

29th day. In other respects, such as caging, cleaning, lighting, temperature and diet, the animals were treated exactly as were non-injected pregnant rabbits. Litters were born within the gestation period found to be normal in this Department (31 ± 2 days).

None of the mothers exhibited normal parental behaviour. When given straw they made no attempt to build a nest and they did not pluck their fur before parturition. After the young were born the mothers showed no retrieval behaviour, but left the offspring lying about the cage for some hours, discouraging attempts at suckling, before chewing them. All members of each litter were eaten or fatally mutilated within 24 h from birth. Although such cannibalism sometimes occurs with normal rabbits⁴ it has been rare in this laboratory. Since the behaviour of the male rabbit is characterized by a comparable initial indifference to offspring followed by cannibalism this phenomenon may perhaps be regarded as a reversal of parental behaviour.

It would be of interest to know why androgens during gestation cause behavioural reversal in some species but not others, and whether such effects are correlated with the presence (in the rat and guinea-pig) or absence (in the rabbit) of a mechanism for the cyclic release of gonadotrophins. The male rat does not exhibit spontaneous cyclic release of gonadotrophins and it has been shown⁵ that intrahypothalamic injections of testosterone in this animal initiate female parental behaviour. However, another mechanism, unconnected with presence or absence of reproductive cycles, may be involved. Spayed rabbits, given daily injections of progesterone, build maternal nests of fur when the administration of the hormone is discontinued⁶, and nest-building in this species has been attributed to the cessation at parturition of progesterone secretion by the corpora lutea⁷. It does not seem likely that this phenomenon is prevented by giving androgen during pregnancy. More probably, the action of testosterone in the pregnant rabbit is to render the hypothalamic regions involved in parental behaviour refractive to reduced blood levels of progesterone. It may tentatively be postulated that disturbances of maternal behaviour including the wish not to suckle in animals and, perhaps, humans may be associated with an abnormal release of androgens from the adrenal cortex occasioned by such factors as emotional stress.

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STATISTICS

Estimating the Malthusian Parameter from Census Data

In reporting¹ the results of experiments designed to examine consequences of the theory surrounding the concept of the innate capacity for increase, or Malthusian parameter^{2,3}, attention was directed to an unexplained discrepancy. From a linear regression of log total numbers on time, the experimental populations increased by an average of 6.082 times per three weeks, with 1 per cent confidence limits of 6.026 and 6.138, whereas age-specific life and fertility data independently obtained suggested that the value should have been 4.478. This discrepancy

alone would have meant no more than that the experimental methods used in obtaining the life and fertility data depressed some or all of the rates of development, etc., but, by coincidence as it now seems, another method of evaluating the census observations suggested a value of 4.664, which is in accord with that calculated from the life and fertility table data. This value was obtained as follows: it was assumed that the population growth could be described as a first order process:

$$Mn_t = n_{t+1}$$

where M is a matrix the elements of which are numerical values of the dependence of stage i at time $t + 1$ on stage j at time t ($i, j = 1, 2, \dots, s$), where there are s morphologically distinguishable stages in the population, and n_t and n_{t+1} are column vectors specifying the number of individuals in each stage at times t and $t + 1$. From census observations made at intervals of 3 weeks, M was estimated for this period by:

$$M = (V^{-1}W)'$$

where V is the variance/covariance matrix between the numbers of individuals at time t and W is the covariance matrix between the numbers of individuals at times t and $t + 1$. The first estimate, that forming the basis of the earlier discussion¹, will be referred to as M_1 and was:

$$M_1 = \begin{bmatrix} 0.250 & 1.998 & 4.734 & -0.009 \\ 1.596 & 0.173 & 25.023 & 12.021 \\ 0.152 & 0.042 & -0.110 & 1.032 \\ -0.133 & 0.854 & 1.022 & -0.231 \end{bmatrix}$$

which has a dominant latent root of 4.664 with an associated stable (column) vector of [0.455 0.875 0.055 0.152]'.

Dr. R. W. Howe, of this Laboratory, pointed out to me that this estimate of M used variances and covariances which had been corrected for the mean; if the experimental methods had achieved the results for which they were designed, namely, the removal of harmful 'density' effects, then regressions should pass through the origin, that is, corrections for the means should not be made. A new estimate of M was then made; this will be referred to as M_2 . This matrix:

$$M_2 = \begin{bmatrix} 0.341 & 1.803 & 4.119 & -0.785 \\ 1.203 & 0.998 & 27.776 & 15.309 \\ 0.125 & 0.101 & 0.085 & 1.264 \\ -0.160 & 0.875 & 0.919 & -0.279 \end{bmatrix}$$

has a dominant latent root of 5.521 with a stable (column) vector of [0.347 0.925 0.058 0.141]'. This latent root is obviously in much closer agreement with the increase implied by the slope of the linear regression estimate of the totals on time.

Since there does not seem to be an algebraic method for the estimation of the standard errors of the latent roots of a matrix, the elements of which have known or estimated variances, it is not clear whether the 1 per cent confidence limits for this latent root include the linear regression estimate. At present, therefore, whether a discrepancy remains is uncertain. Further investigation of the underlying distributions^{1,4} and their implications will be necessary before this problem can be solved.

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