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LIFETIME REPRODUCTIVE SUCCESS IN BARN OWLS NEAR THE LIMIT OF THE SPECIES' RANGE

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ABSTRACT.—I studied 357 nesting attempts by a minimum of 473 Barn Owls (*Tyto alba*) in northern Utah from 1977 to 1995, and documented lifetime reproductive success for 262 owls. Mean age of first breeding was 1.06 years (range <1 to 3), mean number of years breeding was 1.30 (range 1 to 7), and mean number of years breeding successfully was 1.03 (range 0 to 6). Eleven percent of the pairs produced two broods in one year. Mean number of eggs produced in a lifetime was 9.76 (range 1 to 66), and mean number of young fledged was 5.58 (range 0 to 50). Eight percent of the females laid 25% of the population's eggs, and 55% laid 75%. Of the females that laid eggs, 22% produced no fledglings. Twelve percent of the females left breeding descendants in the population with up to four generations traced; the number of direct descendants from these females ranged from 3 to 69. Longer-lived owls produced more eggs and fledglings in their lifetimes, but age that breeding began did not strongly affect lifetime reproductive success. Breeding age had a weak but nonsignificant effect on clutch size and the number of fledglings produced in a breeding season. Habitat variability did not affect LRS, but sites with higher usage were correlated with higher nesting success. Variability in the severity of winter weather had a strong influence on LRS through mortality of adults, reduction in clutch size, and in the likelihood of producing two broods in one season. Severe winters, though, had little effect on the number of fledglings in a brood in the following breeding season. Age and sex of Barn Owls had very little influence on individual LRS. *Received 5 July 1996, accepted 31 March 1997.*

VARIATION IN REPRODUCTIVE SUCCESS among individuals has attracted considerable attention, and the evolutionary significance of lifetime reproductive success (LRS; the total production of offspring during an individual's life) is still debated (Newton 1989b, Murray 1992, Barrowclough and Rockwell 1993). Newton (1985) made a strong case that measurements of LRS offer several advantages over cross-sectional studies in understanding a species' reproduction. First, better than other measures, LRS reveals the extent that reproduction varies among individuals because a few individuals produce a disproportionate percentage of the next generation, and small differences in annual success among individuals may become large differences over entire life spans (Newton 1985, 1988, 1989a; Clutton-Brock 1988). Second, lifetime measures are not affected as much by short-term factors, e.g. poor breeding years brought on by low prey numbers or bad weather conditions (Newton 1989b).

Information on LRS is valuable for understanding reproductive strategies, but determining LRS is difficult because many marked individuals must be followed throughout their reproductive lives. Largely for this reason, LRS has been reported in only six raptor species: Eurasian Sparrowhawk (*Accipiter nisus*; Newton 1985, 1988, 1989a), Osprey (*Pandion haliaetus*; Postupalsky 1989), Tawny Owl (*Strix aluco*; Wallin 1988), Ural Owl (*Strix uralensis*; Saurola 1989), Boreal Owl (*Aegolius funereus*; Korpimäki 1992), and Eastern Screech-Owl (*Otus asio*; Gehlbach 1989). Most of these species are long-lived, and all but the Osprey are forest inhabitants.

In contrast to the above species, the Barn Owl (*Tyto alba*) is short-lived and inhabits open lands. Thus, its pattern of LRS might differ from other raptors. Barn Owls are amenable to the study of LRS because they: (1) readily accept nest boxes for breeding, permitting easy access for documenting reproductive performance; (2) tolerate human presence; and (3) are very sedentary as breeders (Marti 1994). Barn Owls breed at an early age, lay large clutches in relation to their body mass, can produce two or even more broods per year, and often breed only once in their lifetime (Marti 1992, Taylor 1994). Thus, the LRS of a Barn Owl population makes an interesting contrast to species with

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long lives, delayed onset of reproduction, and low productivity (Southern 1970, Newton 1977, Saurola 1989).

Previously, I reported the cross-sectional pattern of reproduction and the effects of weather on reproduction in a population of Barn Owls living close to the northern limit of the species' range (Marti 1994). That study left a major gap in understanding Barn Owl reproduction because it did not explain longitudinal patterns, i.e. differences in reproductive success among individuals. Here, I fill this gap and contrast patterns of LRS in Barn Owls with those of other birds. I identify the life-history attributes that have important influences on LRS, present individual variation in LRS, and quantify the effect of some environmental factors on LRS. These attributes show that Barn Owls have a reproductive strategy more typical of that of passerines.

METHODS

Study area.—The study area was a narrow (12 to 25 km wide, 500 km²) valley between the Wasatch Mountains and Great Salt Lake in Box Elder, Weber, and Davis Counties, north-central Utah, and is close to the Barn Owl's northern range in the Intermountain Region (Marti 1992). This area formerly was a shrubsteppe desert, but that community is now entirely supplanted by irrigated agriculture and urban development. Hot, dry summers and cold winters characterize the region; mean temperatures for July and January are 23.9°C and −3.5°C, respectively. See Marti et al. (1979) and Marti (1994) for more details on the study area and owl nesting sites.

Data collection and analysis.—From 1977 through 1995, I visited nesting sites (all of which were in nest boxes) year-round at least once per month. I made additional visits as needed to record clutch and brood sizes and to band and color-mark nestlings and adults. Visits were minimized during the incubation period when Barn Owls may desert their nests if disturbed. In 1996, I revisited all of the nesting sites to document whether any of the marked owls were still breeding. The number of suitable nesting sites in the study area was quite limited, and most of the nest boxes that I provided were used by owls (Marti et al. 1979). Thus, I believe that I monitored the nests of most of the population. I captured breeding owls each year to determine their identity and age. Most females were caught by hand in nest boxes. Males occurred in boxes less often, so I sometimes used nest-box traps to capture them (see Saurola 1987). For owls not banded as nestlings, age was determined by wing-molt pattern. Barn Owls do not begin molting primaries until 13 months of age (P. Bloom pers. comm., Lenton 1984, Taylor 1994). Thus, in the spring, breeding owls with one generation of primaries are in their first year of life, and those with two generations of primaries are at least two years old. Only individuals whose entire reproductive lives occurred in the study period were included in these analyses.

Statistical analyses were performed using the Statistical Analysis System (SAS Institute 1988). I used Mann-Whitney *U*-tests and Kruskal-Wallis tests to compare means, Wilcoxon signed-rank tests to compare means of paired samples, and simple linear regression to examine relationships between variables; all tests were two-tailed.

RESULTS

From 1977 through 1995, I recorded 357 nest attempts (at least one egg laid) by a minimum of 473 breeding Barn Owls, among which I documented the complete reproductive lives of 262 banded individuals (179 females and 83 males). None of these 262 bred or was found alive in 1995 or 1996, and all were assumed to be out of the breeding population. Twenty-one additional breeding owls were still alive in 1995, but only nine of them were still breeding in 1996. Thus, eliminating the small number of individuals that remained alive at the end of the study (8% of 262), coupled with the very short average life span of these owls, had little effect on LRS calculations. The following analyses are based on those 262 owls unless otherwise noted.

Variables affecting lifetime reproductive success.—The age that breeding begins is an obvious life-history attribute that contributes to differences in LRS among individuals. The earlier that an individual starts breeding, the more opportunity it has to produce offspring (although early breeding also may have costs in adult survival and later reproduction; Lindén 1988). Most owls in my population began breeding in their first year of life; mean age of first breeding was 1.06 ± SD of 0.32 years (range <1 to 3 years; Fig. 1). Both sexes began breeding at the same age (females, $\bar{x} = 1.04 \pm 0.25$ years; males, $\bar{x} = 1.12 \pm 0.44$ years; $U = 1.57$, $P = 0.12$). Three individuals (two males and one female) bred at seven to nine months of age, but none of them nested successfully (i.e. they produced no fledglings).

A second important variable in LRS is the number of times that a bird breeds in its life. Few owls in this population bred more than

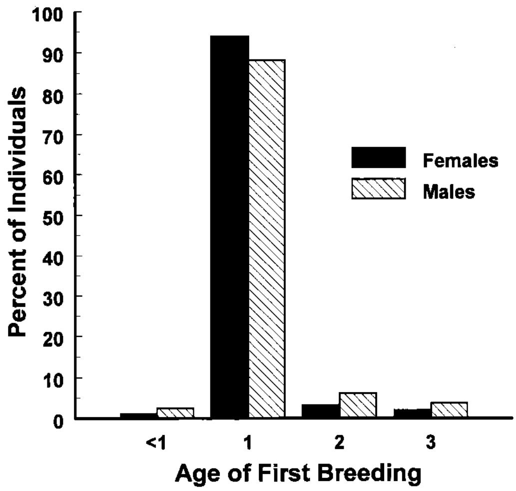

FIG. 1. Age of first breeding by Barn Owls in northern Utah.

once, and the mean number of years of breeding was 1.30 ± 0.79 (range 1 to 7 years; Fig. 2). Females, on average, bred for 1.36 ± 0.86 years and males for 1.19 ± 0.59 years, a difference that was not significant ($U = 1.69$, $P = 0.09$). The number of years that an individual breeds must be partitioned into successful and unsuccessful attempts because the unsuccessful ones add nothing to LRS. Barn Owls bred successfully on average only 1.03 ± 0.83 years (range 0 to 6 years; Fig. 2), and the number of years of successful breeding did not differ between the sexes (females, $\bar{x} = 1.09 \pm 0.91$; males, $\bar{x} = 0.92 \pm 0.61$; $U = 1.00$, $P = 0.32$).

Most raptors produce only one brood per year (Newton 1979, Johnsgard 1988), but producing multiple broods could increase annual productivity and LRS. Only 11% of the Barn Owls produced two broods in one reproductive season (females, $\bar{x} = 0.13 \pm 0.40$ second broods; males, $\bar{x} = 0.10 \pm 0.30$ second broods; $U = 0.52$, $P = 0.60$; Fig. 3). Producing second broods apparently did not shorten life spans of these owls. Indeed, individuals that produced second broods had longer breeding lives than those that did not (sexes combined, $\bar{x} = 2.07$ years with second broods [$n = 29$] vs. $\bar{x} = 1.21$ years without [$n = 233$]; $U = 5.71$, $P = 0.0001$; females, $\bar{x} = 2.2$ [$n = 21$] vs. 1.3 [$n = 158$] years, $U = 5.03$ $P < 0.0001$; males, $\bar{x} = 2.1$ [$n = 8$] vs. 1.1 [$n = 75$] years, $U = 2.46$, $P = 0.01$). The relationship between life span and the production of second broods probably resulted be-

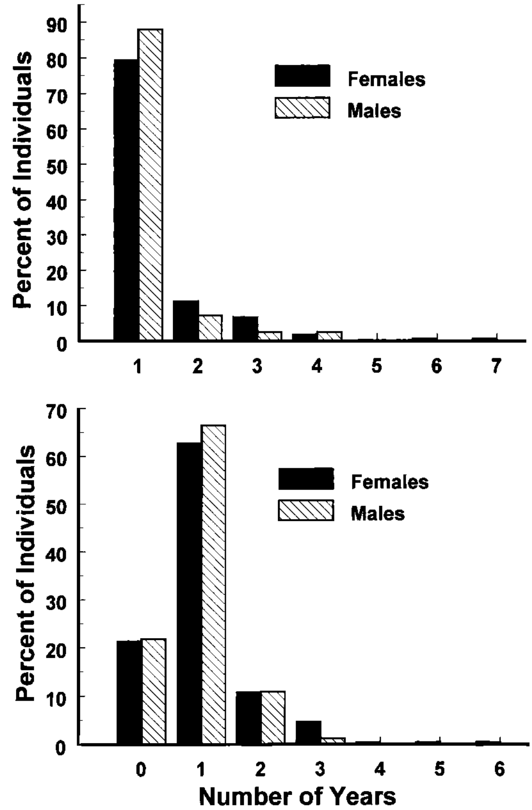

FIG. 2. Number of years Barn Owls bred (upper graph) and number of years Barn Owls bred successfully (lower graph) in northern Utah.

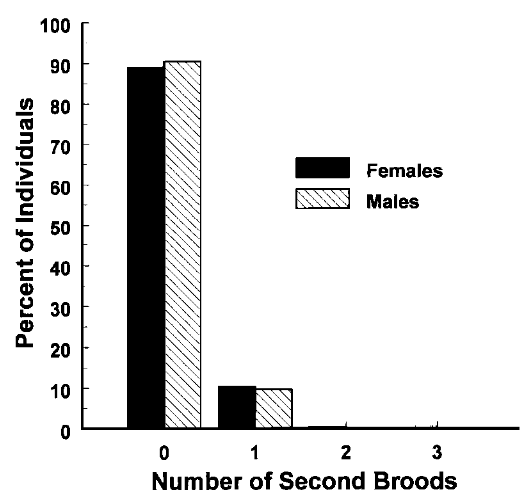

FIG. 3. Production of second broods by Barn Owls in northern Utah.

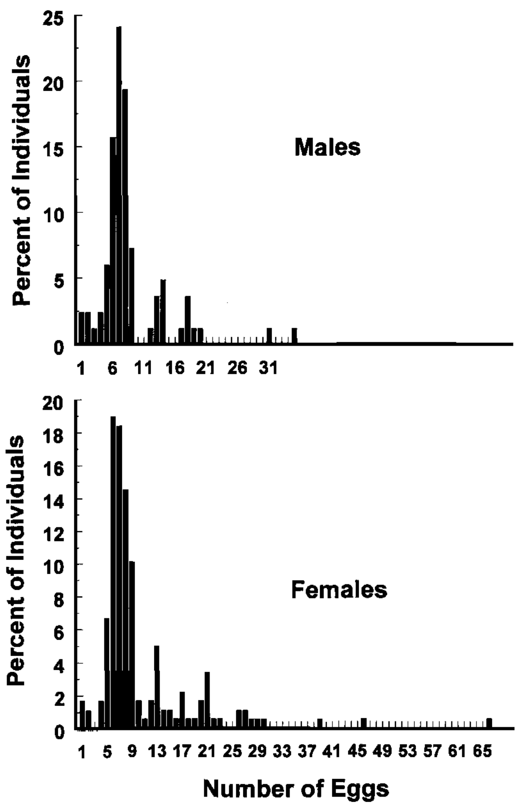

FIG. 4. Lifetime production of eggs by male and female Barn Owls in northern Utah.

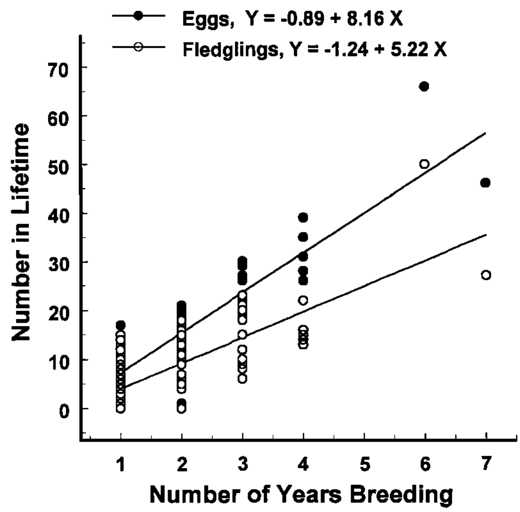

FIG. 5. Relationship between the number of years that Barn Owls bred and lifetime production of eggs (sexes combined, $F = 1024.97$, $r^2 = 0.80$, $P = 0.0001$, $n = 262$) and fledglings (sexes combined, $F = 299.88$, $r^2 = 0.54$, $P = 0.0001$, $n = 262$).

cause owls that lived longer had more chances to produce second broods. However, this relationship seems to show that producing second broods did not result in shortened lives as has been reported in some birds (Bryant 1979, Bennett and Harvey 1988). Attempting second broods in one season might be a good strategy in view of the short life expectancy of these owls.

The power of tests between mean values of males and females was low because sample sizes were small in relation to the slight differences between the sexes. To achieve a power of 0.80 (probability of rejecting the null hypothesis if the means are different), sample size to detect a difference in the age of first breeding was adequate for females but would have to be increased by 112 for males. To attain a power of 0.80 for the other variables, sample size would need to be increased for: (1) number of years breeding, by 197 for females and 178 for males; (2) number of years breeding successfully, by 158 for females and 143 for males; (3) number of second broods, by 2,268 for females and 1,752 for males; (4) number of eggs in lifetimes, by 203 for females and 182 for males; and (5) number fledglings in lifetimes, by 138 for females and 112 for males.

Lifetime reproductive success.—Females that attained breeding status laid from 1 to 66 eggs in their lifetimes ($\bar{x} = 10.2 \pm 7.87$; Fig. 4), and breeding males tended 1 to 35 eggs in their lifetimes ($\bar{x} = 8.7 \pm 5.46$; Fig. 4); the difference between the sexes was not statistically significant ($U = 1.16$, $P = 0.24$). The longer that Barn Owls bred, the more eggs they laid (Fig. 5). Males and females were slightly different in this parameter, with females laying more eggs in their lives than males tended (females, $F = 787.35$, $r^2 = 0.81$, $P = 0.0001$; males, $F = 193.80$, $r^2 = 0.70$, $P = 0.0001$). An even more robust relationship was evident between the number of years that Barn Owls bred successfully and the number of eggs in their lifetimes (females, $F = 423.92$, $r^2 = 0.71$, $P = 0.0001$; males, $F = 59.19$, $r^2 = 0.42$, $P = 0.0001$; Fig. 6). The lifetime production of fledglings ranged from 0 to 50 for females ($\bar{x} = 5.98 \pm 6.28$) and from 0 to 17 for males ($\bar{x} = 4.72 \pm 3.87$); again, the difference between the sexes was not significant ($U = 0.98$, $P = 0.33$). Of the owls that attempted to breed, 22% produced no fledglings in their lifetimes, but the pattern was

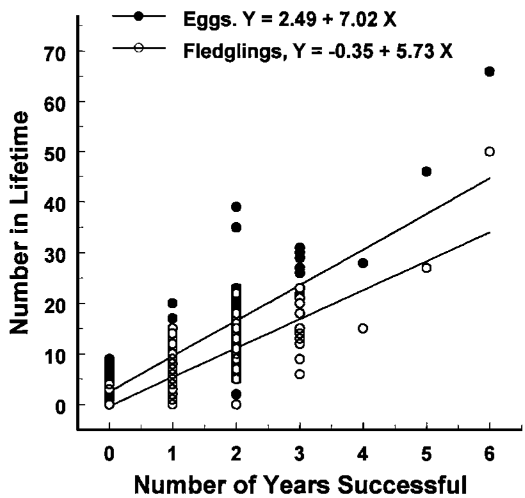

FIG. 6. Relationship between the number of years that Barn Owls bred successfully and lifetime production of eggs (sexes combined, $F = 490.09$, $r^2 = 0.65$, $P = 0.0001$, $n = 262$) and fledglings (sexes combined, $F = 643.65$, $r^2 = 0.71$, $P = 0.0001$, $n = 262$).

similar to that of lifetime egg production (Fig. 7). Again, females exhibited a stronger association between number of years breeding and number of young fledged (females, $F = 249.78$, $r^2 = 0.58$, $P = 0.0001$; males, $F = 34.90$, $r^2 = 0.30$, $P = 0.0001$), and number of years breeding successfully and number of young fledged (females, $F = 526.50$, $r^2 = 0.75$, $P = 0.0001$; males, $F = 89.54$, $r^2 = 0.52$, $P = 0.0001$; Fig. 6). Success at two stages of reproduction, production of clutches and production of fledglings, was parallel. The number of young fledged correlated strongly with the number of eggs laid or tended by individual owls (females, $F = 690.94$, $r^2 = 0.80$, $P = 0.0001$; males, $F = 103.86$, $r^2 = 0.56$, $P = 0.0001$; Fig. 8). The age at which Barn Owls started breeding, though, was not strongly related to the number of eggs laid (females, $F = 0.10$, $r^2 = 0.0006$, $P = 0.75$; males, $F = 3.89$, $r^2 = 0.05$, $P = 0.05$; Fig. 9) or the number of young produced during an individual's lifetime (females, $F = 0.15$, $r^2 = 0.005$, $P = 0.70$; males, $F = 1.51$, $r^2 = 0.02$, $P = 0.22$; Fig. 9).

From an evolutionary viewpoint, a better assessment of an individual's LRS may be the number of descendants that survive to become breeders. On my study area, 21 females (12% of the sample of females with LRS data) produced descendants that bred. In lineages up to four generations, six females produced more

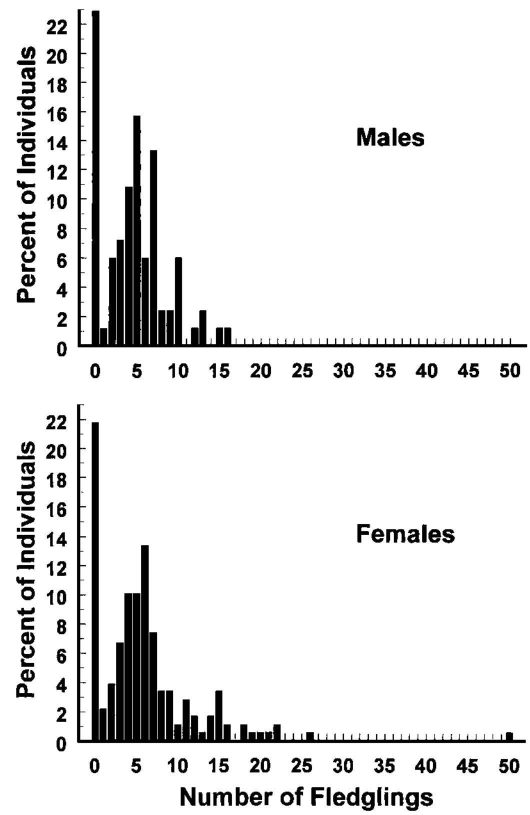

FIG. 7. Lifetime production of fledglings by male and female Barn Owls.

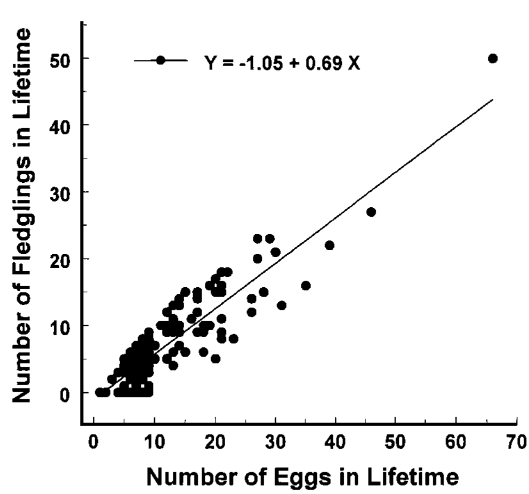

FIG. 8. Relationship between lifetime production of eggs and fledglings by Barn Owls (sexes combined, $F = 804.09$, $r^2 = 0.76$, $P = 0.0001$, $n = 262$).

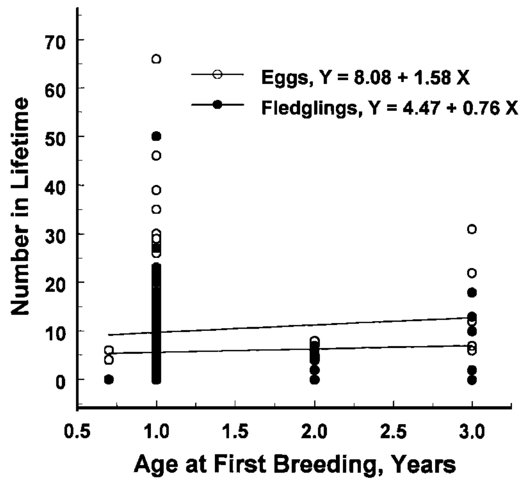

FIG. 9. Relationship between age that Barn Owls started breeding and lifetime production of eggs (sexes combined, $F = 1.30$, $r^2 = 0.005$, $P = 0.26$, $n = 262$) and young (sexes combined, $F = 0.49$, $r^2 = 0.002$, $P = 0.49$, $n = 262$).

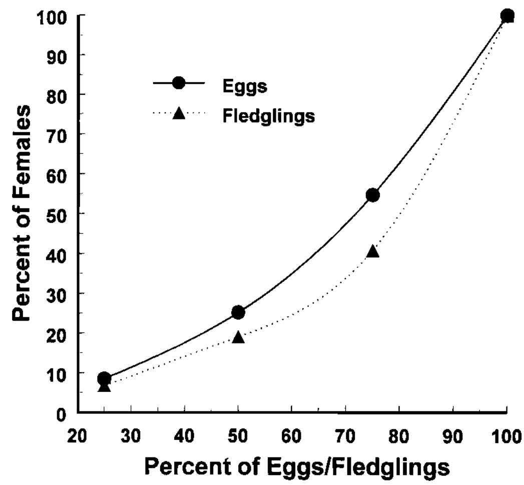

FIG. 10. Percent of eggs and fledglings produced by varying proportions of female Barn Owls.

than 30 descendants each (not all of them became breeders), one female produced 69 total descendants in just three generations, and one female left seven breeding descendants. The mean number of breeding descendants per female was only 0.26, however, and many left none. Descendants of three of the 21 females were still alive at the end of the study, but other hereditary lines either had died out, or the survivors had dispersed from the study area. As noted above, 22% of the females left no surviving offspring, and the remaining 78% produced from 1 to 69 offspring. Unfortunately, knowing the reproductive history, including the number of breeding descendants, was not possible for individuals that dispersed off my study area. It was quite clear, though, that for those that bred on the study area, the contribution of offspring to future generations varied greatly. Twenty-six percent of the breeding females produced 50% of the eggs in the population, and only 19% of the breeding females produced 50% of the fledglings (Fig. 10).

Environmental correlates of lifetime reproductive success.—Environmental factors such as habitat quality and weather may have important influences on LRS. Habitat characteristics across the study area were homogeneous, but some nesting areas might have been of a higher quality than others in prey density or other factors. To evaluate this, I compared reproductive success among nest boxes that were available for at least 15 years; these sites were ranked from 1 to 11 based on the proportion of years they were used relative to the number of years they were available. Annual nesting success was strongly associated with rank, i.e. the higher the percentage of years a site was used, the higher the frequency of successful breeding attempts at that site (Fig. 11). However, clutch size, number of fledglings per brood, and num-

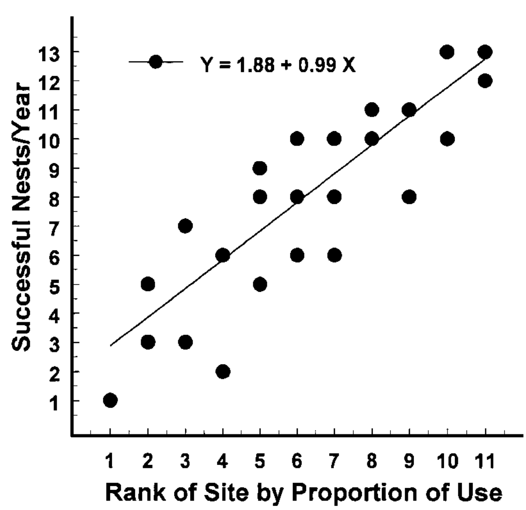

FIG. 11. Relationship between quality of Barn Owl nest sites (1 = worst site) as determined by frequency of use and success of individual nesting attempts ($F = 792.5$, $r^2 = 0.72$, $P = 0.0001$, $n = 302$).

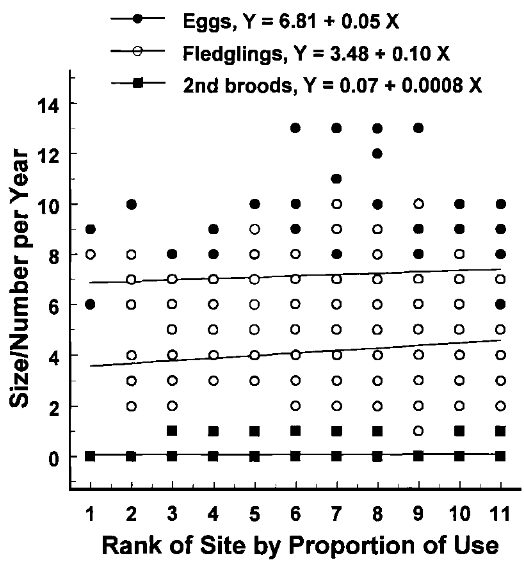

FIG. 12. Relationship between quality of Barn Owl nest sites (1 = worst site) as determined by frequency of use and clutch size ($F = 2.75$, $r^2 = 0.009$, $P = 0.10$, $n = 302$), number of fledglings produced ($F = 2.75$, $r^2 = 0.009$, $P = 0.10$, $n = 302$), and number of second broods produced ($F = 0.01$, $r^2 = 0.0001$, $P = 0.90$, $n = 302$).

ber of second broods showed little association with the frequency of use (Fig. 12). Thus, although some sites had higher usage and success of breeding across years, productivity varied little among owls that were successful at any site.

Winter weather affected the breeding density and reproductive success of Barn Owls (Marti 1994), with severe winters causing very high mortality (Marti and Wagner 1985). Weather also could have had an important influence on an individual's LRS, especially because most of these owls only bred in one year. An owl born by chance in a year preceding a mild winter would be much more likely to produce offspring compared with one born before a harsh winter. I ranked years from 1 to 18 based on an index combining the mean daily winter temperatures and the number of days the ground was covered with deep snow (see Marti 1994). The strength of association between the harshness of the preceding winter and various measures of reproductive performance varied considerably. Harsh winters strongly reduced the number of nesting attempts and successful nests in the following breeding season (Fig. 13).

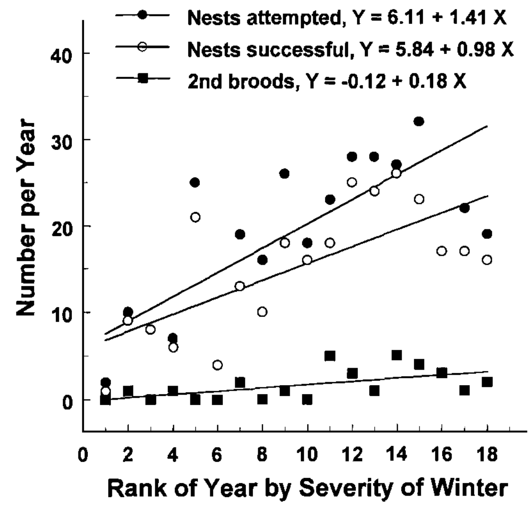

FIG. 13. Relationship between severity of winter weather (1 = most severe) and annual number of nests attempted ($F = 20.98$, $r^2 = 0.56$, $P = 0.0003$, $n = 18$), successful nests ($F = 15.39$, $r^2 = 0.49$, $P = 0.001$, $n = 18$), and second broods ($F = 7.58$, $r^2 = 0.32$, $P = 0.01$, $n = 18$) by Barn Owls.

Harsh winters also reduced clutch size in the following breeding season (Fig. 14), but the number of fledglings per brood showed very little relationship to the preceding winter weather (Fig. 14). Second broods occurred

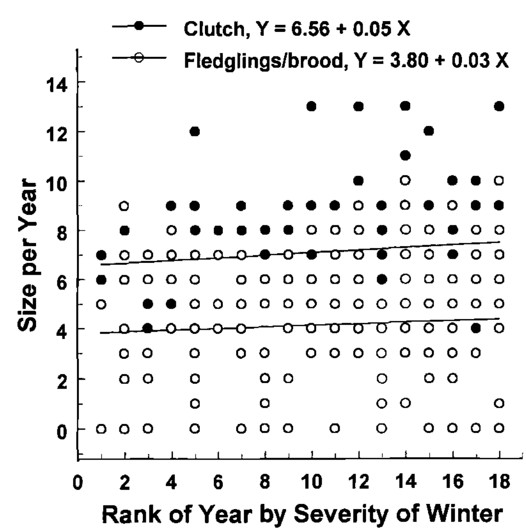

FIG. 14. Relationship between severity of winter weather (1 = most severe) and annual clutch size ($F = 8.18$, $r^2 = 0.02$, $P = 0.01$, $n = 338$) and number of fledglings/brood ($F = 1.03$, $r^2 = 0.003$, $P = 0.31$, $n = 338$) by Barn Owls.

TABLE 1. Reproductive success ($\bar{x}$ ± SD) of female Barn Owls in northern Utah partitioned by age of female.[a]

Age (years)	n	Clutch size	No. of fledglings
1	175	7.13 ± 2.08	3.99 ± 2.08
2	36	7.33 ± 1.96	4.72 ± 2.21
3	17	7.47 ± 1.55	4.53 ± 3.04

[a] Kruskal-Wallis tests comparing age classes: Clutch size, $H = 2.01$, df = 2, $P = 0.36$; No. of fledglings, $H = 2.84$, df = 2, $P = 0.24$.

more often in years following mild winters (Fig. 13), mainly because first broods were started earlier, which left more time for a second brood. These analyses suggest that variation in weather from year to year can affect individual LRS, primarily by shortening breeding life spans.

Fifteen females bred both in a year after one of the six mildest and in a year after one of the six harshest winters. These females exhibited no appreciable difference in the number of eggs laid (Wilcoxon's signed-rank test, $T = 1.38$, $P = 0.19$, $\bar{x}$ difference = 0.80) or the number of fledglings produced ($T = 0.10$, $P = 0.92$, $\bar{x}$ difference = 0.07), but they produced more second broods after mild winters than after harsh ones ($T = 2.08$, $P = 0.06$, $\bar{x}$ difference = 0.53). Although this sample was small, it suggests that some females were better equipped to survive severe winters and that their LRS was less affected by weather variations.

Influence of age on reproductive success.— Among all females studied, owls ≥2 years old produced larger clutches and fledged more young than did 1-year-old inexperienced breeders. The differences were not large (Table 1), but they resulted from experience gained with age because the means of clutches and broods for 36 females that reproduced successfully in both their first and second years were larger in the second year. These differences, however, were not statistically significant ($T = 1.34$, $P = 0.19$, $\bar{x}$ difference in clutch size = 0.56; $T = 1.07$, $P = 0.47$, $\bar{x}$ difference in number of fledglings = 0.47). Seventeen females bred successfully in their first, second, and third years, and even years one and three for those females were not significantly different in reproductive output ($T = 1.74$, $P = 0.10$, $\bar{x}$ difference in clutch size = 0.88; $T = 0.57$, $P = 0.58$, $\bar{x}$ difference in number of fledglings = 0.47). These analyses comparing productivity of the same females at different levels of experience suggest that the increased productivity, though very slight, is attributable to experience and not simply to poor-quality birds dying early.

Sample sizes for paired tests on the same females at different ages were adequate to produce a power of at least 0.80 in tests between number of fledglings produced in years one and two, and in clutch size between years one and three. To achieve a power of 0.80 when testing between clutch size for the same females in their first and second years of breeding, sample size would have to be increased by 13 pairs. Another 52 pairs would be needed to attain a power of 0.80 for the test between the number fledglings produced in years one and three.

DISCUSSION

In a variety of animal species, many individuals do not contribute offspring to future generations (see Clutton-Brock 1988, Newton 1989b); non-contributors are those that die before breeding (42 to 86%; Newton 1989b) and those that attempt to breed but produce no offspring (5 to 49%; Newton 1989b). Furthermore, the productivity of individuals that produce offspring varies widely; some produce only a few, and some produce large numbers (Newton 1989b). Barn Owls in northern Utah showed the same pattern, but I could not determine what percentage of them died before breeding because an unknown proportion of the fledglings died undetected or dispersed from the study area.

Juvenile Barn Owls sometimes disperse great distances from their natal site (Stewart 1952, Bairlein 1985), and other studies have estimated that Barn Owl mortality in the first year is around 70% (Frylestam 1972, Juillard and Beuret 1983). Of the owls on my study area that survived to their first breeding attempt, more than 20% raised no young. If 70% of Barn Owls in northern Utah died before breeding, then 24% of the owls that hatched produced the following generation, and a mere 5.4% of them produced 50% of the next generation.

Barn Owls have an almost passerine-like reproductive strategy (short but highly productive) that is quite unlike that of most other raptors. For example, the Song Sparrow (*Melospiza melodia*) is a small (ca. 4% of the body mass of a Barn Owl) passerine that has a life span almost identical to that of Barn Owls in northern Utah (maximum of 8 years). Based on studies by Hochachka et al. (1989), Song Sparrows breed at one year of age, usually produce two clutches of three to four eggs each year, and produce a maximum of 30 fledglings in their lifetimes (less than half that for Utah Barn Owls). The Florida Scrub-Jay (*Aphelocoma coerulescens*) is a larger passerine (ca. 14% of the mass of a Barn Owl) that usually delays reproduction until two years of age. On average, scrub-jays rarely produce second broods, lay clutches of 3.3 eggs, and produce 7.4 fledglings in a lifetime (Woolfenden and Fitzpatrick 1996), which is higher than the mean lifetime production I recorded in Barn Owls. The Eastern Screech-Owl (*Otus asio*) is a small owl (ca. 36% the mass of a Barn Owl) with a maximum life span comparable to that of the Barn Owl, but most breeders live longer than most Barn Owls. Gehlbach (1989) found that screech-owls usually breed at one year of age and produce clutches of four eggs. Mean lifetime production of fledglings is only 2.8, much less than that of Barn Owls. The Ural Owl has a mass about 30% larger than the Barn Owl. In Finland, the mean age of first breeding is 4.1 years, and mean life span is 7.9 years (Saurola 1989). On average, Ural Owls produce more fledglings in their lifetimes than do Barn Owls (8.2), but their maximum is only 35, less than half that of the maximum for Barn Owls. Thus, Barn Owls achieve equivalent or greater productivity compared with these four species, but usually in a much shorter time, especially when compared with the larger Ural Owl.

Life-history strategy in relation to LRS.—Although the concept of *r*- and *K*-selection has fallen into disrepute among certain ecologists (Parry 1981), the concept can be useful for comparing life-history strategies. For example, Barn Owls seem to fit many correlates of *r*-selection proposed by Pianka (1970). At least near the northern extreme of their range, they: (1) exist under variable and uncertain climatic conditions, (2) face catastrophic mortality from adverse weather, (3) exhibit early reproduction, (4) are essentially semelparous, and (5) have a short life. Additionally, juveniles often disperse widely from their natal sites, allowing them to use new or ephemeral resources (Brown 1971, Stewart 1980, Lenton 1985). This suite of characteristics results in a need to reproduce quickly and abundantly. The best chance for a Barn Owl to maximize its LRS is to produce two large broods in its first year of life because it most likely will not be alive to breed in the next year. A few Barn Owls in northern Utah managed to produce up to 16 fledglings in one year using this strategy.

The life-history strategy of Barn Owls differs from that of other owls. Species of *Strix*, for example, fit the correlates of *K*-selection—they usually delay breeding until two or three years of age, produce small clutches, never produce second broods, and are long-lived and sedentary (Southern 1970, Saurola 1989, Gutiérrez et al. 1995).

Environmental correlates of LRS.—Breeding by chance in favorable years can greatly enhance LRS (Hochachka et al. 1989), especially for short-lived species like the Barn Owl because most that breed do so in only one year. Individuals having the misfortune of entering the breeding population in an unfavorable year may suffer reduced LRS. In northern Utah, harsh winters strongly affect the number of nesting attempts and the number of successful nests the following breeding season. Clutch size, number of fledglings per brood, and number of second broods decline after harsh winters, but the effect on these variables is less than that on the numbers of owls breeding. The high mortality caused by severe winters reduces to zero the LRS of owls that die before they have bred, and it reduces the population's reproductive success. Nevertheless, the subsequent productivity of owls that survivie such winters is not reduced appreciably.

The quality of nest sites used by owls also may impinge on the LRS of individuals, but may be a less stochastic force than variability of winter weather. Depending upon population density, owls probably choose sites that may improve their productivity over sites that offer less; however, they cannot choose the best weather for nesting. Some northern Utah sites had a better record of producing fledglings, but the variation in clutch size, brood size, and number of second broods was largely independent of site quality based on degree of use. The homogeneous nature of my study area may have made it very difficult to evaluate the effects of site equality on LRS. A better test would be among sites that contrast strongly in quality.

The Barn Owl is the most widespread owl species in the world (Marti 1992), making it a good candidate for understanding how various environmental factors affect LRS. Unfortunately, even though literature on Barn Owl reproduction is extensive, very few studies have provided data needed for LRS determination. Most published works originated in northern latitudes (Mikkola 1983, Marti 1992). Notably lacking are data from tropical and subtropical climates where conditions may favor quite different reproductive responses compared with north-temperate regions. For example, survival is higher for southern populations than northern ones in the United States (Stewart 1952, Henny 1969) and could be even higher in tropical areas. Two studies of Barn Owl reproduction in tropical regions were cross-sectional (Lenton 1984, Wilson et al. 1986) and provided no details on individual owls; i.e. age of first breeding, breeding life spans, and lifetime reproductive success. They did, though, document large mean clutches (6.05 in Mali and 6.6 in Malaysia) and the common occurrence of second broods. In Malaysia, most pairs produced two broods per year, and two pairs produced three broods in a year (Lenton 1984). Long-term studies of survival and reproduction of individual Barn Owls in tropical areas would make an interesting comparison to those done near the northern limits of the species' range.

Sex and age differences in LRS.—Barn Owl sexes had similar LRS, as did the small number of other bird species having LRS data for both sexes (Newton 1989b). I found only small differences between male and female Barn Owls in several important factors that affect LRS (age breeding begins, number of years breeding, number of years breeding successfully, and number of second broods). Although differences between males and females were not statistically significant, means for females differed from those of males in the direction that would promote higher LRS. Thus, although it appears that the sexes did not differ in these parameters, any significant biological difference could only be detected with larger samples sizes.

In some species older birds are more productive than younger ones (Hamerstrom 1969, Newton 1976, Clum 1995), but in others reproductive output does not increase with experience (Pietiäninen 1988). In my study population, productivity apparently does not differ among females of different ages (sample sizes for males were too small to test). Thus, age seems to make little difference in annual increments to the LRS of Barn Owls.

Summary.—Barn Owls are similar to other species (including raptors) in that reproductive success varies widely among individuals, and that a few individuals produce a disproportionate number of the following generation. Barn Owls, though, have a markedly different overall reproductive strategy from the other raptors for which LRS is known—one shifted strongly in the direction of trading a long life for quick and intense reproduction. Their early maturation, large clutch size, multiple clutches, and low survival rates are characteristic of species that have evolved in harsh environments (Lindén and Møller 1989) and require that Barn Owls reproduce quickly and intensely to maximize their fitness.

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