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Intraspecific variation in biology and ecology of deer: magnitude and causation

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Abstract. It has been noted that the search for patterns in biology to assist our understanding, often leads to over-simplification. That is, we are satisfied with statements that ‘the species as a rule does this’ or, ‘males of this species do that’. But within such generalisations are masked what are often important variations from that supposed norm and in practice there is tremendous variation in morphology, physiology, social organisation and behaviour of any one species. The focus on a supposedly mean optimal phenotype has diverted attention away from variation around that mean, which is regularly regarded as a kind of ‘noise’ stemming merely from stochastic effects, and thus irrelevant to evolution. Yet it is becoming increasingly clear that this variation is by converse extremely significant and of tremendous importance both to evolutionary biologists and to managers. Such intraspecific variation (IV) may be directly due to underlying genetic differences between individuals or populations within a species, but equally may include a degree of phenotypic plasticity whether as ‘non-labile’, traits which are expressed once in an individual’s lifetime, as fixed characteristics inherited from the parents or as more labile traits which are expressed repeatedly and reversibly in a mature individual according to prevailing conditions.

Recognition of the extraordinary degree of IV which may be recorded within species has important consequences for management of cervids and conservation of threatened species. We review the extent of IV in diet, in morphology, mature bodyweight, reproductive physiology, in population demography and structure (sex ratio, fecundity, frequency of reproduction) before also reviewing the striking variation to be observed in behaviour: differences between individuals or populations in ranging behaviour, migratory tendency, differences in social and sexual organisation. In each case we explore the factors which may underlie the variation observed, considering the extent to which variation described has a primarily genetic basis or is a more plastic response to more immediate social and ecological cues.

Additional keywords: cervids, phenotypic plasticity.

Introduction

Barash¹ has noted that the search for patterns in biology to assist our understanding, often leads to over-simplification. That is, we are satisfied with statements that ‘the species as a rule does this’ or, ‘males of this species do that’. But within such generalisations are masked what are often important variations from that supposed norm and in practice there is tremendous variation in morphology, physiology, social organisation and behaviour of any one species, as it adapts feeding habits, social behaviour – even reproductive behaviour – to changing environmental circumstances. The focus on a supposedly mean optimal phenotype has diverted attention away from variation around that mean, which is regularly regarded as a kind of ‘noise’ stemming merely from stochastic effects and thus irrelevant to evolution. Yet it is becoming increasingly clear that this variation

is by converse extremely significant and of tremendous importance both to evolutionary biologists and to managers.

Such intraspecific variation (IV) may be directly due to underlying genetic differences between individuals or populations within a species, but equally, phenotypic variation between individuals of a common genotype may result from differences in their ontogeny under rather distinct environmental conditions.* Such phenotypic plasticity² (hereafter PP) includes ‘non-labile’ traits, which are expressed once in an individual’s lifetime, as fixed characteristics inherited from the parents or as part of ontogenetic development. But in addition, PP also includes labile traits, which are expressed repeatedly and reversibly in a mature individual according to prevailing conditions.

Thus it is clear that, especially in relation to aspects of behaviour or ecology, there may be considerable plasticity of

*Differences in ontogeny among similar genotypes are also sometimes referred to as ‘developmental plasticity’.

response even within a given individual, if exposed to different environmental circumstances – and that many aspects of behaviour and ecology are not fixed elements of an individual's response, but may show significant variation in expression under different circumstances. Such individual variation (often referred to more formally as phenotypic flexibility³), while more commonly recorded in relation to behavioural or ecological responses, may also relate to reproduction (e.g. timing of reproduction and the number or size of offspring produced), or morphological characters that are regularly regrown.⁴ Such plasticity may influence enzyme products, morphological development, learned behaviours and even an organism's response to the effects of disease.⁵ As environmental conditions include both external surroundings of an organism and the internal conditions affecting gene expression, PP clearly encompasses a tremendous diversity of kinds of variability.⁶

Recognition of the extraordinary degree of IV which may be recorded within species has important consequences for management of cervids and conservation of threatened species.

In this paper we aim to review some of the extent of IV shown by different species of deer. In a short paper we must necessarily be selective both of topic and of the species used to illustrate particular examples. In addition: since differences in social behaviour (grouping tendency, group size, group structure, degree of sexual and social segregation, mating strategy) are often the most notable, and also the ones most relevant to managers, we will focus primarily in this paper on variation in social and sexual behaviour. It would be wrong, however, completely to ignore other contexts of variation, and we will start with a brief review of recorded variation in habitat use, diet, morphology and reproductive physiology. In each case we explore the factors which may underlie the variation observed, considering the extent to which variation described has a primarily genetic basis or is a more plastic response to more immediate social and ecological cues.

Variation in habitat occupied and diet

It is almost a *sine qua non* – that deer species with a wide geographic distribution will show gross variation in the range of habitats occupied and in their adaptation to different abiotic conditions. Extensive plasticity is to be expected among species which historically or currently are distributed over a wide geographical range, subsisting in a variety of environments, along gradients of rainfall, temperature and soil type. Any given species may occur (or may have occurred) from sea level to high mountains, flat to steep terrain, and various distinct habitats (forest, swamps, grasslands, deserts) and different populations are likely to show specific adaptation to the differing environmental conditions.

In response to such variation in environmental condition, there is also significant variation in a series of physiological traits (e.g. in relation to development, heat, water availability, basal metabolic rate, digestion) as a major mechanism permitting survival of populations over the wide range of environmental conditions.⁷ *Rangifer*, for instance, have a lower critical temperature of about -50°C ,⁸ but also have a large capacity for heat resistance ($43\text{--}45^{\circ}\text{C}$),⁹ and *Capreolus*¹⁰ may endure from

below -60 to $>40^{\circ}\text{C}$ – although it is perhaps unclear in this instance whether or not such wide tolerances are a species-wide phenomenon or actually reflect more specific local adaptation in different temperature zones.

As another example, compensatory extension of the gestation length is known for several deer species, with differences being almost twice the oestrous cycle length (moose *Alces alces*;¹¹ red deer *Cervus elaphus*;^{12,13} sika *C. nippon*;¹⁴ reindeer *Rangifer tarandus*¹⁵).

Alongside such gross variability in habitats occupied, individual patterns of habitat use even within a given locality will also show significant inter-individual variation,^{16,17} influenced by availability and disposition of habitats, as well as intra- and interspecific competition, and presence of predators which may affect the spatial distribution.^{18,19}

In exactly the same way, it is clear that, for widely distributed species, the diet must vary from place to place since relative and absolute availability of different forage species varies geographically. Thus, individual studies of the diet composition of European roe deer (*Capreolus capreolus*) in the UK show enormous variation in actual species composition or relative importance of different forage species of animals in different geographic areas, or different contexts (continuous forest, farmland with scattered woodland areas etc.^{20–22} and, to a lesser extent, season,²³ and throughout their European range they may consume literally hundreds of different species. The same is broadly true for other species; in essence, while, within any particular area, deer may indeed show feeding preferences for certain species of plants among those available, dietary intake must otherwise respond opportunistically to availability, within the constraints imposed by physiology, foraging 'style', competition and predation pressure. However, we must recognise that deer can adapt to changing forage quality, to some extent at least, by altering the extent of selective feeding, by increasing forage retention in the rumen, by varying gut length and gastrointestinal anatomy, by changing gut microbial communities, by adjusting body size and reproductive output, among others.^{24–26} For instance, as the vegetation changes, feeding behaviour in some deer species can change substantially, moving from pure 'grazers' through 'intermediate' feeding to pure 'browsers'^{27,28}. Once again, variation in feeding behaviour between deer of the same locality also can be very high, as stomach contents of European roe deer had from 0 to 93% of any individual food item,²³ which is likely linked to habitat availability and individual variation in diet and habitat use.¹⁷

However, to some extent this type of variation is circumstantial and self-evident; variations in environment occupied do not necessarily reflect underlying individual differences in physiology or behaviour since all members of a given species might have appropriate environmental tolerances to all circumstances encountered across their distributional range. Likewise, variation in patterns of habitat use or diet between individuals in localities of different habitat availability, or forage species composition does not necessarily reflect specific adaptation but may simply reflect a direct (and essentially trivial) response to resource availability. Therefore, for the purpose of this paper, we will not elaborate further on these subsystems of IV.

Morphology and reproductive physiology

Once again, within any species of deer with a comparatively wide geographical distribution, it is clear that there is an enormous variation in actual body size across this geographic range. Some of the difference may well reflect underlying genetic differences between geographic races or subspecies²⁹ or may reflect separate adaptation to extremes of climate³⁰ or to differences in habitat and diet quality. In other cases, differences in morphology (including mature bodyweight) may simply reflect resource restriction due to combinations of poor overall habitat quality, or due to competition for available resources in herbivore populations at high density.

Among red deer for example, there is enormous variation in adult body size, and body mass across their European range attaining a difference of 7.6-fold among males.^{31,32} Even within their more limited distribution from the south of England to the north of Scotland, average liveweight of mature males (5 years or older) vary from 89 to >160 kg (of course some individuals were heavier than these population averages), while average weights of mature females vary from 72 to 130 kg.³³ This variation relates in part to a latitudinal variation in body size, but also to a difference in the quality of the habitat occupied (woodland or woodland with farmland, in the south of England, versus open moorland habitat in the north of Scotland), as well as population density.³³ In a similar way, marked variation has been demonstrated in mature bodyweights of adult female reindeer from different populations across Norway,³⁴ which seems to relate to the fact that after they have reached breeding age, females in the more resource-restricted populations simply stop growing, while those in areas where resources are more abundant may continue to increase in size and mass.^{34,35}

Besides variable body sizes, substantial IV in sexual dimorphism has been documented for several species, for instance when size of males (but not females) varies with population density.^{36,37}

Variations in body proportions

Body conformation commonly varies substantially between, but also within deer populations: long and lean versus blocky or stocky; short versus long muzzles; short- versus long-legged.^{32,38} In the following we focus on limb proportions which differ substantially between populations of different habitats and locomotor needs.

In contrast to femur or tibia, distal limb segment (metapodial) lengths vary freely with habitat and exercise,^{39,40} making the long bones of the leg highly variable.^{39,41–44} As species fill the landscape along a wide spectrum of habitats, from source to sink areas, we can expect that body shape will vary within species. Individual differences in appendicular bones, like proportional length or stoutness, are mainly due to adaptations following ecogeographical rules, nutritional and physiological constraints, and in response to average muscle work required as a function of terrain, disturbances and food density.^{42,45}

Leg proportions among reindeer vary greatly, with the metatarsus proportionally up to 70% longer, and the ratio of hind foot length to body length up to 3.1 times larger between different herds.^{39,46} Svalbard reindeer have even shorter metatarsals (N. Tyler, pers. comm.) than populations earlier

described by Klein *et al.*⁴⁶ Relative leg length is also considerably greater in forest reindeer than in mountain reindeer,⁴⁷ and shoulder height is reported to differ by 15 cm between forest- and alpine-wintering groups, without differences in other body measurements or proportions.^{48,49} Importantly, changes in leg proportions in reindeer populations have been observed within one single population after only 30–35 years of nutritional stress.⁴⁶

In another example, mule deer (*Odocoileus hemionus*) in Alaskan rain forests had proportionally longer legs than those further south,⁵⁰ and comparisons of two neighbouring populations showed deer in good habitat to have 16.3% longer metapodials than deer in poor habitat.⁵¹ White-tailed deer (*O. virginianus*) from two different environments could also be clearly distinguished based on proportionally different hind foot length.⁵²

Age and weight at maturity and reproductive demography

It is well established among mammals that puberty and especially the onset of ovulatory cycles in females is less related to actual age than to achievement of a critical body mass – or more properly among cervids, a combination of mass and the amount of accumulated body fat.⁵³ Given the variation in adult bodyweight noted above, it is perhaps no surprise to find that there is similar variation in the age at which both male and female deer may breed in different environmental contexts.

Most continental European red deer reach breeding condition by 18 months and have their first calf at 2 years of age, as indeed do woodland red deer in the UK.⁵⁴ By contrast, in the more extreme climatic conditions of northern Scotland, and with much slower growth rates, females may take much longer to reach breeding weight. There is some level of compensation for this slower growth, in that the critical threshold weight for ovulation is itself reduced and females do not have to reach quite such a high bodyweight before ovulating.^{55,56} Despite this, females in open habitats in northern Scotland often do not conceive until they are 3 years of age or more and thus do not calve for the first time until 4 years old.^{57–59}

Further, while in more productive environments females will calve each year following reproductive maturity, females in resource-restricted populations may breed only every alternate year (or with even lower frequency) since the energetic demands of lactation for the current year's calf prevent the mother from building sufficient body reserves by the following autumn to reach the same ovulation threshold.^{33,53,59} Similar observations are reported for reindeer where adult females weighing <53 kg (i.e. low fat reserves) in one herd had a pregnancy rate <8% whereas 80% of yearling females >46 kg (but high fat reserves) in another herd were pregnant.⁶⁰ Moreover, variation between populations in the relationship between bodyweight and fecundity, similar to that observed for red deer by Albon *et al.*^{55,56} is reported in moose, with bodyweight having to be 22% more for some populations to achieve the same probability of ovulation.^{61,62} Even within a cohort maturity was reached by resident females but not by dispersing ones, indicating a cost of dispersal.⁶³

Among polytocous species, average litter size may also vary between populations, with maternal bodyweight (affected by

habitat quality) apparently as the major factor which determines litter size. For instance, extensive fat reserves in white-tailed deer at the beginning of the rut were required to produce multiple versus single fawns, and females ovulating early had the largest fat reserves.^{64,65} For roe deer, variations in the number of fetuses carried by individual females also seem to relate strongly to maternal condition (as evidenced by bodyweight) and maternal age. Above that critical minimum weight for ovulation, number of fetuses successfully implanted increases as mother's bodyweight increases. In tandem with this there are also clear (but non-linear) effects of age. Thus the fecundity of youngest age classes is more closely affected by condition than those of mid-aged females, whose fecundity appears generally to be far less dependent on bodyweight.⁶⁶ Critical threshold weights for ovulation (and minimum weights at which a female may be expected to carry one, two or even three offspring) do vary between roe deer populations; there is no fixed threshold across the species as a whole, at which one may expect ovulation at all, or one, two, or three embryos. But this ability to adjust ovulation thresholds does not entirely compensate and we may detect very clear differences in fecundity between discrete populations of animals. For the most part, this variation appears to be related to habitat quality and competition.^{66,67}

In addition to these primary effects of environmental quality and population 'condition', however, it would appear that one additional factor has a profound effect upon fecundity: local population genetics. Roe deer again provide an ideal 'study system' within which to explore this. Roe deer became extinct throughout much of the UK in the Middle Ages; by the beginning of the 18th century they are believed to have disappeared from England and Wales and to survive in Scotland only in a few relict populations in the north and west.⁶⁸ An increase in woodlands during the 18th century led to a range expansion in Scotland, but populations in England stem largely from local reintroductions of stock translocated from Scotland or imported from continental Europe. From these introductions, roe have spread throughout much of eastern, northern and southern England during the course of this century. Thus, these populations have different origins and population genetics.^{66,69,70} Based on cranial morphology, Hewison found that 21% of the observed variation in fecundity between these populations was attributable to population genetics, once variation due to environmental factors had been accounted for.⁷¹ Populations of Germanic origin tended to have generally higher fecundity (see also⁷²). Fecundity and fetal growth rates of white-tailed deer have also been shown to depend in this way on both environmental factors and genetic variation.^{73,74}

Behaviour

Home-range behaviour, migrants versus residents, and seasonal movements

Variation in home-range size

Home-range behaviour often reflects habitat and food availability, and this is another aspect of deer biology in which we may expect to find enormous IV. Home-range sizes of female red deer in the UK for example may vary from 200 to 400 ha on Rum,⁷⁵ from 900 to 2400 ha in the eastern Highlands with one

recorded range of >8000 ha,⁷⁶ and averaged 430 ha (range 275–711 ha) in south-west England.⁷⁷ Range size clearly relates to habitat and are generally larger in more open country; in plantations in Scotland, range size related to forest structure, 400 ha in open habitats with intimate mixtures of food and cover to more than 1000 ha when ranges include more unplanted ground or older forest.^{78,79} But even within a given landscape type, where differences are not so exaggerated, there remain enormous differences in average range size. What factors may be involved in determining the size of range occupied?

Among European roe deer, summer territory sizes of adult males have traditionally been considered to be directed towards maximising mating opportunities.^{80,81} The expressed size of summer ranges of females and winter ranges of both sexes are usually considered some response to securing adequate food resources but we are aware of few studies which explicitly test this, except for the unpublished studies of Tim Johnson⁸² (see also⁸³) and work of Tufto *et al.*⁸⁴ These authors showed that home-range size of females increases in response to decreasing food supply with a suggestion that home-range size is determined by the minimum area required to sustain nutritional requirements. However, both studies found that food availability offered only a partial explanation of home-range size, indicating that even for females, range size is not determined purely in response to foraging requirements and suggest that more complex social factors must play a role – a conclusion also reached by Vincent *et al.*⁸⁵ who found strong evidence for a decrease in overall range size within a single population as population density itself increased.

Such illustrations, in exploring the possible causes for facultative variation in size of home range occupied, implicitly emphasise the degree of individual variation apparent even between individuals within a single geographic region; changes in range size of the same individuals between seasons or between years, further emphasise that such responses are the result of underlying plasticity of individual behaviour in adapting to local environmental conditions.

Sedentary and migratory behaviour

Part of the apparent geographical variation in range size is also accounted for by the fact that at higher latitudes (or higher altitudes) many species have quite markedly different summer and winter ranges – and inclusion of both areas within an overall annual range clearly makes this larger than that of an animal resident year round in a single more equable home range. Indeed, for some species and some populations, individuals may have distinct winter, summer and rutting ranges.^{59,75,86,87}

Such seasonal use of range is, as noted, most pronounced in populations of more northerly latitudes or higher altitude, where adverse weather conditions over winter may force animals to move to distinct winter ranges on lower ground. For example, in the Alps^{87,88} or in the north of Scotland, red deer show a marked distinction in seasonal ranges,³³ with males in particular moving to low ground in winter and returning to the better grazings of higher altitude in summer. Females show a less pronounced movement, and it is not unusual that males are found lower than females in winter, but higher during mid summer.⁸⁹ Most

notably, migratory patterns to summer areas of low food quality also develop, and offspring of wintering females migrating to these low quality areas also adopt this pattern, indicating that habitat quality is not the only cause for migratory behaviour (e.g. white-tailed deer;⁹⁰ sika⁹¹).

Where suitable summer and winter habitats are widely separated, such seasonal movements may involve travel over considerable distances and in the extreme, some populations may develop clear seasonal migrations between summer and winter range. While, for example, European roe deer are largely sedentary within a comparatively small home-range area, some populations, especially towards the east of Europe may show more pronounced seasonal movements. Significant movements have been noted in the Alps,⁸⁶ in Finland,⁹² in parts of Russia and in the Baltics (where deer move west to east with remarkable regularity every spring, crossing the same 15-km section of the Narva River).⁹³ In one radio-tracking study within the Belgorod region of Russia, Sokolov *et al.* recorded movements of some individuals over distances in excess of 10 km in a single day.⁹⁴ Seasonal migrations are apparent over the entire range of Siberian roe (*C. pygargus*) and some of these seasonal movements are extremely extensive with summer and winter ranges of deer in the Far East separated by as much as 400–500 km.^{95–97} Some of these movements also involve large numbers of animals migrating together, with groups of 200, 300 and even 600 roe reported by Barancheyev.⁹⁸

As one final example of this variability, we may note that while many populations of reindeer in Northern Europe or North America may remain faithful to a given home range throughout the year (merely making general movements around that wider range), populations of more northerly latitudes may make pronounced and protracted group migrations between winter and summer ranges. Forest caribou moved on average 136 km with maximal 300 km, whereas barren-ground caribou averaged 4355 km with maximal 5055 km.⁹⁹

As deer species expand their distribution, migration distances may increase over several generations by individuals returning to ancestral winter ranges,^{100–102} resulting in great variation of migration distances and directions. As a result, many deer species have simultaneously sedentary populations as well as migrants going 100–300 km (roe deer,^{93,100} red deer,^{99,103} sika,¹⁰¹ mule deer,^{99,104–106} white-tailed deer,^{100,107} moose⁹⁹).

Sedentary and migratory movement patterns represent behavioural phenomena with much individual variability, and members of migratory populations may not go to their traditional winter range when climatic conditions are mild, remaining on the summer range.^{86,93,100,104,108–112} Moreover, even within regularly migratory populations, some individuals may not migrate in every year, or migratory females may later disperse to a new area and remain there as non-migratory.^{113–115} In the same context, swapping of summer and/or winter ranges is not uncommon.¹¹⁴

This tremendous IV in movement patterns results from seasonal migration being a facultative behavioural trait which originates from sedentary populations as part of the process of colonisation of new areas.^{101,104,116} Migratory or sedentary traditions are transmitted vertically as cultural traits,^{104,117} being perpetuated within family units^{90,100,103,104,113,118–120} and even copied by others.¹⁰²

Variation in social organisation and behaviour

Sexual and social segregation

Among the more social species of deer, there is commonly some degree of segregation between the sexes, both in separation into distinct social groups (groups of mature males; groups of females and juveniles) but also, commonly, actual geographical separation of those social groups – with distinct habitat preferences, or distinct and non-overlapping home ranges. Several non-exclusive mechanisms leading to patterns of sexual segregation have been proposed. Among them the ‘predation risk hypothesis’, the ‘forage selection hypothesis’ the ‘activity budget hypothesis’, the ‘social affinity hypothesis’ and the ‘reproductive strategy’ are frequently mentioned.¹²¹

We should note, however, that sexual segregation is in fact a complex phenomenon with several components: ‘social segregation’, where males and females form distinct social groups even within the same habitat, and ‘spatial segregation’ where the two sexes may utilise different habitats or even distinct geographical areas. Social segregation would appear to be the norm among dimorphic ungulates; by contrast, spatial segregation appears to be facultative and dependent on local population and ecological conditions.^{122,123}

For our purposes here it is sufficient to note that the degree of segregation between the sexes (whether social, or spatial separation) is highly variable between populations. Thus, by way of example, a considerable degree of variation in sexual segregation is reported for red deer. While through much of their European range adult males and females segregate for most of the year except during the rut^{89,124} such rigidity of segregation is not encountered in all situations, and in some populations, segregation is far less complete; among mature Crimean red deer for example, only 18–20% of stags and 50–56% of hinds were seen in segregated parties.¹²⁵ In yet another study it was found that some males leave the rutting area and migrate to high-elevation sites for the remainder of the year, where females are absent, whereas other males leave and migrate to lower areas which contain females all year and other rutting males.¹²⁶

In fallow deer (*Dama dama*), groups of adult males and female groups, (which include males up to 20 months of age) may be separate for much of the year in most populations but degree of social and spatial segregation is equally very variable.^{127–131} In many populations, adult males remain in female areas only during the autumn breeding period, and then move to distinct geographical ranges where they may associate in ‘bachelor groups’. In the New Forest of southern England, for example, over 95% of groups encountered between December and September were either exclusively male or females with males <20 months old.¹²⁷ However, in other populations, males remain in the female areas long after the rut and in largely open landscapes, or in populations with few adult males, aggregations containing adults of both sexes remain frequent throughout the year.^{127,132}

Several other species are known to vary in segregation patterns. In white-tailed deer, some populations showed strict sexual segregation (outside the period of the rut), whereas other populations had mixed groups all year.^{133,134} Among mule deer, mixed groups of adults occurred all year, making up 13–30% of

all groups encountered.¹³⁵ In roe deer, home ranges of adult males and females overlap all year¹³⁶ and mixed-sex groups can be common all year, particularly outside of the period when some males establish breeding territories.^{136,137} In huemul (*Hippocamelus bisulcus*), adult males and females can overlap all year,^{138–140} but single-sex groups are common. Males were commonly seen alone, or as groups averaging 2.5 individuals, while female groups averaged 2.9 individuals.^{140–142} In another population, huemul sexes segregated and adult males and females associated only twice out of 104 group sightings.¹⁴³ Moose, considered a rather solitary species, may nonetheless occur in mixed groups throughout the year, along with male groups, or single male and single female groups,¹⁴⁴ with mixed-sex groups being more in populations with proportionally more females.

The degree of segregation observed in different populations would appear to relate strongly both to the habitat variability (facilitating or preventing spatial separation), population density and population sex ratio. Differences in habitat selection between male and female red deer are greatest at high population densities,¹⁴⁵ while in populations with a comparatively low proportion of adult males, there may simply be too few adult males available to form viable single-sex groups of adequate size. In his studies of fallow deer in agricultural areas, Thirgood¹²⁷ found the degree of social separation between the sexes far lower than that encountered within woodland populations. While in the open agricultural landscape, large group sizes are appropriate (see below), densities of deer overall are rather low, and due to uneven culling, densities of males in particular are extremely low. A fallow buck in such a context attempting to adopt the group size appropriate to the environmental character must of necessity join up with groups of females to form a mixed-sex herd.

Group size

For bovids, Jarman¹⁴⁶ noted that social structures seemed closely to reflect habitat structure, feeding style and predation risk, with a remarkable consistency in group sizes adopted by animals of similar ecology. Exactly the same principles may be applied among the Cervidae, and indeed – for very much the same reasons one can detect a very close fit between social group size and these same factors (e.g. see fig. 4.1 in Putman¹⁴⁷).

While recognising these differences between species, Jarman also pointed out even in his original analysis in 1974, that there was variation within species too: that the close match of social group size to ecology meant that different individuals even of the same species, living in different environments, would have the social organisation appropriate to the habitat. Jarman illustrated this by pointing out that African buffalo, when living in the open grasslands of the East African savannahs, characteristically occurred in herds of hundreds or even thousands strong; but buffalo also occur in dense woodland environments too – and here they are encountered as solitary individuals or in pairs.

Among the deer, too, IV in social organisation with ecological habit is as striking within a species as the fit of social group size to ecological circumstances between species, and responds to very much the same environmental cues. Perhaps this was first highlighted among deer by the classic work of Hirth¹³³ on the variation present in group size of white-tailed deer in relation

to habitat. Hirth noted that for this essentially social species, group sizes were larger in more open habitats and generally considerably smaller in closed habitats (see also¹⁴⁸).

Most readers are by now aware of the way in which European roe deer – traditionally regarded as solitary in habit for the greater part of the year, associating in small groups only over the winter months, have adapted to the open conditions of the agricultural prairies of middle Europe so that almost a distinct ecotype, the so-called ‘field roe’, is found living right out in the open, with no woodland or hedgerows for cover – and how in response to this, these ‘solitary animals’ are found grouped together into loose aggregations of 80 or more individuals.^{149–153} We may see how both the solitary habits usually considered characteristic of this species and this grouping tendency in open environments are each the appropriate adaptation to the closed or open character of the environment.

Fallow deer too show a striking difference in average group size when encountered in woodland or forest areas than when found in the open or in agricultural mosaics,^{127,154} and while red deer in their more typical woodland habitat are more generally encountered singly or in pairs – as a hind and calf, a solitary stag or a pair of younger beasts – the red deer of the Scottish uplands are characteristically found in large herds which may number in the hundreds. Similar variation has also been noted in many other species including moose,¹⁴⁴ axis deer (*Axis axis*),^{155,156} mule deer,^{157–159} taruca (*Hippocamelus antisensis*),¹⁶⁰ huemul,^{161,162} with the greatest range in social group size perhaps found among roe deer, hog deer (*Cervus porcinus*), red deer^{163,164} and fallow deer (e.g. review by Putman¹⁴⁷).

In general, within a given species, herd size tends to increase with habitat openness: groups are small in forest and dense thickets, and are ordinarily much larger in grassland and other open landscapes. Group size also tends to increase with population density.^{144,147,155,156,163,165}

We should note at this point that all the adaptations to environmental character described thus far are ‘immediate’ responses to the prevailing circumstances. IV in social structure of different populations of a given species does not simply imply that the populations – each characteristic of different environmental contexts – are themselves different in some way, each with a different, fixed social organisation appropriate to its context; rather each individual has the capacity to alter its social habit with environmental circumstance. Of course, where animals of the same species occur in an environment which is comparatively homogeneous and unchanging – where one particular group size is consistently appropriate – social groups may be maintained over long periods and both the size and composition of the group may seem comparatively inflexible. But where animals live in rather diverse environments with a mix of habitats available to them, the size of the social group adopted is always appropriate to the habitat occupied at the time and group sizes change as animals move from one habitat to another.

Group size is thus seen to be an emergent property, resulting from multiple fusion and fragmentation events, and which is sensitive to variations of population density.^{165,166} In the New Forest in southern England, fallow deer when encountered in woodland are most commonly seen in pairs, but may be found in groups of up to four or five individuals;¹²⁷ the same animals, when found feeding out on the forest grassland – or out in

agricultural crops beyond the forest boundary at night, are seen in aggregations commonly of a dozen or more, or even herds of up to 100 when aggregating on particularly favoured feeding grounds. Red deer in the commercial coniferous plantations of afforested uplands in Scotland are likewise seen in ones or twos within the forests themselves: but cluster into much larger groups when leaving cover to feed in plantation or clear-felled areas, or when venturing onto the open heath.¹⁶⁷ Roe deer have also been shown to fit this model,¹⁶⁸ and the speed at which the transition from forest to field behaviour has happened emphasises that the presence of larger groups in open environments is probably not a fixed phenomenon as the result of natural selection,¹⁵² but a result of adaptive behaviour or PP.

Group dynamics

Regular changes in group size of animals living in mixed environments have several implications. With groups continually forming and dissolving as animals move from closed cover out into the open – and then return again to cover, group composition, in terms of individual membership is equally fluid. In such environments animals are essentially individuals, joining and leaving larger groups or aggregations as appropriate as they move between open and closed environments.

Through regular fission-fusion, there is a tremendous turnover in the individual composition of groups and there appear to be few if any permanent associations between individual animals regularly found together.

This was particularly well exemplified in studies of sika living in mixed landscapes in southern England.¹⁶⁹ While groups of sika might be observed on the same open areas of heathland on successive occasions, the actual individual membership of that group would vary from one occasion to another with individually marked females observed in several different groups (and different association) within their home range on successive nights, occasion to occasion. Group size always remained closely linked to habitat occupied,^{169,170} but membership of those groups showed great variability. Within such loose associations, social ties seem relatively casual.

By contrast, where animals of the same species occur in an environment which is less variable – where one particular group size is consistently appropriate, social groups may be maintained over much longer periods, and real relationships developed among members of a group of relatively constant composition. Such realisation perhaps resolves the apparent contradiction between results reported for social organisation in red deer from work by Ratcliffe and others in commercial coniferous forests in Scotland¹⁶⁷ and those presented from long-term studies of red deer on the Isle of Rum.^{75,145} On Rum, clear matriarchal social groupings are found among females, with groups of relatively constant composition, within which is expressed a clear hierarchy of social dominance; the red deer of Ratcliffe's studies in coniferous forests behaved essentially as individuals, even though they might be observed in groups of equivalent size when feeding out on open ground. Such aggregations on open ground are, in such circumstances, of brief duration only; the groups break up as animals return to the denser cover of the forest – and different groups will form on the next excursion into the open (see also^{163,171}). With such constant flux and change, there is

no opportunity for long-term associations to develop between individuals or groups. By contrast, in the more open environment of Rum, larger groupings are permanently more appropriate; there is no need for continuous change in group size. With relatively little flux in group size and composition, individuals become members of a much more permanent social grouping: within which the more complex structures of dominance hierarchies and associated social behaviours may be developed.

In huemul, also, groups were found to be very fluid with members coming and going¹³⁸ and members of female–male pairs switched regularly such that no long-term pairs were observed.¹⁴² Similarly, Frid¹⁴⁰ noted that almost all huemul associated with a completely different set of individuals at some point during a 2-week period, and Smith-Flueck¹⁶¹ found that radio-collared adult males and females in the Tamango National Reserve associated with different animals throughout the day, with group composition continually changing. In the sister species taruca, individuals also frequently change groups.¹⁶⁰ Multiple fusion and fission resulting in constant and transitory mixing of individuals and group size is also documented for moose, axis and roe deer.^{144,156,168}

Variation in sexual strategy

We have demonstrated above that social tolerance, degree of sexual segregation, group size and flux, the fixity of social groups in terms of individual membership may change in relation to environmental character. And a similar variation may be observed in terms of mating strategy. Here too the conventional stereotypes for each species do not stand up to closer examination, and are found to conceal a variation of pattern just as wide as that we have described in social organisation – and just as explicable in terms of environmental character.

It is now quite widely accepted that mating systems develop as the outcome of the reproductive 'choices' of individuals, rather than as the evolved characteristics of species. Variation in mating strategies is thus expected both within and between populations as a consequence of the adaptive adjustment of individual behaviour to the ecological, social environment and individual condition.^{132,172–175} There is indeed a general consensus that male mating strategies are influenced primarily by the spatial and temporal distribution of receptive females, which is in turn affected by variations in resource distribution, predation pressure and the activities of other males.^{132,173,176–179} Additionally, the adopted strategy depends on individual circumstances like physical condition, age, experience, and 'personality' (aggressiveness^{180,181}) and may change in a given male in the course of a mating season.

Large IV in male mating systems have been reported in other ungulate species such as pronghorn,¹⁸² topi,¹⁸³ Uganda kob¹⁸⁴ and lechwe.¹⁸⁵ This same flexibility of rutting behaviour within cervids was first reported in fallow deer – and it is in fallow that it has perhaps been explored in most detail.^{132,186,187} However, now that we have begun to look more closely, it is clear that there is equal variation in the rutting behaviour of red deer, sika and even roe – and one must suspect that the same potential flexibility may become apparent in other species too, were we to look. Conventional wisdom describes for fallow deer that during

autumn, mature males move into those geographical ranges used by females and their followers, where they compete for traditional mating grounds (or rutting stands), to which they may attract females for mating.^{188–191} These traditional mating grounds are each widely separated from the next and are usually considered exclusive territories held by a single powerful male and actively defended against other males. Such rutting stands do exist but are by no means a universal phenomenon. In some populations studied, males do indeed hold such 'classic' rutting stands. In other populations, while mature bucks still hold exclusive territories – and stands are of much the same size as in the 'traditional' scenario, they are not at any distance from each other, but clustered in space, so that two or three such stands may all abut each other closely in the same area – with common boundaries (called clustered territories or 'multiple stands'). In a further variant of this basic strategy, the number of males clustered together increases, the size of territory defended becomes vanishingly small – really nothing more than standing room only: and a cluster of up to 20 or 30 males forms a communal display area in the equivalent to a blackcock lek. Such leks among fallow deer have also been recorded by others.^{132,186,192–197}

Nor are all variants of the mating strategy based on territorial ownership of land. In some populations of fallow deer, bucks do not establish rutting stands or display grounds at all – or if they do, do so only temporarily until they have attracted a group of females; then they switch completely and transfer ownership and defence to the females themselves, holding them as a classic harem^{198,199} (a mating strategy perhaps more commonly associated with red deer). In other populations, bucks compete for neither territories nor harems: males and females mix in large mixed-sex herds containing adults of both sexes; in such multi-male groupings, bucks seem to compete for simple dominance within the herd, with dominance rank conferring right of access to oestrus does. Finally, other males seem to avoid competing altogether, but become wanderers, travelling widely throughout the females' ranges, mating opportunistically with oestrus females as they come across them.¹⁵⁴

In an analysis of the main factors influencing the adoption of these different mating strategies of fallow deer, Langbein and Thirgood¹⁸⁶ divided the entire continuum of reproductive options into three main categories: non-territorial strategies (dominance within mixed-sex herds; harem-holding; wandering males), single male territorial strategies (classic rutting stands; temporary stands) and multi-male territorial strategies (multiple stands; leks). In complete accordance with the more general expectation (above) that male mating strategies are influenced primarily by the spatial and temporal distribution of receptive females, which are in turn affected by variations in resource distribution, predation pressure and the activities of other males, they concluded that the main factors determining the dominant mating strategy within any given population of fallow deer were male density, density (or absolute number) of breeding females and the amount of tree cover within the population's home range.^{132,186}

It has since become apparent that a similar range of mating strategies may be encountered in other species, too. In some parts of their range sika appear to be territorial, with mature males establishing classic rutting stands, defending them against

rivals,^{169,200} often marking trees within the stand by bole-scoring,^{201,202} whistling to attract oestrus females. In other areas, males are described as holding harems – and there have always also been occasional 'wanderers' foraging for oestrus females.^{154,170} Finally, Bartos *et al.*^{203,204} revealed that the sika of populations in the Czech Republic and Austria are known to form a lek.

In red deer, too, a species widely described as strict harem breeders,^{75,171} Carranza *et al.*^{205,206} have recently reported the existence of territorial behaviour at the rut. In their study area in south-western Spain some 58% of mature stags established territories during the rut, defended them against all other males even in the absence of females, and courted females only within the territorial boundaries. Similarly, red deer males in Patagonia were found to defend territories ranging from 0.8 to 2.5 ha in size in open feeding areas attractive to females, in the form of clustered territories whose boundaries may slightly shift occasionally between successive hours and days.²⁰⁷ Only males of larger body and antler mass held territories, remaining there the entire day, even when females were absent, often bedding down in the middle of the day. The fact that males reacted aggressively to other males regardless of the presence of females within their territories indicates that males were not defending a harem but rather their area. Subordinate satellite males remained at the transition zone bordering these areas, but occasionally would enter the territories, causing the dominant male to engage in defence activity. An individual male's strategy sometimes changed during the course of a breeding season due to a social status change or when a territorial site suddenly became vacant. If a dominant male, for instance, left the main breeding area to migrate to his winter range, a less dominant stag would replace him, often males beyond the prime breeding age. Subordinate males, unable to compete on these territories, adopted an alternate strategy by taking advantage of the female's daily movement patterns. Although some females might remain on the open feeding areas the entire day, many females returned to the brushy forested slopes of surrounding hills to bed down. Feeding activity in the late afternoon was initiated by female groups moving slowly down the hillside, accompanied by subordinate males in a pseudo harem fashion, but only as far as to the next waiting territorial male. Other subordinate males remained in a waiting zone bordering territories, waiting for transient females to pass on their way. Upon terminating their rut, some prime males migrate to areas at lower elevation full of females and other rutting males, but would no longer take active part in the rut. Observations of rather silent rutting by prime males occurring in other nearby habitat types like closed forest, tending small groups of females, indicate that several strategies are being employed simultaneously across this heterogenous landscape.²⁰⁷

While such observations primarily refer to variation within the polygynous breeding systems of the more social species, we are not even safe in relying on the stereotype for comparatively solitary territorial species such as roe. Seasonally territorial, mature roebucks establish exclusive territories each spring, holding these until the autumn; males in general hold territories somewhat larger than the home ranges occupied by females – and the accepted wisdom is that males mate with those females whose ranges lie within their territories. However, it

is rapidly becoming clear that roe deer also show remarkable flexibility in mating behaviour – and females do not necessarily mate, as traditionally supposed, with the adult male whose breeding territory overlaps with their own range. Recent studies in Sweden^{208,209} have shown that such territorial bucks often have a satellite male associated with them, that females not uncommonly mate with two males (after all, male territorial boundaries do not precisely coincide with the boundaries of female ranges: any one female's range may well fall within the territorial preserves of more than one male). Finally, studies of the movement patterns of females reveals that they do not necessarily mate with the males whose territories overlap their own anyway: 44–55% of radio-collared females leave their normal range during oestrus and make extensive excursions through the ranges of other males – perhaps actively sampling male quality – before finally mating with one of these.^{209–212} Moreover, whereas roebucks tend to be territorial in forests,^{136,213} they are not in open-field agricultural habitats.^{152,214} It is thus not surprising that Vanpé *et al.* found 14% of polytocous litters sired by more than one buck,²¹⁵ as also documented for white-tailed deer^{180,216} and sika.²¹⁷

Flexibility in mating systems also occurs in huemul. At higher densities, a system of dominance hierarchy is commonly seen, with up to six males remaining together at close range.^{139,142} At lower density mature males may be more dispersed and overlapping with small groups of mature females and offspring. Breeding is rather at random as subordinate males bred in consecutive years in areas of dominant males, females being bred by neighbouring males, and females moving into areas of other males to return after mating.^{138,139,142,218,219} Nonetheless, the repertoire of strategies used is incompletely known, because current populations exist in only a fraction of habitat types used formerly, and at very reduced densities.¹⁶²

Discussion and conclusions

It is clear from this review that many species of deer show a tremendous plasticity of response both in behaviour and physiology in adaptation to altered social and ecological circumstances, with enormous differences apparent between individuals and populations. However, the understanding of causes and consequences of PP is still in its infancy.²²⁰ It is clear that both individual elements and higher-order architectural features of the genome result in enormous complexity of phenotypic expression, involving innumerable networks among genes, gene products, epigenetic factors and gene expression.⁶ Gene expression can also be influenced by external conditions, whether during ontogenetic development of some fixed character, or through reversible modifications in some morphological or behavioural trait which respond to particular environmental circumstances in the shorter or longer term. The many epigenetic effects on multilayered genetic regulatory networks, including epigenetic inheritance, underscores that intraspecific phenotypic variation and plasticity is expected to be very profound, ranging from obvious to more cryptic variations (in terms of our perception and capacity for detection), making every individual different from another, even if they were perfect clones.

Indeed such is this flexibility that it caused Thirgood to consider the problem the other way round;¹³² that is to say – given this apparent adaptability of response, why are some species apparently so inflexible? Thirgood himself noted for example the clear contrast in mating system flexibility between pronghorns and the largely sympatric bison: asking why, while pronghorn seem to be so flexible in their mating system,^{182,221} bison have never been observed to defend harems or territories and simply consort with one oestrus female at a time – despite huge variations in density, sex ratio and age structure that exists in bison populations. Currently the most powerful prediction on the factors promoting evolution of plasticity of response is that plasticity increases with environmental variability.^{222,223} Such variability is thus more the rule than the exception in heterogeneous terrestrial systems.

Significantly: the social and sexual behaviour of any one species of deer changes markedly with environmental context and character. This has, among other things, profound implications for the manager: if a species such as roe is likely to be territorial only under some circumstances, while in other situations territoriality is suppressed or not apparent, then the whole approach to managing the roe population will be affected in the two distinct sets of conditions. Likewise, while in the majority of circumstances rigid social segregation may be observed between the sexes of fallow deer with bucks forming quite separate groupings distinct from those of females and their followers, if under other conditions – in more open habitat types or areas of low buck density – no clear segregation into separate sex groups occurs, or if in some environmental types group sizes are consistently larger or smaller than those formed in other situations. These sorts of considerations may well affect fundamental management decisions. For a start, estimates of effective population size in a given area will be affected by whether the animals observed are territorial or non-territorial, by typical group size or by distance travelled by a given social group; errors of assumption here may lead to gross misjudgement of the actual density of deer within the management area.

Further, most managers seek to plan their cull in such a way as to maintain the natural social structure of the population targeted (not least because disruption of the natural sex- or age structure of the population, or distortion of the social structure may in itself lead to an increase in damage sustained by agricultural or forest crops through an increase in aggression). But if natural social structure itself changes with local conditions, then the manager cannot simply aim for the 'typical' structure reported in the standard texts: for this may itself be entirely inappropriate in his particular environmental conditions and not represent the social structure that would naturally be adopted in his area at all. That is why it is so important to understand what causes the variation, what factors in the environment do affect the social structure expressed. If we recognise that group sizes are generally larger in more open habitats, that sexual segregation is less marked in areas of low buck density, territoriality of roe less pronounced at low density, or in open landscapes, rutting behaviour affected by both density of females and density of mature bucks, and if we know which direction the behaviour changes in response to variations in these environmental cues, then from a knowledge of local environmental conditions we can hope to predict what should

be 'normal' or at least expected in any given area or for any given population – and aim our management towards that endpoint rather than some textbook norm.

IV has also important consequences for conservation of threatened cervids. Commonly, a certain phenotype in a given population is equated to individual 'quality', for instance, by using the proxy of numbers of offspring produced. However, the continued existence of polymorphism suggests that no single morph is the most fit in all situations, and 'losers' in a particular study population likely become 'quality' winners when environmental conditions change.²²⁴ Focusing on a mean 'optimal' phenotype diverts attention away from variation around the mean, even discarding 'outliers' as noise, to better fit the chosen model. For spatio-temporal heterogeneous environments, maintenance of IV also is an essential ingredient for the continuous existence of a species.

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