monogamous for having only one mate. The word monogamous is complicated because it can mean having only one mate at a time or having only one mate for life. Having one mate does not necessarily mean that the individuals of one pair copulate; the word copulate means to join, couple, unite, or connect but does not specify insemination. It will be shown in the following section that Craig's use[1] of the word monogamous is peculiarly inappropriate for the mosquito *Aedes* (*Stegomyia*) *aegypti* (L.).

The second aspect of this problem concerns a seemingly simple direct observation of whether an individual female *A. aegypti* copulates more than once during her lifetime. It was originally believed that *A. aegypti* females copulate with many males under free-flying conditions in the laboratory[5]. Roth[6] observed that one male in a cage with 16 virgin females copulated 30 times in 30 min, and that 11 males copulated 50 times in 1 h with a single previously virgin female. Wheeler and Jones[6] found that male *aegypti* could be forced to copulate with some newly-emerged females but did not inseminate them. This was influenced by the secretions of the corpora allata and varied with the strain of *aegypti*[7]. Male *aegypti* could not be force-copulated with freshly inseminated females[8]. While under free-flying conditions many of the once-mated females copulated a second, although significantly shorter, time than the first[9]. While Gwadz and Craig[2] stated that *aegypti* females may copulate repeatedly, it was subsequently concluded, from observations with tethered females[3], that they copulate only once and falsely seem to copulate thereafter. Gillett[10] reported many individual and sequential (single pair) matings of *aegypti*, and that one free-flying female mated with 40 different males.

My observations were made on the Bangkok strain of *A. aegypti*. To demonstrate whether free-flying females would copulate (or seem to copulate) with only one male and with this male more than once, ten individual couples were placed in separate cages and observed under undisturbed conditions 4 h per day for 5 to 7 days. Most of the couples copulated (or seemed to do so) more than once with a given partner under these strictly monogamous conditions. The maximum number of copulations occurred on the third day of monogamous cohabitation, when the caged mosquitoes flew about more often than on other days. Over a 7-day period, four out of five couples made 75 genital contacts during 28 h of direct observation; one couple was never seen to copulate. I conclude that females will copulate repeatedly with the same male when only one is available. Females in cages with many males have also been seen to couple repeatedly with one male.

It was possible in many cases to distinguish clearly between pseudocopulations and true copulations among free-flying mosquitoes in a cage. Most pseudocopulations were very short contacts (less than 1–4 s); the males either attached their claspers to a female's cerci or else clasped her terminal sternum and in either case only lightly. Often the males made a series of rapid thrusts with their terminalia in the direction of the female's terminalium without actually clasping any structures of the female.

To determine whether females would copulate with more than one male, a female which had had 13 observed genital contacts with one male over a 6-day period was sequentially placed in a series of 5 cages, each with a different virgin male, and the cages were manually agitated periodically for 5 min to induce flight activity. While only pseudocopulations were seen with each of the first 4 males, the fifth male definitely copulated with this female and for an abnormally long time (250.7 s). After this, a series of virgin females of known ages (1 to 13 days old) were individually blown into a cage of 20 highly active males and observed for 5 min. The 52 females were continuously disturbed to fly whenever they landed, and appeared to copulate with from 1 to 12 males in 5 min with an average of about 5 males. During these tests, 2 males, were seen attempting to copulate simultaneously with one female in 14 cases, 3 males were observed trying to establish genital contact with one female at the same time in 9 cases, and more than 3

males were found trying to mate with a single female concurrently on 4 occasions. Similar activities can be observed in colony cages. In a special test, one female was observed to copulate (or pseudocopulate) with a total of 15 different males over a period of 3 days.

The duration of the first genital contact versus the longest subsequent contact was recorded for 47 couples during these studies. It was found that in 57.4% of the cases, the longest copulation was not the first one. In general, the second genital contact (when it occurred shortly after the first copulation) was significantly shorter than the first one and was often a pseudocopulation.

When virgin females were placed in cages with 5 virgin males and the cages manually shaken for 5 min, first copulations almost invariably resulted in insemination, if the individuals remained in genital contact for 6 s. It was necessary to use only virgin males in these tests because it was found that when 43 virgin females were individually blown into a cage containing 20 unchanged males, only 74% were inseminated by the first copulation.

I conclude that while *Aedes aegypti* may copulate repeatedly with only one mate over a period of days under strictly monogamous conditions, under normal laboratory conditions this species is a polygamous insect, and that the female normally copulates more than once with one or many males but usually gets inseminated only once if she is a virgin when she copulates. This is in agreement with the earlier work of Roth[5] and Gillett[10], but not with Gwadz *et al.*[3], that the female of this species copulates only once during her lifetime.

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[1] Craig, G. B., jun., *Science*, **156**, 1499 (1967).
[2] Gwadz, R. W., and Craig, G. B., jun., *Mosq. News*, **30**, 355 (1970).
[3] Gwadz, R. W., Craig, G. B., jun., and Hickey, W. A., *Biol. Bull.*, **140**, 201 (1971).
[4] *The Shorter Oxford English Dictionary on Historical Principles* (edit. by Onions, C. T.) (Clarendon, Oxford, 1933).
[5] Roth, L. M., *Amer. Midland Nat.*, **40**, 265 (1948).
[6] Wheeler, R. E., and Jones, J. C., *Anat. Rec.*, **138**, 388 (1960).
[7] Lea, A. O., *J. Insect Physiol.*, **14**, 305 (1968).
[8] Jones, J. C., and Wheeler, R. E., *J. Morph.*, **117**, 401 (1965).
[9] Spielman, A., Leahy, M. G., and Skaff, V., *Biol. Bull.*, **132**, 404 (1967).
[10] Gillett, J. D., *Mosquitoes* (Weidenfeld and Nicolson, London, 1971).

Competitive Exclusion in Herbaceous Vegetation

In maintaining or reconstructing types of herbaceous vegetation in which the density of flowering plants exceeds 20 species/m²—the so-called "species-rich" communities, success is often frustrated by competitive exclusion. Here I describe an attempt to identify criteria with which to assess or anticipate the effect of competitive exclusion both at individual sites and in different types of vegetation.

Herbaceous plants have been classified according to the extent to which certain competitive attributes are evident in the genotype. Four consistent features of "competitive" species may be recognized[1–14]. They are (1) tall stature; (2) a growth form (usually a large densely-branched rhizome or expanded tussock structure) which allows extensive and intensive exploitation of the environment above and below ground; (3) a high maximum potential relative growth rate,

Table 1 Examples illustrating the Derivation of the Competitive Index

| | Attributes | | | | Competitive |
Species	a	b	c	d	index (total/2)
Chamaenerion angustifolium	5	5	5	2	8.5
Arrhenatherum elatius	5	4	4	3	8.0
Brachypodium pinnatum	3	4	3	5	7.5
Ranunculus repens	3	5	3	1	6.0
Helictotrichon pratense	3	2	3	2	5.0
Taraxacum officinale	3	1	4	1	4.5
Festuca ovina	2	1	3	2	4.0
Campanula rotundifolia	2	2	3	0	3.5
Arenaria serpyllifolia	1	0	4	0	2.5

a, Maximum plant height (Clapham, Tutin and Warburg[15]). 1, < 26 cm; 2, 26–50 cm; 3, 51–75 cm; 4, 76–100 cm; 5, > 100 cm. *b*, Morphology (Clapham, Tutin and Warburg and personal observations). 0, Small therophytes; 1, robust therophytes; 2, perennials with compact unbranched rhizome or forming small (< 10 cm diameter) tussock; 3, perennials with rhizomatous system or tussock attaining diameter 10–25 cm; 4, perennials attaining diameter 26–100 cm; 5, perennials attaining diameter > 100 cm. *c*, Maximum potential relative growth rate (Grime and Hunt, unpublished). 1, $RGR_{max} < 2.1$ mg g^{-1} h^{-1}; 2, 2.1–4.0 mg g^{-1} h^{-1}; 3, 4.1–6.0 mg g^{-1} h^{-1}; 4, 6.1–8.0 mg g^{-1} h^{-1}; 5, > 8.0 mg g^{-1} h^{-1}. Where no estimate is available a provisional score of 3 has been used. *d*, Maximum accumulation of persistent (from one growing season to the next) litter produced by the species (personal observations). 0, None; 1, thin discontinuous cover; 2, thin continuous cover; 3, up to 1 cm depth; 4, up to 5 cm depth; 5, > 5 cm depth.

and (4) a tendency to deposit a dense layer of litter on the ground surface. It is practicable to score plant species with respect to each of these features and to use the sum of the scores to provide a competitive index (CI) over a scale of 0–10 (Table 1).
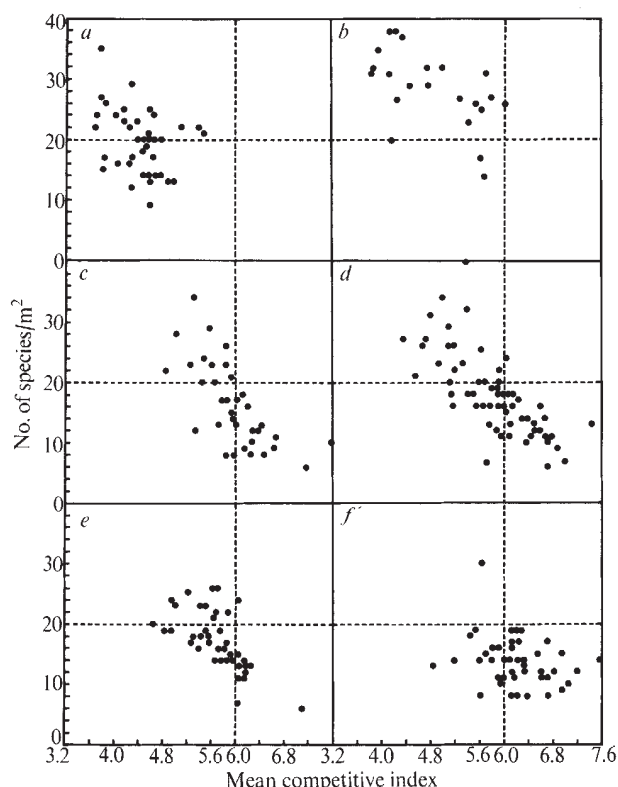

Fig. 1 Relationship between "mean competitive index" and species density in six habitats sampled widely from the same geographical area (Grime and Hodgson, unpublished). *a*, Limestone outcrops with discontinuous soil cover; *b*, unenclosed limestone pastures; *c*, enclosed pastures; *d*, derelict limestone grassland; *e*, meadows; *f*, road verges. The contribution of each species to the mean competitive index is weighted in proportion to its frequency in the m² sample of vegetation.
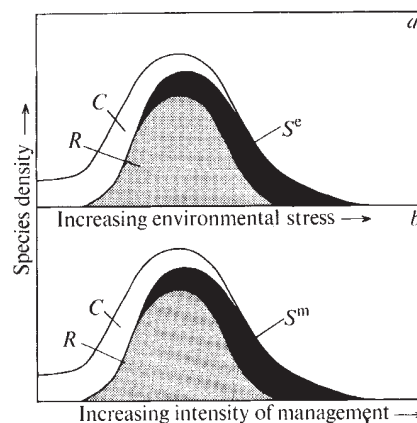

Fig. 2 Diagrams representing impact upon species density of (*a*) intensity of environmental stress and (*b*) intensity of grazing, mowing, etc. *C*, Species of high competitive index. $S^e, S^{g,m,b,t}$, Species (or ecotypes) of high resistance to the prevailing stresses imposed by environment or by grazing, mowing, burning or trampling respectively. *R*, Remaining species.

As it has been calculated in this paper, the CI incorporates a subjective component, fails to take account of ecotypic variation and ignores certain competitive attributes such as the release of phytotoxic compounds. Despite this lack of refinement, however, the index appears to be informative.

In Fig. 1 the CI has been used to assess the importance of competitive exclusion in the control of species density in six types of vegetation sampled from the same geographical area. For each square metre sample of vegetation a mean value calculated from the competitive indices of the component species has been plotted against species density. The data confirm that where species of high CI are prominent (that is mean CI>6.0) species densities are consistently low (<20 species m⁻²). The results indicate a low incidence of competitive exclusion on limestone outcrops and in limestone pastures. In contrast, there is strong evidence that competition is a causal factor in the maintenance of the rather low species densities encountered in the samples from road verges. In the three remaining types (enclosed pastures, derelict limestone grassland and meadows) species density varies widely but in each there is a marked decline with increasing mean CI.

On the basis of previous studies[7,11,14,16–29] and the results of this investigation, I suggest that two mechanisms may bring about the low incidence of species of high CI in vegetation of high species density. One is the result of environmental stress induced by factors such as drought and mineral nutrient deficiencies, and the other is brought about by phenomena such as grazing, mowing, burning and trampling, which by defoliation or by causing other forms of damage to the vegetation tend to prevent potentially competitive species from attaining maximum size and vigour and reduce litter accumulation.

A parallel exists, therefore, between the influence of increasing environmental stress and that of increasing damage intensity, by grazing or mowing for example, on species density. According to the model proposed in Fig. 2*a*, under conditions of low environmental stress productivity is high and species of high CI attain maximum vigour and species density is low owing to competitive exclusion. Under conditions of increased environmental stress, the competitive species decline in vigour and species of lower competitive ability are able to survive. With further reductions in productivity species density falls as conditions of extreme environmental stress are reached and species density is limited by the scarcity of species tolerant of the specific conditions limiting productivity. This model is consistent with the observation of Odum[30] that "the greatest diversity occurs in the moderate or middle range of a physical
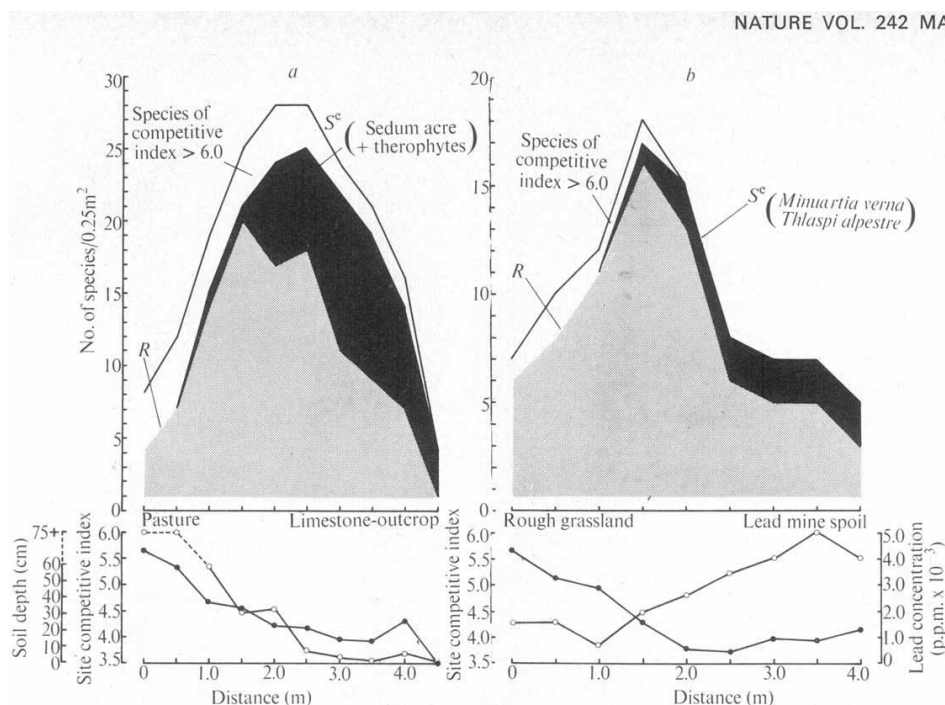
Fig. 3 Transects along natural gradients of increasing environmental stress. *a*, Boundary between rough pasture and a limestone outcrop (Coombsdale, Derbyshire). *b*, Margin of a spoil heap at a derelict lead mine (Winster, Derbyshire). Lead was extracted from the surface soil (0–3 cm) using normal ammonium acetate adjusted to pH 3.0. Shading and symbols as in Fig. 2.

gradient." Data conforming to the model have been obtained from transects along naturally-occurring gradients in environmental stress (Fig. 3).

With respect to the gradient of increasing intensity of grazing, mowing, etc. (Fig. 2*b*), the pattern is essentially similar. Assuming that productivity is sufficiently high, competitive exclusion will occur at low intensity of defoliation and damage. At higher intensities, species of high CI are suppressed and conditions favourable to less aggressive species occur. At the highest intensities species density would be expected to fall as a situation is reached in which only a small number of species are tolerant of the specific form of damage sustained. It is difficult to find situations in the field which illustrate all features of the latter model. Gradients in intensity of factors such as grazing, mowing and burning rarely extend over the full range represented in Fig. 2*b*. A possible exception to this arises in conditions of excessive trampling (Fig. 4) although here it is recognized that effects such as soil compaction may be involved, causing environmental stress.

From a practical standpoint, therefore, there is a need to determine the relative importance of such extrinsic factors in maintaining high species density at particular sites. A possible solution to this problem is to recognize the inverse relationship between net environmental stress and productivity and to use the maximum potential relative growth rates (RGR_{max}) of the perennial species present at each site to derive an index of the latter. A correlation between RGR_{max} and site productivity may be inferred from a number of studies[19,31–34] and comparisons such as that illustrated in Fig. 5 confirm that there is a consistent difference between productive and unproductive vegetation with respect to the potential growth rates of the component perennial species.

An index based upon RGR_{max} would appear to be promising not only in field assessments of the intensity of grazing, mowing, burning or trampling necessary to initiate or maintain high species density but also as a guide to the

stability of herbaceous vegetation. It is to be expected that vegetation composed of species with high potential growth rates (especially where some are suppressed specimens of species of High CI (Fig. 5*a*)) will show a rapid decline in
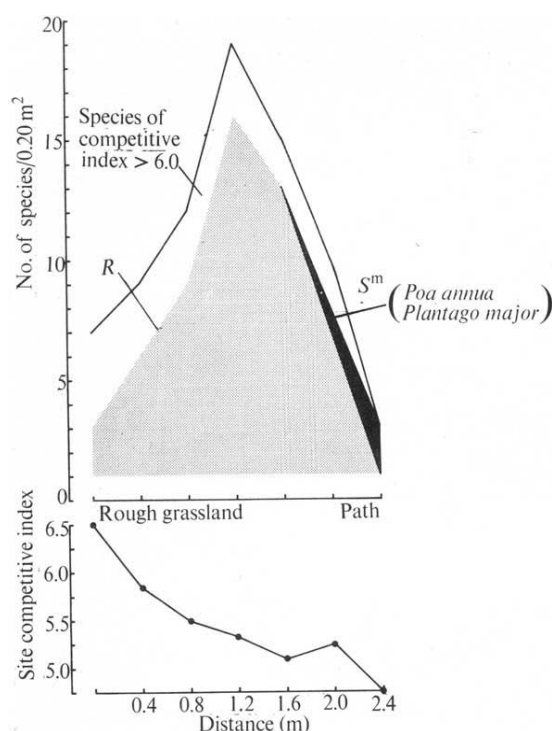

Fig. 4 Transect across the margin of a path through rough grassland (Maltby Low Common Nature Reserve, Yorkshire). Shading and symbols as in Fig. 2.
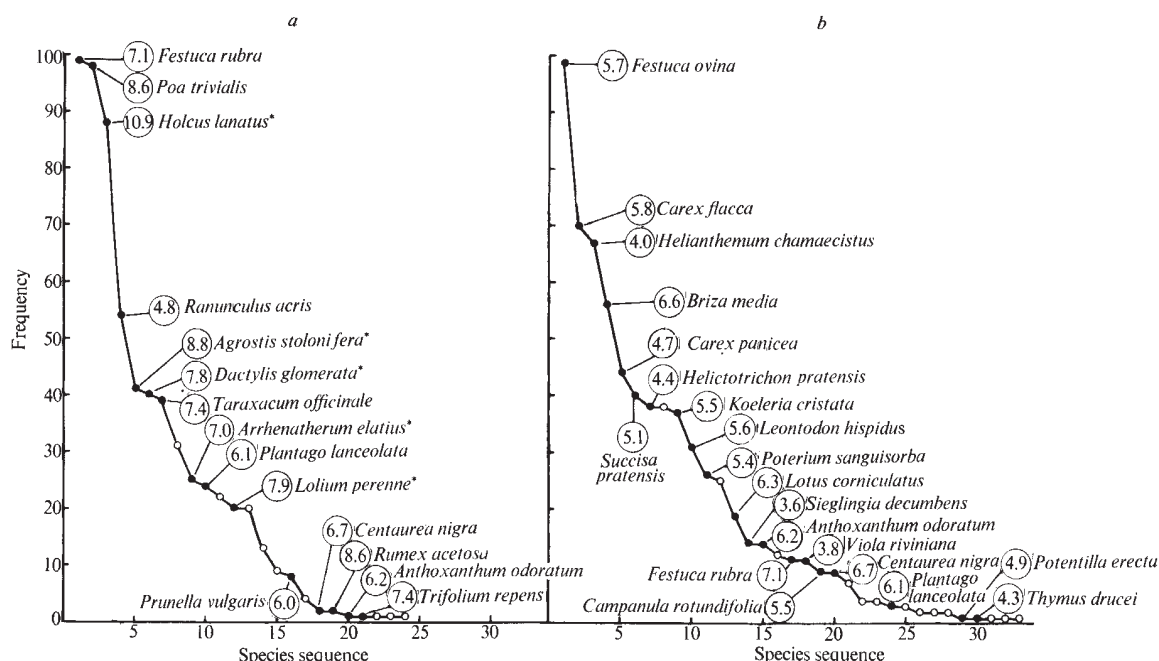
Fig. 5 Comparison of two m² samples of species-rich vegetation with respect to the potential growth rates of the component species. *a*, Productive meadow (Coombsdale, Derbyshire). *b*, Ancient limestone pasture (Cressbrookdale, Derbyshire). (Grime and Hunt, unpublished.) In each figure the species are arranged in order of decreasing % occurrence in 10×10 cm subdivisions of the m² quadrat. The encircled values refer to the RGR_{max} of the species. The open circles indicate species for which no growth-rate estimations are available. * Species of high (>6.0) competitive index.

species density when grazing or mowing is relaxed. Where values for RGR_{max} are low the ensuing reduction in species density is likely to proceed at a relatively slow rate.

Here differences in species density have been related to variation in stress imposed by environment or by certain forms of management and to variation in the frequency and vigour of species of high competitive ability. The impact of additional factors such as site accessibility and degree of niche-differentiation upon species density will be reported elsewhere.

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1 Olsen, C., *J. Ecol.*, **9**, 1 (1921).
2 Greig-Smith, P., *J. Ecol.*, **36**, 339 (1948).
3 Monsi, M., and Saeki, T., *Jap. J. Bot.*, **14**, 22 (1953).
4 Watt, A. S., *J. Ecol.*, **43**, 490 (1955).
5 Black, J. N., *Aust. J. Agric. Res.*, **9**, 299 (1958).
6 Donald, C. M., *Aust. J. Agric. Res.*, **9**, 421 (1958).
7 Thurston, J. M., *Ann. Appl. Biol.*, **47**, 716 (1959).
8 Black, J. N., *Aust. J. Agric. Res.*, **11**, 277 (1960).
9 Palmer, J. H., and Sagar, G. R., *J. Ecol.*, **51**, 783 (1963).
10 Ellenberg, H., *Vegetation Mitteleuropas mit den Alpen, in Kaus-aler, Dynamischer und Historischer Sicht.* (Stuttgart, 1963).
11 Willis, A. J., *J. Ecol.*, **51**, 353 (1963).
12 Grime, J. P., *J. Ecol.*, **51**, 391 (1963).
13 Smith, C. J., Elston, J., and Bunting, A. H., *J. Br. Grassld. Soc.*, **26**, 213 (1971).
14 Maarel, E. Van der, in *The Scientific Management of Animal and Plant Communities for Conservation* (edit. by Duffey, E., and Watt, A. S.), 45 (Blackwell, Oxford, 1971).
15 Clapham, A. R., Tutin, T. G., and Warburg, E. F., *Flora of the British Isles* (Cambridge, 1964).
16 Clarkson, D. T., *J. Ecol.*, **55**, 111 (1967).
17 Higgs, D. E. B., and James, D. B., *J. Ecol.*, **57**, 553 (1969).
18 Pigott, C. F., and Taylor, K., *J. Ecol.*, **52** (Suppl.), 175 (1964).
19 Grime, J. P., in *Light as an Ecological Factor* (edit. by Bain-bridge, R., Evans, G. C., and Rackham, O.), 187 (Blackwell, Oxford, 1966).
20 Hutchinson, T. C., *J. Ecol.*, **55**, 291 (1967).
21 Loach, K., *New Phytol.*, **66**, 607 (1967).
22 Parsons, R. F., *Oecologia Plantarum*, **3**, 121 (1968).
23 Parsons, R. F., *Amer. Nat.*, **102**, 595 (1968).
24 Newhouse, M. E., and Madgwick, H. A. I., *Forest Sci.*, **14**, 27 (1968).
25 Loach, K., *New Phytol.*, **69**, 273 (1970).
26 Tansley, A. G., and Adamson, R. S., *J. Ecol.*, **13**, 177 (1925).
27 Hope-Simpson, J. F., *J. Ecol.*, **28**, 386 (1940).
28 Jeffrey, D. W., in *The Scientific Management of Animal and Plant Communities for Conservation* (edit. by Duffey, E., and Watt, A. S.), 79 (Blackwell, Oxford, 1971).
29 Yemm, E. W., and Willis, A. J., *Weed Research*, **2**, 24 (1962).
30 Odum, E. P., *Ecology* (Holt, Rinehart and Winston, New York, 1963).
31 de Boer, T. A., and Ferrari, T. J., *Versl. Landb. Onderz.*, **62**, 1 (1957).
32 Bradshaw, A. D., Chadwick, M. J., Jowett, D., and Snaydon, R. W., *J. Ecol.*, **52**, 665 (1964).
33 Kruijne, A. A., *Jaarb. Inst. Biol. Scheik. Onderz. Landb.*, 175 (1960).
34 Hunt, R., thesis, Univ. of Sheffield (1970).

Gestation Period for Australopithecus

LEUTENEGGER[1] has provided estimates of the foetal size at birth of two species of *Australopithecus*. Huggett and Widdas[2] drew attention to the relationship between foetal age and weight in mammals, and we have been assessing both specific foetal growth rates and length of gestation (J. F. D. F. and A. St G. Huggett, unpublished data). It is quite clear that in the higher primates the foetal growth rate is 0.06. Using this and the estimates of foetal sizes at birth in the Huggett/Widdas formula[2] we obtain gestation periods for *A. africanus* of 257 days and *A. robustus* 300 days.

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1 Leutenegger, W., *Nature*, **240**, 568 (1973).
2 Huggett, A. St G., and Widdas, W. F., *J. Physiol.*, **114**, 306 (1952).