

22  
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## Chapter 3

### Demographic Constraints on Behavior and Social Organization

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The quality of the habitat may influence population densities and the sizes of groups, but factors such as birth intervals, longevity, and the duration of the period prior to sexual maturity will also influence the demographic composition of a group. Altmann and Altmann call our attention to the feedback mechanisms that relate life history processes to demography to social organization to ecological pressures and back to life history processes. If selection is considered to be operating on life history processes, then these parameters will influence demographic rate processes, which, in turn, set the limits on social structure.

The reproductive performance of an individual in any one year must not be considered to be a direct reflection of evolutionary selective forces in animals such as the primates. It should be clear that it will be reproductive success over the individual's entire lifetime that will determine genetic fitness. Short-term cross-sectional studies may inadvertently focus our attention on short-term processes, causing us to neglect the more significant long-term consequences.

Crucial examples are provided by the few longitudinal studies of nonhuman primates that are available. Such studies revealed the importance of kinship to social organization and our attention was then riveted to this parameter by recent advances in population genetics theory and the resulting attention to kin selection. Altmann and Altmann remind us, however, that most

of the longitudinal studies of primates have taken place at provisioned sites and that, given unlimited food and protection from various sources of mortality, even K strategists like the primates can show r strategy type expansion. When this occurs, matrilineal proliferate and large numbers of surviving kin surround each new infant.

The Altmanns contrast this with their own long-term observations of baboons at Amboseli, living in a more undisturbed state, and point out the consequences of provisioning to natural life history processes. When populations are at equilibrium, what kinds of group structure result? How many kin surround the infant under these conditions? How do life history processes influence the effects of kinship on playmate selection, infant association and care patterns, female association and agonistic aiding patterns? A small change in factors influencing demography may thus have profound consequences on social organization.

## Introduction

The thesis that we shall develop can be stated very simply. First, the size and composition of social groups, in terms of age, sex, and kinship, affect behavior and social relationships. Second, demographic processes provide delayed feedback on behavior because they affect group size and composition and are altered, in turn, by the effects of behavior on demographic parameters.

This cycle of effects—of behavior on demographic processes, of the latter on group size and composition, and of these last, in turn, on behavior—is loosely coupled because behavior and other life history processes are affected not only by demographic and behavioral factors, respectively, but by other environmental factors as well (Figure 1). Consequently, an environmental change may have both short-term effects on behavior, through direct responses of individuals to it, and long-term effects, through responses of these individuals or their descendants to the altered demography of the local population.

First we shall consider briefly the two better-known links in the cycle, traditionally regarded as part of a unidirectional chain of influence. We then turn to the effects of group composition on behavior, thereby completing the cycle. The existence of two-way causal relationships between demography and behavior has no doubt been tacitly assumed by many people, but has rarely been discussed in the literature (cf. Mason, 1978). The ramifications of this duality are virtually unexplored.

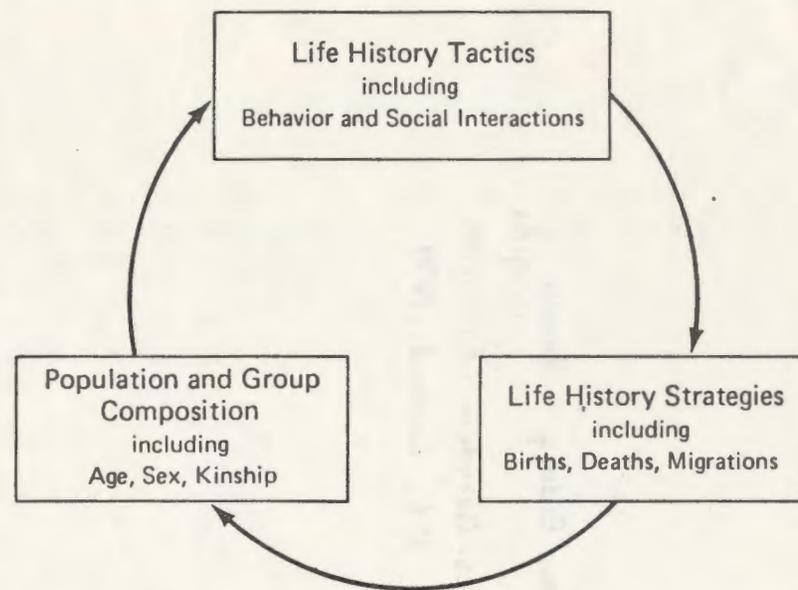


Figure 1.

## The Cycle

### *Life History Processes Affect Demography*

In 1954, Lamont Cole published a remarkable paper that succinctly laid out many demographic consequences of life history processes. The significance of that paper was largely unrecognized at the time, and for over a decade, it seldom received more than token citations in the literature. Matters changed quickly thereafter. Publications by Lewontin (1965), Gadgil and Bossert (1970), and Emlen (1970) were among the first substantial contributions to life history theory after Cole. In the last few years the blossoming of this holistic approach to biology has resulted in the publication of several theoretical papers, as well as extensive research on life history phenomena in many species.

Cole's approach was to measure the evolutionary impact of a life history phenomenon by its effect on the intrinsic rate of increase of the population, and that approach has been followed by most subsequent authors. An alternative approach, measuring the effect on reproductive value (Fisher, 1930), was proposed by Medawar (1952), but Charlesworth's recent analysis (1973) suggests that Cole's approach is preferable.

The life history concept has come to include two closely

related sets of phenomena: the basic demographic variables (primarily natality, mortality, and dispersion rates) and the biological means by which the values of these variables are altered or maintained. This distinction between means and ends is significant. For example, it might be biologically important to know whether a decline in fertility with age results from reduced access to mating partners, from decreased frequency of ovulation, reduced litter size, higher rates of spontaneous or induced abortion, or, in humans, from increased use of contraceptives. For most demographic purposes, however, only the resulting age-specific birth rates matter. To distinguish between life history means and ends, we shall call them life history tactics and strategies, respectively. (Demographers regard the latter as demographic indices or parameters.) Sheps and Menken (1973) have explored some of the relations between the two: the reaction of natality indices to variation in reproductive physiology. Stearns (1976) reviewed literature on the adaptive significance of life history tactics, which he defines as sets of coadapted traits that are designed, by natural selection, to solve particular ecological problems.

Evolutionary biologists analyze the adaptive significance of traits at various levels of organization, for example, biochemical, histological, anatomical, and behavioral. The development of life history concepts has meant recognition that selection may act on life history components as well. The life history approach has a much greater significance, however. Differential reproduction between genotypes—that is, natural selection—depends on differences between genotypes in one or more components of a species' life history strategy, and this, in turn, requires a difference in the underlying life history tactics. For some of the latter, such as litter size and age at menopause, a change will, in the absence of compensating changes in other components, directly affect one or more of the demographic variables. Others, including most forms of behavior, will affect life history strategies less directly. In either case a change in life history tactics is a prerequisite to natural selection.

As a result, natural selection acts simultaneously on life history parameters and on the heritable component of any traits that affect them. Suppose, for example, that in a population of animals some individuals are, for genetic reasons, more aggressive, that they thereby get more to eat, and thus have larger litters and raise more offspring to maturity. The result is simultaneous selection for greater aggressiveness and for larger

litter size. Changes in life history parameters are the channel through which selective evolutionary changes are brought about, regardless of level of organization.

The implications for behavioral biology are clear: the selective advantage of one mode of behavior over another depends on its effects on life history strategies. Thus, it is not surprising that in recent years behavioral biologists have placed increasing emphasis on the life history consequences of behavior and social organization. King (1973) and Gauthreaux (1978) have summarized what is now known about the effects of agonistic behavior on age at sexual maturity, fertility, age-specific mortality, and patterns of dispersion. Unfortunately, no comparable surveys are available for other modes of behavior.

### *Demographic Processes Affect Group Size and Composition*

The number and distribution, according to age, sex, and kinship, of potential social partners are produced by demographic processes through effects of the latter on group size and group composition. Changes in the size and composition of a group are brought about by just seven processes: birth, death, emigration, immigration, maturation, group fusion, and group fission, each of which is susceptible to small-sample fluctuations (demographic "drift"). At present, we do not have a formal model for predicting group size and composition from all of these processes. A model that predicts the equilibrium distribution of group size (but not composition) from the first four of these processes, that is, birth, immigration, death, and emigration (hence, the BIDE model), was developed by Cohen (1969, 1972), based on earlier work by Kendall (1949) and others. The BIDE model predictions are close to those observed in several populations of wild primates, including colobus (*Colobus guereza*), langurs (*Presbytis entellus*), howlers (*Alouatta palliata*), gibbons (*Hylobates lar* and *agilis*), and baboons (*Papio cynocephalus*, *ursinus*, and *anubis*) (Cohen, 1969; Keiding, 1977). Distributions predicted by the BIDE model are those of the negative binomial and poisson distributions. According to the BIDE model a population in which the per capita annual rates of birth, death, and emigration are 0.177, 0.173 and 0.55, respectively, and in which the immigration rate is 0.548 individuals per group—all reasonable values for Amboseli baboons (*Papio cynocephalus*)

lus)—will have an average group size of about 50. However, in such a population about 9% of all individuals will be in groups smaller than 30, and 11% will be in groups larger than 140. Therefore, any effects on behavior and social relations of such very large and very small groups will be recurring phenomena, a point to which we shall return. The literature on primate social groups contains numerous speculations about the adaptive significance of group size. In the BIDE model the chances that an individual gives birth, emigrates, or dies in any time period are assumed to be constant, regardless of group size, and thus the group rates for these processes are proportional to the number of individuals in the group. Additionally, immigrants are assumed to ignore group size, so that all groups in a population acquire immigrants at the same rate. Thus none of these processes would correct, except fortuitously, for any deviations of a group's size from any optimum, if any optimum exists. The equilibrium distribution in the BIDE model is not a dynamic equilibrium, with compensating feedback, but a long-term, large-sample, statistical equilibrium, the result of many replications of groups, each developing independently. That is, in the BIDE model, group size is a consequence of autonomous birth, death, and migration processes. If the BIDE model is correct, natural selection must act on the birth, death, and migration rates rather than on group size per se, and thus it is these rates, not group size, for which it is appropriate to seek evolutionary explanations. Although Cohen's modelling of group demography needs to be extended in several ways (Altmann, 1972), it is by far the most elegant attempt yet made to account for the size distribution of social groups on the basis of the underlying demographic processes.

Perhaps more important than group size as a determinant of behavior is group composition, that is, the age-sex distribution and kinship relationships within social groups. The general problem of how natality, mortality, and dispersion determine the distribution of surviving kin of each class, by age and sex, in a system of groups has not yet been solved. However, recent developments in demographic theory (Keyfitz, 1977, Chapter 10) make it possible to estimate the expected number of surviving kin of each type in a population, for an individual of specified age and sex.

A few rough estimates, calculated under simplifying assumptions, will serve to illustrate the great potential for large differences in social milieu. We look first at the kin composition of a social group. The expected numbers of any class of relatives

available in a group depends on that group's recent demographic history. In a population in which births greatly exceed deaths and dispersal from natal groups is low, each individual will grow up surrounded by relatives. That is exactly what happens in rapidly expanding primate populations. By contrast, consider a group of primates at or near a stationary condition, Alto's baboon group in Amboseli as of 1975. In such a group, what is the chance that a liveborn neonatal infant has a living next-older sibling? From our data (J. Altmann *et al.*, 1977 and in preparation) on mean interbirth interval and female life expectancy, we estimate that on the average the number of offspring in an adult female's lifetime is eight. Since one out of eight infants therefore will be the offspring of a primiparous female, only seven out of eight individuals have any older sibling, living or dead. The probability that such a sibling will survive from conception to age 22 months (the mean interbirth interval with a surviving infant) is 0.46. Thus the probability that a liveborn infant will have a living next-older sibling is  $L(0.46)M^{0.40}$ . In such a stationary primate population, most adult females will not survive long enough to be grandmothers. Thus, an infant's available playmates usually will not include either siblings, nieces, or nephews. Cousins (probably offspring of half-sibs) are more likely. However, even this likelihood will be reduced because two reproductively mature sibs may not produce offspring sufficiently close in time.

Grandparents, especially of first- or second-born infants, and older siblings, especially of later-born infants, may play an important role in an infant's life if they survive. Moreover, the occasional cases of many surviving close kin may be quite dramatic in the impact on the social group as a whole, as well as on the individuals involved. Our aim is to point out that numerous surviving close kin will be uncommon, not that they will be unimportant.

The preceding examples were based on mean values, but in small social groups chance deviations from mean values are likely to be very large. To illustrate this, we consider gender of playmates rather than kinship. What is the chance that an infant will have in its group a potential playmate of the opposite sex that is within three months of its age, that is, another infant born during the six-month period centered on a given infant's birth date? Suppose that the infant lives in a group of 50 baboons, a size that would seem to be large enough to be buffered against small-sample effects and that is about average size for stationary baboon populations. Alto's Group is a group of that size.

During 1975 the 15 adult females of this group gave birth to 5 infants per 6-month period, none stillborn. Assuming equal sex ratios at birth, the probability that 5 out of 5 infants would be of the same sex is about .06, so that even if all infants survived, about 6 infants out of every 100 in social groups of this size would not have any available playmate of the opposite sex within 3 months of their own age. Furthermore, the probability that exactly 4 out of 5 infants will be of the same sex is about .30, which means that in groups of this size, almost a third of all half-year cohorts will include an individual with no same-sex associate. If some of these infants do not survive the first year of life, the chance that, at the time these individuals enter the juvenile play groups, some will have no choice in the sex of their playmates becomes even greater; mortality during the first year of life among liveborn baboons in Ambelosi has been 29% (J. Altmann *et al.*, 1977). Beyond that, lack of a sharply defined breeding season would further increase the chance that some infants will be born at a time of year in which few (or many) others are born, thereby exaggerating variability due to small-sample effects.

In our discussion of the BIDE model we pointed out that even if life history parameters are uniform throughout a population, some individuals will, by chance, find themselves in a much smaller group than will others. They will therefore be more susceptible to effects of small-sample fluctuations in number, gender, and kin relatedness of available playmates.

### *Group Size and Composition Affect Behavior*

That brings us to the missing link in the system: the influence of group size and composition on behavior and social organization. We shall describe some of the few published examples. Perhaps the paucity of literature on this topic stems primarily from the fact that people have been largely unaware of the likelihood that demographic characteristics of groups will influence behavior, and therefore have not looked for such effects until recently.

**EFFECTS OF HIGH DENSITY AND LARGE GROUPS** The most extensive studies of demographic constraints on behavior and other biological processes are the experimental rodent population studies, pioneered by Calhoun (1963, 1973) and Christian (1961, 1971). These studies have dealt primarily with effects of crowding, and have demonstrated alterations in a wide variety of

physiological, behavioral, and social processes when population density is high:

In general, raising the population density increases the rate of individual interactions, and this effect triggers a complex sequence of physiological changes: increased adrenocortical activity, depression of reproductive function, inhibition of growth, inhibition of sexual maturation, decreased resistance to disease, and inhibition of growth of nursing young apparently caused by deficient lactation. (Wilson: 1975:84)

There are, in addition, numerous natural history descriptions of the effects of crowding on many aspects of behavior, including aggression, territoriality, competition, mating behavior, and so forth. Many species of vertebrates switch over from territoriality to dominance hierarchies when population density gets above a certain point (Wilson, 1975). If two large groups of blue monkeys meet at a fig tree, a fight ensues, whereas small groups coalesce peacefully (Aldrich-Blake, 1970). Numerous other density-dependent responses have been reviewed by Wilson (1975). The single most widespread response to increased population density throughout the animal kingdom is emigration.

Those interested in potentially adverse effects of crowding on people living in cities have referred to the effects described in the literature. Yet Draper (1973) has pointed out that !Kung bushmen living in their traditional, crowded bush camps show fewer signs of stress than do those !Kung who live in sedentary villages with more personal space and privacy. She suggests that crowding *per se* may not be stressful for humans.

Although many anthropological publications treat population growth as an effect of cultural practices, there is growing recognition that the causality may be reversed, that is, that cultural practices may be a result of population size and growth (Polgar, 1975). For example, it has been widely accepted that the development of agriculture during the Neolithic Age resulted from technological advances and may have been one cause of the subsequent population explosion, but Boserup (1965) proposed that the technology for some agricultural intensification is readily available to most primitive, nonagricultural peoples, and that the primitive farmer is inhibited from employing this technology by the fact that more intensive land use systems are more labor-demanding in terms of output per man-hour: "gather-

ing" requires only, or primarily, the harvest component of agriculture. Increased population density resulted in an increased demand for food and a decreased availability of land per person, creating the pressure for agriculture (compare Bronson, 1975). Important though population size or density may be, in what follows we emphasize effects on behavior of the particular composition of the local population or group.

**EFFECTS OF INCREASED LIFE EXPECTANCY** The vast majority of animal species do not live for any appreciable period after they produce zygotes, thereby precluding parental care or any other family-specific relationships that extend beyond one generation. Furthermore, many species that do outlive their own zygote production are spatially isolated from their offspring because the offspring are put into a special habitat (for example, marine turtle eggs) or because the zygotes are spewed out into the environment and dispersed (for instance, most aquatic invertebrates). Parental care is precluded unless there is generation overlap in time and space. Long life expectancy and low dispersal rates are prerequisites to kin-based social systems.

**EFFECTS OF OVERLAPPING REPRODUCTIVE PERIODS** If overlap between generations extends beyond the onset of reproduction of the filial generation, parent-offspring incest becomes possible. However, Slater (1959) pointed out that for purely demographic reasons, the likelihood of incestuous mating in humans under primitive conditions is very small: at sexual maturity, an individual is unlikely to have a surviving parent, or to have a surviving sibling that is sexually mature and of the opposite sex.

Consider, again, Alto's Group of baboons. A female will, on the average, give birth to her first infant at the age of six. In the 10-11 years before her death she will produce about 8 infants at intervals of 19 months. Even if her first offspring is a male who survives to maturity (an improbable event:  $p = .10$ , if male mortality rates were as low as females', which is unlikely), a mother would be unlikely to live past the age at which even her firstborn son first reaches full adult status, at about 8-10 years of age, and is breeding. Thus, mother-son incest will be rare, even with no special mechanisms (migration, taboos, and so on) to prevent such mating.

Since daughters breed at a younger age than sons do, it would at first seem that father-daughter incest would be more likely. However, by the same token, fathers are older than are

mothers when they first produce offspring. Moreover, changes in adult male dominance rank, correlation of rank with reproductive success, and mortality rates that probably are higher than those of adult females may make such an event at least as unlikely as mother-son incest. The available data indicate that a father is unlikely to be in high reproductive rank positions when his daughter matures five to six years later (Hausfater, 1975; Saunders and Hausfater, 1978), thus making father-daughter incest even less likely.

As a result, the only form of incest that could occur with an appreciable frequency is between brother and sister, particularly between older brothers and younger sisters. In a moderately promiscuous society, such as that of savannah baboons, the siblings are usually half-sibs. In monogamous primate species, such as gibbons, *Hylobates lar* (Carpenter, 1940) and titi monkeys, *Callicebus moloch* (Mason, 1966, 1978), in which siblings are usually full sibs, dispersal of the young before sexual maturity may be an important mechanism for reducing such potentially detrimental inbreeding.

**EFFECTS OF MALE-FEMALE COMPOSITION** Increased levels of aggression among adult males coincide with the onset of estrus in adult females in many group-living mammals, including several primate species, for example, rhesus, *Macaca mulatta* (Chance, 1956; Wilson and Boelkins, 1970), baboons, *Papio sp.* (Hall and DeVore, 1965) and ring-tailed lemurs, *Lemur catta* (Jolly, 1967). Dunbar (this volume, Chapter 4) has explored some of the consequences of variations in adult sex ratios for socio-sexual interactions in gelada baboon groups. Hausfater (1975) showed that in yellow baboons, the rate of agonistic behavior in adult males was significantly lower on days when at least one female was in estrus than when none were, possibly as a result of greater intermale spacing. However, when at least one female was in estrus, males were more frequently involved in inconsistent dominance interactions, a prerequisite to rank change, and were wounded more often; that is, when at least one female was in estrus, fights involving males were less common but more dangerous. Since the expected number of females simultaneously in estrus is a probabilistic function of the number of females in the group (Altmann, 1962), the rate of aggression in a group will depend on its adult composition.

**EFFECTS OF SMALL-SAMPLE FLUCTUATIONS** Effects on behavior of small-sample demographic variations are poorly understood,

but the potential is enormous. Anyone who has read the recent literature on the rhesus monkeys of Cayo Santiago cannot but be impressed by the pervasive influence of kin relationships on almost every aspect of social behavior and group organization in these animals (Sade, 1972, 1977). We pointed out above that an abundance of close kin is characteristic of expanding primate populations.

Consider social play. Among several species of cercopithecine primates, it has been shown that when given a choice, monkeys tend to play with other monkeys of the same sex and same age class. Conversely, Chivers (1974) believes that the low frequency and intensity of play in small, monogamous groups of siamangs (*Hylobates syndactylus*) may be attributable to the large age gap, at least two or three years, between infants. As we indicated above, the range of available social partners such as playmates may be sharply curtailed in a small population by the recent pattern of births and deaths. The resulting differences in social environment may have major effects on behavioral ontogeny. For example, Green (1978) has claimed that in humans the incidence of homosexuality depends on the composition of peer play groups at age 8–10. In a small !Kung band the play group usually consists of children of both sexes and a wide range of ages (Draper, 1976). Draper has suggested that this play group composition determines the type of play that is feasible and excludes competitive games.

Here is another example. By chance, six out of seven of the surviving 1973 infants in Alto's Group of baboons in Amboseli are female. Furthermore, there are no surviving females who were born in 1971 or 1972. For several years matters remained relatively calm and the female dominance hierarchy quite stable (Hausfater, 1975 and in preparation). This continued until mid-1976, when this entire cohort of juvenile females reached three years of age and began challenging adult females to whom they had previously been subordinate. Since then, many changes in dominance rank have occurred. The agonistic behavior has involved other individuals as well, including younger siblings of these adolescent females. It seems likely that these younger siblings will effect their own dominance changes at a younger age than did their sisters, partially as a result of their involvement in their older sisters' interactions. Neither the remarkable peacefulness of the group before this time, nor the chaos since then make much sense without knowing the demographic history of the group.

This phenomenon of composition-specific social relation-

ships should temper our comparisons of species or even populations that have been studied at different demographic stages. For black and white colobus monkeys (*Colobus guereza*) Dunbar and Dunbar (1976) have described between-group differences in behavior that appear to be related to differences in group size and composition. These demographic characteristics of colobus groups may change in a systematic way over time as one group type develops into the next. Altmann (1968) and Altmann and Altmann (1977) have described techniques for using class-specific rates of behavior and interactions obtained from samples on one population to generate expected values for another population with a different composition.

**EFFECTS OF DISPERSAL** We have mentioned the dispersal of offspring from their natal group. Among animals in which there is considerable variability between species or groups in such dispersal, it may be a major cause of differences in social structure. For example, the phenomenon of "helpers at the nest," when it involves sibling assistance in parental care, is well developed in some species of birds (Skutch, 1976), but is largely precluded in many others because of post-fledgling dispersal of the young.

Dispersal of primates from their natal group has been observed in a number of field studies. We have already mentioned the role such migration might play in preventing incest between brothers and sisters. In almost all primate species most migrants are adult or subadult males. In a few cases, we now have good descriptions of the direct effects that such intergroup movements have on the behavior of the migrants and on those individuals whose groups the migrants join. Perhaps the most extreme case is that of langurs (*Presbytis entellus*), in which adult males, after immigrating into a group, kill the infants in it (Mohnot, 1971; Hrdy, 1974, 1977; Sugiyama, 1967). In addition, intergroup migration may have considerable indirect effects resulting from alterations in group composition.

It would be especially informative to know whether such intergroup migration tends to stabilize group composition, that is, whether there exists, for any age-sex class, a level of representation (number or proportion of individuals) in social groups above which emigration by members of that class tends to exceed immigration, and conversely when that class is under-represented (Altmann and Altmann, 1970, Figure 11). If so, such demographic processes will tend to stabilize corresponding composition-dependent social relations.

## Inherited Social Environment

We have presented a brief survey of demography-dependent behaviors. Clearly, we are dealing primarily with terra incognita, but no less important for that.

What are the consequences for behavior of the feedback loop that results from the influence of behavior on life history processes, and thus on group composition? Surely it would be premature to attempt to answer that question, but we would like to point out one tantalizing implication of these relations. The variance in some behaviors has a heritable component; that is, some differences in behavior can be attributed in part to differences in genotype. The remainder of the variance is attributable to environmental differences, broadly speaking, and we have tried to make a case for the importance for behavior of one aspect of the environment, namely, group composition—or if you will, the social environment. But if group composition is the result of life history processes, and if these life history processes, in turn, have a heritable component, then some part of the variance in the social environment is heritable!

The concept of a heritable component to the environment may explain why the behavior of animals often exhibits a degree of species-typical stereotype that is much narrower than one would expect from their experimentally demonstrable capacity for learning and for other environmentally induced variability. If, as seems often to be the case, the members of a species develop certain forms of behavior and social responses through interactions with their parents, their siblings, and other members of their social group, such group processes are made possible by life history patterns that have a heritable component. Imprinting is practical only when there is a reasonable guarantee that the appropriate social partners will be available at the right time in an individual's life history.

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## References

- Aldrich-Blake, F. P. G. 1970. Problems of social structure in forest monkeys. Pages 79-101 in *Social behavior in birds and mammals*. E. J. H. Crook. New York: Academic Press.
- Altmann, J., Altmann, S. A., Hausfater, G., and McCuskey, S. A. 1977. Life history of yellow baboons: Physical development reproductive parameters, and infant mortality. *Primates* 18:315-330.
- Altmann, S. A. 1962. Social behavior of anthropoid primates: Analysis of recent concepts. Pages 277-285 in *Roots of behavior: Genetics, instincts, and socialization*. Ed. E. L. Bliss. New York: Hoeber-Harper.
- Altmann, S. A. 1968. Sociobiology of rhesus-monkeys III: The basic communication network. *Behaviour* 32:17-32.
- Altmann, S. A. 1972. [Review of] *Casual groups of monkeys and men: Stochastic models of elementary social systems*, by Joel E. Cohen. *Am. J. Phys. Anthropol.* 36:447-449.
- Altmann, S. A., and Altmann, J. 1970. Baboon ecology. *Bibliotheca Primatol.* 12:1-220.
- Altmann, S. A., and Altmann, J. 1977. On the analysis of rates of behavior. *Anim. Behav.* 25:364-372.
- Boserup, E. 1965. *The conditions of agricultural growth*. Chicago: Aldine.
- Bronson, B. 1975. The earliest farming: Demography as cause and consequence. Pages 53-78 in *Population, ecology and social evolution*. Ed. S. Polgar. The Hague: Mouton.
- Calhoun, J. B. 1963. The ecology and sociology of the Norway rat. Paper No. 1008, U. S. Dept. of Health, Education and Welfare, Public Health Service.
- Calhoun, J. B. 1973. Death squared: The explosive growth and demise of a mouse population. *Proc. Roy. Soc. Med.* 66:80-88.
- Carpenter, C. R. 1940. A field study in Siam of the behavior and social relations of the gibbon (*Hylobates lar*). *Comp. Psychol. Mon.* 16: 1-212.
- Chance, M. R. A. 1956. Social structure of a colony of *Macaca mulatta*. *Br. J. Anim. Behav.* 4:1-13.
- Charlesworth, B. 1973. Selection in populations with overlapping generations. V. Natural selection and life histories. *Amer. Nat.* 107: 303-311.
- Chivers, D. J. 1974. The siamang in Malaya: A field study of a primate in tropical rain forest. *Contrib. Primatol.* No. 4:1-335.
- Christian, J. J. 1961. Phenomena associated with population density. *Proc. Nat. Acad. Sci.* 47:428-449.
- Christian, J. J. 1971. Population density and reproductive efficiency. *Biol. Reprod.* 4:248-294.
- Cohen, J. E. 1969. Natural primate troops and a stochastic population model. *Amer. Nat.* 103:455-477.

- Cohen, J. E. 1972. Markov population processes as models of primate social and population dynamics. *Theo. Pop. Biol.* 3:119-134.
- Cole, L. C. 1954. The population consequences of life history phenomena. *Quart. Rev. Biol.* 29:103-137.
- Draper, P. 1973. Crowding among hunter-gatherers: The !Kung bushmen. *Science* 182:301-303.
- Draper, P. 1976. Social and economic constraints on child life among the !Kung. Pages 199-217 in *Kalahari hunter-gatherers*. Eds. R. B. Lee and I. DeVore. Cambridge, Mass.: Harvard University Press.
- Dunbar, R. I. M., and Dunbar, E. P. 1976. Contrasts in social structure among black-and-white colobus monkey groups. *Anim. Behav.* 24: 84-92.
- Emlen, J. M. 1970. Age specificity and ecological theory. *Ecology* 51: 588-601.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. 272 pp. Oxford: Clarendon Press.
- Gadgil, M., and Bossert, W. 1970. Life history consequences of natural selection. *Amer. Nat.* 104:1-24.
- Gauthreaux, S. A., Jr. 1978. The ecological significance of behavioral dominance. Pages 17-34 in *Perspectives in ethology*, vol. 3. Eds. P. P. G. Bateson and P. H. Klopfer. New York: Plenum Press.
- Green, R., 1978. Sexuality and aggressivity: Development in the human primate. Pages 515-528 in *Recent advances in primatology*, vol. 1. Eds. D. J. Chivers and J. Herbert. London: Academic Press.
- Hall, K. R. L., and DeVore, I. 1965. Baboon social behavior. Pages 53-110 in *Primate behavior: Field studies of monkeys and apes*. Ed. I. DeVore. New York: Holt, Rinehart and Winston.
- Hausfater, G. 1975. Dominance and reproduction in baboons (*Papio cynocephalus*). A quantitative analysis. *Contrib. Primatol.* no. 7: 1-150.
- Hrdy, S. B. 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol.* 22: 19-58.
- Hrdy, S. B. 1977. *The langurs of Abu (Female and male strategies of reproduction)*. 336 pp. Cambridge, Mass.: Harvard University Press.
- Jolly, A. 1967. Breeding synchrony in wild *Lemur catta*. Pages 3-14 in *Social communication among primates*. Ed. S. A. Altmann. Chicago: University of Chicago Press.
- Keiding, N. 1977. Statistical comments on Cohen's application of a simple stochastic population model to natural primate troops. *Amer. Nat.* 111:1211-1219.
- Kendall, D. G. 1949. Stochastic processes and population growth. *J. Roy. Stat. Soc., Ser. B* 11:230-264.
- Keyfitz, N. 1977. *Applied mathematical demography*. 388 pp. New York: Wiley.

- King, J. A. 1973. The ecology of aggressive behavior. *Ann. Rev. Ecol. Syst.* 4:117-138.
- Lewontin, R. C. 1965. Selection for colonizing ability. Pages 79-94 in *The genetics of colonizing species*. Eds. H. G. Baker and G. L. Stebbins. New York: Academic Press.
- Mason, W. A. 1966. Social organization of the South American monkey, *Callicebus moloch*: A preliminary report. *Tulane Stud. Zool.* 13: 23-28.
- Mason, W. A. 1978. Ontogeny of social systems. Pages 5-14 in *Recent advances in primatology*, vol. 1. Eds. D. J. Chivers and J. Herbert. London: Academic Press.
- Medawar, P. B. 1952. *An unsolved problem in biology*. 52 pp. London: Lewis.
- Mohnot, S. M. 1971. Some aspects of social changes and infant-killing in the hanuman langur, *Presbytis entellus* (Primates: Cercopithecidae) in western India. *Mammalia* 35:175-198.
- Polgar, S. 1975. *Population, ecology, and social evolution*. 354 pp. The Hague and Paris: Mouton.
- Sade, D. S. 1972. A longitudinal study of social behavior of rhesus monkeys. Pages 378-398 in *The functional and evolutionary biology of primates*. Ed. R. Tuttle. Chicago: Aldine-Atherton.
- Sade, D. S., Cushing, K., Cushing, P., Dunaif, J., Figueroa, A., Kaplan, J. R., Lauer, C., Rhodes, D., and Schneider, Jr. 1977. Population dynamics in relation to social structure on Cayo Santiago. *Yrbk. Phys. Anthropol.* 20:253-262.
- Saunders, C. D., and Hausfater, G. 1978. Sexual selection in baboons (*Papio cynocephalus*): A computer simulation of differential reproduction with respect to dominance rank in males. Pages 567-561 in *Recent advances in primatology*, vol. 1. Eds. D. J. Chivers and J. Herbert. London: Academic Press.
- Sheps, M. C., and Menken, J. A. 1973. *Mathematical models of conception and birth*. 428 pp. Chicago: University of Chicago Press.
- Skutch, A. F. 1976. *Parent birds and their young*. 503 pp. Austin: University of Texas Press.
- Slater, M. K. 1959. Ecological factors in the origin of incest. *Amer. Anthropol.* 61:1042-1059.
- Stearns, S. C. 1976. Life-history tactics: A review of ideas. *Quart. Rev. Biol.* 51:3-47.
- Sugiyama, Y. 1967. Social organization of hanuman langurs. Pages 221-236 in *Social communication among primates*. Ed. S. A. Altmann. Chicago: University of Chicago Press.
- Wilson, A. P., and Boelkins, R. C. 1970. Evidence for seasonal variation in aggressive behaviour by *Macaca mulatta*. *Anim. Behav.* 18: 719-724.
- Wilson, E. O. 1975. *Sociobiology: The new synthesis*. 697 pp. Cambridge, Mass.: Harvard University Press.