REPEATABLE REPRODUCTION IN SONG SPARROWS

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ABSTRACT.—I looked for evidence of consistent variation in individual quality of breeding females in a population of Song Sparrows (*Melospiza melodia*). Consistent differences in individual quality were detected by looking for correlations in reproductive parameters between nesting attempts. Seven reproductive traits were examined for evidence of variation in individual quality. In addition, I determined whether the degree of repeatability was affected by differences in conditions among years, by female age, or by success of previous nesting attempts. There were consistent differences among females in the date of initiation of nesting, clutch size, egg mass, and nutritional condition of offspring. The differences in egg mass between females may be heritable. There was evidence that repeatability of nestling condition is influenced by the success of previous nesting attempts. Although consistent differences were found in quality of female sparrows, there were no "superparents." Females that were good at one given aspect of reproduction were not proficient at all facets of reproduction. *Received 3 April 1992, accepted 25 November 1992.*

THE EXISTENCE of heritable variation in reproductive success is a cornerstone of evolutionary biology (Darwin 1878, Endler 1986). More recently, nongenetic variation has been incorporated into the evolutionary framework (e.g. Högstedt 1980, van Noordwijk and de Jong 1986, Price et al. 1988). Nongenetic differences in individual quality may be due to variation in environment such as territory quality (e.g. Högstedt 1980, Fitzpatrick et al. 1988), or may be permanent effects of environmental conditions during early development (e.g. Richner et al. 1989, Cooch et al. 1991). Identifying the existence of variation in reproductive success ("quality") among individuals is important in a number of fields. In tests of life-history theory, an optimal fecundity for a population may only be demonstrable once one realizes that each bird (or class of birds) has its own individual optimum (e.g. Pettifor et al. 1988, but see Nur 1984). Studies of lifetime reproductive success indicate large differences in the fitness of individuals within populations (Clutton-Brock 1988, Newton 1989), and population and conservation biology deal with source and sink populations (e.g. Pulliam 1988). These differences within and among populations are manifestations of variation in individual quality, and identifying the sources of variation would further population ecology and management.

Considerable evidence exists for variation in individual quality in birds (e.g. Coulson and Porter 1985, Nol and Smith 1987, Birkhead and Goodburn 1989, Mills 1989). These studies indicate that either an aspect of reproductive success (e.g. clutch size; Nol and Smith 1987) or reproductive success itself (e.g. number of offspring raised annually; Mills 1989) differs consistently among individuals. However, many questions remain about variation in individual quality. Where such variation exists, one does not know whether some birds are better at all facets of reproduction than others, or whether only a single aspect of reproduction (e.g. clutch size) differs consistently among individuals. If the latter is the case, then there may be a single critical resource or period of time that determines reproductive success. Understanding causes of variation in reproductive success depends on identifying such critical periods or resources.

Where individuals do not display consistent quality, there may be nonrandom variation in quality within individuals. The most studied example is variation in reproductive success with age (e.g. Sæther 1990). For instance, learned differences in foraging ability may lead to variation in reproductive success with age. Interannual variation in environmental conditions may also affect the degree of consistency of individuals. For example, in relatively good and poor years the degree of variation among individuals may differ. There are also intrinsic reasons why some individuals should not be

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consistent. Parents should not repeat the conditions that caused previous failure of reproduction. For example, divorce may follow failed nesting by Black-legged Kittiwake (*Rissa tridactyla*) pairs (Coulson and Thomas 1983).

In this paper I examine the phenomenon of individual quality in a population of Song Sparrows (*Melospiza melodia*). This population is a good candidate for such a study as evidence already exists for environmental (Hochachka et al. 1989) and genetic (Schluter and Smith 1986) variation in reproductive success. To determine whether parents are repeatable in one or several facets of reproduction, I examine seven independent reproductive parameters. Where significant repeatabilities are found, I consider whether these differences were genetic or environmental. I also test for effects of three factors that might cause nonrandom changes in repeatability of reproductive success: annual fluctuations in environmental conditions, female age, and success of previous nesting attempts. As this population of Song Sparrows is multiple brooded, I was able to examine repeatability both within and among years. Analyses are conducted only on females; variation in quality of males is not considered. Although repeatabilities were detected, analyses indicate that there were not, overall, high-quality or low-quality parents. Instead, two independent suites of traits represented repeatable differences in individual quality.

METHODS

Data in this paper are from the population of Song Sparrows on Mandarte Island, British Columbia, Canada (roughly 25 km NNE of Victoria, British Columbia). The island and general study methods are described in Tompa (1964) and Smith (1981). All Song Sparrows on Mandarte are individually color banded, and almost all (roughly 97%; Hochachka et al. 1989) were banded as nestlings on the island. Hence, ages of breeding females are known. Females in this population are multiple-brooded (Smith 1982, Hochachka 1990), with birds producing on average about 2.5 nests each year (range 1–7). Birds are true multiple brooders: renesting occurs even after young are successfully fledged from a previous nest. Essentially all nests that survive for more than a few days are located; however, some nests that fail early (i.e. during egg laying) are not found. Failure is almost entirely due to nest predation. Thus, when "first nests" and "second nests" are referred to in this paper, these may not always be the true first and second nests that a bird has started in a year. Repeatabilities are calculated for females

and not the territories that they occupy; however, female and territory are almost synonymous. Only 9% of surviving females had completely nonoverlapping territories in successive years, and a smaller proportion of females changed territories between nesting attempts within a year. Data collected on reproductive success allow me to examine repeatabilities of five classes of traits: timing of nesting, clutch size, egg mass, nest failure, and nestling condition. The number of offspring surviving to independence from parental care is also known, and is used in this paper as the "ultimate" measure of annual reproductive success. Within any one year, the number of independent offspring a parent raises is highly correlated with number of offspring recruiting into the breeding population (Hochachka et al. 1989).

There are three separate variables related to timing of nesting: date of first nest of year, date of last nest of year, and internest interval. Data for all three come from the years 1975–1979 and 1981–1990. Date of first nest is the date on which a female laid the first egg of her first clutch in a year. Date of initiation of laying was determined either from finding a nest during laying, or by back dating from nestlings of known age. The date of the last nest is the date on which a female laid the first egg of her last nest of the year. Internest interval is the time between the first egg of one nest and the first egg of the subsequent nest.

The other parameters used in this paper were measured in different sets of years. Clutch size, nest failure (failure of a nest to fledge any young), and number of independent offspring produced were available for all years (1975–1979, 1981–1990). A restricted subset of clutches was used. First, because Brown-headed Cowbirds (*Molothrus ater*) often parasitize Song Sparrows, and because female cowbirds often remove a sparrow egg on laying one of their own (Smith 1981), nests with a cowbird egg were excluded from analyses. Furthermore, because only about 11% of clutches are not of sizes 3 or 4, clutch size is essentially a binomial variable. I excluded from analysis all clutches not of three or four eggs to render the data for clutch size completely binomial, and used statistical techniques appropriate for binomial data (see below). Exclusion of extreme clutches did not affect the qualitative results of analyses involving clutch size (unpubl. analyses). Egg mass was only measured in the years 1985–1990. Nestling condition is an index derived from nestling mass and wing length (see Hochachka and Smith 1991), and data were available for the years 1982–1990. Sufficient data were available to examine repeatabilities for three separate age classes: yearlings, two-year-olds, and three-year-olds.

Data corrections.—To maximize likelihood of detecting repeatabilities, a number of corrections were imposed on the data set. Most of these corrections were used to allow combining of data from several groups, thus increasing sample sizes in analyses. However, while data corrections allowed greater

chance of detecting variation in quality, these same corrections also inflated the estimated repeatabilities above the values that would be observed in nature. Essentially, I have pulled repeatability in reproductive success out of its ecological context in order to examine more closely this one aspect of variation in reproductive success of individuals.

Eggs were not weighed on the days that they were laid, and values for egg mass had to be corrected to account for water loss through incubation. I assumed that 15% of initial mass was lost through incubation and that the rate of loss was constant, as was previously done by Arcese and Smith (1988). Knowing the date that eggs were weighed and the date of hatching (directly or by back dating from known aged nestlings), it was possible to determine the stage of incubation when eggs were weighed. All eggs were corrected back to mass at laying.

Values for internest interval also needed to be corrected, because internest interval increased with increasing numbers of offspring fledging from a nest (Smith and Roff 1980). Values for internest interval were all corrected down to the expected values for females that failed to fledge any offspring. This was done by subtracting the average extension in interval for each brood size (9.2, 15.4, and 18.5 days, for broods of size 1, 2, and 3–4, respectively) from each observed value. The correction factors were determined by quadratic regression of internest interval on number of offspring fledged. The relationship between internest interval and brood size did not vary among years.

The density of Song Sparrows on Mandarte has varied by over an order of magnitude through the course of the study, and reproductive success is strongly influenced by population density (Arcese and Smith 1988, Arcese et al. 1992). Whenever possible, data from all years were combined to maximize sample sizes in analyses. Hence, interannual/density-dependent variation in reproductive parameters had to be corrected for when they were present. The method for standardizing among years was to transform each year's data to a mean of zero and standard deviation of one. This is only applicable for data that are nonbinomial: dates of first and last nests, internest interval, nestling condition, egg mass, and number of independent offspring. Average egg mass and nestling condition did not vary significantly among years and, hence, no corrections for interannual variation were made to these variables. Dates of first and last nests, internest interval, and independent offspring differed significantly among years; dates of first and last nest, and independent offspring also varied significantly with female age. Because the age structure of the population varied from year to year, using the overall population means in standardizing the data would partially confound year and age effects. To avoid this, I standardized data from each age group relative to the annual mean and standard deviation for yearling females. The other option was to stan-

dardize each age class by its own annual mean and standard deviation. I opted against this strategy because annual samples for older birds, particularly three-year-old females, were very small in some years. I felt that standardizing around values determined from small sample sizes was dubious. The largest samples were invariably from yearling females, so they represented the logical age class to standardize around. In no case was there a year × age interaction, so annual variations in population parameters for yearlings accurately indicate the relative values for two- and three-year-olds.

Statistical analyses.—Where repeatabilities within a year could be examined (clutch size, egg mass, nestling condition, nest failure, internest interval), I tested for repeatability between first and second nests within a year; for internest interval the times between first and second, and second and third nests were compared. Separate tests were conducted for females of each age. Repeatabilities among ages were calculated between ages 1 and 2, 1 and 3, and 2 and 3. I only examined interannual repeatability of first nests, even though for some traits data from second nests were available, in order to reduce the number of statistical tests conducted. Because several repeatabilities were calculated for each variable, the level of acceptance for any single test was adjusted by sequential Bonferroni correction (see Rice 1989). Adjustments of probability of rejection of the null hypothesis were made such that for each trait α was 0.05.

Statistical significance of repeatability was determined in one of two ways, depending on the parameter being analyzed. For continuous traits (dates of first and last nests, nestling condition, egg mass, and internest interval), repeatability was evaluated with Pearson product-moment correlations. The two binomial traits (clutch size and nest failure) had to be treated differently. These were analyzed with logistic regression (using BMDPLR; Dixon et al. 1983). Statistical significance was not based on correlations; instead, I tested whether the value for one nest could predict the value for another nest (e.g. whether clutch size for first nest in a year was a significant predictor of clutch size of second nest). Note also that, because clutch size and nest failure were binomial, there was no simple way to correct for interannual variation in these two parameters, even though both varied significantly among years. Interannual differences were largely due to varying population density (Arcese et al. 1992); hence, population density was entered as a covariate in the logistic regressions to account for interannual variation. Where values for correlations between two binomial traits are presented, these correlation coefficients are the averages of correlations calculated separately for each year's data; the coefficients being averaged were weighted by their sample size when the means were calculated.

Correlation coefficients measure repeatability on a population level, but another measure of repeatability

is needed to examine how repeatability of individuals is affected by external conditions (i.e. year, age, or success of previous nest). For each individual, I calculated the absolute value of the difference in a trait between two nests. A zero results from identical values (i.e. indicates perfect repeatability) and larger numbers indicate poorer repeatability. I am explicitly interested in change per se and not the direction of change between nests; hence, the use of absolute values in statistical analyses. These individual values for repeatabilities are termed "repeatability scores" in the text.

The interpretation of statistical tests that fail to reject a null hypothesis is typically done incorrectly. Failure to reject a null may mean that the alternative hypothesis is incorrect (the typical interpretation), but may also indicate that samples sizes are too small to detect a small but biologically real effect. To avoid this problem, the statistical power of tests was calculated where methods were available (from Cohen 1977). I do not know of appropriate power analyses for logistic regression or combined probabilities tests, and so no power analyses are presented for these tests. The results of power analyses are given as β, the probability of failing to reject a false null hypothesis given the observed effect; larger values of β (which varies from 0 to 1) indicate less certainly that the null hypothesis is correct.

In the Results, I present repeatabilities within years and between years separately, under the assumption that different forces may act on reproductive traits within and among years. For instance, the supplies of food on different territories may not fluctuate in parallel within a given year, but some territories may consistently have more at the very beginning of each year. If food availability controls a reproductive parameter, then one would find low repeatability within a year, but high repeatability between years. In the text, I refer to a trait as showing significant repeatability if any single repeatability (within or between years comparisons considered separately) was statistically significant. This relatively lenient criterion for the presence of repeatability was used because of the low power (probability of detecting biologically real repeatabilities) of the statistical tests.

Calculation of heritabilities.—Heritabilities were calculated for traits that were found to be statistically repeatable in order to test for a genetic basis to the repeatability. The heritabilities were calculated between females of the same age because of variation in reproductive parameters (date of first nest and clutch size) with female age. Heritabilities of date of first nest, egg mass, and nestling condition were calculated using mother-offspring regressions (Falconer 1981). Separate heritabilities were calculated for females one and two years of age, because of the possibility that selective mortality of poor females (Nol and Smith 1987) would decrease environmental variance between these ages. Heritability of clutch size had to be calculated in a different manner than for the other three traits. As noted above, clutch size is essentially a binomial trait in the population of sparrows; most clutches either contained three or four eggs. The most appropriate way to calculate heritability of clutch size is to treat clutch size as a threshold trait (Falconer 1981). If the individuals being compared in the heritability analysis were observed under different environmental conditions, the effects of environmental variation are amplified. It becomes less likely that a genetic component of variation will be detected. Thus, the effects of environment should either be corrected for statistically (i.e. by standardizing data among years), or be minimized by comparing individuals occupying the same environment. One major source of variation in clutch size is variation among years due to differences in population density (Arcese and Smith 1988, Arcese et al. 1992). Clutch size, being binomial, cannot easily be standardized among years and, hence, comparisons have to be made within individual years or sets of very similar years. Because heritabilities were calculated between birds of the same age, mother-offspring comparisons could not be made (i.e. mother and daughter are one year old in different years and, therefore, at different population densities). Thus, heritability of clutch size was calculated between full siblings.

All available data were used for date of first nest and egg mass, but because of the problems noted above, data for clutch size came only from two years (1982, 1983; data for these two years with similar average clutch sizes of 3.5 and 3.3, respectively, were combined). Also, because of the problem of variation among years, heritability of clutch size was only calculated for yearling females; sample sizes were too small to permit calculations for two-year-olds.

RESULTS

Repeatable variation in individual quality.—Statistically significant consistency between years (female ages) was found for four reproductive traits: date of first nest, clutch size, egg mass, and nestling condition (Table 1). Even though repeatabilities of these traits were not statistically significant at all ages, the patterns were qualitatively the same (i.e. successful birds at one age also were successful at other ages). Note that the statistical power of these analyses was consistently low. The statistically significant results should be interpreted as identifying the strongest repeatabilities, and not as suggesting that some traits are not repeatable.

Consistent differences in female quality within a year could only be examined for five traits, of which two—clutch size and egg mass—showed significant repeatabilities (Table 2).

TABLE 1. Between-year repeatabilities of reproductive traits. Where repeated measures available for a year (e.g. clutch size), repeatabilities calculated between first nests of each year. Because of Bonferroni corrections of critical α levels, $P \leq 0.05$ does not indicate a significant repeatability. Bonferroni correction used to keep traitwise $\alpha = 0.05$ for within- and between-year repeatabilities combined. For each trait, information presented includes correlation coefficient (sample size in parentheses) in top row, and probability of Type I error (probability of Type II error in parentheses) in bottom row. Power analyses could not be conducted for clutch size or failed nest, the two binomial traits.

Age 1–2		Age 1–3		Age 2–3	
Date of first egg					
0.19	(97)	0.25	(65)	0.38[a]	(50)
0.07	(0.67)	0.05	(0.63)	0.007	(0.38)
Clutch size					
0.09	(82)	0.73[a]	(46)	0.10	(48)
0.74		0.0001		0.25	
Egg mass					
0.47[a]	(18)	0.76[a]	(17)	0.63[a]	(17)
0.05	(0.50)	0.0004	(0.09)	0.007	(0.31)
Nestling condition					
0.32[a]	(74)	0.15	(44)	0.19	(53)
0.005	(0.44)	0.33	(0.95)	0.18	(0.89)
Failed nest					
0.02	(129)	0.07	(78)	−0.06	(81)
0.18		0.46		0.52	
Internest interval					
0.03	(59)	−0.14	(28)	0.14	(35)
0.82	(0.99)	0.47	(0.98)	0.44	(0.97)
Date of last nest					
0.02	(124)	0.06	(77)	0.02	(72)
0.87	(0.99)	0.60	(0.97)	0.88	(0.99)

[a] $P \leq 0.05$ after sequential Bonferroni correction.

TABLE 2. Within-year repeatabilities of reproductive traits. Where repeated measure available for a year (e.g. clutch size), repeatabilities calculated between first nests of each year. Because of Bonferroni corrections of critical α levels, $P \leq 0.05$ does not indicate a significant repeatability. Sequential Bonferroni correction used to keep traitwise $\alpha = 0.05$ for within- and between-year repeatabilities combined. For each trait, information presented includes correlation coefficient (sample size in parentheses) in top row, and probability of Type I error (probability of Type II error in parentheses) in bottom row. Power analyses could not be conducted for clutch size or failed nest, the two binomial traits.

Age 1		Age 2		Age 3	
Clutch size					
0.17	(115)	0.29[a]	(74)	0.12	(31)
0.12		0.001		0.21	
Egg mass					
0.70[a]	(26)	0.67[a]	(27)	0.76[a]	(27)
0.00007	(0.06)	0.0001	(0.07)	0.000004	(0.01)
Nestling condition					
0.03	(61)	−0.13	(54)	0.29	(28)
0.82	(0.99)	0.36	(0.96)	0.14	(0.87)
Failed nest					
0.09	(210)	0.05	(132)	−0.17	(73)
0.18		0.46		0.35	
Internest interval					
−0.25	(44)	0.21	(39)	0.31	(18)
0.11	(0.85)	0.19	(0.92)	0.22	(0.93)

[a] $P \leq 0.05$ after sequential Bonferroni correction.

Again, the repeatability of clutch size was not statistically significant at all ages, but no evidence exists of negative correlations. The lack of repeatability of nestling condition within a year is puzzling. Whereas clutch and egg mass both showed significant differences in female quality both within and between years, nestling condition was only significantly repeatable between years. There was even a negative correlation between condition of offspring from first and second nests for females two years old.

Correlations among traits.—Consistent differences in female quality may have been due to a common cause for the variation in all traits. This would be indicated by high correlations between traits; correlations are presented in Table 3. Note that the correlations for one- and

two-year-old birds are not independent; the birds of age 2 are a subset of those in the age 1 correlations. The only probability values presented are those for the traits in which significant repeatabilities were detected; the rationale is that I am only interested in determining whether the repeatable traits are controlled by the same underlying mechanism. To have conducted statistical tests on all possible correlations would, through use of Bonferroni corrections, have lowered the critical α of each test to an extremely low value. The nonrepeatable traits are included for descriptive, comparative purposes.

None of the traits showing consistent differences among females was significantly correlated with any other reproductive trait, at either female ages 1 or 2 (after levels of acceptance were adjusted with Bonferroni corrections). A decline in clutch size with later laying in yearlings, and decline in nestling condition with increased clutch size for two-year-olds both approached significance. Both patterns are ex-

TABLE 3. Correlations between reproductive traits. Calculation of correlations for binomial traits (clutch size, and nest failure) explained in text. Probability values given only for correlations between statistically repeatable traits. Correlation for yearling birds below diagonal, and for two-year-old birds above diagonal. Where data from first and second nests within a season were available, correlations were between first nests alone. For each trait, information presented includes correlation coefficient (sample size in parentheses) in top row and, where applicable, probability of Type I error (probability of Type II error in parentheses) in bottom row. Power analyses could not be conducted for clutch size or failed nest, the two binomial traits.

	Date of first nest	Clutch size	Egg mass	Nestling condition	Nest failure	Internest interval	Date of last nest
Date of first nest	—	−0.12 (52) 0.13	−0.42 (14) 0.14 (0.90)	−0.003 (24) 0.99 (1.0)	−0.02 (52) —	0.13 (52) —	−0.18 (28) —
Clutch size	−0.29 (50) 0.02	—	−0.24 (11) 0.34	−0.44 (24) 0.04	−0.003 (101) —	−0.02 (80) —	0.10 (59) —
Egg mass	−0.32 (15) 0.40 (0.95)	−0.26 (9) 0.41	—	0.57 (12) 0.05 (0.79)	0.12 (17) —	−0.24 (16) —	0.17 (17) —
Nestling condition	−0.11 (25) 0.60 (0.99)	0.30 (29) 0.11	−0.05 (15) 0.86 (1.0)	—	−0.29 (21) —	−0.11 (23) —	−0.18 (28) —
Nest failure	0.13 (55) —	0.02 (138) —	0.09 (22) —	−0.003 (46) —	—	−0.21 (91) —	−0.36 (67) —
Internest interval	0.09 (52) —	0.02 (98) —	−0.02 (20) —	0.11 (36) —	0.04 (125) —	—	0.20 (57) —
Date of last nest	0.15 (64) —	0.10 (54) —	−0.26 (9) —	−0.04 (29) —	−0.09 (61) —	0.11 (36) —	—

pected for this population of Song Sparrows (Hochachka 1990, Hochachka and Smith 1991). The correlation between egg mass and nestling condition is also quite large for two-year-olds; however, for yearlings the correlation is close to zero, suggesting that the higher correlation for older females may be spurious. In general, it appears that the four repeatable traits (date of first nest, clutch size, egg mass, and nestling condition) are not tightly correlated. However, samples sizes are small, particularly for correlates of egg mass. Again, the statistical power of the analyses was very low. These results should be interpreted as indicating that correlations between traits, if present, were relatively small. Considering the entire correlation matrix, the magnitudes of correlations among traits were relatively small for yearlings, with correlation coefficients being no larger than 0.32, and 11 of 16 coefficients being under 0.15. For two-year-olds, some correlations were larger.

Heritabilities of repeatable traits.—One potential cause of repeatability is a genetic basis for traits. Repeatability provides an upper bound on the size of the heritability. For none of the traits was there a statistically significant heritability, but the sample sizes and power of the analyses were small (Table 4); hence, there is no clear indication that traits are not heritable. If the calculated heritabilities (h^2) are biologi-

cally real, then date of first nest had the lowest heritability and egg mass the highest.

Interannual variation in repeatability.—The degree of repeatability in individual quality may vary among years because of interannual variation in environmental conditions. Repeatability scores for individuals were compared using ANOVA (logistic regression in the case of clutch

TABLE 4. Heritabilities of statistically repeatable traits. For clutch size, heritability calculated as threshold trait from sib-sib data. For all other traits, heritability calculated by mother-daughter regression. Significance of clutch size heritability tested by contingency-table analyses. For all other traits, test was for significant regression slope. One-tailed probabilities presented.

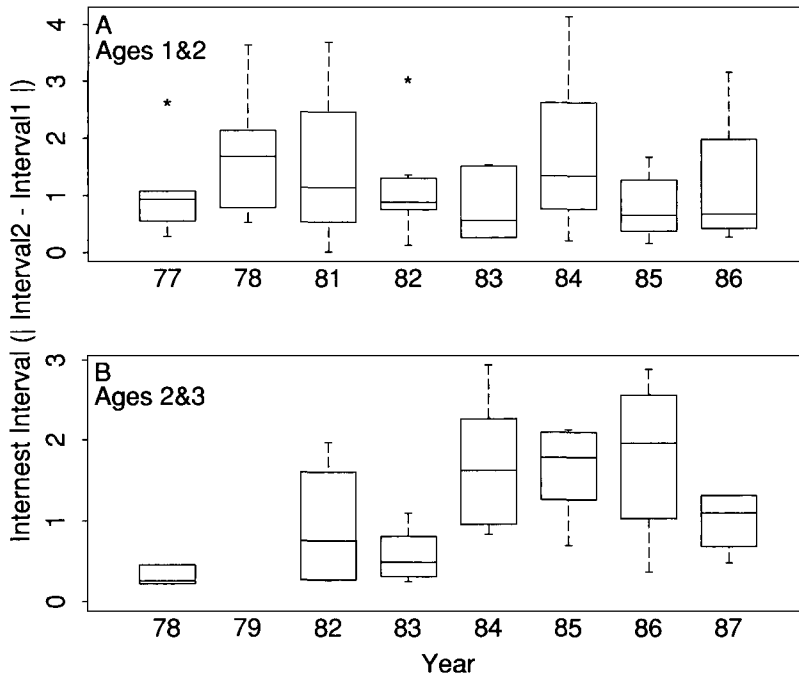| Age	h^2	n	P	β
Date of first egg				
1	−0.01	35	0.99	0.98
2	0.27	29	0.24	0.90
Clutch size				
1	0.61	8	0.74	0.91
Egg mass				
1	0.47	6	0.33	0.95
2	1.00	9	0.09	0.74
Nestling condition				
1	−0.18	46	0.78	0.92
2	0.11	54	0.38	0.95

Fig. 1. Box plots of variation between years in repeatability scores for internest interval. Larger values on the vertical axis indicate lower repeatability. (A) Probability of annual variation in repeatability was small ($P = 0.40$) between ages 1 and 2, but (B) between ages 2 and 3 approached significance ($P = 0.12$, with $\alpha = 0.01$ after Bonferroni correction). Figures are aligned so that birds from the same cohort are shown directly above each other in the two panels. Horizontal lines in middle of boxes indicate median values, bottoms and tops of boxes indicate 25% and 75% quartiles, vertical lines above and below boxes enclose farthest data value within 1.5 times the interquartile range, and asterisks indicate all data values beyond these limits.

size). Because the degree of repeatability also may vary with past success (see below), success of previous nests had to be controlled. I used successful fledging of one or more offspring as my criterion of whether a previous nesting attempt (or nesting year) was successful. Success was either 0 (no offspring fledged), or 1 (at least one offspring fledged). In analyzing the effect of year on repeatability, I looked only at repeatabilities of the larger of these two groups; in most cases these were the successful parents. Year and success were not entered into two-way ANOVAs because sample sizes for unsuccessful females were often very small. In over one-half of the years there were no unsuccessful females for which I had repeatability scores.

The repeatability of individual quality did not vary significantly among years. However, differences in repeatability scores for internest interval approached significance between ages 2 and 3 (Fig. 1). Internest interval was not a statistically repeatable trait within females (Tables 1 and 2), so the observed pattern is one of

interannual differences in the magnitude of variation and not whether a trait is repeatable in some years and not in others. The evidence for lack of interannual differences in repeatability is weak due to the low statistical power of analyses. The smallest probability of erroneously failing to detect a biologically real difference (β) was 0.36, and 14 of 19 tests had a β of 0.8 or higher.

Previous success and repeatability.—Whether a bird was successful at raising offspring in one nesting attempt may influence parental behavior in a subsequent nesting attempt. Repeatability scores of birds that had fledged at least one offspring in their first nesting attempt were compared with scores of birds that had failed to fledge any offspring in their first nests. Only comparisons between first and second nests in a year were made, and not comparisons between years. This was done because effects of previous success are more likely to be felt within a year than between years; conducting tests on interyear repeatabilities would have low-
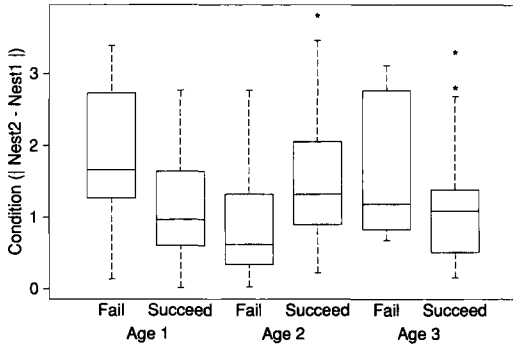
Fig. 2. Box plots of repeatability scores of nestling condition as a function of success of first nest of year. Larger values on vertical axis indicate poorer repeatability. At age 2, birds whose first nest failed to produce any fledglings were more consistent in condition of their offspring than birds whose first nest was successful ($P = 0.003$). Differences not statistically significant at other ages. See caption of Figure 1 for description of information represented by box plots.

ered corrected α levels substantially. Data from all available years were combined in the analyses. Data for egg mass, nestling condition, and internest interval were analyzed with t-tests, and for clutch size with contingency tables.

Only for nestling condition was there a significant effect of success of first nest on repeatability (Fig. 2). The effect, found only for two-year-old females, was that previously successful females were less repeatable than unsuccessful females. Again, note that lack of statistical effects of previous success are poor indicators of lack of biological effects as statistical power of analyses was consistently low ($\beta \geq 0.90$ for all traits except nestling condition, where the probability of failing to reject a false null hypothesis varied from 0.67 to 0.88).

Repeatability and reproductive success.—Repeatabilities of reproductive traits only affects individual quality inasmuch as a repeatable trait is correlated with reproductive success. The measure of reproductive success used below is the number of offspring from the first two nests in a year that reached independence from parental care. For those traits where data from first and second nests were available, the average value for the two nests was used in analyses. Product-moment correlations with data from all years combined were used to test for significant relationships between reproductive traits and numbers of independent offspring for all traits except clutch size and nest failure. For these

TABLE 5. Correlations between reproductive traits and number of independent offspring. For traits where data from first and second nests present, average value for these nests used. Because of Bonferroni corrections, the critical $\alpha = 0.025$. Bonferroni corrections made to keep traitwise $\alpha = 0.05$. For each trait, information presented includes correlation coefficient (sample size) in top row, and probability of Type I error (probability of Type II error) in bottom row. Power analyses could not be conducted for clutch size or failed nest, the two binomial traits.

Age 1	Age 2
Date of first egg	
−0.16 (91)	−0.13 (88)
0.14 (0.78)	0.24 (0.86)
Clutch size	
0.25 (189)	0.34[a] (119)
0.09	0.002
Egg mass	
0.13 (26)	−0.15 (27)
0.53 (0.95)	0.46 (0.93)
Nestling condition	
−0.07 (58)	−0.03 (51)
0.60 (0.96)	0.86 (0.98)
Failed nest	
0.65[a] (189)	0.60[a] (116)
<<0.0001	<<0.0001
Internest interval	
−0.03 (129)	0.09 (91)
0.72 (0.97)	0.39 (0.92)
Date of last nest	
−0.10 (105)	−0.11 (111)
0.30 (0.89)	0.27 (0.87)

[a] $P \leq 0.05$ after sequential Bonferroni correction.

two binomial traits, interannual variation could not be corrected. Hence, correlations between these traits and the number of independent offspring were conducted separately for each year's data; probabilities are from combined probability tests (Sokal and Rohlf 1981:780) on the annual P-values.

As clutch size increased and total nest failure decreased, more independent offspring were produced (Table 5); none of the other traits were significantly correlated with the number of offspring produced. However, the power of all analyses was quite low, so biologically real correlations may exist, although such correlations would be relatively small. For instance, decreased reproductive success with later laying and lower nestling condition have both previously been demonstrated for this population of Song Sparrows (Hochachka 1990, Hochachka

and Smith 1991), although the current analyses (Table 5) show these patterns to be not statistically significant. The most important determinants of individual quality are clutch size and the frequency of total nest failure.

DISCUSSION

The primary aim of this paper was to determine whether female Song Sparrows were either consistently good or poor parents; in general, females were consistent in ability from nest to nest, as evidenced by only 5 of 36 repeatabilities (14%) being negative (Tables 1 and 2). However, even with moderately large sample sizes the only statistically significant repeatabilities found were for date of first egg, clutch size, egg mass, and nestling condition. Statistical power analyses showed that the calculated repeatabilities were generally too small for us to conclude that these repeatabilities were not biologically real. I conclude that, although my data suggest that parents are consistent in reproductive potential, the degree of repeatability is generally very small, even from one nest to the next within a single year.

Nestling condition is unusual in that there was a significant repeatability between years (Table 1), but none within a single year (Table 2). This result is consistent with Hochachka (1990), who showed that average nestling condition was greater for later hatched offspring, and there was no evidence of consistent differences in ability of parents to produce nestlings in high condition. Instead, the low repeatability of nestling condition within a year may be because condition of nestlings from second broods was related to the success of the first nesting attempt (Fig. 2). These data suggest that although a bird starts each year putting the same effort into raising offspring, success of the first nest affects the amount of effort put into subsequent nests in a year. This has been demonstrated previously for Song Sparrows (Nol and Smith 1987) and other species (e.g. McGillivray 1983, Tinbergen 1987).

Given the basic patterns outlined above, I examined whether the statistically significant repeatabilities could be caused by genetic differences among parents by calculating heritabilities (Table 4). For none of the traits was there enough statistical power to demonstrate a statistically significant genetic component to repeatability. For some traits there is evidence that the calculated heritabilities are highly unreliable. The change of sign of heritability of nestling condition between ages 1 and 2 (Table 4) suggests that these heritabilities are not biologically real. Even if there was a small heritability, it cannot account for the presence of significant repeatabilities of nestling condition between years, but lack of repeatability between first and second nests within one year. The large difference in calculated heritability of date of first egg between ages suggests that the large value for two-year-old females (Table 4) is an overestimate. A heritability for clutch size (Table 4) that is larger than the repeatability (Tables 1 and 2) also suggests that the calculated value is an overestimate. In contrast, egg mass had both consistently high heritabilities and repeatabilities. If biologically real, the calculated heritabilities are sufficient to account for most or all of the repeatability found for egg mass. It appears likely that repeatability of egg mass is largely genetically based, but that repeatability of other traits is principally nongenetic.

I also examined three factors that might obscure repeatability of reproductive success; there was no other clear evidence of such obscuring effects for the variables examined. Repeatabilities in reproductive traits did not systematically change with female age (Tables 1 and 2), nor did degree of repeatability vary with year of nesting (Fig. 1). However, the power of these analyses was small enough that subtle variation could not have been detected.

Given some repeatability of reproductive traits (Tables 1 and 2) and little evidence for a genetic basis for repeatabilities (Table 4), one might expect that highly repeatable traits will be closely tied to reproductive fitness (e.g. Gustafsson 1986, Cabana and Kramer 1991). However, in this study repeatable traits were not consistently correlated with reproductive success. Clutch size (repeatable) and nest failure (not repeatable) were the traits most strongly (and the only ones significantly) correlated with fitness (Table 5).

Also expected is that birds proficient at one aspect of reproduction will be good at all aspects of reproduction. However, the data indicate there are no "superparents"—birds that are consistently better at all aspects of reproduction (i.e. producing bigger clutches of larger eggs, and offspring of better nutritional condition). Correlations between repeatable traits were generally low (Table 3). The low statistical power of the correlations indicates that any inter-

pretation should be made with caution. Still, most associations between repeatable traits were negative. Note that the negative correlation between laying date and clutch size represents a positive association between two fitness-related traits; earlier nests have higher survival of individual offspring (Hochachka 1990), more eggs laid and offspring raised. A decrease in clutch size with later laying has been demonstrated for this population of Song Sparrows (Hochachka 1990) and is ubiquitous in birds (Klomp 1970). The other negative correlations between traits are cases where being successful in one aspect of reproduction was associated with lack of success at some other facet of reproduction.

My findings indicate that variation in individual quality or quality of territories exists in Song Sparrows, although the degree of consistency within parents may be very low. The data also show that individual quality is not a single trait with a single cause. There were two main ways for birds to be "good parents": through variation in date of initiation of breeding/clutch size; or through variation in the nutritional condition of offspring. Females that consistently lay the largest clutches are not those that consistently produce the heaviest offspring. These data contradict the individual-optimization hypothesis (Pettifor et al. 1988), which suggests that individuals that produce the largest clutches should also be those best able to care for a large number of offspring. The low or negative correlations between these two sets of reproductive traits suggest that there is no single strategy that can be followed to be a successful parent. Although some adults are capable of being more successful parents than others, this potential can be modified. An example of this modification is the way repeatability of nestling condition within a year was affected by the success of the year's first nest (Fig. 2). "Individual quality" is clearly not a simple characteristic of an individual.

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