

sexual and asexual progeny were thus planted in the locations to which seeds would naturally have been dispersed, because our hypothetical mutant presumably would not alter both the mode of reproduction and the mode of dispersal. The transplanted tillers were similar both in size and in age to seedlings which had germinated the previous fall in the field. We acknowledge that our simulation was a first-order approximation of the natural progeny dispersal pattern in the field, and that it did not incorporate data on density-dependent germination and seedling survivorship. As far as we are aware, few data on this point exist. Nevertheless, our previous experiments have shown remarkably little response of adult tillers and seedlings of *Anthoxanthum* to density variation in the field^{2,3}. Further, the relative advantage of sexual progeny in *Anthoxanthum* is not strongly affected by changes in planting density². We suspect, therefore, that our simulation of progeny dispersal is not particularly unnatural.

Shaankar and Ganeshaiah again seem to confuse asexual reproduction with vegetative reproduction when they argue that inflorescence number is an inappropriate measure of fitness. Hypothetically, asexual progeny could produce apomictic seeds, and hence gain fitness through inflorescences and spikelets. (Using the number of vegetative tillers as an estimate of fitness, our data still show a significant advantage for sexual progeny. The relative fitness of sex is 3.34 ± 0.71 when calculated using the number of vegetative tillers at the end of the second year as an estimate of fitness.)

Our experiment was not designed to test the spatially varying environment hypothesis, and difficulties in testing this hypothesis arise because distance from parent is confounded with progeny density. Nevertheless, the choice of 2 m as the maximal distance for planting was entirely appropriate in *Anthoxanthum*, as 99 per cent of all seeds is dispersed within 2.0 m. Hence, although experiments we have done do show a greater advantage for sexual progeny at greater distances (10 m) from the parent⁴, such considerations are not relevant to explaining how a twofold advantage for sexual reproduction could arise, unless rare long-distance dispersal yields a considerable advantage for the sexual progeny, such as in a colonization event. The plant community within which the present experiments were conducted is relatively stable⁵, and hence it is unlikely a significant short-term advantage for sex arises in this *Anthoxanthum* population from long-distance dispersal.

Shaankar and Ganeshaiah are correct to note that the degrees of freedom for parents, distance \times parent, and parent \times sex should be 24, not 25. However, the effect of this error was to deflate the *F*-values. The correct *F*-values are of

higher significance, and our conclusions are unaffected. In summary, we believe our results are sound and provide clear evidence for a short-term (within a generation) advantage for sexually reproducing females.

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Thoroughbred breeding

SIR—Gaffney and Cunningham¹ and Hill² have addressed a biological dilemma with important consequences by illustrating that although TIMEFORM ratings for thoroughbred horses are increasing by about 1 per cent per year, the winning times for the English classic races have not changed appreciably since 1930. I propose that there is insufficient variation in speed realistically to expect significant reductions in winning times, and improvement in TIMEFORM ratings may be due to components of racing ability other than speed.

The genetic principle under investigation is that of a correlated response in winning time to selection based on TIMEFORM ratings. The expected correlated response per generation (CR) can be calculated from the formula³ $CR_s = ih_s h_r r_G \sigma_s$, where *S* represents speed, *T* the TIMEFORM rating, *i* the intensity of selection, *h* the correlation between phenotype and genotype, σ the phenotypic standard deviation, and r_G the genetic correlation between speed and TIMEFORM rating.

One proposition to explain the contradiction is that the standard deviation for speed is very small. Data to compute this statistic directly are unavailable and so σ_s is estimated here from observations of trial races of 1,200 metres (six furlongs). A high proportion of horses trained for racing compete in such trials in which the distance between first and last seldom exceeds 70 metres. A typical winning time for 1,200-metre races is 72 seconds⁴, and therefore a distance range of 70 metres represents a time range of about 4 seconds. Assuming that this range spans 95 per cent or 4 standard deviations of the population the standard deviation for time to run 1,200 metres is 1 second. From Gaffney and Cunningham $(i_m + i_r)/(L_m + L_r) = 0.132$ and $h_r = 0.6$. Substituting these

values in Falconer's formula: $CR_s = 0.132 \times 0.6 \times 1 \times h_s r_G = 0.079 h_s r_G$ seconds per year and taking 0.6 and 0.8 as arbitrary values for h_s and r_G respectively, $CR_s = 0.04$ seconds per year or 2 seconds per half century. This represents a response in speed of 2.7 per cent which is considerably lower than the 5 per cent predicted by Hill, but is still greater than the improvement indicated by Gaffney and Cunningham. But the predicted response will approach zero if the values of h_s and or r_G are lower than assumed above.

Why, then, have TIMEFORM ratings improved by 1 per cent per year whilst winning times have not changed significantly? A possible explanation is that breeders have difficulty in ranking animals across years. In this instance the problem may be compounded by TIMEFORM rating being subjectively assessed and influenced principally by a horse's ability to win races. Although such ratings may accurately rank animals within age group, their reliability as a measurement from which to estimate rates of genetic change should be addressed.

On the other hand, the improvement in TIMEFORM ratings may be a true reflection of genetic progress for ability of horses to win races. This 'ability to win' encompasses many traits such as strength, temperament, speed and desire to win. The fact that winning times are not changing may simply mean that speed has become a relatively unimportant component of 'ability to win' in thoroughbred horses during the past 50 years.

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CUNNINGHAM REPLIES—Eckhardt *et al.*⁵ in their comment on our paper¹ suggest that the record times for the Derby in 1987 and 1988 provide evidence that racehorses are becoming faster. These two times do not invalidate our general point that winning times have been nearly static for more than 50 years. The main conclusion of our study¹ was in fact that genetic improvement in racing ability of the thoroughbred population as a whole has been very close to what selection theory predicts. We made the point that winning times of the best horses in the most prestigious races are not an accurate measure of genetic change in the population as a whole.

The speculations of Eckhardt *et al.* about the reasons for slow genetic improvement in thoroughbreds, although interesting, are not necessary, and are also debatable. Eckhardt *et al.* suggest that racing ability calls on such a wide range of structural and physiological factors, some of which are antagonistic to each other, so that improvement in net effect is more difficult than it is for economic traits in other domestic animals. A high-perform-