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THE EVOLUTIONARY SIGNIFICANCE OF LIFETIME REPRODUCTIVE SUCCESS

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ABSTRACT.—Recent studies have reported lifetime reproductive success (LRS) as empirical counts of fledglings, yearlings, or breeders produced by individuals during their lifetimes. In this paper, I show how the mean LRS of the breeding individuals of a population can be calculated from age-specific probabilities of survival and fecundity. An analysis of a simulated population shows that the LRS of males and females from the same population can be different, even though the rates of change in numbers of males and females are identical. Thus, although LRS may be a measure of individual fitness, differences in LRS, even among individuals with different phenotypes and genotypes, cannot be construed to have evolutionary significance. The proper measure of fitness is the Malthusian parameter (m_{ij}). *Received 5 March 1991, accepted 30 July 1991.*

THE ANALYSIS of data from long-term studies of marked birds has resulted in the measurement of lifetime reproductive success (LRS), which refers to the actual production of offspring of specific individuals (Brown 1988, Partridge 1989). Lifetime reproductive success is the product of an individual's reproductive life span (L), fecundity per reproductive year (F), and offspring survival (S; e.g. Brown 1988, Grafen 1988). Usually, investigators calculate the means and variances of LRS and its components (see studies in Clutton-Brock 1988a and Newton 1989a).

There is general agreement that LRS is not a measure of Darwinian fitness (e.g. Grafen 1988, Newton 1989b, Partridge 1989). Nevertheless, Newton (1989b:441) suggested that "it provides a better basis for estimating biological fitness than any other measure yet available," and Partridge (1989:435) indicated that "it is probably a good approximation to [fitness] for many bird populations."

In this paper I will show how the mean LRS of a group of breeders can be calculated from life-table probabilities and, having done that, I will discuss the evolutionary significance of lifetime reproductive success.

A SIMULATED POPULATION

The examination of the relationships between annual reproductive success (ARS), lifetime reproductive success (LRS), and a population's life table requires considering a simulated population because suitable data from field studies are not yet available. I have constructed such a population for this purpose (Tables 1 and 2). In this population some males are polygynous, others monogamous. All females are monogamous, but some are primary females, others secondary females. Females produce no more than one brood in a year. Males begin to breed at age 3 yr, whereas females begin at age 1 yr. Not all males of breeding age, however, actually breed. Because of territorial behavior or other factors, only 95.12% of males of ages 3 yr and 4 yr breed. Because of illness or other factors, only 99.29% of females of ages 1 yr, 2 yr, and 3 yr breed.

In order to simplify analysis, I have constructed a population that is in a steady-state (neither increasing nor decreasing in size) and has a stable (nonchanging) age structure. In the long term, populations that have not become extinct are in what I have called an evolutionary "steady-state," or E"SS" (Murray 1991a). Populations (groups of individuals of the same species within a circumscribed area) that have been studied for a long period of time may increase or decrease in numbers from year to year, but rarely, if ever, will they increase or decrease continuously over a long period of time. This does not mean that a species cannot increase in total numbers continuously for long periods by expanding its range outside the circumscribed area. Demographic data should reflect the fact that populations seldom have continual increases or decreases over a long time period. Furthermore, to simplify the computation, I have assumed no differences in fecundity or in ARS with respect to age. These simplifying assumptions should not affect the points to be drawn from the analysis.

Annual survivorship (s_x) from age class x to

TABLE 1. Survivorship for simulated population. There are 2,523 males of breeding age of which 2,400 breed, and 3,928 females of breeding age of which 3,900 breed. Q for males = 2,400/2,523 = 0.9512. Q for females = 3,900/3,928 = 0.9929.

	Numbers (N_x)		Survivorship (l_x)	
Age	Males	Females	Males	Females
0	10,000	10,000	1.0000	1.0000
1	3,619	2,352[a]	0.3619	0.2352
2	2,352	1,106[a]	0.2352	0.1106
3	1,529[a]	470[a]	0.1529	0.0470
4	994[a]	0	0.0994	0.0000
	18,494	13,928		

[a] Breeders.

TABLE 3. Life table for males and females of simulated population.

Age (x)	s_x	l_x	m_x	l_xm_x
		Males		
0	0.3619	1.0000	0	0
1	0.6500	0.3619	0	0
2	0.6500	0.2352	0	0
3	0.6500	0.1529	3.9635	0.6060
4	0	0.0994	3.9635	0.3940
				1.0000
		Females		
0	0.2352	1.0000	0	0
1	0.4702	0.2352	2.5458	0.5988
2	0.4250	0.1106	2.5458	0.2815
3	0	0.0470	2.5458	0.1197
				1.0000

age class $x + 1$ in this steady-state population is N_{x+1}/N_x. Survivorship (l_x) is the product of age-specific survivorship from birth to age class x. Fecundity (m_x) is the number of newborn individuals (N_0) divided by the number of breeders (N_B). The life tables for males and females show that this population is in a steady-state (i.e. $\Sigma\, l_xm_x = 1$; Table 3).

ANNUAL REPRODUCTIVE SUCCESS

To calculate LRS, we need to know the annual reproductive success (ARS). The ARS of polygynous (pg) males in terms of number of young reared (k) through fledging (f) is a variation of equation 8 in Murray (1991b),

$$\mathrm{ARS(pg,\ k,\ f)} = Q \sum_{g=1} \left(F_g \sum_{r=1} c_r s_r k_r \right), \qquad (1)$$

where F_g is the frequency of males mated to g number of mates, c_r is the average number of clutches laid by their rth mate, s_r is the probability that a clutch laid by the rth mate is successful, k_r is the mean number of fledglings per successful clutch of the rth mate, and Q is the proportion of members of breeding age that, in fact, are breeding. The breeding population is defined as all females (or males) of breeding age, including experienced but nonbreeding

TABLE 2. Reproductive data for simulated population.[a]

Clutch number	Primary female			Secondary female			All females		
	C	S	F	C	S	F	C	S	F
				Monogamous males (F_1 = 0.3750)					
1	900	315	819						
2	585	234	608						
3	103	52	134						
	1,588	601	1,561						
				Bigamous males (F_2 = 0.6250)					
1	1,500	420	1,092	1,500	300	600			
2	780	312	812	810	243	486			
3	137	69	177	0	0	0			
	2,417	801	2,081	2,310	543	1,086			
				Totals					
1	2,400	735	1,911	1,500	300	600	3,900	1,035	2,511
2	1,365	546	1,420	810	243	486	2,175	789	1,906
3	240	121	311	0	0	0	240	121	311
	4,005	1,402	3,642	2,310	543	1,086	6,315	1,945	4,728

[a] C is number of clutches laid, S is number of successful clutches where fledglings were reared, and F is number of fledglings reared.

"loafers," but not including inexperienced birds that are not breeding and have never made a breeding attempt (see Murray 1991b). Values for F_g are given in Table 2, and values for c_r, s_r, and k_r for males of the simulated population are given in Table 4. With these values, then,

$$\begin{aligned}\text{ARS(pg, k, f)} &= 0.9512\{0.3750(1.7644 \times 0.3785 \times 2.5973) \\ &\quad + 0.6250[(1.6113 \times 0.3314 \\ &\quad \times 2.5980) + (1.5400 \times 0.2351 \\ &\quad \times 2.0000)]\} \\ &= 1.8739. \qquad (2)\end{aligned}$$

The equation for calculating ARS of monogamous (m) females in terms of young reared (k) through fledging (f) is equation 4 in Murray (1991b),

$$\text{ARS(m, k, f)} = Q \sum c_n s_n k_n, \qquad (3)$$

where c_n is the number of clutches laid in producing the *n*th brood, s_n is the probability that an *n*th-brood clutch will successfully produce young, k_n is the average number of young produced from a successful *n*th brood. Thus,

$$\begin{aligned}\text{ARS(m, k, f)} &= 0.9929(1.6192 \times 0.3080 \times 2.4308) \\ &= 1.2037. \qquad (4)\end{aligned}$$

As expected in a population with polygynous males and monogamous females, the ARS of males is greater than that for females. Furthermore, the ratio of ARS of females to ARS of males equals the ratio of breeding males to breeding females (Murray 1991b). Thus, 1.2037/1.8739 = 2,523/3,928 = 0.6423.

LIFETIME REPRODUCTIVE SUCCESS

I propose that the mean LRS of the breeding individuals in a population is given by

$$\text{LRS} = \sum F_b LRS_b, \qquad (5)$$

where F_b is the proportion of individuals that survive *b* number of breeding seasons and LRS_b is the lifetime reproductive success of individuals that survive *b* number of breeding seasons;

$$F_b = l_b - l_{b+1}, \qquad (6)$$

where l_b is the probability of surviving from age of first breeding to subsequent breeding seasons.

TABLE 4. Values for components of annual reproductive success for males and females of simulated population.

c_1	s_1	k_1	c_2	s_2	k_2
		Males			
	First mate			**Second mate**	
1.7644	0.3785	2.5973	—	—	—
1.6112	0.3314	2.5980	1.5400	0.2351	2.0000
		Females			
	First brood			**Second brood**	
1.6192	0.3080	2.4308	—	—	—

The calculations are presented in Table 5. Considering the females, the rationale is that 100% of the breeders survived to breeding age ($x = 1$), 47.02% survived to begin a second breeding season, and 19.98% survived to begin a third breeding season. Thus, 52.98% survived to begin only one breeding season, 27.04% survived to begin two breeding seasons, and only 19.98% survived to begin all three breeding seasons. The expected LRS of individuals that survive *b* number of breeding seasons is LRS_b, which is $\Sigma_1^b ARS_b$, where ARS_b is the ARS of individuals in their first, second, third, etc., breeding season. The LRS_b of females that breed in only the first breeding season is the average ARS of females (one could work out age-specific ARS if one had the data, but in this example, we have assumed no age-specific differences in ARS). The LRS_b of females that breed in two breeding seasons is the sum of the ARS of their first year and the ARS of their second year, and so on. Lifetime reproductive success of all breeding females is the sum of the proportionate contributions of the females that breed in one, two, three, etc., breeding seasons (i.e. $\Sigma\, F_b\, LRS_b$). In the simulated population, the LRS of females is 2.0102 (Table 5). The LRS of males in the same population is 3.0920 (Table 5). The ratio of female LRS to male LRS, 0.650, is close to the sex ratio of breeders, 0.642.

Now, I will determine "empirically" the mean LRS from the "field" data (Tables 1 and 2) as the product of the breeding individuals' mean reproductive life span (L), mean fecundity per reproductive year (F), and mean offspring survival (S). The census shows that 2,352 females survived to breed in one breeding season, 1,106 in two, and 470 in three. Thus, 1,246 females bred in only one breeding season, 636 bred in two breeding seasons, and 470 bred in three

TABLE 5. Lifetime reproductive success of males[a] and females[b] of simulated population.

Age (x)	s_x	b	l_b	F_b	ARS_b	LRS_b	F_bLRS_b
				Males			
0	0.3619	0	0	—	0	0	0
1	0.6500	0	0	—	0	0	0
2	0.6500	0	0	—	0	0	0
3	0.6500	1	1.0000	0.3500	1.8739	1.8739	0.6559
4	0	2	0.6500	0.6500	1.8739	3.7478	2.4361
			1.6500				3.0920
				Females			
0	0.2352	0	0	—	0	0	0
1	0.4702	1	1.0000	0.5298	1.2037	1.2037	0.6377
2	0.4250	2	0.4702	0.2704	1.2037	2.4074	0.6510
3	0	3	0.1998	0.1998	1.2037	3.6111	0.7215
			1.6700				2.0102

[a] LRS(pg, k, f).
[b] LRS(m, k, f).

breeding seasons. The mean number of breeding seasons for these females is $[(1{,}246 \times 1) + (636 \times 2) + (470 \times 3)]/2{,}352) = 1.67$. Note that L is the $\Sigma\, l_b$ in Table 5. The fecundity per reproductive year, F, is 2 m_x (Table 3), which is 5.0916 (= 2 × 2.5458). The probability of surviving from birth (as an egg) to fledging, S, is the 4,728 fledglings produced from 20,000 eggs (Table 2), which is 0.2364 (assuming in this example that the sex ratio at fledging is 1). From these numbers,

$$\begin{aligned} \text{LRS} &= \text{L} \times \text{F} \times \text{S} \\ &= 1.67 \times 5.0916 \times 0.2364 \\ &= 2.0101. \end{aligned} \tag{7}$$

This is the value of $\Sigma\, F_b\, LRS_b$ calculated from the life table (Table 5).

In general, LRS has been referred to as the reproductive success of individuals (Brown 1988, Newton 1989b, Partridge 1989). In practice, the mean LRS is the mean of individual LRSs rather than the product of mean L, mean F, and mean S (David Brown, pers. comm.), although with large samples both values of LRS should be the same. With small samples, it is not (see studies in Clutton-Brock 1988a, Newton 1989a). Nevertheless, by placing LRS within the context of a life table, one should be better able to evaluate its evolutionary significance.

Before doing so, I point out that the method described here assumes that all individuals of a sex begin breeding at the same age. In fact, this is often not the case. When individuals begin breeding at different ages, they may have differences in age-specific survivorship and fecundity as well (e.g. the Florida Scrub Jay, *Aphelocoma c. coerulescens*; Fitzpatrick and Woolfenden 1986, Fitzpatrick et al. 1988, Murray et al. 1989). For such populations,

$$\text{LRS} = \sum \eta\, LRS_\eta, \tag{8}$$

where η is the proportion of individuals beginning to breed at age x and LRS_η is the LRS of individuals beginning to breed at age x.

DISCUSSION

The interpretation of the evolutionary significance of lifetime reproductive success depends on one's view of the process of evolutionary change (e.g. Clutton-Brock 1988b, Grafen 1988, Newton 1989b). My view (Murray 1979, 1985, 1988, 1990) can be briefly summarized. Populations comprise individuals that differ genetically. Some genetic differences result in phenotypic differences that affect survivorship and fecundity of the possessors of particular genotypes. Natural selection (i.e. changes in the frequencies of alternative genotypes) occurs as a result of differences in the probabilities of surviving, reproducing, or both among individuals of alternative genotypes. The genotype with the greatest rate of increase (often called the Malthusian parameter; m_{ij}) is the one that is expected to prevail, unless lost early due to drift.

I have considerable information about a simulated population (Tables 1-5). Yet, it does not provide information about the evolution of traits within the population because what is not known about the population turns out to be critical. One does not know whether the data refer to a clone (a population of genetically identical individuals), a genetically diverse population, or a portion of a genetically diverse population whose members share a particular genotype.

If the population under consideration is a clone, then differences in LRS among individuals or the average LRS of breeders have no evolutionary meaning because natural selection cannot occur among genetically identical individuals (even though "selection," in the sense of being a cause of "observable changes within a generation in the means, variances and covariances of phenotypic distributions" [Arnold and Wade 1984] is occurring). At the other extreme, if the population is genetically diverse, differences in LRS among individuals or in the average LRS of breeders, again, have no evolutionary meaning, this time because individuals with the different relevant genotypes have not been separated into subpopulations.

Suppose, however, that the simulated population is comprised of only the *WW* individuals of a genetically diverse population, the relevant alternatives being *Ww* and *ww*. Suppose, also, that the LRS of the *Ww* and *ww* subpopulations are known. Assume, for example, that LRS of female *Ww* is 2.5 and of female *ww* is 3.0. It still is not known which genotype is increasing at the expense of the others. This fact is established easily by noting that the LRS of male *WW* is 3.0920 and that of female *WW* is 2.0102, even though the Malthusian parameter is identical for both ($m_{ij} = 0$; neither males nor females are increasing or decreasing). By analogy, differences in LRS between alternative genotypes need not reflect differences in m_{ij}. It is for this reason that I have proposed that the Malthusian parameter, the rate of change in numbers of a particular genotype or phenotype, is the best measure of individual fitness (Murray 1979, 1985, 1988, 1990).

Furthermore, the same arguments apply to the interpretation of the variance in the components of LRS (not measured in the simulated population). A trait can vary even in genetically invariable populations. The variance of the components of LRS of a clone could be great and differences between the variances of components could be great; nevertheless, they would have no evolutionary significance. The variance of the components of LRS in genetically diverse populations could be a reflection of genetic variation, environmental variation, or both. Inasmuch as the genetic basis of the variances of components of LRS in studies so far undertaken (see, especially, papers in Clutton-Brock 1988a and Newton 1989a) is unknown, evolutionary implications drawn from analysis of the components of LRS in these species seem premature.

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