

AGE-SPECIFIC FECUNDITY IN EUROPEAN BLACKBIRDS (*TURDUS MERULA*): INDIVIDUAL AND POPULATION TRENDS

ANDRÉ DESROCHERS^{1,3} AND ROBERT D. MAGRATH^{2,4}

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, United Kingdom; and

²Edward Grey Institute of Field Ornithology, Department of Zoology, University of Oxford,
South Parks Road, Oxford OX1 3PS, United Kingdom

ABSTRACT.—We studied age-related variation in fecundity in six cohorts of European Blackbirds (*Turdus merula*) in Cambridge, United Kingdom. Clutch-initiation date, breeding-season length and clutch size varied significantly with age. First-year females started breeding the latest, had the shortest breeding seasons, and had the smallest clutches. Fecundity varied with female age in a nonlinear way; on average, clutch-initiation dates were earliest at the age of 3.7 years, and breeding-season length peaked at 3.6 years of age. Clutch size increased gradually in the range of ages considered (one to six years). After controlling for year effects, significant variation in the age-fecundity relationships remained among cohorts. Longitudinal analyses showed that the increase in fecundity was mainly the result of individuals' intrinsic changes. Given females started breeding earlier, had longer breeding seasons, and laid larger clutches as they became older, independently of the age of their mate. After controlling for the age of their mate, given males showed no increase in fecundity with age. Logit analyses failed to detect positive relationships between the fecundity of first-year females and their survival to the next breeding season. Thus, the increase in fecundity with female age was more the result of intrinsic individual causes than of natural selection resulting in an increased proportion of high-fecundity individuals among older birds in the population. Received 21 November 1991, accepted 27 May 1992.

LIFE-HISTORY and demographic models (e.g. Williams 1966, Charnov and Krebs 1974, Stearns 1976, Charlesworth 1980) typically assume that the age of individuals affects their fecundity. This assumption is borne out by correlations between age and fecundity in many bird species (Sæther 1990). However, as Curio (1983) pointed out, age-fecundity correlations may arise from physiological development or learning (combined here under the term "intrinsic"), correlations between fecundity and longevity, social status, cohort effects, reproductive restraint, or a combination of these factors. Moreover, since the ages of the parents are often highly correlated (Reid 1988), an apparent age effect in one sex may simply be the result of an age effect in the other sex.

Despite numerous claims that age affects life-history traits, most studies have not considered other correlates while seeking to explain the

variation of fecundity with age. For example, 88 of 95 papers cited by Sæther (1990) do not address the changing individual composition of age groups through mortality when comparing fecundities. The shortcomings usually arise from insufficient data or inadequate statistics, and studies on reproduction have only recently started to examine relationships between parental age and fecundity while simultaneously controlling for likely confounding variables (e.g. Clutton-Brock 1988, Newton 1989a).

It is critical that we understand more about the mechanisms causing age effects if we are to develop further the study of life-history strategies. Here, we report on the relationship between parental age and fecundity in a wild, multiple-brooded population of European Blackbirds (*Turdus merula*). Our aim is to address the problem of possible correlations between survival and fecundity by measuring them directly and by using analyses of individual variation, while controlling for the age of mates. We use dates of breeding onset, breeding-season length, and clutch size as measures of fecundity. Other aspects of reproductive success will be discussed elsewhere.

³ Present address: Département de biologie, Université Laval, Ste-Foy, Québec G1K 7P4, Canada.

⁴ Present address: Division of Botany and Zoology, Australian National University, G.P.O. Box 4, Canberra 2601, Australia.

TABLE 1. Age composition and breeding population size of European Blackbirds in Cambridge Botanic Garden, 1985-1990.

	1985	1986	1987	1988	1989	1990
Males						
Yearling	8	22	16	33	16	27
Older	35	61	78	73	96	75
Unknown	31	19	4	2	2	0
Females						
Yearling	3	20	15	38	23	33
Older	20	47	67	67	91	69
Unknown	51	35	16	3	0	0
No. pairs	74	102	98	108	114	102

STUDY AREA AND METHODS

We conducted this study from 1985 to 1990 in the Cambridge University Botanic Garden, Cambridge, United Kingdom. The Botanic Garden is a 16-ha mosaic of lawns, hedges and areas with shrubs and trees that provides a wide range of nesting and feeding sites for European Blackbirds. We studied about 100 pairs of color-banded European Blackbirds each year (Table 1). Most pairs produced two or three clutches each year. We banded as nestlings 31% and 17% of breeding males and females, respectively. Throughout the study, we determined the age (yearling or older) of immigrants by looking at the contrast between flight feathers and upper wing coverts (Svensson 1984). The proportion of birds of known age varied from 45% (1985) to 100% (1990; Table 1).

Each year, we made daily surveys from late winter to the end of the breeding season to find nests, to record dates of laying (first egg), and to determine the size of each clutch. We recorded laying dates by direct observation (64% of clutches were found before the end of laying) or by estimation from the date of hatching. Our laying-date estimates were based on the observation that the mean incubation time was 13.5 days (Magrath 1989a). Late initiation dates may have resulted from not discovering abandoned or depredated clutches earlier in the season, but we assume that this was rare, since we made thorough and systematic searches of potential nest sites throughout the season, each year. While searching cover thoroughly, we almost never found abandoned nests that had not been recorded before. Thus, it is unlikely that unrecorded nests in the study area would affect the results. Some pairs may have also nested at least once outside the perimeter of the study area, but we dealt with this problem in two ways: (1) by studying only pairs that were present within the limits of the botanic garden each week throughout the breeding season; (2) by making a few surveys each year of the layer of territories surrounding the botanic garden to identify color-banded individuals. Birds repeatedly seen outside the study area were not included in the analyses.

Clutch sizes were included in the analysis only when the females were seen incubating two or more days after laying the last egg. Other (abandoned or depredated) clutches were not included in the clutch-size analysis. We also estimated clutch sizes from nests that were discovered less than two days after hatching by assuming that no eggs or hatchlings were taken away since the end of laying. This assumption was probably false in some cases, but it should have little effect because single eggs disappeared very rarely (Magrath 1989a). Birds that had a territory in previous years were classified as dead when they were not seen later than 31 March.

Data analysis.—Clutch-initiation dates were recorded in days following the end of the previous year. For each individual, breeding-season length was defined as the difference between first and last clutch-initiation dates in a given year (zero in the case of single-clutched birds). Breeding-season length, therefore, was a measure of how long birds were prepared to raise young. We consider this measure more useful than the number of clutches, because the latter tends to be high in territories where nest predation is high, simply because birds are forced to produce replacement clutches (Desrochers and Magrath in prep.).

We adjusted data on clutch-initiation dates and season lengths for year effects by subtracting annual population means from raw data. Population means were computed after excluding yearlings to avoid variation due to changes in age structure (yearling : adult ratio of breeders) among years. All references to clutch-initiation dates and breeding-season lengths in this paper refer to these residuals.

Because of consistent seasonal variation of mean clutch size (Fig. 1), we adjusted clutch sizes by laying date before considering year effects. We used a multiple regression of clutch size with laying dates (linear and quadratic) to account for seasonal variation in clutch size. We then calculated residuals about the fitted regression. We used only pairs composed of two-year-old or older parents to calculate the regression, because birds of different ages nested at different times of the year (see below).

We used parametric methods whenever sample sizes were large and the errors did not greatly depart from the assumptions of normality and homoscedasticity (Sokal and Rohlf 1981). All analyses were performed with the SPSS/PC+ statistical program (Norusis 1986, 1988).

RESULTS

Mean dates of first clutches varied between 31 March and 9 April (range among pairs was 28 February–5 June), and variation among years accounted for 4.6% of the variance of first laying dates (yearlings excluded to control for changes in age structure; $F_{5,472} = 3.8$, $P = 0.002$). Mean breeding-season length varied between 24 and

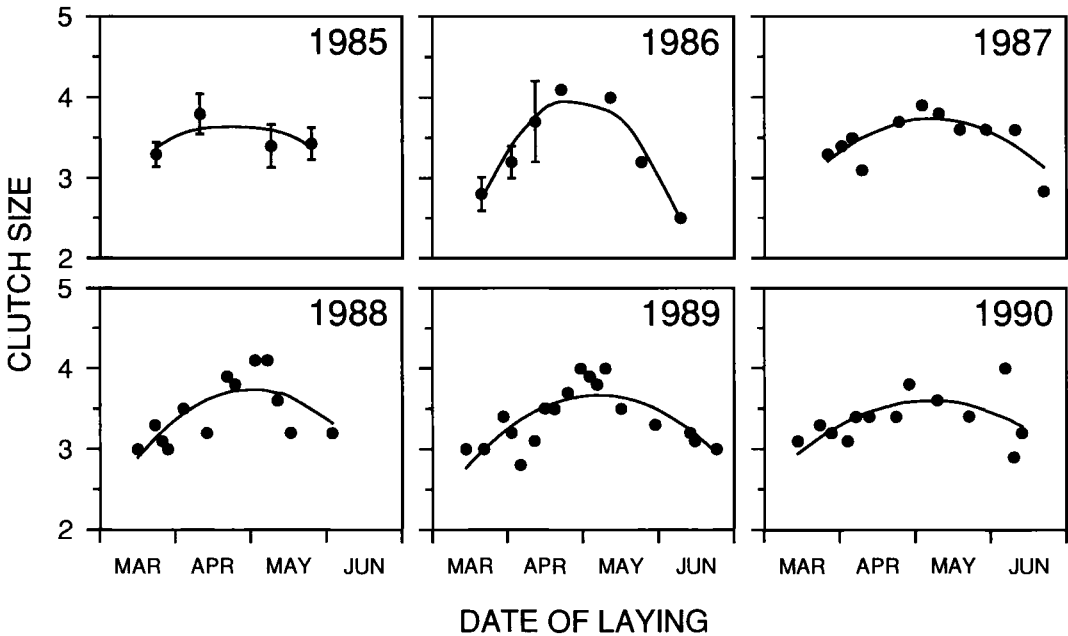


Fig. 1. Seasonal variation of clutch size in European Blackbirds at the Cambridge Botanic Garden. Each point represents a mean (with SE bars) for 10 clutches. Curves calculated by least-squares method. Quadratic regression coefficients were significantly different from zero ($P < 0.05$) in all years except 1985. With years pooled, laying date (linear and quadratic) explained 13% of variation in clutch size.

44 days (data ranging from 0 to 106 days), and annual variation accounted for 5.6% of the total variation in breeding-season length (yearlings excluded to control for changes in age structure; $F_{5,411} = 8.7, P < 0.001$). The latest clutch in the study was initiated on 12 July.

Clutch sizes ranged from one to five eggs. Laying dates accounted for 13% of variation in clutch sizes (Fig. 1; linear and squared date effects in regression, $F_{2,629} = 46.8, P < 0.001$). To determine whether seasonal clutch-size variation was independent of female age, we conducted a log-linear contingency analysis (effect of clutch by laying date by female age) with clutch sizes grouped in two categories (relative to median) and laying dates in five categories (based on quintiles). The seasonal variation of clutch size was similar with one-year-old and older females, ($G = 3.0, df = 2, P = 0.2$). The estimated "between-year" component of variance of clutch-size (s^2) was negative; thus, there was no evidence of variation of clutch size among years after controlling for seasonal variation.

Our measures of fecundity reflected measures of reproductive success later in the breeding cycle (Table 2).

Changes in fecundity with parental age can result from true improvement of individual performance with age, or from natural selection changing the composition of cohorts with time (Curio 1983). To avoid confounding these two factors, we did an analysis of individual variation in clutch-initiation dates by comparing data for given individuals in their first and second breeding seasons. In addition, to control for possible confounding effects of age correlations within pairs, we selected only cases where mates were either in their first breeding season in both years (because of mortality or divorce), or in a second or later breeding season in both years. This selection of cases allowed direct measures of separate male and female age effects. Individual females started nesting nine days earlier, had breeding seasons longer by about 21 days, and laid 0.4 eggs more per clutch as their age increased from one to two years (Fig. 2). With males, there was no statistical evidence of change in fecundity when the age of given individuals increased from one to two years, although the mean changes were in the same direction as those of females (Fig. 2).

Males that had a breeding season longer than average by one month were 10% more likely to

TABLE 2. Correlations among annual life-history parameters in study population. Data from 396 pairs in six years (one datum per pair-year). All correlations statistically significant ($P < 0.01$). Low values for initiation dates indicate early nesting.

	Breeding- initiation date	Breeding- season length	Clutch size	Fledg- lings/ year
Breeding-season length	-0.50			
Clutch size	-0.24	0.21		
Fledglings/year	-0.34	0.44	0.19	
Independent young/year ^a	-0.22	0.27	0.14	0.65

^a Alive >3 weeks after fledging.

return in the following year, although the error on the estimate was large (Table 3). Females that laid on average one more egg per clutch than the population mean had a lower return rate by 32% (Table 3). No other relation between fecundity and subsequent survival approached statistical significance.

Since variation in laying dates beyond the age of two may obscure age relationships when nonyearlings are grouped in a single age category, we examined the relationship between first laying dates and actual ages of males and females (in years). Even if we examine residuals about population means for a given time, there may remain significant differences among age-fecundity curves for different cohorts (years of birth). To account for this variation, we did analyses of covariance (ANCOVA) of our three fecundity measures by female cohort, with fe-

TABLE 3. Relationship between survival to following year (1 April) and fecundity measures in yearling European Blackbirds.

	Effect (SE) ^a	<i>n</i>	Chi- square	<i>P</i>
Males				
Initiation date	-0.001 (0.01)	89	0.002	0.96
Season length	0.024 (0.01)	71	4.54	0.03
Clutch size	0.193 (0.45)	88	0.19	0.7
Females				
Initiation date	-0.010 (0.01)	88	0.53	0.5
Season length	<0.001 (0.01)	61	<0.01	1.0
Clutch size	-1.359 (0.51)	87	8.42	0.004

^a "Effects" represent *B*-values in $P[s] = 1/(1 + e^{-A+Bx})$, where $P[s]$ is probability of survival, *A* and *B* are fitted parameters, and *x* is one of above fecundity measures. Large *B*s represent large increases in survival per unit increase in fecundity. See Hosmer and Lemeshow (1989) for more details on logit models.

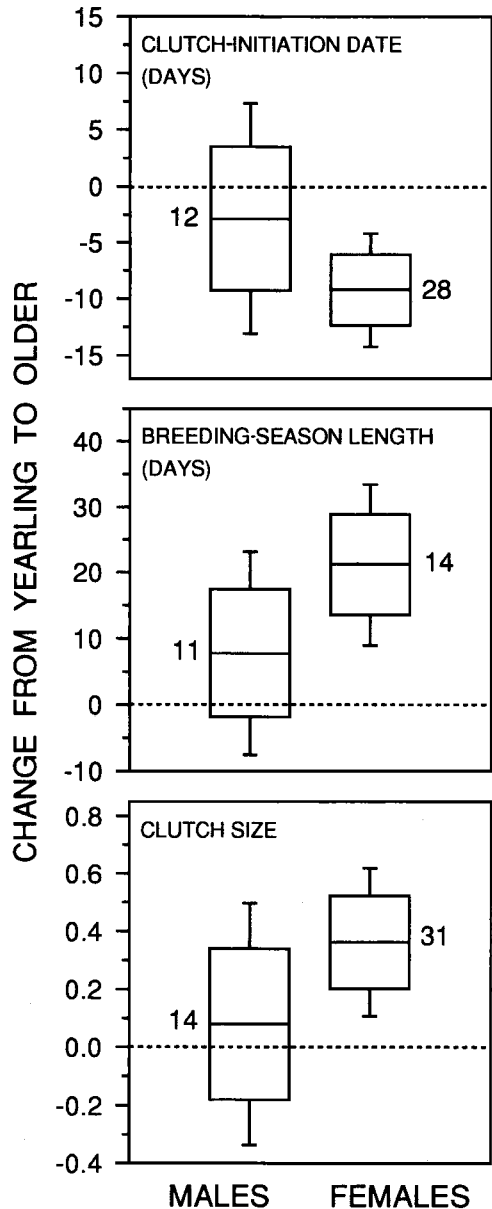


Fig. 2. Change with age in clutch-initiation date, breeding-season length, and clutch size based on measures for the same birds in successive seasons ("older" value minus "yearling" value). All data are values relative to population mean. Clutch-initiation dates are in days following the end of previous year. Boxes represent means (\pm SE); tails represent 95% confidence limits. Sample sizes shown. We included only cases where mate(s) of a given individual were in same age group (yearling or older) in both years.

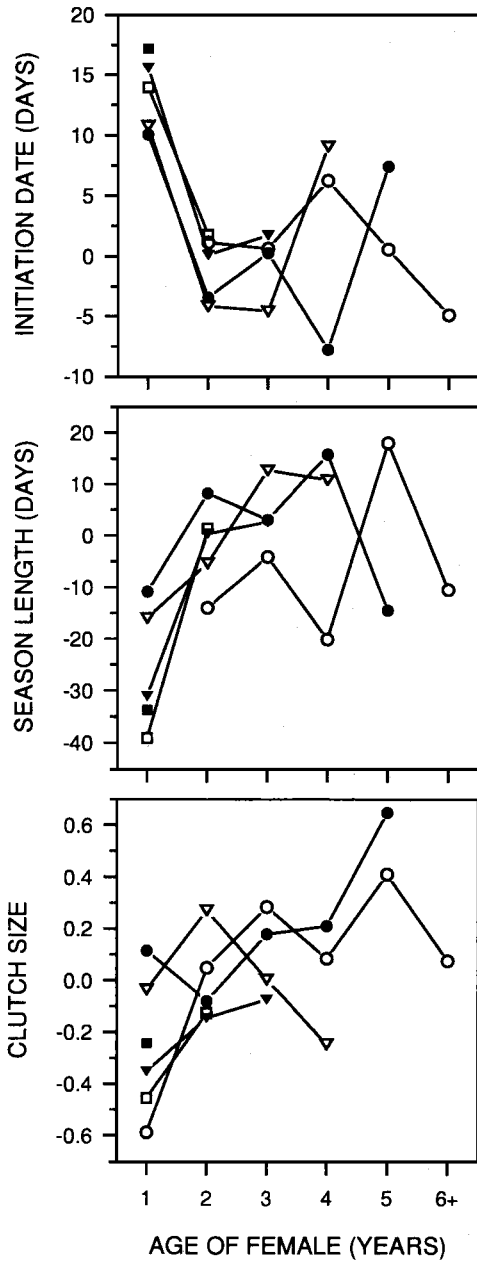


Fig. 3. Changes in fecundity with female age in 1984-1989 cohorts. In each graph, cohorts from 1984 to 1989 represented by open and solid circles, open and solid triangles, and open and solid squares, respectively. Data points represent age-specific means relative to population mean. Curves based on a mean of 47 individuals (range 13-153). Clutch-initiation dates are in days following the end of previous year.

TABLE 4. Analyses of covariance on fecundity measures, with female cohort as a main effect and variables indicating female age as covariates. Cohorts with data from less than three years (1988-1989) excluded from analysis to allow calculation of quadratic terms. Sums of squares (SS) and R^2 -values calculated hierarchically (i.e. only prior effects controlled) in order shown in table.

	SS	R^2 (%)	df	F	P
Clutch-initiation date					
Female age	3,232	8	1	15.5	<0.001
Female age ²	2,082	14	1	10.0	0.002
Female cohort	338	15	3	0.5	0.7
Age × cohort	355	15	3	0.6	0.6
Age ² × cohort	2,307	21	3	3.7	0.01
Residual	30,594	100	147		
Breeding-season length					
Female age	7,036	8	1	15.0	<0.001
Female age ²	8,049	18	1	17.1	<0.001
Female cohort	3,553	22	3	2.5	0.06
Age × cohort	2,177	25	3	1.5	0.2
Age ² × cohort	3,397	29	3	2.4	0.07
Residual	59,213	100	126		
Clutch size					
Female age	5.6	4	1	15.3	<0.001
Female age ²	0.1	4	1	0.3	0.6
Female cohort	5.1	8	3	4.7	0.003
Age × cohort	2.0	9	3	1.8	0.2
Age ² × cohort	3.7	12	3	3.4	0.02
Residual	119.7	100	331		

male age (linear and quadratic) as covariates. There was an overall increase of all three measures of fecundity with female age to six years, irrespective of cohorts (Fig. 3, Table 4). However, the overall shape of age-fecundity relationships was nonlinear, at least for initiation dates and breeding-season lengths (Fig. 3, Table 4). The first derivatives of regression equations for initiation dates and season lengths show that, on average, initiation dates and season lengths peaked at 3.7 and 3.6 years of age, respectively. There was no apparent overall peak for clutch size (no overall age² effect; Table 4). Female fecundity peaked at different ages in different cohorts (interactions with age² in Table 4), at least for initiation date and clutch size. In the case of clutch size, the lack of overall age² effect suggests that there were cohorts in which clutch size increased approximately linearly with age. Little can be said about overall fecundity differences among cohorts irrespective of age (i.e. cohort factor in Table 4), since they reflect the unequal distribution of data points among age groups in different cohorts.

DISCUSSION

Factors intrinsic to females, rather than differential mortality, were the most influential factor leading to variation in fecundity among age classes, although we also found cohort effects. Our study is consistent with other accounts of age-related fecundity (European Blackbirds, Snow 1988; other birds, Sæther 1990), but more importantly, it is one of few studies (see below) that have examined independent effects of the age of mates, mortality, and cohorts on bird life history. The differences among cohorts in relationships between age and fecundity have been ignored in other studies.

Cross-section vs. longitudinal approaches.—Positive correlations between fecundity and longevity may lead to a spurious increase of fecundity with age in cross-sectional analyses (Curio 1983, Clutton-Brock 1988, Newton 1989a). Such correlations are common (e.g. Högstedt 1980, Smith 1981, Coulson and Porter 1985, Gehlbach 1989, Wooller et al. 1990) and may arise because of variation in resource availability or quality among individuals (van Noordwijk and de Jong 1986). Therefore, it is insufficient to use cross-sectional analyses alone to draw conclusions about age effects on fecundity.

In our study, the postbreeding survival of yearlings was insufficient to account for age-specific changes in fecundity. Although yearling males with short breeding season tended to be "weeded out" of the population, there was no apparent correlation between male age and breeding-season length. We found no other positive correlations between fecundity and longevity that could result in the observed changes in fecundity among age groups. In other words, individual (longitudinal) variation in fecundity closely matched our within-cohort (cross-sectional) results. Thus, the general improvement in fecundity with age in our study was mainly due to intrinsic rather than "selection" effects at the population level (Curio 1983) by which the proportion of high-quality individuals changes among age groups. In one case our cross-sectional data may even underestimate the real effect of age, because yearling females with large clutches were more likely to disappear than "poorer" females.

Intrinsic age-related effects may include learned and morphological components, which cannot be distinguished here. Foraging ability

improves with age in the European Blackbird (Desrochers 1992b), as is often the case in young birds (reviewed by Marchetti and Price 1989). A low foraging success of young birds is generally invoked as the main constraint limiting fecundity of young breeders (e.g. Lack 1968: 304), but this claim has received little direct support (but see Heinsohn et al. 1988, Heinsohn 1991, Desrochers 1992a). Using the same population of European Blackbirds, Desrochers (1992a) showed that a daily food supplement early in the season was sufficient to eliminate age-related differences in dates of first clutch initiation, demonstrating the link between parental age, foraging success and fecundity. Alternatively, Williams (1966) and others showed that adaptive restraint of reproductive effort at an early age may lead to the increase of fecundity with age. However, the importance of adaptive restraint in determining avian age-related fecundity should be studied through experimental manipulation (Clutton-Brock 1984, Reznick 1985). The analyses presented here do not allow us to discriminate between the "constraint" and "restraint" hypotheses linking fecundity with age, but a field experiment made on this population supports the constraint hypothesis (Desrochers 1992a).

Relatively few studies of birds have shown that given individuals increase their fecundity as they get older (Kluijver 1951, Davis 1975, Brooke 1978, Ekman 1984, Harvey et al. 1985, Hamann and Cooke 1987, Nol and Smith 1987, Scott 1988, Dhondt 1989, Lessels and Krebs 1989, McCleery and Perrins 1989, Newton 1989b). Only the study by van Noordwijk et al. (1981) looked for and failed to find an increase in fecundity of given females as they became older, despite a large sample size.

Role of sexes.—While longitudinal studies have dealt with confounding effects of mortality on comparisons between age groups, they have generally not distinguished male and female effects; since the ages of mates are often correlated (reviewed by Reid 1988), it is difficult to assess the relative importance of the ages of males and females. To date, our investigation and that of McCleery and Perrins (1989) are the only studies of age effects that simultaneously address the roles of males' age, females' age, and fecundity-related mortality. Female's age, when grouped as "yearling" or "older," had more influence than male's age on fecundity, a result similar to that found by McCleery and

Perrins (1989) for Great Tits (*Parus major*). Ignoring mate age effects can lead to misleading conclusions, especially if the effects of the two sexes are in opposite directions (Lamprecht 1990). Therefore, in species where males provide resources to offspring, future work should address the separate influence of male and female characteristics on fecundity.

We cannot establish why females' age influenced the fecundity of pairs more than males' age, but it is likely that energetic constraints acted directly on females before laying eggs (Perrins 1970, Magrath 1992). Numerous experiments on vertebrates have demonstrated that resource limitation can delay breeding onset (reviewed by Boutin 1990). The addition of food supplements to the territories of European Blackbirds leads to earlier laying and possibly larger clutches (Magrath 1992, Desrochers 1992a). Food shortage late in the season (Török and Ludvig 1988, Magrath 1989b) also may cause young female European Blackbirds to breed for a shorter period than older females, if we assume that yearlings suffer greater reproductive costs than older individuals because of their lower foraging ability (Desrochers 1992b). Thus, it seems likely that the poorer foraging success of younger European Blackbirds results in a later start in the season, a shorter breeding season, and possibly smaller clutches.

Individual females did not adjust their clutch size according to the age of their mate, even though older males presumably provided better parental care (through proficient foraging; Desrochers 1992b) than yearling males. The small role of the age of males may arise from the females' lack of ability to assess the quality of their mate. Alternatively, young females may be prevented from laying larger clutches because of the costs of laying or incubation. Reproductive restraint early in life (Williams 1966) also may influence clutch size of females regardless of the quality of their mate. Though the age of males was not in itself correlated with fecundity, old males still tended to rear larger clutches (and broods) than yearlings, because their own age tended to be similar to that of their mate.

Cohort effects.—Data from population studies of birds and other vertebrates often come from distinct cohorts of individuals that shared similar environments at an early age. Yet, cohorts are nearly always ignored in data analyses from field studies, leading to a failure to meet the

assumption of independence of errors in statistical tests (Bacon and Andersen-Harild 1989). We showed that age-related variation in fecundity itself can vary among female cohorts. Gustafsson and Pärt (1990) showed experimentally that fecundity early in life can have long-term effects on an individual's life-history traits, thus affecting the age-fecundity curve. A similar pattern could occur in our population, as suggested by the lower survival rate of females that laid large clutches as yearlings, compared to less-fecund yearling females.

Senescence.—To date, little information on senescence is available in birds, but available evidence points to its existence (reviewed by Newton 1989a and Sæther 1990). We found that breeding-season length did not increase linearly with age, but tended to peak at the age of three to four years. By contrast, clutch-size variation did not suggest senescence, although further work may reveal it. Dhondt (1989) and Nol and Smith (1987) found a fecundity peak at two to three years of age in other songbirds, but most other data on avian senescence were obtained from long-lived species (Newton 1989a).

Like most other studies of fecundity, ours did not include nonbreeders in comparisons among age groups. In territorial species like European Blackbirds, large numbers of individuals may have access to food, yet be denied the opportunity of breeding (Brown 1969). Such "floaters" typically are young individuals, at least in birds (e.g. Smith 1978, 1989, Smith and Arcese 1989). Floaters were observed, but were mobile and inconspicuous, as in other species (e.g. Smith 1978, Arcese 1987) and, thus, difficult to study. Nevertheless, limiting the scope to breeders in our study and others probably leads to an underestimate of the actual difference in mean fecundity between yearlings and older birds.

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LITERATURE CITED

- ARCESE, P. 1987. Age, intrusion pressure and defence against floaters by territorial male Song Sparrows. *Anim. Behav.* 35:773-784.
- BACON, P. J., AND P. ANDERSEN-HARILD. 1989. Mute Swan. Pages 363-386 in *Lifetime reproduction in birds* (I. Newton, Ed.). Academic Press, London.
- BOUTIN, S. 1990. Food supplementation experiments with terrestrial vertebrates: Patterns, problems, and the future. *Can. J. Zool.* 68:203-220.
- BROOKE, M. DE L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater *Puffinus puffinus*. *J. Anim. Ecol.* 47:477-495.
- BROWN, J. L. 1969. Territorial behavior and population regulation in birds: A review and re-evaluation. *Wilson Bull.* 81:293-329.
- CHARLESWORTH, B. 1980. *Evolution in age-structured populations*. Cambridge Univ. Press, Cambridge, United Kingdom.
- CHARNOV, E. L., AND J. R. KREBS. 1974. On clutch size and fitness. *Ibis* 116:217-219.
- CLUTTON-BROCK, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *Am. Nat.* 123:212-229.
- CLUTTON-BROCK, T. H. (Ed.). 1988. *Reproductive success: Studies of individual variation in contrasting breeding seasons*. Univ. Chicago Press, Chicago.
- COULSON, J. C., AND J. M. PORTER. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: The roles of clutch size, chick grown rates, and parental quality. *Ibis* 127:450-466.
- CURIO, E. 1983. Why do young birds reproduce less well? *Ibis* 125:400-404.
- DAVIS, J. W. F. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus*. *Ibis* 117:460-473.
- DESROCHERS, A. 1992a. Age-related differences in reproduction by European Blackbirds: Restraint or constraint? *Ecology* 73:1128-1131.
- DESROCHERS, A. 1992b. Age and foraging success in European Blackbirds: Variation among and within individuals. *Anim. Behav.* 43:885-894.
- DHONDT, A. A. 1989. Blue Tit. Pages 15-33 in *Lifetime reproduction in birds* (I. Newton, Ed.). Academic Press, London.
- EKMAN, J. 1984. Density-dependent seasonal mortality and population fluctuations of the temperate-zone Willow Tit (*Parus montanus*). *J. Anim. Ecol.* 53:119-134.
- GEHLBACH, F. R. 1989. Screech-Owl. Pages 315-326 in *Lifetime reproduction in birds* (I. Newton, Ed.). Academic Press, London.
- GUSTAFSSON, L., AND T. PÄRT. 1990. Acceleration of senescence in the Collared Flycatcher *Ficedula albicollis* by reproductive costs. *Nature* 347:279-281.
- HAMANN, J., AND F. COOKE. 1987. Age effects on clutch size and laying dates of individual female Lesser Snow Geese (*Anser caerulescens*). *Ibis* 129:527-532.
- HARVEY, P. H., M. J. STENNING, AND B. CAMPBELL. 1985. Individual variation in seasonal breeding success of Pied Flycatchers (*Ficedula hypoleuca*). *J. Anim. Ecol.* 54:391-398.
- HEINSOHN, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding White-winged Choughs. *Am. Nat.* 137:864-881.
- HEINSOHN, R. G., A. COCKBURN, AND R. B. CUNNINGHAM. 1988. Foraging, delayed maturation and advantages of cooperative breeding in White-winged Chough, *Corcorax melanorhamphos*. *Ethology* 77:177-186.
- HÖGSTEDT, G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. *Science* 210:1148-1150.
- HOSMER, D. W., AND S. LEMESHOW. 1989. *Applied logistic regression*. John Wiley and Sons, New York.
- KLUIJVER, H. N. 1951. The population ecology of the Great Tit, *Parus m. major* L. *Ardea* 39:1-135.
- LACK, D. 1968. *Ecological adaptations for breeding in birds*. Methuen, London.
- LAMPRECHT, J. 1990. Predicting current reproductive success of goose pairs *Anser indicus* from male and female reproductive history. *Ethology* 85:123-131.
- LESSELLS, C. M., AND J. R. KREBS. 1989. Age and breeding performance of European Bee-eaters. *Auk* 106:375-382.
- MAGRATH, R. D. 1989a. Hatching asynchrony and brood reduction in the Blackbird *Turdus merula*. Ph.D. dissertation, Univ. Cambridge, Cambridge, United Kingdom.
- MAGRATH, R. D. 1989b. Hatching asynchrony and reproductive success in the Blackbird. *Nature* 339:536-538.
- MAGRATH, R. D. 1992. Seasonal changes in egg-mass within and among clutches of birds: General explanations and a field study of the Blackbird *Turdus merula*. *Ibis* 134:171-179.
- MARCHETTI, K., AND T. PRICE. 1989. Differences in the foraging of juvenile and adult birds: The importance of developmental constraints. *Biol. Rev.* 64:51-70.
- MCCLEERY, R. H., AND C. M. PERRINS. 1989. Great Tit. Pages 35-53 in *Lifetime reproduction in birds* (I. Newton, Ed.). Academic Press, London.
- NEWTON, I. 1989a. *Lifetime reproduction in birds*. Academic Press, London.
- NEWTON, I. 1989b. Sparrowhawk. Pages 279-296 in *Lifetime reproduction in birds* (I. Newton, Ed.). Academic Press, London.

- NOL, E., AND J. N. M. SMITH. 1987. Effects of age and breeding experience on seasonal reproductive success in the Song Sparrow. *J. Anim. Ecol.* 56: 301-313.
- NORUSIS, M. J. 1986. SPSS/PC+ advanced statistics. SPSS, Inc., Chicago.
- NORUSIS, M. J. 1988. SPSS/PC+ V3.0 Update manual, for the IBM PC/XT/AT/ and PS/2. SPSS, Inc., Chicago.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242-255.
- REID, W. V. 1988. Age correlations within pairs of breeding birds. *Auk* 105:278-285.
- REZNICK, D. 1985. Cost of reproduction: An evaluation of the empirical evidence. *Oikos* 44:257-267.
- SÆTHER, B. E. 1990. Age-specific variation in reproductive performance of birds. *Curr. Ornithol.* 7:251-283.
- SCOTT, D. K. 1988. Breeding success in Bewick's Swans. Pages 202-236 in *Reproductive success* (T. H. Clutton-Brock, Ed.). Univ. Chicago Press, Chicago.
- SMITH, J. N. M. 1981. Does high fecundity reduce survival in Song Sparrows? *Evolution* 35:1142-1148.
- SMITH, J. N. M., AND P. ARCESE. 1989. How fit are floaters? Consequences of alternative territorial behaviors in a nonmigratory sparrow. *Am. Nat.* 133:830-845.
- SMITH, S. M. 1978. The "underworld" in a territorial sparrow: Adaptive strategy for floaters. *Am. Nat.* 112:571-582.
- SMITH, S. M. 1989. Black-capped Chickadee summer floaters. *Wilson Bull.* 101:344-349.
- SNOW, D. W. 1988. *A study of Blackbirds*, 2nd ed. British Museum (Natural History), London.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman, San Francisco.
- STEARNS, S. C. 1976. Life-history tactics: A review of the ideas. *Q. Rev. Biol.* 51:3-47.
- SVENSSON, L. 1984. Identification guide to European passerines, 3rd ed. Privately printed, Stockholm.
- TÖRÖK, J., AND E. LUDVIG. 1988. Seasonal changes in foraging strategies of nesting Blackbirds (*Turdus merula* L.). *Behav. Ecol. Sociobiol.* 22:329-333.
- VAN NOORDWIJK, A. J., J. H. VAN BALEN, AND W. SCHARLOO. 1981. Genetic and environmental variation in clutch size of the Great Tit. *Neth. J. Zool.* 31:342-372.
- VAN NOORDWIJK, A. J., AND G. DE JONG. 1986. Acquisition and allocation of resources: Their influence on variation in life history tactics. *Am. Nat.* 128:137-142.
- WILLIAMS, G. C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. *Am. Nat.* 100:687-690.
- WOOLLER, R. D., J. S. BRADLEY, F. J. SKIRA, AND D. L. SERVENTY. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *J. Anim. Ecol.* 59:161-170.