

ment are similar or identical to those necessary for development of the filarial larvae.

The life cycles of many parasites involve insects as intermediate hosts. An *in vitro* method for investigating this phase of development of a parasite, offering conditions closely approximating the environment in the insect, is highly desirable. Insect cells in culture may provide this method.

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Types of Group Selection

THE terms group selection and intergroup selection^{1,2} have been used in referring to a variety of phenomena including recently the evolution of behavioural social systems involved in population control^{3,4}. Since the phenomenon of group selection promises to receive greater attention from students of evolution in the future, I feel that a clarification of terms at this time will help to prevent confusion. The "groups" under consideration may be quite different from each other and the action of natural selection on them will depend on the nature of the group.

At least two extreme types of group can be recognized: the family or lineage group and the population. Intermediate types occur, especially in species in which culture is important, but only the extreme types will be discussed here. The lineage group is a sub-group within a population, and is defined on the basis of kinship. A population in the ecological sense, although it may also have a common lineage, is generally defined from other populations spatially, irrespective of lineage. Theoretically the two concepts can overlap, but in practice this is not embarrassing. The term kin selection may be applied to lineage groups (following Smith⁵ in part). The evolution of parental care, whether behavioural, morphological or physiological, may be attributed to kin selection.

The simplest lineage group is composed of one or more parents and their offspring. In the typical case the family group disperses before the first generation has reached maturity. In some social insects, a few species of birds, and in some other animals, the young remain with the parents and help to raise subsequent broods, as in some cases of "helpers at the nest"⁶. Among birds, in the Mexican jay (*Aphelocoma ultramarina*)⁷, fairy wren (*Malurus cyaneus*)⁸, Australian magpies (*Gymnorhina dorsalis*)⁹ and *G. tibicen*¹⁰, and some other species¹¹, territories may be defended by social groups larger than pairs, in which incipient communal behaviour may occur; but the most extreme development of this evolutionary potentiality in birds appears to be the situation found in certain anis (*Crotophaginae*) in which all phases of breeding may be communal¹¹. In the latter cases, the extent to which inbreeding determines the genetic composition of successful groups is not known but deserves study.

Assuming lineage to be important in the latter cases, we can then recognize a continuum among various species in the importance and complexity of the family or lineage group and in the number of generations in which it may stay together as a unit. The existence of such a continuum is provided for in the expression "inclusive fitness" in Hamilton's¹² model for kin selection. It is possible at all positions on this continuum to recognize the existence of competition between lineage groups. This may be done whether the unit is a pair of titmice and their brood and the competition influences the evolution of

Table 1. CHARACTERISTICS OF TWO TYPES OF GROUP SELECTION

	Kin selection		Interpopulation selection	
	Simple extreme	Complex extreme	Slight ecogeographic separation	Large ecogeographic separation
Lineage relationship	Simple family	Communal group	Irrelevant	Irrelevant
Duration of group	One generation	Indefinite	Indefinite	Indefinite
Gene exchange between groups	Unrestricted	Partially restricted by social behaviour	Partially restricted by geography	Nearly absent
Competition between groups	Sympatric	Sympatric	Allopatric	Allopatric

clutch size¹³ (simple extreme in Table 1) or if the unit is a flock of anis (*Crotophaga* spp.) and the competition determines the social organization and behaviour of the flock and species (complex extreme in Table 1). The critical point in all these cases is that the group is characterized (to varying degrees) by a common lineage, which is characteristically maintained by social bonds within a population and with no important ecogeographic isolation from other such groups. The evolution of the ability to form such social bonds is also provided for in Hamilton's¹² model.

Smith⁵ has referred to one extreme of this continuum as "group selection" and to the other extreme as "kin selection". In my opinion, because these cases may be recognized as lying along a continuum (provided for in Hamilton's¹² model) they should all be interpreted as representing one phenomenon, which may conveniently be called kin selection, or perhaps lineage selection. To use the term "group selection" for any of these cases is confusing, as Wynne-Edwards^{3,4} has used "group selection" and "intergroup selection" in explicit reference to intraspecific interpopulation competition, which is quite a different phenomenon. In order to avoid confusion I propose the following definitions: selection between lineage groups within populations will be called kin selection; selection between spatially defined (allopatric) populations of a species will be called interpopulation selection (see Table 1).

Whether the term group selection will eventually prove useful as a generic term to include both kin selection and interpopulation selection remains to be seen. The differences between the two are significant. Kin selection depends on sympatric competition between lineage groups within a population and can be treated theoretically in a manner comparable to individual selection¹², since the basic time unit is most frequently the generation and the lineage groups are not prevented from interbreeding except partially in the complex cases, as in species with communal territories. Intergroup selection depends primarily on allopatric competition; the basic time units are the time constants for extinction and colonization, and it may require a different type of mathematical expression, such as game theory¹⁴.

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