

PROBABLE EXAPTATIONS WITHIN THE « DISTRIBUTED » HERD

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In a recent review, Parker and Maynard Smith (1990) remind us of the aims and methods of evolutionary biology and behavioural ecology. They insist, in particular, on the fact that the evolutionary models do not aim at proving the omnipotence of natural selection, but rather that they « help us to test our insight into the biological constraints that influence the outcome of evolution ». In this perspective, the concepts of « optimality » and of « Evolutionarily Stable Strategy », which make up the framework of the approach, appear to be reliable instruments which allow specific cases of evolution and adaptation to be dealt with, and especially biological constraints susceptible of being involved in evolutionary processes to be pointed out.

It is clear, however, that the optimization models and the theory of evolutionary games are not our only means of analysing the « constraints » and the proximate processes involved in biological systems. Developmental biology (see, for example, Saunders, 1984) and the systemic approaches dealing with the operation of animal groupings (Deneubourg and Goss, 1989), analyse the proximate mechanisms underlying the biological phenomena, most often without making direct reference to the action of natural selection.

In the present paper we would like to illustrate a proposition that is symmetrical in regard to that of Parker and Maynard Smith (1990), *i.e.* that taking into account the proximate processes underlying the biological phenomena can, in turn, shed light on the evolutionary processes and modify the way in which we consider evolution. Our approach will therefore be very close to that of Gould and Lewontin (1979) who think that the knowledge of proximate mechanisms may help us to improve our insight into the evolutionary processes whether specific or general. The examples used here will be taken from the field of social-ethology of wild even-toed ungulates (Artiodactyla), where the observed phenomena are usually dealt with in the way indicated by Parker and Maynard Smith (see for examples Hamilton, 1971 ; Vine, 1971 ; Jarman, 1974 ; Wilson, 1975 ; Wittenberger, 1980 ; Eisenberg, 1981 ; Clutton-Brock *et al.*, 1982).

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I. — MECHANISMS UNDERLYING SOME « SOCIAL » EMERGENCES IN POPULATIONS OF WILD EVEN-TOED UNGULATES

In wild even-toed ungulates the spatial distribution of food resources can of course affect the size and composition of their groupings through the attraction that zones where food is particularly abundant exert on the individuals (Crook *et al.*, 1986 ; Putman, 1988). Nevertheless, *the formation of groups remains essentially based on the attraction (often differing according to age and sex classes) that individuals exert on one another* (Focardi and Toso, 1987). In this light, the structural characteristics (size, composition, etc...) and the functioning of the groups appear to be *emergences* resulting from local interactions between the individuals of a population (Deneubourg and Goss, 1989).

This point is well illustrated by the simple following example concerning the Pyrenean chamois *Rupicapra pyrenaica* (Fig. 1) : the strong link (i.e. the very strong inter-attraction) between mother and young just after the birth of the kids is at the origin of the preponderance of even-sized groups and therefore brings out a particular group-size distribution. This particular distribution is a property all the more clearly emergent as, in the population, there are no individuals whose behaviour could be defined by an algorithm such as « associate preferentially with groups of such and such a size ». In more general terms, there are not, in the elements of the system, any interaction algorithms corresponding *directly* to the emergence. This is a very frequent property of « distributed » systems *i.e.* systems composed of distinct interacting elements (Varela, 1989 ; Deneubourg and Goss, 1989 ; Théraulaz *et al.*, 1991).

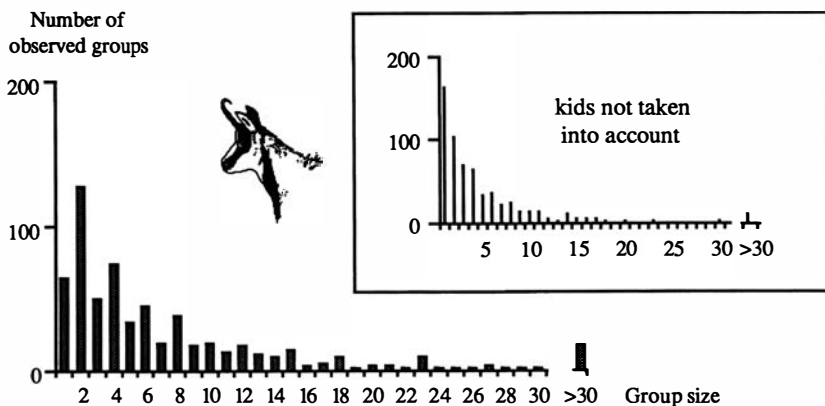


Figure 1. — Frequency of observation of Pyrenean chamois (*Rupicapra pyrenaica*) groups according to their size in summer (June to September) in Orlu National Reserve (Ariège, France). Preponderance of even-sized groups disappears when kids are not taken into account (from Gerard & Richard-Hansen, 1992).

The « social » emergence mentioned above probably has no particular significance from an evolutionary point of view and would doubtless be conside-

red as an « epiphenomenon » by evolutionists. It is indeed difficult to see what advantage there is to be gained from the preponderance of even-sized groups.

So, let us now consider three « social » emergences occurring in groupings of even-toed ungulates, which are often considered as having definite consequences on the fitness of the individuals involved.

1. *Mean group size and probability of perceiving congeners*

Groups of wild even-toed ungulates are most often dynamic and unstable in that they frequently split up or join together, individuals being constantly coming and going (Schaal, 1982 ; Clutton-Brock *et al.*, 1982 ; Lott and Minta, 1983 ; Fichter, 1987 ; Hillman, 1987 ; Barrette, 1991). So, the formation of groups necessarily depends on the possibilities for the animals to perceive one another, and it can therefore be easily assumed that the mean group size is related to the probability of any individual perceiving another.

This process could well be one of the main mechanisms explaining why groups of even-toed ungulates generally increase in size with the openness of the habitat, even when food resources seem to be evenly distributed (Schaal, 1982 ; LaGory, 1986 ; Cibien *et al.*, 1989 ; Barrette, 1991). Let us recall that a positive correlation between the mean group size and the openness of the habitat has been observed on a set of phylogenetically close species (African Bovinae : Jarman, 1974) but also within various species when they occupy different habitats (Bovinae : Leuthold, 1970 ; Walther, 1972 ; Evans, 1979 ; Caprinae : Alados, 1985 ; Cervidae : Hirth, 1977 ; Schaal, 1982 ; Maublanc *et al.*, 1985, 1991 ; Putman, 1988 ; Barrette, 1991 ; Suidae : Gerard *et al.*, 1991).

The same mechanism could, in addition, explain that an increase in the population density, which also increases the chances of one individual perceiving others, also generally results in an increase in mean herd size (Caughley, 1964 ; Spinage, 1969 ; Brezinski, 1982 ; Wirtz and Lörcher, 1983 ; Barrette, 1991 ; Vincent and Bideau, 1992).

2. *Ontogeny and positioning of the young in the group*

Apart from the fact that they are generally unstable, groups of wild even-toed ungulates are also often composed of animals of different age and sex. As a first approximation, it can be considered that each class of individuals presents its own behavioural profile and interactive competence. The young, in particular, present behavioural profiles that are richer and more « exuberant » than those of adults, as well as a greater tendency to initiate interactions or to respond to them (Richard-Hansen, 1992, in the Pyrenean chamois). When in the same group, this trait leads them to preferentially interact amongst themselves (collective « play ») much more frequently than would adults (Carranza and Arias de Reyna, 1987, in the Red deer ; Gomendio, 1988, in *Gazella cuvieri*). In this way, the distances between young are, on average, closer than between adults in groups containing both age classes (Richard and Pépin, 1990a, in the Pyrenean chamois).

For quite simple geometrical reasons (Fig. 2), the short distances between young lead them to occupy a statistically more central position in the herd (Hall, 1983 ; Arnold and Grassia, 1985 ; Alados and Escos, 1998 ; Richard and Pépin, 1990b) : the sub-group of adults, occupying a larger area, can often surround the

sub-group of young individuals whereas the opposite is generally not true (Fig. 2A). Moreover, if the two sub-groups happen to separate, the surface areas that they occupy lead to the young taking up less of the periphery of the whole group than the adults (Fig. 2B). In any case, this situation seldom occurs owing to the proximity of the young and their mothers (Carranza and Arias de Reyna, 1987).

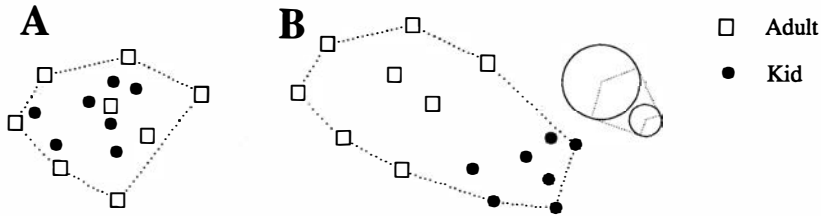


Figure 2. — A shorter mean distance between young animals than between adults leads to the young occupying more central positions in the group.
 Note : the position of the adults amongst themselves is the same in the two theoretical examples given, as is that of the young. The difference between cases A and B is the relative positions between the sub-group of young as compared to that of the adults. The dotted line joins the individuals at the periphery of each group.

3. *Ontogeny and emergence of « leader » status*

When individuals attract each other, any animal presenting particular motor abilities or moving with less heed of the behaviour of its congeners than the other individuals will be followed by the rest of the group (possibly even against its « will ») and will therefore play the role of *leader* (Geist, 1971 ; Arnold, 1977 ; Carranza and Arias de Reyna, 1987). The fact that older animals are behaviourally more stereotyped, and at the same time more individualistic than the young, could explain why they generally lead the group even though, apparently quite paradoxically, they are also more often solitary than younger animals (Pfeffer, 1967, in the Mouflon *Ovis orientalis* ; Geist, 1971, in the Bighorn *Ovis canadensis*).

Note that, in these conditions, the age and sex composition of the population will very probably influence the mean group size. A large proportion of older animals will obviously increase the proportion of solitary animals. Moreover, each old animal will represent, because of its more individualistic behaviour, a potential leader able to eventually split large groups into smaller units.

II. — ADAPTATIONS OR EXAPTATIONS ?

It is generally accepted that even-toed ungulates were originally forest animals which were not particularly sociable, and that they later became more gregarious as they colonized open spaces (Estes, 1974 ; Eisenberg, 1981 ; Putman, 1988 ; Janis, 1991). As already mentioned, the three « social » emergences just discussed are generally considered as having a positive influence, in open habitat or in animals living in groups, on the (*inclusive*) *fitness* of the individuals

concerned. Indeed, the formation of large groups in open country must help in spotting predators at a distance (Vine, 1971 ; Pulliam, 1973 ; Jarman, 1974 ; Treisman, 1975 ; Clutton-Brock *et al.*, 1982). The central position of the young within the groups would also tend to protect the offspring from being preyed upon (DeVore, 1965 ; Carranza and Arias de Reyna, 1987 ; Alados and Escos, 1988). Finally, following an older animal would give the young the opportunity of benefitting from its experience in the distribution in space and time of food supplies or shelters against predators (Festa-Bianchet, 1986).

Does this, however, mean that the *proximate mechanisms* underlying these emergences were established by natural selection over the generations *because of the functions that they presently fulfil* in even-toed ungulates living in open habitats? The answer is not straightforward since a characteristic can have a certain function (*i.e.* an effect on the fitness of the individual bearing that characteristic) but could have appeared during evolution for reasons other than that current function. This is the type of characteristic that Gould and Vrba (1982) term « *exaptations* » as opposed to « *adaptations* » which spread through populations and species because of their function.

In the cases considered here, a *purely* adaptive process seems in fact difficult to uphold because the proximate mechanisms underlying the « social » emergences mentioned are most certainly not those of even-toed ungulates living in open habitats.

1. *General inter-attraction between animals*

Although forest-dwelling and apparently « not very sociable », the individuals belonging to species at present considered as « primitive » in the two main families of even-toed ungulates (like the Serow *Capricornis sumatraensis* for Bovidae and the Water deer *Hydropotes inermis* for Cervidae) still present a certain attraction for their conspecifics (Schaller, 1977 ; Bützler, 1990). Whatever its « origin », *this inter-attraction theoretically enables the individuals of these species to group together into herds if their surroundings were suitable.*

The European roe deer *Capreolus capreolus*, which is generally considered to be a forest-dweller not very or not at all gregarious, seems to provide a good demonstration of the last assertion. Indeed, roe deer groups reach very rarely 8 animals and include scarcely more than 2 individuals on average in forest habitats (Bideau *et al.*, 1983). Basing their conclusions on morphological, anatomical and physiological considerations, some authors like Eisenberg (1981) and Stüwe and Hendrichs (1984) moreover consider this small deer to have evolved in an *exclusively* wooded environment. Nevertheless, since the mechanisation of agriculture led to the creation of larger fields, and since the setting up of hunting quotas, *i.e.* for a few tens of years, roe deer have started colonizing open cereal plains (Kaluzinski, 1974 ; Maublanc *et al.*, 1991). And *from the start*, groups were composed of 6 to 10 individuals on average, reaching 30 to 70 animals on occasions (Reichholf, 1980 ; Brezinski, 1982 ; Stüwe and Hendrichs, 1984 ; Maublanc *et al.*, 1985 ; Cibien *et al.*, 1989).

2. *Enhanced inter-attraction between young*

A *purely* adaptive scenario is especially hard to accept in the case of the enhanced inter-attraction between young giving rise to a central position of kids

within the group. As mentioned above, the strong attraction that the young exert on one another seems to arise from the fact that they present a behavioural and interactive profile which is simply more exuberant than that of the adults. The capacity for « play » is not a characteristic limited to young gregarious ungulates, but one that seems to be general among young mammals and even among young endothermic vertebrates (Fagen, 1982). The exuberance of the behavioural and interactive profile of the young could be considered as a continuation of pre-natal autonomous motility (Bekoff and Byers, 1985) and in general it seems to be closely related to the development of the nervous system. As a matter of fact, the appearance of « play » and nerve cell multiplication were found to be correlated at the end of each winter in hibernating mammals (both Carnivores *and* rodents) whether young or adult (Fagen, 1982).

3. *Increasing desinterest for congeners with advancing age*

Like « play », the increase of behaviour stereotypes with age is again certainly not limited to gregarious ungulates. It is a phenomenon observed to occur in the ontogeny of most animal species, which seems to originate from the same developmental process as the progressive disappearance of « play » with age (Fagen, 1982).

The steady increase of behaviour stereotypes paralleled by a growing relative disinterest for congeners (whose behaviour is not always compatible with the behavioural stereotypes of the older individual) could mean that, in group life, the individual starts by benefitting from the knowledge of more experienced group members, before relying on its own knowledge of the environment. This does not necessarily mean that it is a characteristic which has been « set up » during evolution to perform that function.

III. — *PROXIMATE CAUSES AND EVOLUTIONARY SCENARIOS*

None of the proximate mechanisms underlying the social emergences considered here therefore seem to be genuine adaptations against predation in an open habitat or towards a better knowledge, in group life, of the distribution of resources in space and time. Natural selection can obviously have adjusted the degree of attraction that individuals exert on one another, or their capacity to perceive one another, or increased the importance of « play » in the young, owing to the functions that these traits still perform in even-toed ungulates having for a long time colonized open habitats. However, the proximate mechanisms involved very probably existed in primitive even-toed ungulates, taking on new functions as the animals moved to open habitats. In this respect, it can be noted that the social emergences concerned occur in both Bovidae and Cervidae, whereas their phylogenetic separation seems to have taken place before colonization of open spaces (Eisenberg, 1981 ; Janis, 1988).

The social emergences discussed here result from local rules of interaction between individuals, based on attractions whose intensity and selectivity vary with age. As in the case of group size frequencies in the Pyrenean chamois (Fig. 1), there does not seem to exist, in any of the components of the population, algorithms corresponding *directly* to the social emergences observed. It should be

noted then that the answer to the question « adaptations or exaptations ? » would be quite different if the social emergences involved were due to the existence, within individuals, of *strategies* (*i.e.* of « preprogrammed rules that an animal obeys » : Dawkins, 1982) such as « form larger groups in open habitats », « stay in the centre of the group » or « follow the elders ». Such algorithms would necessarily have been set up by natural selection after even-toed ungulates started to colonize open habitats and to form large groups.

This shows clearly, in our opinion, the importance of studies on proximate mechanisms in evolutionary biology and behavioural ecology. In the field of social ethology such studies should, in particular, allow « confusions of levels » (*i.e.* the attribution to one level of organisation of the properties of another level) to be avoided.

SUMMARY

In wild even-toed ungulates, the increase in group size in more open habitats and the fact that the young are rarely at the periphery of the groups are often considered to be anti-predatory « strategies ». Also, the fact that groups are usually led by older animals is supposed to allow the young to benefit from their experience. In terms of proximate causes, these three social phenomena most probably emerge from quite simple « distributed » processes. Firstly, the animals must be able to perceive one another in order to form groups : this implies that the mean group size depends on the possibilities the animals actually have of perceiving one another. The central position of the young originates from the fact that they interact preferentially amongst themselves thus forming a compact sub-group within the whole group. Finally, the older animals probably become leaders because while moving about, they take less heed of the behaviour of their conspecifics than do the young. Natural selection might have adjusted the degree of attraction of individuals towards their congeners or the importance of playing in the young. Nevertheless, it seems unlikely that the appearance of these characteristics was due to the functions they fulfil in modern even-toed ungulates living in open environments. The notion of « exaptation » introduced in evolutionary biology by Gould and Vrba appears here to be enlightening.

RÉSUMÉ

Chez les Artiodactyles, un accroissement de la taille des groupes avec l'ouverture du milieu et le fait que les jeunes soient rarement à la périphérie des groupes, sont généralement considérés comme des « stratégies » anti-prédatrices. Le fait que les groupes soient régulièrement menés par des individus âgés permettrait par ailleurs aux jeunes de profiter de l'expérience de ces derniers. En termes de causalité immédiate, ces trois phénomènes découlent vraisemblablement de mécanismes particulièrement simples. En premier lieu, les animaux doivent se percevoir pour former des groupes, si bien que la taille des groupes doit dépendre des possibilités qu'ont les individus de se percevoir. Les positions centrales des jeunes découlent sans doute de ce qu'ils interagissent entre eux de façon privilégiée et forment ainsi des sous-groupes compacts au sein des groupes auxquels ils

participent. Enfin, les individus âgés deviennent probablement « meneurs » du simple fait qu'ils se déplacent en tenant moins compte du comportement de leurs congénères que ne le font les jeunes. La sélection naturelle peut avoir ajusté le degré d'attrance des individus pour leurs congénères ou l'importance prise par le jeu chez les jeunes. Il paraît cependant bien peu vraisemblable que ces caractéristiques soient apparues en raison des fonctions qu'elles remplissent actuellement chez les Artiodactyles vivant en milieu ouverts. La notion d'« exaptation », introduite en biologie évolutive par Gould et Vrba, paraît ici éclairante.

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