

AGE-SPECIFIC DISPERSAL STRATEGIES IN ITEROPAROUS SPECIES:
WHO LEAVES WHEN?

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Received May 12, 1981; August 3, 1982

ABSTRACT: Optimal dispersal age was determined by maximizing the expected fitness gain of emigrating individuals versus those staying at home. When fitness is estimated by reproductive value, age-specific dispersal depends only upon the cost/benefit analysis of expected reproductive value of dispersers relative to non-dispersers. Dispersal costs for pre-reproductives are mainly in terms of reduced survival, whereas for reproductives there are both survival and fecundity costs. Consequently, when dispersal is adaptive for all age classes, young individuals gain the most by dispersal, and should disperse even when older age classes should not. When an estimate of inclusive fitness is used in the cost/benefit analysis however, young individuals may emigrate to maximize individual fitness, or may be driven out by parents attempting to maximize their inclusive fitness. In the latter case, a dichotomy of age-specific dispersal strategies occurs because parents eventually reach an age when their progeny's contribution to inclusive fitness is greater than their own. Lastly, in species where reproductive value is a saw-toothed function with age, dispersal strategies of different age classes may follow an annual cycle. An explicit test of the model was not possible, nevertheless, dispersal data from field studies of small mammals are consistent with predictions of the cost/benefit analysis.

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INTRODUCTION

The age-specific expectation of present plus future offspring, reproductive value, is a good estimate of fitness (Fisher, 1930). Because this estimate is calculated from age-specific fecundity and survival schedules, reproductive value plotted against age has a distribution of scores which reflects jointly the survival and fecundity probabilities of various age classes.

This means that any age-specific life history strategy which is related to reproduction or survival can be evaluated by its effect on reproductive value. The problem given a particular environment, is to determine the optimal age-specific strategy which maximizes lifetime reproduction, or alternatively, the optimal strategy which maximizes reproductive value for a particular age class. This kind of cost/benefit analysis has been used to model such adaptive strategies as the timing and number of reproductions, clutch size, longevity, age-specific reproductive effort, habitat selection and population dynamics (Charnov and Krebs, 1973; Charnov and Schaffer, 1973; Cody, 1966; Cohen, 1966, 1967; Cole, 1954; Gadgil and Bossert, 1970; Levins, 1968; MacArthur and Wilson, 1967; Rosenzweig, 1974; Schaffer, 1974 a,b; Schaffer and Rosenzweig, 1977; Schaffer and Tamarin, 1973; Stearns, 1976).

Dispersal is one attribute which has not received a detailed age-specific cost/benefit fitness analysis. Assuming that dispersal is adaptive to individuals (Lidicker, 1962, 1975; Murray, 1967), what age-specific patterns of dispersal maximize reproductive success?

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Evolutionary Theory 6: 53-65 (September, 1982)

The editors thank Mark Boyce and another referee for help in evaluating this paper.

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AN EVOLUTIONARY MODEL

An individual should disperse whenever its expected reproductive value through dispersal is greater than its expected reproductive value of not dispersing plus any dispersal cost. This difference is called the dispersal threshold. If dispersal is instantaneous and without cost, the dispersal decision is trivial. Dispersal is selectively advantageous whenever

$$(1) \quad V_{xD} / V_{xH} > 1$$

where V_{xD} is the expected reproductive value of the individual aged x after dispersal to location D , and V_{xH} is the expected value by not dispersing from location H .

All dispersal movements will take time. Now the dispersal decision will have to evaluate reproductive value in both D and H at the conclusion of movement, and also adjust the threshold for any cost. Dispersal is advantageous whenever

$$(2) \quad V_{(x+t)D} / (V_{(x+t)H} + \Delta V_t) > 1$$

where t is the duration of dispersal, and $\Delta V_t = V_{xH} - V_{(x+t)H} > 0$; else $\Delta V_t = 0$ represents the positive difference in reproductive value of dispersing individuals relative to homebodies caused by reduced survival and lost opportunities for reproduction during t .

Other dispersal costs such as mortality risks or weakened physical condition associated with dispersal can be incorporated as age-specific survival and fecundity probabilities in the calculation of $V_{(x+t)D}$. To predict age-specific dispersal strategies when these costs are negligible, we need only to know the general form of reproductive value against age in the two habitats.

This comparison will be easiest for similar populations where fecundity and survival are monotonic functions of age. As shown in Figure 1A, when t is less than the difference between the age at independence and the age at first reproduction, dispersal is equally advantageous for individuals which arrive at D at or before the age at first reproduction. This corresponds to but is slightly different from, MacArthur and Wilson's (1967) similar proof that the best colonists are those which arrive at D when reproductive value is maximal. Even younger animals will be selectively superior dispersers if pre-reproductive survival is greater in D than in H . Dependent upon the relationship of t to the difference in reproductive value between D and H , older animals too may gain by dispersal, but they will not gain as much as younger ones (Fig. 1B). This is simply because dispersal cost for young animals is only in terms of survival, whereas for older individuals, dispersal cost also includes lost fecundity during potential reproductive episodes.

These differences in dispersal cost for pre-reproductive and reproductive individuals can be shown more explicitly in terms of residual reproductive value, V_x^* , where for a constant population

$$(3) \quad V_x^* = (l_{x+1} / l_x) V_{x+1}$$

and l_x and l_{x+1} are the age-specific survival probabilities at ages x and $x+1$ respectively (Pianka and Parker, 1975; Williams, 1966). Dispersal cost for pre-reproductives is a survival risk during t , and therefore the dispersal decision of pre-reproductives will depend only upon V_{x+t} and the survival probabilities until age $x+1$. Dispersal of pre-reproductives is selectively advantageous at age x only when

$$(4) \quad ((l_{x+t})_D / l_x) (V_{x+t})_D > ((l_{x+t})_H / l_x) (V_{x+t})_H$$

where the left term is the expected residual reproductive value gained through dispersal to D ; the term on the right is the expected residual reproductive value by remaining at home in H , and $(l_{x+t})_D$ is the probability of survival to $x+t$ given dispersal to D .

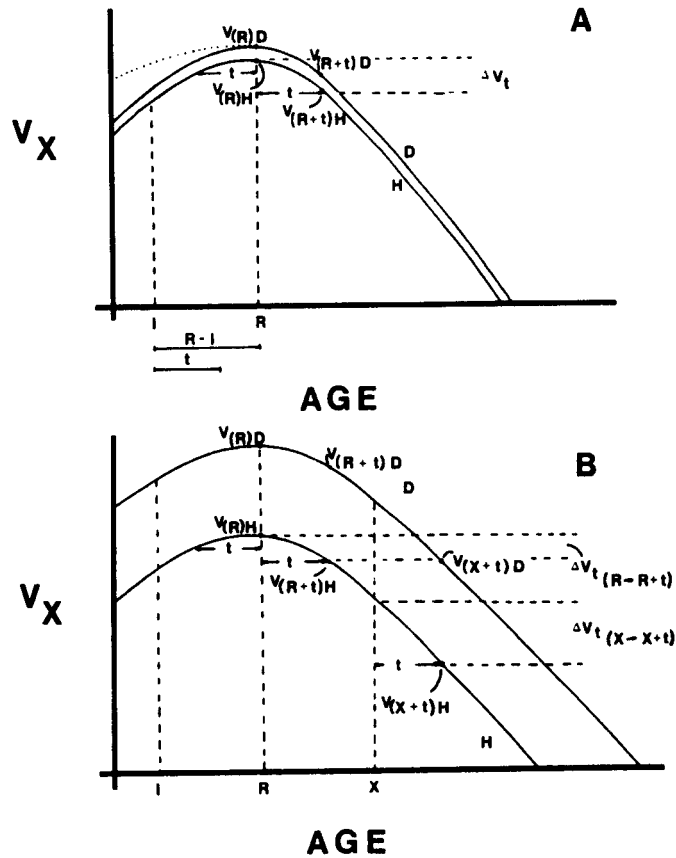


Figure 1. A. Dispersal strategies of pre-reproductive and reproductive age classes when fitness rewards in D and H are approximately equal. I is the age at independence, R, the age at first reproduction which here corresponds with maximal reproductive value. First consider the right hand side of the figure. Reproductive individuals dispersing at R or any later period are at a disadvantage because $V(R+t)_D / (V(R+t)_H + \Delta V_t) < 1$ in all cases. Now, examine the left hand side. Pre-reproductives should disperse because $V(R)_D > V(R)_H$. Note that on the left side, ΔV_t is defined as zero because there is no loss in reproductive value of dispersing individuals relative to homebodies. The decision for pre-reproductives where $t < R-I$, is to maximize $V(x+t)_D - V(x+t)_H$. Consequently, if pre-reproductive reproductive value is asymmetrically higher in D than in H (dotted line), dispersal is maximally advantageous at that first age which maximizes the difference between D and H (age I in the example). Conversely, pre-reproductive dispersal age should be postponed if survival in D is initially lower than in H. B. Dispersal strategies of different age classes when expected fitness in D is much greater than in H, and the dispersal threshold is surpassed by all age classes. First consider dispersal at age X. Dispersal is advantageous because $V(X+t)_D > V(X+t)_H + \Delta V_t(X \rightarrow X+t)$. Now consider dispersal at age R. Again, dispersal is advantageous because $V(R+t)_D > V(R+t)_H + \Delta V_t(R \rightarrow R+t)$. The difference between D and H is constant, but because $\Delta V_t(X \rightarrow X+t) \gg \Delta V_t(R \rightarrow R+t)$, dispersal is of more benefit to younger individuals. Now examine the left side, where $V(R)_D > V(R)_H$, and because $\Delta V_t = 0$, pre-reproductives gain more by dispersal than any other age group. Age-specific dispersal depends upon the shape of V_x with age, t, and the difference between D and H.

However, the dispersal decision of reproductive individuals depends upon lost reproductive value during dispersal (both survival and fecundity costs) as well as residual reproductive value at the end of t . Again for simplicity, assuming a constant population with discrete age classes, reproductive value is approximated by the relation

$$(5) \quad V_x = \sum_{t=x}^{\infty} (l_t/l_x) m_t$$

where m_t is the age-specific fecundity at time t (Pianka and Parker, 1975). Part of the dispersal cost for reproductives is lost reproduction during t . This loss can be estimated in common terms of reproductive value as

$$(6) \quad \sum_{s=x}^t (l_s/l_x) m_s$$

where s is the discrete age interval of reproduction, and t is again, the duration of dispersal. The remaining dispersal cost as for pre-reproductives is in terms of reduced survival. The cost/benefit analysis for reproductive individuals in this example predicts that the dispersal threshold occurs when

$$(7) \quad ((l_{x+t})_D/l_x) (V_{x+t})_D > ((l_{x+t})_H/l_x) (V_{x+t})_H + \sum_{s=x}^t (l_s/l_x) m_s.$$

Consequently, if all age classes face similar mortality risks during dispersal, dispersal is much less expensive for non-reproductive individuals (compare inequality 7 with inequality 4). Non-reproductives can accept a greater cost, and this may result in a dichotomy of dispersal strategies where non-reproductives emigrate farther and over greater periods of time than do reproductives. Note however, that when $t \leq s$, dispersal cost is equivalent for all age classes which then share the same dispersal strategy. The magnitude of t would seem to depend upon the spatial and temporal mosaic of potentially colonizable habitats.

But using reproductive value as the sole criterion for dispersal decisions is misleading because reproductive value may not be a good estimate of inclusive fitness (Hamilton, 1964). An appropriate estimator is the reproductive value of the parent plus the summed reproductive values of offspring and close relatives, all discounted for their respective contributions to parental fitness. Parental fitness for sexually reproducing organisms with no inbreeding can be estimated as

$$(8) \quad W_{PT} = V_{Tx} + V_{TP}$$

where W_{PT} is parental fitness at time T , V_{Tx} is the reproductive value of the parent aged x at T , and V_{TP} is the summed reproductive values of variably aged progeny at T for each F_1 through F_n generation, and each generation is weighted by its expected genetic contribution to W_{PT} . The right hand term can be expanded;

$$(9) \quad \begin{aligned} V_{TP} = & 1/2 (V_{I_{ToF_1}} (l_I) + V_{II_{TpF_1}} (l_{II}) + \dots V_{i_{TqF_1}} (l_i)) \\ & + (1/2)^2 (V_{I_{TrF_2}} (l_I) + V_{II_{TuF_2}} (l_{II}) + \dots V_{i_{TvF_2}} (l_i)) \\ & + \dots (1/2)^n (V_{I_{TWF_n}} (l_I) + V_{II_{TyF_n}} (l_{II}) + \dots V_{i_{TzF_n}} (l_i)) \end{aligned}$$

where Roman numerals designate different clutches, within generations, of (1) offspring aged o through z at T , and $(1/2)^n$ is the weighting term for genetic relatedness of each F_n generation to the parental individual.

As the parent ages, less and less of W_{PT} is contributed by the parent's own reproductive value, and successively more is contributed by progeny. For the discussion of dispersal strategies I am interested only in those individuals

remaining with the parent in H. Equation (8) becomes

$$(10) \quad W_{PT} = V_{Tx} + V_{TP}(1-d)$$

where d is the weighted proportion of F_1 through F_n progeny which have already dispersed.

I first assume that fitness rewards in D and H are equivalent, except that H is colonized and D is not, and that both dispersing and not dispersing have costs. The cost of not dispersing is represented by intraspecific density effects on fitness, ΔV_I . Now dispersal cost (ΔV_t) is related to the distance, duration and risks of dispersal; the cost of not dispersing is related to increased resource competition, increased susceptibility to disease, predators, parasites and other density-dependent mortality and fecundity vectors, and again have costs for both individuals and their relatives. When the expected fitness in D is the same as that in H and $\Delta V_I > \Delta V_t$ dispersal is selectively advantageous. But who gains the most from dispersal?

Different age classes will have different dispersal and non-dispersal costs. For example, very young and very old individuals may be more susceptible to predation (Morse, 1980 p. 83), especially in unfamiliar environments during dispersal. For these age classes dispersal cost is high. But the relative age-specific costs of not dispersing may be very different. Old animals in familiar surroundings may be relatively secure from predation and negative intraspecific influences, whereas young inexperienced animals again may be at high risk. For species with reproductive value functions such as those in Figure 1, old animals have much less to lose reproductively by remaining in H than do younger animals at or near their maximal reproductive value. For young animals, $\Delta V_I \approx \Delta V_t$, whereas for older animals, $\Delta V_I \ll \Delta V_t$. Again, most dispersers should be young individuals.

Where the main dispersal cost is time lost from breeding, dispersal may be much less expensive for young than for old animals. In this example, ΔV_I can be represented as a general reduction of reproductive value in H, and the problem of identifying the dispersal threshold is the same as for the case where the expected fitness in D is greater than in H (Fig. 2).

This view is too simple however, because parental reproductive success (W_{PT}) is both a function of V_{Tx} and $V_{TP}(1-d)$. For old animals, V_{Tx} is small, but $V_{TP}(1-d)$ may be large. As long as

$$(11) \quad V_{Tx} > V_{TP}(1-d)$$

most of the parent's expected reproductive success is due to its own reproductive value and the parent should be more concerned about its own survival and fecundity than that of its offspring. But when $V_{Tx} < V_{TP}(1-d)$, then because descendants contribute more to the parent's expected reproductive success than the parent itself, descendants should receive priority. This means that for the parent, ΔV_I increases, because by remaining, the parent contributes to intraspecific pressures on its descendants. And if dispersal costs are small, then $\Delta V_I \approx \Delta V_t$, for both young and old animals, and both should emigrate.

Accordingly, the age of parental dispersal for parents not providing parental care should be at that first age when $V_{Tx} < V_{TP}(1-d)$, (Fig. 3).

Parents capitalizing on size, strength and experience may forcibly eject offspring, thus exhibiting some control over d , and concomitantly, their own age at dispersal. When the fitness in D is the same or greater than that in H, and dispersal costs are small, this will only tend to reinforce emigration by young which gain by dispersal in any event. But when the fitness in D is less than in H, or dispersal costs are high ($\Delta V_I < \Delta V_t$), this form of parental behavior results in a conflict of interest between parents and progeny such as that discussed by Trivers

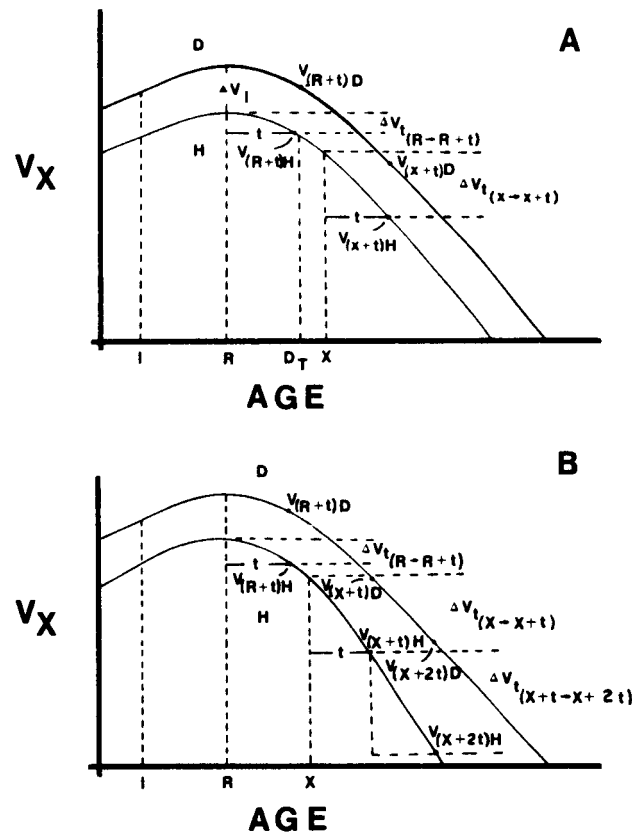


Figure 2. A. Age-specific dispersal strategies for individuals emigrating to D from H when expected fitness in D equals that in H, and intraspecific costs of not dispersing (ΔV_I) are the same for all age classes, so that H is perceived as less suitable than D. Young individuals gain by dispersal (eg., $V_{(R+t)D} > V_{(R+t)H} + \Delta V_t(R \rightarrow R+t)$; ($\Delta V_I > \Delta V_t$)), but older individuals do not (eg., $V_{(X+t)D} < V_{(X+t)H} + \Delta V_t(X \rightarrow X+t)$; ($\Delta V_I < \Delta V_t$)). In this example, the dispersal threshold (D_T) occurs at age $R+t$ because $V_{(R+2t)D} = V_{(R+2t)H} + \Delta V_t(R+t \rightarrow R+2t)$; $\Delta V_I = \Delta V_t$. Again dispersal depends upon age, t , and the difference between D and H, here represented by ΔV_I . B. Age-specific dispersal strategies as in 2A, except that now ΔV_I varies with age. For example, aggressive and territorial individuals could be more susceptible to intraspecific crowding than younger more socially tolerant individuals. This age-dependent effect is incorporated as an asymmetrical perception of reproductive value with age in H. In this example, because ΔV_I increases with age, pre-reproductive and older reproductives who disperse are at selective advantages (ie., dispersal at age R and age $X+t$ is advantageous because $\Delta V_I > \Delta V_t$, but for intermediate aged individuals at X , dispersal is not selectively advantageous because $\Delta V_I < \Delta V_t$). Age-specific variation in dispersal risks can be modelled similarly, or by varying t with age.

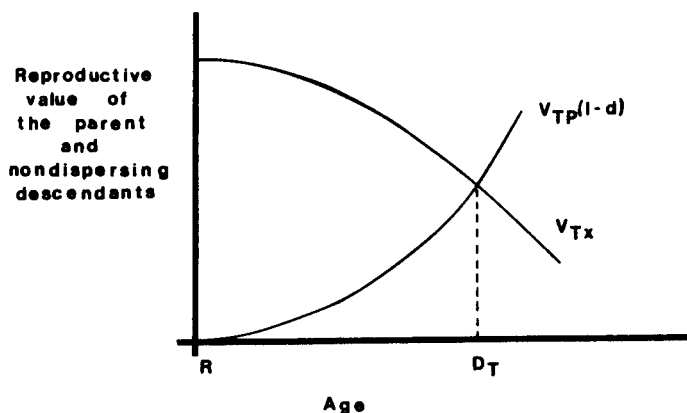


Figure 3. One example of the dispersal threshold (D_T) for parental individuals where reproductive value against age is a monotonic function. At D_T , the parent's reproductive value and the weighted sum of the reproductive values of descendants are equal; to the right, descendants are worth more to parental fitness than the parent itself. The optimal age of parental dispersal is that first age to the right of D_T .

(1974). Because of the size, strength and experience asymmetry in parent-offspring conflict (Alexander, 1974), parents gain the most by driving off early parity offspring as soon as the conflict begins. That is, when offspring are in the most inferior position to challenge parental authority. Because parent-offspring conflict decreases with parity (Trivers, 1974), offspring dispersal age should increase with subsequent parental reproductive episodes. The limits are the ejection of uniparous offspring at the inception of conflict, and total tolerance of offspring from the terminal reproduction. However, it will be to the advantage of offspring to eject the parent when $V_{Tx} < V_{Tp}(1-d)$. In general, because the parent in this case controls d , parental dispersal should not occur until V_{Tx} is less than one half the summed reproductive values of current offspring,

$$(12) \quad V_{Tx} < 1/2 \sum_{i=1}^n (V_{i,Tq}) (1_i).$$

A particularly interesting dispersal strategy may exist in species where survival and fecundity probabilities are complex functions of age. For example, in multiparous lizards, V_x and V_x^* are high early in the breeding season when the probability of producing additional clutches is also high, but drop precipitously during breeding, only to rise to another high level during the subsequent breeding period when the probability of multiple clutches is again high (Pianka and Parker, 1975). Where some young are capable of breeding in the season of birth, or where residual reproductive value annually drops below the net reproductive rate ($R_0 = \sum l_x m_x$), the age at dispersal and parent-offspring relations with parity may follow an annual cycle. The parent gains by re-establishing itself in a new area every year (Fig. 4). This strategy depends on the relation between the positive and negative slopes of the saw-toothed V_x^* functions, on their respective maxima and minima, and on the interval

between subsequent reproductions. It can be shown that whenever the residual reproductive value of the parent at the end of the breeding season is greater than the net reproductive rate (assuming stable population size), annual cycles of dispersal strategy are possible only if the positive slope is steeper than the decline in parental residual reproductive value. Otherwise, the parental residual reproductive value function and that of the offspring of the previous litter never intersect until the parent's final reproductive season.

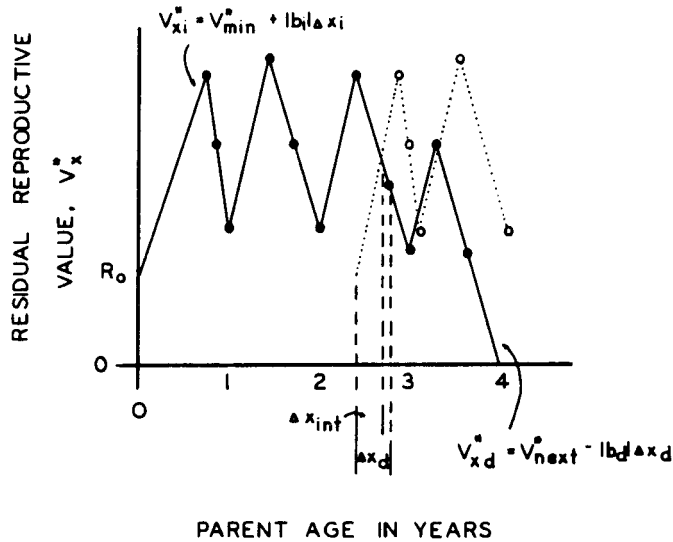


Figure 4. Saw-toothed residual reproductive value versus age plots for the iteroparous parent (solid line) and third year (7th reproduction) offspring (dotted line). Closed circles represent reproductions for the parent and open circles represent those of the offspring. Other symbols are the same as those in the text. Here, $|b_i| > |b_d|$, and for third year offspring $\Delta x_{int} < \Delta x_d; (V_{x_{int}}^* > V_{next}^*)$. The offspring curve intersects the parent curve prior to a subsequent reproduction. In asexual species, the parent should disperse because more of its residual reproductive value is due to the single offspring than to itself. For adult dispersal to be advantageous in sexual species, $V_{x_{int}}^* > 2V_{next}^*$, or when multiple offspring compete with the parent, their summed reproductive values exceed V_{next}^* (analogous to inequality 12). The periodicity of the cyclical dispersal strategy depends on how frequently during the lifetime of the parent the conditions for these V_x^* intercepts are upheld. In this example, if all offspring curves were drawn, annual dispersal strategies are possible. For empirical V_x^* curves see Pianka and Parker (1975).

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In the simplest case, assume these saw-toothed functions to be linear, then

$$(13) \quad V_{x_i}^* = V_{min}^* + |b_i| \Delta x_i \quad \text{and}$$

$$(14) \quad V_{x_d}^* = V_{next}^* - |b_d| \Delta x_d$$

where $V_{x_i}^*$ is the age-specific residual reproductive value during increase, $V_{x_d}^*$ is the residual reproductive value during decrease, V_{min}^* is the residual reproductive

value at a minimum (analogous to the V_x^* intercept, and equivalent at birth to the net reproductive rate R_0), V_{next}^* is the level of parental residual reproductive value at the next reproductive episode, $|b_i|$ is the absolute value of the slope of V_x^* with age during increase, $|b_d|$ is the corresponding value during decrease, Δx_i is the range of x during increase where x is age, and Δx_d is the range of x between subsequent reproductions during decrease.

For offspring, $V_{1_i}^*$ always starts at R_0 , and

$$(15) \quad V_{1_i}^* = R_0 + |b_i| \Delta x_i.$$

If the offspring residual reproductive value increasing function is to intersect the decreasing parental function prior to the subsequent reproduction, then

$$(16) \quad R_0 + |b_i| \Delta x_i > V_{next}^* - |b_d| \Delta x_d.$$

Where the slopes of the increase and decrease functions are the same, intersection can only occur when $R_0 > V_{next}^*$ and we conclude that whenever $R_0 < V_{next}^*$ and the curves intersect, then $|b_i| > |b_d|$ and furthermore $\Delta x_{int} < \Delta x_d$ to obtain annual cycles of dispersal strategy, where Δx_{int} is the range of x between birth and intersection. The possible outcome of an annual cycle depends on R_0 , V_{next}^* , the slopes of the increase and decrease functions, and the interval between subsequent reproductions.

AN ADMONITION

As noted by Pianka and Parker (1975), there are serious limitations to demographic models which assume all individuals equivalent and that age-specific mortality and fecundity are invariant. This hidden variation could conceivably mask any overall age-specific pattern of dispersal. My implicit assumption is that individual variation is substantially less than age-specific differences, and that population averages of life history traits are representative of individual expectations. I further assume that population dynamics do not significantly alter the predictions of the dispersal model. For the sake of parsimony, it would seem appropriate to first test for age-specific dispersal patterns predicted by a simple model based on population averages, before attempting the more difficult to impossible tests of models of dynamic populations with the assumption that individual variation in life history is more important than mean expectation.

DISCUSSION

This life history cost/benefit analysis assumes that dispersal is adaptive to individuals, and consequently the age-specific dispersal strategy will be that strategy which maximizes individual reproductive success. Evaluating the model requires reliable and complete life tables as well as age-specific dispersal data. Unfortunately, most life history studies are unable to differentiate between mortality and emigration (Krebs, 1978), and I am unaware of an available data set which is suitable for an explicit test of this model. There are several reports in the literature on small mammals however, where the age of known dispersers has been determined. These sorts of data are sufficient for preliminary tests because the model makes general predictions about the expected age at dispersal.

Oversimplifying, the model predicts that most dispersers should be either young animals which have not yet attained maximal reproductive value, or much older individuals whose probabilities of future reproductions are very low. On average, in all but declining populations, the youngest age class has the largest number of individual members, and often times orders of magnitude more members than older reproductive age classes. Accordingly, by sheer numbers alone, most dispersers should be young animals. Do the available data support this prediction?

Is dispersal selectively advantageous to individuals?

Most studies of dispersal in small rodents have shown that dispersing animals are characteristically younger and weigh less than residents (Gaines and McClenaghan, 1980; Krebs and Myers, 1974). Also, both pre-reproductive and reproductive individuals disperse. It would be very interesting to know more accurately the respective ages of these dispersers to see if they truly represent examples of the dichotomy in dispersal strategies predicted in this paper. Unfortunately, most dispersal studies on rodents have been designed to test proximate models of dispersal such as those reviewed by Gaines and McClenaghan (1980), or theories of population cycles, rather than to test an evolutionary model such as I propose here.

More complete data are available from a variety of studies on sciurid rodents. Since the purpose of many of these has been to test proximate models of dispersal, I evaluate the fit of data to both proximate and evolutionary explanations. The largest single class of dispersers in sciurids is that of pre-reproductive males (Armitage and Downhower, 1974). Because many sciurids are territorial and have polygynous mating systems, the usual explanation for young male emigration is that these animals are driven off by aggressive encounters with adults. Because juvenile females have a low probability of dispersal, parental males may eject male offspring, reducing competition for copulations, and increasing the likelihood of father-daughter matings (P.K. Anderson, pers. comm.). In California ground squirrels, Spermophilus beecheyi, most dispersing individuals are pre-reproductive males, however they continue to emigrate even after adult males have begun estivating (Dobson, 1979). Dobson (1979) suggested that such a pattern is inconsistent with a competition for mates hypothesis, and that high rates of juvenile male dispersal may function as an outcrossing mechanism. But such an explanation would seem to be at odds with the increased probability of consanguineous matings between fathers and non-dispersing daughters. Perhaps the high rate of juvenile male dispersal, even in the absence of adult males, is less costly than estivating at or near the natal site, and facing aggressive interactions from larger and more experienced fathers at the beginning of the next breeding season. Dunford (1977a) too, noted a high proportion of male dispersal in related round-tailed ground squirrels, Spermophilus tereticaudus. This dispersal was not related to density, food availability or aggression (Dunford, 1977a). Female mate choice could explain this sexual asymmetry in dispersal. If females prefer large adult males, then young males who disperse away from such competitors may be at a selective advantage. Bekoff (1977) provided yet another explanation. He proposed that dispersers are those individuals which fail to establish permanent social ties with their parental group. Accordingly, aggression is not necessary to stimulate dispersal. In each of these cases, it would be interesting to know if the probability of juvenile male dispersal decreases with parental male age as predicted by the evolutionary model.

Fewer female sciurids disperse than males (Armitage and Downhower, 1974), and some female emigrants are adults. In black-tailed prairie dogs, Cynomys ludovicianus, for example, adult females disperse to new territorial units leaving their daughters behind (King, 1955). Dispersing adult females may be at a selective advantage for two reasons. First, by leaving, they reduce intraspecific density pressures on their daughters. Second, by dispersing, they should have a higher probability of consanguineous matings with sons. Daughters gain by not dispersing because of high probabilities of mating with their fathers.

Why the asymmetry in strategies between sexes? The answer may depend upon predation which is a major population vector in these animals, and which could be responsible for their advanced social organization (Carl, 1971; King, 1955). Many sciurids form matrilineal social groups (Wilson, 1975), and related females may assist one another in the detection of predators (Dunford, 1977b; Sherman, 1977).

Mother-daughter co-operation probably contributes to parental fitness, and parental females which drive off young could be more susceptible to predation. Male-male aggression however, should be common if males compete for copulations.

By similar reasoning, male offspring should delay dispersal in patrilineal species. This is common in co-operative breeding birds (Gaston, 1978).

Barash (1974) proposed that in the genus Marmota, dispersal is related to environmental quality. Where growing seasons are short, animals may be unable to accumulate sufficient energy reserves to disperse successfully and may delay dispersal until subsequent growing seasons. But where growing seasons are longer, individuals have more time to physiologically prepare for dispersal and should disperse at a younger age. Support for his model is found in the dispersal ages of three marmot species occurring along elevational gradients (Barash, 1974). Woodchucks (Marmota monax), which live at lower elevations with long growing seasons, disperse at weaning. Olympic marmots (M. olympus) live at high elevations with short growing seasons and disperse as two-year olds. Yellow-bellied marmots (M. flaviventris) live at intermediate elevations and disperse as yearlings. Equally as interesting, woodchucks become sexually mature as yearlings, yellow-bellied marmots first breed as two year olds, and olympic marmots are not sexually mature until their third year of life. The age of dispersal in these three congeners differs, but more importantly, the timing of dispersal is the same. In all three species, dispersal is predominantly by pre-reproductives as predicted by the evolutionary model. Barash's model may be a proximate mechanism for reducing the costs of dispersal.

Further support that dispersal is adaptive to individuals can be found in Bekoff's (1977) paper on the ontogeny of behavioral phenotypes in mammals, which tends to confirm the importance of parent-offspring conflict in dispersal decisions. In many mammal species reviewed by Bekoff, aggressive behavior in young is delayed as predicted by Trivers (1974), and dispersal is related to this ontogeny as predicted here. Bekoff also provided numerous examples of variable dispersal "strategies" within and among species. These proposed behavioral and age-specific dispersal polymorphisms may be better understood in the context of a more general evolutionary model of dispersal. For example, Bekoff noted polymorphisms in the age at dispersal which he attributed to opposing selection on behavioral phenotypes. But the evolutionary model predicts just such polymorphisms, given the assumption that dispersal is advantageous to individuals.

The adaptive value of dispersal to dispersing individuals or their relatives, appears confirmed. Therefore it would seem expedient to conduct life history studies oriented toward comparisons of age-specific survival and fecundity schedules with predicted age-specific and parity dependent dispersal strategies. These observational studies could be complimented by experiments manipulating fitness rewards between natal and dispersal sites, or by varying dispersal costs of emigrants. In addition to their obvious empirical importance, such comparisons and experiments would represent definitive tests of the evolutionary model proposed here.

ACKNOWLEDGEMENTS

Thanks to John Addicott, Paul Anderson, Peter Grant, John King, William Lidicker, Jan Murie, Tom Nudds, Eric Pianka and anonymous reviewers for their suggestions to improve this manuscript. Special thanks to Mark Boyce for a thorough criticism of an earlier version.

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