ELSEVIER

Ecological Constraints on Marriage in Rural Ireland

Beverly I. Strassmann
Department of Anthropology, University of Michigan, Ann Arbor, Michigan
Alice L. Clarke
Department of Environmental Studies, Florida International University, Miami, Florida

Behavioral ecological studies of cooperatively breeding birds suggest that delayed dispersal and reproduction are caused by ecological constraints on independent breeding opportunities. Here we use census data on marriage and reproduction among the 19th and 20th century rural Irish to determine if the ecological constraints hypothesis can be extended to humans and what modifications might be required. We focus specifically on the following predictions: (1) marriage rates for farmers varied directly with the availability of farms; (2) the incidence of celibacy among male heirs increased as size of farm decreased; (3) emigration increased as economic opportunities in rural Ireland decreased; (4) emigration rates were inversely related to farm size; and (5) emigrants improved their chances for marriage by leaving Ireland. Despite important differences between humans and other species, we conclude that the rural Irish fall within the scope of ecological constraints theory. Unmarried siblings who remained on the home farm potentially gained some indirect fitness benefits because (1) the labor of unmarried siblings probably enhanced farm wealth; and (2) heirs of wealthier farms had higher reproductive success. The latter prediction implies that increased wealth, whether due to siblings or other causes, was reproductively valuable.

KEY WORDS: Celibacy; Age at marriage; Cooperative breeding,; Ecological constraints; Emigration; Dispersal; Helping behavior; Irish historical demography.

Since the mid-1800s, Ireland has had one of the highest percentages of individuals who postpone marriage or who never marry of any country in the world (Arensberg 1937:96; Arensberg and Kimball 1940:103; Kennedy 1975:1,139; Messenger 1969:67) (Table 1). For example, in 1936, 74% of

Received October 4, 1996; revised November 26, 1997.

Address reprint requests and correspondence to: Dr. Beverly I. Strassmann, Department of Anthropology, 1020 LSA Building, University of Michigan, Ann Arbor, MI 48109-1382, U.S.A. E-mail: bis@umich.edu, Phone: (313) 936-0428, Fax: (313) 763-6077.

Evolution and Human Behavior 19: 33–55 (1998)

655 Avenue of the Americas, New York, NY 10010
1090-5138/98/$19.00
PII S1090-5138(97)00103-7

Table 1. Postponed Marriage in Selected Countries, 1930s and 1960s

	Percentage single among persons aged 25 to 34 years			
	Females		Males	
Country and exact years	1930s	1960s	1930s	1960s
Ireland (1936, 1966)	55	31	74	50
Northern Ireland (1937, 1966)	47	20	55	29
Finland (1930, 1965)	44	19	50	28
Sweden (1930, 1958)	43	16	54	30
Norway (1930, 1960)	43	15	51	32
Scotland (1931, 1966)	41	13	44	21
Austria (1934, 1967)	41	19	53	30
Iceland (1940, 1966)	40	14	55	26
Switzerland (1930, 1960)	39	23	46	35
Spain (1940, 1960)	35	28	46	39
England, Wales, (1931, 1966)	33	12	35	21
Italy (1936, 1966)	32	21	41	38
Netherlands (1930, 1967)	30	12	36	22
Belgium (1930, 1961)	22	12	29	20
United States (1930, 1967)	18	7	29	14
France (1936, 1967)	15	14	17	27

Note. Source of data: United Nations. Demographic Yearbook, 1960, Table 10, pp. 408, 420–430; 1968, Table 7, pp. 226, 248–264. United Nations, New York. As cited in Kennedy 1975:141.

Irish men and 55% of Irish women between 25 and 34 years of age had remained single, as had 34% of men and 25% of women between 45 and 54 years of age (Table 2). These features typified marriage practices in Northwestern European countries from at least the 18th century onward (Hajnal 1965), but delayed marriage and celibacy in Ireland reached an extreme. In each decade from 1871 to 1966, less than 4% of all Irish births occurred outside marriage (Central Statistics Office 1966b:6, Kennedy 1975:174). Thus, delayed marriage has led to delayed reproduction.

What drove the extreme postponement of marriage and reproduction in rural Ireland? Here we will argue that economic success (especially land ownership or occupancy) and other correlated forms of social success (high status) were necessary for marriage and reproduction. As population pressure outstripped the resource base, increasing numbers of individuals acquired these socioeconomic prerequisites late in life or not at all. Most opted for emigration rather than accept negligible prospects for finding a mate or establishing a family. Emigration did not necessarily improve the material standard of living or even enhance life expectancy, but it provided an escape from celibacy. Previous investigators have attended to socioeconomic influences on Irish historical demography (Arensberg and Kimball 1940; Guinnane 1991a; Kennedy 1975; McGregor 1989; Schellenberg 1991), but have not given enough weight to the link between socioeconomic success and reproductive success. They see socioeconomic striving as an end in itself, despite a growing body of evidence that humans have evolved proclivities to seek socioeconomic gains because these gains translated into reproductive advantage over human evolutionary history (Irons 1979; reviewed in Betzig 1997).[1] Striking similarities between Irish

[1]Whether wealth enhanced fitness in more recent societies, such as 19th century rural Ireland, is an empirical question that must be answered on a case by case basis.

Table 2. Percentage Never Married by Sex and Age, Ireland, 1841–1986

	Males				Females			
Year	20–24 years	25–34 years	35–44 years	45–54 years	20–24 years	25–34 years	35–44 years	45–54 years
1841[a]	NA[b]	43	15	10	NA	28	15	12
1851	NA	61	21	12	NA	39	15	11
1861	92	57	24	14	76	39	18	14
1871	93	57	26	16	78	38	20	15
1881	94	62	27	16	82	41	19	16
1891	96	67	33	20	86	48	23	17
1901	96	72	38	24	88	53	28	20
1911	97	75	44	29	88	55	31	24
1926	96	72	45	31	87	53	30	24
1936	96	74	44	34	86	55	30	25
1946	95	70	43	32	82	48	30	26
1951	95	67	40	31	82	46	28	26
1961	92	58	36	30	78	37	23	23
1966	90	50	33	29	75	31	20	21
1971	NA	41	29	28	NA	26	18	19
1979	NA	34	18	20	NA	22	12	16
1981	NA	34	19	24	NA	22	11	14
1986	NA	38	18	20	NA	26	11	12

Note. Source of data: Central Statistics Office. Census of Population of Ireland, 1966, Vol. II, Table VII, p. xii. Dublin: Stationary Office, 1966. Census of Population of Ireland, 1981, Vol. II, Table G, p. xiv. Dublin: Stationary Office, 1984. Census 86: Summary Population Report, Tables 5B and 5C, pp. 9–10. Dublin: Stationary Office, 1987.

[a] Age groupings for 1841 were 26–35, 36–45, and 46–55 years;

[b] Not available.

demography and the more general phenomenon of delayed reproduction in birds and mammals also have gone unnoticed. We begin our analysis with a cross-species comparative approach that allows us to consider the Irish case in light of this broader phenomenon.

ECOLOGICAL CONSTRAINTS THEORY

In birds and mammals with delayed reproduction, sexually mature offspring may remain with their parents (or another breeding group) rather than disperse in search of opportunities to initiate independent reproduction. Delayed reproduction is found in less than 3% of bird and mammal species; in over 90% of these species, individuals who remain with the natal group help the resident breeders to rear their young, a pattern known as cooperative breeding (Brown 1987; Emlen 1991, 1995; Koenig and Mumme 1990; Riedman 1982; Solomon and French 1997; Stacey and Koenig 1990; Woolfenden and Fitzpatrick 1984). Evidence from more than two decades of research suggests that delayed dispersal is unlikely to be a fitness defying choice, but instead arises when ecological constraints limit independent breeding opportunities (Emlen 1982, 1991; Koenig and Pitelka 1981). Under this hypothesis, offspring are predicted to remain on their natal territories when the expected inclusive fitness pay off from philopatry exceeds the expected inclusive fitness payoff from dispersal (Emlen 1995).

The potential benefits of philopatry include: (1) increasing the helper's probability of survival; (2) increasing the probability that the helper will eventually become a breeder; (3) increasing the probability that the helper will inherit a high-quality territory; (4) increasing the helper's fecundity and success in rearing offspring once breeding status is attained; and (5) increasing the production of nondescendent kin such as siblings (Stacey and Ligon 1987; Walters et al. 1992a; Zack and Rabenold 1989). The expected inclusive fitness payoff from dispersal is diminished by any of the following: (1) a shortage of high-quality territories (habitat saturation); (2) a high risk of mortality; (3) a low probability of finding a mate; and (4) poor odds of succeeding in reproduction once established as a breeder (Brown 1987; Koenig 1981; Koenig and Pitelka 1981; Woolfenden and Fitzpatrick 1984). The benefits of philopatry and the costs of dispersal are alternative semantic emphases, but not alternative hypotheses on delayed dispersal (Emlen 1994; Koenig et al. 1992).

The ecological constraints hypothesis is supported by evidence that more individuals become helpers when adverse conditions increase the costs of independent breeding (Emlen 1982). For example, in the white-fronted bee-eater (*Merops bulockoides*), as rainfall decreased insects became scarce and the percentage of the population helping increased (Emlen 1982). In the acorn woodpecker (*Melanerpes formicivorous*), the percentage of yearlings who remained on their natal territory to assist the breeding pair increased as the proportion of available territories decreased (Emlen 1984; MacRoberts and MacRoberts 1976; Stacey 1979; Stacey and Bock 1978).

In the Superb fairy wren (*Malurus cyaneus*), the adult sex ratio was male biased and, as the skew grew more severe, the percentage of groups with a male helper increased (Emlen 1984; Rowley 1965, 1981). The experimental reintroduction of females had the opposite effect: more males gave up helping and dispersed to breed (Pruett-Jones and Lewis 1990). The experimental removal of males to create breeding vacancies also caused a switch from helping to breeding in 31 of 32 birds (Pruett-Jones and Lewis 1990).

Habitat saturation can interact with territory quality in the decision to stay or disperse. In the Seychelles warbler (*Acrocephalus sechellensis*), 93% percent of yearlings hatched on high-quality territories stayed on as helpers, but only 69% of yearlings from medium-quality territories and 29% from low-quality territories did so. Birds on high-quality territories could achieve higher lifetime fitness if they delayed reproduction until they assumed the position of breeder than if they dispersed and bred immediately on territories of poor quality (Komdeur 1992).

Male red-cockaded woodpeckers (*Picoides borealis*) also were much more likely to remain on high than on low-quality territories (Walters et al. 1992a). Males who previously acted as helpers usually inherited territories, and the benefits of inheriting a good territory appeared to act as strong incentives for helping. Females did not inherit territories and dispersed rather than act as helpers. Experimental data show that the critical resource in red-cockaded woodpeckers is nest cavities in pine trees (Walters et al. 1992b). These cavities take from 10 months to several years to excavate (Jackson et al. 1979). When cavities were created experimentally by humans, birds took up residence in 18 of 20 experimental sites, but in none of 20

control sites in which cavities had not been created. Thus, the creation of new cavities led to new opportunities for independent reproduction.

The ecological constraints hypothesis explains delayed reproduction as a flexible behavioral response that promotes inclusive fitness (Komdeur 1992). Within a species, no genetic variation is posited with respect to helping behavior: helpers in one season may be breeders in another. Instead, the problem-solving capabilities of organisms have been shaped by past selection, which has equipped them with adaptive decision rules and other proximate mechanisms that permit adaptive flexibility in behavior. The relative fitness advantages of the "stay and help" versus "disperse and breed" options depend on such factors as the quality of the natal territory, dominance rank, sex, and genetic relatedness to the breeders, all of which influence observed choices (reviewed in Emlen 1995).

The ecological constraints hypothesis is well supported by field studies of birds and has been invoked, in a preliminary way, for a couple species of mammals (Jennions and MacDonald 1994; Powell and Fried 1992; Solomon and French 1997). But can it be extended to humans? Emlen (1995) has developed an "evolutionary theory of the family" in which he argues that the family dynamics of species with delayed reproduction "often have direct parallels in human society." He does not, however, provide examples of these parallels, and his literature review is confined to nonhuman vertebrates (Davis and Daly 1997). Turke (1988) considers the role of daughters on Ifaluk, a Pacific atoll, as "helpers at the nest." His focus is on the hypothesis that: (1) elder daughters help their parents' future reproductive success more than do elder sons; and (2) daughters with many younger siblings have fewer children themselves. Voland et al. (1991) suggests that celibate brothers on German farms in the Krummhörn may have acted as "helpers," and Clarke (1993) proposes that Swedes served as "helpers" prior to marriage. Clarke and Low (1992) report that the probability of dispersal for sons and daughters in 19th century Sweden was negatively correlated with local availability of resources, as well as individual access to resources. Other evolutionary studies of human social behavior demonstrate that, in predemographic transition societies, resources are important for reproductive success (Betzig 1986; Blurton Jones 1987; Boone 1988; Borgerhoff Mulder 1987; Chagnon 1988; Cronk 1991; Dickemann 1979; Flinn 1986; Hill and Hurtado 1996; Hughes 1986; Irons 1979; Low and Clarke 1991; Røskaft et al. 1992; Strassmann 1997; Turke and Betzig 1985; Voland 1995). While these studies have generated a great deal of relevant data, they do not provide explicit tests of the ecological constraints hypothesis as developed to explain delayed reproduction in cooperatively breedings birds. Here we ask: Does the ecological constraints hypothesis help explain the Irish pattern of delayed marriage and celibacy?

THE IRISH

We begin with a brief introduction to the economy and inheritance patterns of Ireland during the late 19th and early to mid 20th centuries. The Irish economy during this period was predominantly agricultural, producing beef, dairy cattle, and pigs as

the principal livestock; potatoes were the primary crop, followed by oats, cabbage, and barley (Arensberg and Kimball 1940:4–5). Until the passage of the Land Acts (1885–1909), most land was owned by Protestant landlords, but was worked by Catholic tenant farmers and landless laborers [see Kennedy (1975) for a discussion of class and religious conflict].

To prevent the fragmentation of holdings, only one child in each generation inherited ownership or the right to become the next tenant farmer (Arensberg and Kimball 1940). Although sons were usually preferred over daughters as heirs, daughters were sometimes chosen, particularly when no sons were available. Birth order did not rigidly influence the parents' choice. In many families the oldest son was preferred, but the youngest was often more likely to be resident at the time the parents relinquished control. By custom, only the heir was allowed to marry and remain home; any siblings who did not disperse were required to remain single (Arensberg and Kimball 1940; Connolly 1985; Fitzpatrick 1985; Kennedy 1975: 151–154).

This type of family organization is known by the term "stem-family" and has been found primarily in Northwestern Europe (Hajnal 1965). The key feature of the stem family is that young people are effectively barred from marriage until they have attained economic independence. In "joint families," the young couple contributes labor to a larger economic unit, and marriage is not delayed by the need to inherit the family farm or complete an apprenticeship. The stem family system was invoked by Hajnal (1965) to explain the late marriages of Northwestern Europeans compared with all other human populations.

Since the stem family system was a response to land scarcity, Hajnal's argument is consistent with the ecological constraints hypothesis. Stronger tests of this hypothesis are possible, however, through the formulation of explicit predictions. In cooperatively breedings species, it has been shown that the frequency of breeding starts is a direct response to the availability of critical resources such as food, territories, nest cavities, and mates. In the Irish context, the ecological constraints hypothesis predicts that: *Marriage rates for farmers varied directly with the availability of farms.* Under impartible inheritance, the number of sons who inherited constrained the number of daughters who could find an heir to wed. On average, therefore, only one son and one daughter could marry locally per family. However, during periods of Irish history when holdings could be subdivided, several sons in one family could inherit a piece of land on which to establish a family. In support of the above prediction, marriage rates during these times became substantially higher (Arensberg and Kimball 1940; Kennedy 1975:152–153).

A major factor that promoted the subdivision of holdings in Ireland, and thereby increased marriage rates, was the introduction of the potato. The potato had become the mainstay of the Irish diet by the last quarter of the 18th century (Connell 1950:90,133). Potatoes are a higher yielding crop than wheat and other previous Irish staples and could sustain more people per hectare (Connell 1950:93). In addition to enabling the subdivision of farms, potatoes increased marriage rates by allowing the expansion of cultivation into mountains and bogs, areas unsuitable for previous crops (Arensberg and Kimball 1940; Connell 1950:90; Goode 1963:43).

During periods when farms were being consolidated, marriage rates were lower because fewer farms were available to be inherited. When two families consolidated their holdings via marriage contracts, only one child per family could marry locally rather than two (Arensberg and Kimball 1940; Kennedy 1975:153). The consolidation of Irish farms was a reaction to previous over subdivision, such that by 1841 almost half of the rural Irish population subsisted on a holding of less than four hectares (Kennedy 1975:154). It also was promoted by the development of labor saving equipment, such as the post World War II transition from horsepower to mechanical power. Smaller farms could not afford such capital investments and competed against larger farms with increasing difficulty (Kennedy 1975:96–100).

In rural Ireland, the poorest counties with the smallest farms had the highest degree of postponed marriage and the largest proportion of permanently single individuals (Arensberg 1937:97; Arensberg and Kimball 1940:104–105, 227). According to McGregor (1989): "It was here that demographic pressure was greatest, and hovels stretching up mountainsides were the concrete expression of the land constraint upon the economy." Thus, as predicted by the ecological constraints hypothesis, celibacy was most common in the most saturated habitats.

A further prediction from the ecological constraints hypothesis is that *the incidence of celibacy among male heirs increased as size of farm decreased*. The percentage never married among male farmers aged 25 to 29 years and 45 to 54 years, by size of farm, is shown in Table 3. In 1946 and 1966, the percentage never married increased as farm size decreased in both age classes (Spearman r_s range from -0.99 to -1.00, $p < .0005$). Although these data support the prediction, the percentage single did not vary significantly with size of farm in 1926.

Kennedy (1975:161–162) suggests that the transition from manual agriculture to animal and machine powered technologies between 1926 and 1966 may have increased the minimum farm size required before a man could marry. He argues that

Table 3. Percentage Never Married Among Male Farmers Aged 25–29 Years and 45–54 Years by Size of Farm, Ireland, 1926, 1946, and 1966

	Age group in years					
	25–29			45–54		
	1926[a]	1946[b]	1966[c]	1926[d]	1946[e]	1966[f]
Sizes of farm in hectares						
81+	65	60	44	20	19	18
40–81	65	61	53	19	24	23
20–40	65	61	63	18	25	27
12–20	63	64	67	18	27	33
6–12	66	66	71	20	31	39
0.4–6	64	70	71	23	33	42
All male farmers	65	66	65	20	28	33
All occupied men	80	80	57	30	31	28

Note. Source of data: Central Statistics Office. Census of Population of Ireland, 1926, Vol. V, Part II, Tables 3A, 6A, 8, pp. 8, 46, 60–64. Dublin: Stationary Office, 1926. Census of Population of Ireland, 1946, Vol. V, Part II, Tables 3A, 4A, pp. 8, 10–12. Dublin: Stationary Office, 1946. Census of Population of Ireland, 1966, Vol. V, Tables 1A, 2A, pp. 5, 10. Dublin: Stationary Office, 1966. As cited in Kennedy 1975:162.

[a]Spearman $r_s = 0.213$, $p = .343$; [b]Spearman $r_s = -0.986$, $p < .0005$; [c]Spearman $r_s = -0.986$, $p < .0005$; [d]Spearman $r_s = -0.353$, $p = .246$; [e]Spearman $r_s = -1.000$, $p < .0005$; [f]Spearman $r_s = -1.000$, $p < .0005$.

farmers were willing to marry, or could successfully attract a wife, if they had 0.4 hectares of land in 1926, but that this amount of land was insufficient a few decades later. According to this argument, nuptiality did not vary significantly with size of farm in 1926 because even farmers with 0.4 hectares could support a family. The increased importance of size of holding from 1926 to 1966 is seen in the decline in celibacy on the largest holdings and the increase on the smallest (Table 3).

In contrast to most sources (Arensberg 1937; Arensberg and Kimball 1940: 106; Fitzpatrick 1985; Kennedy 1975; Walsh 1985), Guinnane (1991a, 1991b), a self-avowed anti-Malthusian, contends that wealthy heads of household were no less likely to be celibate than those who occupied smaller holdings. His conclusion is for the years 1901 and 1911, and is based on a very small sample, whereas the data in Table 3 are countrywide. Although Guinnane's conclusion is in opposition to most sources, he does point to an interesting fact of Irish demography: some farmers with more than enough land to marry nonetheless remained celibate and heirless. This pattern conflicts with the ecological constraints hypothesis and has not been reported in other species.

Celibacy among the wealthy can be explained by socioeconomic restrictions on mate choice, which were formalized through the system of arranged marriage and dowry. A designated heir was not free to choose whoever he fancied; instead, a marriage was usually arranged for him in which the principal players were the father of the bride and groom and a "matchmaker" or marriage broker. A prospective bride had to have a "fortune" or monetary dowry that was commensurate with the value of the groom's farm. By "walking the land" together, the two fathers confirmed that the "fortune" on offer was suitable for the value of the farm (Arensberg and Kimball 1940:110). This "fortune" was indispensable because it provided for the groom's siblings who did not inherit the farm; in particular, it furbished the dowry for one (or more) of his sisters (Arensberg and Kimball 1940:115–116; Kennedy 1975: 152,154). Even if the father was deceased, the heir was obligated, on behalf of his siblings, to find a wife of appropriate dowry. Plenty of mates would have been available if the heir were allowed to marry a woman who lacked a dowry, but such marriages were opposed within the family (O'Danachair 1985) and put an heir in conflict with his siblings.

In the search for a mate, the heir's prospects were diminished if he or members of his family suffered from poor health (especially tuberculosis or mental illness) or if their reputation was in any way tarnished. In the observation of Arensberg and Kimball (1940:225): "instances of families of brothers and sisters who stuck together celibate until old age, are more often examples of the force of failure to find a mate of acceptable status than of any other cause." Marrying distinctly "down" could occur only through elopement ("runaway matches") and characteristically led to the severing of any material support from the wealthier of the two families (Arensberg and Kimball 1940:118). Thus, preservation or enhancement of social and economic status was a central concern in Irish marriages (Kennedy 1975:151–152), as in marriages in other human populations (Dahal and Fricke 1993). In the case of wealthy farmers who remained celibate, status consciousness impeded reproductive success. However, these cases were the exception, not the rule.

In contrast to the sons and daughters of farmers, hired laborers were perma-

nently excluded from opportunities to own or lease land. They had no motivation to delay marriage while waiting for an inheritance or a dowry since there would be none. Nor had they much chance of marrying up into a higher social class; consequently, marriage took place early (Arensberg and Kimball 1940:106; Guinnane 1991a, 1991b). Despite their youthful marriages, landless laborers tended to achieve lower reproductive success than the landed. For example, in 1958, Catholic farmers and farm managers had a mean fertility rate of 6.6 births per married woman versus 5.6 for agricultural laborers; the respective values for non-Catholics were 5.4 versus 4.3. These data were for marriages of at least 45 years duration in which the wives were 20 to 34 years of age at marriage (Central Statistics Office 1958:222). Data from other premodern populations imply that these fertility differences may have been even greater prior to the demographic transition[2] (Low 1990; Low and Clarke 1991; Røskaft et al. 1992; Stys 1957; Voland 1995). For example, in regard to the Krummhörn, Voland (1995) estimates: "a prosperous farming couple of the eighteenth century had almost twice as many gene replicates in the local population 100 years after wedding than an average family."

In an econometric analysis, Guinnane (1991b:162–163) concludes that males in the most prosperous farm families were more likely to remain celibate than even the landless laborers. In the farm families, however, Guinnane's sample includes "the household head, the head's son, or his brother." Thus, in this particular analysis, Guinnane collapsed data on heirs and nonheirs together. He did not distinguish marital outcomes for the truly landed versus the landless. Similarly, in the Krummhörn parishes of Germany in the 18th and 19th centuries, sons of farmers were reported to be significantly more likely to remain celibate than sons of landless laborers, but again, data for heirs and nonheirs were aggregated (Voland et al. 1991). When a distinction has been made between the truly landed versus the landless in 19th and early 20th century European populations, the landed have been found to have a higher probability of marriage (Low 1990 and Low and Clarke 1991 for Sweden; Røskaft et al. 1992 for Norway).

In determining the relationship between farm wealth and offspring celibacy, it also would be useful to control for family size. Prior to the demographic transition, completed family size increased with size of farm (Kennedy 1975:190, see below), which means that under unigeniture there were more nonheirs on the wealthier farms. Nonetheless, as predicted by the ecological constraints hypothesis, heirs of wealthier farms had higher marriage rates than heirs of smaller farms (Arensberg 1937; Arensberg and Kimball 1940:106; Fitzpatrick 1985; Kennedy 1975; Walsh 1985; cf. Guinnane 1991a, 1991b).

Reproductive Options for the NonInheriting

Fitzpatrick (1985) observes: "(T)wenty-year-olds in rural Ireland consciously confronted three alternative futures: to be matched, to be dismissed as unmatchable, or

[2]The causes of the demographic transition, in evolutionary perspective, are beyond the scope of this paper, but see Cronk et al. (In press).

to emigrate." The second option meant celibacy, and it was by far the least popular. A cohort of 1,000 males was followed from 1861 (when they were age 5 to 9 years) to 1901 (when they were age 45 to 49 years) (Guinnane 1991a). Over this 40-year interval, only 75 had remained celibate in Ireland; 240 had married, and 685 had either died or emigrated. The statistics for females of this cohort are similar: only 81 had remained celibate in Ireland; 288 had married, and 631 had died or emigrated (Guinnane 1991a). Because emigration and celibacy were alternative choices, when all else was equal they tended to be inversely related (Kennedy 1975:164). However, during harsh times, such as the famine decade 1841 to 1851, both increased, and during prosperous times, both decreased (Kennedy 1975:166–167).

The majority of never-married adults in rural Ireland were individuals who had stayed on their home farm and who continued to function as an integral part of its economy (Arensberg and Kimball 1940; Guinnane 1991a). For example, in 1951 there was a mean of 73 relatives assisting and 34 employees for every 100 heirs (Central Statistics Office 1958:82). Thus, most individuals worked on the farm of a relative rather than do wage-labor on the farm of a nonrelative. The tendency for unmarried adults to remain on the family farm also has been noted elsewhere in Europe (Clarke 1993; Duplessis-Le Guelinel 1954; Homans 1960:138–139; Krause 1959; Voland et al. 1991).

Did unmarried adults who labored on their family farms enhance the indirect component of inclusive fitness? If so, then heirs who were assisted by celibate siblings should have had higher reproductive success than they would have had if unassisted. As we have no data on assistance in the form of child care, we will focus on the economic contributions of siblings. If these contributions increased the reproductive success of heirs, then the following predictions should hold: (1) *the labor of unmarried siblings should have enhanced farm wealth*; and (2) *heirs of wealthier farms should have had higher reproductive success.* If the second prediction does not hold, then it is unreasonable to expect the economic contributions of siblings to have promoted the reproductive success of heirs. We do not suggest that farm wealth was only a reflection of the labor of unmarried siblings. The point is simply that as long as unmarried siblings promoted farm wealth and extra wealth translated into extra offspring for the heirs, then assisting relatives promoted their indirect fitness.

We first consider the prediction that the labor of unmarried siblings enhanced farm wealth. Assisting relatives could have increased farm wealth through increased productivity per hectare. The fruits of their labor also may have helped finance additional leases, enabling more land to be brought into cultivation. But if unmarried siblings who remained on the home farm were a net drain on farm resources, or had no effect on farm resources, then the prediction would be falsified.

Arensberg and Kimball (1940) and Connell (1950) mention that additional sons made for wealthier farms but their information is anecdotal. For example, Connell (1950) states that "a father measures his (material) wealth by the number of his sons." In contrast, Kennedy (1975:155) assumes that the presence of unmarried siblings was an economic burden on the heir, especially for small farmers. This is probably true when land could be worked by one couple, but on the larger holdings addi-

Table 4. Size of Farm and Mean Number of Relatives Assisting and Employees per Heir, 1951

	Size of farm in hectares[c]							
	1	3	5	9	16	30	60	80
Relatives assisting[a]	.51	.53	.57	.65	.76	.89	.94	.87
Employees[b]	.06	.05	.06	.08	.18	.48	1.09	3.05

Note. Source of data: Central Statistics Office. Censuses of the Population of Ireland, 1946 and 1951, General Report, Table 62, p. 82. Dublin: Stationary Office, 1958.
[a] $r_s = 0.929$, $p < .0005$; [b] $r_s = 0.958$, $p < .0005$; [c] Average of each size class indicated.

tional labor was potentially useful. Table 4 shows that the number of relatives per heir increased linearly by size of farm ($r_s = 0.929$, $p < .0005$), as did the number of hired laborers (0.958, $p < .0005$). Since extra laborers were sufficiently beneficial that they were worth hiring for pay, we doubt that the labor of siblings was superfluous. One might expect large farms to attract freeloading relatives. However, the number of relatives assisting *per hectare* declined substantially with farm size. Although these data do not establish unequivocally that the unmarried siblings were productive, the census takers of the time chose to refer to these siblings as relatives assisting rather than as dependent relatives, implying that their interpretation was that the unmarried siblings did in fact assist.

The prediction that heirs of wealthier farms had higher reproductive success is at least partially testable (Table 5). Among Catholics there was a significant correlation between the value of farms, as assessed for tax purposes, and mean completed family size in 1946 (Spearman $r_s = 1.00$, $p < .0005$). Farm values were not significantly correlated with family size among Protestants. At every level of farm values, Catholics had more children than Protestants, indicating that Protestants took more measures to limit their fertility. Catholics, by contrast, were encouraged to have large family sizes by the Catholic Church (Kennedy 1975:189–191). Thus, the smaller than expected family sizes of wealthier Protestants may reflect the establishment of the fertility transition within Ireland.

The positive correlation between farm wealth and family size among Irish Catholics is by no means unique. Data from Eastern Europe, China, and India show similar relationships (Stys 1957), as do data from Sweden (Low and Clarke 1991) and Germany (Voland 1995). For example, Polish mothers born between 1855 and

Table 5. Value of Farm for Tax Purposes and Mean Completed Family Size by Religion, Ireland, 1946

	Mean number of children per woman (among women aged 25–29 years at marriage and married for 25–29 years)	
Value of farm in pounds	Catholics[a]	Non-Catholics[b]
< 4	5.09	3.27
4 and under 10	5.11	3.56
10 and under 20	5.28	3.89
20 and under 50	5.33	3.82
50 and over	5.49	3.44

Note. Source of data: Central Statistics Office. Census of Population of Ireland, 1946, Vol. IX, Table 15A, p. 177. Dublin: Stationary Office, 1946.
[a] Spearman $r_s = 1.000$, $p < .0005$; [b] Spearman $r_s = 0.300$, $p = .312$.

1880 tended to have significantly higher reproductive success if they lived on larger farms ($r_s = 0.98$, $p < .0005$). Rich peasant women were more sought after as mates, married earlier ($r_s = -0.98$, $p < .0005$), and therefore were married during a larger percentage of their potentially fertile years ($r_s = 0.99$, $p < .0005$). They also gave birth to more children per year, on average ($r_s = 0.97$, $p < .0005$), and bore children up to a later age ($r_s = 0.90$, $p < .0005$). Stys (1957) suggested that children on larger farms suffered lower mortality rates, but our statistical analysis of the Polish data does not support this conclusion ($r_s = 0.24$, $p = .265$).

Although it is unclear why Irish Catholics living on more affluent farms had larger completed family sizes, we note that in rural Ireland wealthier families ate better than poorer ones (Arensberg and Kimball 1940:20–21). For example, in Westmeath, a county with large farms, the average annual consumption of meat from cattle, sheep, and lambs by dressed weight was 34 pounds per person in 1926. In Mayo, a county with predominantly small farms, an average of only 13 pounds per person was consumed (Arensberg and Kimball 1940:20–21).

If undernourishment affected child survivorship in rural Ireland, then the effect was probably greatest for females. From 1871 to 1940, female mortality was consistently higher than male mortality between the ages of 5 and 20 (Central Statistics Office 1967; Kennedy 1975:60). Kennedy (1975:63) proposed that female death rates were higher because "sons received preferential treatment both in rural and urban regions, and . . . males generally were favored in the allocation of vital resources in Irish rural areas." Daughters were not fed as well as sons and contracted more infectious and parasitic diseases (Kennedy 1975:63). For example, among children aged 5 to 14 years, the female death rate due to tuberculosis was 6.4-fold higher than the male death rate. Daughters were subservient to all family members and often had to wait until the males had eaten before they could take their turn (Arensberg and Kimball 1940).

Although the proximate pathways remain to be elucidated, the foregoing evidence is consistent with the prediction that the labor of unmarried siblings generally enhanced farm wealth. More direct tests of the proposition that the helpers actually helped would be desirable, but are not permitted by the available data. The prediction that heirs of wealthier farms had higher reproductive success was supported among Catholics, but not Protestants. The implication is that prior to the demographic transition, assisting relatives potentially gained some indirect fitness benefits from their economic activities on the home farm.

Until designation of the heir, the labor of assisting relatives also may have increased their chances for inheriting. The farm was much more likely to be passed on to a son who had remained at home, rather than to one who had emigrated. Therefore sons often waited until ownership of the farm was transferred and left only if they had not been designated as heir (Arensberg and Kimball 1940). Daughters who remained on the family farm were more likely to be chosen by their father and the father of a neighboring heir for a match. Thus, by working on the family farm, unmarried relatives might have promoted both their direct and indirect fitness.

An interesting question about Irish inheritance practices is why did fathers often wait until whey were in their 60s and even 70s, and the heir himself was in his

late 20s or 30s, before relinquishing control of the farm? By lengthening the generation time, fathers who delayed the transfer would seem to diminish their inclusive fitness. An Irishman whom we consulted helped shed light on this issue. This man's father says he must retain ownership of the family farm, although the designated heir is of marriageable age, as long as he has younger children to support. When marriage is late (especially for men) and women produce children until the end of their fecund years, then the patriarch may be in his 60s or 70s before his youngest child is old enough to be self-sufficient.

The genetic interests of the patriarch and his heir are not identical. The heir is 50% related to his own children, but only 25% related to his nieces and nephews; for this reason aid to siblings may be a poor reproductive investment for the heir. The patriarch, on the other hand, while investing most resources in the heir, may wish to make a small but potentially fitness enhancing investment in his other children (who are no less related to him). By retaining control of the farm, he is able to support them until they are old enough to be an economic asset or to go out and provide for themselves. Rather than emphasize the risk that the heir could not be counted on to assist his younger siblings, our informant's father put it tactfully: "it would be unfair to burden (the heir) with their support." As evidence that familial assistance was not guaranteed, even the support that the heir owed his parents after the transfer of property (a room in the house, kitchen privileges, use of the potato field and so forth) was customarily specified in detail in the inheritance papers (Arensberg and Kimball 1940).

An alternative hypothesis is that long delays between intergenerational wealth transfers are a strategy for the long-term preservation and concentration of wealth. Every time the inheritance is partitioned, even if one son inherits the land, wealth flows out of the farm (Voland et al. 1991). However, this hypothesis is less compelling because, in the ideal Irish match, wealth loss is balanced by wealth gain in the form of dowry.

Emigration

During the period from 1850 to 1913, more than 4.5 million people emigrated from Ireland and the population fell from 6.5 to 4.4 million people (Aalen 1963; Hatton and Williamson 1993; O'Rourke 1995). At its peak in the 1850s, emigration averaged 19 people per thousand per year. For the remainder of the 19th century, Irish emigration exceeded even that of Italy and Norway (O'Rourke 1995). Net emigration remained high up to World War I (Guinnane 1994), and a positive net migration balance was reached for the first time in the 1970s (Schellenberg 1991).

As late as the 1960s, Ireland's marital fertility rate, 195 births per 1,000 married women per year, was much higher than that of other developed countries (United Nations 1964). For comparison, marital fertility in England and Wales in 1964 was 108 births per 1,000 married women. High marital fertility was a stimulus for emigration because it meant the procreation of many more people than the land base could support. Moreover, the option of emigration meant that extra children could support themselves abroad, which gave parents little incentive to limit family

sizes (Fitzpatrick 1985). The Irish fit the tendency, observed across a wide range of species, for individuals in so-called "colonizing" populations to have high fertility (MacArthur and Wilson 1967). In sum, the high marital fertility of the Irish appears to have been both a cause and a consequence of the high emigration rate.

Irish emigration is often interpreted as a "flight from famine" (but see Kennedy 1975:41–65). Even before the potato famine (1845–1849), however, Ireland already had the highest emigration rate in Europe (about 7 per 1,000 per annum from 1821 to 1841). Moreover, the potato famine cannot explain the continuation of emigration into the 20th century (Hatton and Williamson 1993). Life expectancy of rural Irish males during the mid-1930s was 3.8 years longer than that of urban American males, which makes it unlikely that emigration at that time was a survival strategy (Kennedy 1975:49). An alternative to the "flight from famine" hypothesis is the view that the emigration stream was, in large part, an exodus of those individuals who had the least opportunity to acquire sufficient resources for marriage; they may well have been forced to remain permanently single if they had stayed in rural Ireland.

Because economic resources are a prerequisite to marriage and reproduction, this hypothesis predicts that *emigration increased as economic opportunities in rural Ireland decreased.* In contrast to a traditional economic hypothesis, material advancement is not seen merely as an end in itself but, rather, as an avenue to mate acquisition and procreation. In particular, we distinguish two components of the economic striving of the rural Irish. First, ethnographic accounts strongly suggest that people consciously recognized that economic achievement, through urban migration or emigration, was the surest avenue to marriage for those who were passed over for a "match." Second, we expect the rural Irish, like other humans (and indeed other species), to have evolved predilections to engage in resource garnering behaviors. Such predilections are expected if economic success tended to promote reproductive success over the human evolutionary past (Irons 1979), but need not be associated with any conscious reproductive motivations.

We now turn to the prediction that emigration rates reflected prevailing economic conditions. In support of this prediction, emigration rates fell as Irish wages rose relative to wages in destination countries (Hatton and Williamson 1993). Emigration rates also fell as the proportion of the population on poor relief declined, housing quality improved, family sizes grew smaller, and opportunities to acquire small holdings ($<$ 5 acres) increased. One or two children per family either inherited or married an inheritor, whereas the "surplus" siblings had to choose between emigration and remaining on the home farm as a celibate helper. Another, but strongly stigmatized, option was to become a landless laborer.

The strongest candidates for emigration were the individuals who faced, simultaneously, the worst economic prospects and the highest risk of celibacy. For a man, this should mean having many brothers to compete with for the farm, and for a woman, having many sisters to compete with for a dowry. In a multivariate analysis, the probability of leaving home was, in fact, significantly influenced by the number of same sex siblings; the number of opposite sex siblings had no effect (Guinnane 1992). Similarly, in the German Krummhörn, farmers' sons were more likely to emigrate if they had many brothers (Voland and Dunbar 1995).

We predict that *the decision to stay or emigrate was strongly influenced by the size of the farm, and that the smaller the holding the fewer the sons who were willing to stay on in hope of inheriting.* In both cross-sectional and longitudinal data, farm size was important for the retention of sons. For example, between 1946 and 1966, the percentage decrease in the number of sons aged 25 to 34 years by size of farm was as follows: 1 to 12 hectares (81% decrease), 12 to 20 hectares (67% decrease), and 40 to 80 hectares (45% decrease). The pattern of decreasing retention of sons with decreasing farm size also held in other time periods (Kennedy 1975:101–107). Small holdings were much more likely to lack an heir willing to farm them, in which case they were sold to other families seeking to enlarge their holdings. Larger holdings were more likely to remain within the same patrilineage (Kennedy 1975:106–107).

This pattern also was observable at the county level: emigration was heaviest from those rural counties where farms were small and there was little urban growth (Aalen 1963; Hatton and Williamson 1993); these regions had undergone farm subdivision and rapid population growth decades earlier. Celibacy was highest in these areas and economic opportunities were most limited (Arensberg 1937:97; Arensberg and Kimball 1940:104–105,227; Hatton and Williamson 1993). The emigrants were usually single individuals between the ages of 19 and 29 years—prime ages for seeking mates and establishing independent reproduction (Aalen 1963), but also prime ages for embarking on new economic pursuits.

Except during periods characterized by British wars (in which many Irish men enlisted) or rapid shifts in agricultural methods, the emigration stream was female biased (Kennedy 1975:82; Hatton and Williamson 1993; Schellenberg 1991). This bias resulted in an excess of males in Ireland. In 1926, there were 123 single men aged 15 and older for every 100 single women (Walsh 1985). Within Ireland, rural–urban migration also was female biased. The heavy outflow of women from the agricultural areas resulted in an extremely male-biased sex ratio in the countryside and a female-biased sex ratio in towns and cities. For example, in rural areas in 1961 there were 244 single men for every 100 single women among persons aged 45 to 54 years, compared with 125 single men aged 25 to 29 years for every 100 single women aged 20 to 24 years (Kennedy 1975:167–169). (Younger women are compared with older men since husbands are usually older than wives.)

Because women migrated from rural areas where sex ratios were high to urban areas where sex ratios were low, Kennedy (1975:72) has argued that rural Irish women did not migrate in order to find husbands. He suggests instead that they left the rural areas to escape male dominance (Kennedy 1975:108). However, the excess males in the rural areas were mostly "relatives assisting" or landless laborers. Ample opportunities for marriage in the rural areas did not exist because landholding families were extremely reluctant for their sons and daughters to be downwardly mobile to the landless laborer class (Arensberg and Kimball 1940; Kennedy 1975:152; O'Danachair 1985). This situation contrasts with that of the Krummhörn region of Germany, where 16% of farmers' sons and 20% of farmers' daughters married landless laborers, implying that class endogamy in the Krummhörn was less strict (Voland et al. 1991). The lower tolerance for hypogyny in Ireland may reflect the existence, or perception, of more favorable opportunities for emigration.

Thus, rather than marry a landless laborer, Irish women emigrated or sought employment in Dublin where they earned income to support emigration or build a dowry. Women who had worked for several years as domestic servants in the United States sometimes returned to Ireland with a "fortune" large enough to permit an upscale match to a farmer (Arensberg and Kimball 1940:114–115).

The refusal of the landholding families to accept downward mobility for sons who did not inherit the farm and daughters who did not inherit a dowry effectively removed these individuals from the local marriage market. These strict rules on class endogamy may be interpreted as a tactic for maintaining the wealth of the lineage (Boone 1986; Voland and Dunbar 1995; Voland et al. 1991). If noninheriting individuals had married locally, they and their descendants in the landless laborer class might have become an economic burden on their relatives in the farming class. It was perhaps easier for farmers to maintain their privileged socioeconomic status (with its reproductive advantages) if they eschewed intermarriage with the lower classes. The exclusion of noninheriting individuals from the local marriage market effectively prevented these individuals from engaging in competition with their kin who were in control of lineage resources. The central strategy was for the farm (the most critical resource in local reproductive competition) to be passed on intact, or enlarged, from generation to generation within the same patrilineage.

We have seen that Irish emigration was motivated by poor economic prospects in Ireland (Hatton and Williamson 1993), but we predict *that it was also reproductively rational, and that Irish emigrants improved their chances for marriage and reproduction by leaving Ireland.* We do not suggest that prospective Irish emigrants calculated the inclusive fitness costs and benefits of the "stay" versus "leave" options. Instead, they most likely sought proximate goals, such as finding a mate, motherhood, or fatherhood, that would have led them to prefer emigration over remaining celibate in Ireland. It is difficult to leave one's home and country permanently, but this option becomes more attractive when the alternative is the forced sacrifice of these deep-seated goals. Seen in this light, it is not surprising that nine times as many people opted for emigration as remained permanently celibate in Ireland (Guinnane 1991a). Economic motives alone provide an insufficient explanation for the exodus. The Irish immigrants generally achieved enough economic success to marry and have families, but they generally filled menial, low-status jobs with long working hours (Carpenter 1927:284–290) and often faced a diminished life expectancy (Kennedy 1975:48). The standard of living on the home farm did not necessarily compare unfavorably with the standard of living achieved in the destination countries. We propose that the chief difference was that emigration offered greater marital and reproductive prospects.

To test the prediction that Irish emigration was reproductively rational, we sought data on the percentage married among Irish immigrants in Great Britain and the United States to compare with the percentage married in rural Ireland. In the 1981 census of Great Britain, the percentage married among 30- to 44-year-old Irish immigrants was higher than the percentage married in this age class in Ireland. Similarly, a comparison of the United States census of 1980 with the Irish census of 1981 (the closest census available) reveals a higher incidence of delayed marriage

among the Irish in Ireland than among Irish-born immigrants in the United States (Schellenberg 1991). These results indicate that the emigrants who went to Great Britain or the United States did, in fact, improve their odds of marriage.

However, nuptiality levels for Irish immigrants in Great Britain were not quite as high as for the general British population. Nuptiality levels for Irish immigrants in the United States also were lower than for the United States population as a whole. English-born immigrants in the United States in contrast, actually married at a slightly earlier age than the general United States population (Schellenberg 1991). Curiously, even sons and daughters of Irish immigrants in the United States had higher rates of delayed marriage than individuals of other descent (Schellenberg 1991). Specifically, in 1970, 14.4% of American women of Irish descent were single in the age group 25 to 44 years, but only 9.1% of Americans of non-Irish descent were single, and only 8.3% of American women of British descent were single (Schellenberg 1991). Similar statistics obtained for men. In the absence of a multivariate analysis that controls for economic and educational status as well as geographic location (city or county) it is best not to overinterpret these results. In the opinion of Schellenberg (1991), however, a propensity toward delayed marriage has become engrained in Irish culture. As he put it, delayed marriage "has become tied in some degree to Irish personality and family characteristics—even though its roots may have been especially in economic exigencies in Ireland."

Reproductive Concerns in Irish Ethnography

The ethnographic record for the Irish supports the view that the economic striving of farm families was not simply an end in itself, but was ultimately directed toward reproduction. In particular, ethnographic descriptions by Arensberg and Kimball (1940) demonstrate the extreme measures undertaken by families to ensure that the means of production stayed with the closest genetic relatives available. For example, if a farmer's marriage was barren, an old custom allowed him to send his wife back to her parents. Catholic law forbade him from marrying again, but his brother could marry and produce the heir (Arensberg and Kimball 1940). An ancient custom called trial marriage served genetic interests by enabling the "fertility of a prospective partner to be tested" (Arensberg and Kimball 1940). Because rural Ireland was strongly male dominated, it is not surprising that genetic conflicts of interest were resolved for the benefit of the husband (Arensberg 1937:92):

> (T)he countryside recognizes only dimly if at all, the right of a woman to hold land in her own person . . . She cannot alienate it from the patrilineal line to which it belongs. If a widow remarries, she and her new husband merely hold the land in trust. The second husband and his children are strangers to the land. The rightful heir by blood, whose name is on the land, may turn them out.

Thus, the Irish farm was a resource that was scrupulously passed on to future generations through genetically related males. Inheritance patterns that exclude nongenetic relatives are predicted by the hypothesis that economic striving is in the service of reproductive striving. A purely economic hypothesis does not make this prediction.

Catholicism: An Alternative Hypothesis

An alternative hypothesis contends that the prevalence of celibacy in rural Ireland was due to sexual Puritanism disseminated by Catholicism (De Freine 1965; O'Brien 1954). Delayed marriage and celibacy, however, also were characteristic of Irish Protestants (Kennedy 1975:145–148). For example, in 1961, 30% of Catholic and 25% of Protestant males aged 45 to 54 years had never married; 23% of Catholic and 23% of Protestant females had never married. Moreover, if the role of the Church was definitive, then it should have had the same effect in other conservative Catholic countries such as Spain and Italy. In the 1930s, the percentages of males who attained the age of 45 years without marrying were 22% in Ireland, 8% in Spain, and 9% in Italy. For females, the corresponding percentages were 24%, 12%, and 12% (Kennedy 1975:148). Thus, Catholicism, by itself, provides an insufficient explanation for Irish marriage practices. Any hypothesis founded on religion also is inadequate for explaining the changes in marriage rates over time and space within Ireland, such as increased nuptiality after the introduction of the potato. Nonetheless, religion probably helped to enforce the sexual abstinence of Irish celibates, which is apparent from the exceptionally low rate of extramarital births (Central Statistics Office 1958). For many, celibacy in Ireland was a deprivation beyond simply not having a spouse.

CONCLUSION

How well does the ecological constraints hypothesis explain the Irish pattern of delayed marriage and celibacy? To answer this question we will use as our benchmark tests of the ecological constraints hypothesis in other species. Some of the strongest tests in birds show that experimentally created breeding vacancies caused former helpers to become breeders (Komdeur 1992; Pruett-Jones and Lewis 1990; Walters et al. 1992b). For example, in the Superb fairy wren (*Malurus cyaneus*), 96.9% of birds accepted the new openings. Although perhaps not a surprising outcome, it nonetheless provides strong support for the ecological constraints hypothesis. In humans, the analogous experiment would entail creating new farms to test the prediction that previously celibate individuals occupy them and establish families. Although we cannot conduct such an experiment, all evidence indicates that the same result would obtain.

Correlational tests of the ecological constraints hypothesis in birds have shown that as ecological constraints grew more severe, more individuals delayed reproduction and became helpers (Emlen 1984). In this study, we extend these findings to mammals. Among the rural Irish, marriage rates varied directly with the availability of farms. Partible inheritence and the expansion of potatoes into previously uncultivated land decreased the mean age at first marriage and decreased the proportion of permanently single individuals. The consolidation of farms had the opposite effect. Throughout Irish history, a change in the land constraint had the expected impact on the marriage rate (Arensberg and Kimball 1940; Connell 1950; Goode 1963; Kennedy 1975).

The ecological constraints hypothesis is fundamentally an economic hypothesis because it argues that organisms compete for scarce resources. It goes beyond an economic hypothesis in emphasizing the importance of resources for reproductive success. Offspring are predicted to stay at home to compete for their natal territories only so long as the expected fitness payoff from this strategy is greater than the expected inclusive fitness payoff from dispersal (Emlen 1995). This prediction was rarely tested in studies of cooperatively breeding species, but an exception is Komdeur's (1992) study of the Seychelles warbler (*Acrocephalus sechellensis*). Warblers on high-quality natal territories could achieve higher lifetime reproductive success by deferring breeding to act as helpers than by dispersing to breed immediately on territories of low quality. Differences in reproductive payoffs predicted actual behavior. Ninety-three percent of yearlings remained on high-quality territories as helpers, but only 69% on medium- and 29% on low-quality territories.

The Irish results are closely parallel in that the size of the home farm was a major determinant of whether sons aged 25 to 34 stayed on as "assisting relatives" or emigrated. Landless laborers, whose parents lacked a farm altogether, had the highest probability of emigrating (Kennedy 1975). Among the farmers, the payoffs from staying depended not only on the size of the farm, but also on the odds of inheritence. Individuals with fewer same sex sibling competitors were more likely to remain on the home farm (Guinnane 1992). Overall, 44% of Irish families had 7 or more children (data for 1911) (Kennedy 1975:184), which meant that the odds of inheritance in most families were quite low. In the cohort born between 1852 to 1856, nine times as many individuals died or emigrated over the next 40 years as remained celibate in Ireland (Guinnane 1991a). Irish immigrants in the United States and Great Britain had higher marital prospects than the Irish in Ireland (Schellenberg 1991) suggesting that, for most of the immigrants, emigration offered the best fitness prospects.

By the standards of the bird literature, the Irish data support the ecological constraints hypothesis. The ideal test, however, would compute the fitness payoffs from alternative life trajectories available to particular individuals; then it would compare these payoffs with observed choices. The data we review are short of this goal, but do provide evidence for reproductively rational decision-making. The analysis would be strengthened by further data on lineage expansion and contraction, particularly for the landed versus the laborers. Data on the fitness achieved by Irish immigrants in the United States in the last century also would be useful. Finally further data are required to test the hypothesis that the concentration of wealth, through class endogamy and unigeniture, promotes long-term lineage survival (Boone 1986; Voland and Dunbar 1995; Voland et al. 1991).

Important differences emerge when the Irish data are compared to those for other species. For example, among the Irish, kin often interceded to prevent hypogynous marriages. Insistence on class endogamy excludes noninheriting individuals from the local marriage market. This particular form of social restriction on mating opportunities has not been reported previously in birds or mammals. In other species, connections with former "family" usually disintegrate upon dispersal (Emlen 1995). Individuals who have gone off to initiate independent reproduction cannot

become a drain on lineage resources. Females, do not have to pay an entrance fee, in the form of a dowry (Gaulin and Boster 1990), when they settle on a territory. Instead female–female competition assumes other forms, such as interpersonal aggression. Moreover, in other species, when an individual ascends to the position of breeder, no direct compensation is offered to siblings.

Another feature peculiar to humans, including the Irish, is the existence of a distinct class of landless laborers who are effectively excluded from competition for land. In the landless laborer class, individuals reach their maximal potential status much earlier in life than do farmers' children and the probability of lineage survival is hypothesized to be much lower. In birds and nonhuman mammals, distinct social classes are absent, and no one group is permanently excluded from the main resource. Dominance hierarchies and social castes do exist, but alliances do not form among members of comparable status in different hierarchies. This feature distinguishes social stratification in humans from that found in other species. Despite these differences, we conclude that there are strong arguments for including the Irish (and other historical populations of Europe) within the scope of ecological constraints theory.

We thank R.D. Alexander, L. Betzig, S. Braude, B. Crespi, M. Daly, B.S. Low, A. McGuire, W.H. Mueller, R. Nesse, P.W. Turke, C. Vincenz, M. Wilson, and H.T. Wright for helpful comments on the present manuscript or an early draft. We are indebted to anonymous Irishmen for informative discussions.

REFERENCES

Aalen, F.H.A. A review of recent Irish population trends. *Population Studies* 17:73–78, 1963.

Arensberg, C.M. *The Irish Countryman: An Anthropological Study.* New York: Macmillan, 1937.

Arensberg, C.M., and Kimball, S.T. *Family and Community in Ireland.* Cambridge: Harvard University Press, 1940.

Betzig, L.L. *Despotism and Differential Reproduction: A Darwinian View of History.* Hawthorne, NY: Aldine de Gruyter, 1986.

Betzig, L.L. *Human Nature: A Critical Reader.* New York: Oxford University Press, 1997.

Blurton Jones, N. Bushman birth spacing: direct tests of some simple predictions. *Ethology and Sociobiology* 8:183–203, 1987.

Boone, J.L. Parental investment and elite family structure in preindustrial states: a case study of Late Medieval–Early Modern Portuguese genealogies. *American Anthropologist* 88:859–878, 1986.

Boone, J.L. Parental investment, social subordination, and population processes among the 15th and 16th century Portuguese nobility. In *Human Reproductive Behaviour: A Darwinian Perspective*, L.L. Betzig, M. Borgerhoff Mulder, and P. Turke (Eds.). New York: Cambridge University Press, 1988, pp. 201–220.

Borgerhoff Mulder, M. On cultural and reproductive success. Kipsigis evidence. *American Anthropologist* 89:617–634, 1987.

Brown, J.L. *Helping and Communal Breeding in Birds.* Princeton: Princeton University Press, 1987.

Carpenter, N. *Immigrants and Their Children. Census Monograph VII.* Washington, DC: U.S. Government Printing Office, 1927.

Central Statistics Office. *Census of Population of Ireland, 1926.* (Vol. V, Part II) Dublin: Stationery Office, 1926.

Central Statistics Office. *Census of Population of Ireland, 1946.* (Vol. V, Part II) Dublin: Stationery Office, 1946.

Central Statistics Office. *Census of Population of Ireland, 1946 and 1951, General Report.* Dublin: Stationery Office, 1958.

Central Statistics Office. *Census of Population of Ireland, 1966.* (Vol. II and Vol. V) Dublin: Stationery Office, 1966a.

Central Statistics Office. *Report on Vital Statistics, Ireland, 1966.* Dublin: Stationery Office. 1966b.

Central Statistics Office. *Report on Vital Statistics, Ireland, 1967.* Dublin: Stationery Office, 1967.

Central Statistics Office. *Census of Population of Ireland, 1981.* (Vol. II) Dublin: Stationery Office, 1984.

Central Statistics Office. *Census 86: Summary Population Report.* Dublin: Stationery Office, 1987.

Chagnon, N.A. Life histories, blood revenge, and warfare in a tribal population. *Science* 239:985–992, 1988.

Clarke, A.L. Women, resources, and dispersal in nineteenth-century Sweden. *Human Nature* 4:109–135, 1993.

Clarke, A.L., and Low, B.S. Ecological correlates of human dispersal in 19th century Sweden. *Animal Behaviour* 44:677–693, 1992.

Connell, K.H. *The Population of Ireland: 1750–1845.* Oxford: Clarendon Press, 1950.

Connolly, S.J. Marriage in pre-famine Ireland. In *Marriage in Ireland,* A. Cosgrove (Ed.). Dublin: College Press, 1985, pp. 78–98.

Cronk, L. Wealth, status, and reproductive success among the Mukogodo of Kenya. *American Anthropologist* 93:345–360, 1991.

Cronk, L., Chagnon, N., and Irons, W. (Eds.) *Adaptation and Human Behavior: An Anthropological Perspective.* Hawthorne, NY: Aldine de Gruyter (in press).

Dahal, D.R., and Fricke, T. The family contexts of marriage timing in Nepal. *Ethnology* 32:305–323, 1993.

Davis, J.N., and Daly, M. Evolutionary theory and the human family. *Quarterly Review of Biology* 72: 407–435, 1997.

De Freine, S. *The Great Silence.* Dublin: Foilseachain Naisiunta Teoranta, 1965.

Dickemann, M. Female infanticide, reproductive strategies, and social stratification: a preliminary model. In *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective,* N.A. Chagnon and W. Irons (Eds.). North Scituate, MA: Duxbury Press, 1979, pp. 321–367.

Duplessis-Le Guelinel, G. *Les Marriages en France.* Paris: Coln, 1954.

Emlen, S.T. The evolution of helping. I. An ecological constraints model. *American Naturalist* 119:29–39, 1982.

Emlen, S.T. Cooperative breeding in birds and mammals. In *Behavioral Ecology: An Evolutionary Approach,* 1st ed., J.R. Krebs and N.B. Davies (Eds.). Sunderland, MA: Sinauer, 1984, pp. 305–339.

Emlen, S.T. Evolution of cooperative breeding in birds and mammals. In *Behavioral Ecology: An Evolutionary Approach,* 3rd ed., J.R. Krebs and N.B. Davies (Eds.). London: Blackwell Scientific, 1991, pp. 301–335.

Emlen, S.T. Benefits, constraints and the evolution of the family. *TREE* 9:282–285, 1994.

Emlen, S.T. An evolutionary theory of the family. *Proceedings of the National Academy of Sciences* 92: 8092–8099, 1995.

Fitzpatrick, D. Marriage in post-famine Ireland. In *Marriage in Ireland,* A. Cosgrove (Ed.). Dublin: College Press, 1985, pp. 116–131.

Flinn, M.V. Correlates of reproductive success in a Caribbean village. *Human Ecology* 14:225–243, 1986.

Gaulin, S.J.C., and Boster, J. Dowry as female competition. *American Anthropologist* 92:994–1005, 1990.

Goode, W.J. *World Revolution and Family Patterns.* London: Collier-Macmillan, 1963.

Guinnane, T.W. Re-thinking the western European marriage pattern: the decision to marry in Ireland at the turn of the twentieth century. *Journal of Family History* 16:47–64, 1991a.

Guinnane, T.W. Economics, history, and the path of demographic adjustment: Ireland after the famine. *Research in Economic History* 13:147–198, 1991b.

Guinnane, T.W. Age at leaving home in rural Ireland, 1901–1911. *Journal of Economic History* 52:561–647, 1992.

Guinnane, T.W. The Great Irish Famine and population: the long view. *American Economic Review* 84: 303–308, 1994.

Hajnal, J. European marriage patterns in perspective. In *Population in History,* D.V. Glass and D.E.C. Eversley (Eds.). London: Edward Arnold, 1965, pp. 101–143.

Hatton, T.J., and Williamson, J.G. After the Famine: emigration from Ireland, 1850–1913. *Journal of American History* 53:575–600, 1993.

Hill, K., and Hurtado, A.M. *Ache Life history*. Hawthorne, NY: Aldine de Gruyter, 1996.

Homans, G.C. *English Villagers of the Thirteenth Century*. New York: Russel and Russel, 1960.

Hughes, A.L. Reproductive success and occupational class in eighteenth-century Lancashire, England. *Social Biology* 33:109–115, 1986.

Irons, W. Cultural and biological success in man. In *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, N.A. Chagnon and W. Irons (Eds.). North Scituate, MA: Duxbury Press, 1979, pp. 257–272.

Jackson, J.A., Lennartz, M.R., and Hooper, R.G. Tree age and cavity initiation by red-cockaded woodpeckers. *Journal of Forestry* 77:102–103, 1979.

Jennions, M.D., and MacDonald, D.W. Cooperative breeding in mammals. *TREE* 9:89–93, 1994.

Kennedy, R.E., Jr. *The Irish: Emigration, Marriage, and Fertility.* Berkeley: University of California Press, 1975.

Koenig, W.D., and Pitelka, F.A. Ecological factors and kin selection in the evolution of cooperative breeding in birds. In *Natural Selection and Social Behavior: Recent Research and New Theory*, R.D. Alexander and D.W. Tinkle (Eds.). New York: Chiron Press, 1981, pp. 261–280.

Koenig, W.D. Reproductive success, group size, and the evolution of cooperative breeding in the acorn woodpecker. *American Naturalist* 117:421–443, 1981.

Koenig, W.D., and Mumme, R.L. Levels of analysis, and the functional significance of helping behavior. In *Interpretation and Explanation in the Study of Animal Behavior*, M. Bekoff and D. Jamieson (Eds.). Boulder, CO: Westview Press, 1990, pp. 268–303.

Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L., and Stanback, M.T. The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology* 67:111–150, 1992.

Komdeur, J. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358:493–495, 1992.

Krause, J.T. Some implications of recent work in historical demography. *Comparative Studies in Society and History* 1:164–188, 1959.

Low, B.S. Occupational status, landownership, and reproductive behavior in 19th-century Sweden: Tuna Parish. *American Anthropologist* 92:457–468, 1990.

Low, B.S., and Clarke, A.L. Family patterns in nineteenth-century Sweden: impact of occupational status and landownership. *Journal of Family History* 16:117–138, 1991.

MacArthur, R.H., and Wilson, E.O. *The Theory of Island Biogeography.* Princeton: Princeton University Press, 1967.

MacRoberts, M.H., and MacRoberts, B.R. Social organization and behavior of the acorn woodpecker in central coastal California. *Ornithological Monographs* 21:1–115, 1976.

McGregor, P.L. Demographic pressure and the Irish famine: Malthus after Mokyr. *Land Economics* 65: 228–238, 1989.

Messenger, J.C. *Inis Beag, Isle of Ireland.* New York: Holt, Rinehart and Winston. 1969.

O'Brien, J.A. (Ed.). *The Vanishing Irish.* London: W.H. Allen. 1954.

O'Danachair, C. Marriage in Irish folk tradition. In *Marriage in Ireland*, A. Cosgrove (Ed.). Dublin: College Press, 1985, pp. 99–115.

O'Rourke, K. Emigration and living standards in Ireland since the Famine. *Journal of Population Economics* 8:407–421, 1995.

Powell, R.A., and Fried, J.J. Helping by juvenile pine voles (*Microtus pinetorum*), growth and survival of younger siblings, and the evolution of pine vole sociality. *Behavioral Ecology* 3:325–333, 1992.

Pruett-Jones, S.G., and Lewis, J.J. Habitat limitation and sex ratio promote delayed dispersal in Superb fairy-wrens. *Nature* 348:541–542, 1990.

Riedman, M.L. The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology* 57:405–435, 1982.

Røskaft, E., Wara, A., and Viken, Å. Reproductive success in relation to resource-access and parental age in a small Norwegian farming parish during the period 1700–1900. *Ethology and Sociobiology* 13:443–461, 1992.

Rowley, I. The life history of the superb blue wren, *Malurus cyaneus. Emu* 64:251–297, 1965.

Rowley, I. The communal way of life in the splendid wren, *Malurus splendens. Zeitschrift für Tierpsychologie* 55:228–267, 1981.

Schellenberg, J.A. Patterns of delayed marriage: How special are the Irish? *Sociological Focus* 24:1–11, 1991.

Solomon, N., and French, J. *Cooperative Breeding in Mammals.* Cambridge: Cambridge University Press, 1997.

Stacey, P.B. Habitat saturation and communal breeding in the acorn woodpecker. *Animal Behaviour* 38: 723–725, 1979.

Stacey, P.B., and Bock, C.E. Social plasticity in the acorn woodpecker. *Science* 202:1298–1300, 1978.

Stacey, P.B., and Koenig, W.D. *Cooperative Breeding birds: Long-Term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press, 1990.

Stacey, P.B., and Ligon, J.D. Territory quality and dispersal options in the acorn woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. *American Naturalist* 130:654–676, 1987.

Strassmann, B.I. Polygyny as a risk factor for child mortality among the Dogon of Mali. *Current Anthropology* 38:688–695, 1997.

Stys, W. The influence of economic conditions on the fertility of women. *Population Studies* 11:136–148, 1957.

Turke, P. Helpers at the nest: childcare networks on Ifaluk. In *Human Reproductive Behaviour: A Darwinian Perspective*, L. Betzig, M. Borgerhoff Mulder, and P. Turke (Eds.). Cambridge: Cambridge University Press, 1988, pp. 173–188.

Turke, P.W., and Betzig, L.L. those who can do: wealth, status, and reproductive success on Ifaluk. *Ethology and Sociobiology* 6:79–87, 1985.

United Nations. *Demographic Yearbook.* New York: United Nations, 1964.

Voland, E. Reproductive decisions viewed from an evolutionarily informed historical demography. In *Human Reproductive Decisions: Biological and Social Perspectives*, R.I.M. Dunbar (Ed.). New York: St. Martin's Press, 1995, pp. 137–159.

Voland, E., and Dunbar, R.I.M. Resource competition and reproduction: the relationship between economic and parental strategies in the Krummhorn population (1720–1874). *Human Nature* 6: 33–49, 1995.

Voland, E., Siegelkow, E., and Engel, C. Cost/benefit oriented parental investment by high status families: the Krummhörn case. *Ethology and Sociobiology* 12:105–118, 1991.

Walsh, B.M. Marriage in Ireland in the twentieth century. In *Marriage in Ireland*, A. Cosgrove (Ed.). Dublin: College Press, 1985, pp. 132–150.

Walters, J.R., Doerr, P.D., and Carter J.H., III. Delayed dispersal and reproduction as a life-history tactic in cooperative breeders: fitness calculations from red-cockaded woodpeckers. *American Naturalist* 139:623–643, 1992a.

Walters, J.R., Copeyon, C.K., and Carter, J.H., III. Test of the ecological basis of cooperative breeding in red-cockaded woodpeckers. *Auk* 109:90–97, 1992b.

Woolfenden, G.E., and Fitzpatrick, J.W. *The Florida Scrub Jay: Demography of a Cooperative Breeding Bird.* Princeton: Princeton University Press, 1984.

Zack, S., and Rabenold, K.N. Assessment, age and proximity in dispersal contests among cooperative wrens: field experiments. *Animal Behaviour* 38:235–247, 1989.