mation of the relative proportions of upland, slope, and lowland. By means of studies of this type, one can compare regions, evaluate various distinctive land forms, and in some cases even determine the extent to which structural control has influenced geomorphic development.

Because the work is fairly quick and simple (a typical analysis takes about an hour), computation of skewness and kurtosis measures does not appreciably increase the amount of time and effort necessary to study a given area. When these measures are coupled with altitude and relief values (such as means and standard deviations), the geologist can list absolute, rather than merely relative, figures to denote degree and kind of geomorphic expression.

WILLIAM F. TANNER
Geology Department, Florida State University, Tallahassee

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Role of Olfactory Sense in Pregnancy Block by Strange Males

Abstract. Pregnancy is blocked in a high proportion of recently mated female mice exposed to strange males. This reaction is virtually abolished by the prior removal of the olfactory bulbs of the female. The smell of the strange male appears to be the primary stimulus in the exteroceptive block to pregnancy in mice.

An exteroceptive block to pregnancy in mice associated with the presence or proximity of strange males has recently been described (*1*, *2*). If the newly mated females are placed with or near strange males, particularly males of a different strain from the stud male, pregnancy and pseudopregnancy both fail in a high proportion of mice. The development of the corpora lutea is inadequate, implantation does not take place, and, typically oestrus returns 4 to 5 days after the stud mating in more than 90 percent of the females in which pregnancy is blocked. Fertile mating takes place at this time if the strange male has access to the female. (Atypically, oestrus may return on day 6 or 7).

Table 1. Effect of the removal of the olfactory bulbs on the incidence of pregnancy block in mice.

Mated females	Blocked pregnancies*	
	No.	Percent
Anosmic females		
Parous† 10	2	14
Nonparous‡ 12	1	
Normal females tested concurrently		
Parous 9	6	78
Nonparous 49	39	

* ♀ returns to oestrus within 7 days of mating.
† Stud mating 8 to 17 weeks after operation.
‡ Stud mating 2 to 4 weeks after operation.

A high degree of discrimination is shown by the female because if she is returned to her original stud male 24 hours after separation from him, her pregnancy is carried to term. The primary stimulus initiating the reaction is almost certainly olfactory, but direct proof of this assumption has so far been lacking. Experiments have now been carried out with female mice in which the sense of smell has been destroyed.

The operation of removing the olfactory bulbs was performed under Avertin anesthesia. A hole was drilled between the eyes of the mouse and the olfactory bulbs were separated from the cribriform plate with a metal probe and removed by suction, as described by Whitten (*3*). The mice used were of the same strain as those initially observed. All the females and the stud males were albino, from a closed colony randomly mated, the P strain, bred in this institute. Mice of the G substrain of CBA (*4*) were used as pregnancy blocking agents. To induce pregnancy block the mated female was removed from the stud male when the vaginal plug was found, housed alone for 24 hours after separation from him, her inside a stock box containing males, or in a basket suspended from the lid of the box, for 3 or 4 days. Both situations have proved satisfactory for the manifestation of the block to pregnancy. Vaginal smears were examined daily. Females in which pregnancy was blocked and those which became pseudopregnant were again paired with a stud male and allowed another mating. Only those which then became pregnant have been included in the results. Altogether, tests were completed on 22 anosmic females. The results are summarized in Table 1.

In marked contrast to intact females the majority of anosmic females remained pregnant or pseudopregnant in the test situation. None of the three females in which pregnancy was blocked showed the typical response, since oestrus returned only on day 6 (in two females) or on day 7 (in one female) after the stud mating. An unusually high pseudopregnancy rate (five out of 22) was shown by the anosmic females. Among the intact females tested concurrently, only one became pseudopregnant. It is therefore most unlikely that the increase in the number of pseudopregnancies among the anosmic females is related to the presence of strange males. Removal of the olfactory bulbs in female mice leads to regression of the ovaries and uteri, to alterations in mating behavior (*3*), and to disturbances of reproduction often more profound than can be explained by ablation of the olfactory bulbs alone (*5*). Much variation in reproductive behavior is therefore to be expected among anosmic females.

The results of these tests emphasize the primary function of olfaction in pregnancy block of exteroceptive origin, since the recently mated females in which the sense of smell had been destroyed were virtually immune to the effects of the presence of strange males. In this respect pregnancy block is reminiscent of other social effects in mice. When females are housed together, instead of singly, oestrus is partially suppressed. In small groups there is such an increase in the number of pseudopregnancies that the latter may account for over 25 percent of the cycles (*6*). In large groups of females, oestrus and ovulation occur only infrequently (*7*). But if such females are paired with males, oestrus returns promptly, and the incidence of mating greatly exceeds expectation (on the basis of a 5-day cycle) on the third day after pairing (*8*). By contrast, stimulation resulting from the presence or proximity of strange males inhibits the establishment of pregnancy in the recently mated female (*1*). These effects are abolished in mice from which the olfactory bulbs have been removed (*3*, *9*).

Other experiments have shown that successive pregnancies in the same female can be blocked. Whitten (*7*) has suggested that the exteroceptive control of the oestrous cycle might to some extent regulate cycles of population density among colonies of wild mice. In the same way the exteroceptive block to pregnancy associated with the smell of strange males might be held to favor exogamy among wild mice.

H. M. BRUCE
D. M. V. PARROTT*
Division of Experimental Biology, National Institute for Medical Research, Mill Hill, London, England

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* Present address: Imperial Cancer Research Fund, Burtonhole Lane, The Ridgeway, Mill Hill, London, N.W. 7, England.

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