Lack of biochemical polymorphism in British fallow deer

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Seven-hundred and ninety-four samples of fallow deer (*Dama dama* L.) blood or tissue were collected from 37 sites in England and Wales. A selection of these samples was screened for electrophoretic variation at each of 30 loci (minimum of 88 samples per locus). No genetic variation was found. Possible explanations for the lack of polymorphism are discussed. It is suggested that European fallow deer experienced a genetic bottleneck during a period of captivity in Mesolithic or Neolithic times.

INTRODUCTION

Electrophoresis has been used to generate genetic data about a number of deer species. To date at least 70 papers and reports have been written in this field. The information obtained has been used to study genetic differentiation between species (Baccus *et al.*, 1983), subspecies (Gyllensten *et al.*, 1983; Dratch and Gyllensten, in press) and populations (Soldal and Staaland, 1980; Ryman *et al.*, 1980; Gyllensten *et al.*, 1983; Dratch and Gyllensten, in press) and to examine population subdivision, giving insights into dispersal behaviour (Manlove *et al.*, 1976; Ramsey *et al.*, 1979; Chesser *et al.*, 1982). Other authors have sought relationships between performance and genotype (Johns *et al.*, 1977; Smith *et al.*, 1982; Cothran *et al.*, 1983) or changes in genotype frequencies over time (Baccus *et al.*, 1977; Chesser *et al.*, 1982), suggesting the action of natural selection. Among practical uses, the discrimination of species from blood spots or tissue scraps is of value in law enforcement (Oates *et al.*, 1979; Lawton and Sutton, 1981; McClymont *et al.*, 1982) and genetic information is of obvious interest to conservationists, for example in the planning of introductions (Smith *et al.*, 1976; Ryder *et al.*, 1981; Gyllensten *et al.*, 1983). A number of uses for electrophoresis studies can also be envisaged in the growing deer farming industry, ranging from the assessment of genetic differences between lines to paternity testing.

Most of the applications mentioned above imply the presence of considerable intraspecific polymorphism in deer, which is certainly true for the four species on which studies have so far concentrated. Most work on the Old World reindeer (*Rangifer tarandus tarandus*) has been limited to a single locus, transferrin, at which major surveys have each revealed between 7 and 12 alleles (Braend, 1964; Turubanov and Shubin, 1971; Zhurkevich and Fomicheva, 1976; Soldal and Staaland, 1980; Røed, in press). The remaining three species have been surveyed extensively both geographically and in terms of the number of loci screened, and table 1 summarises the principal studies. Points to notice are that none of the species completely lacks detectable variation and that the white-tailed deer shows an apparently higher level of genetic variation than moose, red deer and wapiti. Indeed, all the white-tailed deer populations and some of the moose and wapiti populations studied have average heterozygosities (H) greater than the H for all mammals ($H = 0.033-0.039$) derived by various authors (Powell, 1975; Nevo, 1978; Avise and Aquadro, 1982; Baccus *et al.*, 1983) which argues further against the generalisation that large mammals are monomorphic (see Ryman *et al.*, 1980).

The present study was undertaken as a first step towards using electrophoretically-detectable variation to investigate the occurrence of inbreeding in fallow deer (*Dama dama* L.) populations (Smith, 1979). Previously published

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Table 1 Summary of the most extensive genetic surveys of deer species to date

Species	Number (and location) of populations surveyed	Number of loci screened	Range of average heterozygosity (<i>H</i>) found	Reference
white-tailed deer (<i>Odocoileus virginianus</i>)	8 (S.E. USA)	35	0.049–0.092	Smith <i>et al.</i> , in press
moose (<i>Alces alces</i>)	18 (Scandinavia)	23	0.006–0.047	Ryman <i>et al.</i> , 1980
red deer and wapiti (<i>Cervus elaphus</i>)	22 (N.W. Europe) 11 (N.W. USA)	34 28	0.000–0.031 0.004–0.060	Gyllensten <i>et al.</i> , 1983 Dratch and Gyllensten, in press

electrophoresis and isoelectric focusing studies of fallow deer include a survey of serum proteins, especially transferrin, by McDougall and Lowe (1968), haemoglobin studies by Maughan and Williams (1967), Butcher and Hawkey (1977) and Lawton and Sutton (1981) and the screening of LDH by Munday *et al.* (1974). Only the Butcher and Hawkey (1977) study suggested a polymorphism in fallow deer. However, besides the small number of loci screened, all the studies mentioned involved limited sampling of individuals and/or populations. Since initial small surveys of the species shown in table 1 also sometimes failed to reveal variation (*e.g.*, transferrin: Braend, 1962; Johnson, 1968; Seal and Erickson, 1969) the previous fallow deer studies do not necessarily indicate the outcome of a more thorough study. Indeed, given the results of existing large surveys of deer species (see above), the widespread, genetically controlled coat colour polymorphism of British fallow deer (Chapman and Chapman, 1975, pp. 23–31) and a suggestion of genetically determined skeletal variation in this species (Chapman and Chapman, 1969), the present survey was fully expected to reveal genetic variation.

MATERIALS AND METHODS

Blood and *post mortem* tissues were collected from fallow deer from the sites in England and Wales shown in fig. 1. In total 794 individual deer from 37 sites were sampled in some way, but we emphasize the heterogeneity of the samples. Blood was obtained by bleeding live deer (389 animals), by *post mortem* sampling (280 animals) and by taking aliquots of samples collected by other researchers (43 animals). *Post mortem* tissue sets consisting of muscle, liver and kidney were collected by stalkers from 179 animals (including 148 which were also

blood sampled) while samples of muscle only were obtained from 51 carcasses in a butcher's cold store.

Fig. 1 also gives a rough indication of the number of animals sampled per site which ranged from one (four sites in Berkshire and Hampshire) to 126 (Margam Park, South Wales). The "sites" themselves consisted of 14 more-or-less enclosed parks and 23 areas holding wild fallow deer.

In addition to fallow deer samples, 133 blood samples and 14 *post mortem* tissue sets were collected from red deer from two sites and blood samples were taken from six muntjac (*Muntiacus reevesi*) from one site, for comparative purposes.

Blood was collected into heparinised tubes (Vacutainer and Sterilin). Blood samples from live deer and from some freshly shot deer were brought to Reading in a vacuum flask containing melting ice and were processed within 48 hours of collection. Blood samples collected by stalkers were posted to Reading and processed on arrival. After centrifugation (3000 rpm for 15 minutes) the plasma was drawn off, separated into aliquots and frozen. All samples were stored at -30°C . Approximately 2 ml of the remaining red cells were washed and centrifuged two to three times in 8 ml 0.85 per cent NaCl solution. When a clear supernatant was produced, the red cells were lysed with 1 ml distilled water, divided into aliquots and frozen.

Post mortem tissues collected by stalkers were stored in domestic freezers until retrieved. The samples were brought to Reading in a vacuum flask packed with solid CO_2 to prevent thawing. The tissues were kept frozen until immediately before electrophoresis when sections weighing approximately 600 mg were homogenised in an equal volume of distilled water. All homogenising was carried out by hand in a ground glass homogeniser (Gallenkamp) or with a pestle and mortar, when 200 mg sterilised sand was added to aid grinding.

Figure 1 Sites in England and Wales from which fallow deer samples were obtained; size of circle indicates number of animals sampled.

Homogenates were centrifuged (3000 rpm for 15 minutes) and the supernatant was then used in electrophoresis.

Electrophoresis was carried out using a mixture of Shandon and home made equipment. General procedure for horizontal starch gel electrophoresis did not differ importantly from that described by Manlove *et al.* (1975). Buffer systems and stain recipes were taken from the literature or followed those in use in the laboratory of Professor R. J. Berry, University College London. In several cases more than one buffer system was tried. Preferred buffer systems, tissues used and references to detailed methods are given in table 2. Full details are given in Pemberton (1983).

Haemoglobin was focused in 0.3 mm thick 7 per cent acrylamide gels containing pH 6–8 Ampholines (LKB) at a concentration of 0.2 per cent. Seventeen chroma Whatman paper was soaked in 1 M H_3PO_4 at the anode and 1 M NaOH at the cathode. Samples were loaded on pieces of 1 MM filter paper laid on the surface of the gel. Voltage was applied *via* a focusing jacket made in the Zoology Department workshop.

The loci screened were chosen because they are known to be polymorphic in deer or other

mammals, because they stain up at the same time as the “target” loci, or because they are cheap to stain or easy to resolve.

In a project with a fixed time limit, the number of loci which can be screened is inversely related to the number of individuals screened at each locus. In the present study, after the first few loci had been screened, calculations were made to help decide how many samples from the “sample bank” needed to be examined at a locus and found to be indistinguishable for that locus to be regarded as monomorphic. Taking a locus in which the rarer allele is at frequency 0.01 as a minimum criterion of polymorphism and assuming Hardy-Weinberg equilibrium, each individual examined gives a probability of 0.98 of not detecting such a polymorphism. The probability of detecting polymorphism is then $(1 - 0.98^1) = 0.02$ after one sample, $(1 - 0.98^{10}) = 0.18$ after 10 samples, etc. Whereas the probability of detecting polymorphism increases rapidly with the first few samples examined, the reward (in terms of increased probability of detecting polymorphism) in return for effort decreases as the probability approaches 1.0. In the present study, it was decided, somewhat arbitrarily, to try to examine at least 100 individuals

Table 2 Electrophoresis methods and sample sizes used in the present study. Key: under "Tissues studied": p = plasma, h = haemolysate, l = liver, k = kidney, m = muscle; under "Reference and Method": gel concentration indicated as %, poly. = polyacrylamide, disc. = discontinuous buffer system

Protein	Reference and Method (electrophoresis on starch gels except where stated)	Tissues studied	No. of loci	No. of animals	No. of study sites
Tf (transferrin)	Manlove <i>et al.</i> (1975). 12.4% lithium hydroxide.	p	1	368	13
Alb (albumin)	As for Tf	p	1	368	13
sag (slow α -globulin)	As for Tf	p	1	368	13
Hb (haemoglobin)	After Lawton and Sutton (1981). Isoelectric focusing, 7% poly.	h	1	224	15
GPD (glycerol-3-phosphate dehydrogenase)	Harris and Hopkinson (1976). 11% tris-EDTA-maleate	l, k	1	88	13
SDH (sorbitol dehydrogenase)	Op't Hof <i>et al.</i> (1969). 12% tris-phosphate.	l	1	100	14
LDH (lactate dehydrogenase)	Manlove <i>et al.</i> (1975). 12.4% disc. tris-citrate.	m	2	134	18
MDH (malate dehydrogenase)	Harris and Hopkinson (1976). 11% phosphate-citrate.	k, l, m	2	109	17
IDH (isocitrate dehydrogenase)	As for MDH	k, l, m	2	109	17
6-PGD (6-phosphogluconate dehydrogenase)	Harris and Hopkinson (1976), under ADA. 11% phosphate.	l, h	1	151	20
GDH (glucose dehydrogenase)	Harris and Hopkinson (1976). 11% tris-citrate.	l	1	115	14
G6PDH (glucose 6-phosphate dehydrogenase)	After Ruddle <i>et al.</i> (1968) 13% tris-EDTA-borate.	l, h	1	132	15
SOD (super-oxide dismutase)	As for LDH and G6PDH.	l, m, h	2	207	22
GOT (glutamate oxaloacetate transaminase)	DeLorenzo and Ruddle (1970). 12% citrate-phosphate.	k, l	2	111	16
AK (adenylate kinase)	Harris and Hopkinson (1976). 11% histidine-citrate.	k, l	2	107	14
PGM (phosphoglucomutase)	Harris and Hopkinson (1976). 11% tris-EDTA-maleate.	l	2	105	15
Est (esterases)	As for Tf.	p	2	230	17
AP (acid phosphatase)	As for 6-PGD	h	1	115	14
CA (carbonic anhydrase)	As for G6PDH	h	2	107	9
GPI (glucose phosphate isomerase)	Harris and Hopkinson (1976). 11% tris-citrate.	k	1	101	16

at each locus, giving a probability of 0.87 of detecting a borderline polymorphism. Table 2 shows the number of individuals examined for each system: the target of 100 was achieved for all except one system, GPD (88 samples, see table 2).

A related decision concerned which samples from the "sample bank" to examine. Previous genetic studies of deer species have revealed considerable between-population variation in the level of polymorphism detected (table 1). Preliminary enzyme surveys of moose and wapiti involving limited sampling of populations (Ryman *et al.*, 1977; Cameron and Vyse, 1978) were taken to indicate that these species had unusually low levels of polymorphism, a finding which was not borne out by subsequent, more extensive surveys (Ryman

et al., 1980; Dratch and Gyllensten, in press). To avoid such problems, each locus screened in the present study was examined in samples representing several sampling sites. Table 2 shows the number of sampling sites represented by the samples screened for each system.

Finally, to maximise the use made of samples, different combinations of samples were used in the screening of different loci.

RESULTS

Under the electrophoresis conditions employed, none of the presumed 30 loci screened in the fallow deer samples showed variation which could be interpreted on a genetic model.

Broadly speaking, band patterns were as expected on the basis of previous studies of deer (*e.g.*, Manlove *et al.*, 1975). The following account uses the locus designations of Allendorf and Utter (1979) in which, when an enzyme is encoded by more than one locus, locus products are labelled from cathode to anode. In brief, IDH-2, G6PDH, SOD-2, Est-2 and Alb zymograms consisted of a single anodal band of high mobility; GPD, MDH-2, GDH, SOD-1, GOT-2, AK-1 and -2, PGM-1 and -2, CA-1 and -2 and slow α -globulin zymograms consisted of a single anodal band of moderate mobility; IDH-1 and 6-PGD zymograms consisted of a single anodal band of low mobility. GOT-1 was revealed as a cathodal band of medium mobility while SDH and MDH-1 products formed a single cathodal band of low mobility. The remaining locus products formed more complex band patterns. LDH-1 and -2 products combined in tetramers to form five isozymes ranging from the origin to the anode, as described in the white-tailed deer (Manlove, *et al.*, 1975). Fallow deer transferrin consisted of a double-banded anodal system of moderate mobility, as described by McDougall and Lowe (1968). Double-banded anodal patterns were also observed for the plasma esterase system designated Est-1 and for AP for which a similar band pattern has been described in other mammals (Harris and Hopkinson, 1976). As recorded by previous workers (Butcher and Hawkey, 1977; Lawton and Sutton, 1981), focused fallow deer haemoglobin also consists of two major bands. The GPI zymogram consisted of three evenly spaced anodal bands, a pattern also observed in other deer species which has prompted speculation that, in cervids, two GPI loci are expressed (Manlove *et al.*, 1975; Ryman *et al.*, 1977; Gyllensten *et al.*, 1983), although there is as yet no firm evidence for this suggestion.

Certain enzymes (notably LDH, MDH, 6-PGD, GOT and CA) tended to produce sub-bands after storage for several months. In the case of LDH, treatment of the samples with dithiothreitol removed the sub-bands indicating that they were due to the formation of sulphhydryl-glutathione bonds during storage (Harris and Hopkinson, 1976). Storage of haemolysates produced met-haemoglobin bands which could be distinguished from the true haemoglobin bands by their brown colour. Blood samples arriving by post which had haemolysed in transit sometimes showed stepwise changes in transferrin band mobility giving an overall pattern like that which might be expected for a transferrin polymorphism. Experiments

revealed that the variants were post-collection changes probably caused by bacterial growth while the samples were in transit (Lowe and McDougall, 1961). Results from posted blood samples were therefore excluded from the final figure for the number of individuals examined for transferrin given in table 2. Occasional aberrant results at other loci did not coincide with the band patterns expected for heterozygotes on the basis of the subunit structure known in other mammals and could usually be attributed to denaturing of the sample. A putative genetic polymorphism in the slow α -globulin region of plasma was discounted on the basis of results from repeat bleedings of individual deer and from deer of known relatedness held in enclosures for breeding studies (Smith and Johnson, 1982).

While failing to reveal genetic polymorphism in the fallow deer samples, the electrophoresis systems detected previously described transferrin and IDH-2 polymorphisms in the red deer (McDougall and Lowe, 1968; Gyllensten *et al.*, 1983) and a previously undescribed transferrin polymorphism in the Reeve's muntjac, involving two alleles. The pH 6-8 isoelectric focusing unambiguously demonstrated foetal haemoglobin in neonatal fallow deer, repeated the finding of haemoglobin polymorphism in Reeve's muntjac (Maughan and Williams, 1967) and revealed variation in red deer haemoglobin patterns, not previously described.

DISCUSSION

The present study does not show that British fallow deer totally lack electrophoretically-detectable genetic variation. The survey involved a sample of loci, buffer systems, sites and individual deer. At each level a different or bigger sample might have led to the discovery of polymorphism. Nevertheless, given the sample sizes employed in the present study (see Materials and Methods) and assuming our electrophoresis was of equivalent resolving power to that of other workers in the field (in support of which we point to the polymorphisms found in red and muntjac deer) it appears likely that British fallow deer really do have a lower level of genetic variation than other deer species studied to date.

We know of no convincing selectionist theory predicting a low level of genetic variation in the fallow deer compared with other deer species. The "environmental grain" hypothesis of Selander and

Kaufman (1973), which predicts low levels of variation in large, highly mobile species and *vice versa* has attracted some interest in the literature (e.g., Cameron and Vyse, 1978) but was not supported by a recent interspecific comparison of large grazing mammals (Baccus *et al.*, 1983). Presumably the environmental grain hypothesis would predict a higher level of variation in fallow deer than in moose, red deer and wapiti, which is not borne out by our findings. We are therefore forced to the conclusion that the lack of variation found in the present study reflects a genetic bottleneck in the history of British fallow deer. Such a bottleneck might have occurred at a number of points in history.

First, a bottleneck might have occurred when the fallow deer was introduced to Britain. Palaeontological evidence suggests that the species died out in Britain during the last glaciation (Chapman and Chapman, 1975, p. 45). It is possible that the introduced animals were few in number and were forced to inbreed for several generations, losing genetic variation in the process (though this is by no means inevitable, cf. the Reeve's muntjac, another species introduced to Britain). A problem with this theory is that there are several documented introductions of fallow deer to Britain since Norman times, when the main introduction was probably made (Chapman and Chapman, 1975, p. 49). For example, introductions were made in 1612 from Norway, in 1661 from Germany (Shirley, 1867) and in the 19th Century from Denmark (Whitehead, 1950, p. 153). If continental European fallow deer have a higher level of electrophoretically detectable polymorphism it is surprising that polymorphism is not found in the British population as a result of introductions. In this context it is interesting to note that a recent survey of 13 loci in a sample of 35 German fallow deer failed to reveal intraspecific polymorphism (H.G. Scheil, personal communication). A more extensive study of continental European fallow deer is clearly desirable.

Alternatively, a genetic bottleneck might have occurred before the introduction of the fallow deer to Britain. Under this hypothesis, mainland European fallow deer would also have a low level of electrophoretically-detectable polymorphism. The idea calls for an examination of the species' earlier history.

It seems that during the last glaciation the European fallow deer went extinct not only in Britain, but also over much of Europe (Lister, 1984). Jarman (1972) reviews data on mammalian remains at 165 Mesolithic sites (*i.e.*, dating from

10,000 to 5000 years before the present) distributed throughout Europe. Although red deer and roe deer (*Capreolus capreolus*) are the first and fourth most widely represented species respectively, there are no definite reports of fallow deer, suggesting the species was scarce or absent at that time. The oldest post glacial finds of European fallow deer are at early Neolithic sites (5000 to 4000 years B.P.) in Greece and Bulgaria (Chapman and Chapman, 1975, p. 44). Subsequent evidence of the presence of fallow deer comes from Hittite, Greek and Roman artefacts (Zeuner, 1963, p. 430; Chapman and Chapman, 1975, p. 46) and these cultures appear to have fostered the increase and spread of the species. Indeed, it seems likely that the entire distribution of European fallow deer outside the South Eastern corner of Europe is due to introductions by man (Chapman and Chapman, 1980).

In the history outlined, there is no obvious date, from the time man started to transport and introduce fallow deer onwards, when a genetic bottleneck affecting the entire descendent population might have occurred. Two main possibilities therefore exist. First, perhaps a natural catastrophe such as the last glaciation, which left only a relict population of European fallow deer surviving in S.E. Europe for the interval 10,000 to 5000 years B.P., was the direct cause of the bottleneck. Alternatively, perhaps the most serious loss of genetic variation took place during enforced inbreeding when man first took the fallow deer into captivity, which was presumably sometime in the interval 10,000 to 3000 years B.P.

History does not relate which of these theories is more likely, but a feature of modern fallow deer may give a clue. European fallow deer have a widespread, genetically-controlled coat colour polymorphism, individuals ranging from all-white, through various spotted types, to all-black. It is difficult to understand how, in a bottleneck caused by the glaciation, coat colour variation could have been retained while electrophoretically-detectable variation was lost. On the other hand, coat colour variation is a notable characteristic of domestic animals (including the most highly domesticated deer species, the reindeer) and is believed to have been selected by man early in the domestication process (Zeuner, 1963). Although there is no information on the origin of the colour varieties of fallow deer, they are generally regarded as human selected (Chapman and Chapman, 1975, p. 73). It is possible that the coat colour varieties were expressed as a result of inbreeding during the initial domestication of fallow deer and were

retained by man, while invisible variation (detectable now by electrophoresis) was lost.

The idea of a genetic bottleneck at least 3000 years ago often provokes suggestions that novel mutation would since have replaced lost variation. Calculation of how many mutations would be expected by now is hampered by lack of information, especially concerning the neutrality or otherwise of mutants and historical population size. However, if it can be assumed that fallow deer selection coefficients are comparable with those of other deer species, one approach is to examine the rate at which electrophoretically-detectable alleles arise and persist in other species of deer. Electrophoresis studies now exist which compare old and new world forms of moose (Reuterwall, 1980), red deer (Baccus *et al.*, 1983; Dratch and Gyllenstein, in press) and reindeer (Baccus *et al.*, 1983) for which the last possible genetic contact (barring recent introductions) was roughly 10,000 years B.P., at the end of the glaciation. The data from these studies suggest that at a single locus, a detectable new mutation becomes established once in every 18,000 to 72,000 years. So, in a sample of 30 loci between one and five mutations would be expected to appear and persist in a 3000 year interval (details of the calculation are given in Pemberton, 1983).

Low as these rough estimates of detectable new mutations are, they should be reduced still further when the population size of fallow deer over the last few thousand years (affecting the absolute mutation rate) is taken into account. What evidence there is (Jarman, 1972, see above) suggests a far larger red deer than fallow deer population in Neolithic Europe. Present day fallow deer population estimates are frequently no more than guesses, but the figures are an order of magnitude smaller than those for red deer, moose and reindeer. Toth (1984), reviewing available estimates, puts the fallow deer population of the world excluding Britain at 164,000. For Britain, Gibbs *et al.* (1975) guess at 50,000 wild fallow deer. Even allowing for enclosed fallow deer in Britain the world population *estimate* for the species would hardly equal the 255,000 red deer living in Scotland alone (Red Deer Commission, 1980). Such considerations suggest that the number of detectable mutations arising at 30 loci since the proposed fallow deer bottleneck could indeed be negligible.

Although we now know that it is wrong to generalise that all species of large mammal have low levels of variation, it does appear that a relatively high proportion of large mammals have little detectable polymorphism. Although additional sampling of populations would be desirable in

some cases, it seems that the Northern elephant seal *Mirounga angustirostris* (Bonnell and Selander, 1974), the Atlantic walrus *Odobenus rosmannus rosmannus* (Simonson *et al.*, 1982), the red fox *Vulpes vulpes* (Simonson, 1982), the beech marten *Martes foina* (Simonson, 1982), the polar bear *Thalarctos maritimus* (Allendorf *et al.*, 1979; Larsen *et al.*, 1983) and the cheetah (O'Brien *et al.*, 1983) all show exceptionally low levels of variation as revealed by electrophoresis. Speculating on the cause of this lack of polymorphism, it is noticeable that excepting the fallow deer all the species with little detectable variation are carnivores. Baccus *et al.* (1983) suggested that "carnivorous species might be expected to have lower heterozygosities due to smaller average population size caused by their position in the trophic pyramid of numbers or the social structure of their populations," but immediately question the theory because the wolf *Canis lupus* (Fisher *et al.*, 1976), the coyote *Canis latrans* (Fisher *et al.*, 1976) and the Macquarie Island elephant seal *Mirounga leonina* (McDermid *et al.*, 1972) all have relatively high average heterozygosities. The theory, of Baccus *et al.*, is certainly unsatisfactory if one imagines that it is the mean population size of a species over a stretch of time *per se* which determines the amount of genetic drift and hence affects the level of variation. However, in fact it is downward fluctuations in population size which cause the greatest loss of genetic variation. Therefore, low levels of variation may be expected in those species which maintain low population sizes and tend to fluctuate. Higher levels of variation are expected either where average population size is high or where fluctuations are rare.

Finally, we consider the possible consequences of a low level of variation for the fallow deer. First, the finding lends support to the idea that British fallow deer experience low levels of inbreeding depression (Smith, 1979) since it suggests that comparatively few recessive deleterious alleles would be expressed on inbreeding. Second, if one accepts that variation at loci detectable by electrophoresis (or at linked loci) is not selectively neutral, various predictions follow. In the context of deer farming, heritabilities of quantitative characters will be lower than in more polymorphic (as revealed by electrophoresis) species and selective breeding correspondingly less successful. Within-herd variance of production characters such as live weight is lower in fallow deer than in red deer on New Zealand deer farms, supporting this prediction (G. Asher, personal communication). In the wild, fallow deer will not adapt to altered environmental

conditions as successfully as other more polymorphic species. Here we point to the low estimated world population for fallow deer (discussed above), the lower rate of spread of introduced fallow deer compared with red deer in New Zealand (Caughley, 1963; Chapman and Chapman, 1980) and the perhaps rather subjective comment that in Britain the fallow deer has nowhere achieved the pest status of red or roe deer.

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