

# Migration and colonization in human microevolution

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# 1 *The study of migration*

## **Evolutionary and ecological perspectives**

### ***Definitions and patterns: migration, dispersal, and gene flow***

Migration is a process with consequences that are important to theory in several disciplines and the term may be used in several senses in these different domains. Biologists study migration both from an ecological and an evolutionary point of view. That is, migration takes organisms into different habitats thereby affecting resource availability and other ecological parameters; likewise, migration may result in gene flow with effects on the gene pool of recipient populations.

The spectacular long-distance to and fro trips of birds and butterflies are more likely to be called 'migration' in biology than one-time, non-return movements that are termed 'dispersal' (Dingle 1996). Both are ecologically similar in that they are usually efforts to improve environmental conditions for the organism and, for Dingle (1996) at least, both types of movements are behaviorally alike in that they involve locomotion not seen at other times in the life cycle. In fact, Dingle would like to reserve the definition of migration for the characteristic pattern of behavior rather than the outcomes of movement (dispersal or aggregation). Moreover, he would exclude accidental or unintentional movement from the definition since these are not behaviors potentially subject to natural selection. Thus migration is 'persistent and straightened-out movement effected by the animal's own locomotory exertions' (Dingle 1996:25) carrying them to new habitats. This behavior will have ecological effects that will determine its evolution.

Evolutionary geneticists on the other hand generally use 'migration' as a synonym for 'gene flow' (Merrell 1981); that is, one-way movement to a new population. Strictly speaking, the migration coefficient in population genetics,  $m$ , is not the number of individuals moving (the quantity of interest to population biologists studying demographic change) but rather a measure of the proportion of gametes contributed by immigrants to the gametic pool making up the next generation in the recipient mendelian population.

This usage is in sharp contrast to Dingle's (1996) behavioral definition since it is an (highly abstract) *outcome* that is the relevant factor.

### ***Population structure: units of analysis***

The study of migration presumes clearly defined populations with migrants moving between them. In demography, populations are generally administrative units ranging from nations (international migration) through various state, county, or metropolitan polities (internal migration). Geneticists and anthropologists define the population unit by focusing on the relevant behaviors linking together the members of the group; interbreeding in the case of genetics, shared language, culture and social interaction for anthropology. Just as there is a hierarchy of political units, social or breeding populations may vary from local groups to ever larger partitions of the species. In practice, then, migration may be measured and modeled between villages, parishes, counties, districts or countries; all are valid units depending on the problem being investigated (Fix 1979).

### ***Causal models***

At the most general, migration is movement to a new location undertaken to improve the environmental conditions for the organism (Dingle 1996). However, simply foraging in search of widely scattered food does not satisfy Dingle's (1996:54) behavioral definition of migration since it does not entail focused movement to a new habitat. Thus organisms in patchy environments might be expected to be nomadic, tracking seasonally shifting or widely dispersed resources. This mobility, while technically not migration in Dingle's sense, may nonetheless involve considerable distances. For instance, Lee (1980) estimated that !Kung women in the Kalahari travel some 2400 km per year, mostly in day-trips of less than 10 km, in the food quest. Many human foragers provide excellent examples of nomadic movement over large ranges exploiting highly localized, often high caloric-return food items. Indeed, this life way has been suggested as part of a key adaptive shift in hominid evolution (Kurland & Beckerman 1985).

Nomadism within a home range may be an appropriate response to patchy resources; however, when the habitat deteriorates or is intrinsically ephemeral, migration to another range may be forced (Dingle 1996:270). In the case of many bird species, long range migration occurs to avoid seasonal shortages (brought on by winter) and to take advantage of short-term abundance (e.g., as occurs during the arctic summer). Temporary abundance may not be only seasonal. For instance, Australian banded

stilts inhabit marshes and salt lakes (Dingle 1996:55). Only after heavy rains fill normally dry lake beds do these birds migrate in great numbers (up to 100,000 birds) to breed. Apparently the temporary abundance of brine shrimp to feed the young birds triggers migration and breeding. Such events may occur at intervals of several years in the arid regions of South Australia.

Bird migrations are often round trips, especially seasonal movements from summer to winter range and return. Such periodicity implies relatively stable or predictable conditions in both ranges. Movement oscillates between two known habitats. One-way migrations, however, are more likely in uncertain or unpredictable environments (Dingle 1996:61). When the environment deteriorates with no indication of when it will improve again, it may be abandoned for a new range.

In theory, it is possible to calculate the costs and benefits of migration just as for any other behavior. These combined with the constraints of the environment, should predict the occurrence and frequency of migration. Migration should evolve as a function of the cost of migration, the availability of alternative habitats, and the basic ecological parameters of population growth rate,  $r$ , and carrying capacity,  $K$  (Dingle 1996:271). This theory has been presented as alternative life histories under the control of different selective regimes called ' $r$  and  $K$ ' (Pianka 1970; see Stearns, 1992 for a critique).  $R$  species inhabit temporary habitats that put a premium on high intrinsic rates of growth,  $r$ . Production of large numbers of quickly maturing young ensures that these offspring can disperse widely in search of ephemeral habitats.  $K$  species tend to occupy permanent habitats with high carrying capacities. Selection under these conditions is for fewer offspring with greater competitive ability rather than large numbers of highly motile progeny. Clearly this is not an absolute dichotomy – species may possess  $r$ -like attributes while at the same time be selected along the  $K$  dimension. For example, humans have many attributes of a quintessential  $K$  species: long life span; relatively few offspring with heavy parental investment; etc. Nonetheless, compared to our closest relatives, the African great apes, we show some attributes that are more  $r$ -like (Lovejoy 1981), especially a shortened birth interval. Thus species or populations exploiting patchy, uncertain environments might be selected for superior colonizing ability ( $r$  selection) *relative* to related species or populations in more stable habitats in which  $K$  selection might be more important. This point is particularly relevant to assessing the ability of humans to rapidly colonize large areas such as the Americas and Australia (see Chapter 5).

The general conclusion to be made is that migration should be more important where habitats are temporally transient or spatially patchy. The

greater the degree of environmental uncertainty, the greater the potential strategic importance of migration.

Caloric considerations are only part of the evolutionary equation, however. Mating and reproduction (genetic effects) must be accomplished if individuals are to leave offspring (and their genes) in subsequent generations. Finding a mate may be an important cause of migration and, indeed, marriage is often the primary determinant of movement from the birthplace in many sedentary human societies.

Of course, marital movement also may have somatic consequences. Tylor's (1888:267) famous aphorism, 'marry out, or be killed out' identifies the political advantages of exogamy. Wide-ranging marital ties extend affinal kinship networks potentially reducing conflict and often allowing access to resources in time of need. Such marital systems might be expected to occur in the same contexts that non-marital migration would be favored; that is, where resources vary greatly in time and space (see Chapter 2 for some examples).

Costs and benefits relating to mating dispersal can be measured in reproductive as well as caloric currencies. Shields (1987) provides an extensive discussion of the fitness effects of philopatry (non-dispersal from natal site) versus dispersal. Table 1.1 is a synopsis of some of these key factors derived from his Table 1.3 (1987:15–16).

A time honored argument for the direct genetic benefit of out-mating is the avoidance of inbreeding depression (for humans, see Aberle *et al.* 1963). Increased homozygosity of rare deleterious recessive alleles leading to the phenotypic expression of genetic diseases would seem an obvious disadvantage of endogamy (or philopatry), in so far as it increased mating with relatives. However seemingly obvious, the actual degree of debility caused by inbreeding in humans has never been satisfactorily documented (Bittles & Makov 1988). In this regard, Shields (1987:19) cites data from acorn woodpeckers showing that some 20 percent of groups were closely inbred, usually within nuclear families. In the same volume (Chepko-Sade & Halpin 1987), a number of studies of other species that also practice high levels of inbreeding are described. Closer to home for anthropologists, the ubiquity of male dispersal in cercopithecine monkeys has been explained as avoidance of incest and thereby inbreeding depression (Bischof 1975). However, other competing hypotheses have not been excluded even in this well known case (Shields 1987).

The other side of the genetic coin from inbreeding depression is the potential cost associated with outbreeding (Shields 1987). When organisms disperse, they may enter environments with different selective conditions than those to which they are adapted. Problems faced by human dispersers

Table 1.1. *Costs and benefits of mating dispersal*


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Potential benefits
I. Genetic
A. Avoid inbreeding depression
II. Somatic
A. Direct fitness benefits
(1) Escape local crowding; gain access to resources including mate
B. Indirect fitness benefits
(1) Avoid competition with sedentary kin
Potential costs
I. Genetic
A. Outbreeding depression
(1) Disrupt potentially coadapted gene complexes
B. Migration load
(2) Enter environment with genotype not locally adapted to disease or other factors
II. Somatic
A. Direct fitness effects
(1) Risk and energy expenditure of migrating
a. Lack of familiarity with new locale reducing foraging efficiency
b. Energy cost of migrating and increased exposure to predators
c. Greater susceptibility to local diseases
B. Indirect fitness effects
(1) Lack of mutual aid and support for non-dispersing kin

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in the island of New Guinea illustrate this situation. Malaria in New Guinea differs greatly in incidence from location to location (Bayliss-Smith 1994). On account of this variability, Bayliss-Smith (1994:305) argues that ‘exogamous marriage is seen as a particularly risky practice in malarial areas’. Where genetic resistance to endemic malaria has evolved, movement bears fitness costs. Strain specific immunity acquired in childhood would not equip a migrant to resist a different strain in the new environment. Similar arguments can be made for any patchily distributed disease – brides or grooms moving to a new area might encounter diseases or strains to which they had no evolved or acquired immunity.

A more tenuous potential fitness cost of dispersal depends on the presence of local coadapted gene complexes. This concept has long been championed by Ernst Mayr (1963) but actual evidence for such sets of interacting genes promoting adaptation to local environments is scarce. Where such complexes exist, migration between groups might disrupt the favorable gene combinations and therefore reduce progeny fitness.

Somatic costs and benefits of dispersal are also summarized in Table 1.1. The general sense of migration as a strategy to improve resource acquisition presented by Dingle (1996) certainly is a primary somatic factor both in the

direct fitness value gained by the disperser or indirectly by no longer competing for local resources with kin remaining in the natal group. On the negative side of the ledger, the energy and risk associated with migration may be high depending on the distance, possible barriers to travel, and risk factors such as predators (including disease micropredators). Where knowledge of local conditions are important for foraging, unfamiliarity reduces efficiency. Particularly for social species such as humans, dispersers may directly suffer due to lack of mutual support provided by kin in the new locale and indirectly due to inability to support kin remaining at home.

A strictly genetic accounting weighs the costs of inbreeding against the costs of breaking up adaptive gene complexes and/or maladaptation to the new environment. But genetic factors can not be considered in isolation from the fitness effects due to somatic factors. Indeed, there is no *a priori* necessity that any one factor, genetic or somatic, will predominate in all cases. While inbreeding has often been seen as the critical problem to be resolved by dispersal, in some species and/or environments other factors may be as or more important. Shields (1987) points out that Bengtsson's (1978) assumption that the genetic costs of philopatry are balanced by the greater somatic costs of dispersal could just as easily be turned around. The cost of philopatry could be increased competition within the natal population (a 'somatic' factor) balanced by the 'genetic' cost of outbreeding depression. Some species tolerate apparent high levels of inbreeding without obvious genetic deterioration; others seemingly accept the high somatic costs of dispersal. Theory can identify the relevant variables but the values taken by each variable may vary with different empirical situations. The diversity of possible outcomes in mammalian dispersal (literally from mice to humans) and evaluations of the causal factors can be found in Chepko-Sade & Halpin (1987).

### **Social science perspectives**

Human migration is the concern of demographers, geographers, anthropologists, sociologists, and economists. All of these disciplines share overlapping interests and concepts; however, particular emphases differ among the fields.

### ***Demographic models***

For demography, migration is one component of the basic demographic equation (Newell 1988:8):

$$P_{t+1} = P_t + B - D + \text{Immigrants} - \text{Outmigrants}$$

where  $P_{t+1}$  is the population after one unit of time which is dependent on the initial population at time  $t$  ( $P_t$ ), the numbers of births ( $B$ ) and deaths ( $D$ ) occurring between time  $t$  and  $t + 1$ , and the number of in- and outmigrants to the population during the same time interval. The difference between the number of births and deaths is referred to as 'natural increase' and 'net migration' is the corresponding migrational differential.

$P$ , 'the population', can be any size unit of interest although usually demographers study nations since these governments provide the statistical data most available to them. The definition of migration in this equation depends on the population referent. Births and deaths occur *within* that unit and migration is something that happens *between* those units. Because of the focus on nation-states, immigration and emigration are defined strictly in international terms while the terms 'immigration' and 'outmigration' are applied to internal movement (Newell 1988). Anthropologists (including anthropological geneticists), in contrast to demographers, are much more likely to be interested in local populations. Nonetheless, many of the same problems of definition and measurement occur at the local level as exist for nations.

The first point to notice about the demographic equation is that only the *number* of individuals migrating in and out of the population are specified. The *structure* of migration, either in terms of the usual demographic markers of age and gender or in terms of spatial location of migrants, is not considered. Elaborate methods for more precisely characterizing births and deaths including age specific fertility rates and life tables have been devised by demographers. Migration, however, has not received such sophisticated treatment.

One reason for this relative neglect of migration by demographers is the intrinsic difficulty of measuring migration. Part of the problem is that of definition. Births are discrete events that occur to women of definable age. Likewise, deaths occur only once to everyone. Both events are recorded in national registries that provide data to demographers. In contrast, migration is less clearly marked, may occur repeatedly, may be reversed (return migration), and therefore is much harder to measure. National migration statistics may be available for some countries but they are not of the same degree of precision as birth and death statistics.

Consider, for example, the conventional definition of an immigrant by a demographer (Newell 1988:84): 'a person who has resided abroad for a year or more and, on entering the country, has declared an intention to stay for a year or more'. Clearly, the arbitrary unit of time and the inference of

intention distinguish migration from the 'natural' events, birth and death. Similarly, for internal migration, a problem arises when the distance of movement is short. Clark (1986:12) reserves the term 'migration' for relatively permanent moves that are 'too far' for continued commuting. Recent trends in Southern California have extended this distance to a previously unimaginable degree with people routinely traveling 40 to 60 miles (64–96 km) one-way daily to work. Clark (1986) also notes the problem of using governmental units to define the scale of migration. 'Internal' migration within the boundaries of the United States, for example, may encompass 2000 miles (3218 km), a distance that would cross many national boundaries in other parts of the world.

These spatial concerns extend the study of migration beyond the disciplinary limits of traditional demography into that of human geography (Clark 1986; Lewis 1982; Robinson 1996). Similarly, the economic and cultural constraints on and consequences of migration make it an important topic of study for economists and anthropologists.

### *Geographic and economic models*

The 'classic questions' defining the domain of study for social scientists are: 'who moves, why do they move, where do they move, and what are the impacts when they get there' (Clark 1986:10).

### *'Laws' of migration*

Historically, models of human migration have been dominated by economic variables. For most of these classic models, movement occurred as individuals were pulled by economic forces to destinations offering better opportunities perhaps having been pushed (also by economic factors) from their home locales. Job seeking thus was the principal motivator for movement. Migration achieved spatial equilibrium in income and employment. Flows of migration were from areas of low wages and demand for labor to areas of higher income and opportunity.

The centrality of economic motivation was established in the first systematic study of migration. Ravenstein (1885; see Grigg 1977; Lee 1966) presented his findings as a set of 'laws' of migration (Lewis 1982). Like many nineteenth-century laws in social science, these were empirical generalizations based on Western societies (census data from Britain later augmented with data from several other countries). Not surprisingly, these rules are specific to time and place and reflect the process of industrialization pulling rural Britons into urban work centers. Thus Ravenstein

observed mainly short distance migration (although his unit of analysis, the county, varied in size, affecting the actual distances traveled by migrants). Similarly, he found townspeople to be less migratory than rural folk, the direction of migration was primarily from rural to urban areas, most migrants were adults (presumably job-seekers), and migration increased as commerce developed and transport improved. Interestingly, he found females to be more migratory than males.

Grigg's (1977) evaluation of Ravenstein's work points out the role of industrialization in structuring migration in Britain. In so far as similar conditions apply in other regions and times, similar patterns might be expected to occur. Thus young adults are often mobile job hunters and jobs are often in urban centers around the developing world. As Grigg notes, however, in Britain itself, migration to towns increased with 'commerce' but by the 1880s was already declining. The key point is that developing and developed commercial societies often depend on a mobile labor force and the volume of economic movement is sufficient to overwhelm other causes of mobility. To conclude that migration is always economically motivated in the narrow sense of the labor market may miss other important attributes of the process.

Despite these caveats, Ravenstein's work identified several important aspects of human migration and is the foundation for later theory (Lee 1966). Indeed, his view that migration stems from the desire of individuals to 'better themselves in material respects' cited by Ravenstein (1889, quoted in Lee 1966) links his ideas to modern biological definitions (recall Dingle's point that migration is directed toward improving environmental conditions for organisms – Dingle 1996). Subsequent causal investigation of human migration has continued to emphasize economics but has added spatial and social variables as important factors.

### *Spatial models*

Human geographers, not surprisingly, are particularly interested in the spatial aspects of migration (Clark, 1986; Robinson 1996). Spatial interaction forms the core of their discipline and the three basic geographic concepts are distance, direction, and connection (Olsson 1965). These concepts are applied in theories of spatial location (Haggett 1966) as well as models of the diffusion of innovations (Hägerstrand 1967) as well as migration (Olsson 1965).

Of the spatial variables, distance has traditionally received the most attention particularly by geneticists (see Chapter 3). Indeed, in some of the classic models of population genetics, distance is the *only* variable – e.g.,

Malécot's (1955) isolation by distance model relates the decline in genetic similarity to distance alone.

Numerous empirical and theoretical studies relate migration intensity to distance (see Lewis 1982). The intuitive perception that distance acts as a barrier to movement has been amply confirmed and the interest has been in specifying more precisely modifying variables including social and historical effects on the migration–distance relationship.

Consideration of the direction of migration has been combined with distance in the so-called *social gravity* model (Lewis 1982) on the analogy of the force of gravity being proportional to the mass of the attracting body. This relationship can be written as:

$$M_{ij} = K(P_i P_j / d_{ij}^b)$$

where  $M$  = migration from place  $i$  to  $j$ ;  $P$  = population size of places  $i$  and  $j$ ;  $d$  = distance between places  $i$  and  $j$ ; and  $K$  and  $b$  are constants specific to the situation.

The basic idea is that some places exert special attraction for migrants, which will bias the direction of movement. 'Mass' is represented by the population size of the destination, large towns and cities being more attractive proportionate to their population.

In so far as population size is an adequate operational definition for 'attraction', the gravity model should predict movement. All other things being equal, job opportunities, for instance, should be proportional to the size of a place. However, empirical studies using the gravity approach have produced mixed results (Lewis 1982) suggesting that population sizes may not be sufficient to define attraction. Other size-independent factors may also be involved. Olsson (1965), for example, cites the special pull of warm climates such as Florida or California for migrants hoping to escape winter's misery.

More comprehensive measures of attractiveness of places have been devised to increase the realism of the gravity model. Morrill (1965) for example, employed an index of attraction,  $A$ , defined in terms of accessibility of the place to the transport system, level of urban growth, and population density in place of the product of population sizes.

Olsson's (1965) classic study of internal migration in Sweden may serve as an example of the geographic approach to spatial interaction models. He examined variation in migration distances as a function of variation in the characteristics of places along with variation in migrants' demographic or economic status. He went on to consider variation in migration intensity as a function of distance. This approach topic also tied the analysis into a broader locational framework, the hierarchy of central places (Haggett 1966).

In order to test the determinants of migration distances, Olsson (1965) used multiple regression analysis. Characteristics of places included areal size, population size, occupational structure, level of income, and geographic situation; for migrant individuals, typical demographic and sociological variables such as age, sex, marital status, occupation, and income level were used. He found that the distances that migrants traveled was positively related to the level of income of the migrant's origin place, to the level of unemployment in both the origin and destination, and to the population sizes of both places. All of these relationships were significant at the 99 percent level (Olsson 1965:18–20). The characteristics of the migrants themselves such as family income and age were less clearly related to distance.

The second stage of Olsson's analysis treated distance as the independent variable in a gravity model to explain the intensity of migration between places. The salient finding in this work was that the effect of distance on migration intensity varied as a function of the central place hierarchy (Olsson 1965:32). That is, for lower levels of the hierarchy (smaller places), the decline of intensity with distance was steeper than for higher levels. The reasoning behind this result is that central place theory defines a hierarchy of *functions* of places. Large centers are the only places that specialized goods and services may be obtained. These marketing centers require a large hinterland of consumers (range) and a threshold population size in order to provide these functions profitably. Smaller markets serve smaller ranges and provide a narrower range of functions. The spatial pattern of the hierarchy depends on the distance consumers will travel. Daily needs will be satisfied locally, but specialized needs may be provided at lower cost (or only be offered) at more distant larger centers. These advantages outweigh the costs of travel. Relating this back to Olsson's findings, the sharper decay of distance among smaller places may reflect the basic similarity and substitutability between these rather uniform places (Olsson 1965:32). Movement between larger, more economically specialized centers is less constrained by distance and therefore shows a more gradual slope.

Another component of increased attractiveness influencing distance decay in the gravity model is information. Morrill & Pitts (1967) showed that social interaction is strongly influenced by the mutually reinforcing factors of nearness in space and amount of information possessed by individuals about a place. Migration and marriage distances, then, would be influenced by map distance and also by the knowledge of conditions and opportunities available in the potential destination. Nearby places might be expected to be better known than more distant locales accounting for

the interdependence of the variables. But, as they (Morrill & Pitts 1967:406) note, 'superior information can overcome great distances'. This basic idea that information held by individuals might determine their behavior was adopted by human biologists in the concept of 'neighborhood knowledge' (Boyce *et al.* 1967) and will be considered in more detail in Chapter 3.

The concern with information fields relates the microlevel processes of behavioral decision-making by individuals or families to the broader patterns of population movement in regions. Focus on the microlevel of analysis highlights the role of non-economic factors such as values, community and social networks, environmental constraints and kinship structure in addition to the usual economic determinants of migration (De Jong & Gardner 1981). Lewis (1982) has reviewed a number of these studies. Theoretical and empirical studies of decision-making with respect to all sorts of behaviors has been presented by C. Gladwin (1989); these models and methods are clearly applicable to the study of migration.

### **Anthropological genetics: integration of social and biological perspectives**

Anthropological genetics, by straddling the disciplinary boundary between social and biological sciences, may relate the socio-economic *causes* of migration to the evolutionary *consequences* of gene flow. Over the course of human history (including prehistory), basic socio-economic features of human populations have varied greatly. The reasons for movement as well as the scale and structure of migration have changed along with cultural patterns. Thus the mass migrations of recent history are the result of the conjunction of particular historical–technological (transport)–economic factors as are the contemporary phenomena of the growth of mega-cities and intra-urban migration. Much current social science research attempts to understand these modern phenomena in terms of locational and economic variables. In addition to these national and international movements, the ethnographic cases to be presented in the next chapter document a wide range of variation in patterns of local migration from extremely sedentary societies with only limited marital exchanges to highly mobile nomads.

The task is to identify the key variables structuring human migration from this great diversity of cultures and histories. As will be seen in the following chapters, patterns of mobility can be correlated with ecological, economic, demographic, and social factors.