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Dispersal in Rodents: A Resident Fitness Hypothesis

PAUL K. ANDERSON

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**DISPERSAL IN RODENTS:
A RESIDENT FITNESS HYPOTHESIS**

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Dispersal in Rodents: A Resident Fitness Hypothesis

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SPECIAL PUBLICATION NO. 9
THE AMERICAN SOCIETY OF MAMMALOGISTS
PUBLISHED 30 MARCH 1989

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Library of Congress Catalog Card No. 88-072153

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ISBN No. 0-935868-40-2

Foreword

Rodent populations are relatively accessible for study and experimental manipulation, and behavior of at least some diurnal species is easily observed. As a result, rodents have attracted the attention of students of behavior and population biology and a massive literature has been generated, so much so that the accumulation of observations threatens to inhibit synthesis and the evolution of cohesive theory. Demographically inclined ecologists, in particular, have found rodents of interest and there has been a major focus on the role of dispersal (narrowly defined as emigration) in population regulation. I believe, as suggested by Jannett (1980), that this demographic emphasis has led to biases and misinterpretations of the available data, and has led the study of dispersal up a blind alley or, as others have put it, to a theoretical impasse (Gaines and McClenaghan, 1980).

If there is indeed an impasse, the blame cannot be laid entirely on the demographers. I propose two other villains, the first of which is the imprecise use of language. Aldous Huxley is said to have declared that language perverts thought. Huxley's point is most appropriate: vague and misleading usages have greatly hindered our thinking about the subject of dispersal. I have focused on semantic difficulties in Chapter I, hoping to lay an unambiguous foundation for what follows. The other source of difficulty, as I see it, is the too-facile assumption that because animals emigrate, there must have been direct selection for emigratory tendency. I refer to this assumption that the evolution of dispersal is founded on benefit to emigrants as "the emigrant fitness hypothesis." Chapter II deals at length with the question of whether this hypothesis is adequately supported.

In Chapter III, I advance an alternative hypothesis: the results of my attempt to approach the topic of dispersal from the perspectives of behavioral ecology and evolutionary theory. The emphasis is place on such concepts as inclusive fitness and parent-offspring conflict, and a consideration of parental strategies that extends beyond the conventional view of parental investment. I present ideas as to dispersal mechanisms on the basis of these parental strategies and their evolution, and suggest deductions that may shed new light on some demographic problems.

Chapter IV deals with the alternative hypothesis in the light of a selective review of the literature. This has been a daunting task, and one that could be continued almost indefinitely. I have tried to be reasonably comprehensive, because that is what testing the hypothesis in this preliminary way requires, but it was neither possible, nor desirable, to be exhaustive. I hope the reader will find the treatment reasonably unbiased and adequate without it becoming tiresome.

In Chapter V, I have ventured a series of predictions and possible tests of the new hypothesis. If the predictions are testable, and at least some suggested tests can be implemented, our understanding will be advanced and this book will have served its purpose, regardless of whether my alternative theory is supported or rejected.

Chapter VI is a brief concluding statement. In it I have tried to draw attention to the elements and implications that I regard as the core of the Resident Fitness view of rodent dispersal.

Like all ideas, those I have expressed could never have evolved without the work of numerous investigators, both those whose work I have cited and others not so mentioned. I am equally indebted to mammaologists whose work I may have criticized, or whose conclusions I have disagreed with, as well as those whose interpretations fit neatly into my perspective.

For critical reading of parts or all of the evolving drafts I am grateful to Kenneth Armitage, Mark Bekoff, Andrew Blaustein, Elmer Birney, John Eisenberg, Michael Gaines, Lowell Getz, Michael Johnson, Robert May, Douglas Morris, Robert Rose, Peter Waser, and two anonymous reviewers. Thankfully, not one agreed with all I have proposed. Their criticism, their willingness to give thoughtful consideration to unconventional ideas, and their suggestions are greatly appreciated.

Very special thanks go to Elmer C. Birney and Carleton J. Phillips for their editorship, and to my wife, Donna Anderson, whose proofreading and checking of citations has been invaluable. Last, but not least, I would like to express my gratitude to The American Society of Mammalogists and its Editorial Committee for the opportunity to present my ideas in the form of a Special Publication.

I dedicate this book to all those small furry travelers whose paths have crossed mine, so often to their distress. May their alleles prosper.

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I

STARTING POINTS

Arguments have been advanced for the adaptiveness of dispersal in both stable (Comins et al., 1980; Hamilton and May, 1977) and variable (Cohen, 1967; Levins, 1968) environments. The latter will most often apply to rodents because extinction and recolonization are frequent in the habitat patches occupied by small mammals (e.g., Myllymäki, 1977b; Pokki, 1981; Smith, 1980; Tomich, 1970). As a result most lineages ultimately persist only through the success of their disseminules. Similarly, environmental stochasticism dictates that the perpetuation of an allele, a gene combination, or a chromosomal arrangement requires the transfer of copies of genetic information, or of individuals that then succeed in transmitting it, to new locations (Van Valen, 1971).

Unlike the perpetuation of an allele or a population, the limited history of an individual can proceed without dispersal. Nevertheless, individual fitness will rarely be unaffected by the choice between philopatry and emigration, and although the individual's requirement for dispersal is less, the cost to the individual may be greater. If an individual emigrates, the process consumes part of a finite life span. Time spent moving may reduce the time available for reproduction, and the movement itself entails risks that must be accepted in return for uncertain rewards. Despite these costs and uncertainties individuals do disappear from their natal sites, transient individuals can be identified, vacant sites are colonized, and individuals carrying new alleles do sometimes become integrated into existing populations. What mechanisms are involved in the emigration of individuals, their subsequent wanderings, and the eventual immigration of those that succeed in reproducing in new locations? How might the genotypes underlying the behavioral phenotypes influencing these processes be selected?

The Terminology of Dispersal

Discussion of dispersal suffers from ambiguous terminology. Vague and varying usages create difficulties in communication, even an inability to understand what we ourselves are thinking or saying. Although nature is not overly friendly to precise definitions, nor bound by them, communication is dependent on precision and consistency. My objectives in the following paragraphs are to establish an unambiguous set of definitions. First, I wish to emphasize that weanlings, juveniles, subadults, adults, residents, emigrants, transients, and immigrants are classes of individuals with distinctly different status in terms of social interaction, demography, and reproductive potential. Failing to recognize distinctions among processes, and among individuals of different status in populations, can only garble our data and befuddle our thinking. Differing, and often indeterminate, classifications of the stages of individual ontogeny can be baffling. Therefore, the first set of terms has to do with ontogenetic stages that I regard as important in the study of dispersal.

Weanling.—Weanlings are recently weaned individuals that are not yet approaching adult size or sexual maturity and that limit their travels to exploration in the vicinity of the natal site.

Natal range.—Unless weanlings show the site attachment, homing tendency, and site-dependent dominance that characterize occupancy of space by resident adults, the term "natal home range" (Bondrup-Nielsen, 1985) seems contradictory. "Natal range" seems a preferable and adequate term by which to refer to the space defined by the initial travels of weanling and juvenile individuals.

Bondrup-Nielsen's (1985) point that space use goes through ontogenetic changes is important, however, because the distinction between adult and non-adult site occupancy is often overlooked.

Failure to implement such a distinction makes such definitions of "dispersal" (=emigration) as movements of individuals in which they leave their home range (e.g., Stenseth, 1983) inappropriate if the majority of emigrants have not previously exhibited the qualities which characterize occupancy of home range in adults.

Juvenile.—The term juvenile has been variously applied. Commonly it refers to pre-pubertal individuals. Following weaning, rodents may progress rapidly into and through puberty (e.g., young microtines born early in the breeding season) or delay puberty for many months (e.g., microtines born late in the breeding season). Although I visualize no clear demarcation between weanling and juvenile stages, it seems best to use the term "juvenile" to refer to a post-weanling, pre-pubertal phase of life history. Juveniles can attain adult size and establish site tenacity without being sexually competent. In some seasonally breeding species, such juveniles can make up the bulk of the population just prior to the initiation of a breeding season. I therefore define a juvenile as a post-weanling, pre-pubertal individual.

Subadult.—I define a subadult as an individual in the process of sexual maturation. Subadults are not treated in the same ways as weanlings or juveniles and can come under social pressure as puberty proceeds. Although subadults are capable of producing viable gametes, they are neither socially nor spatially established and are unlikely to breed. Puberty is often the period when parent-offspring conflict peaks and the period when offspring cease to be recipients of parental investment and come to be treated in the same way as other relatives. Although such individuals might be repeatedly encountered in the natal range, one cannot assume that they have developed the site attachment, or the associated psychological and social status, of residents.

Adult.—Most rodents are seasonal breeders and a fully grown individual might or might not be sexually active. Traditionally, adulthood has been equated with sexual maturity. If this is to be the sole criterion, an "adult" can be defined as an individual that is either sexually competent or has been so. If there are good grounds for the position that socio-spatial status is as important as sexual status, an adult is an individual that conforms to the sexual criteria above and is either established in a spatio-social context (i.e., occupies a home range) or has been so in the past. I use the term adult in this way because otherwise definitions of "dispersal" (=emigration) such as "movements of individuals in which they leave their home range" (Stenseth, 1983) are inappropriate if the majority of emigrants have not previously been spatio-socially established.

Resident.—A resident individual can be defined as a juvenile, subadult, or adult that has established a home range. In the past, tests for residency and non-residency often have not been satisfactory. Empirically, residency usually has been identified by consistent presence within a limited area. A better experimental criterion for residency is that a resident individual should attempt to "home" when displaced. Karlsson (1984) demonstrated residency as a difference in orientation in a laboratory apparatus. Overwintered and sexually active (adult), and overwintered but not yet sexually active (juvenile), *Clethrionomys* oriented toward the homesite, whereas young of the year did not. Because homeward orientation was displayed in spring, Karlsson's results indicated that juveniles had established their residency in winter.

The use of homing as a criterion by which to distinguish between residents and non-residents should be explored further. Although home range should be a dynamic concept (Madison, 1985), site tenacity and associated behaviors are a distinctive aspect of rodent ecology and must be fully taken into account.

Emigrant.—Once weaned, an individual is physically capable of leaving the natal site. To refer to any such one-way movement I will follow here a usage proposed in an earlier paper dealing specifically with microtines (Anderson, 1980); the terminology is close to that of Moore and Ali (1984). Emigration will refer specifically to departure of an individual from either its natal range or the home range on which it had been established. An emigrant is an individual in the process of departure. The important elements that define emigration are one-way movement, extraction of the individual from any reproductive and social relationships in which it has participated, and extraction of the genetic information it carries from the local gene pool. In practical terms, extraction from the previous set of social contacts can be defined as movement

beyond the boundaries of the area of previous activity that are in excess of one home range diameter. This criterion serves to distinguish between emigration and range shifts or changes of home site that are not sufficient to remove an individual from former social relationships and potential or actual mates. Beyond that limit there seems to be no reason why either distance or directionality should be specified.

Lidicker (1975) proposed two categories of emigration, which he referred to as "pre-saturation dispersal" and "saturation dispersal." The former described emigrants that moved out of an area before peak density was reached, the latter those that emigrated at or subsequent to a peak in density. Lidicker predicted that individuals in the pre-saturation category would be healthy individuals with a high potential for survival and reproduction, whereas those in the saturation category would be physiologically inferior, with low potential for survival and reproduction. It is not clear whether we should expect a bimodality or the extremes of a continuum, but Lidicker visualized pre-saturation dispersers as having "a particular sensitivity to increasing density" (Lidicker, 1975:106).

Although the pre-saturation/saturation dichotomy is attractive at first sight, I believe it should be discarded. It seems to me that the evidence reviewed below shows that young are inherently philopatric, and will be likely to maximize fitness by establishing at the natal site. Further, it is a logical and semantic trap to accept the *a priori* assumption that emigration is density dependent. I suggest emigration can be expected only when a potential emigrant perceives its physical and social position untenable (i.e., its personal environment "oversaturated"). As perceived by the emigrating individual all emigration may be "saturation" emigration. Such individual perceptions may have no relation to density as measured by a demographer.

I also find it difficult to see how Lidicker's terminology can be made operational because (from the population viewpoint) "saturation" can only be defined after the fact on the basis of whatever peak density happened to precede a decline, or by assuming a fixed carrying capacity. The alternative of defining "saturation" emigrants (or transients) on the basis of individual condition is unsatisfactory because not all ill, old, injured, starved, or socially outcast individuals are likely to be associated with peak density, and healthy individuals should be as quick to leave as unhealthy ones if their habit is destroyed. Furthermore, in practice the locations from which most transients departed are unknown and therefore the conditions from which they took leave cannot be determined.

Stenseth (1983) proposed abandonment of Lidicker's terminology on the ground that there was no theoretical reason why "saturation dispersal" should be an adaptive phenomenon. He proposed the alternatives of "adaptive (or evolutionarily stable strategy) dispersal" and "non-adaptive dispersal," referring to the latter as characteristic of "surplus" individuals. The point made by Stenseth would seem to be that movements are adaptively irrelevant unless emigrants are successful in immigrating. Stenseth's approach avoided some of the biases inherent in a preoccupation with density, but not others. Like Lidicker's terminology, Stenseth's carries unjustified implications. It is not clear to me whether the term "surplus" refers to the carrying capacity of the habitat, or to the "needs" of the population. It is reasonable to suppose that individuals may move in the face of habitat destruction, or that individuals on the verge of death may lose site tenacity. Stenseth did not, however, directly address the question of whether emigrants do gain fitness, nor did he consider the possibility that the emigration of individuals that eventually die without reproducing might benefit former associates that did not emigrate.

Perhaps the most telling point with respect to these attempts to define classes of emigrants is the absence of data. I have not found in the literature any case where the existence of two significant and distinct classes of emigrant has been convincingly demonstrated. The important point that Lidicker (1975) raised is the need to explain emigration when it appears that there are adequate resources at or near the site from which an individual departs. The alternative dispersal hypothesis proposed in Chapter III deals with this point, and seems to me to account for the observations that originally led Lidicker to propose the pre-saturation/saturation dichotomy.

Transient.—Upon emigration from a natal range or an established home range, and losing contact with mates or other familiar individuals, an emigrant becomes a transient until a site attachment is established. I specifically distinguish this definition from that of Flowerdew (1978) who defined a transient as “any individual which is emigrating or immigrating.” I regard emigration and immigration as specific states different from transiency.

Settler.—Transient status ends when a new site attachment is established. An individual can then be referred to as a settler. Settlement implies residency but it does not imply reproduction. If a transient settles in unoccupied habitat it is not required to establish itself in a resident group (i.e., to immigrate).

Immigrant.—I will use immigration to refer to the process of establishment of a settler in a new spatial, social, and reproductive context. Demographically, immigration need not imply breeding, but from an evolutionary point of view immigration implies production of fertile offspring in the new situation. In a genetic sense an immigrant has completed dispersal when such young reproduce.

Mihok et al. (1985a) used “recruitment” as a synonym for immigration. In an evolutionary sense this is misleading because recruitment does not necessarily imply movement from the natal site, whereas immigration implies origin elsewhere.

Dispersal.—Despite common usage to the contrary, I strongly believe that the term “dispersal” should be used only in its full evolutionary sense. Throughout this volume dispersal implies emigration followed by immigration. In other words it will be equivalent to “effective dispersal” (Greenwood, 1980) or “transfer” (Moore and Ali, 1984). I suggest it is best applied with the understanding that the offspring produced after immigration must be both fertile and reproductively successful.

The use of “dispersal” as a synonym for emigration is confusing, unnecessary, and generally misleading. Although this misuse of the term is unfortunately imbedded in the literature, I hope it eventually can be discontinued. Emigration is distinct from dispersal in that unless emigration is followed by immigration it is in most respects the evolutionary equivalent of death.

With the possible exception of some spermophiles, I question the need to distinguish between “natal dispersal” and “breeding dispersal” (Greenwood, 1980, 1983) in rodents. Although specific data are scanty, it is my impression that rodents generally disperse only once, or not at all. No one has shown that resident individuals forced to emigrate at the start of a breeding season (e.g., Fairbairn, 1977a, 1978a) are subsequently successful breeders (i.e., immigrate) elsewhere. Ground squirrel populations in which successfully breeding males move to new homesites at the termination of the breeding season (e.g., Sherman, 1980) may be an exception, but there is little evidence as to the success of such males in overwintering and breeding a second time. It is noteworthy that males that have not bred do not emigrate, and generally breed in the subsequent season.

I also feel that the word “disperser,” as commonly used in literature, should be avoided because of its ambiguity and its implication of goal or purpose. “Emigrant” is a simple, precise, and readily understood alternative that describes an individual departing from a natal site or home range. Similarly, “transient” accurately defines a wandering individual. If the term “disperser” has any justifiable use, it is merely as a catchall to include emigrants, transients, settlers, and immigrants whose exact status is unknown. As such, it is primarily a way of expressing ignorance about the actual status of individuals and has little scientific value.

The foregoing definitions apply to dispersal in terms of an individual. There seems to be no alternative to using dispersal in one sense for individuals and in another for populations. Within populations, dispersal, as defined above, influences the evolutionarily effective population size and the spatial distribution of an individual’s genetic contribution to subsequent generations. Panmixia, which defines a population in an evolutionary sense, is a result of continuity of dispersal. Attenuation of dispersal defines population boundaries. Between populations dispersal determines gene exchange and introduces new alleles and gene combinations. Where habitat has been vacant, dispersal may lead to founding of new populations. Krohne et al. (1984) attempted to deal with

this problem by defining dispersal as movement within a demographic unit (in practice a trapping grid) and emigration as movement out of a demographic unit. This definition of dispersal is counter to common usage in both population genetics and island biogeography and although I understand their objective I feel their suggestion is likely to be confusing and counterproductive. "Intra-population" and "inter-population" dispersal might suffice, provided the boundaries of the deme have actually been determined.

Brooks and Banks (1973), Jannett (1980), Myllymäki (1977a), Tast (1966), and others have described shifts of homesite and home range that I feel do not qualify as dispersal. In the individual sense of dispersal as described above, a range shift qualifies as dispersal only if the individual establishes a new set of social contacts and a new set of potential and/or actual mates. In a population sense, range shifts may imply dispersal only if they transfer genetic information to another population.

I would like to deal here with another term proposed by Lidicker (1975). Individuals that would otherwise emigrate may be prevented from doing so by physical or social barriers. When physical barriers are imposed as part of an experimental regime, behavioral and physiological abnormalities often result (Anderson, 1961; Calhoun, 1962b; Krebs et al., 1969). Lidicker proposed the term "frustrated dispersal" for such situations. It is not clear whether the term applies to the inability of individuals to emigrate, or to the consequences of that inability for individuals, or for populations. Bondrup-Nielsen and Karlsson (1985) regarded Lidicker's term as internally contradictory because emigration has, by definition, not occurred. I concur, and in my view it is preferable to discuss the separate phenomena of obstacles to emigration, their effects on individuals, and the consequences for populations, without use of an ambiguous umbrella term.

The emigration sink.—In the context of the definition of dispersal used here, "dispersal sink" (Lidicker, 1975) is self-contradictory. "Sink" can be used in two senses. In the individual sense the term implies absorption or dissipation of individuals: a "graveyard" (Stenseth, 1983). Individuals moving into a space in which they eventually die without leaving descendents have entered a sink. Individuals written off demographically and reproductively, have, by my definition, failed to disperse. I therefore prefer the term "emigration sink."

Complications arise when the sink concept is used in the population sense. With respect to the source population, the disappearance of emigrants acts as a "behavioral vent." Relative to that population it is of no immediate consequence whether the resulting transients enter a graveyard, join another population, or found a new population.

The common ground between individual and population viewpoints is that emigration results in the elimination of individuals. This does not, however, completely resolve the problem. Although any space into which an individual moves that is beyond the limits of the family or deme from which it emigrated serves as a "sink" from the point of view of the source population, transients, settlers, and immigrants are, in varying degree, still part of the metapopulation (*sensu* Wilson, 1973). To avoid this difficulty I will use "emigration sink" only in the individual sense.

Philopatry.—In a spatial sense, a rodent is philopatric if it establishes residence at its natal site, within the home range of a parent, or in contact with the home range of a parent. In a reproductive and genetic sense it is philopatric if it makes a reproductive and genetic contribution to the ongoing lineage or local population to which a parent belonged. This approach implies a definition of natal philopatry somewhat broader than that of Waser and Jones (1983) in that individuals establishing home ranges in contact with those of parents or other closely related residents would be considered to be philopatric in a population sense even though as individuals they have dispersed when they establish home ranges and centers of activity, and breed, at locations more than one home range diameter away from the natal site as specified above.

From the population viewpoint we are forced to think of dispersal within the population as the factor binding the population into a genetic unit, and dispersal beyond the population perimeter as a process that removes genetic information from the gene pool (emigration in the genetic sense) and introduces it to other gene pools (immigration in the genetic sense).

Territoriality and spacing behavior.—The term "spacing behavior" appears to be coming

into fashion. I have not found a reference in which a formal definition has been offered and my impression is that it has become popular as a substitute for territoriality. The essential characteristics of territoriality are a fixed area of activity, and acts by the resident that serve to evoke escape or avoidance by some class of potential occupants, leading to the exclusion of the latter (Brown and Orians, 1970). Gauthreaux (1978) suggested that territoriality implied space-related dominance which gave priority of access to a resource. He noted that status as a territory holder might involve individual recognition and might serve in reducing the costs of interaction. "Spacing behavior" seems to imply a broader scope, including individual distance and avoidance of contact, but not necessarily requiring site attachment.

Perhaps what makes "spacing behavior" attractive is that it avoids two difficulties that often cause misunderstanding with respect to territoriality. One is that animals may behave in a territorial fashion with only partial success. For example, Wolff (1985b) noted that, in microtines, exclusive home ranges may decrease in size to a minimum as density increases. He believed that at high density at least some degree of exclusivity is lost. The latter point seems open to question. In any event it is not clear that animals would cease to behave in a territorial manner, even though they have been unable to prevent overlap. The second difficulty has to do with the provision that a class of conspecifics is excluded. Many authors regard overlap of home ranges in one sex as evidence that animals of that sex are not territorial. This misses an important point. If, for example, there is overlap among male home ranges in a *Microtus* population, the overlap may be limited to less than a half dozen mutually familiar adult individuals; others (the class of unfamiliar or, possibly, unrelated adult males) may be excluded. Because a class of conspecifics is still being excluded, perhaps as a result of cooperative site-specific dominance, my view is that the behavior of the residents is territorial, as is the social system. Where site-specific dominance is evident, it may still be best to refer to behavior of residents that appears to have evolved as a consequence of its exclusion of any class of conspecifics (defined by sex, age, familiarity, etc.) as territorial behavior.

Parental investment and parental disbursement.—A semantic dilemma arises in Chapter III in the discussion of the strategies of residents toward their offspring. Trivers (1972:139) wrote that parental investment was "*any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring.*" So defined, parental investment includes the metabolic investment in the primary sex cells but refers to any investment (such as feeding or guarding the young) that benefits the young. It does not include effort expended in finding a member of the opposite sex or in subduing members of one's own sex in order to mate with a member of the opposite sex, since such effort (except in special cases) does not affect the survival chances of the resulting offspring and is therefore not *parental* investment."

The two essentials specified in Trivers' definition are increased success of offspring and parental cost in the form of restriction of the parent's further reproduction. Suppose, however, that we view parents as producing offspring as a means of transmitting parental alleles into the future, rather than as ends in themselves. From this perspective it is possible to think of both investment *in* offspring (Trivers' meaning) and investment *of* offspring. In the latter sense a parent might "invest" an offspring in perpetuation of parental alleles at the natal site (this could be called philopatric investment of the offspring) or in disseminating those same parental alleles to other locations (this could be called disseminative investment). In unstable environments parental fitness could well depend on the mix of the two. If parents do in fact behave so as to determine the fates of offspring, as I argue below, they are the effective agents in both types of investment, and both are therefore "parental."

Reviewers have argued cogently that Trivers' original meaning should be kept clear (a sentiment with which I concur), and thus I have endeavored to find some alternative term by which to refer to parental investment *of* young. Although no totally satisfactory term has turned up, I will refer, in those cases where a specific term is convenient, to the process of allocation of young to philopatry or emigration through parental acts as *parental disbursement*. One important

difference between parental investment and parental disbursement is that in the former, as defined by Trivers (1972), parents invest in offspring at a cost to further parental reproduction. In parental disbursement, expulsion of offspring may facilitate further parental reproduction.

Practical Aspects of Categorization

Applying a set of coherent and consistent definitions to the categories of animals involved in dispersal is difficult on paper and still more difficult in the field. Residents are commonly defined as individuals repeatedly captured in live traps at a set of stations within a sampling area (typically a trapping grid) for a specified length of time, or simply as any animal captured one or more times at the same or closely associated stations on an area designated as a "control" grid (e.g., Reich and Tamarin, 1980). The method positively identifies some proportion of residents. The uncertainties lie in the proportion of residents detected, and the proportion of non-residents included. Such samples may be highly biased because conventional live traps might not adequately sample the individuals present. Boonstra and Krebs (1978) and Beacham and Krebs (1980) found that close to 50% of *Microtus* present in areas trapped concurrently with conventional live traps and pitfall traps were caught only in the pitfalls. Overall, eight times as many voles were caught in pitfalls as in conventional traps, and the pitfall sample was biased toward smaller, faster-growing individuals. In enclosures more males than females avoided live traps and males that avoided live traps did so over a longer period.

Establishment of practical conventions for identification of non-residents (inclusive of emigrants, transients, and immigrants) has proven especially difficult. Identification of emigrants on the basis of simple disappearance (Hilborn, 1975) does not discriminate between emigration and death in situ. Other than disappearance, the most common criterion for non-resident status has been capture on a plot from which residents have been removed (e.g., Joule and Cameron, 1975; Krebs et al., 1978; Krohne and Miner, 1985; Myers and Krebs, 1971; Reich and Tamarin, 1980; Reich et al., 1982). The problems with this approach lie in the numerous unjustified assumptions and the superficial interpretations that have prevailed. All individuals encountered in such a "vacuum" have been assumed to have emigrated at some previous time and have been regarded as representative of emigrants. Transients have not, in most cases, been distinguished from settlers. Unless provision is made for a correction (e.g., Baird and Birney, 1982a) such samples may include an unknown proportion of residents making sorties outside neighboring home ranges. Initially, removal grid samples may also include a high proportion of individuals that were previously present but invulnerable to trapping (Verts and Carraway, 1986). Consideration of the evidence leads me to the conclusion that the individuals captured on removal grids are a mixed bag of nearby residents, transients, settlers, and immigrants. Most appear to be derived from a pool of transients whose origin and past experience are unknown. It is an enormous leap of faith to assume that a removal grid sample is representative of any specific group of individuals at the time they emigrated.

Misinterpretation of the removal grid results has been most serious where the intention was to compare philopatric and emigrant individuals originating from a nearby control plot and measure emigration rates. Even if the settler-transient component is clearly discriminated, it need not represent the original emigrant set from which it was derived. Age-specific weight, reproductive status, wounding, and aggressiveness of transients are likely to have been altered in transit, either through change in the individuals themselves (growth, experience, maturation), settlement elsewhere, habitat choice, or mortality. Further bias could result from interaction among settlers, so that they are even less likely to be representative of emigrants than are the members of the transient pool. The origins of transients could be diverse in time, distance, and habitat, and are likely to be unknown; most transients could have originated at distant localities.

The transient pool may be so large as to lead to gross overestimates of emigration rate. Boutin et al. (1985) compared emigration rate of arctic hares (*Lepus* sp.) as measured from radio-collared individuals with that obtained by the removal grid approach. They showed that the removal grid estimate of emigration rate was approximately 28 times too high.

Removal grids do not simulate immigration into an established group (Dueser et al., 1981, 1984). To remedy this Dueser et al. (1981) attempted to identify a non-indigenous component in unmanipulated populations, proposing that all individual voles first entering the trappable population above a specified body weight could be assumed to have originated external to the trapping grid. Their results, like those of Boutin et al. (1985), imply that there may often be a very large pool of transient individuals. For identification of emigrants, the approach of Dueser et al. (1981) is subject to most of the same deficiencies as the removal technique. Like the latter, it is also open to question if it relies solely on live traps to which all categories of individuals may not be equally vulnerable (Andrzejewski and Rajska, 1972; Beacham and Krebs, 1980; Crowcroft and Jeffers, 1961; Gliwicz, 1970). It can be criticized as well on the grounds that the body weight criterion is unacceptably arbitrary (Tamarin, 1984). Growth rates might vary seasonally (Schwarz et al., 1964) and, as Sauer and Slade (1986) have emphasized, seasonal patterns of change in growth rate make mass a poor predictor of age in voles. Further, Bietz et al. (1977) have shown that voles may suffer differential weight loss in live traps.

Identification of transient individuals by use of drift fences is subject to similar difficulties. Verner and Getz (1985) concluded that most individuals passing through gates in a fence were resident on adjacent home ranges. The use of enclosures with exit doors to identify emigrants (Gaines et al., 1979b) has the advantage that the origin of the sample is known. One then only needs to discriminate between true emigrants and residents making sorties beyond their normal home ranges, but this is not easily accomplished. Singleton (1985) found that many *Mus* caught in "exit" traps in fences around haystacks subsequently re-entered the haystacks.

Methods based on travel of individuals across, or occurrence in, atypical or unsuitable habitat (Beacham, 1979a; Hestbeck, 1986; Pickering et al., 1974; Tamarin et al., 1984) are subject to a bias through variations in willingness to enter the atypical habitat, enclosure effects, and the problem of unknown origin and history of the transients so identified. The filter-cropping system used by Hestbeck (1986) resulted in the classification of most large male *Microtus californicus* as emigrants, perhaps because they tended to make forays outside their ranges. Beacham (1979a) and Beacham and Krebs (1980) combined a mowed boundary strip with both pit and live trapping in an enclosure. Their results were encouraging: the sample of individuals that crossed the boundary strip was biased toward those vulnerable to pit traps. Thus the live-trap sample was biased toward sedentary individuals, the pit-trap sample toward emigrants.

Each of the techniques discussed above has merits as well as deficiencies. In part the problem has been one of not giving sufficient critical thought to what each technique does or does not do. The best approach might be through stepwise designs that begin by discriminating individuals that are fully resident and those that are not. Residents might be clearly identified through displacement of individuals over short distances from which those that had established residency would be expected to home. To my knowledge this approach has not been tested.

Even if resident and non-resident categories can be clearly distinguished in nature, the problem of discriminating between philopatric individuals and emigrants remains. To solve it, definitions must be clearly formulated. Distinctions that are based on two or more criteria will be desirable (Tamarin, 1984). Radio-tracking and isotope marking possibly have the greatest promise for identifying instances of emigration and, thus, the emigrants themselves.

Ultimately non-residents, emigrants, and non-emigrants should be discriminated within specific cohorts and even litters. Similarly, precise techniques must be devised to discriminate among transients, settlers, immigrants, and residents on exploratory forays.

Baseline Observations

Site fidelity is strongly developed in rodents. If established residents are experimentally displaced, they generally return to their home ranges, or appear to attempt to do so (Anderson et al., 1977; Bovet, 1980; Griffo, 1961; Murie, 1963; Robinson and Falls, 1965; Stickel, 1968). Settlement of displaced residents at a distant release site has been observed only rarely (e.g.,

Bovet, 1980). Home ranges appear to be important commodities to which young rodents must aspire.

Each rodent is born on the home range of its female parent but not necessarily within the home ranges of any other conspecifics. The common factor for all rodents is that life begins in the context of the mother-young unit and the maternal home range. This natal range has proven itself adequate for maintenance and reproduction, and is inhabited by one or more relatives that might benefit by altruistic behavior toward the young born there. Young might establish themselves with minimal risk and effort within the maternal range.

Most young that survive and reproduce appear to do so within a short distance of the natal site. The effective dispersal distances (*sensu* Shields, 1982) so far reported in rodent populations are not very great. Even if data are biased in favor of short dispersal distances, the high frequency of short distance movements is still significant. Because rodents appear physically capable of traveling great distances, the evident high frequency of philopatry and the predominance of very short dispersal distances suggest that rodents have philopatric tendencies and that emigration requires a causal explanation.

Fitness: What and for Whom?

Horn (1983) observed that natural selection within populations seems likely to be biased against emigration. In environments where local populations are exterminated, however, only individuals that leave their natal site can exploit the vacated habitats and found new populations. Horn illustrated his point by reference to the situation described by Gill (1978) in the red-spotted newt (*Notophthalmus viridescens*). Although the patchiness of rodent habitats is less obvious than that of pond dwelling newts, rodent habitats might be similarly discrete, the cost of moving between them could be similar to that for newts, and the stability of rodent environments could be considerably less than that of the lakes in which newts spend their early larval and adult stages. If we assume that local populations exist as discrete units, and that there is great variation in survival and reproductive success of these units, it is evident that there may be a selective advantage in dispersal. We must ask, however, whether the advantage lies with the "metapopulation," local population, resident parent, or emigrant offspring.

As suggested by Gaines and McClenaghan (1980), theories proposed to explain the evolution of dispersal phenomena in rodents can be categorized on the basis of whether they see selection as generating differential fitness among individuals (e.g., Murray, 1967) or among populations (e.g., Van Valen, 1971). The currently prevailing view is that evolution operates primarily, if not exclusively, on the basis of selection among individuals. In this essay I have focused primarily on questions of loss and gain in individual fitness and follow Stenseth (1983) in defining individual fitness as the relative number of *successful* offspring.

Fitness for whom? My focus on individual fitness does not resolve the question in favor of resident or emigrant, nor does it preclude examination of the implications for differential evolutionary success of lineages or local populations. The next chapter examines the assumption that emigrants gain fitness.

II

THE EMIGRANT FITNESS HYPOTHESIS

The expressed or implied assumption in numerous influential publications dealing with dispersal in rodents has been that emigration occurs because there is, on average, a gain in fitness to individuals that emigrate (e.g., Bekoff, 1977; Chitty, 1967; Fairbairn, 1978*a*; Holekamp, 1984; Holekamp et al., 1984; Howard, 1960; Krebs, 1978*a*, 1978*b*, 1979; Krebs and Myers, 1974; Lidicker, 1962, 1975, 1985*b*; Murray, 1967; Myers and Krebs, 1971; Tamarin, 1978). Much theory and many years of empirical investigation have been based on this assumption.

The belief that dispersal phenomena in rodents have evolved through gain in fitness to emigrants is the essential point of what I refer to hereinafter as the Emigrant Fitness Hypothesis (EFH). I think it is erroneous. It is therefore appropriate to examine the assumptions that underlie the EFH, consider the possible criteria for its falsification, and critically review the supporting arguments in the light of the available evidence.

Assumptions of the EFH

The first assumption of the EFH is that there is inherited variability in tendency to emigrate. The second assumption is that this variability exists in populations because the ancestors of individuals carrying alleles favoring emigration have gained fitness as a result of their expression. Phenotypic expression of the relevant alleles has been supposed to be either spontaneous (Howard, 1960) or responsive to environmental conditions and stimuli (most other authors).

Suggested mechanisms by which emigrants gain fitness include a higher probability of survival, access to higher quality habitat, contact with more conspecifics with the possibility of more frequent matings, wider dispersion of genetic material, greater fitness of offspring through an increase in heterozygosity, higher probability that offspring would have new and desirable genetic combinations, and avoidance of competition or of population crashes through departure from crowded habitats (Lidicker, 1962).

Falsifiability of the EFH

The EFH is not easily falsified. We can neither prove the non-existence of alleles programming individuals to emigrate spontaneously nor the non-existence of stimuli when emigrants depart from a natal site. We can, however, ask whether emigrants gain or lose fitness. If it can be shown that, on average, emigrants lose fitness the hypothesis is disproven. If we find no evidence that emigrants differ genetically from non-emigrants, and discover that the arguments for a gain in fitness by emigrants are illogical, are opposed by the bulk of available evidence, or both, the EFH comes under grave suspicion. If an alternative can be offered that provides a better explanation of the evidence, the case against the EFH is strengthened even though an hypothesis with a better fit to the data does not constitute disproof. In the following discussion I will consider the processes that have been supposed to lead to increased fitness for individuals that emigrate, beginning with the arguments for increased survival through emigration.

Increased Fitness Through Emigration: Survival of Emigrants

How do survival rates of philopatric and emigrant young compare? Philopatry has advantages that may contribute to survival (Michener, 1981). Emigrants lose these advantages. Does the average gain offset the average cost? Although the data are biased by the greater technical difficulties of measuring survival rates of the individuals that leave their natal sites (especially those individuals that move long distances), studies of populations of rodents and other small

mammals equate a high probability of survival with philopatry and a lower probability of survival with emigration (e.g., Cockburn and Lidicker, 1983; Michener, 1981; Smith and Ivins, 1983). In the only direct comparison I have found, survival of *Dipodomys spectabilis* that settled on the natal site was 50% higher relative to those that established themselves away from the natal site (Jones, 1986).

What is the immediate (pre-establishment) effect of emigration on survival? When an individual emigrates it must, for some period, become a transient. Survival rates during the travel period are critical to the argument for the EFH. The activities and fates of transient individuals are difficult to monitor; there is need for much more investigation of transients and their destinies, but the information available is consistent. Experimental studies (e.g., Ambrose, 1972; Metzgar, 1967) indicate that unestablished voles and mice are more vulnerable to predators than are residents. Observational approaches lead to the same conclusion. High disappearance rates of juvenile and yearling male Richardson's ground squirrel correlate with their relatively greater movement, and loss to predators appears to account for the high female bias in adult sex ratio in ground squirrels (Michener and Michener, 1977; Schmutz et al., 1979). Errington (1943, 1946, 1963), in his analyses of muskrat mortality, showed that most individuals killed or consumed by mink were either transients, or present in peripheral and inferior habitats. Errington argued that death of transients was so highly probable as to approach the inevitable. Korpimäki (1985) attributed the male bias among voles caught by kestrels to wider and more frequent movements of that sex. Pielowski (1962, cited in Petrusiewicz, 1966) found that European vipers preyed selectively on unestablished mice and voles. Young rodents (potential emigrants) are characteristically over-represented in prey of raptors (e.g., Beacham, 1979c). Myllymäki et al. (1962) observed that transient *Lemmus* remained in the open, behaving aggressively toward human observers (and presumably other formidable potential predators), but residents in similar situations quickly took cover. Despite the conclusion that the aggressive behavior of transients might have adaptive value in some encounters, the observation supports the concept of transient vulnerability.

Many factors are likely to contribute to lower survival of transient animals. Lack of access to prepared runways may increase vulnerability to a variety of stresses, as well as to predation. Numerous other studies (e.g., Beacham, 1979a; Bergeron, 1980; Boonstra, 1977a; Frank, 1957) concur on the relative vulnerability of unestablished microtines to predation, disease, and inclement weather. Beacham and Krebs (1980) found that *Microtus townsendii* caught in pitfall traps (a sample biased toward unestablished individuals) had more wounds and a higher incidence of botfly infestation than did a live-trap sample.

By definition, transients must spend time in unfamiliar areas. It is reasonable to assume that when traversing unfamiliar terrain, survival of transients may be affected by the efficiency with which they are able to find and utilize food and cover. Kozakiewicz (1976) attributed lower mean body weight of transient *Clethrionomys* to poor nutrition and to exposure due to lack of prepared nesting sites. Vulnerability of emigrants also may be significantly affected by social status. Presumed transients are commonly found to be socially subordinate to residents (e.g., Fairbairn, 1978b; Myers and Krebs, 1971). Subordinates tend to avoid resident conspecifics (Armitage, 1974; Clough, 1968) and may thereby lack access to resources (Baird and Birney, 1982b; Calhoun, 1963; Noyes et al., 1982). Access to resources bears on survival in many ways. Daan and Slopeema (1978) found that per-capita risk of kestrel predation was least at times when the number of active resident voles was greatest. Because subordinate rodents tend to time their activity to avoid dominants (Calhoun, 1963), unestablished individuals may be more vulnerable to predation as a result of shifts to less favorable activity cycles. Subordination to dominants may also imply habitat in which vulnerability to predators is increased. Spencer and Cameron (1983) found that *Sigmodon hispidus* inhabiting patches with less cover were subordinate to individuals inhabiting patches with better cover (their study, however, failed to reveal a significant difference in survival rates). Roberts and Wolfe (1974) produced some contrary evidence as to vulnerability to predation. In a room in which cotton rats were exposed to predation by either a domestic cat

or a red-tailed hawk, subordinate rats were taken most frequently by the hawk, whereas dominants were more often taken by the cat.

Socially subordinate cotton rats are less likely than dominants to enter either baited traps or traps scented by dominants (Summerlin and Wolfe, 1973). In large outdoor enclosures subordinate male *Mus* were less likely than dominants to occur at sites where food was provided (Noyes et al., 1982). Tardiff and Gray (1978) found that resident *Peromyscus leucopus* were food specialists, whereas immigrants were food generalists. Thus transients may find food less efficiently, spend more time seeking it, and as a consequence be more likely to be caught by predators.

Results of concurrent trapping with pit traps and conventional live traps (Andrzejewski and Rajska, 1972; Beacham and Krebs, 1980; Boonstra and Krebs, 1978) showed that unestablished voles are less vulnerable to baited live traps than are residents. Captures in pitfall traps sometimes increase sharply at the time when emigration tends to be most pronounced, although this might vary interspecifically (Boonstra and Rodd, 1983, 1984). Differential vulnerability to pitfall and baited traps may have several non-exclusive explanations. Baited traps may soon become marked by the scent of residents, particularly when traps are left in place between sampling periods. A significant possibility is that transients are less likely to investigate and utilize unfamiliar food sources, either because they lack the confidence to do so, or because confrontations with dominants are avoided and habitats with food and cover are occupied by resident conspecifics. If low vulnerability to baited traps reflects low foraging efficiency, high vulnerability to pitfall traps could indicate that transients are accident prone; accidental death or injury in unfamiliar environments could contribute to the low survival of transients (Errington, 1943, 1946).

Andrzejewski and Wroclawek (1961) found that transient voles succumbed more readily than residents to the stress experienced in live traps. A transient individual might be physiologically less competent than it would be if it were established on a home range. Any nutritional stress would be expected to increase vulnerability to climatic extremes. If an individual has become transient as a result of defeat in an agonistic encounter, further defeats are probable (Anderson and Hill, 1965). Adrenal function can be impaired as a result of repeated defeats (Archer, 1970; Vale et al., 1970). Social subordinates are likely to be physiologically stressed (Christian, 1963) and puberty, in itself, is a time of physiological stress for most individuals (Seabloom et al., 1978; Seabloom, 1985), thus compounding the total stress experienced by transients.

Summarizing, the material reviewed above includes experimentally and observationally documented vulnerability of unestablished individuals to predation as well as considerations that are more tenuous and largely unexplored. It implies clearly that transiency and lowered survivorship are correlated, and, thus, that individual fitness rarely will be increased by high survival during transiency, regardless of habitat. Logically, a transient can be expected to spend at least some time in habitat that is less than "suitable" so as soon as an individual emigrates it enters a high-risk (transient) category. Except in cases where the site of origin has become physically uninhabitable, I have not found evidence indicating that transient existence per se increases the probability of survival. The total risk depends on the duration of transiency, but survivorship of transients seems inadequate for selection of alleles that promote emigration behavior.

Increased Fitness Through Emigration: Avoiding Competition

The tenets of the EFH with respect to competition can be stated in various ways. It may be implied or explicitly stated that emigrants leave to avoid competition, that competition induces emigration, that emigration leads to reduced competition, that emigrants gain fitness as a consequence of this reduction in competition, or that the reduced competition cost experienced by emigrants selects for emigratory tendency. Still another possibility is that emigrants contribute to the success of relatives by their departure.

Murray (1967) argued that as philopatric young would face parental competition for food and shelter, young might gain fitness by emigrating. Similarly, Brown and Gibson (1983) supposed that a more distant location is always likely to be more favorable than the exact birthplace, in

part because distant locations would be free of parental and sibling competition. Moore and Ali (1984) concluded that most intersexual differences in the probability of emigrating were due to differences in intrasexual competition, and that competition underlies mammalian patterns of emigration in general. Dobson (1982) and Dobson and Jones (1985) argued that competition did not explain all mammalian dispersal patterns, but granted it an important role. Trivers (1974) pointed out that offspring are likely to lose in competition with parents, and that offspring succeeding in maximizing their own reproductive success at the natal site might be doing so at the expense of parents or siblings sharing similar genotypes and thus incur a cost in inclusive fitness.

It is clearly logical that competition among siblings and between parents and offspring can occur, and that fitness could be increased when competition is avoided. It is logical, as well, to postulate that young might be less effective competitors than fully grown individuals; this will be considered in greater detail in later sections. It is also possible that genetic similarity of parents and their offspring might intensify competition. Although parent-offspring conflict has not been intensively studied in rodents, all of the above appear to be reasonable arguments. Such considerations do not demonstrate, however, that an emigrant offspring departs the natal site in order to avoid competition, that it will encounter less competition if it leaves the natal site, or that it is the avoidance of competition on the part of the emigrants through which selection operates.

The fundamental point is whether competition becomes more or less severe when an individual emigrates. Despite the issues raised above, and contrary to the EFH, there are strong reasons to expect that an emigrant should anticipate more competition, and more damaging competition, as a result of departure from the natal site. As distance away from the natal site increases, relatedness presumably decreases. Parents and other close relatives have a vested interest (the potential gain through inclusive fitness) in the welfare of potential emigrants. Restraint may temper competition among relatives or familiar individuals, all of whom may behave altruistically. As a transient moves into a new area, competitive interactions with residents are not likely to be buffered in this way. More distantly related conspecifics resident in other habitats will lack any incentive for restraint, and will compete unreservedly in their own interest and the interests of their own relatives. By this argument both interference and resource competition could increase away from the natal area. Simultaneously, the potential immigrant, as a result of lack of familiarity with the area, is likely to be at a competitive disadvantage. Intruders, almost without exception, are approached aggressively, and defeated, by residents (Petrusewicz and Wilska, 1959).

There is evidence for this argument that competition may be significantly restrained at the natal site. Brown and Brown (1984) have shown that in the more communal jays, parents may increase their own fitness by facilitating inheritance of the natal site by their offspring. Davis (1984) found that those female *Spermophilus richardsonii* that associated with near relatives shared more of their core area with neighbors, spent more of their time feeding, spent less time in aggressive interactions and vigilance, and had higher breeding success than those not so associated. Although prairie dogs do not appear to discriminate between close kin (offspring, full sibs) and other kin (half sibs, nieces, nephews), and although the degree of nepotism varies with the intensity of competition, both sexes interact more amicably with kin than with non-kin (Hoogland, 1986). Yellow-bellied marmots show higher rates of cohesive behavior and greater overlap of foraging areas among closely related individuals (Armitage and Johns, 1982).

Irrespective of relatedness, it appears that familiarity, per se, is likely to buffer competitive interactions. Deer mice are less aggressive toward neighbors than toward strangers (Healey, 1967). In the laboratory familiar *Acomys* are more likely to share food and huddle together than are strangers (Porter et al., 1980, 1981).

Even before site-specific dominance is fully established, a potential emigrant may be a more effective competitor on the natal range than it would be on unfamiliar terrain. I know of only one study in which access to resources, as determined by competition, can be compared before and after dispersal. Unfortunately the study was done in an enclosure so that the dispersal option was limited, but the results still merit consideration. Calhoun (1963) studied a population of

Rattus norvegicus of wild stock in a large enclosure with a central food distribution area. The introduced parent stock settled and bred close to the food source. Emigrants moving out from it lost rank in competitive interactions. Their access to the central food source was reduced, and reproduction declined or ceased.

Some transients must eventually discover suitable habitat that is either vacant or characterized by low density. Because rodents interact socially, however, one can assume neither that competition is directly proportional to density nor that fitness is inversely proportional to density, as the competition argument seems to imply. Competition is a relative phenomenon.

I conclude that competition may well exist at a natal site, but is likely to be more intense and less benign elsewhere. As Greenwood (1983) has said, there is considerable evidence that the advantages of philopatry to young may often outweigh any costs of competition that are specific to the natal site. The argument that selection might operate to create emigratory tendencies because emigrants gain fitness as a result of reduced competition overlooks important mitigating factors present in philopatry, evidence that competition may be more intense elsewhere, and the low probability of finding unoccupied habitat.

Increased Fitness Through Emigration: Opportunity for Breeding

Emigration might lead to increased fitness if it were a prerequisite for reproduction, or if transients contacted more potential mates, mated sooner, or mated more often than non-emigrants (Lidicker, 1962). All of these consequences are possible. Emigration exposes individuals to environmental change and such change may be a reproductive stimulus. Laboratory experiments have shown that social and other changes in environmental conditions can serve to break down reproductive inhibitions in confined *Mus* colonies (Crowcroft and Rowe, 1958; Petrusiewicz, 1963). Sheppe (1966) found that introduction of *Peromyscus leucopus* to uninhabited islands induced unseasonal breeding.

Laboratory studies raise the possibility that philopatry may cause puberty to be delayed. In confinement, continuous close association with conspecifics delays puberty in *Meriones unguiculatus* (Ågren, 1981, 1984a), *Peromyscus maniculatus* (Dewsbury, 1982c; Hill, 1974; Terman, 1980), *Microtus californicus* (Lidicker, 1979), *M. ochrogaster* (Carter et al., 1986; Getz and Carter, 1980; Hasler and Nalbandov, 1974; McGuire and Getz, 1981; Richmond and Stehn, 1976), *M. pinetorum* (Schadler, 1983), and *Mus musculus* (Drickamer, 1974; Massey and Vandenbergh, 1980). In most cases the effect is due to pheromones produced by members of the same sex. If similar inhibition occurs in nature in these species, emigration might release maturation, resulting in earlier reproduction (Carter et al., 1986). Bronson (1979) has specifically suggested that the pheromone system that influences puberty in *Mus musculus* could have evolved as a result of its effectiveness in promoting colonization.

In a polygynous species suppression of puberty in males could, at least in the abstract, deprive the inhibited individual of a large number of possible matings. The reduction in number of matings would be less if the mating system is monogamous, but the proportion could be the same. For females the potential effects would be equivalent irrespective of mating system. Because the number of litters a female can bear has a physiological limit, delayed mating may limit the number of young primarily through the restriction set by the length of the breeding season.

Is inhibition of maturity by parental pheromones a mechanism that favors breeding through emigration? If suppression of puberty by the direct effect of adult pheromones were to enhance fitness through emigration, two requirements must be met: exposure to same-sex adults must be sufficient to induce suppression in unconfined natural populations and potential emigrants must respond to suppression by emigrating. Evidence on the first point is suggestive, but scant and equivocal. Lidicker (1979) observed inhibition of maturity in *Microtus californicus* housed in small outdoor enclosures. Wasser and Barash (1983) and Armitage (1986b) reported evidence suggestive of such inhibition in marmots.

King (1983) proposed a "mate search hypothesis" to explain emigration, based on the assumption that emigration would shorten the time to first reproduction. He suggested that at

sexual maturity *Peromyscus* and other small rodents leave the natal area to search for mates. As potential mates are generally available at the natal site, arguments for King's hypothesis, and for earlier or more frequent mating through emigration, presume either delayed maturity or postmaturity bars to philopatric mating. The key assumption in King's hypothesis is that an individual would respond to the lack of a mate by traveling in search of one. This does not seem to happen. Howard (1949) observed that when one member of a breeding pair of *P. maniculatus* disappeared the other member might remain on the home range for many months without a mate. Jannett (1982) has observed similar behavior in *Microtus montanus*. Getz et al. (1987) observed the breakup of 98 monogamous pairs of *M. ochrogaster* and determined that only 11% of the surviving partners acquired new mates. Carter et al. (1986) stated that in such cases it was rare for a survivor to move and establish a breeding unit elsewhere. Because these observations relate to residents that have lost mates they are, however, not direct tests of King's suggestion that pubertal young might emigrate in search of mates.

The evidence as to breeding condition of transient young is ambivalent. Fairbairn (1978a) found that *Peromyscus maniculatus* emigrating during the breeding season were "mainly light weight non-breeding males" and that less than 25% of either female recruits, or female transients, were in breeding condition when they first entered the trappable population. Myers and Krebs (1971), in contrast, reported that the proportion of small male *Microtus townsendii* with scrotal testes was higher on a removal grid than on the control.

Are transients in breeding condition likely to breed? The probability that an individual will mate is likely to depend on social rank. Although most tests of aggressiveness have been carried out in "neutral" arenas and should be sceptically evaluated, there are grounds for assuming that residency is likely to be associated with dominant status and non-residency with subordinate status (e.g., Turner and Iverson, 1973). Social subordination has repeatedly been directly associated with impairment of sexual function (Bronson, 1976; Bronson et al., 1973; Calhoun, 1962a, 1962b; DeFries and McClearn, 1970; Dewsbury, 1981; Huck and Banks, 1982a, 1982b; Singleton and Hay, 1983; Vale et al., 1970). Dominance and aggressiveness are positively correlated with body weight (Brenner et al., 1978; Reich et al., 1982). Comparison of body weight of resident and transient individuals has been confused as the result of the difficulty in consistently determining residency status, as well as by failure to take seasonal trends in growth and movement into account. However, if non-residents are lighter (Boonstra and Krebs, 1978; Fairbairn, 1978a, 1978b) and socially subordinate to residents (Christian, 1970; Fairbairn, 1978b; Healey, 1967; Krebs et al., 1978; Mackintosh, 1978; Myers and Krebs, 1971; Petruszewicz and Wilska, 1959; Spencer and Cameron, 1983), they are unlikely to dominate heavier competitors and usurp ranges or mating rights. The most appropriate tests of the relationship between residency and dominance so far published (Wolff et al., 1983) support the prediction that even if they are not heavier, residents are likely to be dominant over non-residents as a consequence of residency itself. Resident *Microtus ochrogaster* males drive off transient males (Carter et al., 1986) and resident *Marmota calligata* males were invariably successful in driving off intruders in 41 encounters (Barash, 1981). Subordinate males are also less effective than dominants in pheromonal activation of sexual activity in females (Lombardi and Vandenbergh, 1977). Although there are species differences (Bronson, 1963), successive exposures to more aggressive individuals can make less aggressive individuals progressively more timid.

Dewsbury (1981) found that prior residence, dominance, and greater mating success were correlated in deer mice, *Peromyscus*, in a laboratory situation. Singleton and Hay (1983) found that subordinate males sired fewer litters than did dominants in enclosed *Mus* populations. In another confined population of house mice, R. J. Wolff (1985) noted that only the founding dominant male bred initially. Subsequently only those males that came into possession of territories bred. In a seminatural experimental environment, dominant male *Mesocricetus auratus* produced more offspring than subordinates (Huck et al., 1986).

Female preference may lower the probability that transient males will mate. In laboratory tests Shapiro and Dewsbury (1986) found that female *Microtus ochrogaster* preferred dominant

males to subordinate males. However, female *M. montanus* failed to show preference. As long as female rodents mate preferentially, socially subordinate transient males are unlikely to compete successfully with resident males or to be as acceptable to resident females as are resident males with which they have mated previously (DeFries and McClearn, 1970; Huck and Banks, 1982a, 1982b; Mihok, 1981; Singleton and Hay, 1983; Webster et al., 1982). Kawata (1985b) found that all *Clethrionomys* litters for which he determined paternity were sired by males that were resident. However, Farentinos (1980) observed that unconfined female tassel-eared squirrels (*Sciurus aberti*) sought out and mated with subordinate males.

Even if transient males are unlikely to mate, the crucial test is whether philopatric males mate sooner than those that emigrate. There is little evidence as to how long a transient might wander before settling. Kozakiewicz (1976) found that the average age of transient *Clethrionomys glareolus* was 4–6 months. Cohorts born early in the breeding season predominated, indicating that animals that emigrated were slow to settle and thus slow to breed. I expect that the interval between emigration and immigration will be highly variable, especially in males, and will be influenced by habitat patchiness, season, and population density.

One exception to sedentarity in breeding males might exist in Richardson's ground squirrels in which females are philopatric but adult males rarely occupy the same area in two successive breeding seasons (e.g., Michener, 1980, 1983b). However, even this does not appear to be an invariable characteristic (Davis and Murie, 1985). Further, there seems to be no evidence as to whether males that move succeed in breeding in subsequent seasons. At present it appears that male transients are unlikely to breed and, thus, that transiency delays breeding. Males are unlikely to decrease time to first reproduction, or frequency of mating, through emigration.

Some aspects of transiency may reduce chances of mating in both sexes. As suggested above, lighter weight may indicate that as social subordinates transients may be less able to find food and more inhibited in approaching it (Calhoun, 1963). Females are likely to be especially sensitive to inadequate nutrition, which is a bar to sexual activity (Batzli, 1975; Cooper and Hayes, 1967; Sinclair, 1975; Strecker and Emlen, 1953). Spencer and Cameron (1983) found that reproductive success was lower in subordinate cotton rats occupying patches in which cover had been experimentally reduced. Tamarin et al. (1984) noted that most female *Microtus* caught in atypical (forested) habitat were non-reproductive.

It appears that establishment on a home range may be the crucial prerequisite for attainment of puberty in some species (Bujalska, 1973; Sadleir, 1965). It would be useful to know whether, as in the case of *Microtus ochrogaster*, transient females are generally unacceptable to resident males, and whether spatial and social establishment of females are consequences of mating or prerequisites to mating.

With the exception of Bujalska's (1973) study we have little field data on the relationship between establishment and first pregnancy. Bronson (1979:291) concluded on the basis of a review of literature on pheromonal cueing in the house mouse that "only after establishing a home in an adult male's territory . . . will the young female attain her pubertal ovulation with any degree of efficiency." Because successful rearing of a litter commonly requires construction of a nest or burrow, and demands access to food resources adequate to support gestation and lactation, female sedentarity should precede or be coincident with the later stages of pregnancy. With few exceptions (e.g., Myllymäki, 1977a) transient females have not been found to be pregnant.

As suggested by Morris (1982), it seems likely that time spent as a transient delays mating and represents a loss of reproductive value. Despite the laboratory data showing that the maturation of philopatric young may be delayed, the balance of the evidence weighs against the hypothesis that transients of either sex might mate sooner or more frequently than non-emigrants. Sexual maturity is commonly a stimulus to, and prerequisite for, emigration (King, 1983). An "early mating" interpretation of puberty suppression appears to make contradictory assumptions: that juveniles must mature in order to emigrate, and that they cannot mature until they have

emigrated. I believe we will eventually discover that the adaptive value of suppressed puberty lies in delaying emigration, rather than stimulating it.

Increased Fitness Through Emigration: Immigration and Breeding

In the previous section I examined the probability that the act of emigrating and becoming a transient would lead to earlier or more prolific reproduction. Here I turn to examination of the process of immigration.

Recall that in the first chapter a distinction was made between settling and immigration. We do not yet know whether settlement is a separate process that must be completed before reproduction can begin. Do transients choose unoccupied areas or do they attempt to settle near conspecifics? Is choice of site influenced by availability of a mate? If a male or non-pregnant female settles in unoccupied habitat, reproduction will be delayed until a mate appears. Settling in an established group may avoid the problems of finding or waiting for a mate, but it requires acceptance by residents. Does relatedness of the settler have a bearing on acceptance? Does acceptance entail some delay in breeding?

Ågren (1984b) observed the founding of experimental colonies of *Meriones unguiculatus* in detail. Males first established themselves in unoccupied areas and females then selected males and/or territories and became aggressive toward other males. We do not know if this pattern characterizes settling in unoccupied areas in other species.

As subordinates, transient males appear most likely to settle where no resident male is present. In such locations females are likely to be less abundant. Bronson (1979) concluded on physiological grounds that young male house mice arriving in a suitable but unoccupied habitat were likely to be in poor reproductive condition. If this is true, delay in the arrival of a mate is not necessarily wholly disadvantageous, deferring competition for mates and allowing time for physiological recovery. On the other hand, transients can become reproductively active quickly after settling in unoccupied habitat. Krebs et al. (1978) concluded that animals taken on removal grids were at least as mature reproductively as were residents on a nearby control grid.

A transient could settle in a recently vacated home range, as opposed to settling in a wholly vacant habitat. Vacancies might be taken up quickly. Price et al. (1986) reported that resident *Tamiasciurus* were replaced within hours by new arrivals. The new territories duplicated those of the former residents.

Although Bovet (1978) estimated that 30% of the woodmice (*Apodemus* sp.) that he displaced settled in the vicinity of the release site, experimentally displaced residents usually do not settle but instead return to their former home ranges. Homing success can vary with habitat (Anderson et al., 1977), but there is much evidence that homing is more advantageous for displaced residents than is settling in the areas where they are released. This probably is because transients cannot readily penetrate established groups. Dahl (1967), who released 474 *Microtus pennsylvanicus* into two inhabited 1-ha plots. In subsequent trapping the original residents were captured repeatedly, but only 31 of the introduced voles were ever captured and only five (four females and one immature male) were classified as having established themselves (i.e., were recaptured on the grids where they had been released when trapping was resumed 3 weeks later).

Direct observations support the prediction that settlers and transients have difficulty penetrating established groups (Andrzejewski et al., 1963; Armitage, 1984, 1986b; Eibl-Eibesfeldt, 1950; Halpin, 1981; Hoogland, 1981; Lidicker, 1976; Metzgar, 1971, 1979; Reimer and Petras, 1967; Rowe and Redfern, 1969). Settlers are unlikely to displace residents (Fitzgerald et al., 1981; Jones, 1984), especially if settlers are less aggressive as suggested by Fairbairn (1978b) and Krebs et al. (1978). If transients have been forced out of their natal or home range areas by aggressive conspecifics they are likely to have been placed at a psychological disadvantage by the process. Effects of defeat may be long lasting (Peters and Finch, 1961).

Residents are generally hostile toward strangers. Cox (1984) reported that *Mus* of both sexes showed a preference for odors of their own group over those of an adjacent group. Young and

Stout (1986) found that food supplements increased the ratio of transient to resident *Peromyscus gossypinus* on their study plot, but that the new arrivals were only briefly present and none settled. Where encounters between resident *Mus* and introduced "immigrants" have been observed, residents initiated agonistic interactions with the "immigrating" strangers (Hill, 1966). In such encounters the initiating individual was usually the "victor" (Parmigiani et al., 1981; Petrusiewicz and Wilska, 1959). Andrzejewski et al. (1963) reported that mice that were added to confined house mouse populations were attacked by residents, lost most fights, had low survival probability, and were relegated to permanent subordinate status. Even with the use of an "introducer" chamber that provided initial protection from attack, and with no opportunity for egress, house mice of both sexes introduced into populations in large outdoor enclosures were rarely able to penetrate established kin groups (Lidicker, 1976). Lidicker concluded that gene flow would be largely the result of formation of new social units.

The probability that a transient will be able to establish itself within a population may be determined largely by the degree of social stability and the extent of breeding activity within that population. Baker (1981a) found that six of 10 female *Mus* introduced into high-turnover populations in chicken barns established themselves and became pregnant. Myers (1974) reported that of 11 house mice making spontaneous moves from one grid to another in a hayfield, six remained at least 1 month. Most moves occurred prior to the start of breeding; none of the individuals she released into her grids during the breeding season became established, but five of seven released in the non-breeding season did so. Females may be more likely to be accepted into social groups (Anderson, 1964; Baker, 1981a, 1981b), but this probably varies with species. These results suggest that penetration of an established house mouse group might be more likely if the would-be immigrant is female and arrives in the non-breeding season and if the social structure of the target population is unstable. Although positive with respect to establishment, unstable social structure and arrival in the non-breeding season could reduce the probability of a gain in fitness.

Aggressiveness of residents toward unfamiliar individuals can vary with density. Wolff et al. (1983) found that at high density, resident *Peromyscus leucopus* and *P. maniculatus* were aggressive and behaviorally dominant (intra- and inter-specifically) on their home areas in 131 of 158 trials. When density was lower, using the same approach in the same area, Wolff (1985a) found residents were not aggressive. The explanation of the contrasting results might be that aggressiveness of residents declined as unoccupied areas became available; that transients or settlers were "expected" to avoid contact when unoccupied space was readily available and thus were not attacked; or that when transients were not able to find unoccupied spaces they turned to challenging residents, thus inducing aggressive interactions.

Individuals that are accepted socially might still fail to breed or might breed only after a considerable delay (DeFries and McClearn, 1970; Festa-Bianchet and King, 1984; Rowe and Redfern, 1969; Singleton and Hay, 1983) during which they are subordinate and occupy marginal parts of the habitat. Metzgar (1979) noted that individuals that were adult when initially encountered during a study of an unconfined population of *Peromyscus maniculatus* were likely to breed only if few established residents were present. At other times newly established adults tended to behave as "non-breeding subordinates." Schwartz and Armitage (1981) observed the fates of 790 marmots (*Marmota flaviventris*) and found that only 40 succeeded in moving to a new colony. Among these 40 settlers, only 15 appeared to have contributed genetically to their new groups.

Reproductive success also could be limited if transients settle in poor habitat. Among herbivores, individuals restricted to marginal areas might eat significantly higher quantities of toxic plant species (Bergeron, 1980) and thus lower their survivorship or reproductive competence. Even if not discriminated against by resident females, males that remain subordinate during a transitional period may lack the capacity to activate females pheromonally (Lombardi and Vandenberg, 1977).

Considering the vast literature on emigration, there are remarkably few data on immigration

rates. Those available suggest that immigrants, as defined in Chapter I, make up a relatively small proportion of most rodent populations. Berry and Jakobson (1974) observed replacement of mates in house mice on Skokholm Island but did not calculate rates. Schwartz and Armitage (1981) found that 5% of 790 marmots succeeded in moving to another colony and only 2% reproduced. Foltz and Hoogland (1983) have estimated immigration rates as 10.4% for male *Cynomys ludovicianus* and 2.8% for females. Bishop et al. (1977) reported that there was no immigration into heavily poisoned *Rattus norvegicus* populations. Boonstra (1980) concluded that at high density, microtine populations were almost closed to immigration. Turner and Iverson (1973) speculated that young were wholly unable to establish home ranges in occupied habitat during the period when litters were being produced. Hilborn and Krebs (1976), examining movement between two grids less than 30 m apart, calculated that the proportion of disappearance accounted for by immigration into a neighboring grid varied between 0.02 and 0.12% of emigrants. The proportion of disappearance accounted for by the appearance of marked individuals in a removal plot 76.2 m distant averaged 11.8%. Immigration into an "unoccupied" habitat (a removal plot) averaged twice that of immigration into the control grids. In striking disagreement with this consensus, Holekamp (1986) reported that immigration was equal to emigration in two populations of *Spermophilus beldingi* and Dueser et al. (1984) concluded that "immigration" rates in populations of *Microtus pennsylvanicus* are very high.

I conclude that breeding is likely to be delayed whether a transient settles in occupied or unoccupied habitat. The evidence suggests that immigrants are not likely to breed immediately because resistance of residents to immigration opposes or delays breeding by new settlers. This further discounts the argument that emigrants will mate sooner or more often than the philopatric members of their cohorts.

Increased Fitness Through Emigration: Establishment in Better Habitat

Brown and Orians (1970) questioned whether lower fitness in poor quality habitat had been adequately demonstrated. However, breeding success has been associated with preferred habitat by Cockburn (1981), Cockburn and Lidicker (1983), Cockburn et al. (1981), and Spencer and Cameron (1983). Diet quality, in particular, may be significant. Batzli (1986) showed that *Microtus californicus* feeding on green vegetation produced more young than those on a less favorable diet of grass seeds. Access to preferred diets would be most critical in periods of resource shortage. At such times only the most favorably situated individuals would continue to reproduce (Cockburn and Lidicker, 1983).

The supposition that emigration will result in acquisition of a site in habitat of better quality is dubious. Gauthreaux (1978) argued that dominance was a means of regulating competition and that dominance rank could be expressed in terms of the quality of the habitat occupied or the distance to which an individual dispersed from its natal site. His argument assumes that transients move to progressively less desirable habitat. Field observations support this view. Young *Clethrionomys* born in poor habitat remained there and most young born in good habitat settled in poorer habitat (Mazurkiewicz and Rajska, 1975). Lidicker (1985b) viewed favorable habitat as islands surrounded by emigration sinks; he cited evidence that the highest quality habitats are the ones most consistently occupied by *Microtus californicus*. Ostfeld (1985a) and Ostfeld and Klosterman (1986) arrived at the same conclusion. Svendsen (1974) noted that marmots classified as "avoiders" on the basis of response to their mirror images lived peripherally to the main colonies and were the least successful reproductively. It follows that highest quality habitats are least available to settlers.

Adler et al. (1984) noted that *Peromyscus leucopus* found in marginal habitats are characterized by smaller body size and lower recapture frequency. They assumed on this basis that individuals found in such habitats had been emigrants. Krohne et al. (1984) described a sink area where *P. leucopus* died out each winter. Among movements that Krohne et al. (1984) identified as "dispersal" (=emigration), 71% were into this sink. Four to nine times as many individuals moved into the sink area as moved out of it. Merkt (1981) found that newly arrived *P. maniculatus*

settled in high quality habitat only when residents were experimentally removed. Van Horne (1981) found that younger deer mice settled into habitat characterized by less proteinaceous foods and low winter survival of mice. Sullivan (1979) observed bursts of movement of *P. maniculatus* into clear-cut forest areas in late summer and fall. Winter survival was poor in these areas compared with uncut forest. Bondrup-Nielsen and Karlsson (1985) characterized movement of emigrant *Clethrionomys* as going from "optimal to low quality habitat." Calhoun (1963) and Metzgar (1971) found that under the conditions of their experiments transients settled in less favorable locations or in the interstices between the territories of established residents. Pokki (1981) observed that transient *Microtus agrestis* settled in wooded rather than in preferred grassland habitat. Observing an unconfined population of arctic ground squirrels, Carl (1971) reported that there was no overwinter survival in areas in which most transients settled.

Although Myers (1974) recorded movement of feral house mice from sparsely vegetated areas to others that she judged to be more favorable, the general trend of the evidence is that dispersal is rarely an upwardly mobile process in terms of habitat quality. Most emigrants might end their lives in sink habitats (Anderson, 1970; Calhoun, 1962a, 1963; Lidicker, 1975; Tamarin et al., 1984). Introductions into apparently suitable habitats not occupied by conspecifics often fail (e.g., Berry et al., 1982).

Even if an animal mates while transient it is unlikely to have gained in fitness through emigration if young are produced in inferior habitats as a result of matings with other transients, or matings with residents of poor quality habitat that are stressed by nutritional deficiencies, exposure, and social discrimination. Emigration is an unlikely road to increased fitness through increased habitat quality.

Increased Fitness Through Emigration: Emigrant Advantage Through Heterotic Mating

As Lidicker (1962) suggested, an emigrant that succeeds in mating will probably share fewer common ancestors with its mate than will a non-emigrant. Outcrosses of laboratory mice (*Mus musculus*) from previously inbred lines give rise to larger litters of more vigorous offspring (Chai, 1959; Green, 1966; Lynch, 1977). Hybrid vigor acquired in this way could also carry over to females of the following generation (Lynch, 1977).

A vital point that is often overlooked is that heterosis is likely to be proportional to the degree to which it has been preceded by inbreeding. It will be most evident when considerable inbreeding has occurred in the past (Green, 1966). In an ideally panmictic population the average outbred mating would not increase heterozygosity. In other words, the potential gain in fitness as a result of heterosis is greatest where there has been a tradition of incestuous mating (parent-offspring, sibling) or close inbreeding (cousin, half-sibling).

Shields (1982) has emphasized that outbreeding entails genetic costs that oppose the possible heterotic gains. Fitness of offspring resulting from outbred matings may depend on whether adaptive combinations of genes and alleles have been disorganized (Selander et al., 1969a; Shields, 1982). Pre-existing combinations would have been pruned by selection so as to be adaptive. Where this is the case, novel combinations resulting from outbreeding are equivalent to mutations insofar as they have a high probability of being disadvantageous. The chances of lower fitness might be slight if an emigrant settles near the natal site, but should increase with dispersal distance and/or difference in habitat.

There is little information on the question of heterosis as a result of outcrossing in natural populations. In a recent experiment in which incrosses and outcrosses of house mice from discrete commensal populations occupying small granaries were compared (Anderson, unpublished), outcrosses led to significant increases in mean litter size at birth. However, Martell (1983) found no differences in litter size of *Peromyscus maniculatus* in newly colonized clear-cuts and undisturbed forest. Juvenile persistence (survival?) was low in newly colonized areas. Demonstration of heterosis at a single locus has proved elusive in natural animal populations except in the case of sickle-cell anemia in man. The sickle-cell case illustrates the point that the adaptiveness of new allelic combinations depends on their appropriateness to the habitat (heterosis at the sickle-

cell locus is adaptive only where malaria is present). Outbreeding as a result of emigration may therefore produce allelic combinations which are less adaptive to the habitat than are the parental combinations.

It could be significant in this context that in some populations there appears to be a strong tendency to associate with close relatives. King (1983) reported that only five of 104 *Peromyscus* born on his study site and remaining until 37–40 days of age were ever found in the company of a non-relative.

Further experiments are needed to determine if the litter-size heterosis observed in outcrosses of house mice from granary populations can be generalized to other species and habitats. Even where such benefits occur, increased fitness is not a necessary outcome because the adaptiveness of larger litter size at birth, like that of larger clutch size in birds (Lack, 1966), will depend on parental ability to provide the necessary nourishment.

The evidence indicates that heterotic gains are possible if there has been previous inbreeding, but that if heterotic gains do occur in nature they could be negated or neutralized by the phenotypic inferiority of immigrant parents, inferior quality of the habitat into which the parents have immigrated, and low status within the new social group.

Increased Fitness Through Emigration: Avoidance of Inbreeding Depression

Some inbreeding occurs in all finite populations. Any consequent reduction in number and viability of young is the reciprocal of heterotic gain. Inbreeding can be deleterious in two ways. It can eliminate any advantage due to heterozygosity, and it can increase the probability that unconditionally deleterious or lethal alleles will occur in the homozygous condition. The probability that recessive alleles will be homozygous increases with the proportion of parental alleles shared by potential mates.

For clarity it is important to keep in mind that inbreeding may occur in the context of a family (parent-offspring, sibling, or half-sibling matings, to which the terms “strong inbreeding” or incest can be applied) or because a species is structured in such a way that deme size is small and matings with cousins, uncles, aunts, nieces, or nephews (close inbreeding) are highly probable. Although the basic problem of shared ancestral alleles is identical in both strong and close inbreeding, the social and behavioral contexts are distinct. The arguments that avoidance of inbreeding would favor evolution of emigratory tendency have been based largely on the potential genetic consequences of incestuous matings (strong inbreeding).

Avoidance of inbreeding depression has appeared to be one of the stronger and more popular arguments for the EFH. Murray and Smith (1983), for example, wrote that “kin-mating aversion may function to promote migration in most mammalian species.” Sherman and Holmes (1985) advanced inbreeding avoidance as the major adaptive force behind kin recognition. Because of the apparent strength of the inbreeding avoidance argument, and because the question has a major bearing on the alternative to the EFH that I propose, a detailed discussion of the evidence on the cost of inbreeding is appropriate.

As pointed out by May (1979) and Moore and Ali (1984), extrapolation from the evidence that forced inbreeding in the laboratory or in other captive situations reduces litter size or viability of young might have led to fabrication of elaborate hypothetical constructs with inadequate foundations. Attempts at a more balanced view (e.g., Bateson, 1983; Bengtsson, 1978; Partridge, 1983; Shields, 1982) have only recently surfaced. These efforts make it clear that the net cost or benefit is dependent on the context in which inbreeding occurs.

The hypothesis that emigration would increase fitness by avoiding the potential cost of mating with a close relative rests on three assumptions. The first is that there will be a net loss of fitness in a mating with a relative. The second is that there is a net gain in fitness through avoidance of inbreeding by means of emigration. The third is that the potential for inbreeding is great enough so that there is a need to emigrate to avoid the net cost, if any.

The theoretical basis for inbreeding cost is straightforward. All individuals carry recessive alleles that are deleterious in the homozygous condition. The more closely potential mates are

related to each other, the more likely it is that two alleles at any given locus will have been derived from the same ancestral allele and the greater the probability that any deleterious recessives present will appear as homozygotes. Much concern has been expressed with regard to costs of inbreeding in small populations of endangered vertebrates in the wild and in captivity. A summary of the results of inbreeding of large mammals in zoological parks (Ralls et al., 1979) showed that with inbreeding coefficients of 0.25 or greater the number of surviving young was lower for the majority of species than when matings took place between less closely related individuals. It is important to note, however, that this was not evident in all species studied.

With respect to rodents, specifically, the evidence for inbreeding cost is inconclusive. Consequences of incestuous matings in rodents have been examined in *Peromyscus maniculatus* (Haigh, 1983a; Hill, 1974) and in more detail for both laboratory and wild stocks of *Mus musculus* (Chai, 1959; Connor and Belluci, 1979; Falconer, 1960a, 1960b; Lynch, 1977; McCarthy, 1965, 1967; Roberts, 1981; Wallace, 1981).

Early work with laboratory stocks of *Mus musculus* compared performance of outcrosses with that of inbred stocks from which the parents were derived. Chai (1959) found that outcrosses between inbred strains tended to have lower mortality in early life and longer mean life spans than the inbred parent strains. Falconer (1960a) began inbreeding with an outbred stock derived by crossing two unrelated inbred laboratory lines. Average litter size in 30 lines maintained through full sib matings dropped by 0.49 young per 10% increase in the inbreeding coefficient; in 20 lines initiated with a double first cousin mating followed by full sib matings mean litter size dropped by 0.56 young per 10% increase. Losses in the second experiment were partitioned as 40% due to lowered maternal fertility and 60% due to reduced viability of the young.

Connor and Belluci (1979) found that although only five of 10 inbred house mouse lines survived 20 generations of inbreeding, litter size decline occurred primarily in the five lines that became extinct. In all 10 lines, survival of young in early life showed an increase up to the 0.50 level. At the end of 20 generations only one of the five surviving lines showed the anticipated degree of homozygosity. In the same series of experiments, stocks held at eight breeding pairs and thus subject to moderate inbreeding failed to show any reduction in fertility.

Because the initial stocks used by Chai (1959), Connor and Belluci (1979), and Falconer (1960a) were inbred laboratory lines, each should theoretically have been purged of deleterious lethals. If this was indeed the case the data must reflect loss of heterosis, rather than expression of recessive lethal homozygotes.

Even where inbreeding does reduce the number of first generation offspring, the consequences may be somewhat ephemeral. An important point with respect to Falconer's (1960a) work is that only half of the inbred lines showed depression in litter size. Lines showing depression died out within a few generations, whereas those not showing depression continued to produce litters as large as those expected under random mating (Falconer, 1960a). If lineages carrying deleterious recessives are eliminated almost immediately, even under laboratory conditions, surviving descendants of inbred matings could benefit sufficiently from their lack of the deleterious alleles to compensate for any initial loss in fitness suffered by the original parental pair.

Use of wild stocks of house mice in studies of strong inbreeding has provided interesting results. Like Connor and Belluci (1979), Wallace (1981) and Lynch (1977) found that inbreeding failed to produce the anticipated reproductive depression. Lynch suggested that wild stocks from which her lines were started were partially inbred so that her initial crosses (with mice collected at random from several farms) were heterotic and that heterotic maternal effects extended to the second generation. Wallace (1981) found that her wild stocks maintained mean litter size at 5.5 young through five generations of sib mating despite a 60% loss of heterozygosity. There was no appreciable reduction in fitness as measured by proportion of fertile females or mortality between birth and 15 days of age.

Under laboratory conditions, inbreeding of house mice taken from wild stocks that were presumed to be outbred thus failed to produce the amount of inbreeding depression that Falconer's (1960a) calculations would lead one to expect. This appears to imply two seemingly contradictory

conclusions: first, that the store of heterozygosity is sufficiently high so that reduction through five generations of incestuous matings does not reduce litter sizes as it apparently did in Falconer's study; second, that there is sufficient inbreeding in natural house mouse populations so that further inbreeding is of little or no consequence because most deleterious alleles and/or lineages carrying them have already been eliminated. In any case it seems evident that in wild stocks of house mice even strong inbreeding is not as costly as basic theory would imply.

Several arguments give some support to the idea of resistance to inbreeding depression in litter size. Unlike the ungulates studied by Ralls et al. (1979), many rodents produce large numbers of ova at each estrus. When larger numbers of eggs are ovulated than can be accommodated as zygotes implanting in the uterus, early losses would reduce intrauterine competition and compensation for pre-implantation losses might be possible. The reduced production of young in Falconer's inbred lines was not due to ovulation of fewer eggs; most loss of zygotes occurred prior to implantation (Falconer and Roberts, 1960) in contrast to other studies reporting more post-implantation loss. For example, in inbred lines McCarthy (1965) demonstrated significant early post-implantation losses and Hollander and Strong (1950) found average mortality was 15%, mostly in the first 3 days post-implantation. Bowman and Roberts (1958) reported a correlation between the number of eggs ovulated and the amount of intrauterine loss, but were unable to demonstrate correlation between loss and number of implantation sites. Although the evidence is ambiguous, the possibility of compensatory intrauterine survival should not be rejected.

Postnatally, reduction of sibling competition might compensate further for any inbreeding depression. Dapson (1979) found that although female *Peromyscus* with large litters weaned more young, the percent of young weaned was higher in smaller litters. Fuchs (1982) reported that in addition to higher survival, smaller litters were characterized by higher individual growth rates.

Some evidence from studies of other wild rodents also suggests that inbreeding depression could be less significant than is generally assumed. Lidicker (1979) reported normal litter sizes in confined populations of *Microtus californicus* that had been initiated with a single pair of adults. Although Hill (1974) reported that sibling *Peromyscus* pairs delayed first reproduction and had lower lifetime reproduction than did non-sibling pairs, Haigh (1983a) found that father-daughter matings did not differ from matings of the daughter with an unrelated male in the proportion of females that conceived, age of the female at first reproduction, size of litters, total number of litters, or total number of young produced. Weights of offspring at 2 days of age and survival of offspring to 21 days were less in incestuous matings, but the difference was slight.

Outbreeding creates a large effective population size (N_e). Deleterious mutations can accumulate in large panmictic units as a consequence of relaxed selection. As Moore and Ali (1984) emphasized, discussions of inbreeding depression often overlook the fact that inbreeding depression will only occur in populations that have had opportunities to accumulate deleterious mutations. If N_e is small, deleterious mutations could decline in frequency (or be eliminated) as a result of drift or selection against homozygotes, or both (Lewontin, 1962). Effective population size is unknown for most rodent populations and there is inadequate justification for the common belief that it is large. Selection pressures in rodents have yet to be extensively documented (Gaines, 1981, 1985). Therefore, neither large population size nor relaxed selection can be assumed.

Any net cost of inbreeding must be balanced against the cost of emigrating to avoid inbreeding. I suspect that inbreeding cost is relatively stable, but the cost of emigrating might be more variable as seasons and population densities change. Cost-benefit relationships have been explored in some detail in the models of Waser et al. (1986). The models predict that even in monogamous species such as *Microtus ochrogaster* it is the cost of inbreeding avoidance (rather than the cost of inbreeding) that will determine whether there will be selection against inbreeding. The models also suggest that inbreeding depression will generally be less costly than mortality during transiency, especially where mating systems are polygynous and a male forfeits few outbred matings

by mating with an offspring, but forfeits many opportunities for incestuous matings if he behaves so as to avoid inbreeding. This seems to imply that where females are strongly philopatric and both male and female ranges are stable, a male should not refrain from inbred matings. The models indicate that inbreeding by males is favored under a wider range of conditions than is the case for females.

An earlier set of modeling studies led Bengtsson (1978) to conclude that where the inbreeding coefficient equaled 0.25, inbreeding would be favored if more than 40% of males produced died as emigrants. He regarded this as an improbably high loss but for populations of small rodents it is probably unusually low. Evidence for low success of emigrant marmots has been cited above (Schwartz and Armitage, 1981). Similarly, success of emigrant male *Spermophilus parryi* appears to be on the order of 15% (McLean, 1982). L. Getz (pers. comm.) has observed success of emigrants to be in the 25–32% range in *Microtus ochrogaster*. Bengtsson (1978) calculated that a strategy that increased inbreeding by 1% would be favored if it simultaneously reduced mortality by 3%. He concluded that if a population had been inbreeding for a long time, eliminating deleterious mutants through selection, no significant gain in fitness would accrue from outcrossing. May (1979) reviewed Bengtsson's model and emphasized that the decision to emigrate or to inbreed must be viewed in a cost-benefit context and pointed to the need for more information on the kinship structure and actual costs of inbreeding in natural populations before inbreeding avoidance is used as a basis for explaining behavioral phenomena.

The models discussed above deal primarily with outbreeding costs in terms of risk of death or failure to reproduce. Another cost has been proposed by Shields (1982). He argued that because most genetic changes can be considered either individual or familial lethals, and favorable alleles and combinations can be shared by members of a family but are unlikely to be shared with members of other families, extrafamilial matings might have an average reduction in fertility (as much as 100% in the case of karyotypic mutations, and as little as 5% or less in the case of point changes).

Shields (1982) proposed that when a point mutation creates a favorable epistatic relationship in the local habitat, maintenance of the coadaptive combination will be favored through intra-familial mating. He argued that the traditional view that inbreeding is disadvantageous stems primarily from consideration of intralocus effects, and reasoned that there will be an optimal level of inbreeding for each species, based on the relative predominance of positive epistasis or inter-locus factors in adaptation. He concluded that while an optimal level of inbreeding would rarely include incest, it might involve close inbreeding within demes in which N_e was under 1,000 individuals.

The third point raised near the beginning of this section was whether the opportunity for inbreeding was sufficient for the evolution of mechanisms that function to prevent it. High inbreeding coefficients require that breeding structure be stable over several generations. For most populations, environments are so variable and the existence of individuals, families, and lineages so transitory, that there might be little opportunity for inbreeding and thus little selection for inbreeding avoidance. Even in long-lived rodents such as marmots the life span of lineages may be so short that any increase in homozygosity due to inbreeding is reversed by subsequent outbreeding (Armitage, 1984). As Greenwood (1983) has said, avoidance of inbreeding as seen in nature is perhaps as likely to be an unselected effect as it is a cause of dispersal.

The best case for emigratory behavior that effectively reduces inbreeding can be made in those ground squirrels in which reproductively successful males shift burrow sites between breeding seasons (Michener, 1980; Sherman, 1981) or in which juvenile males emigrate before their first hibernation (Sherman, 1981). Even here it is perhaps too easy to conclude, as has Holekamp (1984), that the data on emigration and immigration are consistent with the hypothesis that dispersal evolved because it could "function to minimize incest." Moore and Ali (1984) gave detailed consideration to the question of whether emigration generally accomplishes this and felt that it did not. They argued that sex differences in emigratory tendency could have evolved on the basis of inbreeding depression only in a group selection context, and emphasized (p. 95) that "since inbred siblings are more closely related than outbred ones, and hence more able to

benefit from kin selection, inbreeding can be seen as a potentially beneficial phenomenon that promotes increased altruism and sociality.” Their conclusion was that although inbreeding is not inherently maladaptive, emigration (usually necessary for outbreeding) probably is, with the result that philopatry and consequent inbreeding should generally be favored. In their view the evidence available from studies of both birds and mammals failed to support the belief that a male/female differential in probability of emigration could be explained on the basis of inbreeding avoidance. They also reasoned that if the mean dispersal distance were nearly equal for the two sexes, dispersal would have little effect on inbreeding.

If emigratory tendency has evolved because of its increment to fitness through inbreeding avoidance, I would expect the sex that has the most to lose through inbreeding to be the one with the highest emigratory tendency. In polygynous species, females seem more likely than their brothers to suffer from inbreeding depression (through proportionately higher loss of reproductive potential), yet male rodents are the emigration-prone sex. In polygynous species where males make little or no post-copulatory investment in offspring and do not sacrifice additional matings, males have little to lose through inbreeding (Smith, 1979). As would be predicted, kin recognition appears to be least developed in males, but it is difficult to argue that the sex with the least to lose through inbreeding should be the one most likely to emigrate.

There is one further argument against the importance of inbreeding avoidance that should be mentioned. Resident rodents resist immigration. If inbreeding is to be avoided and outbreeding is advantageous, then this resistance is surprising.

Summing up, inbreeding in natural populations of rodents may not be inevitably costly, may be less costly than has been conventionally assumed, or may be advantageous. Reduced litter size could be compensated for by reduced sibling competition, and inbreeding could speed elimination or oppose accumulation of deleterious alleles. Provided that an inbred mating does not occur at the cost of an opportunity for an outbred mating, any residual costs must be balanced against loss of inclusive fitness through disappearance, mortality, and/or reduced success of emigrant relatives as compared with non-emigrants, or through disruption of co-adapted gene combinations (Bateson, 1983; Partridge, 1983; Smith, 1979). The tendency to view the laboratory evidence on inbreeding depression as *prima facie* evidence that inbreeding will be avoided in nature is not justified. It is difficult to reconcile the observation that in mammals the female sex, which has the most to lose through inbreeding depression, is the least likely to emigrate. Avoidance of inbreeding is not an automatic, or even probable, source of emigrant fitness.

Increased Fitness Through Emigration: Avoidance of Population Crashes

Lidicker (1962:29) suggested that emigrants should benefit if they were able to “avoid getting involved in devastating population crashes (whatever their cause) by moving out of potentially congested places.” There is little evidence to show that a “population crash” as such should have an adverse effect on individual survival or reproduction, and it is not intuitively obvious that emigrating from a habitat occupied by a declining population should increase individual fitness as long as food, cover, and mates are available. As crude density declines, per capita resource availability should increase, and exposure to contagious disease or stress resulting from social pressure or resource depletion would presumably be reduced. Because site-tenacious or philopatric survivors could benefit as a result of reduced competition in such a situation it is difficult to see how “avoidance of a crash” could select for an emigratory tendency.

Observational evidence suggests that the number (and presumably the proportion?) of individuals emigrating tends to decline in declining populations (e.g., Gaines et al., 1979*b*). For emigration to function as a means by which individuals avoid population crashes, emigrants would have to possess a means of sensing the impending crash (response to crowding?) and leave before the decline took place. Mass emigration at this time should, however, serve to reduce the chance of a catastrophic decline, making the reasoning somewhat self-defeating. Most evidence shows that the survivors of sudden declines are in the optimal habitats, not in marginal habitats as Lidicker (1962) imagined.

An alternative argument might be that groups in which young inherited a tendency to emigrate

would be less likely to suffer "overpopulation" and therefore be less susceptible to "crashes." However, the departure of emigration-prone genotypes would strip the groups of the relevant alleles, destroying the supposed group advantage in the process.

The Evidence for Emigration-Prone Genotypes

The EFH is, at the very least, strongly linked to the concept of genetic variation in innate migratory tendency. As Lidicker put it, the EFH "requires that migratory tendencies can indeed be controlled genetically" (Lidicker, 1962:30). Inherited variation in tendency to emigrate seems to me to be essential to the "innate disperser" concept proposed by Howard (1960) and the "pre-saturation" concept proposed by Lidicker (1975, 1985a). Although some may not accept the argument that the hypothesis is totally dependent on the existence of alleles programming emigration, the importance of the issue cannot be denied.

The initial suggestion that such innate programming existed in rodents (Howard, 1960) was based on data on the distribution of dispersal distances. Available distribution data are leptokurtic. As Murray (1967) argued, and Waser (1985) has demonstrated with a model, a leptokurtic distribution of dispersal distances can be explained without a requirement for a specific polymorphism for migratory tendency.

In many invertebrate populations, specialized forms or life history stages equipped morphologically or behaviorally, or both, for long distance movement are well known. However, no studies have convincingly demonstrated parallel polymorphism in rodents despite numerous attempts to demonstrate correlations between biochemical phenotypes and tendency to emigrate. These efforts to correlate such phenotypes with emigration have either failed to show any correlation (Berry and Jakobson, 1974; Blackwell and Ramsey, 1972; Gaines and Krebs, 1971; Gaines et al., 1979b; Krohne et al., 1984; Myers, 1974; Schwartz and Armitage, 1981; Singleton, 1983) or have relied on designs that are suspect because they did not unambiguously distinguish non-emigrant and emigrant categories, or because they did not specify the source of the emigrants. I think it worthwhile to review these technical weaknesses in some detail.

The majority of such studies categorized individuals captured on removal plots as emigrants (commonly referred to as "dispersers"), and compared this sample with the original residents, or with animals resident on a "control" area somewhere in the vicinity (Baird and Birney, 1982a; Fairbairn, 1978a; Gaines and Johnson, 1982; Hilborn, 1975; Keith and Tamarin, 1981; Krebs et al., 1976; Massey and Joule, 1981; Myers and Krebs, 1971; Pickering et al., 1974; Stafford and Stout, 1983; Tamarin, 1977a). As discussed earlier, removal plots appear to draw on a pool of unestablished animals. These may be diverse in microgeographic origin (Baird and Birney, 1982a, 1982b; Desy and Thompson, 1983; Dueser et al., 1981; Krebs et al., 1976, 1978; Schroder and Rosenzweig, 1975; Small and Verts, 1983; Williams and Cameron, 1984). Typically, only a small proportion originate on any nearby "control" area. For example, Krebs et al. (1976) reported that only 15% of the animals captured on their removal plot came from the nearby control. The fraction of removal grid settlers known to originate on the control plot appears to have been approximately the same in the study of Myers and Krebs (1971). Stafford and Stout (1983) noted that only 11 of 88 *Sigmodon* captured on two removal grids came from nearby control grids. Mihok et al. (1985b) trapped a "depleted" grid for 78 marked *Microtus* that disappeared from a nearby 3.24-ha control grid. Among 106 animals captured they found only one of the marked voles. In another investigation, Mihok et al. (1985a) concluded that *Clethrionomys* appearing on a removal grid had come from an "inexhaustible" pool over a large surrounding area. Taken together, these observations support speculation that the majority of individuals captured on removal grids come from considerable distances (Boutin et al., 1985).

With a few possible exceptions (e.g., Foltz, 1981b; Foltz and Hoogland, 1983; Keith and Tamarin, 1981), rodent populations show temporal and/or microgeographic genetic variation in allelic frequencies (Anderson, 1964; Berry, 1963; Berry and Jakobson, 1975; Bowen, 1982; Chessier, 1983; Dunn et al., 1960; Gaines et al., 1978; Jannett, 1981b; Kawata, 1985a; Krohne et al., 1984; Massey and Joule, 1981; Myers and Krebs, 1971; Patton and Feder, 1981; Schwartz and Armitage,

1981; Selander, 1970a, 1970b, 1976; Semeonoff and Robertson, 1968; Singleton, 1983; Smith et al., 1978). If the vast majority (80 to 90%) of animals captured on removal plots are of unknown spatial and temporal origins, differences between total removal plot samples and any specific resident ("control plot") sample in allelic and heterozygote frequencies are to be expected on the basis of microgeographic variation alone. It is this uncertainty with regard to the origin of removal samples in space and time that invalidates the majority of resident/emigrant comparisons, because only those transients and settlers known to have originated on the control area can legitimately be used in a comparison of emigrant and philopatric members of the control population.

Most studies have also failed to take into account the reports that frequencies of biochemical variants could change seasonally due to shifts in selection pressure (e.g., Berry and Murphy, 1970; Fedyk and Gebczynski, 1980). If such variation occurs, comparison of sedentary (or philopatric) and emigrant animals must also be restricted to members of the same seasonal cohort. Studies reporting correlation between migratory tendency and biochemical phenotype have not met this criterion.

Because it is frequently cited in support of the view that emigrants are genetically different from non-emigrants, I have chosen the study of Myers and Krebs (1971) to illustrate the misinterpretations risked in the removal-grid approach. The conclusion of this study (based on comparison of the transient-settler sample on the removal area with that from the nearby controls) was that "Tf-E and Lap-S phenotypes were more common among dispersing animals" (Myers and Krebs, 1971:53). This was interpreted as indicating a possible association between the underlying genotypes and tendency to leave the control area, or equivalent areas with similar gene pools. Fortunately, the data presented by Myers and Krebs (1971) allow comparison of frequency of these alleles on the control grids (I and F) with the sample of animals actually known to have moved from grid I to the removal grid K. Data were presented for six seasonal samples for each of these alleles in *Microtus pennsylvanicus*. In only two of the six samples of males was Tf-E more common in those *known* to have moved from Grids I and F than in the control sample (residents on grids I and F). Tf-E was also more frequent in only two of six samples of females known to have moved from grids I and F to grid K. In only one of the six samples was the frequency of Lap-S higher in animals known to have moved from grids I and F to grid K (Krebs and Myers, 1971: tables 10, 11, 12; pp. 66-68). Therefore the valid comparison (emigrants vs residents from the same source) shows a trend just the opposite of that reported by Myers and Krebs (1971) in 13 of 18 comparisons.

Removal techniques recently have been criticized on still other fundamental grounds (Dobson, 1981; Krohne et al., 1984). I believe the evidence for genetic differences between emigrant and philopatric individuals based on removal studies done to date cannot be accepted. Alternative approaches to demonstration of inherent migratory tendency taken by Beacham (1979b), Hilborn (1975), and Garten (1976) are equally open to criticism, failing either to satisfactorily discriminate comparable emigrant and non-emigrant groups, or to eliminate other sampling, maternal, or environmental factors that could account for the differences observed.

As Gaines and McClenaghan (1980) pointed out, failure to find a correlation between electromorphs and tendency to emigrate does not prove that there are no alleles programming an migratory tendency. The chance of finding a correlation between any particular electromorph and such a complex behavior is indeed quite small. If the EFH in general and the specific "innate" and "pre-saturation" hypotheses proposed by Howard (1960) and Lidicker (1975) require such polymorphism, the failure of the numerous attempts to demonstrate polymorphism weakens the credibility of the EFH, but does not disprove it.

Rejection of the EFH?

The EFH has never been explicitly explored in detail. It would be good if some adherent would do this. How does the EFH account for maternal nepotism toward daughters, for the greater tendency of daughters to philopatry, or for the tendency of male dispersal distances to

exceed female dispersal distances? What behavioral predictions can be based on the EFH and are they supported by the available information?

To date, the EFH has been accepted almost casually. Its essential core is that emigratory tendencies have evolved because emigrants gain fitness relative to non-emigrants. There have been no direct and systematic tests of this assumption, although Jones (1986) has shown that philopatric *Dipodomys spectabilis* survive better than even those members of their cohorts that do succeed in settling elsewhere. I think it is fair to state that the main support for the core concept of the EFH has been the reasoning that because animals emigrate, the assumptions of an average net gain in fitness to emigrants and the existence of polymorphism for emigratory tendency must be correct. In this superficial acceptance of the EFH, the costs of emigration and establishment at a new site have been ignored (Dobson, 1982). The preceding review indicates that, contrary to the reasoning above, emigrants are unlikely to gain fitness, and the adaptiveness of emigration for emigrants, even in the best possible light, is uncertain (Festa-Bianchet and King, 1984). There is good reason to conclude, as did Moore and Ali (1984), that emigration is maladaptive for emigrants, most of which find their way into emigration sinks.

The suggestions that emigration has evolved because individuals that emigrate have a higher probability of surviving and reproducing, are likely to occupy better habitat, produce larger litters, or otherwise accrue higher fitness than conspecifics that do not emigrate have been shown to be poorly supported. Although it is possible that emigrants may avoid costs of inbreeding depression through matings with near relatives, or gain fitness through matings that produce heterotic offspring, these gains are not certain and are likely to be exceeded by the costs of emigration, transiency, and immigration. As it stands, I feel that the EFH is a poorly supported hypothesis. It should be rejected if a better one can be developed. This is not to say that emigration is never the best or the only available strategy. It does suggest that the phenomena encompassed by the term dispersal are unlikely to have evolved on the basis of benefits to emigrants.

III

THE RESIDENT FITNESS HYPOTHESIS

The dispersal hypothesis presented in this chapter rests on the propositions that emigration arises from an interaction between dominants and subordinates, that parents are dominant to their offspring, and that the behavioral processes evolved on the basis of parental benefit.

Among others, Beacham (1979*b*), Christian (1970), Gauthreaux (1978), and Krebs (1978*b*) have concluded that behavioral interaction between dominant and subordinate individuals is likely to be the proximal cause of emigration. Established residents are generally dominant over other categories of individuals. Parents are established and young are not, and it is in parental interest to control the distribution of propagules (Comins et al., 1980; Hamilton and May, 1977; Horn, 1983). Fitness is dependent not only on the number of offspring born and reared, but also on the amount of competition between parents and their maturing young, and on the spatial distribution of those offspring that reproduce. Disbursement of young is thus an important aspect of parental strategy. If, as Alexander (1974:340) stated, "the entire parent-offspring interaction evolved because it benefited one of two individuals—the parent," it follows that dispersal has evolved on the basis of the fitness of resident parents, and that parents behave so as to achieve an optimal allocation of offspring to philopatry or emigration. This approach expands, and examines with specific reference to rodents, the suggestion of Hamilton and May (1977) that parental manipulation might play a role in the evolution of dispersal systems.

The focus of this Resident Fitness Hypothesis (RFH) can be brought out clearly by an analogy. Operationally, breeding rodents can be as sedentary as plants. Like plants, therefore, their fitness is strongly influenced by the dispersal of their offspring. Like plants also, they can face competition from offspring that establish at the natal site. Angiosperm "young" (embryos) are non-motile. Plant propagules are distributed by means of adult adaptations (Howe and Smallwood, 1982); well-known examples include the height and position of seed-bearing structures, and the coatings of parental tissue that may be wing-like, hooked, sticky, nutritious, or attractive. Adult plants also have defenses (such as shading, root competition, and allelopathy) that restrict competitive establishment of their propagules (philopatry) or those of other conspecifics (immigration). Angiosperm dispersal is a matter of parental adaptation and can be analyzed in terms of parental strategies that cope with both competitive parent-young interactions and optimization of the balance between inbreeding and outbreeding (Levin, 1981; Price and Waser, 1979). The RFH proposes that emigration of young rodents similarly is based on adult adaptations, and that mobility of rodent young is exploited by established residents to control philopatry and emigration and to block immigration of less related individuals. Exploration of these ideas as to how residents behave and offspring might respond requires consideration of inclusive fitness (Hamilton, 1964*a*, 1964*b*) and parent-offspring conflict (Trivers, 1974).

The players in the dispersal game are residents and potential residents. The latter consist of offspring of the residents (closely related potential recruits) and transients (more or less distantly related potential recruits). The resident role with respect to transients is relatively simple. Transients are competitors, distantly related at best, and rarely to be tolerated even as potential mates. The parent-offspring relationship is much more complex and dynamic. Initially, offspring are the currency of classical fitness. As offspring mature, parent-offspring conflict over emigration is inherent (Horn, 1983). Maturing offspring can become both competitors and potential mates, yet they remain relatives with whom we should expect interactions to be governed by the rules of inclusive fitness. Parents can be expected to behave so as to further the survival and reproduction of their offspring, but must also behave so as to minimize competition that jeopardizes parental

reproduction, competition that threatens survival of and reproduction by their own siblings, and competition among young that threatens survival or reproduction of their own offspring. Parents and offspring of the opposite sex can offer each other matings in which a higher proportion of the alleles transmitted to the subsequent generation are identical by descent. It may be advantageous to parents, in order to minimize competition, to force offspring to emigrate, despite the heavy odds against successful establishment elsewhere. Wide distribution of the genetic contribution of the offspring may, in itself, be important enough to parents to justify the cost of lowered offspring fitness, but offspring may gain most by avoiding the cost of emigration and settling on the natal site. However, this conflict is not a static state. Optimal strategies for both parents and offspring shift with the resource supply, the residual reproductive value of the parents, and the period of seasonal breeding available to offspring. This dynamism is especially acute in species in which females are polyestrous, and maximum life span encompasses a single annual cycle. As parental investment can be expected to vary with expectation of future survival and reproduction (Clutton-Brock, 1984; Morris, 1982), parental behaviors and offspring response will be specific to successive litters as the breeding season progresses.

The immediate goals at stake in the dispersal game are resources that are "fixed" in space. These resources, to which home range and social position are the keys, are sex-specific. Resident males can compete for females; females can compete for nutritional resources, for sites in which to rear young, or for such paternal investment as the mating system makes available. These resources, however, are merely means toward the ultimate goal of both parents and offspring: relative representation of alleles, identical by descent with those they carry, in the gene pool of the future. Resident parents are constrained in their treatment of offspring by the fact that the offspring represent their primary genetic contribution and are also relatives through whose welfare there may be parental benefit. Offspring are constrained by the relatedness of their parents.

Because offspring compete in different ways and share different sets of alleles with male and female parents they relate to each parent differently. Offspring fitness is also influenced differently by siblings of the same and of the opposite sex. As offspring approach maturity their requirements and those of their parents increasingly coincide. In order to breed, an offspring might require a home range of its own (philopatric or not), but it might also benefit through helping its parents to rear further young. The least expensive way to obtain a home range, from the point of view of offspring, is to settle on the natal range. A home range encompassing all or part of the parental range could become available to one or more offspring through parental death, parental emigration, or nepotism. Forceful takeover of the parental range by an offspring is unlikely. Parental cooperation or the death of the parent is required. Parental cooperation (nepotism) can only be expected when the parent will gain more through use of that range by an offspring than by using the range itself (e.g., when parental reproductive value is so low that the offspring can contribute more to the parent's fitness than the parent can).

Small size and inferior social status limit the options open to offspring. Offspring could emigrate when given no other choice, minimize or avoid competition by delayed growth and/or maturity, or contribute sufficiently to parental reproduction to compensate for the competitive cost of continued offspring presence.

The crux of the RFH is that residents control the game. Residents can prevent transients from settling or immigrating. Residents can drive out offspring and benefit by reduced competition either through their absence or possible success elsewhere, or both. Residents also could suppress maturation of offspring and thereby reduce competition, gain benefit through the assistance or presence of near relatives, or eventually hand over part or all of the resources they control. The RFH postulates that parents with a high residual reproductive value will benefit in most cases by forcing their offspring to emigrate.

In this chapter I explore the strategies that seem likely to serve the interests of residents, and the responses of offspring in the face of these resident strategies. The first step is to review the context in which the proposed strategies and counter-strategies operate.

Habitat Heterogeneity

A basic assumption of both the EFH and the RFH is that rodents do not experience habitat as homogeneous. Instead, spatial and temporal habitat variability create dynamic mosaics on which behavioral strategies evolve and are expressed. Over the long term in a spatially and temporally variable environment, an individual's contribution to the species gene pool is dependent upon the transfer of alleles to other populations (Roff, 1975).

The role of habitat heterogeneity was first given strong emphasis by workers in the USSR (Fenyuk, 1937). Recently, descriptive models of this sort and their implications have been discussed by Anderson (1970, 1980), Hansson (1977), Lidicker (1985b), Naumov (1972), Smith et al. (1978), and Stenseth (1980). The thrust of the concept of habitat heterogeneity is that some habitat patches are relatively stable over time and support behaviorally defined groups of related individuals more or less continuously. These patches are "core" or "survival" habitats. Other patches are subject to wide fluctuations in habitability and are frequently recolonized following recovery from seasonally predictable or stochastic declines in carrying capacity. These are "colonization" habitats. Patches of the former type could produce the majority of emigrants, whereas the latter sort, and even less suitable areas, receive most of the immigrants (Anderson, 1970). The RFH can be understood and its implications worked out only in the context of a concept of habitat that is patchy in space and time. It is a point of considerable importance that emigration much exceeds immigration in the more favorable or stable patches (Anderson, 1970; Hansson, 1977). An illustrative comparison of the dynamics of two vole species in three habitat types has been published by Getz et al. (1979).

Fine scale habitat variability has been described for *Microtus californicus* by Cockburn and Lidicker (1983) and Ostfeld et al. (1985). Breeding females aggregated, and individuals remained in the trappable population longest, in high quality habitat, defined by proportionally high coverage of a perennial grass. The sex ratio was biased toward females in these high quality habitats, per-capita reproductive success was high, and immigration was lower than in poor quality habitats (Ostfeld and Klosterman, 1986).

Although some habitats are of higher quality, and some are more stable than others, neither quality nor stability are constant. Most rodents about which information is available inhabit environments that are highly seasonal. As a result, the relative advantage of r-selected or K-selected strategies can vary with the annual cycle. Evolutionary success depends to a considerable degree on flexibility and on the degree to which bets can be hedged (Stearns, 1976; Stearns and Crandall, 1981a). The stochastic component of change might be high and dispersal strategies that generate a degree of serendipity (Anderson, 1978) would be especially advantageous.

Strategies for Resident Rodents

I assume that residents will maximize their fitness by optimally regulating both emigration of offspring and immigration of other conspecifics. What factors will be important in the adaptive strategies of residents toward potential emigrants and potential immigrants?

Parents might benefit through dispersal of their offspring if the latter become established in more than one habitat patch (Horn, 1983). This could help avoid lineage extinction and permit the testing of variable offspring in different environments. The higher the risk of local extinction, the more young should be exported if the benefit is to be achieved. On the other hand parents might benefit through philopatry of their young by allowing the young to avoid the costs of emigration, provided the cost of retaining the young does not exceed the benefit of their continued presence. If, toward the end of a breeding season, parental mortality rates are likely to exceed those of young, the best parental strategy could be to suppress development of young if this functions to limit filial competition and thus avoid the need to force their emigration.

Frequent and copious emigration has been commonly predicted for r-selected species, but it has also been shown that emigration may be adaptive for K-selected species (Hamilton and May, 1977). The probability that parents can benefit by forcing emigration of offspring may vary with

the probability of nearby vacancies. The optimal strategy of residents will also vary with the qualities of the individual residents, and those of the conspecifics toward whom the resident strategies may be directed. Residents vary in sex, nature and level of sexual activity, resource requirements, age, and residual reproductive value. All other conspecifics (including offspring) are competitors for food, space, and shelter. Conspecifics of the same sex can compete for mates. Unrelated adults and their young can occupy space that could be occupied to greater advantage by relatives. Strategies toward offspring are the most complex and the most difficult to analyze.

The concept of inclusive fitness applies to these relationships, but is easily misunderstood (Grafen, 1982). Ideally, fitness might be defined as the relative contribution of the alleles making up an individual's genome to the ongoing gene pool of the population. Inclusive fitness incorporates the incremental (or decremental) influences of individuals on the reproductive success of kin, multiplied by the degree of relatedness of those kin (Hamilton, 1964a, 1964b). Successful offspring are the direct measure of parental fitness. They are also, in a sense, merely currency representing the ultimate wealth (alleles) that determines fitness.

Although the alleles offspring carry are the direct component of parental fitness, offspring are also subject to the positive or negative influences arising from parental behavior. The important point is that behavioral strategies that maximize the inclusive fitness of resident rodents require that social behaviors are determined on the basis of relatedness (e.g., critical resources may be shared to a greater extent with relatives than with non-relatives). Selection will act on this basis, favoring behaviors specific to each particular combination. With respect to their offspring, residents must compromise between maximization of their own reproductive value and gain in inclusive fitness through interactions with their progeny. As suggested by Armitage (1986b), resident fitness could be increased in patchy environments if residents behave so as to retain relatives, including direct descendants, in the natal area provided advantageous compromises are possible where parent-offspring and male-female interests are in conflict. On the other hand, if gain through realization of their own reproductive potential plus inclusive gain from the reproductive success of their offspring at the natal site is outweighed by loss due to intra-familial competition, parents can maximize fitness by exporting competing or potentially competing offspring.

The first step in assessing resident strategy is to consider the choice faced by a resident with respect to incestuous matings. Should the resident force an offspring of the opposite sex to emigrate, or allow it to settle as a potential mate? Are inbred matings beneficial because the resulting offspring are especially closely related to their parents and more likely to behave altruistically?

Calculations quantifying the options with respect to mating from the point of view of a resident parent are shown in Table 1. I have used the house mouse as an example and accepted the estimate that if a mating is incestuous there will be an average loss of approximately 0.56 young for each 10% increase in the inbreeding coefficient (based on the estimate of inbreeding cost published by Falconer, 1960a, 1960b). In a parent-offspring mating the inbreeding coefficient (F) is 0.25. As a measure by which to estimate relative potential increment to parental fitness, I have used the number of haploid equivalents of the parental nuclear genome (mitochondrial DNA is not included in my model) contributed to the population gene pool at the time of birth of the resulting litters. If the parent avoids an incestuous mating, and the offspring fails to mate (option A), the resulting litter (estimating 5.5 as mean litter size for *Mus musculus*) is represented by 5.5 parental haploid equivalents. In an incestuous mating (option B) the proportion of the parental resident's alleles represented in each zygote becomes 75% (it's own 50% contribution, plus 25% contributed by the offspring). The net gain from this 50% increase in representation, however, is limited by the assumed inbreeding cost to 11.8%.

The calculation that an incestuous mating is preferable, despite the cost of inbreeding depression, assumes that the offspring has no other opportunity to breed. If only options A and B in Table 1 are possible, a parent would benefit by choosing B, but if emigration of the offspring results in both parent and offspring mating successfully with "unrelated" partners, option C is

TABLE 1.—Gains through proportional representation versus inbreeding cost in *Mus musculus*, based on Falconer (1960).*

Mating type and inbreeding coefficient (<i>F</i>)	Expected litter size	Total resident genomes transmitted**
A. Outbred mating by resident (<i>F</i> = 0)	5.5	$(5.5 \times 2)/2 = 5.5$
B. Incestuous mating (<i>F</i> = 0.25)	$5.5 - [0.56 \times (0.25 \times 10)] = 4.1$ ***	$(4.1 \times 2) \times 0.75 = 6.15$
C. Outbred matings by resident and offspring (<i>F</i> = 0)	$5.5 \times 2 = 11$	$(5.5 \times 2)/2 = 5.5$ + $0.25 \times (5.5 \times 2) = 2.75$ total = 8.25
D. Outbred matings but probability of offspring surviving and reproducing = 0.19	$5.5 \times 2 = 11$	$(5.5 \times 2)/2 = 5.5$ + $0.25 (5.5 \times 2) \times 0.19 = 0.53$ total = 6.03

* Falconer estimated 0.56 young lost per 0.10 of inbreeding coefficient.

** A genome is defined here as the equivalent of a haploid set of chromosomes.

*** $[0.56 \times (0.25 \times 10)]$ = loss due to inbreeding depression.

clearly superior. Option C, however, assumes that dispersal has no cost. Option D is more realistic. It assumes that the chance of the offspring emigrating, settling, and reproducing (dispersal in its full sense) is only 19%. Option B (incestuous mating) then remains advantageous (provided there is no cost due to competition for food, matings, and so forth). A still less favorable option (not illustrated in the table) would be that the resident did not mate and benefited solely through reproduction by the offspring. In this case the resident's genome would be represented by a mere 2.75 haploid equivalents. This option would be advantageous only if the probability of A was very low.

Dawkins (1979) has pointed out that, as Table 1 shows, independent outbred matings by both parent and offspring outweigh the proportional gain of an inbred mating in potential total contribution of parental alleles to the next generation. The situation varies with the sex of the resident and the mating system. For a female parent, option C gives the best return. In the case of a male parent in a polygynous social system, mating incestuously need not sacrifice an outbred mating; the combination of an incestuous mating and an outbred mating are possible, resulting in 11.65 haploid equivalents.

The resident parent's "choice" of mating with or exporting an offspring must then take into account the inherent value and the possible costs. Option D illustrates one such cost (the low probability that the offspring will survive and reproduce if it emigrates). Other outbreeding costs include any time spent by an emigrant offspring as a transient and settler, and any recombinational costs such as the breakup of coadapted combinations. Inbreeding costs include those of competition and inbreeding depression.

The foregoing exercise shows that parental "decisions" respecting strong inbreeding cannot be regarded as a simple matter of avoiding inbreeding depression. The point I wish to make most clearly is that proportional gain from incestuous matings can legitimately be taken into account, along with other benefits and costs of possible strategies, and that the strategies of male and female residents are likely to differ as a result.

My earlier discussion of parental investment and "parental disbursement" becomes particularly relevant here. The definition of parental investment (Trivers, 1972; Kleiman and Malcolm, 1981) requires that parental behavior increases the probability of survival of offspring at a cost to the parent [as emphasized by Clutton-Brock (1984), it is important to maintain a distinction between energetic costs in calories expended and reproductive costs in negative effect of breeding on potential for future survival and reproduction]. If the fitness of a resident is measured at the time its offspring reproduce, a resident parent that expended energy (a parental cost) to export offspring might be facilitating its own further reproduction (at a cost to the offspring). Neither the parental expenditure of energy, nor the cost to the offspring of its manipulation by the parent, represent parental investment in Trivers' sense. They are, however, costs of parental disbursement and as such are relevant to parental strategies. To be of the greatest possible

advantage to the parent, the expulsion of offspring must maximize the reproductive success of those offspring that manage to survive the rigors of emigration and transiency and reproduce.

If parenting is a selfish activity in an evolutionary sense, the same kind of argument applies to other resident options. Suppression of maturation of young by adult (parental) pheromones has been put forward as an adaptation that functions to force young to emigrate. Is it any less logical to consider suppression as functioning to limit competition from offspring while the parent's reproductive value is high, simultaneously conserving the young in the natal area, either as helpers or to avoid the costs of their premature emigration? If the probability of emigrant survival is very low, retention of young and either suppression of sexual development or incestuous mating will be the best strategy. Parents should force offspring of the opposite sex to emigrate, however, if the cost to the parents' own reproduction through filial competition exceeds the net gain of retaining philopatric offspring. The outcome of the equation will be determined in part by the residual parental reproductive potential (Morris, 1982). Offspring should be exported when the parent's residual potential is high relative to a high competitive threat and a low potential inclusive contribution through the offspring. As parental potential declines relative to the potential reproduction of retained offspring, parents should behave so as to encourage philopatry. Parental strategy might also vary with site quality. Parents occupying high quality sites would gain most in fitness by passing those sites on to their offspring. For every resident of a high-quality site there may come a time for nepotism.

As the young approach puberty, the close parent-offspring relationship weakens and offspring might be perceived merely as relatives. The behavior of residents can no longer be viewed exclusively from the perspective of parental investment, but must be considered on the basis of the impact of competition versus the potential gain through inclusive fitness. Residents, having fulfilled parental duties, must defend resources required for their own residual reproduction, provided their former offspring cannot contribute more to parental fitness than can the parents themselves. In either event, it is important that matters be managed altruistically. As Morris (1982) suggested, export of propagules should be conducted by the parent in such a way as to minimize the degree to which the fitness of the offspring is compromised. If young are forced to leave, it is to the benefit of both residents and their offspring that the parting be peaceful. Wounding, physical or psychological, represents a potential cost to the offspring's fitness and is therefore costly, on average, to the parent as well.

Dispersal (emigration followed by immigration, including reproduction) of a propagule of either sex, from the parental viewpoint, represents a successful gamble. Is it better to gamble with sons, or daughters? This will depend on both the cost of the offspring (parental investment) and the return on a particular strategy (reproductive success of offspring, and any inclusive contribution to parental fitness). In some mammals males grow much larger than females and are relatively expensive to produce. This could have a significant effect on parental strategies (Clutton-Brock et al., 1985; Trivers and Willard, 1973). Even though rodent mating systems are commonly polygynous, sexual dimorphism in size and morphology is less obvious than in red deer, and it has been less well studied. Differences in growth rates and body size may not become apparent until after weaning (e.g., Drickamer and Bernstein, 1972; McClure and Randolph, 1980). However, McClure (1981) found, as predicted by Trivers and Willard (1973), that nutritionally stressed female woodrats weaned more daughters than sons. Male and female offspring might, therefore, differ in cost to the mother and, on that basis, should be valued differently as disseminules.

The sex of an offspring can determine the potential benefit of a strategy to parents, the timing of the return on parental investment, and the odds that the benefit will be forthcoming. Parental strategies should vary with potential benefit, as well as with the cost of the offspring. Sons and daughters contribute equivalent quanta (0.25) of the autosomal genomes of each of their parents to a mating. A daughter has a potential for only a few matings and these will be separated by intervals of pregnancy and lactation. In polygynous and iteroparous species with a short breeding season and low post-breeding survival, a successful son is capable of more numerous matings.

As expressed by Carl (1971), a son completing the dispersal process can make a "jackpot" contribution to parental fitness. Whether it is more advantageous to export sons, however, will depend on the relative chances for success of male and female disseminules. If variance in success of emigrant male offspring is higher than that of females (as it may be if sons move farther, take more risks, and are less likely to immigrate) export of sons may be no more advantageous than export of daughters.

Although parental strategies should be conditioned by the return on disbursement of young, as well as by that on investment in young, I suspect that the average net value of offspring, after disbursement "decisions" have had their effects, should be equally divided between male and female offspring. Fisher (1958:159) concluded that at the moment when parental expenditure on behalf of young ceases, "the total reproductive value of the males . . . is exactly equal to the total value of all the females, because each sex must supply half the ancestry of all future generations of the species." This same reasoning should apply with respect to disbursement strategies, and parental disbursement behaviors should be adjusted so as to generate an equal return, through sons and daughters, in terms of contribution of parental alleles to future gene pools. If, for example, high potential success of emigrating sons is only partially counterbalanced by high costs of male emigration, parents should make up the difference by nepotism toward daughters.

I predict, on the basis of the above, that the strategies by which resident males and females maximize fitness can be expected to be specific to both the sex of the resident and that of the offspring. An offspring of the same sex is more likely to compete with a parent than an offspring of the opposite sex. Offspring are less significant as competitors to their parents prior to sexual maturity. Therefore it would be advantageous to parents to exercise control over the sexual maturation of progeny of the same sex. Pheromonal means of regulating maturation of young might serve as a way of regulating competition and thereby deferring disbursement decisions.

Because transients are less closely related to residents than are the residents' own offspring, they should be prevented from immigrating if the cost of competition with the residents or their offspring exceeds possible benefits, such as those that might accrue from outbred matings. Furthermore, because resident strategies are specific to the sex of both resident and offspring, the strategies of male and female residents toward offspring could be in conflict (Armitage, 1982*b*, 1986*b*) and it is appropriate to examine separately, and in detail, the strategies by which males and females allocate young to philopatry or emigration.

Strategies for Resident Males

In a situation where food and cover meet minimal requirements and males contribute little beyond insemination to the production of offspring, male strategies ought to be founded on securing and defending copulatory rights to one or more females.

Wittenberger (1980) postulated that mammalian polygyny evolved on the basis of female sociality. He suggested that female aggregation led to selection for males that successfully associated themselves with female groups. Matrilineal clusters appear to be common among rodents (e.g., Armitage, 1986*b*; Jannett, 1980) and might turn out to be the general rule. Males of most rodent species should therefore be responsive to female patterns of spacing (Armitage, 1986*b*; Greenwood, 1980) and male strategies therefore could be expected to vary with female defendability and with assurance of paternity.

For polygynous rodents, paternal investment is not likely to be supplied at the cost of passing up additional matings (Trivers, 1972). The benefits of paternal care favor monogamy in only a few rodent species, such as beavers (Busher and Jenkins, 1985), beach mice (Blair, 1951; Foltz, 1981*b*), and prairie voles (Getz et al., 1981; Thomas and Birney, 1979).

Defense of space by males is advantageous insofar as it enhances or guarantees exclusive access to females and assurance of paternity. How does this translate into strategies of resident males toward male siblings, sons, and male transients? If they can do so, individual males should benefit by excluding all other sexually mature males. Where individual defense of space is ineffective,

cooperative defense by several related males might still be advantageous, with or without a dominance hierarchy, particularly if the males forming a cooperative group were relatives and could benefit through inclusive contributions to fitness. This potential should be highest among male siblings, or between fathers and sons.

At sexual maturity, male offspring become potential competitors for the limited supply of copulations available. Because sons are able to contribute only half as many of a male parent's alleles to a mating as the male parent can contribute, it is likely to be in a resident male's interest throughout most or all of his sexually active life to cause sons to emigrate, or to prevent them from mating if they fail to emigrate.

Resident males have greater cause to repel potential male immigrants than they do to expel pubertal sons. Potential male immigrants will share fewer alleles with resident males than do sons, might have the potential to block recently established pregnancies, and might behave infanticidally toward young sired by a resident male. In the process of establishing themselves, immigrant males might also cause premature emigration of the resident male's sons. Resident males should behave so as to repel male immigration during, and in anticipation of, the breeding season.

The strategy of a breeding male toward daughters should reflect the fact that daughters represent potential matings. Paternal males will benefit if daughters remain on the natal range and become sexually mature at an early age. As I have shown, a polygynous male has little to lose in an incestuous mating even if the high proportional representation of the paternal genome fails to fully compensate for inbreeding costs. Emigrant daughters represent lost copulations. Smith (1979), discussing father-daughter mating in fallow deer, has treated incest as a form of altruistic behavior on the part of the female. Assuming the ability of a male to mate with any other available female is unaffected by an incestuous mating, Smith (1979) reasoned that in an outbred population the male risks loss of fitness only if the coefficient of inbreeding depression is at least 0.33. If persistent inbreeding has reduced the frequency of deleterious lethals, the level at which a male will lose fitness is proportionately reduced. Daughter success elsewhere lacks the jackpot potential of male offspring. Therefore resident males should be less likely to cause daughters to emigrate than sons.

How should resident males behave toward transient females? In polygynous species resident males should not inhibit female immigration because transient females represent potential copulations and these should be free of any inbreeding costs. In monogamous species, behavior of a mated male toward transient females should be influenced by the degree to which such females represent threats to previous or future paternal investment.

Implications of Strategies Postulated for Resident Males

A great deal of research effort during the past 35 years has been based on the assumption that male aggressiveness would prove to be a significant factor in limiting population density. Postulated mechanisms include death or morbidity arising directly from agonistic interactions (Southwick, 1955a, 1955b), physiological responses to such interactions (Christian, 1963), establishment of dominance hierarchies leading to expulsion or inhibition of subordinates (Christian, 1970), inhibition of immigration (Healey, 1967; Sadleir, 1965), emigration of "surplus" individuals (Lidicker, 1975), and selective pressures leading to maladaptive shifts in gene frequency (Chitty, 1967; Krebs, 1978a, 1978b). The assumption about male aggressiveness was founded on the observation that sexually active, unfamiliar males fight when forced to face each other in an arena. Combat under these peculiar circumstances is a logical outcome of male competition for copulations but it need not be directly relevant to the behavior of resident males with respect to sons, or transient males, in nature. The RFH postulates that such combat is abnormal, particularly where father-son contests are involved.

Contrary to the assumption that has guided so much past research, the RFH predicts that male aggression will only rarely have a significant restraining influence on population increase. Population growth in polygynous species could mean that there will be a larger number of potential copulations available to a resident male. Male fitness would be increased as a result of

a local increase in female density and any male behavior that would restrict population growth would be selected against. In such a scenario males would lose fitness by expelling female offspring or resisting female immigration. Export of sons and exclusion of transient males would only partially counter the increase in density through production of young, because young males become competitive threats only at maturity. According to the RFH, resident males should behave to resist increase in density of related or unrelated females only if shortages of food and cover threaten prior paternal investment sufficiently to outweigh the gain that would be derived from increased female availability. Similarly, sexually inactive male relatives should be excluded only if prior or future investment is threatened by their presence. Male defense of space should be more evident in monogamous species because of the value of protecting a relatively high level of paternal investment in young.

Male aggressiveness might, on the basis of the RFH, have a significant effect on pre-breeding emigration of males. If females reach estrus more or less simultaneously when a breeding season is initiated, males can most efficiently attend to the business of locating and mating with receptive females if mating rights have been settled previously. Male competition prior to the breeding season could establish a hierarchy with respect to copulatory privileges and/or force emigration of subordinate males.

Once estrous females cease to be available as the end of breeding activity approaches, and/or resident males' residual reproductive values decline, the RFH predicts that male nepotism toward male offspring should occur. This is because males with low expectations of breeding in another season would lose fitness by forcing the costs of emigration on sons that might be able to claim mating rights at the natal site in the new breeding season. Males cannot be certain of paternity, but if males sharing the same or neighboring space are relatives, tolerance of young males might extend to all potential close relatives. If resident males would benefit near the end of their own reproductive lives by tolerating settlement of young males born nearby, any residual density-limiting effects of male aggressiveness are predicted to decline sharply at this time. Establishment of sons and transient males is predicted to contribute to the end-of-breeding increase in density.

Strategies for Resident Females

Females are not likely to have to compete for copulations. Instead, resident female fitness may be limited by competition for the nutritional resources required for gestation and lactation and for territories that will provide such resources along with secure nest sites for their litters. Females should choose among potential mates, but because resources can determine the survival and/or success of an entire litter, females should give priority to habitat choice over mate choice. Further, paraphrasing a conclusion reached by Alexander (1974), if females make a greater per-offspring investment than do males, they should be proportionately more influential in controlling the emigration of those offspring. According to the arguments summarized by Wittenberger (1980), the behavior of high-ranking females should control the size and composition of any social groupings.

Because female requirements change over the course of estrus, pregnancy, parturition, and lactation, female behavior toward potential emigrants and potential immigrants can be expected to vary with stages of the female-reproductive cycle. Emigration induced by resident females might coincide with the peak of female aggressiveness. This occurs during lactation (Ostermeyer, 1983). In monestrous species and also at the start of breeding in polyestrous species emigration induced by resident females could result in a well-defined pulse of emigrants.

If female strategy reflects resource needs, resident females should be more responsive than males to food shortage and more active than males in defense of space containing resources. Perceived or predictable shortages ought to lead females to behave so as to induce emigration of offspring whose competitive roles outweigh their contribution to maternal fitness. Sexually active daughters represent a greater threat to resources required by resident females than do sons. Why, then, are females more nepotistic toward daughters than toward sons? In the absence of competition for matings or resources, resident females should conserve daughters (i.e., avoid

the loss of fitness inherent in the high risk and low gain emigration equation) and behave nepotistically toward them. Females ought to induce emigration of daughters only when resource shortage becomes an overriding threat to residual maternal reproductive value. Sons should be preferentially exported when the breeding system is polygynous and at times when the probability is high that a successful son will mate soon and mate often. If male emigrants have an advantage in potential total matings and/or dispersion of matings in space, females may respond to resource shortages selectively, expelling sons before expelling daughters. If the preweaning cost of producing male offspring is greater than the cost of producing daughters, maternal females that respond to nutritional stress by favoring daughters before weaning (Clutton-Brock et al., 1985; Trivers and Willard, 1973) should behave so as to conserve sons and export daughters after weaning.

Female strategy should also reflect mate choice. In polygynous species any mating in which there is a net loss through inbreeding depression will represent a more significant proportion of a female's potential lifetime reproductive investment than is the case with a resident male. Sons will also be less attractive as mates than reproductively proven and familiar males that have demonstrated their effectiveness as mates and their competitive ability in contests with other males. Previous mates are likely to be effective in preventing immigration and reducing any chance of pregnancy block or infanticide. Therefore, I think it unlikely that females will show mating preference for sons over older resident males who have sired their previous litters. They might, however, be likely to conserve sons as future mates in the absence of resident males with whom they have mated previously. If pair bonding and paternal care are unimportant, females might also hedge against poor mate choice through multiple paternity of their young, but this should not significantly affect resident female strategy with respect to expulsion or retention of young of either sex in the natal area.

Female residents, like males, should expel offspring with as little detriment to the young as possible. The behaviors encouraging emigration of daughters might promote maternal fitness most effectively when maternal reproductive value is high and emigrant daughters have the greatest chance of finding available habitat. It has been suggested that the optimum time to export young is when density is low and carrying capacity is expanding (Morris, 1982). At times of increasing or surplus resource availability, however, the advantages of maternal nepotism may be high. Maternal females then may optimize by shifting nest sites or moving to a contiguous area, if they are better able than their daughters to accept the costs of movement and to establish themselves on the periphery of their former ranges. Abdication might also be an advantageous strategy when a female's residual reproductive value is low. Such maternal behavior would serve to minimize cost to daughters, maximize daughter success, and retain the opportunity for inclusive gains through further altruism. If abdication is primarily a way of assuring resources to offspring, females would not be predicted to make such moves to benefit sons.

Resident females have reason to resist incursion of unrelated conspecifics of any sex and age. Other females and their potential offspring represent the greatest threats to a resident female's resource base. Resident females should be especially hostile toward transient females, but resident females should be tolerant of female neighbors and their young to the extent that they are related.

Resident females also should be aggressive toward male intruders; contact between resident females and transient males should be limited. To whatever extent experimental induction of pregnancy block and male infanticide can be extrapolated to nature, unfamiliar males are threats to current or prior investment. If possession of a home range is a useful criterion for choice of a mate, transient males should also be repelled as less desirable than established, familiar, resident males.

Implications of Strategies Postulated for Resident Females

The differences between male and female strategies have significant consequences. The copulations on which male fitness depends come in discrete and mobile packages (females). The actual copulatory opportunities are ephemeral. The resources of prime importance to females

are generally more widely and thinly dispersed, fixed in space, and continuously (though variably) present and in demand. Therefore the resources needed by females require territorial defense and are amenable to it. If potential immigration greatly exceeds carrying capacity (Redfield et al., 1978b), then strong selection for defense of space by females can be anticipated. It follows that female territorial behavior, because it functions to assure the resource base available for their own and perhaps their daughters' reproduction, might be responsive to contacts with neighbors or transients (perceived density?). The RFH predicts, therefore, that emigration-inducing and immigration-restricting behaviors of females ought to be more sensitive to crowding than those of males. Because females have a means (pregnancy) of anticipating increased resource requirements (during subsequent lactation), female behaviors that induce emigration could rise prior to attainment of peak density. As resources wax and wane in seasonal environments, female-governed emigration should show concordant trends.

As potential immigrants of either sex threaten the resource base on which the past, current, and future reproductive value of a resident female depends, resistance of resident females to immigration in both monogamous and polygamous mating systems should be effective in preventing increase in population density through immigration. Such resistance might be density dependent (increasing with perceived density). Territorial behavior of females, when linked to resource availability, is a potentially significant factor in limiting increase in population density. The effects of female control of immigration and emigration should be more significant demographically and more complexly seasonal than those of males.

The RFH predicts that male immigration, opposed by residents of both sexes, is likely to be rare. It follows that pregnancy block and male infanticide are unlikely to be of any demographic significance.

Conservation of daughters by resident females leads to matrilineal groupings. As a consequence, the maternal female could benefit by the cooperation of close relatives. The major advantage of female aggregation in ground squirrels has been thought to be protection against predators through giving alarm calls that alert kin (Michener, 1983b). On the basis of the RFH it might be assumed that matrilineal groupings in ground squirrels arise as a result of conservation of daughters and the inclusive benefits of having amicable neighbors, and that alarm calls are a secondary development in habitats where predators, and warning calls, can be detected at a distance.

The common failure to demonstrate density-dependent emigration (Gaines and McClenaghan, 1980) should not be unexpected if only crude density (i.e., total individuals per unit space, irrespective of sex and age classes) is measured. If the RFH is correct, more intelligible results should be obtained if sex and age effects are carefully considered, and the relationship between emigration and density of breeding females per unit of space or per unit of some measurable nutritional resource is subjected to close examination. Unlike male aggression, female aggressiveness should have the potential, under all mating systems, to act as a density-limiting mechanism by inducing emigration and preventing immigration.

Strategies for Offspring

To the best of their abilities, offspring must cope with their environments in ways that maximize their own fitness. The RFH approach views the pre-existing strategies of parents and other residents as major environmental factors in the context of which offspring are forced to respond. I emphasize that the topic here is offspring fitness, not emigrant fitness. The latter term applies only to strategies an individual might adopt as it is forced to emigrate.

To recall another point raised in Chapter I, weanlings, when they leave the nest, cannot be equated with residents on established ranges. The transition from nestling through weanling, juvenile, and subadult to established resident is a critical process in the life of an individual rodent. A home range is established during some period after weaning. We know almost nothing about the process by which home range and its associated psychological security, social dominance, and tendency to return if displaced, are acquired. I believe it is extremely important to recognize that most animals that emigrate are leaving from a natal site, not from a home range.

Establishment at or near the natal site is likely to be advantageous (Jones, 1986). The natal site has been proven adequate for survival and reproductive success: residents may have constructed burrows or runways or accumulated food stores; it is an area inhabited by near relatives, which could benefit by altruistic behavior and which could behave altruistically in turn. The potential emigrant has some familiarity with the local area. It can have no knowledge of unexplored habitat elsewhere. Philopatry avoids costs in energy, time, and risk. Whether or not local resources have been depleted by use, the natal site has at least some of these advantages over other areas.

The RFH assumes that the primary strategy for offspring is to behave so as to maximize the opportunity for philopatry. Philopatry (defined as establishment within breeding distance of the natal site) might be especially crucial to survival in those rodents that depend on hibernacula or communal stores for survival through unfavorable seasons. This tendency of offspring to settle on the natal site, or as near to it as possible, may be in conflict with the interests of residents, including parents (Horn, 1983).

As Trivers (1974) emphasized, young are likely to be ill-equipped, physically or psychologically, to contest territorial rights against aggressive and established parents. The young face a dilemma: confrontation with unrelated conspecifics, whose actions will be unconstrained by the dictates of inclusive fitness, will be even less likely to be successful. The strategies of young must combine behaviors that maximize the possibility of local establishment, but also optimize the outcome of emigration if it is forced on them.

Inbreeding depression resulting from the homozygous expression of deleterious alleles may be of minor consequence in determining the strategies of offspring. Offspring, like parents, may gain high proportional representation in the descendent gene pool through incestuous matings. When such gains are coupled with the advantages of avoiding the risks of emigration, inbreeding costs are likely to be outweighed.

Given the resident strategies postulated, young may adopt strategies that increase the chance of philopatry, or they may optimize the timing of their emigration. Conditions may be favorable for philopatry at the beginning of a new breeding season when there has been overwinter mortality, at times when resources are expanding (e.g., during the spring flush of growth or when a new seed crop appears), or when parental reproductive potential has been expended and parental replacement can be anticipated (Jannett, 1981*b*). Appropriate delays in maturation may serve either to avoid emigration and increase the chances of establishment at the natal site, or to allow an unavoidable emigration at the most favorable time and stage of ontogeny (Frogner, 1980; Morris, 1982; Stearns and Crandall, 1981*a*, 1981*b*).

Will competition with siblings affect emigration? If, on average, each parent is to be replaced by a single young, it is at the time when parental gain through enforcing emigration of young is waning that competition among siblings may be most significant. This competition could be for safe hibernacula (some ground squirrels) or for some other resource important to survival during the non-breeding period. On the other hand, there might be advantage in maintaining an aggregation over a winter season (Madison, 1984, 1985; Madison et al., 1984).

The RFH predicts that in most seasonal breeders terminal litters should be the most philopatric. Emigration should cease at this time, and settlers may come from the transient pool as predicted above on the basis of the relaxation of resident defenses. The high recruitment at this time may give a false impression that emigration is high.

Is it more advantageous that offspring emigrate singly, or in the company of siblings? If emigration is "companionate" should the companion be of the same or the opposite sex? Irrespective of sex, transients might benefit from companionship of kin through increased tolerance to climatic stress (i.e., huddling at low temperatures) and reduced risk of predation (i.e., lower risk per individual). If opposite-sex siblings traveled together, they could avoid mating delay if available habitat were located. Dispersal with a sibling, as with choice of a mate at the natal site, would invoke the equation of high proportional representation versus inbreeding depression. Emigration with a sibling might have significant advantages, although any gains would be measured by selection against costs such as inbreeding depression or delayed maturity in the

presence of a familiar sibling. Companionate dispersal might facilitate retention of co-adapted allelic combinations, and through cooperation siblings might also be more effective in contesting for territorial rights as has been suggested for lions (Bertram, 1976).

Strategies for Male Offspring

Paternal pressure can be expected as male young approach sexual maturity. Young males are unlikely to displace either paternal males or resident males elsewhere. Delayed maturity may be a useful recourse. Although delayed maturity incurs a cost in time lost for reproduction, this cost may be balanced by the benefits of philopatry or of emigrating at an optimal time. A young male that avoids expulsion may eventually replace a resident male parent if the latter should die or become sexually inactive. Delay may allow for greater physical growth and improve chances of competitive success.

In seasonally breeding polyestrous species with long breeding seasons, the most favorable time for male emigration might be determined by availability of females. Space that overlaps home ranges of females could be available at the beginning of the reproductive season as a result of overwinter mortality. Females that have not yet become reproductively active at this time might be less aggressive and might not have established male affiliations. Female availability could rise again in mid-season as overwintered males die and young females are forced to emigrate.

As the end of the season approaches and the residual reproductive value and sexual activity of resident adult males decline, philopatry through delayed maturity will become an increasingly valuable option. In many seasonal breeders, males that overwintered in the previous year are likely to fail to overwinter a second time. Delayed maturity at the end of the breeding season (and on through the winter) will allow accumulation and conservation of physiological reserves.

Delayed sexual maturity might not enable young males to avoid maternal pressure. Lactating females might be especially active in defending resources. A decline in per-capita resources will bring on emigratory pressure from resident females whether a male is mature or not. Because maternal needs for resources for gestation and lactation extend beyond the time when competition for copulations has ended, the strategy of young males should be to avoid aggressive females until the last litters are weaned.

At sexual maturity, young males might have a third option, that of persistence in interstices or on the periphery of ranges of larger-breeding males. At least two advantages to such a "floater" strategy are possible: true emigration and its attendant risks might be avoided, and "sneak copulations" with resident females might establish bonds that will reduce or eliminate emigratory pressure from the females, as well as increment the males' fitness through immediate reproduction.

Implications of Strategies Postulated for Male Offspring

To the extent that male offspring emigrate as a consequence of paternal strategies, the RFH predicts that their emigration should show little dependence on the density of resident adults. When young males emigrate in response to female pressure, however, density-dependence might be apparent (e.g., during a mid-season resource shortage in a seasonally polyestrous species). In long-lived species such as ground squirrels, female aggression might also generate density-dependent emigration of young males. If female aggressiveness increases with density, it could operate in such a way as to conserve resources for daughters, or for future litters. In polygynous species, emigration of young males will have little effect on the birth rate, depressing the realized rate of increase only through the loss of male emigrants.

Because of the advantages of delayed maturity, young males should often become sexually mature later in the season than their sisters. In polygynous species, at least, males have the potential to compensate for delays by numerous matings once the opportunity arrives. Because it will be to paternal advantage to export maturing sons throughout most of the breeding season, emigration of young males would be expected to begin early in the season and to precede that of female siblings unless postponed by delayed puberty. Emigration of young of both sexes would be expected to begin concurrently when both are forced to move by maternal pressure associated with a shortage of nutritional resources. The RFH predicts that in comparison with that of female

siblings, male transiency should be more prolonged, and emigration-associated male mortality should be higher. In monogamous species, where male investment is higher and paternity more certain, male offspring should be more successful in settling at the natal site.

In confined situations (island populations or experimental enclosures) the consequences of blocked emigration of young males will depend largely on the effectiveness of mechanisms delaying their sexual maturity. If these mechanisms break down, contests with adult males and among maturing male offspring will lead in the short term (experimental confinement) to fighting and other behavioral and physiological pathologies, and result in wounding and mortality (primarily of younger males). In the long term (island situations), selection might act against male aggression and further reduce its demographic impact.

Male emigration might not be very effective in reducing inbreeding. If male emigrants move the minimum distance possible, and their offspring do this in their turn, inbreeding will remain high (Bateson, 1983; Moore and Ali, 1984). If males travel farther, export of males might reduce inbreeding, and parents could benefit through the wider distribution of their alleles.

Strategies for Female Offspring

Like sons, daughters should attempt to remain on or associated with the natal site, especially if resources are abundant. The RFH predicts that daughters will be subject to maternal aggression whenever resource shortage and high maternal residual reproductive value coincide, but will rarely be subject to paternal aggression (perhaps only in monogamous species). Female offspring should, unless inbreeding costs are overriding, exploit maternal nepotism and settle in, or at the periphery of, the maternal home range.

Because females commit a significant proportion of potential reproduction to each mating, however, any net inbreeding cost may weigh more heavily in the balance with the advantages of philopatry than is the case with their brothers. If so, behavior of young females is more likely to show evidence of inbreeding avoidance than that of male siblings. When in estrus, young females would be more likely than their mothers to accept nearby male residents as mates. As these males are likely to be close relatives (uncles or half brothers) matings will still be inbred, although less strongly so than with parents or siblings. If any daughters emigrate to avoid inbreeding, they might leave before male siblings as a result of earlier maturity, but their higher probability of immigration should lead to shorter dispersal distances. If inbreeding depression is a deciding factor, philopatry of daughters should also be negatively correlated with residual reproductive value of male (paternal) residents.

Should daughters be directly sensitive to resource shortage (i.e., respond in the manner anticipated by the EFH) or responsive only to maternal pressure? In general, a resource shortage should induce maternal pressure earlier than it could induce a response in the young because resident (breeding) females will have the greatest nutritional demands, the greatest sensitivity to shortage, and the best basis for detecting resource deterioration. This suggests that maternal pressure is likely to cause filial emigration before young of either sex have an opportunity to emigrate spontaneously.

In resource-stimulated emigration, the timing of resource shortage in relation to puberty could be an important variable. Sexually activated daughters are more threatening to current and future reproductive investment than are pre-pubertal daughters and more likely to be subject to maternal pressure. Young females might gain fitness by delaying sexual maturity if the resource shortage is temporary, or if the maternal female will soon become sexually inactive (at the end of the breeding season). If offspring (of either sex) delay maturity when there is a mid-season resource shortage, they could benefit by functioning as helpers in rearing siblings.

The effectiveness of a delayed-maturity response depends on the strategy of the maternal female. If maternal nepotism is best invested in her last litter, maternal aggression may continue, or even increase, through her final lactation, then decline abruptly. In this event, daughters might be under greater pressure to emigrate, relative to sons, than was the case earlier in the season. Female young in penultimate litters might gain the most by delaying sexual maturity and/or attempting to persist at the periphery of maternal ranges.

Once transient, young females should settle in the first unoccupied site where resources are adequate for reproduction. Proximity to the natal site would minimize delay in appearance of, and mating with, a male. Although it would reduce the chances of an outbred mating, it would maximize the potential for altruism on the part of neighbors.

Should female young mate prior to emigration, while transient, after settling, or as part of the immigration process? At times when the probability of finding unoccupied sites is high, female young forced to emigrate might gain fitness by an incestuous mating prior to emigration, or a (presumably outbred) mating while transient. In such matings, fitness would not be reduced by delay in finding a mate if and when a young female succeeded in settling in available habitat. Unaccompanied pregnant females might commonly initiate populations in new locations under such circumstances. As long as males are more likely to emigrate than females, however, emigrant females should have little difficulty in finding a mate.

If most sites were occupied, and if immigration were dependent on acceptance by a resident male, estrus might enhance the probability that a resident male would accept an unfamiliar female. Pregnancy block, if it occurs in nature, could have a similar effect. A female could hedge bets by mating prior to emigration, but having a potential for blocking pregnancy and returning to estrus on prolonged contact with an unfamiliar male if an opportunity to immigrate could arise by that means. This, rather than some of the commonly postulated advantages, might be the selective basis for the pregnancy-block phenomenon. In species where resident males are aggressive toward unfamiliar females, estrous females might be less likely to be driven out and might, as the result of copulation, achieve immigration.

Implications of Strategies Postulated for Female Offspring

Emigration of daughters should follow a different seasonal cycle from that of their male siblings, beginning later in the season and showing greater variation (with per-capita resource availability) in timing and amplitude. If measures of economic density can be devised, emigration of daughters ought to show density-dependence in the form of a positive correlation with competition for resources as perceived by resident adult females.

Because emigratory pressure is predicted to be linked to sexual maturity of daughters only indirectly (via resource shortage), and because nepotism promotes maternal advantage only so long as resources are adequate, daughters should be less likely than sons to delay maturity. If female offspring delay sexual maturity, delay should be associated with a shortage of nutrients or of space (as representative of nutrient availability). In a seasonally polyestrous species, a point in the breeding season will normally be reached where selection favors delay until the following year. The point at which young females delay maturity, like that at which resident females expel daughters, is likely to vary with resource availability. Both emigratory tendency and sexual maturation of female offspring might become resource-dependent in the latter part of the breeding season. When resources are abundant, both maturation of adolescent females and philopatry might be stimulated and females will remain and breed at or near their natal sites. This creates a potential for exploitation of surplus resources, and rapid increases in population density. Reproduction under these circumstances might continue beyond the normal breeding season (e.g., during "mild" winters or "wet" dry seasons). The RFH therefore includes an explanation for late-season reproduction by young females. The mechanism should be both sensitive and responsive to resource availability. Breeding of late season cohorts should be highly variable in response to environmental conditions. Prolonged breeding and recruitment of these cohorts into the breeding population might generate "plague" densities.

Strategies for Transients

Once an individual has been forced to emigrate it can wander in search of suitable habitat that is not claimed by a resident, or it can attempt to maintain position as a "floater," peripheral to areas occupied by residents.

Floater strategy may be advantageous if close relatives behave altruistically, if familiar in-

dividuals are less aggressive than strangers, or if a parent of the same sex is ill or near the end of reproductive life. Occupancy of marginal areas surrounding any high quality habitat could offer some of these advantages. Emigrants might opt, temporarily or permanently, for floater strategies.

When contact with the natal range has been lost, there will be little opportunity to benefit through altruism. On the other hand, residents would have little to gain by opposing passage of transients as long as the latter do not contest resident rights to resources or mates. The optimal transient strategy might be to avoid residents and marked territories, and settle on the first available space. I suggest five reasons for this. First, if a mate is available, time lost from lifetime reproduction will be minimal. Second, because rodents might prefer mates that are only slightly different from themselves, mutual acceptability might decline with distance. Third, high-risk travel through unfamiliar habitat will be ended. Fourth, the possibility that matings will suffer outbreeding depression as a consequence of hybrid breakdown will be reduced. Lastly, selective pressures will be more like those at the natal site if the transient is able to settle nearby.

Implications of Strategies Postulated for Transients

The reasoning in the preceding section points to the conclusion that long-distance movement might be common but long-distance dispersal will be rare. Once the floater strategy has been abandoned, individuals might wander indefinitely in search of opportunities for establishment. There may, in consequence, be a considerable transient pool available to take advantage of any local catastrophe (such as an epidemic or a removal grid) or opportunity (such as a swathed field of grain) that makes space available. The existence and extent of the transient pool would be difficult to determine if transients are not highly vulnerable to conventional baited traps. If members of such a pool are trappable, investigators could get false impressions of immigration rates or overestimate mortality rates. The most significant quality of such a transient pool would be its potential to lead to massive increases in numbers whenever environmental conditions permit mass settling and breeding.

Summary

Because it involves interaction of individuals whose close genetic relationship puts considerable weight on costs and benefits that determine inclusive fitness, dispersal can best be understood in a broad context that includes both classical selection and kin selection. Dispersal, in the sense that it encompasses both emigration and immigration, resembles a game in which established residents have the advantage and always make the first moves. This leads to the proposal that selection has generated dispersal phenomena in the first instance through advantage to residents. The responses of non-residents are secondary. They are the result of selection among offspring and transients and consist of behavior that is the most effective response to resident strategies. It is on this basis that I have referred to this way of looking at dispersal as the Resident Fitness Hypothesis.

The working concepts of the RFH are that rodents are fundamentally philopatric and sedentary, that the interests of parents and offspring come into conflict with respect to philopatry, that dispersal is controlled by behavior of resident adults, and that the maximization of parental fitness requires "judicious" management of the disbursement of offspring.

Although it is not critical to the RFH, considerable attention was paid to the cost-benefit balance of inbred and outbred matings and it was concluded that inbreeding avoidance is unlikely to be the most significant factor in resident strategies or those of their offspring. This conclusion is in agreement with the views of authors such as Moore and Ali (1984) and Waser (1985), who have emphasized the importance of competition as a driving force in emigration, but my examination of competition has been more detailed and more specific. The RFH assumes that resident males compete primarily for copulatory rights, and that resident females compete primarily for the resources required for gestation and lactation. Both the strategies of residents

and the response strategies of offspring and transients are assumed to be conditioned by the spatial and seasonal patchiness of the environment as experienced by small mammals.

The strategies attributed to residents imply that aggressive behavior of resident males would oppose male immigration but not female immigration, lead to expulsion of maturing male offspring for as long as resident males retained high reproductive value, and rarely be responsible for emigration of daughters. As a result, male aggressiveness might not be an effective restraint to increase in population density. If females respond to resource shortage as the hypothesis predicts, however, female aggression is predicted to be dependent on economic density and to have significant density-limiting effects. The hypothesis predicts that as long as resources are abundant, breeding female residents will behave nepotistically toward daughters, leading to the formation of matrilineal groups. Nepotism will also be favored when the residual reproductive value of a female resident falls below that of an offspring. Suppression of maturity by parental pheromones is favored where it is to mutual advantage to limit intrafamilial competition and at the same time conserve offspring at the natal site.

The strategies of offspring have been predicted on the basis of three assumptions. The first is that the greatest advantage lies in "inheritance" of the natal site. The second is that selection operates on the behavior of offspring as a response to prior behaviors of parents and other residents. The third is that individuals emigrate when they perceive their personal environments as intolerable. In the absence of habitat disruption, the environment of a potential emigrant in a mother-young group could become intolerable when a mother behaves in a threatening (even though non-damaging) manner toward a weaned offspring. Such an unacceptable personal environment need bear no relation to the density of the population as measured in demographic terms. An isolated family group would expel offspring in essentially the same way as one imbedded in a dense aggregation of family groups.

Failing to establish philopatrically, offspring should behave so as to optimize dispersal. That means emigrating at the most favorable time and moving as short a distance as possible. The major tactic available to offspring in avoiding, or timing, emigration is delayed maturation. Delay postpones competition with residents and/or facilitates benefit through altruism toward, or from, kin. Suppressed development may increase chances of philopatry, or delay emigration. The value of the tactic will vary with the nature of the annual reproductive cycle, the point in the cycle, the residual reproductive values of residents, and the potential for establishment elsewhere. In polygynous species, a daughter that mates with her father can provide an additional mating that would not otherwise be available to him. Although incest might carry a net inbreeding cost, it might also increase the chance of philopatry in species where males defend territories.

The resident fitness model assumes variability in genotypes that influence behavior of residents but it does not require the existence of discrete polymorphisms specifically controlling tendency to emigrate. It accounts for both seasonal and interannual demographic patterns on the primary basis of the responses of resident females to resource availability.

IV

TESTING THE RESIDENT FITNESS HYPOTHESIS AGAINST OBSERVATIONS IN THE LITERATURE

In behavioral ecology, theories as to the way things "ought to be" have tended to outstrip the empirical data (Bekoff, 1981). If it is true that there is unfounded theorizing about rodent dispersal, it is also true that there is a veritable avalanche of empirical data against which theory might be evaluated. The difficulty lies in synthesizing the data to the point where it can be applied to theory. In the last chapter I attempted to provide a new theoretical base from which to study rodent dispersal. In this chapter I bring together the available data in a format that explores the fit of the hypothesis.

The Site Tenacity of Resident Rodents

The RFH requires that breeding adults be sedentary. There is an enormous quantity of trapping data indicating that for most individuals of most species, home ranges, once established, are effectively permanent for the duration of an individual's reproductive life (Behrends et al., 1986; Blair, 1951; Brown, 1966; Fairbairn, 1978a; Harris and Murie, 1984; Hofmann et al., 1984; Howard, 1949; Jewell, 1966; Krohne et al., 1984; Madison, 1980a, 1980b; Maza et al., 1973; Michener, 1979; Sadykov et al., 1985; Watts, 1970; Wolff and Durr, 1986; and many other authors). Exploration (Shillito, 1963) and scent marking at regular intervals (Bronson, 1976; Christiansen, 1980; Eisenberg, 1963) continuously reinforce site fidelity. The crucial importance of a home area is indicated by the remarkable development of homing behavior in rodents, and the rarity with which displaced individuals settle at the sites where they are released (Dahl, 1967; Stickel, 1968).

As demonstrated by Karlsson (1984), site fidelity may actually be the most precise criterion for discrimination between subadult and adult social status. Site tenacity and reproduction are strongly correlated. Pregnancy has been reported only occasionally among apparently transient animals (Kozakiewicz, 1976; Myllymäki, 1977a). Lactating females occupy permanent home ranges even in species with precocious young (Rood, 1970). Although in a few cases males appear to roam widely in search of mates (e.g., Kutenkov, 1979; Linsdale and Tevis, 1951) or shift breeding areas between seasons (Michener, 1979; Sherman, 1980), male breeding activity seems always to be based on a home area. The evidence is scant that the successful male ground squirrels that shift ranges breed elsewhere in the next season and although such shifts have been reported in some populations (Michener, 1979) they apparently do not occur in others (Davis and Murie, 1985).

In a few species, shifts of homesite within the home range have been observed (Kikkawa, 1964) or range boundaries have varied (Madison, 1980a, 1980b); in a few others females may make stepwise range shifts following progressively shifting food supplies (Tast, 1966) or after weaning of litters (Jannett, 1978; Myllymäki, 1975, 1977a). King (1983) reported that female *Peromyscus maniculatus* moved nest sites between litters without shifting home range boundaries. Lemmings of both sexes move between summer and winter habitats (Kalela et al., 1961). In my view, adjustments such as these do not constitute dispersal as defined here because they do not alter the social and genetic milieu. They therefore do not nullify the concept of site

tenacity. The evidence is strongly in favor of the view that once residency has been established persistence at the same site approximates the individual's ecological life expectancy. Rose and Dueser (1980) found that more than 16% of voles that met their criterion of residency (three or more captures) persisted on their grids for at least 35 weeks, and 5% persisted for at least 52 weeks.

Although these lines of evidence support the concept of lifetime site tenacity, there remain: 1) the observation that most disappearances cannot be accounted for; 2) the fact that the previous history of most transients is unknown; and 3) some evidence of long distance movement by previously resident animals. Myllymäki (1977a) concluded that the dynamism of the home range in microtines is so great that the concept of life-long home range cannot be considered realistic. Lidicker (1985a) suggested that "adult dispersal" is common and Viitala and Hoffmeyer (1985) also challenged the concept of site tenacity, arguing that it may be absent in *Microtus agrestis*, *M. arvalis*, *M. pennsylvanicus*, and *M. xanthognathus*. Porter and Dueser (1986) claimed that the majority of studies designed to identify "dispersers" have shown that large, sexually mature individuals frequently emigrate. This assertion was based on removal studies and on the criterion of large body size at first capture. It is difficult to evaluate these arguments at present. Neither the removal grid technique nor the body size criterion specifies the age, residency status, sexual maturity, or social status of transient animals at the time they began their wanderings. Definitions of "adult" often have been vague or variable. Most available data have been biased by the relative trappability of larger individuals in live traps. Beacham and Krebs (1980) found that pitfall traps primarily caught small voles, whereas live traps primarily caught large voles. In an enclosure, nearly half of the animals caught in pitfall traps never appeared in live traps and those that did so appeared after a delay of more than a month.

Clear exceptions to the rule that a home range, once selected, is permanent for the life of an individual are hard to find. When the "adult" categorization has been made entirely on the basis of body size or sexual activity there generally has been no evidence that the individual was "adult" in the sense of having had a fully developed site attachment elsewhere. In other instances, no distinction has been made between range shifts and dispersal in the sense used in the present discussion. Those studies where appropriate definitions were adhered to suggest that, once established, fewer than 10% of residents emigrate. Watts (1970) designed a trapping grid that covered the entire 27 ha of Marley Wood specifically to detect long-distance movements. Of 341 resident adult *Clethrionomys glareolus*, only eight dispersed. Correcting for the differences in trap spacing in the design, Watts calculated that adult dispersal per adult lifetime was 6.2% for male and 2.1% for female *Clethrionomys*. With fewer data, his estimate for *Apodemus sylvaticus* was 2–3%. Bondrup-Nielsen and Karlsson (1985) estimated the rate of emigration of mature female *Clethrionomys* sp. as less than 5%. Howard (1949) reported a single pre-partum movement in *Peromyscus*. Dice and Howard (1951), however, reported that 15% of female and 25% of male *Peromyscus* bred at more than one site during a single season, with intervening distances of up to 180 m for males and 442 m for females. Getz and Hofmann (1986) followed the history of "breeding units" (a pair or trio occupying a specific nest) in *Microtus ochrogaster*. In 12% of pairs the partners separated and each moved to a different part of the study area; 16.7% of pairs changed nest sites together. When one member of a pair disappeared, 84% of females and 64% of males continued to reside at the site following the loss of the partner. Getz et al. (1987) reported that of 98 such individuals, only 11 acquired new mates. Crawley (1969) recorded a move of a male *Apodemus* from one home site to another 150 m distant. Meredith (1974) observed post-breeding movements of *Eutamias amoenus* of up to 1 km.

A study of radio-isotope marked *Clethrionomys* (Sadykov et al., 1985) has produced unusual data on site utilization. Each "micropopulation" maintained continuous occupation of a stable core of habitat throughout the year. From this core, voles moved out to forage in a surrounding area; the extent of the movement depended on season and on favorability of environmental conditions. In winter, voles fed along the perimeter of the core area, not traveling more than 100 m to feed. At other seasons they foraged out as far as 500 or 600 m. Young of the year

settled in the peripheral feeding zone and fed up to 1,500 m from the colony core when conditions were favorable. In species whose trap-revealed daily movements were only 5–15 m, excursions of up to 1,000 m appeared to be typical and possibly routine.

Some young male ground squirrels either emigrate prior to hibernation (Sherman, 1980); others are driven off the following spring by their mothers (Michener, 1979). Adult males that have bred in one season move (driven by resident females?) away from the area where they have bred. Some, at least, might survive to breed a second time. Most of these, but not all (Davis and Murie, 1985), do not breed at the same site or with the same females in subsequent seasons. It is not clear that they shift to different demes, nor is it known how many survive and breed again at a new location. Hoogland (1981) noted that few male black-tailed prairie dogs remained in the same coterie long enough to mate with their mothers or daughters, although 94–99% of surviving females remained in the same coterie in successive years. Although 86% of males born into a colony remained in the natal coterie in their first (non-reproductive) year, most survivors bred in coterie or wards other than those in which they were born. Careful observation and analysis of behaviors and post-breeding fates of successful males in these and other diurnal species will be important in evaluation of RFH and EFH hypotheses.

Despite the questions raised by a few investigators, permanent establishment appears to be a basic part of rodent life history strategy. Most claims of “adult emigration” are based on inadequate and overgenerous definitions of “adult” and/or of “emigration.”

The Prevalence and Importance of Philopatry

The RFH postulates that in most cases in which an individual emigrates, it does so because it was driven from the natal site by residents, primarily its own parents, and that it would have remained at the natal site if it had been given an opportunity to do so. It is well to remember that data are likely to be biased in favor of detecting philopatry. One is most likely to discover the place of residence of philopatric individuals and least likely to detect establishment elsewhere.

Greenwood (1983) and Waser and Jones (1983) found few exceptions to philopatry. Among 36 species in 12 families for which Waser and Jones (1983) found published data, clear evidence of philopatric tendencies was lacking only for males of two sciurid and two cricetid species. Jones (1986) found that of 147 young *Dipodomys spectabilis* that became established, 24 males and 13 females acquired their natal mounds. Young of both sexes remained in the natal mound until able to occupy vacant sites nearby. Seventy-nine percent of 97 male juveniles and 77% of 99 female juveniles settled within 50 m of natal sites or points of first capture. The median dispersal distance in this species was 17 m for males and 30 m for females. Among individuals eventually successful in establishing themselves, survival over the first post-establishment year was 50% higher among philopatric settlers than among those settling elsewhere (Jones, 1987).

Disappearance of either parent increases the probability that an offspring of that sex will be successful in establishing residence (e.g., Dickman et al., 1983; Dixon, 1958; Slade and Balph, 1974; Svendsen, 1980). It has yet to be demonstrated, however, that all young will settle on the natal range if not actively expelled.

Given a general and presumably inherent tendency to philopatry, success rates vary. Most data show the expected bias in favor of females. Dice and Howard (1951) found that 38% of female and 28% of male *Peromyscus maniculatus* settled at their natal sites. Mean breeding distances of 10 male and 10 female *P. leucopus* were 75.5 and 39.3 m, respectively, from known birth sites (Goundie and Vessey, 1986). Wolff and Lundy (1985) reported that some overwintering groups of *P. leucopus* and *P. maniculatus* consisted of mothers, offspring, and possible fathers; most also contained individuals not known to be relatives. By spring all the autumn-born male *P. leucopus* had disappeared from their natal ranges, but 30% of autumn-born females bred within the range of a possible father. Three of seven male and two of eight female *P. maniculatus* bred within their natal ranges in the spring following their birth (Wolff and Durr, 1986). Baker (1981b) found that less than 1% of house mice living in chicken coops moved between buildings; individuals carrying an introduced allele tended to be located near their putative mothers.

Mackin-Rogalska (1975) examined the fidelity of *Microtus arvalis* to family burrow systems in an enclosed 1-ha field. She concluded that fidelity to a burrow system was not apparent among males or in young born early in the season. However, she did not consider possible disruptive effects of confinement. Stoddart (1971) observed that recruitment was largely philopatric in *Arvicola terrestris*. He reported that early season young were philopatric, but those born after 1 July were not. Female *Clethrionomys rufocanus* settle as close to the natal site as possible and as long as density is low matrilineal lines are discernible (Viitala, 1977; Viitala and Hoffmeyer, 1985). Kawata (1985a) found greater heterogeneity in frequencies of electromorphs of female than of male *Clethrionomys* and attributed this to greater philopatry in females. According to Getz and Carter (1980), most female *Microtus ochrogaster* that succeeded in establishing home ranges did so within 30 m of their natal nest. Among young *M. ochrogaster* that survived to the age of maturity, 68% of males and 75% of females occupied their natal sites for their entire lives (Getz and Hofmann, 1986; Getz et al., 1987). Although male dispersal distances are greater in most species, long-distance dispersal in *D. spectabilis* was biased in favor of females (Jones, 1987).

Female philopatry is very strongly developed in ground squirrels (Armitage, 1984; Hoogland, 1981; Michener, 1983b; Sherman, 1980). More than 60% of female yellow-bellied marmots in harems were found to remain in the colonies into which they were born, but the proportion of males doing so was extremely low (Schwartz and Armitage, 1981). At 60 days of age 92% of female *Spermophilus beldingi*, but only 26% of males, remained in their natal areas (Holekamp, 1984).

Data showing the relevance of philopatry within superficially homogeneous habitat have recently been provided by Cockburn and Lidicker (1983). Within continuous grassland, variations in habitat quality between areas the size of individual home ranges in *Microtus californicus* made a significant difference in individual persistence and reproductive success.

Shields (1983) reviewed various models explaining the trend to philopatry among higher vertebrates. He rejected models based solely on low vagility, and regarded as more powerful those models that took into account the risks of movement, the ability of individuals to function efficiently in a familiar area, the value of local adaptation, and the compatibility of alleles in local gene pools. In his view, philopatry should prevail in organisms in which the environment is relatively coarse grained, although wide distribution of propagules would be beneficial if habitats were ephemeral. Both of these criteria apply to rodents, and the resulting contradiction might be resolved through the bias toward male emigration and greater male dispersal distances in the majority of species.

Specific studies that would determine whether philopatry is an inherent and universal tendency are lacking, although the available evidence is favorable to that view. New techniques (e.g., Dickman et al., 1983; Sheridan and Tamarin, 1986; Tamarin et al., 1983; Wolff and Lundy, 1985) are becoming available for identifying litters and following their dispersal. These show promise of greatly improving our ability to determine paternity, to distinguish among philopatric individuals, emigrants, and transients, and to determine patterns of dispersal. I expect them to confirm that philopatry is an innate tendency in rodents.

Discrimination Among Relatives, Associates, and Transients

Because it places emphasis on parent-offspring interactions and inclusive fitness, the RFH depends on evidence that residents make social discriminations among familiar individuals (mates, neighbors, offspring, and parents); between familiar individuals and strangers; and between individuals that are transient and those that are resident. The RFH relies heavily on mutual recognition among relatives (adults and their own offspring), and requires that adults (males at least) detect the onset of puberty in their young. Discriminatory abilities are also fundamental to nepotism; to preference for, or avoidance of, inbreeding (Holmes and Sherman, 1982; Hoogland, 1982); and to exclusion of non-kin and "judicious" selection of whether (and when) to allow philopatry or to force emigration of kin. Do rodents have the required discriminatory abilities?

Recognition of conspecifics and discrimination of their sexual and social status is based primarily on odor in rodents (Schultz and Tapp, 1973; Stoddart, 1976). Odors serve to announce stages of sexual development and activity to conspecifics of all ages and to regulate intraspecific behaviors (Bronson, 1979; Brown, 1979; Fass and Stevens, 1977; Ropartz, 1977; Stoddart, 1974; Thiessen and Rice, 1976; Whitsett et al., 1979). In *Mus musculus* both individual and group recognition on the basis of odor have been demonstrated. Dominant individuals produce odors different from those of subordinates, and urine of dominant males contains an aversive factor lacking in the urine of subordinate males. Stressed individuals emit distinctive odors; female odors tend to inhibit aggression by males (Ropartz, 1977). Stoddart (1977) showed that sebaceous secretions of young differ from those of adults in *Apodemus* and *Arvicola*, and that the secretions of young males closely resemble those of adult females (a camouflage inhibiting adult male aggression?). In *Arvicola terrestris*, Stoddart et al. (1975) showed by means of gas-liquid chromatography that flank gland secretions differed between sexes, between adults and juveniles of each sex, between families reared under identical laboratory conditions, and between populations in the field. They also suggested the existence of olfactory dialects. Wolton (1984) showed that *Apodemus sylvaticus* of both sexes could be trained to discriminate between odors of urine or feces of two conspecifics of either sex. Much remains to be learned about the role of scent, but it is clear that there are: 1) olfaction-based responses to social and sexual status; 2) adaptations for chemically marking territories; and 3) correlations between olfactory familiarity and agonistic interactions.

On what basis does olfactory discrimination among relatives operate? Holmes and Sherman (1982) and Blaustein (1983), viewing recognition as functioning to regulate nepotism or balance inbreeding and outbreeding, have considered four possible mechanisms on which kin recognition, nepotism, or inbreeding avoidance (or preference) might be based: 1) individuals might recognize kin through proximity to the home range or natal site; 2) recognition might be based directly on association in the natal nest (Porter et al., 1978, 1981, 1983; Porter and Wyrick, 1979); 3) recognition could be ascertained by phenotype matching if an individual compared its own phenotype (morphological, olfactory, or behavioral), or those of familiar relatives, with that of an unknown; and 4) there could be a direct (unlearned) response to "recognition alleles." Yamaguchi et al. (1981) and Yamazaki et al. (1976, 1980) presented data interpreted as showing that relative to identical females, male *Mus* preferred females whose genotypes differed from their own at the H-2 locus. Nevertheless, Holmes and Sherman (1982) concluded that use of recognition alleles was doubtful and might be impossible to demonstrate.

Empirical data (Gavish et al., 1984; Godfrey, 1958; Grau, 1982; Halpin, 1978, 1981; Kareem, 1983) suggest that both experience and genetic similarity might be involved in kin recognition. Maternal and sibling recognition might be established shortly after birth (Porter et al., 1978; Quadagno and Banks, 1970; Stoddart, 1976) or might require several weeks (Michener, 1983b). Michener (1974) noted that recognition was mutual between maternal *Spermophilus richardsonii* and their own young before young opened their eyes, but she has subsequently emphasized that individual recognition (as opposed to discrimination between familiar and unfamiliar conspecifics) has not been demonstrated in ground squirrels (Michener, 1983b). Recognition persists over long periods of inactivity in hibernating species (Michener and Sheppard, 1972).

Laboratory studies provide both direct and circumstantial evidence that extends the functional importance of recognition. Physiologically, pregnancy can be terminated by intense and prolonged contact with non-stud males or their pheromones (Bronson and Eleftheriou, 1963; Bruce, 1959; Chipman and Fox, 1966a, 1966b; Jannett, 1979; Stehn and Richmond, 1975). Similarly, young can have sexual development activated or accelerated by contact with unfamiliar adults of the opposite sex (Bronson, 1979; Carter et al., 1980; Milligan, 1980). In confinement, newly parturient female voles discriminate between males with which they mated and other males, behaving amicably toward stud males but persistently attacking non-stud males. The latter will kill young that they have not sired (Mallory and Brooks, 1978, 1980). In contrast, stud males are unlikely to attack their own young when introduced to the natal cage under these conditions (Labov, 1980; vom Saal and Howard, 1982). I suspect that infanticide by non-stud males may be induced by maternal aggression in a confined space.

Reviews of the topics of sibling recognition (Bekoff, 1981) and mother-young recognition (Gubernick, 1981) have concluded that recognition is learned, but as Blaustein (1983) pointed out, the empirical evidence for recognition mechanisms remains compatible with both learned and unlearned recognition. Non-learned recognition could, for example, be based on glandular secretions (Stoddart, 1976), but learning, on the basis of self-perception, would be difficult to rule out. Holmes and Sherman (1982) found that sibling *Spermophilus beldingi* and *S. parryii* reared apart differed from non-siblings in interactions when encountering each other for the first time in a test situation, but Holmes (1984) did not find evidence for such "innate" discrimination in *S. tridecemlineatus*. He concluded that differential responses of *S. tridecemlineatus* in arena encounters could be fully explained on the basis of familiarity. As Holmes (1984) pointed out, however, the methods varied somewhat and exact comparisons are not possible among various species. Grau (1982) seems to have demonstrated discrimination of kin independent of prior contact in *Peromyscus leucopus*, and a recent study by Porter et al. (1984) also argues strongly for a non-learned component. Comparisons of responses of *P. leucopus* to familiar and unfamiliar siblings and non-siblings in paired arena encounters appear to demonstrate an ability to discriminate between related and unrelated strangers housed in identical conditions, the responses to unfamiliar siblings being more cohesive and amiable than those to unfamiliar non-siblings. Females reacted cohesively toward unfamiliar, related males (more approaches and more investigation, but no difference in time spent huddling) and aversively toward unfamiliar, unrelated males (more chases). There were marked differences between male and female response patterns: males behaved most positively toward familiar relatives, less positively toward unfamiliar relatives, and least positively toward unfamiliar non-relatives; females displayed positive interest most strongly toward non-familiar relatives. Davis (1982) cross-fostered *Spermophilus richardsonii* within 24 h after birth. After being isolated for 110 days, beginning 1 week after weaning, the test animals demonstrated recognition of biological siblings in arena tests, behaving more cohesively toward siblings than toward non-siblings. Holmes (1986a) showed that female *S. beldingi* were less agonistic in their interactions with unfamiliar kin than with unfamiliar non-kin. These results seem most compatible with a phenotype matching hypothesis.

De Jonge (1983) found evidence of species differences in response to relatives among microtines. When tested in laboratory arenas at 6–10 weeks of age, *Microtus arvalis* that had been separated from their siblings within 24 h of birth investigated siblings without any fighting, but fought with non-siblings. *M. agrestis*, under the same regime, fought with both siblings and non-siblings.

Whatever the mechanism, the general trend in discriminatory behavior is toward more amicable relationships with familiar individuals of either sex, whether relatives or neighbors. Residents tolerant of associates have been reported to be aggressive toward unfamiliar conspecifics that are experimentally introduced in both laboratory and natural environments (Anderson and Hill, 1965; Armitage, 1974, 1975; Armitage and Johns, 1982; Eibl-Eibesfeldt, 1950; Fairbairn, 1978b; Healey, 1967; Hill, 1966; Lidicker, 1976; Reimer and Petras, 1967; Rowe and Redfern, 1969; Sadleir, 1965).

Given that rodents are capable of making fine discriminations among conspecifics, much remains to be learned as to how the observations on olfactory discrimination relate to social and reproductive structuring. McLean (1982) found that immediate neighbors among breeding female *Spermophilus parryii* were not closely related. However, females that were closely related tended to move newly emerged young into common burrows whereas distantly related females did not. Close female kin also had more overlap among home ranges and interacted more amicably than did less closely related females. Distant relatives that had not associated as young were intermediate between close kin and non-relatives in these respects. McLean postulated that aggregating behavior might enable cousins to learn to recognize each other and thus serve to facilitate extended nepotism. Armitage and Johns (1982) found that among yellow-bellied marmots, mother-daughter and sister pairs were more amicable than expected on the basis of frequency of occurrence of such pairs in the population.

Carefully integrated field and laboratory observations by Jannett (1980) showed that parous female *Microtus montanus* tolerated the presence of only their own young and familiar males

within their home ranges. In monogamous stocks of *M. ochrogaster* confined in extensive artificial runway systems, Getz and Carter (1980) observed that all members of any social group attacked experimentally introduced subadults of either sex, but that the breeding male was the most aggressive toward both male and female strangers.

Recognition of neighbors, per se, has yet to be investigated adequately. Healey (1967) observed that male *Peromyscus maniculatus* were less aggressive toward neighbors than toward strange males. Vestal and Hellack (1978) reported that *P. leucopus* behaved less agonistically toward neighbors than toward strangers in laboratory arena encounters, but failed to observe equivalent discriminatory behavior in *P. maniculatus*. Madison (1980a) noted evidence that microtines, when placed in arenas, are less aggressive toward neighbors than toward strangers; in large semi-natural enclosures, however, territorially established resident *Microtus* tolerated introduced strangers ("transients") but attacked neighbors at territory boundaries (Skirrow, 1969). Female *Clethrionomys* have been reported to be tolerant of neighbors and aggressive toward unfamiliar conspecifics (Viitala and Hoffmeyer, 1985). Getty (1981) observed general overlap among chipmunk territories, in conjunction with avoidance of actual contact, and concluded that territorial behavior was primarily important in deterrence of immigration by non-neighbors. At this point it appears that neighbors are probably recognized as distinct from transients, but the consequence may vary with the degree of relationship, the species, and a number of other variables. Like other interactions, those among neighbors are likely to depend on the sex of the participants. Armitage (1982b, 1986b) suggested that because males and females compete intrasexually for different resources, overall rodent social systems actually are composed of separate but interlocking male and female systems.

Recognition of offspring by males, or of paternal males by offspring, has been little studied. Males of many rodent species do not share nests with females and young and thus there would seem to be less opportunity for discrimination based on close contact. Paternal males are actively excluded from the nest by the maternal females in some cases. However, if young acquire the maternal scent, and males respond positively to the scent of females with which they have copulated, male recognition of offspring could be facilitated. In some caviomorphs, where males do not share the nest and the maternal females are aggressive toward even stud males, males take advantage of the females' absences to scent-mark their offspring (Kleiman, 1977).

Although much remains to be learned as to the basis and function of recognition mechanisms, the discriminatory abilities of rodents appear adequate to meet the demands of the RFH.

Cohesiveness Among Kin

Emigration and immigration might be greatly influenced by whether kin repel or attract each other. Repulsion might result from high inbreeding costs, whereas attraction might result from opportunities to accrue fitness through altruism or positive assortative mating. Hamilton (1964a, 1964b) predicted that the advantages of positive response among kin would cause parents to behave so as to minimize competition among their offspring.

Familiar odors generally evoke positive responses, and this persists after weaning. In laboratory tests, young rodents show preferences for odors with which they are familiar (Carter and Marr, 1970; Marr and Lilliston, 1969). Stoddart (1982) found that *Microtus agrestis* preferred traps with their own odor over those scented with the odors of other voles. Gubernick (1981) reviewed the literature of parent-offspring recognition in *Rattus*, *Mus*, and *Acomys*, and concluded that young learn to recognize their mother on the basis of olfactory and gustatory perceptions, and that innate parent-offspring attachment was not required to explain the observed patterns.

Evidence of cohesion and cohesive behavior among kin has been found in both laboratory and field studies. Sibling *Acomys* were more likely to share a food source and more active in exploring novel environments than were non-siblings of the same age (Porter et al., 1980). Savidge (1974) observed that young *Peromyscus maniculatus* that had been ejected by their mother tended to travel together when they crossed a barrier. In arena tests, female *Peromyscus* investigated unfamiliar sibling males and chased unfamiliar non-siblings (Grau, 1982). Grau's inter-

pretation was that females investigated the unfamiliar siblings in order to avoid incestuous matings.

For both *Mus* (Lidicker, 1976) and *Peromyscus* (Howard, 1949; King, 1983; Madison, 1977), there is evidence that littermates associate and travel with parents and siblings later in life. A tendency for opposite-sex littermates to disperse together has been observed in *Peromyscus polionotus* (Smith, 1968). Field evidence indicates that unrelated *Peromyscus* tend to avoid association. King (1983) found unrelated *Peromyscus* together in only 7.5% of 598 observations of groups. Litters were more cohesive in fall, whereas juveniles were most likely to be encountered alone in spring and summer. Among 10 male and 10 female emigrant *P. leucopus* followed by Goundie and Vessey (1986), there was evidence of cohesion in one litter and no evidence of active avoidance among littermates in the others. Patton and Feder (1981) found no evidence of cohesion among kin in pocket gophers colonizing a trapped-out area.

Lidicker (1976) found that *Mus* released into large outdoor enclosures established and maintained kin groups, despite the pressure of very high densities. Genetic evidence showing that similar group individuality and integrity was maintained in unenclosed populations (Selander, 1970a) demonstrates that kin grouping was not an artifact of confinement.

Sibling cohesiveness apparently varies with species in voles. After a period of separation, *Microtus arvalis* behaved affiliatively toward kin even in an unfamiliar environment, but *M. agrestis* showed no evidence of affiliative behavior toward kin (De Jonge, 1983). Overwintering groups of *M. pennsylvanicus* are formed among kin. Reduction in relatedness within such groups appears to be a consequence of predator pressure rather than loss of group cohesion. Infusion of unrelated individuals follows loss to predators because lone individuals join depleted groups, taking advantage of huddling to protect themselves from the stress of low temperature (Madison, 1984, 1985; Madison et al., 1984). Getz (1972) did not find any evidence that sibling *M. pennsylvanicus* behaved cohesively during emigration, and Wilson (1982) reported that sibling *M. pennsylvanicus* behaved less cohesively under the same conditions than did *M. ochrogaster*. The evidence of greater cohesiveness in *M. ochrogaster* seems paradoxical with respect to female reproduction if association with unfamiliar males is required for sexual maturation and if, as Carter et al. (1986) report, natal territories are rarely visited by unrelated males. It is unclear how cohesiveness evolved in this species if it inhibits reproduction. Hilborn (1975) and Beacham (1979b) obtained data that they interpreted as indicating that littermate *M. townsendii* might emigrate synchronously, possibly in company.

Formation of kin-clusters as a result of amicable and cohesive behaviors among related females is evident to some degree in all the well-studied terrestrial sciurids and is most marked among females (Armitage, 1986b). In *Marmota flaviventris*, relatedness increased the amount of the foraging area shared (Frase and Armitage, 1984). However, cohesiveness might depend on philopatry and continued association. When a group of eight juvenile marmots were introduced into a new and unoccupied habitat, kinship was unrelated to the frequency of social interaction (Armitage, 1982a).

Young *Spermophilus richardsonii* behave cohesively toward the female parent and submissively toward other adults (Michener, 1974) and establish site-specific dominance over non-kin in the season of their birth. Less physical spacing is maintained between kin than between non-kin. Amicability toward kin is maintained into the first breeding season, and kin-clusters result (Michener, 1981). Waterman (1986) observed that on emergence juvenile female *S. columbianus* differed from males in greeting the mother more often, playing preferentially with sisters, and staying nearer the natal burrow over the first 10 days. Related female *S. parryii* might actively facilitate cohesion by transporting their litters to communal burrows just prior to weaning (McLean, 1982). Cross-fostered ground squirrel pups reared together behave cohesively (Holmes and Sherman, 1982) as do cross-fostered *Microtus* pups (Gavish et al., 1984). Female ground squirrel sibs reared apart, however, also show less aggression in dyadic laboratory encounters than similarly reared non-sib females, providing evidence that both association in early life and relatedness per se may be involved in cohesion of kin (Holmes and Sherman, 1982). Holmes

(1986b) reported that half-sib *S. beldingi* females were less antagonistic toward each other than comparable unrelated yearlings, but that this difference was not evident in male-female or male-male pairs. Hoogland (1986) found that both male and female *Cynomys ludovicianus* interacted more amicably with kin than non-kin. Nepotism was least among males during mating and least among females at the time when competition for burrows was at its peak. Even when competition was most intense both sexes were more amicable toward kin than non-kin.

Schaller and Crawshaw (1981) observed that capybaras (*Hydrochoerus hydrochaeris*) formed large aggregations during the dry season. Within these aggregations, groups that presumably consisted of relatives or families maintained their integrity. Young followed their mothers for up to 1 year after birth.

It appears that cohesion develops in the nest in most species and thus is most probable between mother and young and among siblings. Among siblings, cohesion is more evident than repulsion. Familiarity facilitates cohesive behavior; cohesiveness, maternal nepotism, and philopatric tendencies of female young can all contribute to development of matrilineal groupings in the field. The picture is much less clear with respect to male-female and male-male cohesion and its relevance to formation of new colonies and to co-dispersal of siblings. Investigators have shown so little interest in cohesion between males, between fathers and daughters, or between brothers and sisters that there is a temptation to assume that it is nonexistent. There are, nevertheless, some suggestions that male siblings emigrate together, and further investigation of inter- and intrasexual cohesiveness among emigrants would be useful. It would also be useful to know if relatedness was high among males sharing common or overlapping home ranges.

Mating Preferences of Residents

Sexual dimorphism in body size is less obvious in rodents than in many other mammals, a fact that might be taken to indicate that sexual selection is weak or absent. As Blaustein (1981) has emphasized, however, chemical dimorphism (differences in odor between males and females) is marked. Scent differences among males could provide an adequate basis for expression of mating preference by females.

Studies of mating preferences in laboratory *Mus* were reviewed by D'Udine and Alleva (1983). A number of generalizations can be drawn from their review. Sexual behavior might be less labile than other forms of social interaction. Relative to females, males tend to be less discriminating in sexual preferences and less fixed in such preferences. Expression of preference by female *Mus* is dependent on an opportunity to associate with the father in the nest. Laboratory strains vary in expression of preference, and females might show preference for familiar males or for males of slightly different genotype, as opposed to either closely or distantly related individuals.

Unfortunately, tests of "preference" in many experiments demonstrate only that females preferentially investigated odors of unfamiliar males. Preference measured in this way might reflect sexual attraction, curiosity, or aggression. On the basis of such experiments, Hayashi and Kimura (1983) reported that female laboratory *Mus* showed no preference within male combinations of unfamiliar related, unfamiliar unrelated, and familiar related males in terms of time spent in neighboring compartments. Even where mating occurs in choice experiments in the laboratory, results cannot be extrapolated directly to mating in the field because the choice is limited in too many ways by the experimental conditions. Hayashi and Kimura's conclusion that the choice of mate is made mainly or entirely by males is unjustified.

In nature also, mate choices by females are likely to be limited. The factors include residency of females, male residency and territoriality, and male social hierarchy. Jannett (1981a) reported that in a population of *Microtus montanus* only those males that occupied territories achieved physiological readiness to breed. Webster and Brooks (1981) observed in the field that a large male *M. pennsylvanicus* remained near a post-partum female for several hours. When other courting males attempted mounts, the female vocalized loudly and the large male drove off the

intruders. Kawata (1985b) was unable to find strong evidence that female *Clethrionomys rufocanus* exercised preference, yet in cases in which paternity was determined there was no instance in which a female had been inseminated by a transient male or by a resident male whose home range did not overlap hers. R. J. Wolff (1985) reported that in house mouse colonies founded in the laboratory with an adult pair and a juvenile male, the adult males were dominant and continued to monopolize copulations until eventually killed by younger males. Thereafter several individual male offspring were able to establish territories within the colony room. Only those males that established territories were able to mate. Mating and parturition took place primarily within the higher quality territories.

Ågren (1984b) studied pair formation in *Meriones unguiculatus* in outdoor enclosures. Females expressed preference (for males and/or territories) only after males had established territories. Females then developed their own site-related dominance. Males subsequently became aggressive toward non-resident females. Females, however, wandered widely when in estrus, and mating was not restricted to cohabiting males. Ågren suggested that females might use male possession of a territory as an index of male quality. One possible further interpretation is that the presence of a male is viewed by the female as a component of habitat choice, and subsequent mate choice is a separate process. Behrends et al. (1986) observed that female *Dipodomys merriami* wandered much more widely when in estrus, and Viitala (1977) reported similar behavior in *Clethrionomys rufocanus*. Such behavior supports the suggestion of Cox and Le Boeuf (1977) that females behave so as to incite male competition. Receptivity of estrous females toward males occupying adjacent home ranges is suggested by the "estrous runs" reported by Viitala (1977), and by evidence for multiple paternity in *Peromyscus* reported by Birdsall and Nash (1973). Multiple matings might also serve to lower the risk of a poor mate choice or reduce inbreeding cost. Female Belding's ground squirrels normally mate with several males (Hanken and Sherman, 1981; Holmes and Sherman, 1982), but it is not clear how general such bet-hedging behavior is, nor whether there is any preference based on relatedness.

How precise can mate choice be? Lenington (1983) reported evidence that female *Mus* showed preference for males homozygous for wild-type alleles over those heterozygous at the t-locus. She found, in arena experiments, that the preference of heterozygous females was stronger than that of those females that were homozygous for the wild-type allele and had less to lose by mating with a male heterozygote. Heterozygous males, however, were dominant over male homozygotes and the high levels of aggression in the experimental context affected female behavior, introducing uncertainty as to how the evidence for female choices should be interpreted. In another experiment females showed preference for the odor of homozygous males in a choice chamber. It is difficult to judge the relevance of these interesting results to the natural context.

There may be considerable variation among species in mate choice. Webster et al. (1982) investigated copulatory preferences in female voles under laboratory conditions, including reinforcement of preferences by successful copulations. When given access to both a male with which they had just mated and an unfamiliar male, female *Microtus ochrogaster* showed preference for the stud male, whereas female *M. montanus* showed no preference. When separated for 2 weeks by a wire mesh barrier from a male in the same cage, female *M. ochrogaster* showed no preference when given a choice between the familiar male and a stranger, whereas female *M. montanus* spent more time with the unfamiliar male.

Behavioral response to an unfamiliar conspecific usually takes the form of an aggressive approach by a resident. Aggression by resident females toward unfamiliar males has been observed in *Neotoma* (Fleming, 1979) and *Microtus* (Jannett, 1980). Such aggression presumably reduces the chances that mating will take place. Getz et al. (1981) found that female *Microtus ochrogaster* in post-partum estrus were receptive and non-aggressive toward previous mates, and less receptive toward unfamiliar males. Reversal of this preference required several days.

Mate choice in *M. ochrogaster* is especially interesting in view of the tendency to monogamy. Although virgin females investigate only the ano-genital odors of unfamiliar males, once a female

has been activated and enters her first estrus she is equally likely to mate with a familiar or an unfamiliar male. This initial mating establishes a pair bond. Females living in established pairs attempt to avoid matings with unfamiliar males (Carter and Getz, 1985; Getz et al., 1981).

Dominance status of males seems to be an important factor in female choice in many rodent species. Female preference for dominant males, or a preferential tendency to investigate odors of dominant males, has been reported in *Mus* (DeFries and McClearn, 1972), *Clethrionomys* (Hoffmeyer, 1982), and *Lemmus* (Huck and Banks, 1982a, 1982b). Shapiro and Dewsbury (1986) found that female *M. ochrogaster* spent more time near dominant males than near subordinate males, both when the males were tethered and when separated from them by wire mesh walls. Under the same conditions female *M. montanus* showed no preference. In most studies dominant males have been observed to copulate earlier and more frequently than subordinates. Hyde and Sawyer (1977) suggested that variation in female aggressiveness over the estrous period might broaden mate choice (i.e., selectivity might be reduced during estrus as a result of reduced female aggressiveness). Female tassel-eared squirrels have been observed to solicit copulations from subordinates (Farentinos, 1980).

After reviewing the literature, Dewsbury (1982b) concluded that male dominance was correlated positively with relative frequency of copulation in the majority of rodents studied, although the correlation did not hold for all conditions. The effects of confinement are difficult to exclude in most studies. The fact that greater reproductive success of dominant male *Peromyscus* was evident in large enclosures but not in smaller ones (Dewsbury, 1981) suggests that in unconfined situations the expression of female preferences is likely to be more, rather than less, effective. This might not be true, however, in the more social species. In black-tailed prairie dog towns, where numerous males occur within a short distance, females mate primarily with males that are members of their own coterie (Foltz and Hoogland, 1981).

Schwartz and Armitage (1980) reported that recruitment of male colony members appeared to be largely from outside the colony in *Marmota flaviventris*. Armitage (1986b) concluded that there was no evidence that female yellow-bellied marmots made choices among males. If a harem male disappeared, females simply remained in the colony without breeding until another male appeared and took control of the harem. It would not be surprising if replacement of males followed this pattern in murine rodents. However, removal of males from house mouse populations produced no evidence of recruitment of mature male immigrants and mating was presumably suspended until male offspring were recruited (unpubl. personal observation).

There are few clues in the literature as to mating preferences of resident females with respect to male offspring. Maternal presence in close confinement has not been reported to inhibit sexual maturity of sons and presence of sons under these conditions has not been reported to inhibit maternal estrus. Grau (1982) interpreted the high frequency of female approaches toward related males as possibly indicative of inbreeding avoidance. However, he also observed that female *Peromyscus leucopus* investigated unfamiliar male siblings but chased unfamiliar non-sibling males, which casts doubt on the inbreeding-avoidance explanation.

Baker (1981b) carried out six experiments in which cages containing small demes were joined. In five experiments the demes merged. Females mated with the "foreign" males in two experiments, but in the other three the females mated with the "local" as long as the opportunity was present, mating with the foreign male only when the local male had been killed. These results seem to indicate that females favored familiar males as long as those males were able to maintain dominant status. Cox (1984) found that female *Mus* from adjacent granary populations selected the odor of their own colony over that of the neighboring colony when offered a choice in an experimental apparatus. They also avoided the odors of males from the alien population. Heth and Nevo (1981) reported that female mole rats (*Spalax ehrenbergi*) from both central and peripheral populations also showed preference for local mates over "foreigners."

In contrast to the abundant evidence on female preferences, there is little evidence that males are selective. In laboratory tests, Godfrey (1958) reported that male *Clethrionomys* showed preference for females from local as opposed to more distant populations. Fleming et al. (1981)

reported that male *Neotoma* spent more time sniffing the urine of familiar estrous females than that of unfamiliar estrous females.

The evidence reviewed implies that females tend to make choices, but that males are less discriminating with respect to mates. Except in monogamous species, and to a lesser extent in highly social species, there is little evidence of male choice beyond a generalized tendency for males to behave aggressively toward unfamiliar conspecifics. Choice by both sexes tends to be in favor of familiar and, therefore, more closely related mates.

All females appear to prefer mates that are familiar and are established and dominant on home ranges. Mate choice in both sexes is restricted primarily by sedentarity, territoriality, and social organization.

How Common Is Inbreeding?

How much inbreeding does occur in nature? Is there widespread evidence for inbreeding depression, or of heterosis, in natural rodent populations? Is reduction of the probability of strong inbreeding an unselected by-product of physiological or behavioral patterns that have evolved on some other basis? Do natural populations and environments exhibit enough stability for behavioral patterns to evolve on the basis of their contribution to inbreeding avoidance? Is the degree of familiarity that acts as a barrier to mating in some species in the laboratory replicated in nature? Is the loss of opportunity for altruism a significant cost when inbreeding is avoided?

Both inbreeding and outbreeding have costs and benefits and the optimal mate choice may be the one that maximizes benefits relative to costs (Bateson, 1983; Shields, 1983). In the following discussion it will be useful to keep in mind the distinction drawn by Moore and Ali (1984) between strong inbreeding (coefficient of kinship 0.25 or more) and close inbreeding (coefficient of kinship between 0.125 and 0.25), as well as the relation of these specific terms to the more general concept of inbreeding as it occurs in demes of less than a few thousand individuals. It is also worth noting that even low levels of inbreeding can have significant effects on the rate of change in gene frequency (Breden and Wade, 1981).

The questions above are important to the evaluation of the emigrant fitness and resident fitness hypotheses of dispersal. Avoidance of incestuous matings has frequently been advanced in support of emigrant fitness, and is in that sense a likely basis for challenge of the RFH. However, it is not essential to the RFH that inbreeding have no net cost. To the contrary, if inbreeding depression does entail a net cost to the parent in an incestuous mating, parents should export young in order to avoid inbreeding cost. If inbreeding has a potential for costs, it also has a potential for benefits. Inbreeding creates a favorable environment for the evolution of altruistic behaviors through kin selection (Breden and Wade, 1981).

The proliferation of reports of presumed inbreeding avoidance obscures the fact that there are many behaviors that could be described as inbreeding facilitation. Mates chosen at random in a population of largely philopatric rodents might on average be no more distantly related than second cousins. The probability of close genetic relationship between mates will be increased if young of either sex tend to remain at the natal site; if parents in some way facilitate inheritance of the natal site (nepotism); if "survival" habitat occurs in small, isolated patches supporting only a few breeding pairs of individuals; if there are tendencies for relatives to behave aggressively toward strangers but in a neutral, affiliative, or altruistic manner toward familiar individuals such as parents or littermates; if populations are founded by a pregnant female or a pair; if there is resistance to immigration; if there are "social fences"; or if there is a tendency for young to emigrate in company with other members of the same litter. Inbreeding is also favored over any time period in which habitat conditions are stable. Inbreeding could be favored by selection if outbreeding leads to breaking up of combinations of alleles whose overlapping effects lead to advantageous phenotypes.

It is worthwhile to examine some of these "inbreeding facilitation mechanisms" in some detail. Parental nepotism strongly favors inbreeding. Female nepotism and the formation of matrilineal groupings is widespread among the terrestrial sciurids (Armitage, 1986b; Hoogland, 1981; King

and Murie, 1985; Michener, 1983b; Sherman, 1980), and the sciurid model could apply to other rodents as well. The formation of matriline implies that the offspring of neighboring females will be closely related and most polygynous males will mate with females that are close relatives, if not sisters or daughters. The degree of inbreeding in such situations will be determined primarily by male dispersal distances, and avoidance of close inbreeding would require that minimum male dispersal distances must be greater than 1.5 female range diameters. The distance would have to be still larger if male home ranges are larger than female ranges.

Dominance hierarchies among males tend to limit mate choice by females and increase opportunities for matings between the dominant male and sisters or daughters. In polyestrous species, philopatry of offspring of either sex during the breeding season creates opportunities for parent-offspring and sibling matings. In seasonal breeders cohesiveness among members of families over the non-breeding season increases the possibility of parent-offspring matings where parents survive to breed again, and of sibling matings if parents are no longer available. Among temperate zone mice and voles, close relatives often overwinter together (King, 1983; Mihok, 1979). Some non-siblings might join overwintering groups (Madison, 1984; Wolff, 1980; Wolff and Lidicker, 1980), but there seems to be no evidence that closely related individuals spontaneously leave or are forced from such groups.

Habitat patchiness accentuates behavioral tendencies toward inbreeding. This is especially likely if patches are well-separated and small relative to territory size. Pairs of individuals taken at random are more closely related to each other in small populations than in large populations (Partridge, 1983). The point can be appreciated easily in a small non-rodent, *Ochotona*. Smith and Ivins (1983) found that well-defined small patches of scree habitat were associated with philopatry and incestuous mating. Although boundaries are often less easily identified in many rodent habitats, I suspect they are similarly discrete from the point of view of their occupants. Exclusive breeding structure is apparent in some small commensal *Mus* populations (Anderson, 1964, 1965; Petras, 1967a) in which habitat boundaries are readily discernible. Goundie and Vessey (1986) observed little movement in or out of woodlots inhabited by *Peromyscus leucopus*, concluding that the short dispersal distances observed indicated that close inbreeding was probable.

Even in superficially more homogeneous environments, patchiness might be sufficient to promote inbreeding, at least when regional density is low. Bowen (1982) reported that in *Microtus californicus* living in continuous grassland, electromorphs from blood samples collected at first capture of voles on four nearby quadrats revealed that genetic heterogeneity (measured as the *F* statistic) was high at low density. Heterogeneity appeared to decrease as density increased over the single breeding season of the study. As Bowen's comparisons were between grids, rather than habitat patches, however, it is not clear whether the decrease in heterogeneity was due to a decline in inbreeding as Bowen believed, or simply the result of the filling in of the interstices between permanently occupied sites by settlers as the breeding season progressed. The latter interpretation is in keeping with the results obtained by Pearson (1960).

As development and application of statistical and electrophoretic techniques have proceeded, it has become possible to make increasingly sophisticated analyses of genetic structure. Studies designed to detect departure from random mating have produced mixed results. Evidence of small effective population size, inbreeding, and genetic drift has been adduced in house mice (Anderson, 1964, 1965; Petras, 1967a, 1967b; Selander, 1970a, 1970b; Selander et al., 1969b; Singleton, 1985), deer mice (Rasmussen, 1964), voles (Nygren, 1980), pocket gophers (Patton and Feder, 1981; Selander et al., 1974), prairie dogs (Chesser, 1983), and marmots (Schwartz and Armitage, 1981). Following studies of house mice in farm buildings, Petras (1967a, 1967c) estimated inbreeding coefficients of 0.06 to 0.30 on the basis of biochemical polymorphisms and 0.18 on the basis of an agouti coat-color locus. He also observed heterozygote deficiencies. Singleton (1985), in a study of house mice inhabiting haystacks, reported that genotypic frequencies at the GPI-1 locus matched Hardy-Weinberg predictions for random mating, but that

there was a deficiency of heterozygotes at the Hbb locus. Nygren (1980) found a general excess of homozygotes in *Microtus agrestis* over the course of a fluctuation in density. Patton and Feder (1981) reported high positive F_{IS} values, indicating heterozygote deficiencies, for most of 11 loci examined in an undisturbed population of *Thomomys bottae*. Following removal and recolonization, F_{IS} values were largely negative or non-significant, suggesting that inbreeding did not occur during recolonization. Despite the evidence for inbreeding in the undisturbed population, Patton (1985) has concluded that microgeographic variation in pocket gophers is due primarily to founder effects, rather than to inbreeding and restriction of gene flow. Parallel conclusions have been advanced for mole rats (*Spalax*) by Nevo et al. (1982).

Heterozygote deficiencies might or might not indicate inbreeding, depending on selective pressures. Most studies have dealt with one or a few loci, and single-locus studies might be poor indicators of breeding structure because it is difficult to show that a given locus would not be affected by strong selection. Experimental matings, designed to compare the fitness of intra-population and inter-population matings, might be an effective alternative approach to detection of inbreeding. Comparison of litter size in within-population and between-population matings of granary house mice showed evidence of heterosis in the latter (larger mean litter size), implying that significant inbreeding was occurring within the studied populations (Anderson, unpublished).

Modeling studies designed to test possible explanations for the persistence of mutant alleles in house mice have supported empirical evidence of inbreeding in that species (Lewontin, 1962; Lewontin and Dunn, 1960). Maynard Smith and Stenseth (1978) suggested, on the basis of modeling, that inbreeding could be responsible for the stability of female-biased sex ratios in litters of some microtines. They also suggested that a high degree of inbreeding might characterize fluctuating microtine populations during periods of low density.

Although sufficiently detailed studies of dispersal are still scanty, some do suggest that inbreeding might be common. Wolff and Durr (1986) found that nearly one third of overwintered, fall-born *Peromyscus leucopus* females bred within the range of a possible father. In *P. maniculatus* a third of the young also overwintered and bred within their natal home ranges. Jones (1984) reported that at least one male *Dipodomys spectabilis* shared a mound with his mother in his first breeding season.

Other investigations have provided evidence for random mating and/or outbreeding tendencies. Genetic evidence for significant gene flow has been found in several house mouse populations. Such evidence has been associated with disturbance due to agricultural practices, experimental manipulation, or both (Baker, 1981b; Justice, 1962; Myers, 1974), or severe overwinter mortality (Berry and Jakobson, 1974, 1975). Petras (1967a) postulated that *Mus* populations on farms might fall into two categories, those that were permanent and those that were relatively ephemeral. In more ephemeral populations the constant turnover of individuals eliminated any opportunity for inbreeding. Foltz (1981a) found no evidence of a departure from panmixia in *Peromyscus polionotus* and his re-evaluation of data from other studies of *Peromyscus* casts doubt on previous analyses suggesting inbreeding in that genus. Foltz and Hoogland (1983) found that all of four polymorphic loci examined in a colony of black-tailed prairie dogs showed an excess of heterozygotes, a possible result of negative assortative mating. Pedigree analysis supported this indication of low levels of inbreeding and Foltz and Hoogland concluded that behavioral observations of these ground squirrels suggested that inbreeding among close relatives would be rare enough to make inbreeding coefficients very low. However, variability across the electrophoretically analyzed loci suggested other explanations, including selection, for the excess of heterozygotes. Foltz and Hoogland (1983) emphasized that it was difficult to attribute heterozygote excess specifically to any of the several possible causes.

Other studies have demonstrated that the laboratory data on inbreeding depression should not be casually extrapolated to the field situation. Davis (1984) manipulated relatedness in *Spermophilus richardsonii* on two areas so that the coefficient of relatedness was much less than 0.5 on one, and close to 0.5 (between 0.25 and 0.5) on the other. In the more inbred group there

was evidence that inbreeding and close relatedness conferred benefits: above-ground time spent feeding was greater; vigilance was less; sharing of core areas among neighbors was greater; interactions leading to chasing and flight were reduced; and breeding success was increased.

Overall, we are poorly informed as to the actual extent of inbreeding in the majority of commonly studied rodent species. At the present time it is not unreasonable to predict that close (near relative) inbreeding is the normal state of affairs in many populations. If this were the case, deleterious recessive alleles would be maintained at a relatively low frequency because of their frequent exposure to selection. Occasional or even frequent close inbreeding might then not be very costly. If laboratory evidence alone is relied on, the logic in support of the notion that inbreeding should be avoided seems clear. The theoretical and experimental evidence as to the possible cost of inbreeding notwithstanding, it is apparent that if populations maintain social stability, matings among close relatives are probable. Further studies are needed to address directly the question of degree of inbreeding, amount of gene flow, frequency of founder effects, and genetic structuring under a variety of conditions. The evidence that gene flow in house mice is promoted in environments where there is frequent disturbance of population structure raises two important questions applicable to many species. Which populations are most representative, stable inbreeding populations or high-turnover outbreeding populations? Is frequent disturbance so sufficient at preventing close inbreeding that other barriers are unlikely to have selective value?

Barriers to Inbreeding

Close inbreeding can be prevented by separation of near relatives in time or space, or by behavioral or physiological restraints. Selection against inbreeding has been an attractive explanation for various behavioral and physiological phenomena. Sherman and Holmes (1985), for example, suggested that greater development of kin recognition in the more nepotistic sex (females) might be due to its potential contribution to inbreeding avoidance.

The attractiveness of such explanations should not be allowed to obscure the fact that the opportunity for strong inbreeding might be limited by factors that are difficult to relate to inbreeding depression. Seasonal breeding, for example, might influence the probability that matings will be incestuous. Mortality over the non-breeding season can significantly reduce the opportunity for parent-offspring or sibling matings, and relaxation of territorial defense during the non-breeding season might eliminate behavioral barriers to immigration and create opportunities for outbreeding when reproduction is resumed. Predation on *Microtus pennsylvanicus* over the winter months, combined with relaxation of aggressive behaviors and a requirement of sufficient group size to make huddling an effective protection against low temperatures, leads to admission of strangers into overwintering families (Madison, 1984). Similar tendencies for development of aggregations of unrelated individuals during the non-breeding season have been reported by Myllymäki (1977a), Wolff (1980), and Wolff and Lidicker (1980, 1981). Seasonal changes in habitat could have similar consequences. Mihok (1984) noted massive immigration of overwintered *M. pennsylvanicus* at the start of the breeding season, associated with a seasonal shift from wintering habitat (forest) to spring, summer, and fall habitat (grasslands). As visualized by Shields (1983), the resulting "injection" of outbreeding might be an effective counter to the decay of heterozygosity in otherwise inbreeding populations. Tropical dry seasons might have effects similar to those of high-latitude winters. In the capybara, for example, large aggregations form near water in the dry season (Schaller and Crawshaw, 1981).

Hoogland (1982) attributed the rarity of parent-offspring and sibling matings in *Cynomys ludovicianus* to emigration of young males, death or emigration of adult males before philopatric daughters reach breeding age (males that survived the first year of life lived only an additional 3–4 years, whereas females lived an additional 4–5 years), failure of philopatric daughters to come into breeding condition when the father remained in the natal coterie, and behavioral avoidance of closely related males by estrous females. Upon further scrutiny, however, Hoogland's data do not appear to support the hypothesis that there are specific adaptations for inbreeding

avoidance. The first of the four mechanisms (male emigration) eliminated the possibility for inbreeding in 90.4% of the instances studied. As Greenwood (1983) emphasized, it is difficult to disentangle cause and effect with respect to the role of emigration as a barrier to inbreeding. If male emigration evolved from other causes, as postulated by the RFH, it does not support Hoogland's (1982) case for behavioral avoidance of inbreeding. The observed deaths of harem males also can be explained without evoking selection against inbreeding.

Hoogland's data show that although a significantly lower proportion (2/26) of yearling females copulated when the paternal male was present in the coterie, only a minority (13/37) of yearling females copulated when the paternal male was not present. This suggests that, as with male emigration, absence of estrus in a yearling female might be due to factors other than incest avoidance. If cause and effect interpretation is suspended with respect to male emigration and delayed reproduction of yearling females, Hoogland's argument for behavioral avoidance then must rest primarily on the cases of seven females that had an opportunity to copulate with a father, son, or sibling. Two did so, but copulated with a less closely related male as well, and a third did so in 2 of 3 years. Three of the remaining four copulated exclusively with the less closely related of two available males; the other copulated in a neighboring coterie and subsequently returned home. There were, therefore, only three instances in which females were known to have mated exclusively with partners less related than immediate family. As there were also three females that did mate with closely related males, and one for which the data are apparently inconclusive, a strong argument cannot be made for inbreeding avoidance.

In yellow-bellied marmots, as in prairie dogs, the major obstacles to inbreeding appear to be the emigration of young males and the death of older males before philopatric daughters mature (Schwartz and Armitage, 1980). The same conclusion applies to other ground squirrels (Dobson, 1979, 1981; Michener, 1980, 1983*b*; Michener and Michener, 1977; Sherman, 1980). In all of these monestrous species, parental mortality prior to sexual maturity of offspring could be the major obstacle to parent-offspring matings.

Inbreeding might be restricted if inhibition of sexual development in juveniles results from exposure to pheromones produced by sexually active adults of the same sex. Confinement of young with sexually active parents or siblings under laboratory conditions can inhibit sexual maturity of young mice or voles (Batzli et al., 1977; Haigh, 1983*b*; McGuire and Getz, 1981; Rissman et al., 1984; Terman, 1980). Schadler (1983) found that presence of a brother sequestered behind wire mesh inhibited matings between female pine voles and unrelated conspecific males (Schadler did not, however, determine whether the presence of an unrelated male was similarly inhibitory). Inhibitory effects such as these are not demonstrable in some species (Batzli et al., 1977; Facemire and Batzli, 1983; Wilson, 1982) and might not be widespread among rodents. These phenomena might be dependent on close, continuous confinement; Milligan (1980) reviewed the data and concluded that ideas about biological significance of almost all laboratory-derived phenomena of this type were speculative. Two-year-old female yellow-bellied marmots are less likely to breed when older females are present in the colony (Armitage, 1986*b*); this would reduce chances of their mating with their fathers. Such behavior could have evolved through selection for mechanisms by which maternal females limit competition and thereby maximize their own production of offspring at the expense of the reproductive success of their daughters. Inhibition in young female voles observed by Bujalska (1970, 1971, 1973) also seems to be related to regulation of competition among females, rather than to inbreeding avoidance. The response of non-adults might then be viewed as a complementary strategy, effective in delaying emigration (Rissman et al., 1984) and facilitating philopatry. Direct inhibition of maturation of female young by adult female pheromones seems most readily explained in terms of female competition, nepotism, and retention of female young as helpers. Maturity delays associated with parental pheromones need not be explicable solely as barriers to incest.

Inadequate stimulation is the alternative to direct pheromonal inhibition of juvenile development. Lendrem (1985) compared age at first estrus of immature female *Mus musculus* exposed to soiled bedding from the cages of more closely and less closely related males. Females exposed

to bedding from the cages of male cousins matured at a significantly earlier age than those exposed to bedding from the cages of fathers or uncles. It appeared that the odors of more distantly related males accelerated puberty.

The most thorough investigations of a behavioral/physiological mechanism with the potential to reduce the frequency of inbreeding were by Getz, Carter, and co-workers on *Microtus ochrogaster*. This species is a special case because of tendencies to monogamy and to postnatal investment by the father. Up to 50% of breeding units in the field are monogamous (Getz and Hofmann, 1986); in the laboratory males provide paternal care in the nest (Thomas and Birney, 1979). Mechanisms inhibiting mating by other than the parental pair while a family group remains together are evident in males as well. Sons do not attempt to mate with their mothers in postpartum estrus, and young males maintained in family groups show reduced tendency to mount when placed in a pen with an unfamiliar estrous female (Carter and Getz, 1985).

As in other microtines, ovulation must be induced by copulation in *M. ochrogaster*. Females copulate only when in estrus. To achieve her initial estrus, a pubescent female must be sexually activated by exposure to a male pheromone. In confinement, at least, young females do not make naso-genital investigations of familiar males. Therefore, they are not exposed to male pheromones and remain sexually quiescent (Gavish et al., 1983, 1984; Getz et al., 1983; McGuire and Getz, 1981). If parents and offspring share a nest in nature, virgin females probably are unlikely to be activated by their fathers or brothers and thus apparently are unlikely to mate for the first time with a near relative. Because a pair-bond is formed at first mating, females are also unlikely to mate incestuously in later matings.

The obstacle to inbreeding in *M. ochrogaster* is familiarity, not relatedness. If urine from a familiar male is placed on the nose of an inactive female, activation and fertile matings are induced. If familiar males are removed for 8 days and then returned, naso-genital investigation occurs and activation of females and mating follow (Getz and Carter, 1980; McGuire and Getz, 1981). This opens the question as to whether inbreeding avoidance is the entire, or even the correct, interpretation. Some of the laboratory data also raise questions as to how activation can occur in nature if the system operates as it does in confinement. The activation process observed in the laboratory requires that a young female remain with an unfamiliar male for 24 to 48 h. However, both pair-bonded males and sexually experienced but unbonded males are aggressive toward unfamiliar virgin females (Gavish et al., 1983). If an activated female is returned to the family group in the laboratory, activation could be suppressed by maternal pheromones. Confinement of two virgin females together prevents sexual activation of one or both (Carter and Getz, 1985). In the field, most females that survive to maturity are philopatric (Getz and Hofmann, 1986; Getz et al., 1987). It seems, therefore, that explanations other than incest avoidance should be considered. Young assist in rearing younger siblings in the laboratory (Gruder-Adams and Getz, 1985). Inhibition of female maturation in *M. ochrogaster* might function to retain female young in the nest as helpers or to limit female competition or both. There is a good case for expecting that familiarity will make father-daughter and sibling matings unlikely, but alternative explanations for the process by which it is achieved should be sought. Parental strategies serving to control emigration and reproduction of offspring might be revealed.

Familiarity reduces the probability of within-litter incest in some other voles as well. Boyd and Blaustein (1985) reported that although sibling and non-sibling pairs produced litters of equivalent size and viability, young *Microtus canicaudus* that had been reared together to maturity produced fewer litters than those that were unfamiliar when paired. Separation for 5 or 12 days did not reduce reluctance to mate. It thus appears that in nature littermates would be less likely to mate than non-littermates. Despite the absence of detectable inbreeding depression, Boyd and Blaustein (1985) characterized the disinclination to mate as an inbreeding avoidance mechanism and speculated that inbreeding might be characteristic at low density because non-littermates might be unavailable.

The evidence for barriers to inbreeding in other rodents is similarly tantalizing but questionable. Dewsbury (1982c) cross-fostered *Peromyscus eremicus* and *P. maniculatus* prior to eye opening, and paired siblings and non-siblings directly and after 4, 8, or 24 days separation. Although fewer

sibling pairs produced litters than non-sibling pairs in *P. maniculatus*, the difference in number of successful pairs was not significant. The non-sibling pairs produced significantly more litters, but within litters there was no difference in the number of pups born or weaned, or in the percentage weaned. In *P. eremicus*, non-sibling pairs were significantly more likely to produce litters than were siblings or pseudo-siblings (fostered). Non-siblings produced more young at birth, more weaned, and a higher percentage weaned. The pseudo-sibling pairs (born to different females but cross-fostered) had the highest percentage of pups weaned, but mean litter size was significantly higher in matings between siblings. Separation of sibling *P. eremicus* for 4 to 8 days did not eliminate differences between sibling and non-sibling pairs, but there was little difference when pairs were mated after 24 days separation.

Skryja (1978) found no evidence of either delayed matings or infertility in father-daughter pairings of *P. eremicus*, but confinement of young females with their mothers and fathers was more inhibitory to daughters than was confinement with the father alone. If the maternal female was absent there was no difference in age at first reproduction between females caged with their fathers and those caged with unfamiliar males. Daughters had no inhibitory effects on maternal reproduction.

If it is assumed that mechanisms for inbreeding avoidance have been selected, it is necessary to explain why kin recognition and reproductive inhibition appear to be sexually asymmetrical. Lack of stimulation that is based on familiarity is unlikely to be effective in preventing father-daughter matings where the father does not inhabit the nest with the young (most rodent species). The higher probability that male offspring will emigrate and the longer dispersal distance of those that do so appear to be the only restraints limiting strong or close inbreeding on the part of males.

Kin recognition and other male behaviors that relate to inbreeding or altruism have been little studied. D'Udine and Alleva (1983), reviewing the work of Yamazaki et al. (1976), concluded that male *Mus* could exhibit either positive or negative choice of female genotypes at the H-2 locus and suggested that males might select for an optimal level of outbreeding. D'Udine and Partridge (1981) found that cross-fostered males showed a preference for siblings whereas males reared by their own mothers preferred non-siblings.

The inbreeding avoidance explanation of direct pheromonal inhibition can be questioned on the grounds that the mechanisms are intrasexual, rather than intersexual. In *Peromyscus maniculatus*, for example, sexual maturation of young males is inhibited by the pheromones released by adult males, but not by those of adult females (Lawton and Whitsett, 1979). In conjunction with pheromonal cueing of maturation of young of the opposite sex, pheromonal inhibition of maturation of young of the same sex may facilitate parent-offspring mating.

Pheromonal cueing has been studied most intensively in the house mouse. Maternal pheromones tend to accelerate maturity in male offspring, and paternal pheromones tend to accelerate maturity in female offspring (Milligan, 1980). This is likely to be the pattern for most rodents. The relationships are consistent with the concept of intrasexual competition, but not with that of inbreeding avoidance. Inbreeding facilitation seems to have been largely overlooked in the enthusiastic search for inbreeding avoidance.

Inbreeding avoidance might be a seductive explanation for interactions that have subtle and more complex foundations. The operation of pheromonal and behavioral systems that have effects on the probability of inbreeding needs to be carefully evaluated under field conditions before conclusions are drawn as to evolutionary significance. More elaborate and more natural experiments are needed before it can be established clearly that the various maturity-delay phenomena observable under laboratory conditions occur in nature, or function there as barriers to inbreeding. Selection on the basis of the cost of inbreeding has a strong basis in mathematical prediction, but a weak one in data from natural populations. In many cases, inbreeding depression might be temporary because deleterious recessives are rapidly eliminated (Templeton and Read, 1984). Behaviorally, inbreeding can be limited by expulsion of offspring, voluntary emigration of offspring or parents, active avoidance, active preference for unrelated mates, failure to discriminate against unfamiliar individuals, sex differential in export of offspring, or sex differential in

site tenacity of parents or offspring. Physiologically, delayed or suppressed sexual maturation of young in the presence of adults or littermates can make inbreeding unlikely. Avoidance of inbreeding depression presents itself as an attractive evolutionary explanation, but none of the behavioral and physiological phenomena described needs to function exclusively, or even primarily, as a deterrent to inbreeding. The lack of evidence for male choice is partly due to lack of investigation, but unselective mating by males is in accord with the prediction that at least in polygynous species males would have little to gain by selectivity.

I suspect that in nature more opportunities for inbreeding are eliminated by mortality, seasonal changes in behavior, and environmental instability than by inbreeding avoidance. Jones (1984) concluded that high mortality was probably the major factor limiting development of groups of closely related *Dipodomys spectabilis*. Patton (1985) has also concluded that low individual survivorship is the dominant force for outbreeding in *Thomomys*. Selection for avoidance of inbreeding is unlikely where there is little opportunity for inbred matings due to frequent habitat disruption, high turnover rates of males due to mortality, or male emigration. Selection against inbreeding is also unlikely if its costs are low relative to the high costs of emigration. Where selection against inbreeding does exist, it might operate primarily against parent-offspring and sibling matings and have little effect on mating at other levels. Because rodents can occupy habitat patches of small size, selection for local adaptation and coadaptation, as defined by Templeton et al. (1986), could be as important as selection against inbreeding. I think it premature to conclude, as Sherman and Holmes (1985) have done, that kin recognition exists largely because it contributes to avoidance of inbreeding depression.

Male Competition for Copulations

Variation in male mating success is likely to be high in most rodent populations because mating systems are polygynous (Kleiman, 1977) and operational sex ratios are biased toward females (e.g., Jannett, 1980; Redfield et al., 1978a; Schaller and Crawshaw, 1981). As expected, intrasexual aggression is correlated with sexual maturity in males. Sexually active male rodents of most species are mutually antagonistic if placed in arena situations, although some species rely more on avoidance and less on combat (Colvin, 1973; Cranford and Derting, 1983). Aggressiveness in males provides strong circumstantial support for the hypothesis that males compete for copulations.

Male aggression appears with the onset of sexual activity both seasonally and ontogenetically. Thereafter, aggression is maintained at a more or less constant plateau, declining as the end of the breeding season approaches. If there is variation during this period it can occur in response to such stimuli as the presence of estrous females or challenges from other males or both.

The association of male aggression with sexual maturity and with the breeding season in nature is well documented (Boonstra, 1978; Fairbairn, 1977a, 1978a; Healey, 1967; Llewellyn, 1980; Perrin, 1979; Sadleir, 1965; Turner and Iverson, 1973). Laboratory studies have shown that male aggression is correlated with high levels of circulating steroids. In *Clethrionomys glareolus*, for example, Gipps (1983, 1984) demonstrated that male fighting and wounding were dependent on the level of circulating androgens, and that prepubertal castration reduced the tendency to fight.

Aggression is also positively associated with the opportunity to copulate. Aggression among sexually mature male *Peromyscus* is enhanced by the presence of females (Dewsbury, 1984; Terman, 1984). The introduction of a female into an all-male group of *Mus* induced aggressive interactions among the formerly compatible males (Petrusewicz, 1963). The probability of aggressive behavior in male *Microtus californicus* increased with proximity to a caged estrous female (Ostfeld, 1985b), and reproductively active male voles have been observed to be mutually aggressive in the field in the vicinity of estrous females (Webster and Brooks, 1981). Removal of female *M. pennsylvanicus* from an experimental plot increased persistence (i.e., survivorship) of adult males on the plot during the breeding season (Boonstra and Rodd, 1983; Rodd and Boonstra, 1984). However, removal of overwintered female *Clethrionomys rutilus* after weaning

of the first litter did not affect persistence of overwintered males (Gilbert et al., 1986). Aggressiveness in male rodents is directed primarily toward individuals that could compete for matings: immature males can be tolerated where mature males would be attacked (Gipps, 1984). Pheromones produced by adult males have been shown to suppress sexual development of young males under laboratory confinement (Bediz and Whitsett, 1979; Lawton and Whitsett, 1979; Vandenbergh, 1971). Male chipmunks congregated in the home ranges of females in estrus (Yahner, 1978), and radio-collared male meadow voles have also been observed to move into the home ranges of estrous females (Madison, 1980a). Males are known to increase the size of their ranges with the onset of breeding (Korn, 1986; Madison, 1985; Randolph, 1977). Ostfeld et al. (1985) reported that the dispersion of sexually active male *Microtus californicus* was affected more strongly by competition for access to females than by competition for access to food.

Male home ranges are typically larger than those of females (Bondrup-Nielsen and Karlsson, 1985; Mazurkiewicz, 1981; Ostfeld, 1986; Scheibe, 1984), despite the higher energy requirements of gestating and lactating females. Ostfeld (1986) found that supplemental food caused a reduction in the size of home ranges in females but had no effect on those of males. During the mating season, male *Spermophilus richardsonii* moved over greater distances and engaged in more fights than females (Michener, 1983a). Male ranges are more likely to overlap than are those of females (Madison, 1985). Lidicker (1985b) stated that recapture frequencies of male *M. californicus* differed from those of females in that the latter were correlated with habitat quality, whereas male recapture frequencies were not. These intersexual differences imply that female availability, rather than nutritional resources, might be the reference system for use of space by males.

Male maturity and inter-male competition typically precede the seasonal availability of receptive females. In most obligately-hibernating ground squirrels, males emerge and establish hierarchical social relationships through agonistic encounters prior to emergence of females (Armitage, 1986b; Michener, 1983a; Sherman, 1981; Yahner, 1978). Overwintered male voles are more aggressive, have larger home ranges, and survive longer than male young of the year (Turner and Iverson, 1973). Dominant and early-emerging males are more successful at mating than subordinates or those that emerge later (Michener, 1983a). Mating success of male *S. tridecemlineatus* is correlated with both age and weight (Schwagmeyer and Brown, 1983). Dobson (1983) reported that male *S. beecheyi* appeared to guard receptive females. Armitage (1986b) has shown that fitness of male marmots increases with harem size.

Male aggressiveness often declines or ceases as soon as receptive females are no longer available. Most ground squirrel species either follow similar patterns to those described or differ in ways that are consistent with intrasexual selection (Michener, 1984).

If successful competition for copulations depends on a claim to space, male territoriality (defined here as scent marking, aggression, or other behavior leading to occupancy of space to the exclusion of some category of conspecifics) is most likely to be expressed in the breeding season. Adult males have been found to occupy home ranges that overlap those of females, but not those of other adult males in marmots (Armitage, 1974), California ground squirrels (Dobson, 1983), house mice (Fitzgerald et al., 1981), woodrats (MacMillen, 1964), pocket mice (MacMillen, 1964), and voles (Jannett, 1980, 1981a; Wolff, 1980).

Overlapping ranges of resident males have been reported in many species, including some of those listed above (Daly and Daly, 1975; MacMillen, 1964; Oakshott, 1974; O'Farrell, 1980; Webster and Brooks, 1981). If males compete intensely, why do male home ranges sometimes overlap? Boonstra and Rodd (1983) postulated that breeding male *M. pennsylvanicus* formed dominance hierarchies among individuals with overlapping ranges. Ostfeld (1985a) has argued that male territoriality is dependent on female strategy, and that male behavior should be territorial when female ranges are mutually overlapping, and non-territorial when female ranges are mutually exclusive.

Perhaps the view that males are not territorial when male home ranges overlap is simplistic and misleading. Territoriality is evident in its simplest and most generally accepted form when

male residents occupy space to the exclusion of all other breeding males. Definition of male use of space as non-territorial wherever there is overlap in ranges of breeding males (Lidicker, 1980; Madison, 1980a, 1980b, 1985; Wolff, 1980) overlooks the possibility that there might be advantages to males in various forms of cooperative or communal defense of space. The possibility that overlap might indicate that males are cooperating in defense of territory, and therefore of mating rights, needs investigation. Cooperative defense of an area by equals, relatives, or members of a dominance hierarchy may exclude neighbors or transients. Communal territories are easily defined in *Microtus pinetorum* (Cranford and Derting, 1983; FitzGerald and Madison, 1983), suggesting that they may be present in other less obvious forms in those microtines where male ranges overlap. Stable groupings of 2 to 4 breeding males, suggesting inter-group territoriality, have been described in *Clethrionomys rufocanus* (Viitala and Hoffmeyer, 1985). In a comparative study of *M. pennsylvanicus* and *M. pinetorum*, Cranford and Derting (1983) concluded that males of the former species maintained individual distance through mutual avoidance. The question of whether overlapping ranges formed a continuum or represented mating "communes" was not addressed, and the degree of relatedness of overlapping males was not considered. The difference between those situations where male ranges overlap and those where they do not may relate to habitat characteristics and the effectiveness with which space can be defended by fighting, chasing, and patrolling, or by scent marking or other means of display. It may also depend on the degree to which other males threaten copulatory success.

Scent marking might play an important role in assertion of male mating rights. Jones and Nowell (1974) showed that urine of male *Mus* contained an aversive substance that caused subordinate males to avoid scent marked areas. Wuensch (1982) found that in the field, traps scented by wild male *Mus* dominant in laboratory encounters were more likely to be visited by resident males than were those scented by males that had been subordinate in the laboratory. This might follow if the presence of a dominant male is more likely to threaten reproductive success, and thus be more worthy of investigation by a resident than the presence of a subordinate. Scent marking could serve as an alternative to combat among adult males, or to damaging attacks by males on their offspring.

Outside of confinement, fighting may be less common and wounding more superficial than in staged encounters in the laboratory. Schaller and Crawshaw (1981) noted that pursuing male capybaras did not appear to make any effort to close the gap between themselves and intruding males they chased. Nevertheless, wounds (mostly on the rump and shoulders) did accumulate over the breeding season and some were fatal.

Competition for copulations might not have spatial reference points in all species. Observing inter-male competition for copulations in an unconfined population of *Spermophilus tridecemlineatus*, Schwagmeyer and Brown (1983) saw no site-specific dominance. Differences among species might be associated with habitat differences, mating systems, whether or not estrus is male-induced, relatedness of the animals studied, or study methods.

Male territorial behavior has been repeatedly implicated as a determinant of density of breeding males (Fairbairn, 1977a; Myllymäki, 1977a; Redfield et al., 1978a, 1978b; Wolff, 1980), and emigration of overwintered males typically shows a peak at the start of spring breeding activity (Boonstra and Rodd, 1983; Fairbairn, 1977a; Perrin, 1979). Myllymäki (1977a) attributed emigration of spring-born males to the aggressiveness of overwintered males. In boreal populations of *M. pennsylvanicus*, males enhanced their probabilities of reproductive success to a much greater extent by early establishment in summer habitat than did females (Mihok, 1984). Mihok et al. (1985b) found that as males came into reproductive condition, there was a high rate of turnover during which most of the fall residents were displaced.

Boonstra and Rodd (1983) systematically tested the hypothesis that male competition for copulations was direct, rather than through territorial claims, in *M. pennsylvanicus*. Removal of females caused a reduction in male density; removal of males led to an increase in male density. They concluded that resident breeding males restricted recruitment of breeding males when breeding females were present. Armitage (1986b) implied that male territoriality in mar-

mots and ground squirrels is oriented primarily toward assertion of exclusive access to females. A male might defend a colony area containing the burrows of females, or defend a burrow near, but not among, those of the females. Barash (1981) explored a series of predictions based on the assumption that male marmots competed for copulations. He found, as predicted, that: 1) males made probes outside of the colony area ("gallivants") more than did females; 2) gallivanting males were invariably driven from neighboring colonies if they encountered the resident male; 3) if the resident male had been removed, gallivanting males copulated with the resident females; 4) resident males attended females more closely during the breeding season and when threatened with cuckoldry by intruders; 5) group-living (harem) males maintained closer watch on females than did monogamous males; and 6) males cohabiting with fertile females guarded the females more than did males with infertile females.

Davis and Murie (1985) suggested that competition among male ground squirrels may include both pre-copulatory competition and post-copulatory mate guarding, both of which reduce the incidence of multiple matings. Male *Microtus* with overlapping ranges concentrate in the territories of estrous females (Madison, 1980a; Webster and Brooks, 1981).

Competitive mating chases have been described for *Microcavia* (Rood, 1970), *Microtus* (Webster and Brooks, 1981), *Tamias* (Yahner, 1978), and *Clethrionomys* (Kalela, 1957; Viitala, 1977). Social dominance has been shown to correlate with breeding success of males under various experimental regimes (DeFries and McClearn, 1970, 1972; Dewsbury, 1984; Lloyd and Christian, 1969; Reimer and Petras, 1967; Singleton and Hay, 1983). Social dominance under field conditions has been associated with mating success in *Clethrionomys* (Kawata, 1985b; Mihok, 1981), *Spermophilus* (Schwagmeyer and Brown, 1983), and *Tamias* (Yahner, 1978). Yahner found that as the number of competing male chipmunks increased, the ability of the dominant male to monopolize copulations was eventually eroded. The dominance/success relationship has been questioned on the basis of laboratory experiments with wild and domestic strains of *Rattus norvegicus* (Barnett, 1958; Dewsbury and Hartung, 1980; Price, 1980).

It is generally assumed that competition among males results in high variance in male success. There are few direct measurements of this in nature, but Sheridan and Tamarin (1986) obtained results suggesting that, at least among established resident males, success was fairly uniform. Among 28 cases where paternity could be assigned in *M. pennsylvanicus*, 82% of the males fathered only one litter and the remaining 18% fathered only two. If these preliminary results can be extended to rodents in general, high variance in male reproductive success may be less common than previously believed.

Exposure of a recently impregnated female to an unfamiliar male under conditions of confinement might block pregnancy and induce estrus (Bruce, 1959; Dewsbury, 1982a; Heske and Nelson, 1984; Mallory and Clulow, 1977; Schadler, 1981; Stehn and Jannett, 1981; Stehn and Richmond, 1975), and introduction of an unfamiliar male into a cage containing a female and her newborn litter can lead to infanticide by the male (Mallory and Brooks, 1978). Both phenomena have been viewed as mechanisms that have evolved through male competition for reproduction (Mallory and Brooks, 1980; Schwagmeyer, 1979). Neither phenomenon has been convincingly demonstrated in the field, in the absence of confinement, and Milligan (1980) has speculated that the pregnancy-block effect might simply be a derailing of the system for maintaining prolactin secretion in early pregnancy and thus a laboratory artifact. Boonstra (1980) has concluded that there is no evidence that male infanticide increases with population density, or is frequent enough to be of demographic significance.

There are a few reports in which male competition did not seem to be clearly oriented toward access to females. Huck and Banks (1982b) observed dominant male lemmings ignoring receptive females in order to seek out and attack subordinate males. Evans and Dewsbury (1978) concluded on the basis of arena experiments with two males and a receptive female *Microtus ochrogaster* that there was no justification for believing that males fought over females or that dominance conferred a copulatory advantage. Dewsbury (1982b) later revised this conclusion somewhat in a more wide-ranging review. Because the confined arena environment in laboratory studies often

distorts behavior and obscures interpretation (Anderson, 1961; Calhoun, 1962*b*; Dieneske, 1979; McClintock, 1983), the few available observations fail to discredit the view that males compete for copulations. This conclusion appears to be as well established as it is possible for a biological generalization to be, despite the cautions expressed by Dewsbury (1981, 1982*b*) and Evans and Dewsbury (1978).

Resident Male Behavior Toward Offspring

If males are to behave paternally, they must be able to distinguish between their own offspring and those sired by others. The fact that fertilization is internal and is separated from the initial appearance of the young by a long interval of gestation makes it difficult for male mammals to be certain of paternity and, as pointed out by Elwood (1983), favors abandonment of females in search of further copulations once a mating has been achieved.

We are largely ignorant of paternal behavior in rodents; Kleiman and Malcolm (1981) were able to cite observations on only 36 species. Elwood (1983) cited observations of paternal care of offspring in nine genera and 23 species. All but a few of these citations referred to studies in which paternal proximity to young was enforced by confinement. Observations of paternal care outside of the laboratory are almost non-existent (Elwood, 1983). As far as the few field observations go, most male rodents have little contact with presumptive offspring, at least until young emerge from the nest, and contact with young might be actively discouraged. Female meadow voles prevented males from interacting with pups in a semi-natural runway system (McGuire and Novak, 1984).

Paternity may be relatively certain in some species, but less so in others in the same genus (Birdsall and Nash, 1973; Foltz, 1981*a*, 1981*b*). Behavior of males toward young should be influenced by the degree of uncertainty. Available data are ambiguous as to the ability of males that have not cohabited in the nest to recognize young they have sired. Males that do not share a nest with females and their litters might recognize offspring directly (e.g., through matching of chemical phenotypes), through association with the maternal female, or through the appearance of young as weanlings within the paternal home range. Encounters with their offspring are probable in sedentary males, but recognition is less likely where males shift ranges after breeding. Males appear unable to distinguish their offspring from those of others in some ground squirrels (Michener, 1980; Sherman, 1977, 1980).

The strongest evidence for paternal recognition might be the fact that although males of many species cannibalize young, males have rarely been observed to kill young that they sired. Males could benefit from infanticide if they killed and cannibalized young for their nutritional value, or as a means of assuring or accelerating paternity (Elwood, 1983). Labov (1980) found no difference in the proportion of pups killed by same-strain and other-strain males when female house mice were placed in the males' cages 3 days prepartum, but his design did not distinguish between stud and non-stud males. Rates of infanticide were low in all cases. Stud male *Dicrostonyx* introduced into laboratory cages containing the maternal females and their own young did not attack the young, whereas non-stud males acted infanticidally in the same situation (Mallory and Brooks, 1978; Webster et al., 1981). It is not clear whether infanticide in such cases involves the paternity of the young in question, or is simply induced by the maternal attack on the non-stud male under conditions of confinement in small spaces, although it has been observed in moderate-sized outdoor pens (Heske and Nelson, 1984). Immigrant male *Spermophilus parryii* tend to kill young in the process of establishing themselves (McLean, 1983). As females are monestrous there is no immediate mating advantage to this behavior. If female young (potential mates) are killed along with males, infanticide could reduce rather than increase the fitness of immigrating males. McLean reported that male *S. parryii* defended territories primarily during the period when young were most vulnerable to infanticide, and that removal of presumptive sires increased the probability of infanticide. Sires appeared to act as lookouts during the period of lactation (McLean, 1983).

When males cannot recognize their own offspring, the best course might be to tolerate all

prepubertal young. Tolerance for prepubertal offspring has been evident in observations of male behavior in *Peromyscus* (Eisenberg, 1962; Horner, 1947; Howard, 1949), *Onychomys* (Horner and Taylor, 1968), and *Microtus* (Thomas and Birney, 1979). In the laboratory, males have been observed to hover over, lick, and retrieve offspring in *Peromyscus* (Horner, 1947; McCarty and Southwick, 1977a), *Onychomys* (Horner and Taylor, 1968; McCarty and Southwick, 1977a, 1977b), and *Rattus* (Horner and Taylor, 1969). Adult male meadow voles investigated young introduced into their home cages, but were not aggressive toward them; this was in contrast to lactating females, which were aggressive toward unfamiliar young (Boonstra, 1984). McGuire and Novak (1984) reported similar tolerance of weaned young by male meadow voles within a semi-natural runway system. Paternal tolerance of offspring is variable among *Microtus* species (McGuire and Novak, 1984, 1986; Oliveras and Novak, 1986; Thomas and Birney, 1979; Wilson, 1982). In the absence of dedicated studies in the field, it appears that in nature the behavior of resident males toward sexually immature young also tends toward neutrality. This is not surprising because males in most species appear to have little contact with young.

Other than guarding against infanticide, it could be that the greatest contribution a paternal male can make to the welfare of offspring of either sex is to facilitate the inheritance of the paternal home range. As in those birds where offspring are retained as helpers (Brown and Brown, 1984), retention of young in the paternal territory could increase survival and future reproduction. Paternal behavior toward offspring can be expected to change when maturing offspring become potential mates or potential competitors for matings, and when paternal reproductive potential is exhausted. In general, offspring should be treated as relatives capable of making a contribution to paternal fitness.

There is no evidence of barriers to inbreeding in the behavior of paternal males toward female offspring. Insofar as paternal pheromones accelerate puberty of daughters (Bronson, 1979), the available evidence on behavior and function of males with respect to daughters suggests that inbreeding is likely to be facilitated.

Svare (1981) commented that male aggression as a paternalistic behavior had been so little studied that discussion of the topic was precluded. There are a few indications of active nepotism by male rodents, but it is not clear that investigators have looked for it. I have found no studies that deal specifically with paternal behavior as an active contribution to philopatry. Early hibernation of breeding males in some ground squirrels might relate to competition among males (Michener, 1984), but could secondarily benefit offspring by reducing competition in the critical period before their first hibernation. Declining male aggressiveness in polyestrous species might be associated with recruitment of young that will overwinter, but the relevant male patterns might be explicable on other grounds, and benefits for offspring, or their fathers, have not been quantified. "Neutrality" sums up the bulk of what is known about male-offspring relationships in nature.

Competition and Aggression in Female Rodents

Female aggressiveness, like that of males, is associated with reproductive activity, but has received much less attention from ecologists and ethologists. This probably is because females are less easily induced to fight in arenas. The aggressiveness of adult females normally declines outside the breeding season, but persists when breeding is extended. For example, Ylönen and Viitala (1985) reported that female *Clethrionomys* remained aggressive when breeding continued over winter.

Although Hyde and Sawyer (1977) reported a peak in female aggressiveness during proestrus, it is evident that resident females are not required to compete for copulations. Pregnancy rates among adult female rodents tend toward 100% (e.g., Dobson, 1982; Mihok, 1981) and female-biased sex ratios in ground squirrels do not result in lower pregnancy rates (Michener and Michener, 1977). Removal of sexually active males did not affect density or reproductive status of female *Microtus pennsylvanicus*, and exclusion of adult female immigration by resident females was not dependent on the density of breeding males (Boonstra and Rodd, 1983).

Female aggressiveness varies with gestation and lactation in ways that reflect both resource requirements and defense of current investment in offspring. Aggressiveness increases with progesterone level (Gleason et al., 1979), and is highest during pregnancy and lactation (Boonstra, 1984; Burt, 1940; Festa-Bianchet and Boag, 1982; Gleason et al., 1980; Nicholson, 1941). Female ground squirrels apparently do not establish territories until pregnant (Holmes and Sherman, 1982). It is during gestation and lactation that nutritional requirements of females are greatest (Sadleir et al., 1973); lactation is also the time when investment in vulnerable nest young is high.

Heightened aggressiveness in females with nest young has been reported by Fleming (1979), Gray (1979), and Mallory and Brooks (1980). Female *Mus* in the laboratory are most aggressive toward unfamiliar juveniles during the first 2 weeks postpartum (Gray, 1979). Non-lactating female *Microtus pennsylvanicus* ignored unfamiliar young introduced into their home cages but lactating females were aggressive toward them (Boonstra, 1984). Female *Peromyscus leucopus* in their home cages showed the greatest aggressiveness toward diestrous conspecific females when in late pregnancy and during the middle portion of lactation. When encounters took place in a neutral cage there was no difference in aggression over the course of pregnancy, and increased aggression was evident only on day 5 postpartum (Gleason et al., 1980). This result illustrates the importance of location, and re-emphasizes the point that "neutral arenas" can give misleading results.

Ostermeyer (1983) has provided a detailed review of the literature on female aggression as it is specifically related to pregnancy and lactation. Such aggression has been recorded in 14 rodent genera. It is viewed as a special category ("maternal aggression") and characterized by a brief latency to attack, high intensity, and damaging attack to vulnerable areas. Maternal aggression has one peak in the first third of pregnancy, and a more intense peak late in the first third or early in the middle third of the lactation period.

Increased aggressiveness during lactation might serve both to conserve resources and to protect reproductive investment from intruding conspecifics. In the laboratory, maternal aggression is most often directed against unfamiliar males, and is site (home cage) dependent but not dependent on the presence of pups. Because females encountering unfamiliar males under laboratory conditions in the first few days of pregnancy could abort their litters, and because pups might be killed and eaten under these conditions by males that did not sire them, the implication is that the primary function of maternal aggression is protection of maternal investment. Ostermeyer (1983) tends to accept this conclusion. However, field data are largely lacking and it is possible that both pregnancy block and male infanticide are results of the agonistic interactions generated by the laboratory situation, rather than the evolutionary precursors of maternal aggressiveness. Mallory and Brooks (1980) have suggested that infanticide by intruding females might be the main threat toward which aggression of lactating females is directed.

There is a strong case for a relationship between female aggression and the acquisition and retention of resources. Female home ranges are more commonly exclusive of same-sex breeding residents than are those of males (Blair, 1951; Bondrup-Nielsen and Karlsson, 1985; Brooks and Banks, 1973; Bujalska, 1973; Daly and Daly, 1975; Dixon, 1958; Eisenberg, 1975; FitzGerald and Madison, 1983; Howell, 1954; Jannett, 1980, 1981b; Kawata, 1985b; Madison, 1980a, 1980b; Metzgar, 1979; Mihok, 1981; Perrin, 1981; Reich and Tamarin, 1980, 1984; Sherman, 1980; Smith, 1978; Stoddart, 1970; Tanaka, 1953). Overlapping ranges of breeding females are reported relatively rarely (Behrends et al., 1986; Morris, 1955; Myllymäki, 1975; Ostfeld, 1986; Wolff, 1980). When they do overlap, the relative extent of overlap might be less than that in males (Behrends et al., 1986). Analyzing sequential catches of *Microtus pennsylvanicus* in multiple-capture traps, Reich and Tamarin (1984) found that breeding females were the population component most likely to occur singly. In a study of sequential captures in traps scented by a previous occupant, breeding females were rarely caught in traps in which a different breeding female had been caught previously. Multiple captures of female *M. pennsylvanicus* have been observed less frequently than would be predicted from the frequency of females in populations (Getz, 1972; Slade, 1976).

There is ample evidence that nutritional resources are important to females. Pfeifer (1982a) reported that female *Spermophilus* holding territories on which earlier snow melt had led to earlier vegetative growth produced the most young. Individual reproductive success of female marmots is significantly associated with food availability (Andersen et al., 1976) and decreases with harem size (Armitage, 1986b; Downhower and Armitage, 1981). In many hibernating sciurids, female emergence is timed to coincide with the spring flush of vegetative growth (Michener, 1984). Where the growing season is very short, emergence and parturition of female yellow-bellied marmots can occur earlier, allowing young to obtain sufficient nutrition to fuel winter metabolism.

Experimental supplementation of food supplies usually caused increased population density and/or induced immigration (Cole and Batzli, 1979; Flowerdew, 1972; Gilbert and Krebs, 1981; Hansson, 1971; Mares et al., 1976; Sullivan et al., 1983; Wolff, 1986). Young and Stout (1986) reviewed 13 food-supplement studies in *Peromyscus* and reported that supplemental food increased the minimum number known alive (MNA) on study grids in most, but not all, studies. Their own data showed that supplemental food increased the MNA primarily through an increase in transient *P. gossypinus*, but did not increase persistence of juveniles, and apparently did not affect the density of *Ochrotomys*. Wolff (1985a) reported that food supplements caused a reduction in the size of home ranges of *P. leucopus* and *P. maniculatus* until an apparent minimum size was reached, after which range overlap and aggressive interactions were evident. Taitt (1981) reported that food supplements maintained reproduction in populations of *Peromyscus* despite winter weather.

Gurnell (1983) viewed most experimental attempts to alter the demography of tree squirrel populations through supplemental feeding as inconclusive. Krebs and DeLong (1965), Cole and Batzli (1978), and Desy and Thompson (1983) all failed to halt population declines in *Microtus* by supplying supplementary food. In other studies, food supplements have facilitated reproduction (Andrzejewski, 1975; Bendell, 1959; Cole and Batzli, 1978; DeLong, 1967; Flowerdew, 1972; Sullivan et al., 1983; Taitt, 1981; Taitt and Krebs, 1981, 1983; Watts, 1970) and increased the proportion of resident females breeding (Desy and Thompson, 1983; Ford and Pitelka, 1984; Taitt et al., 1981). Reproduction-enhancing effects of food supplements do not require an increase in the density of breeding males (Fordham, 1971). Radiotelemetry revealed that home ranges of female *M. californicus* decreased in size when food was supplied, that overlap of ranges increased, and that some females shifted ranges into the area where supplemental food was available (Ostfeld, 1986). In northern Finland, female *M. oeconomus* shifted nest sites to follow the progressive appearance of new vegetation behind receding spring meltwaters (Tast, 1966).

Seasonal appearance of new vegetation may control vole reproduction directly in at least some species. Seasonal activation of female *M. montanus* can be induced through physiological responses to intake of substances associated with seed germination and growth of vegetation (Berger et al., 1981; Negus and Pinter, 1965; Negus et al., 1977).

There is room for a great deal of further study of the role of nutrition in the strategies of female microtines (Batzli, 1985). Survival of female *Microtus* can vary with patch quality, and increased quality through supplementary food, watering, or fertilizing generally has resulted in an increase in density, litter size, and persistence of adult females (Ostfeld, 1985a). Myllymäki (1977b) concluded that female *Microtus agrestis* were capable of coming into breeding condition whenever high quality food was abundant. In a season of high density and food abundance, female *Dipodomys spectabilis* tended to abandon natal sites to offspring, thereby increasing offspring survival without apparent cost to themselves (Jones, 1986).

The RFH predicts that female aggressiveness in defense of resources would be high in times when resource demands would increase or peak, and that resource defense should be directed toward other females because they represent greater threats to resource availability than do males. Pre-eminence of nutritional resources should place a premium on habitat selection by females.

The limited comparisons of habitat selection in males and females to date have been incon-

sistent. Bowers and Smith (1979) evaluated habitat quality on the basis of water potential in the vegetation in arid areas of western North America and concluded that female *Peromyscus* chose habitat of higher quality than did males. Morris (1984), working in more mesic habitats in the northeast, concluded that males selected the higher quality habitats. Krohne et al. (1984) noted a significant female-biased sex ratio among *P. leucopus* settling in a seasonally available habitat, and a male-biased sex ratio among individuals moving between trapping grids inhabited throughout the year. This is unexpected under the RFH, but might reflect a focus on mates as resources by male transients, and a focus on uncontested access to food and other "habitat" qualities by female transients.

Female aggressiveness can be reduced under appropriate circumstances. McShea and Madison (1984) observed sharing of nests by two lactating *Microtus pennsylvanicus* in spring and suggested that thermal advantages at this time (when resources were perhaps superabundant) might make sharing an advantageous strategy for closely related females. Cooperative nesting was not observed later in the season, when resources might have been in less abundant supply. Overlapping female ranges are found primarily in the more social of the sciurids (Armitage, 1975; Hoogland, 1982; King, 1955). The data from this group suggest that whenever such overlap of female home ranges is observed, the maturity and genetic relationship of the females involved should be taken into account. McLean (1982) found that among arctic ground squirrels close female kin (sisters, mothers, and daughters) had more overlap of home ranges and interacted more amicably than unrelated individuals. Close female kin also clumped their young on emergence. Distant relatives that had not associated on emergence were intermediate in these characteristics between close kin and unrelated individuals.

Food resources may not be the only focus of female competition. Pfeifer (1982a) found that female reproductive success in ground squirrels varied with the quality of the maternity burrows. Poor burrows might increase the chance of infanticide by neighboring females, who could increase their own fitness by killing the litters of unrelated neighbors (Sherman, 1981, 1982). Sherman (1981) suggested that infanticide by female Belding's ground squirrels that had lost their own litters to predation could represent a competitive move by means of which the perpetrator replaces an unrelated female on a safer burrow site.

Michener (1980) reported that differential female reproductive success in *Spermophilus richardsonii* was achieved by production of female-biased litters. She considered that, in such female-philopatric and matrilineal species, investment in daughters and nepotism toward them is highly advantageous. The utility of this strategy may be limited by effects of resource shortage on survival of offspring (Downhower and Armitage, 1981). However, reproductive success of sons has not been examined in sufficient detail to permit comparison.

Female aggression, like that of males, is associated with the breeding season. Unlike that of males it has a cyclic expression associated with gestation and lactation. This is specifically referred to as maternal aggression, and is closely related to investment in young. Females compete for resources, and female territoriality can be expected to function in defense of both resources and young. These observations suggest that female aggression could significantly affect both emigration and immigration.

Resident Female Nepotism

Although male rodents often have little opportunity to contact young, females can readily identify and form bonds with their young at birth and are generally able to recognize their own offspring (Beach and Jaynes, 1956a, 1956b; Downhower and Armitage, 1981; Holmes and Sherman, 1982; Michener, 1973; Michener and Sheppard, 1972; Sherman, 1977, 1980). Mother-young associations established at birth and during lactation often continue after weaning. The certainty of relationship, the prolonged period of association, and the high maternal investment all underlie maternal nepotism. Options open to the mother include conservation of young at the natal site, selective export of offspring, inbreeding, avoidance of inbreeding, or manipulation of offspring

in ways that optimize between inbreeding and outbreeding (Moore and Ali, 1984). Mother-young recognition makes possible the formation of persistent matrilineal groupings of related individuals in which there can be exchange of altruistic behaviors.

Kin recognition and maternal nepotism have been studied in greatest depth among ground squirrels (Davis, 1984; Sherman, 1980; Sherman and Holmes, 1985). Recruitment, where carefully documented, appears to consist largely of individuals born into local groupings, whether in ground squirrels (Hoogland, 1981; Michener, 1983*b*; Sherman, 1977, 1980) or house mice (Lidicker, 1976).

Females initially behave nepotistically toward their entire litters, regardless of the sex of the offspring. Nevertheless, as predicted by the RFH, recruitment from a given litter is usually sex-biased. Associations between mothers and daughters are more persistent than those between mothers and sons, reducing the likelihood of mother-son matings, favoring the formation of mother-daughter clusters and matrilineal lines, and increasing opportunity for father-daughter matings.

Mother-daughter relationships can be readily observed in some ground squirrels. In such cases females persist in cohesive behavior toward their daughters even as they grow older (Armitage and Johns, 1982). In species that hibernate, mutual recognition and bonding between mothers and daughters remain evident after emergence (Michener, 1974; Michener and Sheppard, 1972). Adult female Columbian ground squirrels allowed daughters to inherit parts of their breeding territories, and if a resident female shifted her range it was usually taken over by a daughter (Harris and Murie, 1984). Because mothers were dominant to yearling daughters, maternal moves were not forced by filial competition; maternal range shifts appear to be a form of parental investment.

Matrilineal groupings in *Spermophilus columbianus* typically included an adult female, a 3-year-old female, and a 2-year-old female. More than 75% of 2- to 4-year-old females had at least one adult female relative in the same breeding group (King and Murie, 1985). Female ground squirrels will attack unrelated young but are less inclined to attack those of their own daughters (Sherman, 1977). Female black-tailed prairie dogs are much more likely to behave amicably toward members of their own coterie than toward members of neighboring coterie (Hoogland, 1981).

Although females behave so as to favor recruitment of daughters, maternal behavior appears neutral or negative with respect to recruitment of sons. Most resident female yellow-bellied marmots are recruited from their natal colonies, but most of the breeding males are recruited from other colonies (Armitage, 1984; Schwartz and Armitage, 1980). Yellow-bellied marmot colonies thus persist as matrilineal lines for many years (Armitage, 1986*b*). The result of maternal nepotism in all intensively studied ground squirrels is that the fundamental social unit is the "mother-headed family" (Michener, 1983*b*). Work on South American caviomorphs occupying similar niches (Rood, 1970) suggests that this generalization applies to that group as well.

Relatively little effort has so far been devoted to determination of the extent of nepotism in other rodents. Evidence of female nepotism toward daughters, similar to that observed in ground squirrels, has been inferred for microtines (Frank, 1957; Jannett, 1978; Madison, 1980*b*; Madison et al., 1984; Wolff, 1980). The primary cause of bias in recruitment in these rodents seems to be male emigration (e.g., Myllymäki, 1977*a*, 1977*b*). Young *Microtus* of both sexes are much more likely to be caught in multiple-catch traps with adult females than with adult males (Slade, 1976).

Abdication of the maternal home range as a form of maternal nepotism has been suggested. Resident females sometimes shift their own homesites, leaving parts of their ranges to their newly weaned litters in *Dicrostonyx* (Brooks and Banks, 1973), *Microtus* (Jannett, 1978, 1980; Madison, 1980*b*; McGuire and Novak, 1986; Myllymäki, 1977*a*), *Tamiasciurus* (Price et al., 1986), *Peromyscus* (Howard, 1949), and *Dipodomys* (Jones, 1986). Jones (1986) reported that survival of philopatric young was higher when maternal *Dipodomys spectabilis* abandoned the natal mound and shifted to another mound on the margin of the natal range compared to that when the

female simply disappeared. Nepotism in female *D. spectabilis* appeared to be impartial with respect to sex. Jones found no difference in the proportion of male and female offspring acquiring natal mounds. The cost to maternal females appeared to be slight. Females moved less than the mean width of a territory, and the survival of those that moved was as high as that of those that did not. Maternal abdication in this species would not reduce the probability of mother-son matings.

Madison et al. (1984) observed that at the end of the breeding season *Microtus pennsylvanicus* in outdoor enclosures formed matrilineal groups in which there was selective retention of males. Communal winter nests were observed to develop around a female and included her immature young and males from the surrounding area. Relatedness was not determined in communal nests shared by lactating *M. pennsylvanicus* in spring (McShea and Madison, 1984) so the persistence of matrilineal groupings beyond the non-breeding season is uncertain.

Behaviorally, maternal nepotism is modified in response to density. Maternal females might become more aggressive toward their offspring as density increases, or they might cease to abdicate nest sites to their litters (Hoogland, 1986; Jannett, 1978).

Given the general evidence of maternal nepotism toward daughters in the wild, what significance is to be attached to the observation that close confinement with a maternal female will inhibit sexual maturation of female young in the laboratory? Getz et al. (1983) suggested that female pheromones blocking sexual activation of female young would serve to restrict breeding to a single pair in a social group. Maximization of direct fitness at the expense of reproductive contributions from offspring is understandable if the retained young can contribute in some way to parental reproductive success. This analysis could apply also to *M. pinetorum*, because in most cases only a single female in a colony is reproductive (FitzGerald and Madison, 1983). The extreme of such pheromonal inhibition is reached in *Heterocephalus glaber*, in which many females are non-reproductive throughout their lives, carrying out specialized tasks in a colony in which a single large female produces all young (Jarvis, 1981). Waser and Jones (1983) have pointed out that *H. glaber* may represent the end of a continuum in social evolution within the Bathyergidae.

Although it would not be surprising to find that in most species maturation of young females can be inhibited by exposure to maternal pheromones under laboratory conditions, it is unclear how common the phenomenon is in the wild. Exposure to the urine of maternal or other adult females blocks the activation of virgin female *Microtus ochrogaster* by males (Carter and Getz, 1985; Getz et al., 1983). Getz (1978) proposed that suppression of maturation in female young was a means of maintaining low densities in stable habitat. Superficially, at least, this is a pattern that would increase the persistence of a group at the expense of individual success.

Interpreted on the basis of maternal fitness, instances of suppression by maternal pheromones can be viewed as a means of conserving offspring and of furthering nepotism. In circumstances where maternal females retain considerable residual reproductive value, maturation of female offspring portends competition, but expulsion of offspring is costly in terms of offspring survival. The RFH encourages a postulate that selection would favor inhibition of juvenile development as a means of regulating export of offspring so as to maximize the chances that they will survive to contribute to the future gene pool at a later date. Observations on a small island (Bujalska, 1970, 1971, 1973) suggest that inhibition of daughters in response to density or resource shortage might have this effect, because disappearance of a breeding female leads to reproduction by a previously inhibited young female. On the other hand, Snyder (1962) reported that removal of adult females from a free-living woodchuck population delayed, rather than accelerated, the maturity of juvenile females.

Maternal nepotism is at least widespread, if not universal, among rodents. It conforms to the predictions of the RFH and can be interpreted as an example of parental manipulation of the philopatry-emigration option for offspring. If females are generally nepotistic, and preference is directed toward daughters, dispersal becomes a matter of emigration from, and immigration into, matrilineal groups. The observation that female nepotism is directed primarily toward

daughters also provides a rationale for the observation that female grouping establishes the basis for polygyny (Wittenberger, 1980).

Inhibition of Immigration by Residents

Evidence of inhibition of immigration falls into three categories: appearance of new individuals when residents are removed; location-dependent dominance by residents; and avoidance of residents by non-established individuals. To a varying degree the information in these three areas can be detailed with respect to factors that modify the probability that immigration will be successful.

Removal studies provide circumstantial evidence that the presence of residents prevents settlement and immigration of transients. New settlers (potential immigrants) typically appear immediately in trap samples when residents are removed from field populations. Removal studies have resulted in increased capture of unmarked individuals in the genera *Apodemus* (Flowerdew, 1978), *Peromyscus* (Fairbairn, 1978a; Healey, 1967; Sadleir, 1965), *Clethrionomys* (Watts, 1970), *Microtus* (Baird and Birney, 1982a, 1982b; Beacham, 1980b; Boonstra, 1978; Hilborn, 1975; Myers and Krebs, 1971), *Sigmodon* (Joule and Cameron, 1975), and *Reithrodontomys* (Joule and Cameron, 1975).

Although it is clear that removal of trappable individuals leads to the appearance, in traps, of previously unencountered individuals, the origin of the new individuals is not specified. We cannot be sure that the presumed immigrants were drawn from a pool of individuals that originated elsewhere. Studies that made concurrent use of conventional live traps and pitfall traps (e.g., Beacham, 1979b; Beacham and Krebs, 1980; Boonstra and Krebs, 1978; Boonstra and Rodd, 1984) have shown that conventional removal studies fail to distinguish among neighbors making sorties outside their home ranges, individuals present but inhibited from entering traps, and transients. Simple removal studies show only that the presence of trap-prone individuals inhibits capture of a broad spectrum of other individuals.

The question of whether residents prevent establishment of transient individuals can be answered by means of introduction experiments. Introduced animals rarely settle in undisturbed populations, but are more likely to settle if residents are removed. Smyth (1968) compared persistence of marked *Clethrionomys* released in a control area and in an area from which adult males and non-lactating adult females had been removed. During the breeding season, persistence of adults released on the removal area was higher than on the control. Persistence of young was less affected by removal of adults. Marked young males survived poorly on both areas, but introduced voles in other categories persisted longer on the removal area. Flowerdew (1978) also combined removal and introduction and compared the persistence of experimentally introduced wood mice (*Apodemus*) in areas where residents were present, and in areas where residents had been removed. Again, establishment of these potential immigrants was more likely in the areas where residents had been removed.

The interaction of residents and presumed or known non-residents has been observed most often in laboratory situations. Conventional arena tests between known residents and presumed non-residents (e.g., Reich et al., 1982) suffer from the basic flaw that neither of the test individuals is resident in the "neutral" arena. Despite this, residents are most often dominant. In a major improvement in arena testing, Wolff et al. (1983) staged encounters in the field between resident and non-resident *Peromyscus*.

In confrontations observed by Barash (1981), resident male *Marmota calligata* were successful in repulsing intruders. In another study (Yahner, 1978), resident *Tamias striatus* of both sexes successfully excluded other conspecifics from core areas around their burrows.

Hill (1966) observed the response of house mice residing in granaries to caged and unrestrained introductions of individuals moved from neighboring populations. Resident mice attempted to enter the cages as if to attack the introduced mice. When Hill released unrestrained strangers they often left the granary even before encountering residents. The majority of those that were not seen to leave of their own volition were attacked by residents (both sexes) and driven out.

None of the 10 males and 10 females released in these observational studies became resident. Hill's approach demonstrated that residents actively and effectively resist the establishment of strangers.

Encounters with residents might not be required to prevent transients from settling. Despite the multitude of studies reporting fighting in arenas, it is not yet clear that fighting (as opposed to avoidance or chasing) is commonly involved in exclusion of potential male immigrants. Where egress is an option, non-residents might retreat rather than engage in combat. It has been observed in both field and laboratory that transient or subordinate individuals respond to resident or dominant conspecifics by avoidance (e.g., Armitage, 1974; Parmigiani et al., 1981). If arena size is increased, for example, unfamiliar male *Peromyscus leucopus* avoid encounters (Vestal and Hellack, 1977). Ostfeld (1985b) also observed that although unfamiliar male *Microtus californicus* exhibited more aggression in small arenas than did females, reproductive males were more likely to flee non-aggressive approaches of same-sex adults than were females when the interaction occurred in a larger area. Price et al. (1986) noted that female *Tamiasciurus* that had lost their territories became wanderers until such time as they were able to discover a vacant territory. Occupancy of the vacant territory was promptly signaled by frequent calling.

If avoidance is the rule in nature, scent marks or visible or audible displays by residents could be adequate to cause potential immigrants to move on, avoiding actual confrontations. Although male scent marks do not appear to function as sex attractants, the quality and quantity of scents produced by male rodents generally peak during the breeding season (Stoddart, 1978). Urine is the predominant substance used by males in scent marking. Male urine marking has important functions in cueing female reproductive activity in the house mouse (reviewed by Bronson, 1979), but it also has adverse effects on subordinate males (Jones and Nowell, 1974), lending support to the hypothesis that male scent marking could also have an important role in excluding potential competitors from scent-marked home ranges.

Introduced females are more likely to become established in introduction experiments than are introduced males (e.g., Anderson, 1965; Redfield et al., 1978b). This suggests that resistance of residents may be specific to the sex of both residents and potential immigrants. Michener and Michener (1977) recorded male immigration in a *Spermophilus* population with a low proportion (0.3/1) of breeding males. Resident female marmots are apparently able to repel intruding females, but are dominated by intruding males. Males repel intruding males, but accept intruding females (Armitage, 1975). In *Microtus pinetorum*, immigration occurred only when no adult resident of the immigrant's sex was present in the colony (FitzGerald and Madison, 1983). Boonstra and Rodd (1983) found that removal of breeding adult *Microtus* stimulated immigration by the same sex, but not by the opposite sex. Redfield et al. (1978a, 1978b) argued that because potential immigration was far in excess of actual recruitment, residents must inhibit immigration. They concluded, however, that removal of female *M. oregoni* and *M. townsendii* did not stimulate female immigration, and that male removal did not stimulate male immigration. Their results might have been affected by the fact that sex ratios of the two species were being manipulated simultaneously.

Restriction of immigration has often been attributed largely or exclusively to the aggressiveness of males (e.g., Adler et al., 1984). Sadleir (1965), Healey (1967), and Flowerdew (1978) all reported that removal of resident males facilitated the immigration of conspecific *Peromyscus*. Flowerdew (1974) obtained parallel results in experimental removal of male *Apodemus*. If males compete for copulations, male residents would be expected to be effective in excluding male immigrants, but to be less effective or ineffective in excluding female immigrants. This prediction is supported by the fact that unfamiliar males of most species of rodents will fight if placed in small cages without cover or possibility of egress, whereas males are less likely to attack unfamiliar females under these "arena" conditions (e.g., Gipps, 1984).

The pattern of same-sex exclusion might not be consistent across species. Cranford and Derting (1983) stated that in a 61-cm² arena, male *Microtus pinetorum* were more aggressive than females in within-sex encounters, but that female *M. pennsylvanicus* were more aggressive than

males under the same circumstances. Sexual distinctions probably arise only with the maturity of the young. Halpin (1981) observed no significant difference among responses of adult male *Peromyscus* to male and female juveniles except that males showed more cohesive behaviors toward older juvenile females than toward younger ones.

There are a few exceptions to the results suggesting that male residents inhibit primarily or exclusively the immigration of adult males. For example, Gavish et al. (1983) found that sexually experienced male *M. ochrogaster* were aggressive toward unfamiliar virgin females in dyadic encounters in the laboratory.

In species in which females are monestrous, males might have relatively minor effects on immigration. Dobson (1979) was not able to induce an influx of immigrants by removal of resident male *Spermophilus beecheyi*. In other species of *Spermophilus*, males leave their breeding ranges when mating is over (Holmes and Sherman, 1982; Michener and Michener, 1977). Male *S. parryii*, however, continue to defend territories during the period when females are pregnant.

There is need for further study on the role of males in excluding immigrants. The available information implies that the role of male aggression in inhibiting immigration can be expected to vary with the sex, age, and reproductive status of the potential immigrant, as well as seasonally and with the mating system and other natural history parameters of the species. In this context, as in the case of male competition for copulations, the nature of territorial behavior needs further definition and exploration. The valid generalizations with respect to the role of males in inhibiting immigration appear to be that male aggressiveness is likely to: 1) be effective primarily in excluding sexually mature males during the breeding season; 2) have little impact on immigration of adult females and sexually immature young of either sex during the breeding season; and 3) have little or no effect on immigration of any category of conspecifics outside of the breeding season. Exceptions can occur where males guard hoarded food, lactating females, or nest and weanling young. Getz and Carter (1980) suggested that transient male *M. ochrogaster* can be driven off by resident males before there is an opportunity for virgin females (daughters of the residents) to be sexually activated. Such behavior would restrict outbreeding and conserve the potential for incestuous matings.

In several studies, aggressive tendencies of females could be specifically related to inhibition of immigration. Female yellow-bellied marmots repel intruding females from their colonies (Armitage, 1986b). Female *Microtus* have been found to be tolerant only toward their own offspring and toward familiar resident males. Comparing immigration of *M. townsendii* into plots from which residents had not been removed with movement into male-removal and total-removal plots, Boonstra (1978) concluded that the higher rate of appearance of immigrants in the total-removal plots was due to the absence of female residents. Boonstra and Rodd (1983) showed that the presence of breeding females restricted recruitment of other breeding females, and removal of resident females induced settlement of sexually mature females during the latter part of the breeding season. Restriction of female recruitment by breeding females was not dependent on the presence of males. Rodd and Boonstra (1984) found that reduction in density of overwintering *M. pennsylvanicus* induced an increase in female home range size during the subsequent spring breeding period. Gipps et al. (1985), however, were unable to detect any difference in the immigration rate on control and experimental grids following removal of resident female *Clethrionomys glareolus* at the start of the breeding season.

Metzgar (1971) found that opportunity for female *Peromyscus leucopus* to settle was negatively correlated with the density of resident females and that transient females could settle only when vacancies were created by disappearance of female residents. Female *P. leucopus* were more aggressive toward intruding females than resident males were toward unfamiliar males.

Exclusion of immigrants is probably strongly dependent on the reproductive state of residents. Male aggressiveness usually declines following the breeding season. Behavior of resident males then could have little or no effect on male immigration. Boonstra and Rodd (1983) found that it was primarily at the start of the breeding season that removal of breeding male *Microtus* led to immigration of older adult males on their open grid. Later in the season removal of resident

males resulted in immigration of sexually mature male young of the year. By removal of females, Boonstra and Rodd also showed that the effectiveness of breeding males in inhibiting recruitment at any time was dependent on the presence of breeding females. This implies that in polyestrous species in which pregnancy and birth of young extend beyond the decline in male aggressiveness, recruitment of the last litter and immigration of young of either sex may be unaffected by aggressive behavior of resident males. Immigration into matrilineal clusters of *Microtus* has been observed to occur only after the breeding season (Madison et al., 1984; Wolff and Lidicker, 1981). Exclusion of immigrants by a resident parent should reduce the probability that the range and its resources will become available to a non-relative. If this behavior thereby increases the probability that the parental range will be inherited by an offspring it is a form of altruistic behavior. As Smith and Ivins (1983) pointed out, it constitutes an indirect form of parental care.

Avoidance of contact and other expressions of male incompatibility appear to inhibit male immigration in *Peromyscus maniculatus* prior to the onset of breeding and throughout the period when matings are available (Healey, 1967; Sadleir, 1965), but Metzgar (1971) concluded that this was not the case in *P. leucopus*. He felt this might be because the large home ranges occupied by males prevented effective exclusion of other males. Range size is more likely to prevent exclusion of transients than of immigrants, however, since settlers can be detected and confronted even where the range is large.

Eibl-Eibesfeldt (1950) observed that house mice were able to establish themselves in a building only if they were able to find a defensible corner and persist there through an initial period of resident hostility. His observation implies that immigration can be influenced by the complexity of the habitat. Defensible space might be more easily located in nature than in simpler environments.

Female house mice introduced into occupied fields by Myers (1974) failed to establish residence, but those introduced into occupied chicken coops by Baker (1981b) did so. The success of Baker in introducing house mice into chicken coop populations where the rate of turnover was high was not matched in low-turnover granary populations (Anderson, 1965; Hill, 1966).

Is resistance to immigration density-dependent? Wolff (1985a) reported that the aggressiveness of resident *Peromyscus* toward non-residents varied with density. At high density the residents were aggressive and dominant. At low density, however, aggressive behavior was rare. This result is significant because it suggests that resistance to immigration might become more intense as density increases and might decline as density decreases. Hestbeck (1986) found that the effectiveness of resident voles in inhibiting movement through an area increased with density. Carter and Getz (1985) reported, however, that pairs of *Microtus ochrogaster* excluded strangers more effectively at low densities than at high densities.

Resident bannertail kangaroo rats (*Dipodomys spectabilis*) are solitary, occupying individual mounds which they defend by footdrumming. Juveniles either take over vacated mounds or establish new mounds in the interstices between those that are occupied. As distances between occupied mounds decrease, residents visit neighboring mounds less and drum more often, suggesting that possession of a territory is more actively advertised as density increases (Randall, 1984).

Taitt and Krebs (1982) were surprised to observe increased female immigration when they treated female *Microtus townsendii* with testosterone implants. This apparently anomalous result is understandable if viewed in the context of the overall masculinization induced by the male hormone. If implants caused the treated females to behave as males, the quantum of "female" behavior in the area was thereby reduced and the observed immigration could have been predicted on the basis of the RFH argument that density is largely under female control.

The references cited above indicate that the presence of residents inhibits other conspecifics from becoming resident, and that the inhibition might be mediated through aggressive behavior or display or both. Despite the flaws in the most commonly used removal and arena techniques, it seems safe to conclude that residents inhibit immigration of same-sex adults. The situation is less clear with respect to juveniles and subadults. Resistance to immigration is likely to be seasonal in seasonally breeding species. It might be influenced by the availability of defensible space for

immigrants, and by the influence of density on the behavior of residents. Field experiments, possibly based on the approaches of Smyth (1968), Flowerdew (1978), Hill (1966), and Wolff et al. (1983), which explore the role of relatedness and season in the resistance offered by residents, will be helpful. Removal of single individuals or small groups (Price et al., 1986) also could be more informative than the mass removal technique that has been used in the past.

The Stimuli for Emigration

Can attractive stimuli induce emigration? One possible interpretation of the mate search hypothesis of King (1983) is that young are attracted from the natal site by the possibility of mating. Another is that emigration might be stimulated by information as to the availability of unoccupied habitat. Jones (1984) suggested that young *Dipodomys spectabilis* might be stimulated to emigrate when they detected a mound made vacant by the death of an established individual. Stickel (1979) recorded movement of 41 house mice from one field to another and interpreted this as a response to the development of more favorable habitat in the new area rather than deterioration in the old area. She did not speculate as to the means by which a distant, more suitable, habitat was detected, although exploratory sallies across the intervening roadway might have served the purpose.

Habitat deterioration and approach to the limits of a resource have been associated with emigration in some instances. Movement could be the only alternative to immediate death in kinds of habitat disturbance such as flooding (Aho and Kalela, 1966; Hansson, 1977). Freezing has been observed to force muskrats out of small bodies of water (Errington, 1946, 1963). Such factors have little relevance to the general problem of dispersal.

Uchmański (1983) explored a model based on the assumption that animals emigrate when food becomes inadequate to sustain them, and Grant (1978) hypothesized that emigration might be stimulated by anticipated resource (nutrient) shortage. Full exploitation of the available food supply triggered emigration of commensal *Mus musculus* (Strecker, 1954), but there was no basis on which to conclude that movement was stimulated directly by hunger rather than mediated by social interaction. Residents might not always emigrate in response to habitat deterioration. Established individuals have been observed to remain on their home ranges despite highly disruptive, or even devastating, habitat change (Friend, 1979; Getz, 1970).

Some data can be interpreted to indicate that emigration of virgin female *Microtus ochrogaster* is stimulated by the absence of suitable male pheromones in the vicinity of their nest (see the summary by Carter et al., 1986). In this species one or more male pheromones trigger sexual maturation and estrus in young females. Emigration in search of such stimulation would be analogous to the mate search hypothesis proposed by King (1983). However, Carter et al. (1986) reported that pair-bonded resident males will not accept a transient female until she is activated, suggesting that a virgin female may need to establish herself on an unoccupied area and either await the arrival of a transient male or activate herself by sniffing scent marks left by nearby male residents. The operation of this relationship with respect to emigration of female *M. ochrogaster* is puzzling in the light of evidence that most surviving females breed within 30 m of the natal site.

One fundamental assumption of the RFH is that inherently philopatric young are forced to emigrate as a result of social stimuli. The RFH predictions are explicit: in other than exceptional circumstances, such as catastrophic habitat deterioration, the proximate external stimuli for emigration are social pressures exerted by dominant residents (usually parents) on subordinate non-residents (usually their offspring). Stimuli received by potential emigrants are expected to be related to competition for the requisites for reproduction, and to have a strong intrasexual component, especially where competition for copulations is involved (males). Timing of stimuli is expected to be related to the breeding season, and to be dependent on the maturation of the offspring and on the residual reproductive value of the residents. The nature of the social pressure, and its intensity, are expected to be influenced by altruism based on the relatedness of the individuals exerting the pressure and those receiving that pressure. Interactions leading to emigration are expected to be intrafamilial, whether the family is matrilineal, nuclear, or extended.

Rodents fall into two categories with respect to parent-offspring relationships and the social environment in which one might seek the proximate mechanisms of emigration. In one class (seasonally polyestrous species), all except the juveniles of the last litter of the season must interact with sexually active male and female residents. In this group, stimuli triggering emigration should be directly discernible if observational difficulties can be overcome. In the other class (seasonally monestrous species), encounters with reproductively active conspecifics do not take place until the young are nearly a year old. The radically different contexts dictate separate discussions of the topic of emigratory stimuli.

In seasonally polyestrous species, emigration occurs in both sexes and is associated with the breeding season. Males are more likely to emigrate than females, transients are frequently younger than residents, dominance is positively correlated with age and size, subordinate status and emigration are frequently associated, social subordinates are often maturing young, and emigration is associated with puberty (Baird and Birney, 1982a; Beacham, 1981; Christian, 1970; Fairbairn, 1977a, 1978b; Gaines and McClenaghan, 1980; Myllymäki, 1977a; Myers and Krebs, 1971; Petticrew and Sadleir, 1974). Many authors have inferred that in these rodents emigration is socially enforced (e.g., Beacham, 1980b; Burt, 1949; Christian, 1970, 1971; Cockburn et al., 1981; Fairbairn, 1977a, 1977b; Krebs and Boonstra, 1978; Sadleir, 1965). Butler (1980) reported that subordinates made up 95% of the "emigrants" crossing a water barrier in a laboratory apparatus.

Does fighting induce emigration? Male emigration, in particular, is strongly correlated with the breeding season. Aggressive behavior of males in many species increases prior to the initiation of breeding (e.g., Flowerdew, 1978). Emigration at this time, as described by Fairbairn (1977b) and Krebs and Boonstra (1978), is likely to be initiated by competition among males for mating rights, and most emigrants should be mature males. To the extent that pre-season contests for mating rights occur between non-relatives, they should be more likely to involve serious fighting. Krebs and Boonstra (1978) found that males were more likely than females to disappear in this pre-season stage, and that the rate of male disappearance, but not of female disappearance, was positively correlated with the incidence of wounding.

Wounding studies are relevant to the questions of whether social pressure takes the form of aggression, and whether parental aggression toward offspring is benign, as the RFH predicts. Unfortunately, the majority of studies of wounding have attempted to establish a relationship between population density and the frequency and intensity of aggression and are inconclusive (Christian, 1971; Krebs, 1964; Lidicker, 1973; Rose, 1979; Rose and Gaines, 1976, 1981; Turner and Iverson, 1973). These studies demonstrated that wounding was associated with reproductive activity. Rose and Gaines (1976:48) stated that "voles of both sexes show substantially higher levels of wounding during the periods of greatest reproductive activity." Christian (1970) reported that immature male *Microtus* born late in the breeding season lacked scars, whereas mature males of the same cohort bore scars. Nevertheless, wounding has not been directly correlated with emigration.

The contention by Rose and Gaines (1976) and Rose (1979) that the highest levels of wounding observed in their studies of *M. ochrogaster* were found after the breeding season seems inconsistent with RFH predictions. Rose and Gaines noted that their results and those of Lidicker (1973) for *M. californicus* suggested high wounding levels in winter. Wounding in *M. ochrogaster* did, however, correlate with sexual competence in males (Rose and Gaines, 1976). Weanling females lacked wounds, and thus were distinct from all other groups. Wounding among males was associated with the transition into the heaviest weight class. Assuming these were the oldest males, and noting the tendency for emigration to be delayed in this species, male aggression might be related to a post-breeding replacement of old males. Gaines and Johnson (1984) concluded, on the basis of regression analyses, that the ratio of transients to residents in *M. ochrogaster* was negatively correlated with season and with male reproductive activity, but positively correlated with the abundance of large males. Because late winter is the period of peak reproduction for *M. californicus*, but not for *M. ochrogaster*, the Kansas and California

situations are not parallel. The confusing evidence could reflect an inadequate allowance for the unusual social structure and the bimodal breeding season in *M. ochrogaster*.

The greatest weakness of wounding studies is that the sex and relatedness of the individual administering a wound and the circumstances (the site and the nature of the interaction) are unknown. Wounding studies have produced only one consistent observation—wounding is related to sexual maturity in males in the reproductive season (Gaines and McClenaghan, 1980). Because wounding data fail to indicate whether the wounds were caused by males or females, and whether wounds are acquired during courtship, mating, defense of territory against immigrants, emigration, or expulsion of emigrants, wounding studies have so far shed little light on the nature of the stimuli for emigration.

Emigratory stimuli given by resident females to offspring should follow a different seasonal pattern than those originating from resident males, and should correlate with the cycle of estrus and gestation, as well as with the reproductive state of female offspring. Females might drive out young at the time a subsequent litter is born, or puberty or pregnancy of female offspring could trigger maternal aggression. Viitala and Hoffmeyer (1985) speculated that most female *M. agrestis* become pregnant while living on the maternal territory and emigrate while gravid.

The implication throughout the literature reviewed above is that emigration is stimulated by aggressive interactions. However, an aggressive encounter and emigration can rarely if ever be tied together. Despite the convergence of evidence and opinion pointing to emigration of subordinate young as a consequence of interaction with dominant adults I have been unable to find any study in which individual episodes of stimulus and emigratory response have been given detailed examination in polyestrous rodents. In particular, I have found no data sufficiently precise to test the assumptions of the RFH.

In part, the inadequacy of the literature might exist because investigators have not focused specifically on stimulus-response relationships leading to emigration. When this is done, several possibilities will need to be considered. Emigration might be triggered by a single agonistic interaction, a series of interactions, or a trend in the nature of interactions. When interactions are between relatives, it could be advantageous if emigration were to be triggered in a single, non-damaging, agonistic interaction. Some observations support a single-episode or key-interaction postulate. In arena-like spaces, social dominance and subordination may be established in the first moments of a brief initial agonistic encounter (Anderson and Hill, 1965). Avoidance is the behavioral response of mice defeated in arena encounters (Parmigiani et al., 1981). Thus, emigration would be a likely outcome of one or a few aggressive interactions in an unenclosed space. Butler (1980) observed a formerly territorial male *Mus* "emigrate" across a water barrier in a laboratory enclosure within 10 min after the loss of a series of fights. Single encounters could have persistent effects. Pituitary-adrenal response to defeat has been shown to be rapid (Archer, 1970; Bronson and Desjardins, 1971) and the behavioral and physiological responses to an initial encounter are rarely reversed. Nevertheless, a key-interaction stimulus system would be difficult to demonstrate in the field. If only one or a few agonistic interactions were required to tip the scale in favor of emigration, the critical rare and ephemeral events might be easily overlooked. An alternative to the key-interaction hypothesis is that emigration is induced by repeated, and perhaps escalating, agonistic interactions. Although chances of observing one or more interactions might be greater, the point at which emigration was elicited might be difficult to determine and the differences in behavior toward emigrants and non-emigrants might be obscure.

If aggression leading to emigration is intrafamilial, the frequency of encounters, and of aggression, need not be determined by crude density. Pearson (1960) monitored activity on runway systems made by *Microtus californicus* and found that each system was used by a family group. The frequency of encounters among individuals did not increase with increasing density in the surrounding area. Indirect evidence obtained by Carroll and Getz (1976) supports Pearson's observation.

Abdication of home ranges by resident females is clearly an exception to the argument that emigration is stimulated by the pressure of dominant residents on subordinate offspring. The

most conspicuous example of emigration under these circumstances has been reported by Price et al. (1986). They observed that maternal female *Tamiasciurus* left their territories to offspring and became transients, wandering until able to claim a vacant territory.

Establishment of a connection between emigration and a triggering stimulus should be easiest in large-sized, diurnal species. Many such species, however, are seasonally monestrous, with life history strategies centered on exploitation of abundant resources in a period of intense foraging activity, followed by hibernation. In consequence, the relationships between emigration and reproduction could be obscured. Holekamp (1984, 1986) has reviewed emigration in diurnal sciurids. On the basis of an intensive study of the proximate causes of emigration in *Spermophilus beldingi*, she proposed that emigration is internally motivated. *S. beldingi* exemplifies the extreme life history pattern for seasonally monestrous species. As outlined by Holekamp (1986), Sherman (1977, 1980, 1981), and Sherman and Morton (1984), emigration takes place in the following context. The winter months are spent in hibernation. Above-ground activity takes place between April and October, but all cohorts are not active throughout this period. Adult males are the first to emerge from hibernation, and competitive interactions leading to a hierarchy that regulates male mating success occurs at that time. Yearling males do not mate and thus do not participate in this competition. Adult females are the next to emerge, and mate within a few days. Males that succeed in mating disappear from the areas where they have mated and settle elsewhere. Adult males that did not mate do not emigrate. Mortality of adult males in both groups is high at this time.

Adult males enter hibernation when young are about 6 weeks old. Because young emerge from their natal burrows at 25–28 days of age, which is after the successful males have departed, there is no opportunity for interaction between males and their own offspring. Nevertheless, sexual bias in emigration in *S. beldingi* is extreme with almost all females being philopatric and almost all male young emigrating at about 10 weeks of age.

An interpretation of the dispersal biology of Belding's ground squirrel requires two hypotheses—one to explain the post-breeding emigration of successful males and the other to explain the emigration of male young from an environment lacking active adult males, some 20 months before they reach puberty. Holekamp (1986) specifically tested 10 hypotheses about proximate mechanisms responsible for emigration of young males in their first summer: demand for food; demand for nest sites; ectoparasite load; ontogenetic switch; intraspecific aggression directed at juveniles; response thresholds to intraspecific aggression; conspecific avoidance of juveniles; juvenile avoidance of conspecifics; avoidance of nearest neighbors; and social facilitation. She concluded that all except the "ontogenetic switch" hypothesis, which she visualized as a sex-linked internal stimulus for emigration of young males, could be rejected. Holekamp's study raises two questions of special importance in the present context. Is the RFH applicable to *S. beldingi*? Further consideration of both the biology of this species and the potential for an RFH explanation for emigration in seasonally monestrous rodents is in order.

Emigration of young male *S. beldingi* begins 16 days after their emergence from their natal burrows. In Holekamp's populations, 74% of young males, but only 8% of young females, had emigrated by 60 days of age. Male emigration appeared to be associated with attainment of a body mass of 125–175 g. Because young males emigrate and most young females do not, Holekamp's search for a proximate cause of emigration was based primarily on comparison of the stimulus environments of male and female young. Because she found no differences between male and female young in mean levels of intraspecific interaction, Holekamp was led to postulate a sex-specific internal trigger.

Holekamp did, however, record some significant differences in the experiences and behavior of male and female young. Between the 7th and 9th weeks of age the frequency of chases directed at males increased, while that directed at females decreased. During the 7th week of life, males spent more time investigating non-natal burrows, and entered more of them. During the 8th week males spent significantly more time climbing, and during the 8th and 9th weeks males moved about at a significantly higher rate. The most interesting difference was derived

from experiments designed to test response to interspecific threats. Between the 5th and 9th week of life, male young re-emerged sooner from refuge burrows following fright reactions induced by a simulated overflight by a predator. This observation calls attention to an important point. The observations of intraspecific interaction dealt only with above-ground activity. Sub-surface interactions could not be evaluated. Re-emergence of males following a surface fright could reflect an inhospitable subsurface environment, and agonistic interactions below ground could have caused male emigration.

Can the RFH provide a rationale for such subsurface antagonism (presumably on the part of adult females or female siblings) and is there any evidence to support it? An hypothesis can be built on the basis of maternal energy demands, female expectations as to further reproduction, and observations on other species. Although Festa-Bianchet and King (1984) found no correlation between dominance status and probability of disappearance of yearling *S. columbianus*, they noted that the timing of yearling disappearance correlated with a peak in aggressiveness in resident females. Yearling female marmots delayed emigration when adult females behaved amicably toward them (Downhower and Armitage, 1981). Young male *S. richardsonii* were philopatric only when maternal females failed to overwinter (Michener and Michener, 1973). Adult female Belding's ground squirrels have a mean longevity twice that of males, and have a high probability of further reproduction at the site where they have produced a litter successfully.

If there is a social stimulus for emigration of male *S. beldingi*, it seems that it must originate with the mother or female siblings. Rapid weight gain after lactation is especially critical for survival of mothers and daughters. Both depend on retention of the foraging area to build fat reserves required for overwinter survival. A significant finding in Holekamp's study, suggesting that there is competition for forage, is that the few females that did emigrate spent more time foraging than did those that were philopatric. Export of young males might give a female and her daughters an important competitive edge over other females.

Requirements of adult females might also influence the emigration of reproductively successful adult males. Breeding success probably demands intensive energy expenditure. If adult males have any chance of breeding in more than one season, emigration to avoid female competition might be adaptive (an EFH explanation?), or be the best way to facilitate survival of presumptive offspring (a male equivalent of female abdication in polyestrous rodents?).

There is ample opportunity for further studies designed to determine what stimuli induce emigration, as well as for reinterpretation of data from previous studies on the basis of new concepts and new data. Although there is support for the roles of dominance and social pressure in inducing emigration, the picture is not sufficiently clear and detailed for evaluation of the assumptions of the RFH. Future investigators might wish to evaluate relatedness in relation to agonistic interaction, and consideration should be given to an examination of the hypothesis that a single agonistic exchange between parent and offspring, moderated on the basis of their relatedness, is sufficient stimulus for emigration.

Resident Behavior as a Cause of Emigration of Offspring

For most rodents the role of parents in the emigration of offspring is unclear. We can expect parental strategies to differ with the parent's sex and residual reproductive value, the sex and potential competitive impact of philopatric offspring, and probable breeding success of the offspring that emigrate. All of these factors vary seasonally, and all will vary with the reproductive pattern of the species. Conclusions as to the role of parental behavior (particularly those made under conditions of confinement) must be drawn with these considerations in mind.

Sadleir (1965) and Healey (1967) attributed disappearance of young *Peromyscus maniculatus* from their natal sites during the breeding season largely to adult male aggression, but Howard (1949) and King (1983) observed no parental aggression in association with emigration of young *Peromyscus*. Halpin (1981) also found few instances of aggression between parents and offspring, although the relevance of her laboratory findings to seasonally variable field environments and

adults of various ages is difficult to evaluate. Young *P. maniculatus* sometimes overwinter with their parents (King, 1983; Mihok, 1979), and Fairbairn (1977a) noted a spring surge in numbers of transient individuals, suggesting that delayed expulsion of young may be characteristic of some populations or cohorts.

The evidence is stronger for parentally-induced emigration in large, diurnal rodents. As indicated above, the distance at which yearling male *Spermophilus richardsonii* settled was correlated with overwinter survival of their mother (Michener and Michener, 1973). According to Downhower and Armitage (1981), yearling male *Marmota flaviventris* are the primary recipients of adult aggression, and harem males are more likely to initiate aggressive encounters with yearling males (which generally emigrate) than with yearling females (which often do not). Emigration of yearling males could not be correlated with the frequency of adult aggression, but was positively correlated with build-up of energy reserves. The timing of emigration of yearling females correlated positively with high rates of aggression among female peers and was associated with above-ground appearance of young of the year. Whether or not yearling females emigrated appeared to be independent of whether or not young appeared. In *Microcavia*, adults of both sexes are aggressive toward adolescent males. Adult females may drive their young away from the home bush at the time a new litter is about to be born, although at least some of the young are allowed to return later (Rood, 1970).

Resident Male Aggression and the Export of Offspring

The interests of male and female residents could conflict with respect to expulsion of young. In marmots, harems often consist of two or more matriline. Matrilineal success decreases with harem size, whereas paternal fitness increases (Armitage, 1986b). Armitage (1984) found no evidence that male marmots inhibited recruitment of yearling daughters into their harems. Harem males might gain by retention of female young, but harem females could lose, especially if retention is indiscriminate among matriline. Females could also lose if resident males discriminate harshly against sons. Although Rood (1970) attributed emigration of adolescent *Microcavia* to aggressiveness of adults of both sexes, female adolescents were not expelled by resident males. These observations are in accord with a general lack of evidence that resident male behavior is such as to reduce the likelihood of father-daughter matings.

If "pre-saturation dispersers" (Grant, 1978; Lidicker, 1975) are largely pubertal males, their emigration might well be due to pressure from adult male residents, but it is difficult to reach a clear conclusion as to the role of males in expelling sons because, in most studies, emigrants have not been identified with sufficient assurance and consistency, or categorized by sex and season. Myllymäki (1977a) recorded that in a large enclosure young male *Microtus agrestis* belonging to the first two spring-born cohorts were "badly treated" by dominant overwintered males and sought corners rarely frequented by the dominant males. Jannett (1981a) observed that only young males in which testes had not descended were able to persist in dense *M. montanus* populations, but he had no direct evidence that young males were expelled after their testes descended. In most other field studies evidence that males become intolerant of sons around the time the latter reach puberty, and that parental aggression results in filial emigration, is even more difficult to pin down.

Gaines and Johnson (1984) applied regression analyses to data obtained in studies of *M. ochrogaster* and found that as the proportion of reproductively active adult males increased, the ratios of apparently transient adult females, subadult males, and subadult females to residents decreased. Thus male reproductive activity was a negative predictor of transient abundance. The negative correlation between reproductive activity of resident males and disappearance of subadult males appears contrary to the RFH, but the data are confusing due to the criteria used to define the various categories, and seasonal effects are difficult to evaluate in the analysis.

The literature also fails to provide any particular relationship between emigration of male offspring and their reproductive condition. According to Krohne et al. (1984), most male *Pero-*

myscus leucopus making long one-way movements had undescended testes; those that successfully dispersed were non-scrotal at the time they emigrated, but became scrotal after settling in a new area. Fairbairn (1978a) followed Sadleir (1965) and Healey (1967) in attributing high juvenile disappearance rates in *Peromyscus* to resident male aggression. Nadeau et al. (1981) came to a similar conclusion. Fairbairn (1978a) believed, despite a lack of direct observation of interactions in the field and without discriminating with respect to sex of offspring, that male aggressiveness caused death of most young *P. maniculatus* born during the period that she designated as the main breeding season. She did not speculate as to the evolutionary process that would lead males to kill or cause death of their own offspring. Wolff and Lundy (1985) reported avoidance but no overt aggression in encounters of same-sex, adult-juvenile pairs staged on the home ranges of resident adult *P. leucopus*. Savidge (1974) found that male *P. maniculatus* were tolerant of young of both sexes in the laboratory. Mihok (1979) reported that in northern Alberta, young *Peromyscus* cohabited with parental pairs over the first winter. King (1983) observed that association of young *Peromyscus* with their fathers increased at the end of the breeding season. Taitt (1981) reported a predominance of males among recruits to populations of *P. maniculatus* during the non-breeding period. More detailed studies are needed to resolve the differences among these studies.

Gipps et al. (1981) failed to influence density in *Microtus townsendii* significantly by treatment of young males with testosterone implants (which were expected to increase male aggressiveness), or with scopolamine (which was expected to reduce it). The scopolamine did appear to slow the decline in numbers of males at the start of the breeding season. Boonstra (1977b) found that experimental reduction of density of *M. townsendii* did not affect male disappearance rates (i.e., neither survival nor emigration of males appeared to be density-dependent), but he did observe that young males became sexually mature at a lighter weight on grids from which adult males were removed. Boonstra and Rodd (1983) reported that removal of adult male *Microtus* had little effect on the persistence of other sex-age cohorts on open experimental plots. Pfeifer (1982b) indicated that juvenile male *Spermophilus elegans* appeared to avoid adult males, but she did not observe agonistic interactions that would suggest active expulsion of young by the adult males.

The literature does not presently provide a satisfactory basis for evaluation of male roles in the emigration of their sons and daughters. We need studies in which such factors as the season, the seasonal cohort, the sexual state of adults and young, the residual reproductive value of the male parent, and the degree of genetic relatedness are precisely specified. It is especially important that these studies be designed in such a way that the relevance of the results to natural situations is unequivocal. Although the general trend of the evidence appears to support the hypothesis that males expel pubertal sons and are tolerant of daughters, the conclusion that this is the case must remain tentative at present.

Resident Female Aggression and the Export of Offspring

Kalela et al. (1961) attributed the early male migration from summer to winter habitat in *Lemmus lemmus* to female aggression. Redfield et al. (1978a) found that removal of female *Microtus oregoni* increased persistence of young, but that removal of males had no effect. Experimental alteration of sex ratios in populations of *M. townsendii* also showed that recruitment of young was inversely related to female density (Redfield et al., 1978b), and that sex ratios biased in favor of adult females reduced persistence and recruitment of juveniles. Young female *Clethrionomys gapperi* occupied areas not claimed by overwintered females, but moved into the territories of the latter when death of residents created vacancies (Perrin, 1979).

Because so much effort has been concentrated on male aggression, evidence as to the influence of females on emigration is scattered. Female aggression toward potential emigrants is likely to be affected by the hormonal cycles associated with gestation and lactation, and by social circumstances. Aggressiveness of female *Peromyscus leucopus* increases with dosage of progesterone

(Gleason et al., 1979). Gray (1979) found that in ICR mice, female aggressiveness toward juveniles peaked during the first 2 weeks postpartum. Virgin females also attacked juveniles, and virgins housed in groups were more aggressive toward juveniles than were those kept in isolation.

If female aggression is based on anticipated resource demands, we might expect females to expel young in association with the birth of a succeeding litter. Female Chinese hamsters (*Cricetulus griseus*) with new litters in a laboratory enclosure became aggressive toward both unfamiliar young and their own older young (Dasser, 1981). Festa-Bianchet and King (1984) noted that the peak in adult female aggression in Columbian ground squirrels came just prior to the time when yearlings disappeared from the colony and that prior to emigration the young shifted the sites of their activities so as to avoid female aggression. In a laboratory environment, aggressiveness of newly parturient females was associated with movement of young *P. maniculatus* across an electrified barrier to an adjacent cage (Savidge, 1974).

When female *Dipodomys spectabilis* abdicated their home mounds to offspring, the settlers were predominantly female. When the female died, the offspring settling on the home mound were predominantly male (Jones, 1986). Such observations support the notion that females, as well as males, may expel male offspring.

If female competition is resource-based, behavior of resident females may be linked to emigration through population responses to food shortage. The RFH anticipation that female-induced emigration should be triggered by food shortage is partially supported. Myllymäki (1977a) attributed increased emigration by voles to decreased availability of food and to aggressive behavior of females toward offspring midway in the reproductive season.

Desy and Thompson (1983) increased persistence of juvenile *Microtus pennsylvanicus* on plots by addition of high quality food, and Cole and Batzli (1979) found that supplemental food increased the proportion of juveniles overwintering in *M. ochrogaster*. Gilbert and Krebs (1981) induced both increased juvenile recruitment and immigration in unconfined populations of *Peromyscus* and *Clethrionomys* by supplying high quality food (sunflower seeds). However, Ford and Pitelka (1984) concluded that persistence of young was not determined by resource availability. They found that food supplementation in the spring lowered persistence of young *M. californicus* in the population.

In an imaginative experiment, Smith et al. (1984) compared heterozygote frequency on food-supplemented and non-supplemented grids. Population density was higher with food supplements and heterozygote frequency was lower. This result was interpreted as indicative of selection for hybrid vigor on the grids with less food. An equally tenable hypothesis is that decreased turnover and increased inbreeding due to retention of offspring explained the low heterozygote frequency on the food-supplemented plots.

The most important and conclusive pair of studies on the relationship between emigration and food resources seem to have been largely forgotten. In confined populations of *Mus*, female reproduction was suppressed by food shortage (Strecker and Emlen, 1953), but in an unconfined population there was no curtailment of reproduction, and emigration began when food was unavailable (Strecker, 1954). Strecker's study unequivocally identified emigration as related to density and implicated emigration and free egress as the essential elements in behavioral responses that limited density in relation to a resource base, although the data do not tell us whether the emigrants responded directly to food shortage or to pressure from residents.

Provision of supplemental food enabled Sheppe (1965) to reduce emigration from populations of *P. leucopus* experimentally introduced on small islands. Pokki (1981) observed that movement of *M. agrestis* between islands peaked in conjunction with vegetation decline.

Following a study on the relationship of forage quality to emigration in voles, Grant (1978) argued that although elements such as Na, N, or P might have been insufficient, initiation of emigration did not coincide with a sharp decrease in nutrient content of the grass. His calculated requirements were, however, based on young males and thus failed to account for female requirements during pregnancy and lactation. Further, each female should adjust behavior on the basis of food quality within her own home range, and because individual ranges can differ

greatly in quality (Cockburn and Lidicker, 1983), a clear-cut relationship such as the one Grant tested would be unlikely.

Madison et al. (1984) regarded the tendency of extended families of *M. pennsylvanicus* in an enclosure to retain male offspring selectively and exclude female offspring as an extension of resource competition by the breeding females. The result was retention of familiar males, especially sons, at times when resource supplies were declining but resource requirements remained high. However, if a mother expels her young in order to preserve resources for her present or future investment, it might be predicted that export of daughters will sometimes take precedence over export of sons. Any bias toward export of daughters would be most likely to occur as daughters approach puberty or parturition and are likely to use more of the available resources. This might explain the observations of Gaines et al. (1979a) that subadult females captured on a removal plot were more likely to be in breeding condition than females of equivalent weight captured on an adjacent control plot. Myers (1974) reported, similarly, that female house mice that emigrated were more likely to have perforate vaginae than those remaining on the natal grid. Gaines and Johnson (1984) found that the ratio of females of adult and subadult weight encountered on a removal plot to density on nearby control plots increased as the percentage of females in breeding condition on the control plots increased. The implication is that expulsion of female voles into the transient population increased with the proportion of resident females that were reproductively active. Although this may be indicative of a female role in expelling female young, it is difficult to exclude other variables or to demonstrate a cause-and-effect relationship on the basis of the available data. Downhower and Armitage (1981) stated that aggressiveness of female marmots was greater in larger harems, and the increase in aggressiveness along the harem-size gradient was directed more toward female yearlings than toward male yearlings.

By experimentally reducing density of resident *M. townsendii*, Boonstra (1977a) was able to lower female disappearance rates. Boonstra (1984) noted considerable behavioral variation among female *M. pennsylvanicus* toward young, but provided no indication as to the cause. Mihok (1981) stated that in arena encounters female *Clethrionomys gapperi* were most aggressive toward female young of the year. Relatedness was not assessed in either study and, additionally, their relevance to field situations is unclear. Contrary to the interpretation of their results by Boonstra and Rodd (1983), there is no clear case for a consistent effect of removal of adult female *Microtus* on persistence of younger females on their grids during the breeding season because the effect varied between years.

The ability of adult females to suppress sexual activity of juvenile or adult female conspecifics pheromonally has been demonstrated in various species in the laboratory (Batzli et al., 1977; Champlin, 1971; Drickamer, 1974; Whitten, 1959). Because it serves to limit demand on resources by restricting recruitment to the breeding population (Getz et al., 1983), it might be an alternative to forced emigration of daughters. Gilbert et al. (1986) reported that when all adult female *Clethrionomys rufocanus* were removed from two areas after the weaning of the first litter of the season, female young of the year bred on these female-removal grids, but not on control or on total-removal grids. These results suggest that the function of reproductive suppression was not to prevent inbreeding or to stimulate emigration of young so that they might reproduce, but instead to prevent premature reproduction of female young and thus prevent philopatric daughters from competing with maternal females. Immigrants to the female-removal plots in this experiment were primarily young of the year. Massey and Vandenberg (1980) found that in "island" populations of *Mus* only females living at high densities produced urine that was capable of inhibiting juvenile female maturation. Coppola and Vandenberg (1987) induced secretion of a urinary pheromone that had the same effect by introducing transient females.

Bujalska (1970, 1971), Mihok (1979), and Perrin (1979, 1981) have all observed that the number of reproductively active female *Clethrionomys* remained relatively constant while overall density on their study plots varied more widely. Bujalska (1970, 1971), studying *C. glareolus* on a small island, demonstrated that breeding was dominated by over-wintered females, and that these

were spaced evenly throughout the available habitat. The number of sexually inactive females varied considerably. Young females from the spring cohorts bred only when they were able to occupy a vacancy created by the disappearance of an older breeding female. Removal of females born in early cohorts increased the proportion of females born in the later cohorts breeding in the year of their births (Bujalska, 1973). Bondrup-Nielsen (1986) also demonstrated that removal of adult female *Clethrionomys* was followed by maturation of previously suppressed young females, and Armitage (1986b) reported that the presence of older female marmots reduced the chances that 2-year-old females would breed.

Myllymäki (1977a) attributed the tendency of female *Microtus agrestis* to leave their newly weaned litters in the nest and shift their own home ranges just before the birth of a new litter to a release of maternal bonds and a spontaneous tendency to emigrate. Contrary to the view that recruitment of young is strongly influenced by the density of females (Boonstra, 1978; Redfield et al., 1978a, 1978b; Taitt, 1981; Taitt and Krebs, 1982, 1983), he concluded that female territoriality had little or no effect on dispersal. Abdication of all or part of the maternal range by females that have weaned their young might represent an alternative outlet for maternal aggressiveness.

Direct evidence that young emigrate in response to female aggression is hard to find. Female red squirrels (*Tamiasciurus*) have been observed to drive young out of their territories at weaning (Rusch and Reeder, 1978). Randall (1984) observed female *Dipodomys spectabilis* chasing female offspring away from the natal mound and driving them away again when they attempted to return. Yahner (1978) believed that young *Tamias* left voluntarily. He stated that he saw no evidence that maternal females expelled their young, but he observed that young returning to the natal site after several days were attacked by their mothers. In the two instances where young settled at the natal site, the maternal female had moved or disappeared.

Increased tolerance of offspring by females has been observed as the breeding season ends and residual reproductive value of the breeding population is exhausted (Jannett, 1978; Perrin, 1979; Viitala, 1977). Decline in the tendency of young to emigrate as the end of the breeding season arrives has been noted in *Apodemus* (Flowerdew, 1978; Watts, 1970), *Mus* (Naumov, 1940), and *Peromyscus* (Mihok, 1979), but a direct connection between increased female tolerance and philopatry of young at this season has yet to be established.

Viewing the evidence, there is much to be learned regarding any role of resident females in regulating dispersal. Most of the recent studies do support the generalizations that females are intolerant toward unfamiliar individuals of both sexes, that female territoriality opposes settlement of transients, and that female residents can inhibit immigration of sexually mature female conspecifics, but the picture of the role of females in opposing immigration is still far from definitive. Female resource competition provides a basis on which expulsion of offspring might function, but direct evidence that females actively expel either male or female offspring is scant. Although the importance of female behavior is being increasingly recognized, more detailed studies on the role of females in emigration of offspring are needed. The present trend favors the RFH prediction that female behavior will have a significant effect on emigration as it relates to density, and will be more influential than male behavior in limiting density increase. Nevertheless, the opinion of such careful workers as Myllymäki (1977a:561) that "it is possible to dispense with the theory that female territoriality and aggressiveness are major demographic forces" cannot be ignored.

Responses of Young to Resident Pressure

There is little evidence that in unconfined populations young are likely to displace parents or other residents through confrontation or other forms of agonistic behavior. Young marmots always lose agonistic encounters with adults (Armitage and Johns, 1982). Evicted individuals sometimes establish themselves near, but out of routine contact with, natal or non-natal colonies. In arena encounters young *Microtus ochrogaster* that had not had an opportunity to establish pair-bonds rarely initiated agonistic interactions (Getz et al., 1981). Metzgar (1971) observed that young

Peromyscus leucopus tended to settle in the interstices between resident home ranges, or to take over ranges vacated by residents. Downhower and Armitage (1981) noted that yearling female marmots delayed emigration when adult aggression was low.

The two physical responses available to young in the face of parental pressure are emigration or adoption of "peripheral" status but, if adult pressure is significantly dependent on the state of development of offspring, delayed maturity might serve as an alternative. From the point of view of the offspring, delayed maturity in response to adult pheromones could be adaptive if it staves off pressure to emigrate and thereby facilitates philopatry.

In most seasonally polyestrous species, persistence of young of both sexes at the natal site probably increases with the end of breeding by residents, although few authors have examined the point critically. It has been specifically reported in *Apodemus sylvaticus* by Flowerdew (1978). Overwinter delay in emigration of males from the last litter of the season has been observed in *Microtus townsendii* (Beacham, 1979b) and *M. montanus* (Jannett, 1978), and reported for *Mus* by Naumov (1940).

Although the interplay of adult pheromones and juvenile response might also reduce the possibility of inbreeding (Rissman and Johnston, 1985; Rissman et al., 1984), the competition-suppression and emigration-avoidance explanations are obviously favored when the relationship is intrasexual. The inbreeding-avoidance explanation is favored when maternal cues are most effective in delaying male maturity (e.g., in *Microtus californicus* as reported by Rissman et al., 1984). The fact that in experimental populations the initial stocks can inbreed freely, and delayed maturity becomes evident only when crowding results from lack of egress (e.g., the "growing" house mouse populations of Brown, 1953), favors the competition-explanation over the inbreeding-explanation, but the two are not mutually exclusive in most situations.

Available evidence supports the assumption that juveniles generally fare best if they avoid challenging residents. Terman (1961) conducted experimental releases of laboratory-reared *Peromyscus maniculatus* in large field enclosures and concluded that the ultimate pattern of dispersion was best explained on the basis of avoidance of same-sex residents by the settlers rather than aggressive defense by the residents. Van Horne (1981) concluded that there was a tendency for young *Peromyscus* to be displaced to less favorable niche space. She observed that when density was high, younger individuals consumed less of certain preferred foods and occupied habitats with less cover. Tardiff and Gray (1978) reported that immigrants sampled a wider range of foods than residents.

The assumption of the RFH that the options available to offspring are determined by the behavior of residents is supported by a variety of observations. If young become transient, encounters with residents, or with indications of occupancy such as feces, urine, or other scent marks, could induce avoidance responses and young could be stimulated to continue wandering. Avoidance could therefore be an important factor in dispersal distance. Neither adults nor young should be expected to be uniform in their behavior, and both stimulus and response are likely to vary with genotype and experience (Armitage, 1986a). Nevertheless, patterns can be expected. There is ample opportunity for direct studies of the behavior of transients in response to runways, scent marks, and encounters with residents under actual or simulated field conditions.

Responses of Male Offspring

Downhower and Armitage (1981) observed that young male yellow-bellied marmots were subject to both maternal and paternal pressure. Although it remains to be demonstrated that this is true in most species, the majority of young males probably emigrate. In studies to date, males have predominated among presumed emigrants and disappearance rates of young males have generally been higher than those of female siblings (Dice and Howard, 1951; Dobson, 1981, 1982; Festa-Bianchet and King, 1984; Gaines et al., 1979b; Gaines and McClenaghan, 1980; McLean, 1982; Myers and Krebs, 1971; Pfeifer, 1982b; Sherman, 1977; and others), and the proportion of young males known to establish near the natal site lower than that of their female siblings (Holekamp et al., 1984; McLean, 1982; Schwartz and Armitage, 1980). Young male

emigrants settle at greater distances from their natal sites than do their sisters (Dice and Howard, 1951; Dobson, 1981; Holmes and Sherman, 1982; McLean, 1982; Michener, 1981, 1984; Pfeifer, 1982b).

There is evidence that as young males enter puberty they avoid adult males. Juvenile male hamsters in a laboratory enclosure showed preference for unoccupied nest sites over those occupied by adults of either sex (Dasser, 1981). Viitala and Hoffmeyer (1985) marked traps with hexadecylacetate, a substance present in the preputial gland secretion of dominant adult males, and found that subadult male and subordinate adult male *Clethrionomys glareolus* avoided these traps. Measurement of aggression in arena encounters might be misleading with respect to responses of juveniles, especially if a juvenile resorts to aggression when means of avoidance are unavailable. This might explain the observation of Perrin (1981), who reported that in *C. gapperi* male young of the year were the most aggressive cohort in arena encounters staged between late June and September.

The correlation in males between sexual maturity and tendency to emigrate could result entirely from internal mechanisms, or from a response by residents to evidence of maturity. Holekamp et al. (1984) postulated that perinatal androgen levels might explain male-biased emigration rates in ground squirrels, but provided no direct evidence to support the fundamental assumption that male emigration was internally induced. In some ground squirrels emigration of young males can occur well before sexual maturity (Holmes and Sherman, 1982). More commonly, young ground squirrel males leave the natal site at or shortly before sexual maturation (Armitage and Johns, 1982; Pfeifer, 1982b), and departure is associated with aggressive interactions with paternal (Armitage, 1974; Christian, 1970) or fraternal (Pfeifer, 1982b) males.

In some species of *Spermophilus*, fathers depart before young emerge from natal burrows and therefore there is little probability of father-son contact (Holekamp, 1986; Michener, 1979). In other species, disappearance of the male parent reduces the probability that sons will emigrate. Armitage (1974) concluded that the presence of an adult male in a colony of marmots was a prerequisite for yearling male emigration. Svendsen (1980) observed that following the death of the father, a young male beaver did not emigrate but instead settled in the natal lodge and was accepted as a mate by his mother. Correlation between absence of a male parent and failure of young males to emigrate is contrary to the argument that emigration is selected on the basis of incest avoidance.

If sexual maturity triggers external pressures (or internal drives) toward emigration there should be a correlation between transiency and sexual status at the appropriate seasons. Data are variable as to sexual maturity of transient males. Transient male *Clethrionomys glareolus* were usually sexually mature (Kozakiewicz, 1976), but Krohne et al. (1984) found that most male *Peromyscus leucopus* that emigrated had abdominal testes. Forty percent of subadult *Microtus townsendii* of both sexes identified as emigrants by Beacham (1981) were in breeding condition, compared with only 15% of non-emigrants. Beacham suggested that sexual maturity at a low body weight predisposed animals to emigrate. Male *M. townsendii* taken in pitfall traps were more likely to have descended testes than were males of equal or greater weight caught in live traps (Beacham and Krebs, 1980).

There are broad associations among male puberty, emigration of male young, higher probability of males emigrating relative to their sisters, and the presence of sexually active adult males. In many species sexual maturity occurs later in males than in their female siblings (Frank, 1957; Holmes and Sherman, 1982; Koponen, 1970; Myllymäki, 1977a; Schwarz et al., 1964; Stenseth et al., 1977). Busher and Jenkins (1985) reported that yearling male *Castor canadensis* behaved less like adult males than did their female siblings. Stoddart (1973) noted that until sexual maturity the tail-gland secretions of young male *Apodemus* show chromatographic patterns resembling those of the mother. Assuming identification of sex and status are olfactory, this could be an example of chemical camouflage offering protection from emigratory pressures. Delayed emergence by yearling male ground squirrels until after the mating season is over (Slade and Balph, 1974) might have a similar effect. However, Porter and Dueser (1986) were unable to demonstrate

suppression of male growth or maturity in *Microtus* when the proportion of large resident males in the population was high, nor early maturity when the proportion of adult males was low.

There is little evidence to suggest that young males challenge male adults for the right to remain on the natal site. If sexual maturity of male offspring triggers agonistic behavior of resident males, delay in sexual maturity may avoid or delay forced emigration and thereby facilitate philopatry. It may be to the advantage of both fathers and their sons if young males postpone emigration when they have little chance of success (e.g., Rissman et al., 1984).

Pheromones produced by adult male *Peromyscus* sp. have been shown to retard the development of the testes and seminal vesicles in young (Lawton and Whitsett, 1979). On the other hand, one or more pheromones carried in the urine of breeding females can accelerate sexual maturation in young males (Drickamer, 1984). This could either increase the probability that male offspring would be expelled by resident males or make young males available as mates for maternal females.

In polyestrous species, adult male pressure on young males is likely to be continuously high until near the end of the breeding season. Turner and Iverson (1973) speculated that young male *M. pennsylvanicus* never establish home ranges during the breeding season of their birth. Overall, there is much circumstantial evidence to support the RFH assumption that emigration of young males occurs in the course of puberty in response to pressure of residents, but there is as yet no definitive picture of the stimulus-response system that leads to emigration or philopatry in young males of any species. Competition among young males is another possible factor but fraternal relationships have received little study.

Responses of Female Offspring

Young females behave as the RFH predicts. Dispersal distances of female ground squirrels were less than those of males in most studies (e.g., McLean, 1982). Exceptions (Holekamp, 1984) and observations that females are in the majority among transients (Dobson, 1981; Jordan, 1971) are rare. Dice and Howard (1951) reported the average distance between natal site and breeding site for female *Peromyscus* that dispersed was 57 m, as opposed to 121 m for males.

Response to paternal aggression is not a factor in emigration of female young in *Marmota flaviventris* (Armitage, 1974). Unfortunately data about this are not available for other species.

Emigration of young females is a response to maternal aggression in *Spermophilus elegans* (Pfeifer, 1982b). Aggression by, or avoidance of, female residents other than the mother also might lead either to emigration or continued transiency in female young. In laboratory enclosures juvenile female hamsters avoided nest sites of adult females but did not avoid those occupied by adult males (Dasser, 1981).

The combination of female nepotism and philopatry might produce a lag effect in emigration of young females. Gaines and Johnson (1984) found that of all sex-age cohorts of *Microtus ochrogaster* encountered on a removal grid, only subadult females differed in comparison with trapping results from a control grid.

As noted above, female young can be inhibited reproductively when kept in continuous close confinement with female kin in the laboratory (Batzli et al., 1977; Drickamer, 1974; Richmond and Stehn, 1976) and by forced exposure to maternal pheromones in the wild (Getz et al., 1983; Massey and Vandenbergh, 1980). In some cases the inhibitory effect on female young of pheromones produced by adult females appears to be dependent on physical contact (Batzli et al., 1977; Terman, 1980). It is not certain that contact outside of captivity would be adequate to suppress sexual maturation, but Saitoh (1981) reported that confinement with overwintered females in outdoor enclosures delayed maturation of spring-born female *Clethrionomys rufocanus*. Removal of adult female *C. rutilus* (Gilbert et al., 1986) from an unconfined population, and of adult female *C. gapperi* from both confined and unconfined populations (Bondrup-Nielsen, 1986), was followed by maturation of young females that otherwise probably would not have matured at that time. Although removal of overwintered females in spring stimulated breeding in young females, removal of overwintered adult females in fall had no effect on young at a

time when breeding was continuing in the overwintered adults (Bondrup-Nielsen and Ims, 1986). Bujalska (1973) found that removal of members of both the overwintered and first spring cohorts in an island population of *C. glareolus* increased reproductive activity of females of the subsequent summer cohort.

Many authors have noted an inverse relationship between rate of sexual maturation in females and population density, and have inferred that delayed sexual maturation is a density-limiting response (e.g., Bondrup-Nielsen and Karlsson, 1985; and references cited therein). In most such instances, crude density peaks at the end of the breeding season, when delayed sexual maturity would be anticipated as a seasonal response. The density relationship therefore may be incidental to strategies specified by the RFH.

A key question in the present context is whether inhibition of sexual maturity acts as a stimulus to emigration or a mechanism to delay emigration. There are a number of possible ways in which delayed sexual maturity of young females could be adaptive for parents or offspring (e.g., Frogner, 1980; Stearns and Crandall, 1981a, 1981b). Depending on season, population density and sex-age composition, and the like, delayed sexual maturity in female young could have one or more of the following effects: 1) limit intra-familial competition; 2) retain young females as helpers to care for younger siblings; 3) optimize the timing of emigration of female offspring; 4) reduce the probability of incestuous matings; 5) conserve young females in the home range for future matings; 6) force females to emigrate in order to breed; 7) be a means by which young females avoid emigration, thereby facilitating philopatry and continuation of matriline. The available data support most of these possibilities.

If a virgin female *Microtus ochrogaster* is caged with a reproductively active adult female, male-induced reproductive activation is suppressed (Getz et al., 1983). Such inhibition of maturity in female young may function to alleviate intrasexual competition. This is supported by the parallel to Bujalska's studies of *Clethrionomys glareolus* (Bujalska, 1970, 1971, 1973), in which suppression of reproduction in young females living within the home range of a reproductively active female seemed to function primarily to regulate the number of breeding females. Viitala and Hoffmeyer (1985) suggested that pheromones produced by adult females could have the effect of limiting female competition in *C. rufocanus*.

Because older offspring might contribute substantially to the care of nestling *M. ochrogaster* (Getz and Carter, 1980; Getz et al., 1981; Thomas and Birney, 1979), the concept of retention of young as helpers is also supported. Midsummer droughts bring about a midsummer lull in reproduction over much of the range of *M. ochrogaster*. At this season, delayed maturity of female young could serve to prevent emigration at an unfavorable time.

Because females fail to become sexually activated by *familiar* males, and in this pair-bonded species familiar males are likely to be related (fathers or brothers), it is also logical to suggest that delayed sexual maturity evolved as a means of preventing inbreeding (McGuire and Getz, 1981). The fact that pre-pubertal confinement of non-related adult-young pairs produces the same inhibition as confinement with relatives (Gavish et al., 1984) weakens the "incest taboo" argument, but does not negate it. Ågren (1984a) found that in *Meriones unguiculatus*, as in *Microtus ochrogaster*, sexual maturity of young females is inhibited as effectively through constant close contact with familiar non-relatives as with relatives.

Is delayed sexual maturity in females a spur to emigration, or a means by which emigration of young females is delayed or avoided? Familiarity barriers to female activation and mating erode when the familiar animals are temporarily separated (Dewsbury, 1982c; Gavish et al., 1984; Hill, 1974; Huck and Banks, 1979; McGuire and Getz, 1981; Porter and Wyrick, 1979; Richmond and Stehn, 1976) and the question of whether contact is constant enough, and familiarity sufficiently strong, to prevent female maturity in the wild has yet to be answered. Although it appears that those female *M. ochrogaster* that emigrate will be the first to enter estrus, there is no evidence that absence of estrus is a stimulus to emigration. Further, it is not known if emigration results in an increased rate of sexual maturation. In laboratory arena tests, mated male *M. ochrogaster* were aggressive toward unfamiliar virgin females. It is therefore

unlikely that transient females would be activated by, or establish breeding relationships with, pair-bonded resident males (Getz and Carter, 1980; Getz et al., 1981).

In seasonally polyestrous species, patterns of growth and maturation vary markedly with the time of birth (Anderson, 1970; Gyug and Millar, 1981; Martinet, 1967; Reichstein, 1964; Schwarz et al., 1964). Failure of female offspring to emigrate in the latter part of the breeding season has been observed frequently (Batzli and Pitelka, 1971; Beacham, 1979b; Lidicker, 1980; Mihok, 1979; Myllymäki, 1977a), and as pointed out above, optimal dispersal strategies for both parents and female young could be served by delayed maturation at that time. McClintock (1983) suggested that delay in sexual maturation of young female voles until they are able to claim a territory, as observed by Bujalska (1970, 1971, 1973), is an adaptive response on the part of the young in that it serves to delay reproduction until adequate resources are available.

If transient females have a higher probability of immigrating than do their male siblings, activation by unfamiliar males could assist in this process. Female transients penetrate established populations (immigrate) more frequently than do males in at least some species (Anderson, 1965; Eibl-Eibesfeldt, 1950; Redfield et al., 1978b). For the present, the conclusion must be that there is no evidence that juvenile females in unrestricted situations normally respond to maternal pheromones or "excess" familiarity with male relatives by delaying sexual maturity. Further experiments like those of Massey and Vandenberg (1980) are needed to resolve the question.

In summary, young females are more likely to settle philopatrically than are their brothers. In a few cases it is reasonably clear that maternal aggression is responsible for emigration of young females. Even so, little is known about the proximate stimuli and responses that determine whether a young female will emigrate or settle at its natal site. It appears that young females are unlikely to experience agonistic interactions with their father; mothers tend to behave in an affiliative or nepotistic manner unless stressed by resource shortages. Maternal aggression, if any, is likely to be associated with pregnancy or parturition. Competition between sisters might be similarly triggered and act as an additional source of pressure to emigrate in some species. Sexual maturation in females of at least some species can be delayed by either maternal pheromones or insufficient contact with pheromones of mature males, but there are many possible functions for such inhibition and their relationship to emigration and other aspects of dispersal remains problematical.

The Confinement Syndrome: Consequences of Lack of Egress

If some individuals are behaving in a way that has evolved because it causes others to emigrate, and emigration is impossible due to physical barriers, the frustration of the normal processes can be expected to lead to abnormal consequences for both those exerting the pressure and those receiving it. Beginning in the 1950's, studies of confined populations of mice, rats, and voles have consistently reported results that seem counterproductive in evolutionary terms and are not readily interpretable except as abnormalities associated with pressure on potential emigrants combined with lack of egress.

The RFH predicts that when egress is blocked, pathological behavioral or physiological effects, or both, should be most immediate and most extreme with respect to the potential emigrants. Established individuals should be the last and least affected as density increases. The effects of confinement therefore should provide clues to the identity of potential emigrants and to the mechanisms that normally induce emigration.

The classic confinement syndrome, in which a confined population grows to a high density, following which growth is terminated by behavioral and physiological abnormality, was demonstrated in studies of house mice by Brown (1953), Christian (1955a, 1955b), Southwick (1955a, 1955b), and Strecker and Emlen (1953). Further examples of confinement effects in house mouse populations were provided by Calhoun (1973) and Lidicker (1976). Calhoun (1962a, 1962b, 1963) described similar patterns in Norway rats. The pathological nature of many of these effects was pointed out by Anderson (1961) and Calhoun (1962a, 1962b). Parallel results were obtained with confined vole populations at an early date (Clarke, 1955; Louch, 1956; van Wijngaarden, 1960).

Attribution of the discovery of such so-called "fence effects" to Krebs et al. (1969) by MacArthur (1972), Tamarin (1978), and others seems inappropriate in view of the numerous earlier observations. What is important here, however, is the existence and nature of the confinement syndrome and its relevance to the RFH and EFH.

The common characteristics of the syndrome, as seen in the references cited above, may include violent fighting leading to wounding and death among sexually active males, loss of weight and condition in subordinate individuals, multiple (and frequently sterile) copulations, infanticide, persecution of juveniles (males in particular) at the onset of sexual maturity, and inhibited sexual maturity or suppressed reproduction of young of one or both sexes. The pattern develops more quickly when unrelated individuals are confined together than when a population is initiated with a single pair (Brown, 1953), implying that the phenomena are not associated with inbreeding. Adrenal hypertrophy, indicative of physiological stress responses among subordinate (potentially emigrant) individuals, has been evident where tests were conducted (e.g., Christian, 1955*a*, 1955*b*, 1956). Male offspring are usually the first to be affected and mortality of male offspring is typically higher than that of females (Singleton, 1985).

Several points stand out in the present context. The first is that young are consistently the first and most severely affected by the confinement syndrome. Two interpretations are possible. The first is that all young are innate emigrants and frustration of their innate impulses generates the pathologies. The second is that the syndrome is the result of pressure exerted by established adults and that both adults and young suffer from the effects of behaviors that fail to produce normal consequences. The evidence is strongly in favor of the second explanation. As predicted by the RFH the young are objects of adult persecution, particularly at the onset of puberty, and established adults (commonly the original founders of the confined populations) are the last affected and show the least response, although they do eventually show stress symptoms and abnormal behaviors. In extreme cases infants are killed, but more often young of both sexes fail to reproduce. Female young, in particular, may fail to mature, and any young males that pass through puberty suffer from attacks by breeding adult males. In view of the evidence that young are philopatric given the opportunity to settle on the natal site, and the observation that young are persecuted by resident adults, the RFH is strongly supported.

Seen in experimental enclosures, the confinement syndrome reduces the fitness of both residents and their offspring, and may eventually lead to extinction of the confined population (e.g., Calhoun, 1973). Rodent populations inhabiting small islands are also confined, although, as shown by Pokki (1981), the surrounding water barriers might be crossed more easily than cage walls. Also, drowning of emigrants may provide a built-in system for disposing of "excess" individuals. The peculiarities of populations of rodents on small islands, reviewed in detail by Gliwicz (1980), reflect the confinement syndrome and/or its evolutionary aftermath.

On very small islands the probability that colonizing populations will succumb to the confinement syndrome may be high. In those populations that survive a confinement syndrome phase and persist for many generations, stringent selection may have acted in several ways to reduce or eliminate the confinement syndrome. The nature of any compensatory adjustment is relevant to evaluation of the RFH. Observed "adjustments" include reduced aggressiveness of adults (Halpin, 1981; Halpin and Sullivan, 1978; Tamarin, 1977*a*, 1978), and delayed or inhibited maturity of offspring (Bujalska, 1970, 1971, 1973). Other characteristics of island populations, listed by Gliwicz (1980), include: high and stable densities; low reproductive rates; low disappearance rates of weaned individuals; density dependent mortality of nestlings; small, closely packed home ranges; and control of recruitment by inhibition of female reproductive activity. The association of demographic stability with lack of emigration sinks, proposed by Tamarin (1977*b*), might actually reflect the general syndrome of resident adaptation to long-term island existence. Island populations that do not display some of these adjustments, and show patterns resembling those of experimentally confined populations (e.g., Adler and Tamarin, 1984), could be of relatively recent origin.

Summary

Although there are many gaps in our information, there is considerable support for the RFH. Site tenacity is well developed, if not universal, among breeding adult rodents. Young are strongly philopatric, settling on their natal sites if permitted to do so. Both adults and young have the ability to discriminate among conspecifics as to sex, sexual status, degree of familiarity, relatedness, and social status. Residents are aggressive toward strangers, and immigrants are more likely to settle if residents are removed than if they are present. There is evidence for considerable inbreeding, and it is questionable whether the costs of inbreeding outweigh the costs of avoiding it. Selection for incest avoidance is compatible with either EFH or RFH; instances of incest avoidance are open to alternative explanations and incest avoidance alone appears inadequate as an explanation of emigration patterns. Evidence is abundant that male interactions are strongly influenced by competition for copulations, and female interactions are similarly influenced by availability of resources required for gestation and lactation. The resulting patterns of behavior are in conformity with the assumptions of the RFH. Mothers are nepotistic, but more so toward daughters than toward sons. Fathers have less assurance of relatedness, interact much less with offspring, and are generally neutral toward prepubertal young. Delayed sexual maturity of young could serve parents as a means of suppressing competition and conserving young at the natal site, and serve young of either sex as a means of avoiding pressure to emigrate. The evidence is largely circumstantial on this, as it is on such topics as mate preference, the actual stimuli for emigration, the responses of potential emigrants to such stimuli, the behavior of transients, and the process of immigration. Although many of the relevant questions remain to be investigated in these areas, the trend of the evidence is compatible with the RFH. Strong support for the RFH is evident in the confinement syndromes exhibited by experimental and island populations.

V

COMPARING THE RFH AND EFH: PREDICTIONS AND TESTS

To what extent do the behavioral, demographic, and genetic patterns implicit in the RFH differ from those of the EFH? To what extent do they provide a basis for tests that could assist in evaluation of the relative applicability of the two hypotheses? In this chapter I have expanded on some predictions, suggested others, and commented on specific approaches that could be of use in testing the relative applicability and significance of RFH and EFH, in explaining the evolution of dispersal among rodents, and in predicting the consequences of dispersal-related behaviors.

Despite the risk of too much preaching, I think it necessary to remind readers of some basic points. If these hypotheses are to be tested, both the concepts under investigation and units used must be unambiguously defined. Emigration must be separated from immigration. Significant stages in ontogeny must be clearly discriminated. Potential emigrant cohorts must be precisely identified and those individuals that emigrate must be compared with those that do not if an investigator wishes to test an hypothesis about the qualities of emigrants. Despite the great difficulty involved, more ingenious and precise ways must be devised to discriminate potential emigrants (including both established residents and unestablished individuals), actual emigrants, transients, and immigrants. It is not appropriate to identify immigrants and transients captured on a removal plot as emigrants. It is particularly inappropriate to regard such a sample as representative of emigrants from an arbitrarily designated area nearby without precise knowledge of the spatial origins of animals in the sample.

Testing the RFH demands that season be taken into account in all analyses of dispersal. Because the RFH predicts seasonal variation in parental tactics and offspring responses, the practice of pooling data on emigration, or emigrant characteristics, for an entire year, or an entire breeding season, cannot be expected to give unambiguous results. In fact, one way of discriminating between EFH and RFH explanations of emigration is through experimental manipulation of parental (established resident) pressure, appropriately timed to test specific RFH predictions.

The RFH rests on several fundamental propositions reiterated here because it is essential that the foundations of the hypothesis be kept clearly in view. They are: 1) that breeding rodents establish fixed home ranges; 2) that emigration of young is caused by the behavior of residents toward non-residents (in particular their own offspring); 3) that behavior of parents toward offspring can change between treatment of young as the output of parental reproductive investment and treatment of young as competing, although related, conspecifics; 4) that young endeavor to settle at the natal site and will do so unless forced to move elsewhere; and 5) that residents effectively resist immigration.

Lidicker (1985*b*) criticized a preliminary version of the RFH (Anderson, 1980) on the following grounds: 1) that it failed to account for observations claiming to have demonstrated a high proportion of adults, especially adult females, among emigrants; 2) that it negated selection as a result of advantage to emigrants; and 3) that the model did not predict that littermates will depart synchronously. As discussed above, I believe that most reports of adult emigration are based on inadequate definitions of adult and/or emigrant status. Littermates would be at least as likely to depart synchronously under the RFH as they would if alleles for the tendency to emigrate were segregating, and Lidicker (1985*b*) was incorrect in stating that the RFH does not predict simultaneous departure of littermates. He is correct, of course, in stating that the RFH

assumes that emigrants are less fit than they would have been had they succeeded in settling at the natal site, and I have summarized evidence indicating that this is the case. Comparisons of the relative success of philopatric and emigrant young (e.g., Jones, 1986) are highly appropriate tests of the two hypotheses.

Behavioral Predictions and Tests

The basic prediction of the RFH is that emigrants depart "because of" rather than "in order to." Emigration "in order to find a mate" (King, 1983) or "in order to find available space" (Viitala and Hoffmeyer, 1985) is not anticipated. Emigrants are not expected to leave spontaneously due to "ontogenetic switches." Behavioral stimuli given by residents are expected to precede emigratory responses on the part of offspring. To the extent that residents resist immigration, the movements of individuals unable to settle on, or adjacent to, the natal range are likely to be prolonged and cover relatively long distances. Because the probability that travel away from the natal site will be detected declines exponentially with distance, and the probability of immigration might do so as well (see below), long-distance dispersal is considerably less likely to be detected than short-distance dispersal. Recorded movements are probably even less representative of distances over which an individual wanders before becoming established (or dying). Despite this difficulty, it would help in comparing the two hypotheses if both dispersal distances and transient movements could be studied more thoroughly and accurately.

The EFH and RFH make different predictions regarding dispersal distances. The RFH anticipates that an emigrant should settle as close to the natal site as possible, benefiting by association with relatives and minimizing risks of movement. Under this hypothesis, data on dispersal distances should vary with season, density, and habitat distribution. Within a single cohort and sex, leptokurtosis should be strong. In contrast, an extension of the genetic polymorphism hypothesis might predict that the distance an individual moved (as well as the tendency to emigrate) would be predetermined, and that dispersal distances might be bimodal or approximate a normal distribution.

Historically, it was the observation that distributions of dispersal distances were leptokurtic that inspired the EFH view that emigration was controlled by the genotype of potential emigrants. Variation in emigratory drive seemed the simplest explanation for this distribution. The superficial application of Occam's law may not, however, provide the best answer in this case. Waser (1985) demonstrated that a model assuming parent-offspring competition and offspring expulsion also predicts a distribution of dispersal distances with a shape that closely approximates the leptokurtic distribution observed for *Peromyscus maniculatus* by Dice and Howard (1951), yet does not require any polymorphism in dispersal tendencies. The data did show two deviations from the predictions of the Waser model: females tended to settle closer to the natal site than expected, and there was an excess of long distance movements. Neither phenomenon has been explained on an emigrant-fitness basis.

The RFH offers explanations for the philopatry and short dispersal distances of female young. It may also suggest some explanations for an excess of long distance movements. As an individual moves farther away from the natal site there will be a decline in the mean relatedness of residents. If individuals are more tolerant of relatives than non-relatives, and if mate choices favor slightly different phenotypes and discriminate against greater differences, the probability of social acceptance might drop off rapidly with dispersal distance. Once a transient has passed an intermediate zone the probability of immigration may be low, and wandering may be prolonged. It may also be that a transient would be influenced by the similarity or dissimilarity of the habitat to that at the natal site. As distance from that site increased, acceptability of the habitat might decrease. These effects could account for long-distance movements. Both the relatedness effect and the habitat effect should be testable.

How far might a transient travel from the natal site? Small rodents clearly have the capability for rapid long-distance movement (Beer, 1955; de Kock and Robinson, 1966; Getz et al., 1978). Sadykov et al. (1985) recorded movements of radioisotope-marked transient *Clethrionomys* as

1,500 m in 24 h. An individual traveling at this rate along a canalizing habitat such as a stream course might cover 10 km in a week. Transients traveling for more than a few hours clearly are capable of moving beyond the limits at which they can be detected in most studies. They almost certainly do precisely that. Hilborn and Krebs (1976) radioactively-tagged 219 *Microtus townsendii* in an attempt to identify and follow emigrants. Only 30 tags were recovered, and Hilborn and Krebs felt that most explanations other than long-distance movement could be ruled out. If rates of movement evident in the study of Sadykov et al. (1985) and implied by the results of Hilborn and Krebs (1976) are typical, then studies of emigration using small grids (or within enclosures) would give misleading results.

The RFH predicts that long-distance movements should be made primarily by males and should be most frequent when competition for mates is high (e.g., in the spring), both of which were observed by Smyth (1968) for *Clethrionomys glareolus* and by Crawley (1969) for *C. glareolus* and *Apodemus sylvaticus*. Females born early in the breeding season should move only short distances. Female dispersal distances should increase for later cohorts. Long-distance dispersal by females would be promoted if females can mate prior to emigration or while transient.

A clear-cut, but difficult-to-test, difference between the RFH and EFH may exist in the relationship between fitness and dispersal distance. This is illustrated in Fig. 1. The EFH predicts that fitness of offspring should increase with distance from the natal site until any advantages of movement are overridden by the costs of reduced survival and/or delayed reproduction, thereby producing a simple convex frequency distribution. In contrast, the RFH predicts that the general trend is for fitness to decline with distance moved. For female offspring this decline should begin at the spatial limit of maternal nepotism. Beyond that zone, further decline in fitness would be a result of time lost in relation to the limited female potential to produce offspring. For males, faced with paternal competition and unassisted by nepotism, a much lower initial fitness and a more drawn-out distribution (reflecting the potential of a polygynous male to mate repeatedly with several females) is suggested.

The timing of emigration might also be useful for discriminating between the EFH and RFH. The RFH predicts that emigration should occur primarily within the breeding season. With the exception of some terrestrial sciurids this prediction is borne out (e.g., Krohne et al., 1984; Myllymäki, 1977a; Smyth, 1968). Patterns such as the burst of emigration of overwintered *Peromyscus* coincident with the initiation of breeding, and leading to colonization of sites made vacant by winter-induced mortality, are consistent with RFH predictions. If breeding is experimentally prolonged (e.g., by supplemental food) emigration should be prolonged as well.

As Horn (1983) suggested, a parent should behave so as to maximize the chance that its offspring will outcompete the offspring of other parents for occupancy of the natal site. It also follows from the RFH, and from models by Hamilton and May (1977) and Comins et al. (1980), that parents should suppress emigration of offspring whenever there is a period of parental reproductive quiescence in which the probability of parental survival is lower (less than half?) than that of philopatric offspring.

In seasonally polyestrous species emigration commonly ceases with cessation of breeding as the RFH anticipates it should, but emigration has sometimes been reported to be high in the immediate postbreeding period. Many such reports, however, deal with the number of transients, rather than the proportion of potential emigrants that actually move. Where this is the case the trend is a reflection of high post-breeding numbers, rather than of high emigration rate. Movement outside of the breeding season, on the basis of the RFH, should be more or less random with respect to sex and age. Singleton (1985), using both "exit" and "entrance" traps in mouseproof fences surrounding haystacks, reported that in non-breeding populations, house mice leaving and re-entering the fenced areas did not differ in sex, age, or mean weight from those that departed permanently.

The EFH and RFH offer different explanations for male bias among emigrants. There has been no specific elaboration of "innate" and "pre-saturation" versions of the EFH in this area, but Greenwood (1980, 1983) has argued that male bias can be best explained on the basis of selection for behavior (by parents or offspring) that restricts inbreeding. An EFH explanation

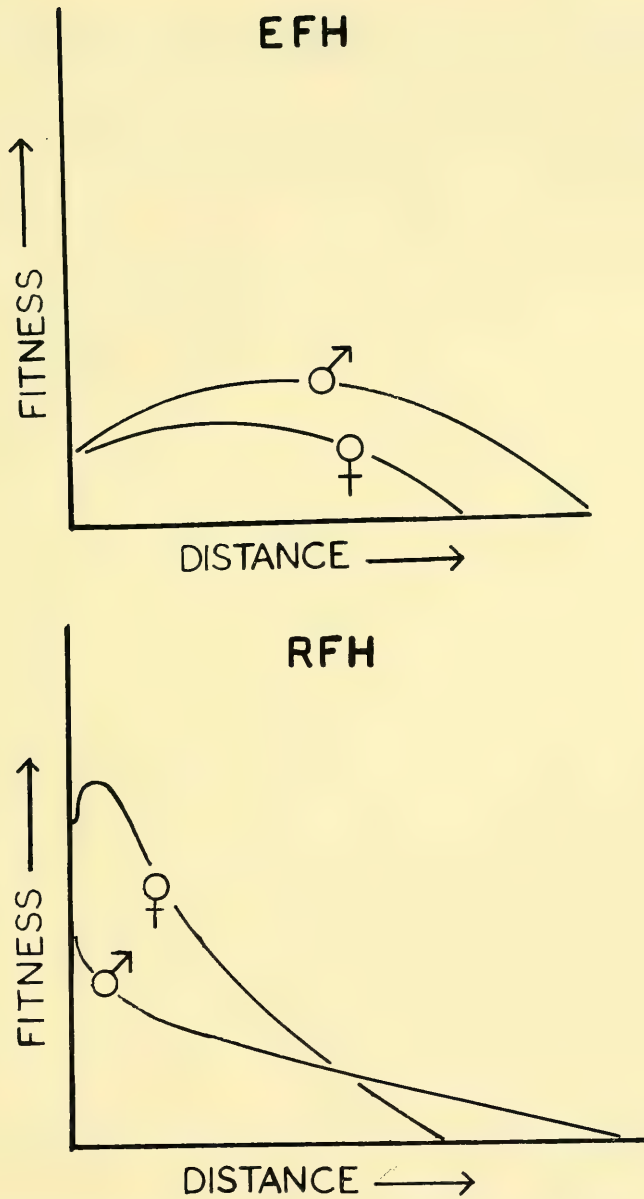


FIG. 1.—Qualitative patterns in the distribution of fitness relative to distance moved during dispersal as predicted by the Emigrant Fitness (EFH) and Resident Fitness (RFH) hypotheses.

based on selection for behavior of male offspring might require that alleles programming emigratory tendency be sex-linked, or sex-limited in expression. The RFH requires neither. It predicts that: 1) emigration will be closely associated with puberty in both sexes; 2) males will be more likely to emigrate than females because male parents tend to expel all male offspring as long as paternal residual reproductive value is high; 3) females tend to expel some males; 4) males do not expel females; and 5) females expel only a few females.

Fisher (1958) and many subsequent theoreticians have examined the question of sex ratio at

birth and generally have concluded that equal numbers of males and females should be produced. Although I do not feel competent to undertake a mathematical approach to the topic, I suspect that the same arguments could be applied to the "return" (transmission of parental alleles to future generations) that parents receive through disbursement of their offspring. If this is correct, the RFH predicts that parents should disburse male and female offspring in such a way that the production of grandoffspring through sons and daughters is equal. This should be reflected in comparisons of the sex ratios among emigrants and immigrants, and the relative reproductive success of the sexes following immigration.

Trivers and Willard (1973) postulated that if males competed for copulations and if large body size were advantageous, then male offspring would be selected for rapid growth and large body size. Where that was true, mothers might benefit by varying the sex ratio of young on the basis of their own available resources. If return is proportionate to parental investment, females in poor condition should produce the less expensive sex, whereas those in good condition should produce the more expensive sex. Trivers and Willard reviewed data that appeared to conform to this hypothesis. This line of reasoning seems applicable to parental strategies with respect to the export of offspring. The point is that if parents behave so as to maximize return on their investment, Fisher's (1958) argument should apply here as well—in other words, the return on disbursement of male and female offspring should be equivalent. In rodents there may be little difference in maternal investment in males and females if there is little dimorphism in body size, but sexual dimorphism in size has not been thoroughly investigated. If the cost of producing sons and daughters is the same, but male offspring have the potential to transfer parental alleles through multiple matings and females have a much lower potential, female offspring should be conserved through nepotism. It also follows that male bias in emigration should be greater in polygynous species.

How should resident strategies vary with population density? The RFH anticipates that resident behaviors toward offspring will be relatively insensitive to crude density. Male behavior, in particular, should show little variation with density. There is little reason for a male to be more aggressive toward sons at high density than at low density. Similarly, although resident females may be less able to abdicate in favor of their daughters and find a nearby range for themselves if all nearby areas are already occupied, full occupancy of available space need not affect the general level of resident female aggressiveness even though females may be forced to expel sons or daughters. In unconfined populations it is not necessary, with respect to either male or female residents, to assume with Krebs (1978*b*) that as density increases there is no alternative to fighting to maintain fitness. Immigration could still be prevented if transients avoid contacts with residents, perhaps by responding to resident scent marks. Emigration of offspring might still be stimulated by parental behavior that is relatively benign. There have been few studies of interactions between resident parents and their offspring in natural contexts, and most of the evidence for parental expulsion of offspring is circumstantial rather than direct.

Still another potentially useful distinction between RFH and EFH exists with respect to the nature of emigratory stimuli. The RFH predicts that the stimuli will be external, but that because parents gain fitness by optimizing the emigration of their offspring, emigrants that are forced to leave should not be damaged. Because fathers can benefit by altruism toward sons, resident males should expel presumed sons without harming them. Paternally administered wounding of young males should occur only when normal processes are obstructed. In confined populations that were regulated by removals, Hestbeck (1986) found that *Microtus californicus* identified as emigrants had a lower incidence of wounds than they did in confined populations not so regulated. Wounding, on the basis of Hestbeck's results, appeared to be a pathology induced by confinement, a result which would be predicted by the RFH but is not inherent in the EFH.

Authors have varied in their thinking as to how potential emigrants should respond to increases in density. Stenseth (1983) suggested that philopatry would be high following a decline in density and restriction of voles to the most favorable habitat patches, and that as density increased, individuals with a tendency to emigrate would be favored. Emphasizing the heterogeneity of

microtine habitat, Lidicker (1985b) suggested that when regional (metapopulation) density was low, small demes with high probabilities of extinction occupied the superior microhabitats, while surrounding and inferior habitats served as "sinks." He envisioned that the probability of an individual's emigration from such a population would be high, and that as density increased, emigration would decline because potential emigrants would be prevented from leaving the natal site by the resistance of surrounding residents (the "social fence" hypothesis of Hestbeck, 1982, 1986). Hestbeck (1986) demonstrated inhibition of emigration with increasing density in a confined population, but it remains to be seen if this would occur in less artificial situations (other than on small islands).

Whether increasing density lowers the emigration rate as visualized in the social fence model depends in part on the interaction between residents and transients. If residents are required to eject transients forcibly, as would be expected on the basis of arena experiments, young might be forced back to the natal area as Hestbeck (1982) and Lidicker (1985b) have envisaged. If transients are not attacked, and are allowed free passage as is indicated by the more tolerant behavior of resident *M. pennsylvanicus* toward strangers than toward unrelated neighbors reported by Skirrow (1969), emigration may not be inhibited by density. Lidicker's model appears realistic with respect to dispersion, but somewhat contradictory with respect to emigration rate because it envisages that panmixia will increase in conjunction with inhibition of emigration (Lidicker, 1985b). It also appears inconsistent with the EFH because emigrants lose fitness whatever the density. They are expected to be largely absorbed by "sinks" when regional density is low, and to be prevented from departing when it is high.

The RFH predicts that philopatric tendency in offspring is essentially constant and therefore insensitive to crude density. This, together with the strategies attributed to residents, should minimize density-dependent variation in the probability that young will emigrate. To the extent that the literature reflects the probability of emigration, this seems to be the case (e.g., see the conclusions of Gaines and McClenaghan, 1980).

Several experimental removal approaches can be envisaged that would be useful in discriminating between EFH and RFH with respect to the relationship between emigration and density. Specifically, the techniques used by Redfield et al. (1978a, 1978b) and Boonstra and Rodd (1983) could be modified and extended through still more selective removals of specific sex-age cohorts. In one pertinent experiment producing results consistent with RFH prediction, Rodd and Boonstra (1984) found that reduction in the density of overwintering *M. pennsylvanicus* improved persistence rates of males in the spring, but did not affect persistence of females.

As suggested earlier, the RFH predicts that within a breeding unit, removal of a resident of one sex during the breeding season should favor philopatric recruitment of an offspring of that sex. Immigration should be similarly favored. Removing residents is the simplest way of varying pressure on young, but mass removals ("removal grids") are bulldozer approaches where surgical precision is needed. I suggest that removal of single resident individuals of one sex or the other from numerous well-separated sites, and monitoring of the fates of potential emigrants (young born on the home ranges of the adults removed, or on adjacent home ranges), should replace mass removal approaches in testing the validity of hypotheses about resident pressure and its effects.

According to the RFH an isolated pair would still export their young according to the strategies outlined in Chapter II. Removal of a male should increase the probability that a son of that male would settle. That probability should be independent of density. Single pairs could be studied in large enclosures or through introductions to islands in order to test this prediction. If it proves correct, alternative and simpler explanations of the observations that have led to the concepts of "pre-saturation" and "innate" departure of young would be available. Removal of maternal females should prevent or reduce emigration of male young in seasonally monestrous species such as *Spermophilus beldingi*.

The work of Stoddart and others (e.g., Stoddart et al., 1975) on the role of scent suggests many possible experiments through which the role of odor in facilitating nepotism and philopatry and

in controlling emigration and immigration can be investigated. The RFH predicts that in populations in which males make little post-copulatory investment in their young, and male-male competition is centered on copulations, emigration of young males should be delayed if female scent is applied to them. Less directly, emigration of young males should be inhibited by removal or neutralization (e.g., castration, hormonal manipulation, olfactory blocks) of fathers or by any measures that delay or prevent maturity of young males.

Holekamp et al. (1984) suggested that emigration might be a direct response to the level of gonadal steroids in male Belding's ground squirrels, arguing that if emigration had evolved as a means of avoiding inbreeding, a direct physiological (EFH) mechanism effecting male emigration independent of environmental conditions might be adaptive. Where this EFH hypothesis predicts an inflexible response, the RFH predicts that increasing steroid levels in potential emigrants would fail to induce emigration in the absence of resident pressure. Taitt and Krebs (1982) reported that residency times of female *Microtus* implanted with testosterone were lower than those of control females, and equivalent to those of males. Disappearance due to death and disappearance due to emigration could not be distinguished, however. The Holekamp hypothesis could be tested by removing male residents while artificially raising androgen levels in their male offspring.

Manipulation of food and cover might also produce informative data if carried out in conjunction with selective removals. The RFH predicts that as long as there is no acute shortage of food or cover, removal of resident males should facilitate philopatry of male offspring exclusively, whereas removal of resident females should encourage philopatry in females. When material resources are short, on the other hand, removal of males might have no effect on philopatry of male offspring because females should then expel male offspring to reserve resources for themselves and their daughters. Food supplementation at a time of resource shortage should encourage female recruitment, but have a less marked effect on male recruitment or male emigration. Application of male scent to female young (olfactory masculinization) should cause their emigration irrespective of resource levels. These predictions are not derivable from the concept of an innate tendency to emigrate that is implicit or explicit in most interpretations of the EFH.

Tests of behavior could also be devised in the area of cohesiveness and mate selection. It will be important to determine if the barriers to inbreeding adduced on the basis of laboratory studies function in nature; the RFH predicts that they would not be significant, whereas the EFH emphasizes avoidance of inbreeding. According to the EFH, for example, probability of successful immigration might be inversely proportional to degree of relatedness. The RFH predicts that probability of immigration should be positively correlated with relatedness. If inbreeding is unimportant, removal of resident males should increase the probability of their sons establishing at the natal site more than it should the probability of establishment of unrelated males.

Experiments designed to test both the incest avoidance hypothesis and various EFH and RFH predictions could be carried out through systematically varied releases onto uninhabited islands or into large outdoor enclosures. Comparison of the histories of populations initiated with sibling, non-sibling, and cross-fostered pairs of colonists in such contexts should be informative. It would also be of interest to know if there is any evidence of incest avoidance among "siblings" belonging to different litters, or among overwintered young. Inbreeding and outbreeding need to be evaluated on the basis of cost versus benefit rather than cost only. Avoidance of inbreeding appears to be one of the stronger and more popular supports of the EFH. Costs of inbreeding are clearly a legitimate point on which to question the RFH, but potential benefits of inbreeding strengthen the RFH.

Because the RFH postulates normal distributions of emigratory tendency among potential emigrants, a variety of direct tests of emigratory behavior might be useful. The individuals to be compared come from the same source population and belong to the same seasonal cohort of young, and tests could be extended to comparison of breeding colonies derived from parents that were assumed to differ in emigratory tendencies. If some criterion were chosen to discriminate between supposed "pre-saturation" and "saturation" phenotypes, for example, colonies derived

from each should be developed. The RFH would predict that comparable cohorts from the two colonies would not differ in behavior under identical test conditions, indicating that the presumed difference was not inherent, but due to external influences. If there is variation in tendency to emigrate, it might be discernible as differences in individual responses among members of the same sex-age cohort to experimental displacement just beyond the limits of the maternal home range.

The greatest void in the study of dispersal is in the areas of recruitment and immigration. As a starting point, the assumption that young are inherently philopatric should be tested thoroughly. The simplest approach is to mark individual litters and explore the effect of removing one or both parents. The generality of the observation that young that do not succeed in obtaining rights to the natal site and settle instead in the first vacancy in suitable habitat, as observed by Baird and Birney (1982b), should be determined.

According to the RFH, females should have higher average success in immigrating than males, and males that emigrate should remain transient longer, wander more widely, and suffer higher mortality following emigration than females. Each of these predictions can be tested by experimental displacements. Female-scented or sexually inactive males should be more successful in establishing residence than sexually active males. Male-scented females should have reduced success. Immigration should be sensitive to manipulation of resident female behavior. As Taitt and Krebs (1982) observed, masculinization of resident females, like removal of females, should result in increased immigration of both sexes. As the RFH would predict, treatment of resident females with the chemosterilant mestranol apparently reduced their ability to maintain resident status (the cause of their disappearance was unknown).

Young of both sexes should benefit by philopatry and by association with kin. Few tests have been made, but Jones (1986) was able to demonstrate that philopatric young *Dipodomys spectabilis* benefited by maternal abandonment of the natal mound. He was, however, unable to find evidence that proximity to kin increased survival. Further tests of this type would be useful.

Habitat selection studies also have a place. Male transients should attempt to select habitat on the basis of female availability. Female transients should select sites on the basis of resources required for rearing young. Getz et al. (1987) have predicted that in *Microtus ochrogaster* new breeding units form when unfamiliar males and females meet in neutral areas.

Short-distance displacements would serve as a test for residency (i.e., individuals that home can be defined as residents, those that do not can be defined as unestablished). At the release site the unestablished individuals are potential immigrants. The RFH predicts that the probability of displaced non-residents immigrating should vary with the relatedness of the residents within whose home range they are released. The effects of season, and of the ontogenetic stage of displaced individuals, would also be of interest when displacement techniques are used.

Demographic Predictions and Tests

If the RFH is to be tested in a demographic context, several precautions need to be kept in mind. The first is that care should be taken to distinguish between the measurements of the number of emigrants or transients and the proportion of emigrants or transients. As Stenseth (1983) pointed out, this distinction has sometimes been overlooked. The second is that the measurement of emigration rates as the proportion of actual emigrants to potential emigrants should be specific to carefully chosen and defined sex-age cohorts at each season. As shown by Beacham (1980a), attempts to correlate emigration rates with demographic trends have often mistakenly interpreted seasonal trends in emigration rate as reflecting "cyclic phases" in demography. Many authors, when relating density to emigration rates, have failed to distinguish between long-term trends ("phases" of population demography) and trends that were part of the annual cycle. On careful examination, the "increase phase" in the majority of purported correlations between emigration rates and supra-annual or multiannual density trends turns out to be synonymous with at least the latter part of the annual reproductive cycle when, as the RFH predicts, populations are open to recruitment of young. Krebs et al. (1973) have argued

that because it frequently appears that emigration in microtines is maximal prior to a population decline, the relationship between population density and emigration must be qualitative rather than quantitative. The RFH correctly predicts the temporal relationship to which Krebs et al. referred. In doing so it provides an alternative explanation through analysis of possible strategies of residents and seasonal cohorts of young. It thus accounts for a relationship between emigration and crude density, which in most, if not all, of the published examples is directly associated with the cycle of seasonal reproduction.

Some data (e.g., Mazurkiewicz and Rajska, 1975) show declining emigration with increasing density. The social fence hypothesis (Hestbeck, 1982) offers one explanation, assuming that resistance to transient movement increases as density increases and that the advantage to dominant individuals in expelling a subordinate should decrease as density increases. Mares et al. (1982) carried out experiments designed to discriminate between the effects of resource availability and density per se on movement patterns in chipmunk populations and concluded that movement was not directly affected by density. The RFH predicts declining emigration as density reaches its seasonal peak, but makes this prediction on an entirely different basis (the advantage to residents of conserving their offspring as their own residual reproductive value declines). I suggest that the demographic observations that the social fence idea was proposed to explain are largely season-based, rather than density-based, and that when season is taken into account the patterns in emigration rate will be explicable without the need of an additional hypothesis.

The RFH implies that although emigration is not strongly density dependent, immigration well may be. It is not inevitable, however, that transient movement, as distinct from immigration, is restricted by increasing density. Tests of density effects should be devised so that it is possible to discriminate between immigration and transient passage. Multivariate analysis of disappearance rates by Gaines and Johnson (1984) pointed to season as the most important variable in explaining the ratio of presumed transients to residents in heavier (older) *Microtus ochrogaster*. For lighter (younger?) individuals season was not as effective for explaining variation in this ratio. This is contrary to RFH expectations. Re-examination of this result and those of other studies would be valuable in order to determine if a large proportion of the unexplained variation may have resulted from difficulties in categorization.

In addition to more precise and relevant categorization, improvement in demographic measures would be helpful. The "replacement rate" or "recovery ratio," defined as total catch on a removal plot divided by the catch on a neighboring control plot (e.g., Fairbairn, 1978a), is an inadequate and probably misleading measure of emigration. It identifies neither the cohort(s) nor the origin(s) of individuals in the sample that the removal plots have drawn from the transient pool; there is little justification for the assumption that it monitors the emigration rate on a nearby "control" plot. If replacement is to be measured, a better approach might be to measure it directly through selective removal of individuals rather than mass removals.

According to the RFH, the emigration rate should be independent of density over a wide range. To the extent that the techniques used to date actually reflect emigration, emigration rates do not appear to be density dependent (Gaines and Johnson, 1984; Gaines and McClenaghan, 1980; Verner and Getz, 1985). Further experimental manipulation of sex ratios along the lines exemplified by the studies of Krebs et al. (1978) and Boonstra and Rodd (1983) should be designed to test RFH predictions as to demographic effects at different seasons.

Boutin et al. (1985) reviewed four hypotheses that have been proposed with respect to the relationship between the emigration rate and the trend in crude density. These were termed the pre-saturation/saturation hypothesis, the kin-selection hypothesis, the selective dispersal hypothesis, and the food shortage hypothesis. In their view, predictions for emigration rate and growth had not been stated explicitly for the pre-saturation/saturation hypothesis, but as interpreted by Stenseth (1983) the emigration rate should be expected to increase with increasing density. According to the kin-selection hypothesis (Charnov and Finerty, 1980, as expanded by Stenseth, 1983), an increase in density would bring about a decrease in the mean relatedness of interacting individuals, leading to higher levels of aggression, and thereby stimulating higher rates of em-

igration. The selective dispersal (emigration) hypothesis postulates that emigration-prone phenotypes predominate in increasing populations. The food shortage hypothesis reduces simply to the expectation that hungry animals will move in search of food. Each of these models appears to me to be too coarse to provide results that are other than superficially plausible or misleading. The analysis of Boutin et al. (1985) illustrates the point that the predictions of the pre-saturation/saturation hypothesis are so vague as to be open to contradictory interpretations. The pre-saturation/saturation and kin-selection hypotheses rely on assumptions regarding the nature and frequency of social interactions that have never been demonstrated in nature, and for which there is contrary evidence. For example, Mazurkiewicz (1981) found that although home range size in *Clethrionomys glareolus* decreased with increasing density, the number of voles per trap station did not increase. The observations of Pearson (1960) also point to the conclusion that social pressure is not simply or directly related to density. The selective dispersal hypothesis likewise postulates undemonstrated phenomena: the existence of innate trends in density, and the existence of phenotypes that detect and make specific responses to such trends.

Although the demographic predictions of the EFH, at least as enunciated to date, are exceedingly vague, those of the RFH are relatively specific and more readily testable. The RFH predicts that although crude density should have relatively little influence on the probability that young will be expelled, density would influence the distance traveled by transients, and the probability of their establishment at a new location. Tests designed to discriminate between the two hypotheses on the basis of density responses should concentrate on family units. The RFH predicts that per capita probability of emigration from a matriline, or other family unit, will be sex, age, and season specific, but largely density independent. Male emigration is expected to increase in seasonal breeders during the pre-reproductive period (in association with male competition and the commonly observed pre-reproductive population decline). Throughout the mating period the probability that young males undergoing puberty will emigrate is predicted to be high whether the population is increasing or decreasing. Female young undergoing puberty will have a high per capita probability of emigrating whenever resident breeding females are stressed by food shortage. Per capita probability of emigration of young of both sexes is predicted to decline in polyestrous seasonal breeders during the period of maximum recruitment at the end of the breeding season.

If there are any density dependent effects on the probability that an individual will emigrate, the RFH predicts that they will be related primarily to resident female density. Female emigration rates are predicted to correlate positively with shortages of food, or unavailability of space. Male emigration will be unlikely to show cause and effect relationships with density. At times when emigration of male young is dependent on paternal pressure, experimental removal of male offspring should have little effect on the probability that remaining male siblings would establish themselves at the natal site, but removal of young females should increase the probability of philopatry for remaining female siblings. Removal of resident males should have no effect on philopatry of female young. As long as resident males are in breeding condition, removal of young females should fail to reduce the probability that their male siblings will emigrate (assuming that food resources are sufficiently abundant to eliminate any resource-related effects).

The RFH can be used to generate specific, testable predictions for demographic histories. Figure 2 presents a family of curves representing the relationships among resources, absolute crude density, economic density (per capita resource availability), effective density (individually perceived density including interference competition), emigration, and recruitment as these might be predicted on the basis of the RFH in a microtine population. Contrasting patterns are outlined for continuously occupied (core) and opportunistically or seasonally occupied (colonization) habitat. A projection as to the evolutionary contribution of animals breeding in the two habitat types, also included in the figure, reflects the relative contribution of residents and emigrants to the ongoing metapopulation inhabiting the surrounding region. The figure illustrates both the specificity of RFH predictions and the many points at which tests could be designed.

In such an RFH model, the emigration rate tracks stochastic patterns of environmental quality

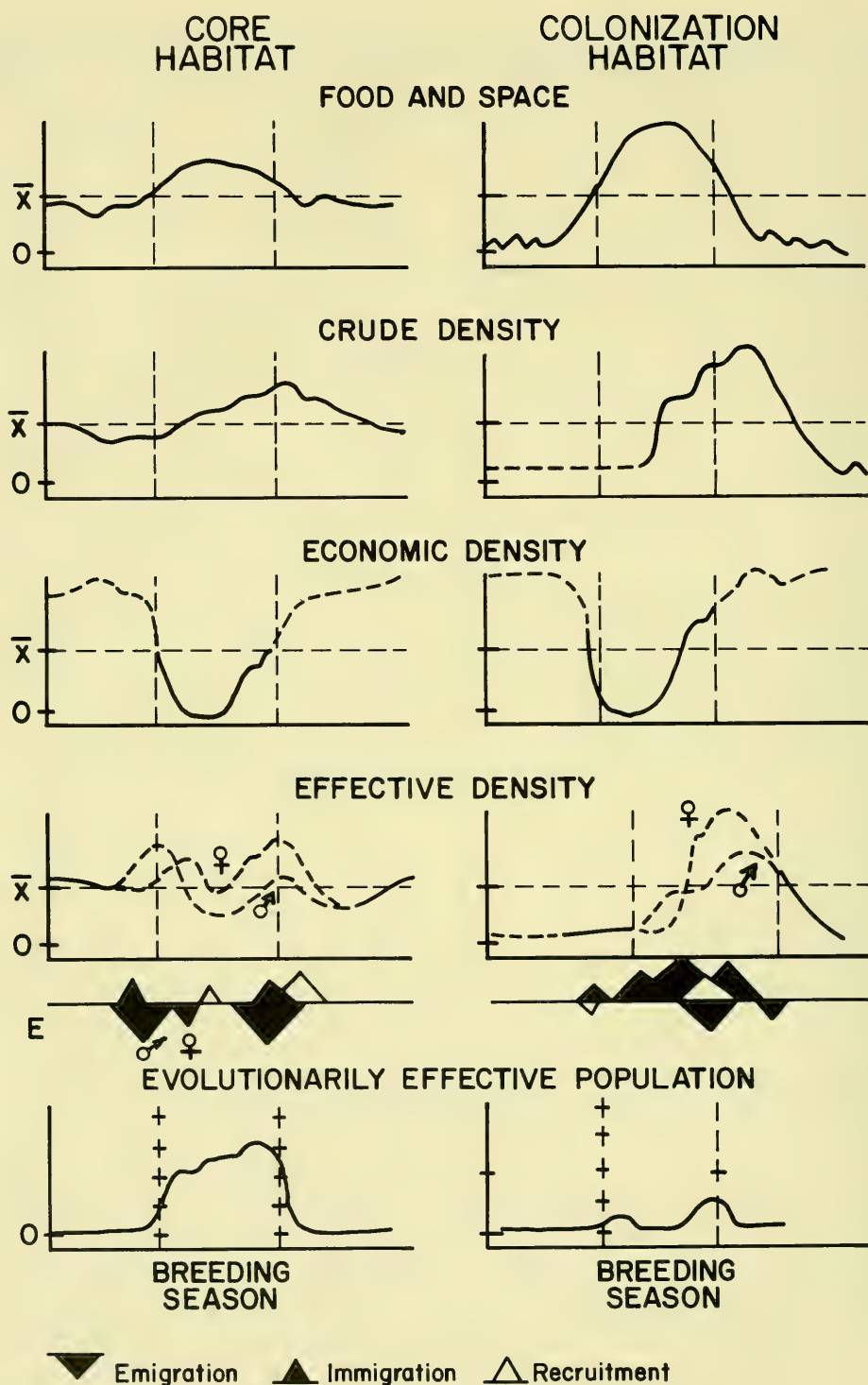


FIG. 2.—RFH-based predictions for a hypothetical vole population, specified for a stable patch of continuously occupied (core) habitat and a patch of seasonally or occasionally suitable (colonization) habitat.

primarily through female assessment of resource availability and consequent emigration of offspring. The predicted pattern of microtine abundance and emigration under "typical" conditions, as shown in Fig. 2, and its possible modifications by variation in weather and resource availability, should be compared with the results obtained in studies of *Microtus californicus* by Bowen (1982) and Cockburn and Lidicker (1983), the 10-year data set provided for *M. pennsylvanicus* by Mihok (1984), and other detailed descriptions of annual and multiannual patterns in microtine demography.

To my knowledge no equivalent EFH predictions have been devised and published. In contrast to specific predictions such as those outlined in Fig. 2, an EFH model would predict relatively little difference between the probability that male and female young would emigrate, no difference in the timing of male and female emigration, a greater response to crude density, and less specificity with respect to season. Alternatively, an EFH model might predict simply that in the absence of habitat destruction or resource shortage a constant proportion of the potentially emigrant cohort should emigrate, regardless of density. The distinctive basic postulate of the RFH is that emigration rates should be primarily responsive to economic density as perceived by breeding females, and to residual reproductive value of residents of both sexes.

A recent study by McShea and Madison (1986) reported that in spring the sex ratio of juvenile *Microtus pennsylvanicus* recruited into the trappable population was strongly biased toward females (61.5 to 67%). In fall the sex ratio among such recruits proved to be even, or biased (70.5%) toward males. Relative weight of nestlings was higher in females in the spring and lower in females in the fall. Nestling loss within litters was negatively correlated with weight, suggesting that ratios could have been influenced by differential survival. Heavier (possibly overwintered) females produced female-biased litters toward the end of the breeding season. This study implies a facultative seasonal bias in investment in nestlings. Such shifting bias is in accord with the RFH, which would predict that females should favor daughters as residual maternal reproductive value declined.

There are other explanations for biased sex ratios. As Trivers and Willard (1973) proposed, a female-biased sex ratio might reflect poor female condition and a consequent maternal disinvestment in male offspring, provided that the variance in male reproductive success is higher than that of females and that when conditions are good investment in male offspring will lead to their greater success in competition for copulations. Early season conditions may indeed be poor. Fairbairn (1977b) noted that early-season breeding is costly to female *Peromyscus*. Laboratory evidence supporting this theory has been provided by McClure (1981), who demonstrated that food restriction led to a bias against males in neonatal growth and survival in *Neotoma*. Trends in maternal pressure on male and female young to emigrate might reflect the interaction of the same kinds of tactical responses.

In most transient-settler samples taken from removal plots, younger animals and males have predominated (Gaines and McClenaghan, 1980). Absence of such biases in samples taken from the transient pool (Joule and Cameron, 1975; Stafford and Stout, 1983) are open to several non-exclusive explanations. As pointed out earlier, emigration is less likely to be governed by resident behavior outside of the breeding season; such "template" results may be obtained when data from an entire annual cycle are aggregated, obscuring seasonal patterns.

Comparison of results of pitfall and conventional trapping may be useful. From a study using

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Resource availability, crude density, density in relation to the resources available (economic density) for lactating females, and density in relation to social pressure and resources combined (effective density, graphed separately for males and females during the breeding season) are shown as related to mean density on the four upper graphs. The timing of emigration, immigration, and local recruitment are indicated by triangles below the graph of effective density. The times at which male and female emigration are predicted to predominate are indicated for core habitat. The lowest graph indicates the pattern of variation in relative size of the group contribution to the subsequent regional gene pool.

pitfall traps, Kozakiewicz (1976) reported that peaks in the pitfall-vulnerable ("transient") component of a population of *Clethrionomys glareolus* occurred in early fall in 1971, and in July and August in 1972. At first glance this appears to be at variance with RFH predictions. However, identification of the birth cohorts to which transients belonged showed that in both years they came from the early and midseason cohorts, as the RFH predicts. Comparison of the results of pitfall and live-trap registration of *Microtus townsendii* (Beacham and Krebs, 1980) showed peaks in pitfall catches at times when the RFH would predict non-resident numbers to be maximal. Trappability in live traps, in contrast, was highest in spring when breeding had been established and the proportion of residents in the populations would be predicted to be at its peak.

Most writers have assumed that the demographic consequence of emigration will be limitation of density. Horn (1983) pointed out, however, that modeling studies are inconsistent. Some have predicted density-increasing effects and others have predicted density-limiting effects. Emigration has also been supposed to be both a destabilizing (Tamarin, 1978) and a stabilizing (Anderson, 1970, 1980; Lidicker, 1962, 1975) factor in the dynamics of rodent populations. The RFH assumes that populations are structured into small units, including local populations and matriline, which collectively make up a regional "metapopulation" along the lines envisaged by Anderson (1970), Lidicker (1985b), and Stenseth (1983). It implies that the strategies of resident females will act to promote stability in the small units occupying favorable habitat by regulating the retention and reproduction of female offspring. Relaxation of intolerance by both sexes during the non-breeding season may serve to stabilize density in the metapopulation by allowing more animals to move into sites where the probability of survival is higher during the non-breeding months. At other times, resident strategies may facilitate colonization of marginal habitats. When the stochastic variations of the general environment make these marginal habitats unusually favorable for long-term reproduction, emigration might be viewed as the causal factor in a consequent population eruption.

Demographic predictions should, therefore, be viewed in the context of both predictable and unpredictable changes in the environment. Mihok et al. (1985b) concluded that continual influx of voles into a removal grid during midsummer tended to refute behavioral regulation of population density. My conclusion is the opposite. Parental (primarily female) behaviors tend to ensure a two-level population structuring in which semi-permanent breeding units export emigrants, maintaining a transient population available throughout the breeding season to fill gaps created by experimental manipulations or environmental stochasticism. These same strategies restrict increase in density and increase persistence of occupation in high quality habitats. The RFH predicts that in the absence of confinement the primary effect of male aggressiveness is to mediate emigration and immigration of males. Further, it implies that because male aggressiveness is probably constant over a wide range of densities, male aggression will have no density dependent effect on the emigration rate.

In polygynous species, male aggressiveness should bias the operational sex ratio toward females at all except the highest densities. Through export of sons and resistance to male immigration, male aggressiveness should increase rather than decrease the reproductive rate and the per capita rate of population growth. In general, male aggressiveness should limit population growth only in situations where increasing density reduces either the opportunity for matings, or the returns to males on post-copulatory reproductive investment. Further refinement of experiments in which resident sex ratio is manipulated along the lines pioneered by Redfield et al. (1978a, 1978b) and Boonstra and Rodd (1983) should be worthwhile.

It is probably not possible to overemphasize the often overlooked need to discriminate carefully among seasonal cohorts of young in behavioral and demographic studies. The subadult stage (encompassing both the puberty transition and the transition to resident status) is critical as each cohort matures, and occurs in a distinctive context for each cohort. The RFH predicts differential recruitment among seasonal cohorts. This is nicely demonstrated in simple form in the study of Stoddart (1971), showing that *Arvicola* born into a discrete population before 1 July were

recruited, but those born thereafter were not. The distinctiveness of cohorts is relevant to the Chitty-Krebs explanation of density fluctuation (Krebs, 1978a). One interpretation of the EFH might predict that a constant proportion of each cohort would be emigration-prone (as suggested by the data of Gaines and Johnson, 1984); another EFH interpretation might lead to the prediction that this proportion would change as the result of selective forces driven by density responses, particularly the aggressive responses of males. It is the second interpretation that is implicit in the Chitty-Krebs hypothesis. The RFH contradicts both of the EFH models just described. Instead of the simple Chitty-Krebs model of emigration driven by density-dependent selection, the RFH proposes that variation in emigration rate is driven by a complex relationship among seasonally variable habitat quality, resource availability as perceived by individual females occupying habitats that vary spatially and temporally in their capacity to support survival and reproduction, and male competition. Accordingly the RFH anticipates that interannual fluctuations should show significant, and sometimes subtle, dependence on variation in annual weather patterns and the phenology of food plants. The RFH model neither explains nor predicts intrinsic periodicities in population density. A more careful examination of the question of whether microtine numbers truly show regular multiannual periodicities than has been undertaken in the past (e.g., Elton, 1942; Finerty, 1976; Krebs and Myers, 1974) might eliminate the notion that such periodicities exist, and thus obviate the need to explain them. The recent review by Taitt and Krebs (1985) suggests that the concept of periodicity may indeed be on the way out.

Seasonal variations in the emigration rate may be useful criteria on which to judge the EFH and RFH. In seasonal breeders the initiation of the non-breeding season is a time of maximum recruitment and increase in density, coincident with onset of less favorable conditions such as food scarcity or lower temperatures. As environmental conditions deteriorate, economic density and competition should increase. The EFH postulates that individuals with a higher sensitivity to competition ("pre-saturation emigrants") should emigrate in response to increasing density and/or deteriorating environmental conditions. On this basis, the EFH predicts that the emigration rate would increase at this time. The RFH, in contrast, postulates that parents should cease exporting young at the time when residual parental reproductive values are nearing exhaustion, density is maximal, and opportunities for breeding are minimal.

Movement into removal plots demonstrates that in most populations there is a "transient pool" of animals available to settle in habitat from which residents have been removed. The RFH and EFH make different predictions as to the way the correlation between resident density and the proportion of animals in the transient pool should vary with the season. Fairbairn (1978a) noted that the number of *Peromyscus maniculatus* captured on a removal grid was significantly correlated with density on a nearby mark-and-release grid but not with the rate of increase on the latter. The ratio between captures on the removal grid and the number of animals currently encountered on a nearby mark-and-release grid (the "recovery ratio" referred to above) was highest in late fall and early winter when recruitment into the sedentary population was occurring. The peak in philopatric recruitment of young into Fairbairn's populations occurred at a time of maximum density, and at a time when transients were relatively numerous. Both observed relationships are difficult to reconcile with an EFH model, but both conform to RFH predictions.

The RFH anticipates that variation in immigration rates should be seasonal, and the inverse of emigration rates, because immigration rates should peak outside the breeding season. Demographic studies of immigration are rare. Andrzejewski (1963) reported that immigrant numbers showed distinct spring and fall peaks in a forested area. Krohne et al. (1984) noted spring immigration of *Peromyscus* into an area where there was no overwinter survival, and Sullivan (1979) noted a burst of recruitment in colonization habitat in clearcut areas in late summer and early fall. As with removal grids, trends in such seasonally vacated areas probably reflect numbers of individuals in the transient population rather than rate of immigration into established populations. If some of the uncertainties regarding the identification of immigrants on the basis of body weight at first capture (Dueser et al., 1984) can be resolved, the method might provide useful insights into immigration, but the approach has many weaknesses (Tamarin, 1984).

Demographically, the RFH is compatible with the view of species populations as composed of small local groups, most often matrilineal, which are subject to frequent extinction and replacement (Anderson, 1970, 1980; Lidicker 1985*b*; Stenseth, 1983). Few studies have been sufficiently enduring and detailed to test predictions as to extinction rates, but the model is well-illustrated by the matrilineal observed by Armitage (1984) in the yellow-bellied marmot. It may be that extinction and recolonization play more important roles in dispersal than we have yet recognized.

Genetic Predictions and Tests

The RFH and EFH differ in their predictions as to the amount of gene flow, the direction of gene flow, and the pathways by which genetic information travels. The EFH predicts a high degree of panmixia and a more or less random exchange of genetic information. The RFH predicts that gene flow is largely one-way: outward from established matrilineal, family groups, and demes occupying patches of favorable habitat. Significant amounts of inbreeding and genetic drift are anticipated within breeding units, and outbreeding is expected primarily in the founding of new groups, making founder effect a significant evolutionary factor in the maintenance of microspatial heterogeneity. Heterozygote frequencies are expected to decline within the life span of breeding units. It is expected that homozygotes will tend to be in excess in more permanent habitats and heterozygote frequency will be higher in temporary habitats.

Examples can be found that fit many of the above predictions, but because they are restricted to relatively few species their generality remains in doubt. The prediction of microspatial subdivision is supported by results reported in studies of marmots (Schwartz and Armitage, 1981), prairie dogs (Chesser, 1983), pocket gophers (Patton and Feder, 1978; Zimmerman and Gayden, 1981), *Peromyscus maniculatus* (Massey and Joule, 1981), *Microtus agrestis* (Semeonoff and Robertson, 1968), *M. californicus* (Bowen, 1982; Lidicker, 1985*b*), and in some house mouse populations (Anderson, 1964; Anderson et al., 1964; Petras, 1967*a*, 1967*b*, 1967*c*; Selander, 1970*a*; Singleton, 1983) but not in all (Justice, 1962). Myers (1974) found that clumping of electromorphs was ephemeral in feral *Mus* inhabiting barley fields plowed and planted at 3-year intervals.

Drift and founder effects have been invoked as explanations of heterogeneity among local populations in most of the examples cited in the preceding paragraph, offering considerable support for the RFH vision of gene flow. Reviewing the evidence for both rodents and mammalian populations in general, Cothran and Smith (1983) found a tendency for concordance between chromosomal and genic divergence, which they interpreted as evidence for population subdivision and the influence of drift and inbreeding. In his study of *Cynomys ludovicianus*, Chesser (1983) found greater differentiation among populations within regions than among regions, suggesting that drift, inbreeding, and founder effects operated within regions, while selection operated across regions.

Drift and inbreeding, predicted by the RFH, should theoretically lead to homozygote frequencies in excess of those predicted by the Hardy-Weinberg model for panmictic populations of more than a few hundred individuals. The EFH predicts high levels of heterozygosity as a result of outbreeding. Results have been variable where homozygote and heterozygote frequencies have been measured. Homozygote excess has been reported in *Cynomys ludovicianus* (Chesser, 1983), *Microtus agrestis* (Nygren, 1980), and *Thomomys bottae* (Patton and Feder, 1981). Some loci in *Marmota flaviventris* showed excess heterozygotes and others a slight excess of homozygotes (Schwartz and Armitage, 1981). Heterozygote excess has been characteristic of some *Mus* populations, but seasonal fluctuation and microspatial variation in heterozygote frequency indicate that both selection and social organization are involved (Berry and Peters, 1977). The evidence is compelling that many factors enter into determination of allelic and genotype frequencies (Berry and Peters, 1977; Peters, 1981; Schnell and Selander, 1981). It appears that some loci may be affected by drift, whereas selection may over-ride drift at other loci (e.g., Patton and Feder, 1981). Each locus, each sex, and each seasonal cohort, may be differently affected by these forces (e.g., see the results obtained by Baird and Birney, 1982*a*). The relative roles of

extrinsic factors determining gene flow also remain in doubt, and it is not clear whether immigration is made possible because social exclusion of immigrants is ineffective, or because social stability is frequently disrupted by environmental stresses or catastrophies. Conclusions have also varied with respect to the relative effect of physical barriers on gene exchange. Zimmerman and Gayden (1981) observed little evidence that a river interfered with gene exchange in *Geomys bursarius*, but Smith and Patton (1984) concluded that physical barriers were of major importance in *Thomomys bottae*.

The RFH does not, in the same sense as the EFH, require sex-linked or sex-limited alleles imparting a tendency to emigrate in order to explain sexual bias in emigratory tendency. Although residents are expected to vary in their behavior toward offspring and other kin, and in their aversive behavior toward non-kin, the RFH does not postulate polymorphism in the same sense as does the EFH.

As anticipated by the RFH, emigrants are unlikely to form a genetically distinctive subset of the sex-age cohort of the local population from which they originate, and emigrants from any given local population should be less variable genetically than transients passing through the area. Shifting patterns in emigration simply reflect the sex-specific tactics of residents in response to their residual reproductive values and to the varying environment. In this scenario, there seems to be little need to invoke a "phenotypic plasticity" hypothesis (Lidicker, 1985a) to explain changing patterns in emigration and immigration.

It is important for comparison of the two hypotheses that we assess the cost-benefit ratio of inbreeding in natural populations. Demonstration of adaptations that prevent strong inbreeding favors the EFH, but if the cost of incest is high, residents should avoid inbreeding under the RFH as well. Absence or ineffectiveness of obstacles to moderate inbreeding are more compatible with the RFH, and the RFH is therefore supportive of the concept of optimal levels of inbreeding (Bateson, 1983; Shields, 1982). Studies designed to determine the significance of inbreeding depression in nature will be of value in testing both the RFH and the concept of optimal breeding structure. Our traditional acceptance of the negative effects of inbreeding seems to me to be out of all proportion to the available data from populations in the field.

One of the more effective genetic tests for population structuring might be comparison of litter sizes or other measures of fitness in intrademe and interdeme crosses. If matrilineal or other population units are inbred, outbred matings should show heterosis; if populations are unstructured, no increase in fitness should be evident.

If female residents are replaced by their daughters more often than males are replaced by their sons, populations will be structured into matrilineal clusters upon which selection can act to produce co-adapted gene complexes. Long distance gene flow will be largely a male prerogative, but will be limited by restrictions on male ability to penetrate established groups. Maternal nepotism leading to retention of daughters and an occasional son in the natal range favors inbreeding. As visualized in the RFH, the major counters to inbreeding are male emigration, mortality, seasonal delay in maturation of female offspring, environmental instability, and the long-term instability and frequent extinction of social groups as described by Singleton (1983) and Pokki (1981). More succinctly, the RFH view is that inbreeding is limited primarily by low survivorship (Patton, 1985). The degree of inbreeding should be highest in habitats that are continuously occupied and lowest in habitats where extinction is frequent and colonization is seasonal or occasional.

In polyestrous seasonal breeders (for example, microtines and many populations of wild house mice) in continuously occupied habitat, the RFH predicts that the incidence of inbreeding will show a seasonal pattern, with outbreeding predominating at the beginning of the breeding season and inbreeding peaking as the females of the first litters become sexually mature and settle in relatively uncrowded natal habitat. If barriers to immigration break down between breeding seasons, each season will begin with outcrossing among inbred, overwintered young. Inbreeding depression in litter size may be eliminated in the first outbred mating (Lynch, 1977). The result of spring outbreeding could be heterosis, leading to larger litters at a time when new habitats

are available to be colonized and resources are rising toward peak availability. Anderson and Boonstra (1979) found that embryo counts in overwintered female voles in spring were larger than those from females of equal weight collected in summer and fall, a relationship that would be expected if spring matings were heterotic. Seasonal shift in mean heterozygosity of offspring suggestive of such a pattern has been noted in the field in several other studies (Baird and Birney, 1982a; Kuryshv and Khvorostyanskaya, 1983; Massey and Joule, 1981; Mihok et al., 1983; Myers, 1974; Petras and Topping, 1983). Although they did not carry out an analysis of the correlation of heterozygote deficiency with the progression of the breeding season, Gaines et al. (1978) noted that heterozygote deficiency increased as density increased.

Berry and Murphy (1970), Berry and Jakobson (1975), and Berry and Peters (1977) have reported data that clearly demonstrate seasonal shifts in selection, but also appear to show increase in heterozygote abundance over the breeding season, contradictory to the seasonal pattern suggested in the preceding paragraph. It is not clear whether their data truly reflect an increase in outbreeding as the breeding season progressed, or whether they reflect a sampling technique that failed to discriminate among residents and transient or peripheral individuals. Further investigations designed to answer that question would be helpful.

Does an annual cycle in inbreeding and outbreeding lend support to the ideas of Charnov and Finerty (1980) as to variation in relatedness during a multiannual cycle? I think not. If, as the RFH assumes, kin groups and matriline are highly impermeable during the breeding season, effects of multiannual trends in density will be buffered by population structuring, and the effect visualized by Charnov and Finerty seems unlikely.

That data on heterozygote frequency are difficult to interpret is illustrated by the study by Petras and Topping (1983). Two stochastic models were developed, based on characteristics of corn-crib house mouse populations in Ontario. The models were applied to loci coding for t-allele and hemoglobin (Hbb). Both models explained the observed frequencies, provided strong selection pressure favoring Hbb heterozygotes was incorporated in the high-gene-flow model. The authors concluded that the high-gene-flow model was more realistic, but this required three assumptions: gene flow must be high because populations were disrupted annually by the emptying of the corn cribs, there must be selection against +t phenotypes (the evidence is conflicting), and there must be selection in favor of Hbb heterozygotes.

Mihok et al. (1983) noted that gene pools in *Clethrionomys gapperi* appeared to be relatively stable and suggested that this might be explained either by restricted gene flow or by selection. Although small deme size predisposes local groups to initial genetic instability as a result of drift and founder effects, inbreeding and maternal nepotism favor sufficient stability so that favorable alleles and combinations will attain intermediate frequencies at which they will be sufficiently buffered against drift for selection to operate. As illustrated by the studies of Baker (1981b) and Myers (1974), immigration (introducing new alleles and increasing recombination) may be largely dependent on resident mortality and disruption of established groups by periodic disturbance. The RFH model envisages the exchange of genetic material as constrained by resident exclusion of immigrants and female nepotism directed primarily toward daughters. This form of genetic structuring is best documented among diurnal ground squirrels, but if the RFH is correct it should be demonstrable in many species of smaller nocturnal rodents as well. The life expectancy of matriline probably varies with the life history strategy followed by a population, with the degree of environmental stochasticism experienced, with habitat quality and with the relative fitness of the available alleles and allelic combinations.

If residents behave as postulated by the RFH, food supplements should reduce emigration and encourage inbreeding. Data showing that heterozygosity at the esterase-1 locus in *Peromyscus polionotus* was highest in areas where food was less abundant was interpreted by Smith et al. (1984) to suggest that scarcity of food selected for heterozygotes. The RFH explanation would be that food supplements increased inbreeding and lowered heterozygosity in the areas where supplemental food was provided.

Depending to some extent on the stability of demes, clines should be relatively narrow. One

TABLE 2.—Qualitative comparison of EFH and RFH predictions relative to behavior.

Behavior pattern	RFH expectation	RFH:EFH trend
Residents		
Male-male aggression	High	≥
Male-female aggression	Low	<
Female-female aggression	High	>
Probability of adult emigration	Low	<
Male territoriality	Variable	>
Female territoriality	High	>
Resident dominance over transients	High	>
Male nepotism	Low	≥
Female nepotism	High	>
Avoidance of incest by female	Moderate	<
Avoidance of incest by male	Low	<
Female range shifts at weaning	Occasional	>
Reciprocal altruism among neighbors	High	>
Resistance to immigration	High	>
Kin recognition by females	High	>
Kin recognition by males	Moderate	≥
Seasonal change in behavior toward young	High	>
Expulsion of young by males	High	>
Expulsion of young by females	Occasional	>
Restraint in contests with young	High	>
Retention of young as helpers	Occasional	>
Offspring		
Philopatry	High	>
Cohesive behavior among kin	High	>
Aggression toward transients	Moderate	>
Male emigration	High	>
Female emigration	Low	<
Ratio of male to female emigration	High	>
Male immigration	Low	<
Female immigration	Moderate	<
Ratio of male to female immigration	Low	<
Male dispersal	Low	<
Ratio of male to female dispersal	Moderate	<
Male dispersal distance	High	>
Female dispersal	Low	<
Female dispersal distance	Low	<
Defense of the natal range by offspring	Moderate	>
Avoidance of incest by females	Moderate	<
Avoidance of incest by males	Low	<

such abrupt cline has been investigated in detail in Danish house mouse populations (Selander et al., 1969a). Where demes are less stable than those of commensal house mice, clines should be broader.

Genetically based removal studies could be useful in testing the RFH. If immigration and mate choice are largely determined by resident females, removal of resident females should be more effective in increasing heterozygosity in a matriline or deme than removal of resident males. Experimental introduction of individuals carrying marker alleles and monitoring of their spread (e.g., Anderson et al., 1964; Baker, 1981b) is the ultimate test of immigration, an effective measure of the effect of structuring on gene flow, and thus an effective means of testing the validity of the RFH.

The observation that genetic individuality of local groups in *Microtus californicus* is high when density of the metapopulation is low, and that this micro-heterogeneity appears to decrease with increased density, has been taken to imply that panmixia increases with regional density

TABLE 3.—A qualitative comparison of EFH and RFH predictions relative to demography.

Demographic parameter	RFH expectation	RFH:EFH trend
Dispersion		
Random or overdispersed	Rare	<
Clumped	Common	>
Kin clusters	Common	>
Family groups	Common	>
Matrilineal groups	Common	>
Emigration		
Crude rate*		
Positively density dependent**	Rare	<
Negatively density dependent	Often	>
Seasonally dependent	Generally	>
Adult male rate		
Positively density dependent	Occasional	≤
Negatively density dependent	Occasional	>
Seasonally dependent	Generally	>
Adult female rate		
Positively density dependent	Rare	<
Negatively density dependent	Occasional	>
Seasonally dependent	Generally	>
Juvenile male rate		
Positively density dependent	Occasional	<
Negatively density dependent	Occasional	>
Seasonally dependent	Generally	>
Juvenile female rate		
Positively density dependent	Occasional	>
Negatively density dependent	Occasional	<
Seasonally dependent	Generally	>
Immigration		
Crude rate	Low	<
Adult male rate	Low	<
Adult female rate	Low	<
Juvenile male rate	Low to moderate	<
Juvenile female rate	Moderate	>
Fluctuations in density		
Intrademe (local) stability	High	>
Metapopulation (regional) stability	Moderate	≤

* Proportion of population emigrating irrespective of sex or age.

** Increases with number of individuals/unit area as measured on a conventional trapping grid.

(Bowen, 1982; Lidicker, 1985*b*). Because the analysis compared grids, rather than matrilineal, the data collected by Bowen (1982) appear to be subject to the alternative interpretation that the decline in heterogeneity was merely due to the occupation of interstitial habitat by cohorts of young, rather than an actual increase in outbreeding. The evidence that resistance to immigration increases with density (Hestbeck, 1986; Wolff, 1985*a*) favors the view that breeding structure was unaffected, but either interpretation is compatible with the RFH.

The EFH predicts that populations will be integrated by gene flow into relatively large units with common genetic and demographic characteristics. Such units would tend toward a regional adaptive compromise, minimal ecotypic or local adaptation, and a relatively high genetic inertia in the face of environmental change. The RFH differs in respect to each of the above characteristics, and leads to the kind of evolutionary model outlined by Patton (1985) for *Thomomys*. Regional metapopulations would be composed of many small, more locally-adapted, and genetically independent groups. In the event of sudden environmental changes some groups would go extinct and be replaced by colonists exported from other groups in which gene combinations chanced to be preadapted. Interdemic selection, in this form, could bring about rapid evolutionary

TABLE 4.—A qualitative comparison of EFH and RFH predictions relative to genetic structure and evolutionary processes.

Genetic/evolutionary parameter	RFH expectation	RFH:EFH trend
Breeding system		
Inbreeding		
In general	Common	>
Seasonal variation	General	>
Outbreeding		
In general	Rare	<
Seasonal variation	General	>
The genome		
Coadaptation in the genome	General	>
Neutral alleles	Common	>
Heterozygote frequency	Moderate	<
Genetic structure in populations		
Extensive panmixia	Unusual	<
Local clustering	General	>
Kin groups and matriline	General	>
Genetic neighborhood size	Small	<
Cline width	Narrow	<
Processes changing the gene pool		
Regional selection	General	=
Local adaptation	General	>
Founder effects	General	>
Drift	Common	>
Kin selection	Common	>
Interdemic selection	Occasional	>

shifts of the type visualized for a self-fertilizing snail by Selander and Hudson (1976) and for rodents by Shvarts (1977). Sequences of such rapid genetic reorganizations in the metapopulation could play significant roles in the swift adaptive radiations that appear to characterize rodents and in the genesis of "punctuations" in evolutionary equilibria.

Krohne and Baccus (1985) suggested that demographic units, defined by demographic homogeneity (similar sex and age structure and synchronous patterns of fluctuation, extinction, etc.), are independent of genetic units (demes). I believe this suggestion should be rejected. As Krohne and Baccus recognize, common demographic patterns are likely to result from common seasonal changes and habitat characteristics. Demographic similarity of this sort does not reflect demographic unity, merely operation of similar external pressures on groups that are in fact independent both genetically and demographically.

The genetic landscape of a species as visualized by the RFH is a little like a restless stream with transient wavelets erupting in an irregular pattern. As it conforms to the surrounding environment it can break at times into a braided pattern of independent streamlets. Some streamlets dissipate in the gravel and disappear, whereas others persist and expand. Most rejoin the main stream, but occasionally a streamlet may drop into a new channel.

Innovation is favored in a model that incorporates founder effects and drift. Coupled with resistance to immigration it allows scope for both individual and collective (kin and interdemic) selection in generating local adaptation. The RFH predicts a genetic and evolutionary landscape that is dynamic. Individual fitness remains a dominant evolutionary force, but because regional metapopulations are highly subdivided, new gene combinations may be preserved and persist long enough to be tested by selection; this advantage of inbreeding is maintained without loss of individual variation. Kin (and even interdeme) selection, founder effects, and drift may become effective agents of change. The pattern reflects a reasonable life history strategy for rodent environments that are spatially and temporally coarse grained and where environmental change

is stochastic. For the metapopulations, such a landscape provides a kind of serendipity, making it probable that adaptive gene combinations will be available in replicate to meet whatever environmental variations occur (Anderson, 1978).

Summary

The RFH postulates control of dispersal by resident behaviors. The EFH postulates control of dispersal by the genes of potential emigrants. My purpose in this chapter has been to stimulate the imagination of future investigators by suggesting the nature and design of investigations that challenge the dichotomy I have proposed. Tables 2, 3, and 4 further summarize the differences between the EFH and RFH. The intention in each of these tables is to indicate the relative trend or emphasis for a series of observable qualities and to imply that although no single test may firmly establish one hypothesis or the other, the two differ in emphasis over a wide range of behavioral, demographic, and genetic topics. The sum of the trends in favor of one or the other, over the tables as a whole, may be the best indication of the power of the competing views.

A CONCLUDING STATEMENT

I believe that the hypothesis that emigration evolved through a gain in fitness to emigrants is weak on many counts. In its place I have proposed an alternative that seems to me to be logically coherent and to be supported by a wide range of observations taken from the literature. Nevertheless there is much to be done before one or the other hypothesis can be fully falsified and the other tentatively accepted. I see it as particularly important that the elements in the central dogma of the RFH (site tenacity, resident dominance, maternal nepotism, offspring philopatry, optimization of relatedness in mate choice) be fully tested.

The RFH alternative has far-reaching behavioral, demographic, and genetic implications. I have tried to suggest predictions that should follow if resident behavior has been selected so as to maximize fitness through manipulation of young by parents in accordance with the dictates of inclusive fitness and kin selection, and if young, in their turn, are basically philopatric, but respond to parental strategies in ways that have been selected according to the same principles. One cannot doubt that emigration can be induced by a variety of proximal mechanisms (Dobson and Jones, 1985), but this need not exclude the possibility that evolution has generated a strategy which characterizes groups with a broad range of life histories. The RFH predicts that emigration will vary with seasonal and other conditions, and I believe it obviates the need for such concepts as pre-saturation dispersal and phenotypic plasticity as envisaged by Lidicker (1975, 1985a).

In the area of demography, the RFH emphasizes the responses of female residents to the resource demands of gestation and lactation as a factor in emigration rates and regulation of local density, and de-emphasizes male aggression as a factor in limiting population growth. It predicts that the probability that a potential emigrant will depart from the natal site is almost entirely independent of density. It requires that analyses of emigration be specific to sex, age, degree of genetic relationship, season, season of birth, residual reproductive value, and resource availability.

The RFH is an hypothesis attractive to those who appreciate environmental heterogeneity and the role of population structuring in buffering population dynamics and limiting gene flow. Dispersal, as visualized by the RFH, takes place in habitats that are patchy, with favorable patches supporting discrete, predominantly matrilineal groups of closely related individuals. Less favorable habitats may be occupied seasonally or intermittently, and may be characterized by outbreeding. In this respect the RFH relies on models of habitat and population structure similar to those recently envisioned by a number of investigators (Anderson, 1970, 1980; Hansson, 1977; Naumov, 1972; Smith et al., 1978; Stenseth, 1983). In temporal terms it also incorporates the notion that distinctive seasonal generations, as described by Anderson (1970), Martinet (1967), Reichstein (1964), and Schwarz et al. (1964), are significant in the demographic and evolutionary dynamics of seasonally breeding polyestrous species. In a general sense, the RFH supports the supposition of Gaines (1985) that changes in the composition of gene pools are most likely to be consequences, rather than causes, of demographic patterns.

The RFH eliminates the need to demonstrate "dispersal genotypes." It predicts that emigrants will be subject to especially intense and variable selective pressures. Although the RFH is based on individual selection, it suggests trends toward demic population structuring that may be sufficient to require that selection interact with chance effects in a dynamic equilibrium. In populations so structured, regional demography and evolution incorporate both the sums and interactions of local events. The evolutionary process is open to the occasional or even frequent operation of founder effects followed by inbreeding under local selective pressure, speeding generation of a diversity of locally adapted demes. Within limits set by the degree to which

emigrants outbreed, differential success in survival, expansion, and dissemination of such local groups could couple individual, kin, and interdeme selection as defined by Wilson (1973) in ways that could significantly influence the speed and direction of evolutionary change.

The Resident Fitness Hypothesis expands and extends to rodents in general an analysis initially applied specifically to microtines (Anderson, 1980). It has been foreshadowed in numerous ways by the theories, observations, and experiments of a host of investigators. I am indebted to all of them. As developed here, I believe the hypothesis offers a new, significant, testable, and predictive model that future studies of behavior, demography, and genetics in rodent populations can explore.

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