is surprisingly little evidence from animal research on the simultaneous measurement of classically conditioned responses, and what evidence does exist is not clear-cut. In studies on the simultaneous recording of heart rate and leg flexion, for example, Gantt found that heart-rate was conditioned before leg flexion (*1*); Jaworska, Kowalska, and Soltysik found that flexion was conditioned before heart rate (*2*); and Dykman, Mack, and Ackerman and Obrist found that heart rate and "nonspecific motor responses" were acquired at roughly the same rate, and both were conditioned before flexion (*3*). For heart rate and bar pressing, the two responses that are our concern in this report, Stebbins and Smith (*4*) have shown that changes in heart rate do occur during suppression of bar pressing, but they have not presented data on the speed of acquisition and on the form (the changes over time) of the two types of response. We now present data on the form and speed of acquisition of the two responses in order to answer the questions posed above.

The subjects were seven naïve, male, hooded rats about 120 days of age. An eighth rat was discarded because of a fault in its implanted electrode recording system. The apparatus consisted of four Skinner boxes controlled automatically by standard Grason-Stadler operant conditioning units.

Two conditioned stimuli (CS) of 70-db intensity were employed. One stimulus was a continuous white noise, and the other was the same white noise interrupted four times per second. The unconditioned stimulus (UCS) was an electric shock of 0.5-second duration and 1.3-ma intensity. A delayed conditioning procedure with a 3-minute CS-UCS interval was employed; that is, the CS lasted for 3 minutes and terminated at UCS onset.

Heart rate was recorded from permately 7.5 cm long ran from the electrodes (*5*). Insulated wires approximately 7.5 cm long ran from the electrodes to an Amphenol "Subminax" connector. The electrodes were inserted through an incision made on the scalp while the rat was under Nembutal anesthesia. They were pushed through this incision under the skin to a position on the ribcage, one on each side of the body. The connector was firmly cemented to the skull. During recording, the connector was attached to a cable which led to a mercury swivel system and then to a Grass polygraph (model 5).

Two days after the operation all animals were placed on a 24-hour feeding schedule and their weight was reduced to approximately 75 percent of the weight they maintained when they had free access to food. Following "magazine training," they were given 2-hour bar-pressing sessions daily, for 8 consec-