

## ORIGINAL ARTICLE

Mary C. Towner

**A dynamic model of human dispersal in a land-based economy**

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**Abstract** This paper presents a dynamic state variable model that examines human dispersal in a land-based economy. In humans, like other animals, many individuals disperse during their lifetimes, with extensive variability in the timing and likelihood of dispersal by individuals of different states. The model places human and non-human dispersal in a common framework, specifically by utilizing a cost-benefit approach. As with other animals, individual access to resources likely plays an important role in shaping human dispersal, and the model explores the mechanisms underlying this relationship. Over a series of time steps, individuals must decide whether to stay in their natal area or disperse, given their states (wealth, marital, and inheritance status) and the environmental constraints on dispersal. Costs of dispersal include time and an initial drop in wealth, while the benefit is the potential of the dispersal area to increase wealth. The model determines whether dispersing or staying results in the highest fitness, where fitness is a function of individual wealth and years married. The model shows that dispersal is favorable under a wide range of environmental conditions, but that it also varies predictably according to individual states. Men of middle wealth values disperse under a wider variety of circumstances than poorer or wealthier men. Wealthy men, who are particularly sensitive to the time cost and mortality risk associated with dispersing, appear to adopt a more conservative dispersal strategy than poorer men, who are more sensitive to the wealth cost and wealth growth rate associated with dispersing. Dispersal behavior is also contingent on its effects on an

individual's probability of marrying or inheriting wealth. Finally, the model fosters an examination of how the interaction of life events, and their directions of causation, can be studied.

**Key words** Dispersal · Migration · Philopatry · Inheritance · Dynamic modeling

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**Introduction**

This paper presents a dynamic state variable model of dispersal in a specific human scenario: a land-based economy where reproduction occurs primarily in monogamous marriages, individuals can inherit wealth from parents, and arable land is accessible via dispersal. As one piece of a larger study of dispersal from a small New England town (Oakham, Worcester County, Mass., about 1750–1850), I use the model to develop predictions suitable to the New England setting and to examine dispersal in general. For the model, I define dispersal as one-way movement between two sites, a natal area and a dispersal area. Such locational dispersal (*sensu* Isbell and Van Vuren 1996) is facultative and not a prerequisite to independent reproduction (a broader view of human dispersal than used by Emlen 1995). For individuals who do disperse, dispersal can occur before or after first reproduction, subsuming natal and breeding dispersal.

Dispersal and its counterpart, natal philopatry, have been the focus of extensive empirical and theoretical research (see Isbell and Van Vuren 1996; Johnson and Gaines 1990; Lidicker and Caldwell 1982; Moore and Ali 1984; Plissner and Gowaty 1996; Pusey and Packer 1987; Swingland and Greenwood 1983; Waser and Jones 1983). Dispersal imposes many possible fitness costs (e.g., lost time, energy expenditure, and predation risk) and philopatry many benefits (e.g., known food sources, familiar conspecifics, and greater potential for kin investment). So why do individuals in so many species

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M.C. Towner (✉)  
Animal Behavior Graduate Group  
University of California, Davis, CA 95616, USA

*Present address:*

National Center for Ecological Analysis and Synthesis  
735 State street, Suite 300, Santa Barbara  
CA 93101-5504, USA  
e-mail: towner@nceas.ucsb.edu  
Tel: +1-805-892-2500

disperse? Ultimate hypotheses fall into three main categories: (1) dispersal reduces an individual's risk of inbreeding, (2) dispersal increases an individual's access to mates, and (3) dispersal increases an individual's access to resources. In many species, including humans, dispersal varies greatly within and across populations, often according to age, sex, resource access, and reproductive state. Consequently, no single hypothesis is likely to explain dispersal for all individuals. Exploring variability in dispersal by individuals of different states, however, can give insights into the underlying mechanisms.

The few behavioral ecologists to consider dispersal in humans have concentrated primarily on resource-based (ecological) explanations for dispersal (Clarke 1993; Clarke and Low 1992; Koenig 1989). In contrast, primatologists emphasize the social dynamics of dispersal and tend to conclude that inbreeding avoidance is the primary explanation for natal dispersal, with later transfers between groups explained by access to mates (Pusey and Packer 1987; model by Alberts and Altmann 1995). This view may reflect a phylogenetic emphasis on Old World monkeys (Di Fiore and Rendall 1994), whose social systems are structured around groups of related females, with strongly male-biased dispersal, polygynous matings, and minimal paternal investment in offspring. For humans, particularly those in agricultural settings, access to viable land or other sources of income is critical to survival and reproduction (Borgerhoff Mulder 1990; Cronk 1991). In addition, in rural New England, many marriage partners came from the same or neighboring towns and dispersal often occurred after marriage (Adams and Kasakoff 1984; Norton 1973; Tracy 1989), so dispersal is unlikely to be explained simply by inbreeding avoidance or access to mates, but instead by ecological constraints.

In many ways, human dispersal shares more with birds, especially cooperatively breeding birds, than with non-human primates. Many bird species have social systems similar to humans', characterized by socially monogamous pairs, paternal investment in offspring, overlapping generations, and the inheritance of "improved" territories (see Emlen 1995; Hrdy and Judge 1993). Also, like human behavioral ecologists, ornithologists emphasize the ecological as well as social aspects of dispersal, finding, for example, correlates with variables such as rainfall, territory vacancies, and nest site availability (Emlen 1991). In addition, cross-cultural data show that the majorities of human societies are patrilocal – men remain with or near their kin after marriage (Murdock 1967). Many men do disperse, however, even in so-called patrilocal societies (e.g., Brettell 1986; Clarke and Low 1992; Koenig 1989). Thus, unlike most mammals, but like most birds, human populations typically exhibit female-biased dispersal, and as with birds, the differences between males and females are not absolute (Clarke et al. 1997; Greenwood 1980).

Against this background, my model considers how individual access to resources and dispersal costs and

benefits impact the dispersal decisions of men in a land-based economy. Specifically, my objective is to determine the effects on dispersal behavior of three individual states (wealth, marital status, and inheritance prospects) under varying environmental conditions (wealth and time costs to dispersing, the probability and size of inheritance, wealth growth after dispersal, and mortality risk). To this end, I have constructed a dynamic state variable model based on evolutionary theory, historical patterns, and empirical data relevant to the dispersal of early New England farmers. This problem is well-suited to dynamic modeling because the technique allows dispersal decisions to occur in successive time steps, incorporating changes in the men's individual states. Of existing evolutionary models of dispersal (reviewed by Johnson and Gaines 1990), few take a state-dependent approach or contain attributes of human dispersal examined here (e.g., the role of inherited wealth).

### Historical setting

One goal of building models should be to infuse enough reality to generate specific hypotheses about how the system in question works, without making it so realistic that analysis becomes intractable or superfluous (Mangel and Clark 1988). This model includes three aspects of life for New England family farmers: (1) family demography, (2) resources and inheritance, and (3) dispersal. The model is simplified by omitting the varied religious, political, and historical events that may have influenced people's decisions.

### Family demography

Life in rural New England was characterized by a surprisingly healthy population with high childhood survival rates and adult longevity (Greven 1970). First marriages occurred at older ages than has been supposed, falling in the mid-twenties rather than mid-teens. With divorce infrequent, high life expectancy meant that marriages generally lasted through a woman's reproductive years. Early New Englanders also experienced high fertility, especially in recently settled regions, leading to large completed families (Vinovskis 1981).

When feasible, specific model parameters are drawn from the life histories of Oakham, Mass. inhabitants (from about 1750 to 1850). Demographic data from Oakham is consistent with the general New England pattern. In a small sample relevant to inheritance, Oakham fathers survived to an average age of 70.6 years (range 23.6–92.8, SD 17.1,  $n=27$ ). Prior to 1815, the average age at first marriage for men was 25 years (SD 4.7, range 18–48,  $n=88$ ) and for women, 23 years (SD 5.3, range 15–42,  $n=111$ ). A sample of 58 married Oakham women had on average eight known births (range 1–13, SD 3.0) and seven children surviving to

maturity (range 1–12, SD 2.8). The majority of Oakham women were only married once and most survived past menopause.

### *Resources and inheritance*

Family farming for personal consumption and exchange was the basic source of subsistence in rural 18th-century New England (Henretta 1978), with communities organized around patriarchal households characterized by patrilineal descent and male-biased inheritance of property (Ditz 1986; Henretta 1978). Household heads (nearly always men) were distinguished from dependents and were the main legal representatives in financial and political ties to the town and other households (Cook 1976). The agricultural economy of the time can be reconstructed through surviving tax lists, which estimated a man's worth by the acres of land, number of animals, and bushels of produce he possessed (Pruitt 1978).

The inheritance system has been identified as “multigeniture” or “preferential partibility” (Ditz 1986), where most children of propertied parents could expect an inheritance of some kind, although not all inherited equally in terms of quality and quantity of bequests. Daughters tended to inherit “moveable” personal property such as furniture, bedding, money, and animals; sons inherited money, land, livestock, tools, and farm buildings and houses. Typically only one or two sons inherited the main house and farm, while any remaining sons would receive money and other property (Ditz 1986; Shammass et al. 1987).

Long reproductive and farming careers meant that many sons would reach maturity while their fathers were still productive; apart from direct bequests, fathers could partition their own holdings or provide financial assistance to sons reaching maturity. Young men could also earn wages as farm hands, although whether such earnings yielded enough to finance land purchases is uncertain (Tracy 1989). Coupled with the economic and inheritance system, men could thus obtain their own farms through some combination of direct purchase, loans, and inheritance. Dispersal to less-developed areas with greater potential for growth may have made such acquisitions easier and perhaps more profitable over time.

### *Dispersal*

Despite early historical views of New England towns as stable, closed systems, movement between communities and to frontier areas was actually quite common (e.g., Adams and Kasakoff 1984; Tracy 1989). Oakham data for instance indicate twice as many dispersers as stayers among individuals reaching maturity (M.C. Towner, unpublished data). Dispersers fell into any of several categories over a lifetime (Adams and Kasakoff 1984). Many dispersers were children who moved with their

parents; young adults moved to other households to earn wages as farm hands and domestic servants (Beales 1991; Main 1994; Ulrich 1980); newlyweds from different places moved to one or the other's home town (more often the husband's); married adults moved to recently settled areas, often selling a farm in their natal area; the elderly moved into households of grown children.

No simple relationship has been found between wealth and likelihood of dispersal, with conflicting results reflecting either true variation within New England or the use of different sampling methods and wealth measures by historians. In the 1740s, approximately half of native-born men, mostly from the middle and bottom of the economic scale, dispersed from Beverly, Mass. (Jones 1981). In contrast, dispersers from Northampton, Mass. were more often from the middle to upper wealth levels (Tracy 1989), acquiring ample land elsewhere to establish their sons. Sons not inheriting land from their fathers often dispersed (e.g., Greven 1970), implying that dispersers were generally resource poor. Inheriting the paternal homestead, however, did not preclude later dispersal. Evidence suggests that sons would sometimes wait until receiving their inheritance, then sell it in order to finance purchases in other areas (Adams and Kasakoff 1984; Tracy 1989).

Local environmental constraints appear to have impacted dispersal rates. For example, sons born to the early settlers of Andover, Mass. tended to stay because fathers could provide multiple sons with land (Greven 1970). By the third generation, however, many Andover men were dispersing to sparsely settled areas elsewhere (Greven 1970), as did Oakham sons when they experienced similar local environmental constraints (M.C. Towner, unpublished data). The dispersal of adults starting farms in new locations seemed to involve the greatest risks, including a considerable investment of time and resources. This type of dispersal led to the expansion of New England settlements (Crandall 1975; Martin 1991) and was most often associated with men (as in this model), although often implicit is that such men dispersed with women and children (e.g., Adams and Kasakoff 1984; Tracy 1989).

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## **Methods**

### General structure

The key components of a dynamic state variable model are a decision (e.g., disperse or remain in natal area), at least one state variable characterizing the individual (e.g., wealth), a series of time steps, and a terminal fitness function (e.g., success as a function of wealth and years married at the end) (Mangel and Clark 1988). At each time step, the state variables may change according to probability distributions in the model and individual decisions. Working backward through each step, the model solves for what an individual of each possible state should do in that time step in the attempt to optimize its terminal fitness, and then saves the solutions in decision matrices. Monte Carlo simulations (described in more detail below) are then used to investigate the behavior and changing states of a population of individuals based on the decisions generated by the backward

portion of the model. [All model programming and analyses were completed in S-PLUS (StatSci 1995). For detailed instruction in the method and use of dynamic state variable modeling in behavioral ecology, see Mangel and Clark (1988); for additional examples of its use in human behavioral ecology, see Anderies (1996), Beauchamp (1994), and Mace (1993, 1996).]

My model examines the optimal dispersal decisions for individuals patterned after male, New England farmers. Individuals are placed in a simplified land-based economy, where increased access to resources can be gained by inheritance and/or dispersal to a less-saturated area. The dispersal decision is analogous in many ways to a classic patch choice problem (see Mangel and Clark 1988), where the choice at each time step is whether to remain in one patch, the "natal area," or attempt to move to another, the "dispersal area." Dispersal entails two main costs: a loss of time and an initial decrease in wealth. In subsequent time steps, however, wealth in the dispersal area grows at a specified rate and can potentially exceed pre-dispersal wealth (the principle benefit of dispersal in my model).

More precisely, the model encompasses the lifetime of an individual who has to decide whether to attempt dispersal or stay in the natal area. To approximate the ages of reproduction and the timing of dispersal decisions, the model includes 32 steps ( $t = 1 - 32$ , where the last period,  $T$ , is 32), representing 1-year intervals between the ages of 18 and 50. Dispersal decisions are based on the choice that maximizes a fitness function of both wealth and years married at the last time step, age 50. Random factors (e.g., illness, weather, social unrest) could conceivably prevent an individual from dispersing in a given year, even if dispersing was optimal. Thus, for each time step, an individual attempting to disperse has a specific probability (0.5) of reaching the dispersal area. An unsuccessful individual may continue to attempt dispersal in subsequent time steps until successful; most would-be dispersers eventually succeed (within four time steps, the cumulative probability of success reaches 0.94). The model assumes that once he has dispersed, the individual remains in the dispersal area for all remaining time steps.

#### State variables and environmental parameters

At each time step ( $t$ ), the individual is characterized by three main state variables: (1) wealth, with  $W(t) = w$ , (2) years married, with  $Y(t) = y$ , and (3) inheritance status, with  $I(t) = i$ . An additional state variable tracks the maximum wealth a disperser can gain relative to starting wealth ( $w_m$ , defined below). Table 1 summarizes the individual state variables and the values they can take. With each time step survived, the individual can inherit (if he has not already), marry (if he is unmarried), accumulate years married (if he is married), and change in wealth (through inheritance and/or dispersal). A set of environmental parameters determines probabilities for such state changes (e.g., inheriting in a given year in the natal or dispersal area); these parameters are drawn from a combination of empirical data and categorical approximations (see Table 2).

Before anything else can occur, the individual must survive the current time step. Probabilities of death per time step in the natal and dispersal areas are given by  $q_n$  and  $q_d$ , respectively. A preliminary survival analysis of vital records for Oakham men ( $n = 67$ ) was used to derive a mortality risk of 0.004 per time step, with  $q_n = q_d$  unless otherwise specified. Corresponding probabilities of surviving from  $t$  to  $t + 1$  are thus  $1 - q_n$  and  $1 - q_d$ . The  $q_n$  and  $q_d$  parameters yield an 88% cumulative probability of surviving to  $T$ , the last time step.

**Table 1** Individual state variables

Variable	Symbols	Values taken
Wealth	$W(t), w$	0–8
Years married	$Y(t), y$	0–28
Inheritance	$I(t), i$	1 (has not) or 2 (already has)
Maximum wealth	$w_m$	0–8

**Table 2** Parameters varied in simulations

Variable	Symbol	Base	Variations
Mortality risk	$q_n$ or $q_d$	=	$q_d = 1.2q_n$
Father's starting age	$a$	medium	young or old
Inheritance size (natal area)	$w_{in}$	2	1 or 3
Inheritance size (dispersal area)	$w_{id}$	2	$w_{in}$ or $w_{in} - 1$
Wealth cost of dispersal	$w_c$	1	0 or 2
Time cost of dispersal	$t_c$	1	0 or 2
Wealth growth in dispersal area	$g$	1.05	1.02 or 1.08

In an analogous manner, the probability of unmarried individuals marrying with each time step is given by  $m_t$ , and is equal in the natal and dispersal areas. The  $m_t$  probability distribution (Fig. 1) is approximated from a sample of first marriages of Oakham men ( $n = 88$ ) with a 15% non-marriage rate (estimated using survival analysis). Once an individual marries, the years married accumulate [ $Y(t+1) = Y(t) + 1$ ] in each subsequent time period. For the purposes of calculating fitness,  $Y(t)$  is limited to 28 (approximating the potential reproductive years of a woman marrying in her early twenties).

The wealth state variable,  $W(t)$ , ranges from 0 to 8 (the maximum wealth allowed) and can be thought of as "farm units" comprised of the land, buildings, animals, farming tools, and personal property that all combine to determine an individual's wealth and ability to support and establish children on their own farms. While wealth can change in later time steps through inheritance and dispersal, the wealth that individuals start with at  $t = 1$  could be wealth derived from a combination of labor and parental investment.

The inheritance state variable,  $I(t)$ , tracks whether individuals have inherited wealth from their fathers ( $i = 2$ ) or not ( $i = 1$ ). If  $i = 1$ , individuals in both natal and dispersal areas have a probability of inheriting wealth with each time step of the model. Inherited wealth is gained by the individual when his father stops farming (probably at or near the end of his life) and is added to whatever starting wealth the individual may have received from parents. The amount of wealth inherited ( $w_{in}$  in natal area,  $w_{id}$  in dispersal area) ranges from 1 to 3 wealth units and represents a function of both father's wealth and how the father distributes his wealth (subsuming variables like family size and birth order). If inheritance occurs,  $i = 2$  for all remaining time steps.

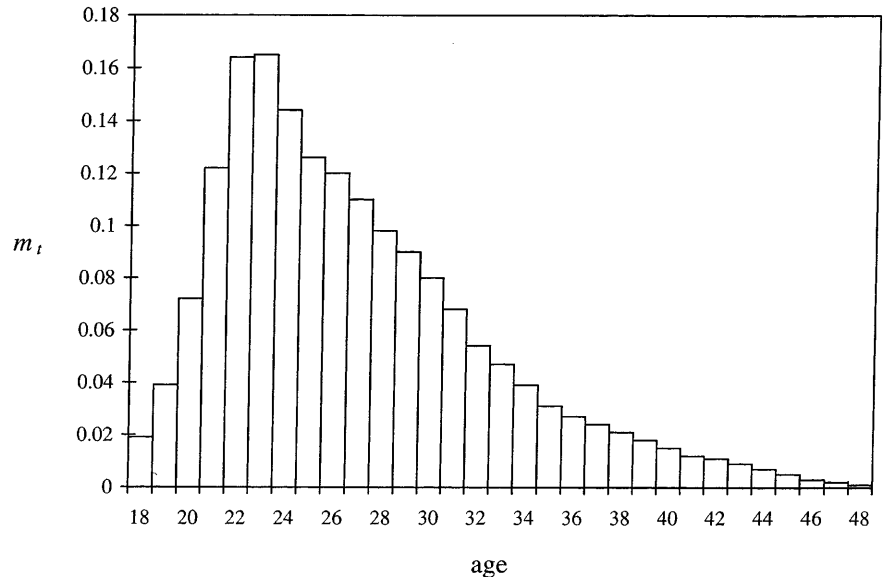
The timing of inheritance is determined by  $p_t$ , the probability the father dies in time step  $t$ , roughly calculated from a sample of Oakham fathers. This probability increases as father's age,  $a$ , increases 1 year with each time step. Several different starting ages ("young," "medium," and "old" fathers) are considered. The formula for  $p_t$ :

$$p_t = \frac{1}{275} e^{0.1a_t} \quad (1)$$

thus yields an increasing risk with each  $t$  and starts at a higher rate with father's age.

Wealth can also change through dispersal. The attractiveness of the dispersal area is measured by the potential wealth gain ( $w_d$ ) that can be acquired relative to  $w$ . Dispersal first confers a wealth cost ( $w_c$ ), the investment needed to move and acquire land in a new area. Dispersal also confers a time cost ( $t_c$ ), during which time wealth holds constant at  $w - w_c$ . In addition, the model incorporates a temporary fertility cost to dispersal by not allowing years married to increase during  $t_c$ . Once  $t_c$  has elapsed, the individual's wealth starts to grow such that  $W(t+1) = gW(t)$ , where  $g$ , the growth rate, is a constant (e.g., 1.05). Wealth growth corresponds to the "improvement" of the land as fields are cleared and planted, buildings are erected, livestock is acquired, and so on.

**Fig. 1** Probability of marriage,  $m_t$ , as a function of age. Distribution based on a sample of first marriages of Oakham males ( $n=88$ ). To adjust for those Oakham men who never married, a 15% non-marriage rate was incorporated (estimated through survival analysis)



Usually within several time steps, the individual will recoup  $w_c$  and in further time steps (assuming survival) will gain up to  $w_d$  more wealth units. Wealth after dispersal can thus increase to  $w_m$ , where  $w_m = w + w_d$ , not to exceed the maximum wealth possible in the model ( $w=8$ ). For example, assuming  $w_d=2$  and ignoring inheritance, an individual of  $w=3$  in the natal area could reach  $w=5$  after dispersing, whereas  $w=7$  could reach  $w=8$ . See Fig. 2 for an example case that illustrates both inheritance and dispersal.

*Dynamic equations*

The solution to the dispersal decision is the choice (stay or disperse) that maximizes expected lifetime fitness for an individual at time  $t$ , given the states and probabilities described above. The expected lifetime fitness associated with the optimal decisions is represented by  $F(w, y, i, t)$ , which at  $T$ , the last time step considered, is equal to the terminal fitness function,  $\phi(w, y)$ . Terminal fitness varies with two main state variables: the individual's wealth and the years the individual has been in a reproductive marriage [I will describe  $\phi(w, y)$  in greater detail after introducing the dynamic equations].

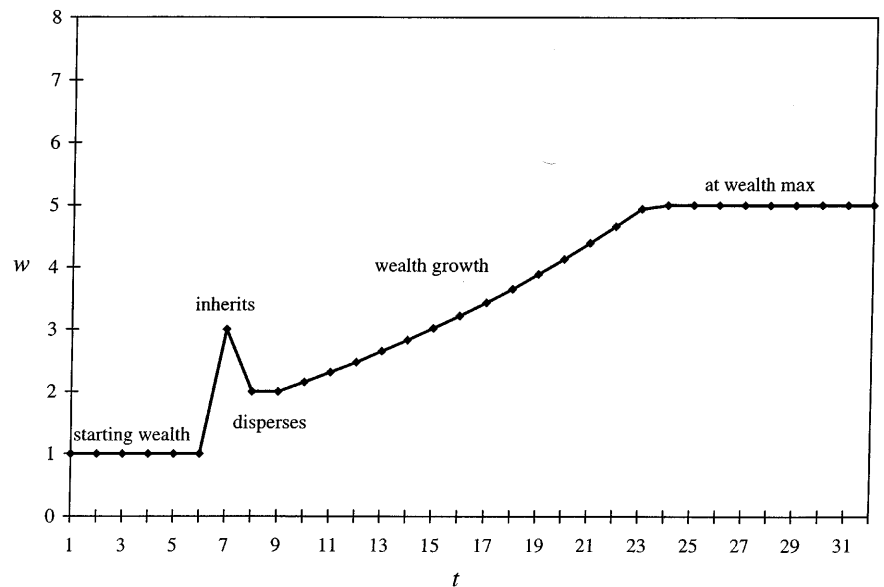
As an example to illustrate the model dynamics, consider the most basic case when the individual is married ( $y > 0$ ) and has already inherited ( $i = 2$ ). In this case, the only stochastic event that can happen is death, and the value of staying in the natal area at time  $t$  can be expressed as:

$$V_s(t) = q_n \phi(w, y) + (1 - q_n) F(w, y + 1, i, t + 1), \tag{2}$$

where  $F(w, y + 1, i, t + 1)$  refers to the expected benefits associated with state changes and decisions in the future. In other words, the value of staying equals the probability that the individual dies during  $t$ , in which case he gains the terminal fitness benefits connected with his present wealth and years married, plus the probability that the individual survives the time period, in which case he gains the benefits expected in future time steps.

Similar dynamic equations are calculated for  $V_s$  when the individual has not yet married ( $y = 0$ ) and/or inherited ( $i = 1$ ), and also for the value of being in the dispersal area ( $V_d$ ) under the various individual state combinations. For instance, the value of being in the dispersal area for the simple case when the individual is married ( $y > 0$ ) and has already inherited ( $i = 2$ ) is:

**Fig. 2** Example of how an individual's wealth,  $W(t)$ , might change over time. At  $t = 1$ ,  $w = 1$ . At  $t = 6$ , inheritance occurs, so  $w = 3$  at  $t = 7$ . The individual then disperses and experiences a wealth and time cost, so  $w = 2$  at  $t = 8$  and 9. Wealth then grows gradually in the dispersal area, until the maximum is reached ( $w_m = w + w_d = 5$  for an individual dispersing at  $w = 3$ )



$$V_d(t) = q_d \phi(w, y) + (1 - q_d)F(gw, y + 1, i, t + 1), \quad (3)$$

The heart of the model, then, cycles through all states and, working backward from  $t = T$  to 1, solves for the maximum of  $V_s$  and  $V_d$  (adjusting for the costs of getting to the dispersal area). This maximum then determines whether the individual will stay or attempt dispersal, and also determines the expected future benefits ( $F$ ).

### Terminal fitness function

Precisely how wealth and fertility interact in determining an individual's fitness is controversial and beyond the scope of this paper (see Judge and Hrdy 1992; Kaplan et al. 1995; Rogers 1990; Vining 1986), but a general fitness currency must be specified to develop the dispersal model. I used a positive function of both wealth and fertility, in effect, child-wealth units (see Fig. 3). The measure is analogous to that used by Mace (1996), where the minimum between number of children or wealth per child determines fitness (hence optimal behavior works to increase both quantities simultaneously). A recent theoretical model developed by Rogers (1995) supports this relationship, as does historical evidence from New England that suggests individual acts to produce children and wealth (Vinovskis 1981).

The terminal fitness function is:

$$\phi(w, y) = cw \frac{y}{b}, \quad (4)$$

where  $y$  (years married) is divided by  $b$  (an interbirth interval of 2 years), and multiplied by  $w$  (wealth) and  $c$ , a scaling constant (0.11) that adjusts the range of  $\phi(w, y)$  to fall between 0 and 12. In effect,  $\phi(w, y)$  is a measure of how many child-wealth units an individual has accumulated (Fig. 3).

### Decision matrices and Monte Carlo simulations

To investigate dispersal decisions for individuals of different states, I run the model multiple times, once for a "base case" and then for 12 separate environmental parameter changes (Table 2). (The base case, a central frame of reference, represents the least number of assumptions about differences between dispersal and natal areas, rather than the most frequent or typical environment.) Each model run yields two components: a decision matrix and a Monte Carlo simulation. The decision matrices, produced by backward iteration of the dynamic model equations, store the dispersal decision ("d" for disperse, "s" for stay) for an individual of a given set of states

(see Fig. 4 for a graphical representation of the base case decision matrix).

In contrast to decision matrices, simulations are produced by forward iteration using the decision matrices and stochastic events. Simulations show how the decisions might play out in a population of imaginary men moving through time, being exposed at each step to the probability of events such as death, marriage, and inheritance. As time progresses, the men begin to differ from one another in individual states as each experiences events at different times, and each individual stays or disperses according to his own states and the given environmental conditions. Because I assume all men have not yet married ( $y=0$ ) or inherited wealth ( $i=1$ ) at  $t=1$ , I emphasize how variation in initial wealth impacts simulation results, using groups of men with three starting wealth levels ( $w=1$ ,  $w=4$ ,  $w=7$ , referred to as low-, middle-, and high-wealth men). Each simulation runs a sample of 8000 men, translating into confidence intervals of about  $\pm 1\%$  (see Fig. 5 for percentage of simulation men dispersing under each environmental condition).

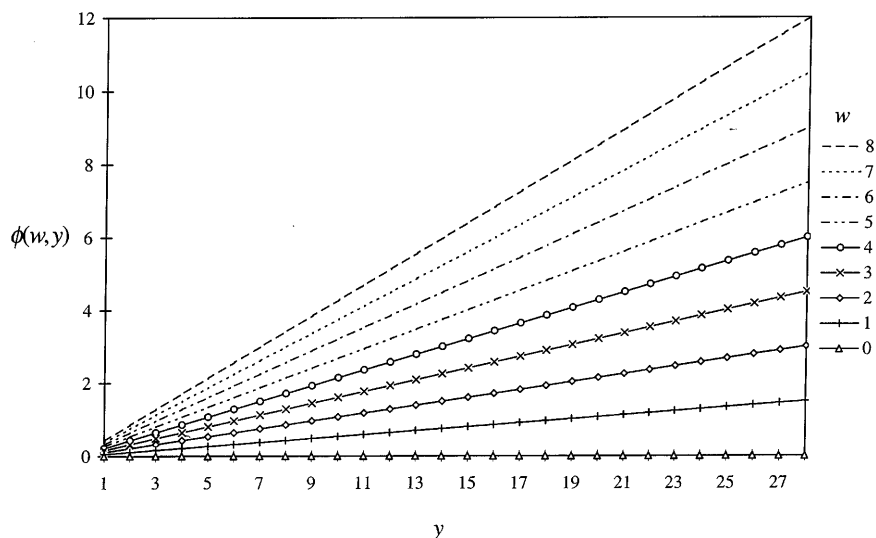
## Results

### Individual states

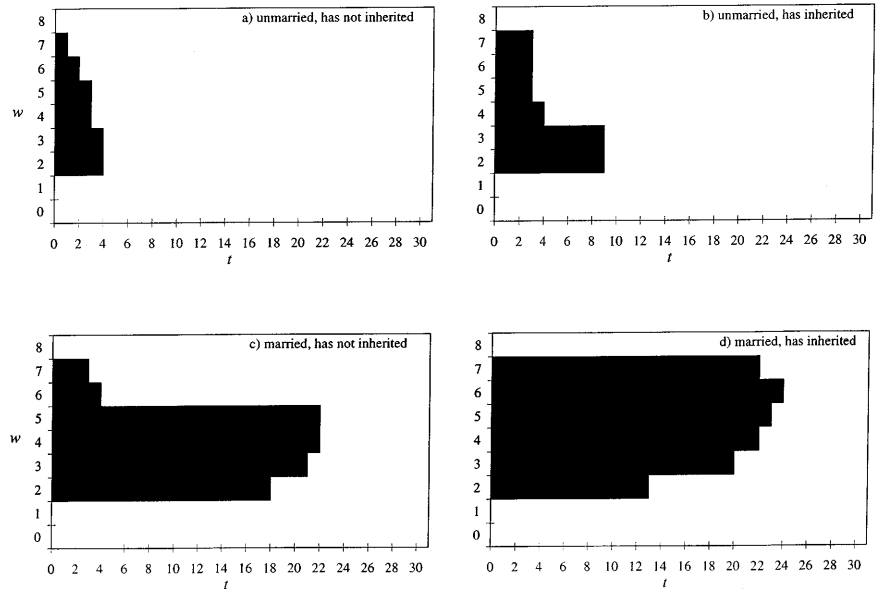
#### Wealth

Overall, the poorest and wealthiest men do not disperse. For instance, in the base case, the decision is never "d" for men in the two lowest wealth categories ( $w=0$  and 1) and the highest ( $w=8$ ), while the decision is sometimes "d" for men of other wealth values ( $w=2-7$ ) (Fig. 4). This result follows from the basic constraints of the model. The poorest men cannot afford the wealth cost of dispersal, while the wealthiest men do not benefit from dispersing because they have already reached the upper wealth limit. In the base case simulations, 36.7% of low-wealth men, 97.1% of middle-wealth men, and 55.4% of high-wealth men eventually dispersed. Because nearly all middle-wealth men disperse, simulation results will tend to refer only to low- and high-wealth men (Fig. 5).

**Fig. 3** Terminal fitness function  $\phi(w, y)$  ranges from 0 to 12 units, with the maximum of 12 gained by individuals married at least 28 years and with highest wealth 8 at  $T$ . The terminal fitness is therefore positively correlated with both  $w$  and  $y$ ; holding  $w$  constant,  $\phi(w, y)$  increases linearly with  $y$ , and vice versa. In addition, the same fitness value can be achieved through multiple combinations of  $w$  and  $y$ ; for example,  $\phi(8, 7) = \phi(4, 14)$



**Fig. 4** Decision matrices for the base case showing time regions over which the decision is to disperse (black area; “d”) or stay (white area; “s”) for each combination of  $W(t)$ ,  $Y(t)$ , and  $I(t)$  (wealth, marital, and inheritance state variables, respectively)

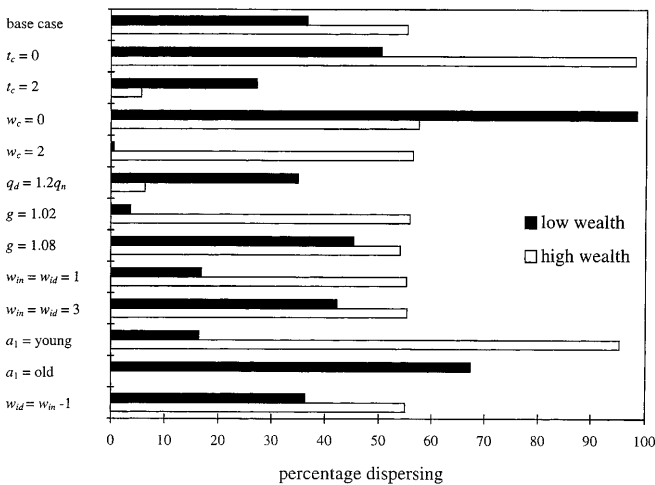


*Marriage*

In general, married men disperse more than unmarried men. For both married and unmarried men, the decision is “d” in early time steps of the base case (for intermediate-wealth values), but “d” occurs over a much longer range of time steps for married men (Fig. 4c compared to 4a, 4d compared to 4b). For unmarried men, who are not allowed to marry during the dispersal time cost, dispersal in all but the first few time steps (when marriage is less likely; Fig. 1) has a negative impact on their lifetime probability of marrying. If unmarried men subsequently marry in the middle of the time frame, dispersal may follow in the very next step as individuals shift from one decision matrix to the other (e.g., from Fig. 4a to 4c).

*Inheritance*

For men who have already inherited wealth, the decision is more often “d” than “s” (Fig. 4b compared to 4a, 4d compared to 4c). Once inheritance has occurred, the only route for men to increase their wealth is by dispersal. If inheritance has not occurred, but inheritance prospects are good (e.g., if the father is wealthy or old), men of middle to upper wealth values are less likely to disperse because the impending inheritance will bring them up to the maximum wealth possible. As in the case of marriage, dispersal may be precipitated by an inheritance event, as an individual shifts from a decision matrix where the decision is “s” for someone who has not inherited, to one where the decision is “d” for someone who has (e.g., from Fig. 4a to 4b).



**Fig. 5** Percentage summaries of men dispersing in simulations over different environmental parameter changes (see Table 2), ordered according to presentation

*Environmental parameters*

*Time cost*

When there is no time cost to dispersal ( $t_c=0$ ), the range of states and time over which the decision is “d” increases dramatically compared to the base case (Fig. 4), particularly for unmarried men, who no longer lose a chance to marry during the time cost. In the simulations (Fig. 5), more low-wealth men (50.5%) and many more high-wealth men (98.0%) disperse when  $t_c=0$ . Conversely, when the time cost is greater than the base case ( $t_c=2$ ), the range of states and time over which the decision is “d” decreases slightly, and in the simulations fewer low-wealth men disperse (27.2%), and high-wealth men drop down to very low dispersal rates (5.7%). Even when there is no explicit time cost, the time necessary to reap the benefits available in the dispersal area places an upper limit on the dispersal decision. Men never disperse in the last few time steps

( $t = 29 - 31$ ), and only infrequently in the last quarter of steps (after  $t = 24$ ).

### Wealth cost

The wealth cost of dispersal shows its effect mostly on men at the lower wealth values, with little impact on middle- and high-wealth men. When there is no wealth cost ( $w_c = 0$ ), the “d” decision expands compared to the base case (Fig. 4) to include poorer men ( $w = 1$ ), whereas an increased wealth cost ( $w_c = 2$ ) limits the “d” decision to men of at least middle-wealth values ( $w = 3$  or more). The simulations (Fig. 5) reveal the effect on low-wealth men: 98.3% disperse when  $w_c = 0$ , but less than 1% disperse when  $w_c = 2$ . The few dispersers in this group are men who inherit in the very early time steps. An increased wealth cost also compresses the time window of the “d” decision (Fig. 4). For married men who have already inherited ( $w = 4$ ), the decision is “d” up to  $t = 26$  when  $w_c = 0$ , but this decreases to  $t = 13$  when  $w_c = 2$ .

### Mortality risk

An increased risk of mortality in the dispersal area relative to the natal area ( $q_d = 1.2q_n$ ) has the biggest impact on high-wealth men, with no substantial changes for poor- and middle-wealth men. For wealthy men ( $w = 6$  and  $7$ ), increased mortality risk reduces the “d” decision (Fig. 4). In the simulations, only 6.4% of high-wealth men disperse when  $q_d = 1.2q_n$ , compared to 55.4% in the base case (Fig. 5). For wealthy men who are married, but have not inherited, the decision is always “s,” whereas in the base case the decision is “d” in early time steps (Fig. 4). If such men have already inherited, dispersal windows result, where in early time steps the decision is “s,” in middle time steps “d,” then in late steps once again “s.” This apparently reduces the total amount of time spent in the higher-mortality area, while still leaving time to accrue the wealth benefits of dispersal.

### Wealth growth rate

When the rate at which wealth increases after dispersal is slow ( $g = 1.02$ ), the “d” decision occurs over a shorter time period compared to the base case (Fig. 4). Conversely, a faster growth rate ( $g = 1.08$ ) extends the time period, because even at late time steps, dispersal can provide a net benefit. The growth rate has its biggest impact on men of low-wealth values, for whom dispersal drops out altogether in some cases when  $g = 1.02$ . In the simulations of low-wealth men, dispersal decreases from 36.7% to 3.7% when  $g = 1.02$ , while the percentage dispersing increases to 45.3% when  $g = 1.08$  (Fig. 5). Because growth is proportional to starting wealth, poorer men’s wealth grows more slowly than that of

wealthier men, even while the possible attainable dispersal wealth is the same.

### Inheritance (wealth amount)

For men who have yet to inherit, the amount of wealth they can expect to inherit has surprisingly little impact on the dispersal decision. However, if inheritance is less than the base case ( $w_{in} = w_{id} = 1$ ; Fig. 4), men of the lowest wealth level ( $w = 0$ ) will still be unable to afford dispersal even after inheriting. Once inheritance occurs, inheritance amount impacts dispersal by potentially placing men in different wealth categories. In the simulations, low-wealth men will still be relatively poor when  $w_{in} = w_{id} = 1$ , and the rate of dispersal drops to 16.9%; a larger inheritance ( $w_{in} = w_{id} = 3$ ) raises low-wealth men to a wealth level where the “d” decision occurs over a longer period of time, and subsequently the rate of dispersal increases to 42.2% (Fig. 5).

### Inheritance (father’s age)

The probability of inheriting (as a function of father’s age) has a bigger impact than wealth amount on the dispersal decision. Compared to the base case (Fig. 4), the “d” decision changes to “s” for men of upper-middle wealth values ( $w = 6$  and  $7$ ) with older fathers (since inheritance, and hence maximum wealth, is imminent). In the simulations, father’s age has a reverse effect on low- and high-wealth men (Fig. 5). For low-wealth men, a young father ( $a_1 = \text{young}$ ), with a lower probability of dying, reduces dispersal to 16.4%, and an old father ( $a_1 = \text{old}$ ), with a higher probability of dying, increases dispersal to 67.4%. For high-wealth men, however, a young father increases dispersal to 95.3%, and an old father eliminates dispersal altogether. This difference occurs because low-wealth men must inherit before being able to disperse, while high-wealth men do not benefit from dispersal if inheritance is assured.

### Inheritance (amount in dispersal versus natal area)

Finally, in the base case, inheritance amount is equal in natal and dispersal areas (inherited wealth is moveable). In the decision matrices as well as the simulations, little changes when the inheritance amount is lower in the dispersal area relative to the natal area ( $w_{id} = w_{in} - 1$ ) because low-wealth men already wait in the natal area to inherit before dispersing, and high-wealth men will reach the maximum wealth capacity even with a reduced inheritance. The only noticeable change is that the “d” decision drops out for all low-wealth men (including  $w = 2$ ), who now delay dispersal until inheritance occurs (compared to Fig. 4).

## Other base case demographic outcomes

### Death

Across the three wealth categories, about 12% of all men died before reaching the final time step (i.e., sometime between the ages of 18 and 50; Table 3). More stayers than dispersers died (e.g., 14.7% versus 6.6% in the low-wealth case), and stayers that died did so at a younger average age (31.8 versus 40.3 years old) than dispersers. These mortality differences occur because some of those stayers that died would have dispersed had they lived long enough (the mean age at dispersal was 31.6, 20.4, and 19.4 years old for low-, middle-, and high-wealth men, respectively).

### Marriage

There is little variation in the overall percentage of men eventually marrying (about 81%), but more variation when dispersers and stayers are compared (Table 3). For example, among men of low starting wealth, 94.7% of dispersers are married, while 74.5% of stayers are married. Dispersers also tend to marry at slightly younger ages than stayers (Table 3). The causal direction stems not from conditions in the dispersal area, but because marriage shapes dispersal behavior. If men do not disperse right away, dispersal may only be favored later, after marriage; also, men who die in early time steps are more likely to be unmarried and more likely not to have dispersed yet, lowering the percentage married among stayers.

### Inheritance

Approximately 84% of all men eventually inherit some wealth from their fathers (all men start with living fathers in the simulations; Table 3). As with marriage, marked variation exists between dispersers and stayers,

especially among men of low starting wealth, with 100% of dispersers inheriting wealth, compared to 74.6% of stayers. The average age of inheritance is also over 10 years younger for low-wealth dispersers than for stayers (Table 3). Once again, the occurrence and timing of inheritance shapes dispersal behavior, and not vice versa. For low-wealth men, inheriting wealth is the only way they can afford the wealth cost of dispersal, hence all dispersers have already inherited. Furthermore, inheritance must come at a young enough age for the dispersal decision to still be “d,” which explains the average age difference in inheritance among dispersers and stayers.

### Terminal fitness outcomes

Table 4 summarizes terminal fitness outcomes in the base case simulations for low-, middle-, and high-wealth men. Overall, mean fitness increases with increasing starting wealth, with the fitness difference between low- and middle-wealth men (3.3 versus 7.5 fitness units) exceeding that between middle- and high-wealth men (7.5 versus 7.7 fitness units). This non-linear relationship occurs because many middle-wealth men eventually reach higher wealth levels (constrained at  $w=8$ ) by the last time step. Mean terminal wealth is 7.6 for middle-wealth men (who started at  $w=4$ ) and 7.9 for high-wealth men (who started at  $w=7$ ), while only 3.3 for low-wealth men (who started at  $w=1$ ). Years married does not differ across wealth categories.

Comparisons between dispersers and stayers across all wealth categories reveal that dispersers have higher mean fitness than stayers due to an increase in both terminal wealth and total years married. Dispersers average roughly three fitness units more than stayers for low-wealth men, and one fitness unit more for high-wealth men. In addition to the wealth increase from dispersal, fitness differences can be attributed to the causality issues already described above; dispersers do not do better simply because of the dispersal environment, but because

**Table 3** Base case demographic outcomes

	Wealth		
	Low	Middle	High
Percent marrying: overall	81.9	81.7	80.6
Percent marrying: dispersers	94.7	83.9	83.1
Percent marrying: stayers	74.5	07.4	77.5
Mean age at marriage: dispersers	24.8	25.5	24.9
Mean age at marriage: stayers	25.6	32.4	26.1
Percent inheriting: overall	83.9	84.9	84.0
Percent inheriting: dispersers	100	85.6	84.7
Percent inheriting: stayers	74.6	59.1	83.2
Mean age at inheritance: dispersers	29.6	36.2	36.4
Mean age at inheritance: stayers	41.4	36.2	36.2
Percent dying: overall	11.7	11.4	12.3
Percent dying: dispersers	6.6	10.6	11.0
Percent dying: stayers	14.7	40.0	13.9
Mean age at death: dispersers	40.3	35.8	35.2
Mean age at death: stayers	31.8	24.6	33.1

**Table 4** Base case terminal fitness outcomes

	Wealth		
	Low	Middle	High
Mean $w$ : overall	3.3	7.6	7.9
Mean $w$ : dispersers	4.7	7.6	8.0
Mean $w$ : stayers	2.5	5.2 <sup>a</sup>	7.8
Mean $y$ : overall	19.9	19.8	19.7
Mean $y$ : dispersers	23.4	20.4	20.6
Mean $y$ : stayers	17.9	1.4 <sup>a</sup>	18.6
Mean fitness: overall	3.3	7.5	7.7
Mean fitness: dispersers	5.3	7.7	8.1
Mean fitness: stayers	2.2	0.1 <sup>a</sup>	7.1

<sup>a</sup> Only 2.9% of middle-wealth men stay, so their fitness outcomes have little impact overall

those men that inherit wealth and marry early (both fitness-enhancing events) are more likely to disperse than their counterparts. The very low fitness value for middle-wealth stayers, for example, occurs because only men who died in the very early time steps stayed.

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## Discussion

### Dispersal and wealth

Wealth shapes many aspects of dispersal behavior. Nearly all men of middle wealth ( $w=4$ ) disperse, regardless of environmental variation tested. Considerable dispersal also occurs by men of low and high wealth ( $w=1$  and  $w=7$ ). However, no simple correlation can be derived across environmental conditions between wealth and extent of dispersal. Under some conditions, low-wealth men disperse more than high-wealth men, while in others, the reverse is true. For example, the wealth cost of dispersal has its greatest impact on low-wealth men; when the wealth cost is removed, almost all low-wealth men disperse, while almost no low-wealth men disperse when the wealth cost is increased. This sensitivity is partly, but not solely, explained by the lower wealth limit set by the model. Dispersers must have at least one unit of wealth left after paying the wealth cost in order for wealth to grow in the dispersal area. This requires men in the lowest wealth categories to first increase their wealth by other means (e.g., inheritance) before dispersal becomes a viable option and also explains why low-wealth men tend to disperse at later ages than middle- and high-wealth men.

A minimum wealth constraint is probably realistic for land-based systems like early New England, where even if land was practically free in some locations, building materials, farming tools, animals, and other necessities were not. Apart from inheritance, working for others and acquiring loans may have provided some relief for men facing this wealth constraint (Greven 1970; Main 1994). As a means for accumulating wealth, however, such options may have been least accessible to the very poorest men who needed to work for their own subsistence. In fact, very poor men without any prospect of inheritance may have dispersed as laborers or even paupers, but without the wealth opportunities enjoyed by the dispersers in the model.

The model predictions concerning the rate at which wealth grows in the dispersal area are strikingly similar to those for the wealth cost of dispersing: a slow growth rate especially decreases dispersal by low-wealth men. Dispersal is less frequent under the high wealth cost and slow growth rate conditions, even for low-wealth men who eventually inherit. Increasing wealth costs and slow growth rates compress the dispersal time window because the wealth cost is only recouped with time, as wealth in the dispersal area grows. With growth at a constant rate, a larger wealth cost thus takes longer to

recoup and time is limited. Simultaneously, men are exposed to more time during which they could die before recovering even the initial dispersal costs. Thus, only low-wealth men who inherit in early time steps disperse, even though they may have sufficient wealth to cover the dispersal cost at a later time.

How wealth changes after dispersal, including dispersal costs, subsequent growth, and limits on growth, significantly impacts model results. The model assumes an initial wealth drop, followed by wealth growth proportional to existing wealth, until a new wealth level is reached. Once this level is reached, wealth remains constant, as in the natal area, unless inheritance occurs. Different patterns of wealth change after dispersal are possible, for example, growth at a constant rate, regardless of starting wealth, or growth that slows down over time. Or perhaps dispersal environments vary in predictability, such that changes in wealth after dispersal have a large stochastic component (for example, due to crop failures), making the benefits of dispersal less certain (as in Switzer 1993).

A related question is how wealth could grow in the natal area. Agricultural intensification, possibly through technological innovations, could potentially increase the value of a farm in a land-based system, but this would be true for both the natal and dispersal areas. Alternatively, natal wealth could potentially decline over time if agricultural practices decreased land productivity. Such parameters might vary considerably in different ecological and economic environments, leading to different predictions about the timing and likelihood of dispersal for men of different states.

### Dispersal and marriage

Marital status is another individual state that produces variability in dispersal behavior. The decision to disperse occurs over a larger range of state variables for married men than for unmarried men (Fig. 4); thus, variability in the timing of dispersal is introduced because not all men marry at the same time, or even at all. Marriage (at least in early New England) is essential to producing children, such that if dispersal in any way decreases the probability of marriage, dispersal might best be delayed until after marriage. In the model, the time cost of dispersing causes such a decrease because marriage cannot take place during dispersal. This helps explain the result that removing the time cost to dispersal increases the frequency of dispersal, particularly for high-wealth men for whom marriage is a more pressing issue than wealth or inheritance. These results point to the need to consider marriage and dispersal together, even when the benefits of dispersal are couched solely in terms of wealth.

While the decision matrices (Fig. 4) suggest greater dispersal by married men, the simulation results indicate that many dispersers are unmarried at the time of dispersal. This is understandable because the decision to disperse tends to occur in early time steps, corre-

sponding approximately to the ages of 18–22, regardless of marital status. If dispersal to establish an independent farm were not feasible for men so young, in other words if the simulations started men at slightly older ages, then, based on the decision matrices, only married men would be expected to disperse. Such conditions in fact apply to low-wealth men, who must delay dispersal until inheritance, and men whose early dispersal attempts are unsuccessful, moving them out of the time period when unmarried men favor dispersal.

For 19th-century Sweden, Clarke and Low (1992) found that dispersing men were more often unmarried than married. Several studies from early New England, however, suggest that dispersers were more likely to be married (Adams and Kasakoff 1984; Tracy 1989; M.C. Towner, unpublished data). In part, this difference might be due to economic constraints on marriage unique to the Swedish sample (Low and Clarke 1991), but more comparable empirical data on dispersal and marriage are needed. While the model's link between the time cost and marriage may help explain the New England pattern, other factors, such as the loss of close social ties, biased sex ratios, and low population densities in the dispersal area, could also serve to lower marriage prospects immediately following dispersal, thus encouraging unmarried men to wait. It could also be the case that the costs of dispersing and establishing a new residence are somehow ameliorated by having a spouse's help, or even that there would be little point to dispersing if there were no family yet to support.

Studying how marriage and dispersal interact clearly requires a broad perspective that includes women. With its focus on resources in a land-based (and patriarchal) system, the model takes a predominantly male perspective. In fact, although the model and results were presented in terms of men, women and even children were dispersing whenever married men dispersed. How the decision to disperse impacts women, however, was not considered, and it would be important to know how conflicts of interest over the dispersal decision might play out between husbands and wives. Another reason to consider women concerns marriage itself. How would women preferentially marrying wealthier men, or men with good inheritance prospects, affect dispersal? For men in the model, marriage was treated as a chance event and the probability of marriage was the same across all men, controlling for age. To marry or not could be treated as its own decision, one that might trade off with individual states like wealth. Such considerations might be particularly important in some polygynous marriage systems, where men can use wealth to acquire additional wives (as modeled by Luttbeg et al., in press).

## Dispersal and inheritance

Inheritance prospects affect dispersal behavior in several ways. Men who have already inherited wealth are more likely to disperse than those who have not. This is true

not only for low-wealth men, who must wait for their inheritance, but also for high-wealth men under certain conditions. When the amount of wealth men can expect to inherit should their fathers die is decreased, dispersal by low-wealth men is slightly reduced, but there is little impact on high-wealth men. In addition, father's age, which correlates with the timing of inheritance, produces an interesting interaction effect with wealth: for low-wealth men, dispersal increases as father's age increases, while for high-wealth men, dispersal decreases with father's age. These results suggest a more complex picture than the common generalization that men who inherit wealth (particularly in the form of land) are less likely to disperse. While this often holds true for the wealthiest men in the simulations, as long as dispersal is an option it might still be favored if wealth can increase.

Considering the inheritance results, together with those for dispersal and wealth, leads to a characterization of two types of stayers: low-wealth men who are responding to unfavorable wealth conditions, and high-wealth men who are generally risk averse. Low-wealth men are particularly sensitive to conditions negatively impacting wealth. The higher wealth cost to dispersing, a slower growth rate, a young father, and a small inheritance all decrease dispersal by low-wealth men (Fig. 5). For high-wealth men, already close to the upper wealth boundary, the high likelihood of inheriting wealth when the father is old makes dispersal unappealing. Likewise, an increased time cost and an increase in mortality risk (Fig. 5) also drastically reduced dispersal for high-wealth men. There is no reason why such environmental conditions would cause more damage to high-wealth men than low-wealth men; high-wealth men simply have the luxury of playing it safe.

The conservative behavior of high-wealth men raises the question of whether an upper limit on wealth is reasonable. Rogers (1995) models the potential long-term impact of inherited wealth on fitness and suggests that: "In a world with heritable wealth, wealth has value over and above its effect on the number of one's offspring. By continuing to earn, a rich person can increase the wealth of descendants several generations removed." Could not even very wealthy men be able to increase their fitness by earning more wealth, perhaps through dispersal opportunities? In early New England, at least, this was probably unlikely. Although some very wealthy men did increase their wealth by land speculation on the frontier, they could do so without actually dispersing, which would be consistent with the conservative dispersal behavior of the model's high-wealth men (e.g., Taylor 1990).

This discussion of inheritance and wealth highlights a significant difference between humans and other animals in which inheritance of territories has been observed (see discussions in Emlen 1995; Hrdy and Judge 1993). For humans with currencies and other exchange systems, the value of inherited wealth can be transported to new areas (Clarke and Low 1992). If conditions are favorable, a piece of inherited land can be sold and that wealth

applied to purchasing more land in a new location. Thus for humans, inheritance of parental resources may facilitate rather than hinder dispersal. A big question remains as to how parents will behave, for example, if they attempt to restrict children from dispersing under such conditions. On the other hand, if children reach maturity and disperse before inheriting, what does this mean for their subsequent likelihood of inheriting wealth (i.e., will they automatically receive less than their philopatric brothers and sisters)? When the model decreased the inheritance amount in the dispersal area compared to the natal area, the simulation results actually changed very little.

### Dispersal and life history analysis

What lessons does modeling have for the interpretation of empirical data on dispersal? Because the causality in the model simulations can be easily identified, we know that differences in individual states between dispersers and stayers (e.g., marital status) are often what favor dispersal in the first place. If these results were instead found in an empirical study of dispersal, notably one trying to identify the costs of dispersal, it would be tempting to attribute differences in the states of stayers and dispersers as arising from dispersal itself. For example, the higher percentage of dispersers versus stayers having married and inherited wealth might suggest that dispersing leads to a higher likelihood of marrying and inheriting.

The model also shows us how dispersal complicates interpretations of causality in population demographic measures (Table 3). Using mortality as an example, the results of the base case simulations show that more stayers than dispersers died and did so at a younger age, on average, compared to dispersers. In this case, the model simply creates the illusion that stayers experience higher mortality rates than dispersers. The base case mortality rates were identical in the dispersal and natal areas; the differences in population measures arise because among those stayers who died, some would eventually have dispersed had they only lived long enough. Studies that have not adjusted for dispersers (or individuals with missing data) may consistently underestimate measures such as life expectancy in local populations, a warning already issued by some historians (Kasakoff and Adams 1995; Ruggles 1992). Survival analysis is one statistical method for empirically estimating mortality and other rates from durational data. In this case, dispersers would be censored at the time they dispersed, so that the years they survived in the natal area would be taken into account.

### Conclusion

When dispersal is linked to resource access in a human agrarian population, the model results confirm its appeal: nearly two-thirds of all men dispersed in the base case

simulations. Dispersal occurs under a wide range of circumstances, despite the costs in time and wealth, and even when other costs, such as an increased mortality risk or a decreased inheritance, are imposed. The key is that a potential benefit, the opportunity to increase wealth to a new level, is available. This benefit need not be large; in the simulations, even men of high initial wealth disperse under many conditions.

The model results also confirm extensive variability in dispersal behavior. Not all men dispersed, and dispersers themselves varied in age at departure. If, as argued above, a potential increase in wealth is beneficial enough to overcome a variety of dispersal costs, then why should any men stay? The answer to this question comes by examining different individual states. In some cases, these states may make staying more desirable than dispersing (as with the very wealthiest men), or in other cases may make dispersing impossible, even if it is the optimal decision (as with the very poorest men).

For any species, this simple model highlights the importance to behavioral ecologists of considering individual state variables and time, and makes it clearer why studies can find different associations between dispersal measures and independent variables, even within a species (see examples in Clarke et al. 1997). And, of course, the natural world is even more complex than this model. For example, real individuals are faced with additional choices: they may be able to select from more than one dispersal area, acquire resources in many different ways, move repeatedly, and return to their natal areas if they are unsuccessful. At the same time, real individuals must make such choices under more complicated circumstances: the costs of dispersal may be less predictable and vary according to age and health, other individuals (e.g., mates and parents) may have conflicting interests in what decisions are made, and environmental parameters may vary in a density-dependent manner according to the dispersal behavior of others in the population. Despite these complexities, modeling provides a powerful theoretical tool for generating and evaluating predictions that, in combination with empirical studies, may lead to the recognition of underlying principles that shape complex behavior such as dispersal.

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### References

- Adams JW, Kasakoff AB (1984) Migration and the family in colonial New England: the view from genealogies. *J Family Hist* 9:24-42

- Alberts SC, Altmann J (1995) Balancing costs and opportunities: dispersal in male baboons. *Am Nat* 145:279–306
- Anderies JM (1996) An adaptive model for predicting !Kung reproductive performance: a stochastic dynamic programming approach. *Ethol Sociobiol* 17:221–245
- Beales RW Jr (1991) Boys' work on an eighteenth century New England farm. In: Hunter JE, Mason PT (eds) *The American family: historical perspectives*. Duquesne University Press, Pittsburgh, pp 75–85
- Beauchamp G (1994) The functional analysis of human fertility decisions. *Ethol Sociobiol* 15:31–53
- Borgerhoff Mulder M (1990) Kipsigis women's preferences for wealthy men: evidence for female choice in mammals. *Behav Ecol Sociobiol* 27:255–264
- Brettell CB (1986) *Men who migrate, women who wait: population and history in a Portuguese parish*. Princeton University Press, Princeton
- Clarke AL (1993) Women, resources, and dispersal in nineteenth-century Sweden. *Hum Nat* 4:109–135
- Clarke AL, Low BS (1992) Ecological correlates of human dispersal in 19th century Sweden. *Anim Behav* 44:677–693
- Clarke AL, Sæther B-E, Røskoft E (1997) Sex biases in avian dispersal: a reappraisal. *Oikos* 79:429–438
- Cook EM (1976) *The fathers of the towns: leadership and community structure in eighteenth-century New England*. Johns Hopkins University Press, Baltimore
- Crandall RJ (1975) New England's second great migration: the first three generations of settlement, 1630–1700. *New Engl Hist Gen Reg* 129:347–360
- Cronk L (1991) Wealth, status and reproductive success among the Mukogodo of Kenya. *Am Anthropol* 93:345–360
- Di Fiore A, Rendall D (1994) Evolution of social organization: a reappraisal for primates by using phylogenetic methods. *Proc Natl Acad Sci USA* 91:9941–9945
- Ditz TL (1986) *Property and kinship: inheritance in early Connecticut 1750–1820*. Princeton University Press, Princeton
- Emlen ST (1991) Evolution of cooperative breeding in birds and mammals. In: Krebs JR, Davies NB (eds) *Behavioural ecology: an evolutionary approach*. Blackwell, Oxford, pp 301–337
- Emlen ST (1995) An evolutionary theory of the family. *Proc Natl Acad Sci USA* 92: 8092–8099
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Greven PJ (1970) *Four generations: population, land, and family in colonial Andover, Massachusetts*. Cornell University Press, Ithaca
- Henretta JA (1978) Families and farms: *mentalité* in pre-industrial America. *William Mary Q* 35:3–32
- Hrdy SB, Judge DS (1993) Darwin and the puzzle of primogeniture. *Hum Nat* 4:1–45
- Isbell LA, Van Vuren D (1996) Differential costs of locational and social dispersal and their consequences for female group-living primates. *Behaviour* 133: 1–36
- Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu Rev Ecol Syst* 21:449–480
- Jones DL (1981) *Village and seaport: migration and society in eighteenth-century Massachusetts*. University Press, London
- Judge DS, Hrdy SB (1992) Allocation of accumulated resources among close kin: inheritance in Sacramento, California, 1890–1984. *Ethol Sociobiol* 13:495–522
- Kaplan H, Lancaster JB, Bock JA, Johnson SE (1995) Fertility and fitness among Albuquerque men: a competitive labour market theory. In: Dunbar RIM (ed) *Human reproductive decisions: biological and biosocial perspectives*. Macmillan, London, pp 96–136
- Kasakoff AB, Adams JW (1995) The effect of migration on ages at vital events: a critique of family reconstitution in historical demography. *Eur J Popul* 11:199–242
- Koenig WD (1989) Sex-biased dispersal in the contemporary United States. *Ethol Sociobiol* 10:263–278
- Lidicker WZ Jr, Caldwell RL (eds) (1982) *Dispersal and migration: benchmark papers in ecology*, vol 11. Hutchinson Ross, New York
- Low BS, Clarke AL (1991) Family patterns in 19th century Sweden: impact of occupational status and land ownership. *J Family Hist* 16:117–138
- Luttbeg B, Borgerhoff Mulder M, Mangel MS (in press) To marry again or not: a dynamic model of marriage behavior and the demographic transition. In: Cronk L, Chagnon NA, Irons W (eds) *Human behavior and adaptation: an anthropological perspective*. Aldine de Gruyter, New York
- Mace R (1993) Transitions between agriculture and pastoralism in sub-Saharan Africa. *Curr Anthropol* 34:363–382
- Mace R (1996) When to have another baby: a dynamic model of reproductive decision-making and evidence from Gabbra pastoralists. *Ethol Sociobiol* 17:263–273
- Main GL (1994) Gender, work, and wages in colonial New England. *William Mary Q* 51:39–66
- Mangel M, Clark CW (1988) *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton
- Martin JF (1991) *Profits in the wilderness: entrepreneurship and the founding of New England towns in the seventeenth century*. University of North Carolina Press, Chapel Hill
- Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? *Anim Behav* 32:94–112
- Murdock GP (1967) *Ethnographic atlas*. University of Pittsburgh Press, Pittsburgh
- Norton SL (1973) Marital migration in Essex County, Massachusetts, in the colonial and early federal periods. *J Marriage Fam* 35:406–418
- Plissner JH, Gowaty PA (1996) Patterns of natal dispersal, turnover and dispersal costs in eastern bluebirds. *Anim Behav* 51:1307–1322
- Pruitt BH (ed) (1978) *The Massachusetts tax valuation list of 1771*. Hall, Boston
- Pusey AE, Packer C (1987) Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) *Primate societies*. University of Chicago Press, Chicago, pp 250–266
- Rogers A (1990) The evolutionary economics of human reproduction. *Ethol Sociobiol* 11:479–495
- Rogers A (1995) For love or money: the evolution of reproductive and material motivations. In: Dunbar RIM (ed) *Human reproductive decisions: biological and biosocial perspectives*. Macmillan, London, pp 76–95
- Ruggles S (1992) Migration, marriage, and mortality: correcting sources of bias in English family reconstitutions. *Popul Stud* 46:507–522
- Shammas C, Salmon M, Dahlin M (1987) *Inheritance in America: from colonial times to the present*. Rutgers University Press, New Brunswick
- StatSci (1995) *S-PLUS for Windows*, version 3.3. MathSoft, Seattle
- Swingland IR, Greenwood PJ (1983) *The ecology of animal movement*. Clarendon Press, Oxford
- Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. *Evol Ecol* 7:533–555
- Taylor A (1990) *Liberty men and the great proprietors: the revolutionary settlement on the Maine frontier, 1760–1820*. University of North Carolina Press, Chapel Hill
- Tracy PJ (1989) Re-considering migration within colonial New England. *J Soc Hist* 23:93–113
- Ulrich LT (1980) *Good wives: image and reality in the lives of women in northern New England 1650–1750*. Knopf, New York
- Vining DR (1986) Social versus reproductive success – the central theoretical problem in human sociobiology. *Behav Brain Sci* 9:167–260
- Vinovskis MA (1981) *Fertility in Massachusetts from the revolution to the civil war*. Academic Press, New York
- Waser PM, Jones WT (1983) Natal philopatry among solitary mammals. *Am Nat* 58:355–390