

Are biochemical-genetic variation and mating systems related in large mammals?

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In some families of large mammals (*Cervidae*, *Bovidae*, *Canidae*), we examined relationships between the various mating systems adopted and biochemical-genetic variation measured in terms of the mean proportion of polymorphic loci (P), mean heterozygosity (H) and derived coefficients, such as the ratio $Pt:P$ and F_{IS} . Our hypothesis was that genetic variability decreases as the degree of polygyny of the mating system adopted increases. Most of the data were in accordance with this prediction, but also some ambiguous results could be observed. Methodological and practical difficulties connected with our synoptical approach, such as the lack of comparability among most electrophoretic studies and the general scarcity of quantitative behavioural data are critically discussed.

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Introduction

In order to assess the relative role of factors influencing the amount and distribution of allozyme polymorphism within and among populations and species, indices of biochemical-genetic variation have been related to various ecological and phylogenetic parameters. In a first attempt to explain differences in the extent of heterozygosity among species by other than stochastic factors, a distinction between small and large animals was established. According to the so called "environmental grain hypothesis" (Selander and Kaufman 1973), small animals were expected to exhibit more genetic variation than large ones, due to their experience of the environment as a set of distinct alternatives ("coarse grained") rather than as a homogeneous mixture of recurrent elements ("fine grained"). This dichotomy was followed by further subdivision of taxa according to strategy of adaptation, nutrition, and geographical distribution. Some examples in mammals are: small vs large species (Wooten and Smith 1985), fossorial vs terrestrial

species, specialists vs generalists (Nevo 1983, Nevo *et al.* 1984), carnivores vs herbivores (Baccus *et al.* 1983), inhabitants of the northern vs southern hemisphere (Sage and Wolff 1986), *r*-strategists vs *K*-strategists (Hartl and Reimoser 1988), phylogenetically basal vs derived species (Hartl *et al.* 1990a, c).

In the present study we examined the relationship between allozyme variation and mating systems, which has comparatively poorly been considered in previous studies (see e.g. Chesser 1983, Ralls *et al.* 1986). Moreover, as in a monofactorial approach the consistency of a pattern may be blurred by biological, ecological, and historical peculiarities of phylogenetically very distinct taxa, we tried to employ a stepwise approach, i.e. to start with comparisons from the lowest possible taxonomic level and proceed to the level of families and orders. In particular, with data from ungulates we attempted to test the hypothesis that the degree of polygyny of a mating system is negatively correlated with genetic variability within populations and positively correlated with differentiation among populations. Using data on canids and ungulates we tested the hypothesis that monogamous species harbour more genetic variability than polygamous ones.

Material and methods

Data on the proportion of polymorphic loci (P) and on overall heterozygosity (H) in cervids (Table 1), bovids (Table 2), and canids (Table 3) were extracted from the literature and averaged over all populations investigated in the respective surveys. Whenever this was possible, expected (H_e) rather than observed (H_o) heterozygosity was used, because the former could be calculated from allele frequencies even if no explicit data on this parameter was given (although the latter would perhaps have been more meaningful for our purpose). Moreover, H_e is less susceptible to sampling bias when only small numbers of individuals were studied. As an additional index of genetic variability, the 'total proportion of loci polymorphic in a species' (P_t) was calculated from the data by summing up all polymorphisms detected in a species rather than averaging them over populations. Since P , \bar{P} and P_t are identical in that case, the P_t index was not considered for further analysis when data from only one population were available. In order to quantify the distribution of polymorphisms present in a species among the single populations examined, we calculated the ratio $P_t:P$. This ratio is expected to be high, if P in the various populations is the result of different sets of polymorphic loci. On the contrary, it should be low, if almost all populations share the same polymorphisms. In order to take into account some loss of heterozygosity within populations due to non-random mating, we also considered the coefficient of inbreeding, F_{IS} (see Hartl 1988). Whenever this was possible, only data based on more than twenty loci and more than twenty individuals were used.

Data on mating systems were extracted from the literature (see Tables) and critically examined. In particular, mating systems were ranked in four classes with respect to the presumed degree of polygyny, i.e. to the standardized variance in male reproductive success (I_m ; Arnold and Wade 1984a, b), according to Clutton-Brock (1988), Clutton-Brock *et al.* (1988), Apollonio (1992). Since to date in ungulates such data is available only on a few species, estimation of the degree of polygyny was based mainly on the size of the breeding party (Clutton-Brock 1987). Other biological variables, such as male territory size, female group size, home range and habitat selection in the two sexes were taken into account (see references in Tables).

The four different types of mating systems are defined as follows:

Lek-breeding (L) – Each of several males defends one territory without any resource apart from the male itself. All those territories are clumped in a cluster that is visited by females for copulating. Females are free to move among different territories whereas the spatial positions of males are fixed.

Harem-breeding (H) – Males defend groups of females and move with them. They do not have a spatial reference for dominance but just defend the females while waiting for them to come into estrus.

Territorial (T) – Males defend spatially separated territories containing a certain amount of resources for females. The quality and quantity of these resources have a strong influence on male mating success.

Roving (R): Males follow single females testing whether they are close to estrus. If so, males try to defend the respective female until copulation is possible. Then they look for other females.

As in various cervids data from different studies were available for the same species, on our purpose we selected the best and the worst combination of H , \bar{P} , $Pt:\bar{P}$, and F_{IS} with respect to our hypotheses. Given the characteristics of our data we employed non-parametric statistics (Spearman rank correlation coefficient).

Results

When examined for a relationship between H or \bar{P} and the degree of polygyny in cervids, there was a significant negative correlation in both cases ($r_s = -0.65$, $p = 0.016$ and $r_s = -0.74$, $p = 0.005$, respectively), but only when the optimal combination of data was chosen. On the contrary, the choice of the worst combination of data revealed no significant results even though there was still a negative relationship in both cases (Table 1).

Due to the scarcity of data, in the bovids it was possible to use only one combination. H proved to be negatively correlated with the degree of polygyny ($r_s = -0.54$, $p = 0.052$) whereas \bar{P} showed only a statistically insignificant trend ($r_s = -0.39$, $p = 0.13$) in the same direction.

The ratio $Pt:\bar{P}$, which could be examined only in cervids (in bovids too many data were based on only one population), was significantly positively correlated with the degree of polygyny of the mating system typically adopted by the species ($r_s = 0.73$, $p = 0.02$), but again only when the optimal combination of data was chosen.

The inbreeding coefficient (F_{IS}) was available in a sufficient number of cases only in cervids. In this family, it was positively correlated with the degree of polygyny when the best combination of values was chosen ($r_s = 0.97$, $p = 0.05$), but it was completely uncorrelated in the case of the worst combination.

In bovids only very few F_{IS} -values were available and they did not reveal any trend.

We tried to check the influence of the adoption of a monogamous (M) vs a polygynous (PO) mating system within families belonging to different mammalian orders by comparing \bar{P} - and H -values for three species of canids (see Table 3) with the corresponding values for cervids and bovids. They proved to be not significantly different in both cases (Mann-Whitney U -test). Moreover, the few inbreeding coefficients available fell in the distribution of ungulates, except for coyotes, whose F_{IS} -value deviated remarkably from our expectations.

Table 1. Genetic variation and mating systems in the *Cervidae*. nI - number of individuals, nPo - number of populations, nL - number of loci studied. Pt - total proportion of polymorphic loci, \bar{P} - mean proportion of polymorphic loci, H - mean expected average heterozygosity, F_{IS} - inbreeding coefficient, MS - mating system. * Source of genetic data: 1 - Randi and Apollonio (1988), 2 - Hartl *et al.* (1993), 3 - Hartl *et al.* (1990b), 4 - Gyllenstein *et al.* (1983), 5 - Dratch and Gyllenstein (1985), 6 - Røed (1986), 7 - Ryman *et al.* (1980), 8 - Ryman *et al.* (1980), 9 - Baccus *et al.* (1983), 10 - Reuterwall (1980), 11 - Sheffield *et al.* (1985), 12 - Smith *et al.* (1986), 13 - Gavin and May (1988), 14 - Hartl *et al.* (1991), 15 - Lorenzini *et al.* (1993). Data on mating system: A - Apollonio *et al.* (1989), B - Clutton-Brock *et al.* (1982), C - Struhsaker (1967), D - Espmark (1964), Lent (1965), E - Geist (1963), F - Hawkins and Klimstra (1970), G - Wallmo (1981), H - Thomas (1975), Macnamara and Eldridge (1987), I - Kurt (1991).

| Species | nI | nPo | nL | Pt | \bar{P} | H | F_{IS} | MS | Source* |
|--|------|-------|------|-------|-----------|-------|----------|------|---------|
| Fallow deer <i>Dama dama</i> | 180 | 1 | 51 | 0.002 | 0.002 | 0.006 | 0.159 | L | 1 A |
| Red deer <i>Cervus elaphus</i> (various European subspecies) | 411 | 7 | 43 | 0.209 | 0.179 | 0.059 | 0.051 | H | 2 B |
| | 277 | 10 | 34 | 0.206 | 0.115 | 0.035 | -0.086 | | 3 |
| | 594 | 22 | 34 | 0.206 | 0.077 | 0.022 | - | | 4 |
| | 243 | 11 | 28 | 0.179 | 0.123 | 0.023 | - | H | 5 C |
| Wapiti <i>Cervus elaphus canadensis</i> | - | 5 | 35 | 0.257 | 0.160 | 0.049 | - | H | 6 D |
| Reindeer <i>Rangifer tarandus</i> | 239 | 3 | 35 | 0.286 | 0.190 | 0.039 | - | | 7 |
| Moose <i>Alces alces</i> | 734 | 18 | 23 | 0.217 | 0.094 | 0.020 | -0.004 | R | 8 E |
| | 165 | - | 19 | 0.158 | 0.158 | 0.017 | - | | 9 |
| <i>A. a. americana</i> | 47 | 1 | 22 | 0.180 | 0.180 | 0.040 | - | R | 10 E |
| White-tailed deer <i>Odocoileus virginianus</i> | 321 | 4 | 29 | 0.172 | 0.161 | 0.062 | -0.011 | R | 11 F |
| | 1549 | - | 19 | 0.421 | 0.368 | 0.078 | - | | 12 |
| | 141 | 6 | 35 | 0.200 | 0.110 | 0.036 | - | | 13 |
| Black-tailed deer <i>Odocoileus hemionus columbianus</i> | 115 | 3 | 35 | 0.230 | 0.180 | 0.043 | - | R | 13 G |
| | 106 | 4 | 35 | 0.200 | 0.160 | 0.036 | - | R | 13 G |
| <i>Odocoileus hemionus hemionus</i> | 52 | 1 | 19 | 0.579 | 0.579 | 0.070 | - | R | 12 H |
| Red brocket <i>Mazama americana</i> | 399 | 20 | 40 | 0.300 | 0.158 | 0.049 | -0.061 | TR | 14 I |
| Roe deer <i>Capreolus capreolus</i> | 227 | 9 | 40 | 0.200 | 0.178 | 0.059 | 0.034 | | 2 |
| | 183 | 4 | 32 | 0.250 | 0.156 | 0.049 | 0.035 | | 15 |

Table 2. Genetic variation and mating systems in the *Bovidae*. nI - number of individuals, nPo - number of populations, nL - number of loci studied. Pt - total proportion of polymorphic loci, P - mean proportion of polymorphic loci, H - mean expected average heterozygosity, Fis - inbreeding coefficient, MS - mating system. * Source of genetic data: 1 - Georgiadis *et al.* (1990), 2 - Bigalke *et al.* (1993), 3 - Hartl (1986), 4 - Sage and Wolff (1986), 5 - Nascetti *et al.* (1987), 6 - Stüwe *et al.* (1992). Data on mating system: A - Leuthold (1977), B - Krämer (1969), C - Geist (1971), D - Aeschbacher (1975), E - inferred from Schaller (1977).

| Species | nI | nPo | nL | Pt | \bar{P} | H | Fis | MS | Source* |
|---|------|-------|------|-------|-----------|-------|--------|------|---------|
| <i>Topi Damaliscus korrigum</i> | 19 | - | 40 | 0.109 | 0.109 | 0.010 | - | L | 1 A |
| <i>Blesbok Damaliscus dorcas phillipsi</i> | 27 | 1 | 45 | 0.022 | 0.022 | 0.011 | -0.091 | T | 2 A |
| <i>Blue wildebeest Connochaetes taurinus</i> | 61 | - | 40 | 0.043 | 0.043 | 0.012 | - | TM | 1 A |
| <i>Hartebeest Alcelaphus bucephalus</i> | 17 | - | 40 | 0.087 | 0.087 | 0.019 | - | T | 1 A |
| <i>Thomson gazella Gazella thomsoni</i> | 33 | - | 40 | 0.196 | 0.196 | 0.055 | - | T | 1 A |
| <i>Springbok Antidorcas marsupialis marsupialis</i> | 24 | 1 | 46 | 0.174 | 0.174 | 0.060 | 0.150 | T | 2 A |
| <i>Alpine chamois Rupicapra rupicapra</i> | 136 | 5 | 38 | 0.240 | 0.127 | 0.031 | 0.041 | R | 3 B |
| <i>Dall sheep Ovis dalli</i> | 18 | 9 | 27 | 0.037 | 0.025 | 0.015 | - | R | 4 C |
| <i>Alpine ibex Capra ibex</i> | 36 | 1 | 33 | 0.151 | 0.151 | 0.040 | - | R | 5 D |
| <i>Nubian ibex Capra ibex nubiana</i> | 39 | 1 | 15 | 0.200 | 0.200 | 0.087 | -0.474 | R | 6 E |

Table 3. Genetic variation and mating systems in the *Canidae*. nI - number of individuals, nPo - number of populations, nL - number of loci studied. Pt - total proportion of polymorphic loci, P - mean proportion of polymorphic loci, H - mean expected average heterozygosity, Fis - inbreeding coefficient, MS - mating system. * Source of genetic data: 1 - Fusco *et al.* (1991), 2 - Kennedy *et al.* (1991), 3 - Fisher *et al.* (1976), 4 - Hamilton and Kennedy (1986), 5 - Simonsen (1982). Data on mating system: A - Sheldon (1992).

| Species | nI | nPo | nL | Pt | \bar{P} | H | Fis | MS | Source* |
|------------------------------|------|-------|------|-------|-----------|-------|--------|------|---------|
| <i>Wolf Canis lupus</i> | 27 | 1 | 39 | 0.077 | 0.077 | 0.020 | -0.200 | M | 1 A |
| | 188 | 9 | 37 | 0.135 | 0.084 | 0.028 | -0.003 | | 2 |
| | 12 | - | 53 | 0.113 | 0.113 | 0.038 | - | | 3 |
| <i>Coyote Canis latrans</i> | 6 | - | 53 | 0.132 | 0.132 | 0.050 | - | M | 3 A |
| | 239 | 20 | 20 | 0.550 | 0.140 | 0.020 | 0.870 | | 4 |
| <i>Red fox Vulpes vulpes</i> | 281 | - | 21 | 0.0 | 0.0 | 0.0 | - | M/PO | 5 A |

Discussion

Empirical studies provided inconsistent evidence for most of the monocausal hypotheses attempting to explain enzyme variation by the biological and ecological characteristics of the animals (e.g. Schnell and Selander 1981, Baccus *et al.* 1983, Wooten and Smith 1985, Hartl and Reimoser 1988, Hartl *et al.* 1988). Also in our case, even though most of the data seem to corroborate the predicted influence of mating systems on genetic variability, we were not free of ambiguous results. The causes of discrepancies could be found in genetic data, in behavioural data, or even in both.

In genetic data, the main sources of bias are unequal numbers of individuals, populations, and loci sampled (see Hartl and Pucek, in press) as well as differences in the composition of genetic loci (see Zouros 1979, Hartl *et al.* 1988, 1990c) and in the range of sampling sites (see Hartl *et al.* 1993) investigated. Regarding the number and composition of isozyme loci, there are objections as to the accurate assessment of overall genetic variation due to various arguments (see Mitton and Grant 1984). Regarding the array of sampling areas, a confrontation of five alpine roe deer populations, separated by mountain barriers (Hartl *et al.* 1991, "western group", Switzerland, western Austria) with five Bulgarian populations, living more or less in a continuum ranging from lowland agricultural areas over transitional habitats to montaneous forests (Hartl *et al.* 1993), may serve as an example. In spite of similar geographic distances among populations, the Bulgarian roe deer did not show any differentiation in terms of the ratio $Pt:P$, whereas in the Alps Pt was 50 per cent higher than P . As a further source of bias, F_{IS} -values may be affected by factors other than inbreeding, such as a Wahlund effect due to inappropriate pooling of individuals in order to increase sample sizes of localities (see Kurt *et al.* 1993).

In behavioural data, the lack of a complete set of comparable data on Im in ungulate species required some extrapolation from the scarce sound information available (Clutton-Brock 1987, Apollonio 1992). Moreover, a certain degree of behavioural plasticity is known to exist in almost all species relevant for our analysis and this could have generated interpopulational differences which were not accounted for. For example, effects of mating systems on levels of genetic variation may be compensated to a certain extent by patterns of dispersal (Chesser *et al.* 1993). Although the species considered in the present study are generally similar in showing male dispersal and female philopatry, these phenomena have not been subjected to a detailed quantitative evaluation in many cases. Thus, in spite of our attempts to minimize all these hypotheses, due to the limited number of thoroughly comparable data available, there were some serious restrictions as to the rigidity of the selection criteria employed. Yet the possibility to choose closely related species avoided too large differences among them in important genetic (homology of loci, preservation of linkage groups, see O'Brien *et al.* 1980, Hartl *et al.* 1990c) and biological parameters (e.g. number of generations per year, number of offspring per year).

Our basic idea in considering relationships between mating systems and genetic variation in ungulates was that genetic variability of a population is reduced with a decreasing number of males participating in reproduction and an increasing Im . This was generally supported by our data on cervids and bovids. However, it is necessary to be aware of the importance of the choice of data. For instance, although essentially the same trend was detected using both the best and the worst combination of data with regard to our hypothesis, it proved to be statistically significant only in the first case. The situation was different with respect to F_{IS} , which fitted extremely well in the optimal case, but did not reveal any trend in the worst. The use of this statistics was limited by the absence of proper data in most of the papers examined. Here we would like to emphasize the necessity of a standardized presentation of electrophoretic results in order to make the data comparable and, thus, suitable for various synoptic analyses. Moreover, F_{IS} -values are influenced not only by the mating system but, for example, also by the geographic structure of sampling areas and by sex-biased dispersal (cf Ralls *et al.* 1986).

A further point to be considered is that also species having experienced bottlenecks in historical times appear in the data sets. Although the data have to be treated with care, in our opinion there is no a priori reason to exclude such species from the analysis: for example, the low level of genetic variability detected in the fallow deer need not necessarily be brought about by genetic drift due to bottlenecking (Randi and Apollonio 1988) but may as well be a consequence of their mating system. In such cases, Hardy-Weinberg equilibrium may be used as an indicator not only for genetic imbalance due to demographic perturbations, but also for extremely polygynous mating systems. A significant excess of homozygous genotypes was, for example, obtained in a fallow deer enclosure, where only two males were available as mates for about one hundred females (Hartl *et al.* 1986). It is noteworthy that almost the same result was obtained in a natural free-ranging population of more than 1000 individuals with a sex ratio of 1:1.7, but with lek as mating system, i.e. the most extreme polygynous mating system known in ungulates (Randi and Apollonio 1988).

The comparisons of \bar{P} and H values of a monogamous and two polygamous families were done in order to test the hypothesis that a higher proportion of the male population participating in reproduction should be reflected by a lower Im , a larger N_e , and, thus, by a higher extent of genetic variability in monogamous than in polygynous species. This assumption was not supported by our data, possibly because, as argued by some authors (Clutton-Brock 1987, 1988), Im is not necessarily higher in polygynous than in monogamous species. Moreover, it could be possible that in some monogamous canids like the wolf the existence of a social rank among males and females, where only the dominant individuals of both sexes do reproduce, contributed to keep N_e small. As a possible methodological reason, the scarcity of allozyme population genetic data available in canids, both with respect to the number of species (populations, individuals) and the number of loci investigated must be taken into account.

The influence of the degree of polygyny on interpopulation genetic differentiation was partly supported by our data. The effect of mating systems characterized by intense intermale competition and, thus, presumably by a high *Im* on the development of quite distinct physical and behavioural characteristics in subpopulations was first noted by Buechner and Roth (1974) in a lekking antelope, the Uganda kob. It seems therefore possible that the presence of some very successful males in various populations of the same species may contribute considerably to differentiate these populations from one another.

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