# BREEDING SEASON QUALITY, AGE, AND THE EFFECT OF EXPERIENCE ON THE REPRODUCTIVE SUCCESS OF THE URAL OWL (*STRIX URALENSIS*)

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ABSTRACT.—I studied the reproduction of female Ural Owls (*Strix uralensis*) in southern Finland in 1977-1986. I compared the age of first breeding and the reproductive success of experienced and inexperienced females in a situation where the birds subsisted on cycling voles.

The proportion of first-time breeders varied annually between 0 and 38%. The breeding seasons were classified into poor, intermediate, and good according to vole abundance and winter quality. More females started to breed in intermediate than in poor or good years. Most first-time breeders were in their fourth year or older. The first breeding attempt was postponed most often because of poor environmental conditions.

Experienced females laid earlier, but not significantly larger, clutches than inexperienced females. Seasonal decline in clutch size was steeper in experienced females than in inexperienced females. Brood size was not related to female experience. Thus, the reproductive output of females did not increase with experience. *Received 6 April 1987, accepted 23 December 1987.*

THE popular concept of a "reproductive strategy" is that underlying traits are evolved responses to an organism's environment (Stearns 1976, Southwood 1977). Age at first breeding is such a trait. In general, differences in the availability of resources or in the pattern of adult mortality affect the observed variation in the age of first breeding (Wooller and Coulson 1977). Potentially long-lived species should delay their first reproduction if their mortality rate is higher in their early attempts than later, which might decrease their lifetime reproductive success—the ultimate evolutionary currency (Williams 1966). Theories predict that an optimal pattern of reproductive effort exists over age classes (Pianka and Parker 1975, Pianka 1976). What we see is a shortage of mates or food affecting the age of first breeding (Newton 1985).

Besides variation in the age of first breeding, young, inexperienced birds generally lay later and have fewer offspring than more experienced individuals (Nol and Smith 1987). Two options explain the variation in the reproductive success of first-time breeders and established breeders. First, novice breeders may put less effort (in terms of time and energy) into their breeding attempt than older individuals. Curio (1983) called this the restraint hypothesis. Second, novice breeders may be less skilled in the various tasks required for successful reproduction. Curio (1983) called this the constraint hypothesis. Nol and Smith (1987) improved the constraint hypothesis by separating the effects of age and experience.

I examined the frequency of female first breeders in a population of Ural Owls (*Strix uralensis*) and their age and breeding success at the first breeding attempt. At the time of laying, the owls mainly eat *Microtus* or *Clethrionomys* voles (Lundberg 1981). The vole populations are cyclic in the study area (Hansson and Henttonen 1985), and it was possible to compare the reproductive success of inexperienced and experienced females in years with different food availability.

## STUDY AREA AND METHODS

I studied a population of Ural Owls in 1977-1986 in an area of about 1,500 km$^2$ in Päijät-Häme, southern Finland (see Pietiäinen et al. 1986 for details). Nearly all pairs nested in nest boxes, and in all years there were more boxes than the birds could use (in 1986 about 160 nest boxes and 85 pairs). Boxes were 3-4 km apart. A few pairs (0-5/yr) used old Northern Goshawk (*Accipiter gentilis*) or Common Buzzard (*Buteo buteo*) nests or stumps. Coverage of the nest-box network was incomplete, and the actual number of pairs was unknown.

I considered females to be first-time breeders if they bred in a previously unoccupied territory ($n$ = 40), they bred in a box erected in the previous autumn ($n$ = 11), or they replaced the former, presumably dead, female of a territory ($n$ = 27). This method is subject to error because older females may have bred somewhere else previously. The error was probably small, as 96% of 576 banded Finnish Ural Owl females moved 0–5 km between two successive breeding seasons (Saurola 1987).

Since 1977, 20 first-breeding females were banded as nestlings. Since 1979 owls were classified into three age classes (2nd, 3rd, and +3rd calendar year) according to their plumage characteristics (Pietiäinen and Kolunen 1986). Thus, the age of 58 more females was known (2nd: 7, 3rd: 4, +3rd: 47). In addition, I used Valkeila's (1976) records of 24 banded females in the analysis of the age of first breeding.

I classified the breeding seasons as poor, intermediate, or good according to the severity of the winter and the availability of voles (Table 1). The food supply was approximated by the amount of damage done to forest-tree seedlings by *Microtus* voles (references given by Pietiäinen et al. 1986). The breeding seasons of 1977–1984 were classified by Pietiäinen et al. (1986). The characteristics of the breeding seasons of 1985 and 1986 were:

1985. Intermediate. Voles were increasing. Extremely hard winter; mean temperature in January and February was −17°C (about 10° below the average in 1931–1960).

1986. Good. The best vole year in the study area in the period 1977–1986. Signs of vole activity could be seen everywhere after the snow had melted. Mean temperature in January (−10°C) and in February (−13°C) was lower than average.

I determined the date of laying for 320 clutches either by a visit to a nest where the female was sitting on her incomplete clutch ($n$ = 130) or by calculating the hatching date from the wing length of the oldest chick(s) ($n$ = 190) based on a growth curve of wing lengths of 35 young (Pietiäinen unpubl.). For these nests I calculated the date of laying by back-dating 32 days as the incubation period in two-egg clutches (assuming that incubation starts from the first egg) and 34 days in larger clutches (assuming that incubation starts from the second egg).

I considered the clutches full if on two successive visits to the nest clutch size did not increase. No one-egg clutches were taken as genuine full clutches because all, except one, were abandoned when found. Ural Owls lay only one clutch annually. A replacement clutch was laid after initial failure in only two cases. The females were banded and the nests were often followed from the prelaying period, so I assumed that the data contain no other repeat clutches. Brood size is the number of young that reached at least the age of banding (2–3 weeks).

When necessary I adjusted laying dates to the yearly medians, and clutch and brood sizes for the effects of the seasonal decline in clutch or brood size and the variation in year quality-class mean clutch or brood sizes. I counted the residuals from the models of the seasonal decline in clutch size/brood size separately for inexperienced and experienced females, and added these to the year quality-class means.

TABLE 1. Quality index of the breeding seasons, number of pairs, number of females laying eggs and their proportion of the number of pairs (%), and number of first-time breeders and their proportion of the females laying eggs (%) in Päijät-Häme, southern Finland. Year quality classes: P = poor, I = intermediate, G = good. See Methods for an explanation of the classification.

| Year | Quality index | No. of pairs | No. of layers | (%) | First breeders[a] | (%) |
|---|---|---|---|---|---|---|
| 1977 | P | 29 | 19 | (66) | 3 | (16) |
| 1978 | I | 48 | 39 | (81) | 9 | (23) |
| 1979 | G | 54 | 47 | (87) | 7 | (15) |
| 1980 | I | 70 | 41 | (58) | 10 (7) | (24) |
| 1981 | P | 67 | 19 | (28) | 3 | (16) |
| 1982 | I | 85 | 63 | (74) | 24 | (38) |
| 1983 | G | 82 | 62 | (76) | 9 (1) | (15) |
| 1984 | P | 75 | 9 | (12) | 0 | (0) |
| 1985 | I | 80 | 53 | (66) | 15 | (28) |
| 1986 | G | 85 | 63 | (74) | 17 (3) | (27) |
| Total | | | 415 | | 97 | (23) |

[a] Numbers of first breeders that bred in nest boxes erected the previous autumn are given in parentheses.

## RESULTS

*Frequency of first breedings.*—There were 415 breeding attempts in 1977–1986 (at least 1 egg laid), and in 97 cases (23%) the clutch was laid by an inexperienced female. The proportion of first-time breeders varied from 0 (1984) to 38% (1982; Table 1). I added new nest boxes during the study, but owls bred in boxes that were erected in the previous autumn in only 11 cases. When breeding seasons were pooled according to their quality, the numbers of first-breeding females differed significantly between breeding seasons of different quality (Table 2). The difference was due to a large number of first breeders in intermediate years. Poor years differed from intermediate years ($\chi^2$ = 5.53, $P$ = 0.019) and intermediate years from good years ($\chi^2$ = 5.33, $P$ = 0.021), but poor years did not differ from good years ($\chi^2$ = 1.04, $P$ = 0.31). The general result held even when the first-time breeders that used new boxes (7 in intermediate years, 4 in good years) were excluded ($\chi^2$ = 7.32, $P$ < 0.05).

*Age of first-time breeders.*—The median age at the first breeding attempt of 31 accurately aged females, in Päijät-Häme, was 3 yr (Table 3A). With Valkeila's (1976) records of 24 banded fe-

TABLE 2. Numbers of experienced and inexperienced females that laid eggs in poor, intermediate, and good breeding seasons. Chi-square test for goodness-of-fit between the distributions.

| | Poor | Intermediate | Good | |
|---|---|---|---|---|
| Experienced | 41 | 138 | 139 | $\chi^2 = 8.87$, $P = 0.012$ |
| Inexperienced[a] | 6 | 58 (7) | 33 (4) | |
| Frequency of first breedings (%) | 13 | 30 | 19 | |

[a] Numbers of females that bred in nest boxes erected the previous autumn are given in parentheses.

males added to this data, the median age reached 4 yr. The higher median age derived from the combined sample is supported by the 47 +3rd-yr first-time breeders in Päijät-Häme.

Second-year initial breeding was more common in the present study than previously suggested (Lagerström 1969, Valkeila 1976). This probably was due to improved techniques of aging the birds (Pietiäinen and Kolunen 1986), rather than to any changes in the breeding behavior of the species. On the other hand, improved aging indicates that +3rd-yr birds are very common among the first-time breeders, as Valkeila suggested. Mikkola (1983) regarded the mean age of 3.5 yr in Valkeila's (1976) data as high and suggested that "Valkeila's study area had been overstocked with Ural Owls, and this led to the unexpected result." My data do not support this.

The proportion of the two youngest age classes (2nd- and 3rd-yr birds) among the novice breeders was significantly larger in good than in intermediate breeding seasons (Table 3B), and no young birds bred in poor years. This suggests that the youngest birds breed only in the very best environmental conditions.

Newton (1985) presented a useful method to approximate the proportion of females in each age class that have started their breeding career. When the number of birds that have started to breed in different ages and the yearly adult mortality are known, the number of birds that survive and the number of birds alive but not breeding when younger can be calculated. Using these figures it is possible to calculate the proportions of birds that have started to breed in different ages. In the Ural Owl females I used 90% as the survival rate of adult females (2nd year or older). Originally, Lundberg and Westman (1984) suggested this figure for breeding females only. In Table 3A females in their 5th year or older were pooled, and females aged as being in their +3rd year were divided into two age classes (4th- and ≥5th-yr) on the basis of the number of breeding 4th- and ≥5th-yr females (Table 4).

Using Newton's (1985) method, 9% of the Ural Owl females started to breed by their 2nd year, 18% by their 3rd, 55% by their 4th, and (by definition) all by their 5th. To test the robustness of these estimates, I used 80% as the survival rate, but the percentages did not change appreciably: 2nd-yr 7%, 3rd 15%, 4th 52%, and 5th 100%. Thus, it seemed reasonable to assume that nearly half of the females did not begin breeding until their 5th year (see also Lundberg and Westman 1984).

*Constraints on the first breeding attempt.*—A median age of first breeding of 4 yr implies delayed breeding. Some information is available on the conditions of the preceding breeding seasons. The 2nd-yr females are logically excluded, because they hatched in the previous season. The sample of 3rd-yr females is small (Table 4). Thus, I considered only the 59 females that started to breed by their 4th year or later. In 10 cases the females could not have bred in the previous year because no nest box was available, and

TABLE 3. (A) Age at first breeding attempt of Ural Owl females. Age in calendar years: 2 = born in the previous spring, +3 = older than 3 calendar years. (B) Number of second- or third-year and older-than-third-year females breeding for the first time in poor, intermediate, and good breeding seasons. Chi-square test for goodness-of-fit between the distributions in intermediate and good years.

| (A) Age | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | +3 |
|---|---|---|---|---|---|---|---|---|---|---|
| This study | 11 | 8 | 9 | 1 | 0 | 2 | 0 | 0 | 0 | 47 |
| Valkeila (1976) | 1 | 2 | 9 | 5 | 2 | 2 | 2 | 0 | 1 | — |
| Total | 12 | 10 | 18 | 6 | 2 | 4 | 2 | 0 | 1 | 47 |

| (B) Year quality | Female age: 2 or 3 | Female age: +3 | |
|---|---|---|---|
| Poor | 0 | 6 | |
| Intermediate | 5 (1/4) | 39 | $\chi^2 = 9.90$, $P < 0.01$ |
| Good | 13 (10/3) | 17 | |

TABLE 4. Number of females that started to breed at different ages (bold face) and their estimated numbers (based on 90% adult survival) at different ages before or after first breeding. Percentages are the proportion of females that bred at appropriate ages (for the method see Newton 1985).

| Age of first breeding | Numbers of different-age females alive (% breeding) in following years: 2 | | 3 | | 4 | | ≥5 | |
|---|---|---|---|---|---|---|---|---|
| 2 | **12** | (9%) | 10.8 | (18%) | 9.7 | (55%) | 8.7 | (100%) |
| 3 | 11.1 | | **10** | | 9.0 | | 8.1 | |
| 4[a] | 22.2 | | 20.0 | | **18** | | 16.2 | |
| | 25.2 | | 22.7 | | 20.4 | | 18.4 | |
| ≥5[a] | 20.6 | | 18.5 | | 16.7 | | **15** | |
| | 36.5 | | 32.9 | | 29.6 | | 26.6 | |

[a] Lower row indicates the estimated number of 47 +3rd-yr birds I divided into age classes 4 and ≥5. First, I added the number of 4th-yr females alive and breeding (9.7 + 9.0 + 18 = 36.7, or 43% of all breeding females older than 3 yr) and the number of 5th-yr birds alive and breeding (8.7 + 8.1 + 16.2 + 15 = 48.0, or 57%). Second, I used these percentages to sort the +3rd-yr birds into 4th-yr (20.4) and ≥5th-yr (26.6) birds.

once the territory was occupied by a different female. On 31 occasions the previous breeding season was a poor one. Overall, approximately 70% of the inexperienced Ural Owl females were constrained from breeding one year earlier because of a lack of nest sites or because of otherwise poor conditions for breeding.

*Timing of laying.*—Yearly median laying dates of the population varied from 23 March (1986) to 23 April (1977; see also Pietiäinen et al. 1986). The owls laid earliest in good years (Pietiäinen et al. 1986). Both experienced and inexperienced females laid 24 days earlier in good breeding seasons than in poor seasons. Regardless of the quality of the breeding season, experienced females laid 3–4 days (laying dates adjusted to yearly medians) earlier than inexperienced females (Table 5A). I analyzed the effect of experience on the date of laying in 54 females that were encountered at least once after their first breeding. Females did not breed every year. The median dates from first to fifth (median date = $2/n$ = 39, 0/49, −2/24, −2.5/24, 1/8) breeding attempt differed significantly (Kruskal-Wallis test, $H = 15.3$, df = 4, $P < 0.01$), and the median laying date was earlier as the females gained more experience ($r_s = -0.27$, df = 144, $P < 0.005$).

*Female mass.*—I analyzed mass in intermediate and good breeding seasons only. In both year classes inexperienced females were as heavy as experienced females (Table 5B). In good years females were heavier than in intermediate years, but the difference was significant in experienced females only ($t = 4.51$, $P < 0.001$).

Mass varied greatly among individuals. The difference between the lightest and the heaviest female was about 350 g in intermediate years

TABLE 5. (A) Median laying dates of experienced and inexperienced females in poor, intermediate, and good breeding seasons. Mann-Whitney *U*-tests for the significance of the differences in medians (z-values corrected for ties: poor = −1.13, intermediate = −3.35, good = −3.29). Numbers of observations are given in parentheses. (B) Mass (g, $\bar{x}$ ± SD) of experienced and inexperienced females in intermediate and good breeding seasons. *t*-tests for the significance of the difference in means.

| | Poor | Intermediate | | Good |
|---|---|---|---|---|
| **(A) Laying date** | | | | |
| Experienced | −0.5 (28) | −1 (90) | | 0 (125) |
| Inexperienced | +3 (5) | +2 (39) | | 4 (29) |
| *P* | =0.26 | <0.001 | | <0.001 |
| **(B) Female mass[a]** | | | | |
| Experienced | | 1,011 ± 70 | *** | 1,059 ± 87 |
| *n* | | 104 | | 121 |
| Range | | 800–1,145 | | 845–1,320 |
| | | NS | | NS |
| Inexperienced | | 1,016 ± 76 | NS | 1,059 ± 129 |
| *n* | | 49 | | 29 |
| Range | | 840–1,160 | | 845–1,335 |

[a] *** = $P < 0.001$, NS = not significant.

TABLE 6. Number of clutches in each clutch-size class and mean clutch size of experienced (E) and inexperienced (I) females in poor, intermediate, and good breeding seasons. Observations in median clutch-size classes are in boldface. The significance of the difference in medians was tested with a Mann-Whitney *U*-test (z-values corrected for ties: poor = −1.29, intermediate = −0.6, good = −1.11).

| | | Clutch size | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *n* | 2 | 3 | 4 | 5 | 6–7 | $\bar{x} \pm$ SD | *U*-test |
| Poor | | | | | | | | |
| E | 34 | **25** | 8 | 1 | — | — | 2.29 ± 0.52 | *P* = 0.2 |
| I | 5 | **5** | — | — | — | — | 2.0 | |
| Intermediate | | | | | | | | |
| E | 120 | 26 | **55** | 33 | 6 | — | 3.16 ± 0.82 | *P* = 0.55 |
| I | 53 | 15 | **22** | 12 | 4 | — | 3.09 ± 0.90 | |
| Good | | | | | | | | |
| E | 127 | 12 | 29 | **43** | 32 | 11 | 4.02 ± 1.14 | *P* = 0.27 |
| I | 29 | 4 | 8 | **11** | 2 | 4 | 3.79 ± 1.21 | |

and about 450 g in good years. The mass of both experienced and inexperienced females varied more in good than in intermediate seasons (experienced: $F = 1.54$, $P < 0.05$; inexperienced: $F = 2.88$, $P < 0.001$). This suggests that the body condition of breeding females varied more in good than in intermediate seasons (see also Pietiäinen et al. 1986). In female raptors mass characterizes body condition (Newton et al. 1983, Hirons et al. 1984).

*Clutch size.*—Within year quality classes, inexperienced females always laid slightly smaller clutches than experienced females, but the differences were not statistically significant (Mann-Whitney *U*-test, two-tailed; Table 6). I studied the effect of experience further by analyzing the variation in the clutch size of 54 first breeders that were encountered at least once in successive breeding seasons. The means of the adjusted clutch sizes did not differ significantly from the first to the fifth breeding attempt (Fig. 1; Kruskal-Wallis test, $H = 9.01$, df = 4, $P < 0.1$). Pietiäinen et al. (1986) did not find significant differences in clutch size in relation to the age of breeding females.

Ural Owls lay progressively smaller clutches as the season advances (Fig. 2; see also Pietiäinen et al. 1986). Seasonal decline occurred in both experienced and inexperienced females (−0.08 ± 0.005 [SE]; $t = 15.54$, $P < 0.001$, $n = 228$ vs. −0.05 ± 0.01, $t = 5.02$, $P < 0.001$, $n = 68$). The rate of this decline was steeper in experienced than in inexperienced females ($F = 6.32$, $P < 0.05$). Unlike earlier work (Pietiäinen et al. 1986), I used calendar dates (31 March = 0), not dates adjusted to yearly median laying dates. This accommodates the marked variation in laying dates (63 days in 1977–1986). If the date is important in determining the clutch size of the Ural Owl (Pietiäinen et al. 1986), proximate control must be based on day length (see also Daan et al. in press). Day length is invariable from year to year, so calendar dates reflect the relationship between date and clutch size.

The rate of the seasonal decline in clutch sizes of the sample of first breeders steepened from −0.05 ± 0.01 ($t = 3.39$, $P < 0.01$, $n = 37$) to −0.07 ± 0.01 ($t = 5.68$, $P < 0.001$, $n = 48$) between first and second attempts, but the difference was not significant ($F = 1.54$, not significant). In the third attempt the slope was −0.08 ± 0.02 ($t = 4.03$, $P < 0.001$, $n = 24$).

The rate of the seasonal decline in clutch size was significantly steeper in experienced than in inexperienced females in good years (−0.09 ± 0.01, $n = 117$ vs. −0.05 ± 0.02, $n = 26$; $F = 6.32$, $P < 0.05$) but not in intermediate years (−0.06 ± 0.01, $n = 86$ vs. −0.03 ± 0.02, $n = 38$; $F = 1.76$, not significant). The clutch size of experienced females declined faster in good years than in intermediate years ($F = 5.10$, $P < 0.05$).

*Brood size.*—In poor years the average brood sizes of experienced and inexperienced females were about equal (Table 7). In intermediate years inexperienced females had larger average broods than experienced birds, but the brood-size distributions did not differ significantly. In good years experienced females had larger average broods than inexperienced females, and the difference in the brood-size distributions was statistically significant (Table 7; Mann-Whitney *U*-tests, two-tailed).

The mean adjusted brood sizes in the first

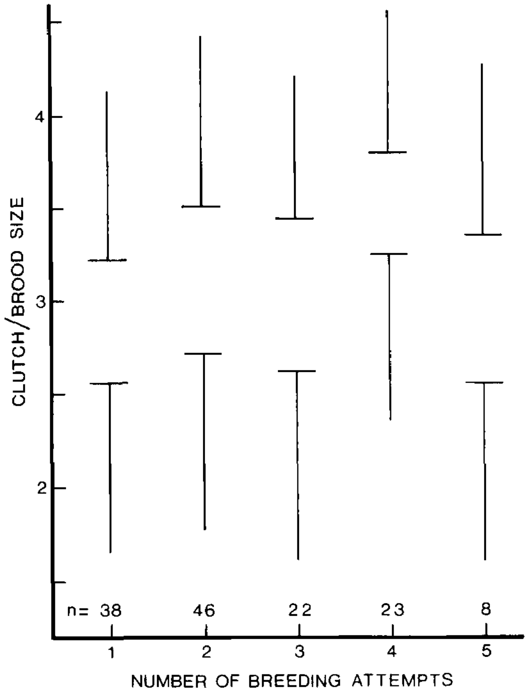


Fig. 1. Adjusted clutch sizes (upper portion of the figure) and brood sizes (lower portion) of female Ural Owls in relation to the number of breeding attempts. Means (horizontal lines) and standard deviations (vertical lines) of adjusted values (residuals of the clutch size/brood size vs. date models for inexperienced and experienced females added to mean clutch size/brood size of inexperienced and experienced females in different year quality classes) are shown. Note that the values could be adjusted only in cases where the laying date was known.

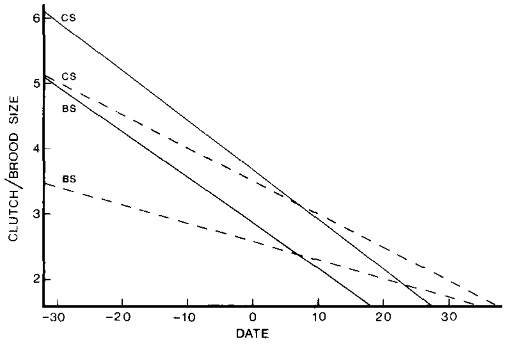


Fig. 2. Seasonal decline in clutch size (CS) and brood size (BS) of experienced (solid lines) and inexperienced (broken lines) female Ural Owls. Laying dates were used as the independent variable because only 2.7% of young die after hatching, while 17.6% of eggs do not hatch (Lundberg and Westman 1984). Dates deviate from 31 March (=0). Kruskal-Wallis test for the difference in means, $H = 9.37$, not significant.

to the fifth breeding attempt of 54 retrapped first breeders did not differ significantly (Kruskal-Wallis test, $H = 9.37$, $P < 0.1$).

I used laying date as the independent variable to calculate the seasonal decline in brood size because only 2.7% of the young die after hatching, while 17.6% of the eggs do not hatch (Lundberg and Westman 1984). When seasonal declines in clutch and brood size were compared, the rates in experienced females were nearly the same (clutch size: $-0.08 \pm 0.005$, $n = 228$ vs. brood size: $-0.07 \pm 0.01$, $n = 235$; $F = 0.58$, not significant; Fig. 2). This implies that loss of eggs or small chicks is independent of date. The nearly identical rates of the seasonal decline also suggest that losses are independent of clutch size. Experienced females averaged 0.8 fewer young in their broods than clutch size would predict, regardless of the date of laying. Inexperienced females lost relatively more young in early clutches, but the difference between the decline in clutch size and brood size was not significant (clutch size: $-0.05 \pm 0.01$, $n = 68$; brood size: $-0.03 \pm 0.01$, $n = 72$; $F = 2.20$, not significant).

## Discussion

Because the Ural Owl breeds slowly, it is difficult to test the hypotheses of the effects of experience and age separately (Nol and Smith 1987). Consequently, I assumed that, irrespective of age, experience should enhance reproductive success. Because of the restrictions of the data, the residual reproductive value hypothesis (the reproductive-restraint hypothesis of Curio 1983) and the selection hypothesis (Curio's bad-quality hypothesis) were not tested adequately.

There is a marked division of labor between female and male birds of prey (Newton 1979). Thus, male experience affects reproductive success. In the Eurasian Sparrowhawk (*Accipiter nisus*) male experience directly affects the reproductive success of a pair (Newton et al. 1981). Male Ural Owls play an important role in the initiation of breeding, as males bring the females into breeding condition by courtship feeding (Lundberg 1980). The male also pro-

TABLE 7. Number of broods in each brood-size class of experienced (E) and inexperienced (I) females in poor, intermediate, and good breeding seasons. Observations in median brood-size class are in boldface. The significance of the difference in medians was tested with a Mann-Whitney *U*-test (*z*-values corrected for ties: poor = −0.20, intermediate = −1.54, good = −2.50).

| | | Brood size | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | $n$ | 0 | 1 | 2 | 3 | 4 | 5 | 6 | $\bar{x} \pm$ SD | *U*-test |
| Poor | | | | | | | | | | |
| E | 39 | 8 | 9 | **19** | 3 | — | — | — | 1.44 ± 0.91 | $P = 0.84$ |
| I | 6 | 1 | 1 | **4** | — | — | — | — | 1.50 ± 0.84 | |
| Intermediate | | | | | | | | | | |
| E | 124 | 30 | 13 | **31** | 37 | 11 | 2 | — | 1.94 ± 1.37 | |
| I | 54 | 5 | 4 | **21** | 18 | 5 | 1 | — | 2.31 ± 1.11 | $P = 0.12$ |
| Good | | | | | | | | | | |
| E | 135 | 13 | 10 | 21 | **42** | 30 | 17 | 2 | 2.93 ± 1.48 | $P = 0.012$ |
| I | 32 | 7 | 3 | **8** | 8 | 2 | 4 | — | 2.22 ± 1.62 | |

vides food for the incubating female and the growing young. The quality of the male as a hunter probably affects the timing of laying, the clutch size, and the resulting brood size. Previous male experience may be influenced by marked variation in the quality of the hunting grounds (Pietiäinen et al. 1986). I did not track the males in my population.

*Vole density and age of first-time breeders.*—The proportion of laying females and the average clutch size varied from year to year (Linkola and Myllymäki 1969, Lundberg 1981, Pietiäinen et al. 1986). Variation in environmental conditions affected the frequency of first-breeding females in the population (Table 1). The highest proportion of first-time breeders was in intermediate years. This was not influenced by providing new nest boxes. Higher adult mortality in poor years may have provided more vacant territories in intermediate years than in good years following intermediate years. This will remain unresolved until reliable estimates of adult mortality in different years become available. Fluctuation in the quality of breeding seasons was also reflected in the age of first-breeding females, especially in the occurrence of the youngest females in the breeding population (Table 3B). In unfavorable years females may have to postpone their first breeding attempt.

In general, the fluctuation in the quality of breeding seasons produced a variable pattern of ages of the first breeding attempt. Fifty-five percent of the Ural Owl females bred in their 4th yr (Table 5). Nearly half of the females began later. Perhaps many females do not breed until in their 6th yr. In some cases the year of birth may affect the age of first breeding (Lundberg and Westman 1984), because good breeding seasons are generally followed by poor ones. The importance of the succession of seasons of different quality was evident in the 2nd-yr females, most of which were born in an intermediate year preceding a good season. Similarly, 17% of female Eurasian Sparrowhawks did not lay their first clutch until in their 5th yr (Newton 1985). Newton found no evidence for delayed reproduction other than shortage of mates or food.

The reproductive-restraint hypothesis suggests that young birds should delay their first breeding if breeding in younger ages increases mortality (Curio 1983). This can be resolved by a comparison of mortalities of birds that have or have not started to breed at a given age. Presently, such data are not available for Ural Owls. Further, the demands of the molt might affect the age of first breeding in the Ural Owl (Pietiäinen et al. 1984). Ural Owls molt about 65% of their flight feathers in their first two molts, 48% in the third, and 53% in the fourth (Pietiäinen et al. 1984). The differences may not be large, but parents with a greater number of dependent young molt fewer of their flight feathers.

*Differences in the reproductive success of inexperienced and experienced females.*—Inexperienced Ural Owl females laid later than experienced females, but neither clutch sizes nor brood sizes increased with experience. The breeding-experience hypothesis (Nol and Smith 1987) predicts that if birds of equal age are compared, individuals with more previous breeding experience should do better. A rigorous test of the prediction requires data where age and experience can be separated. Because Ural Owls do not breed each year, my data are not sufficient for this test. Breeding success also may improve with age, but no age-related effects on clutch size have been found (Pietiäinen et al. 1986). A further complicating factor is the efficiency of the male, which I did not examine.

Surplus-feeding experiments have provided substantial evidence of the importance of food in determining the timing of annual reproduction (Daan et al. in press; see also Pietiäinen et al. 1986). Daan et al. concluded that "food availability in spring primarily affects laying date and . . . laying date in turn determines clutch size, either via an internal annual programme or via some external variable independent of food, e.g. daylength." The difference between inexperienced and experienced female Ural Owls in the rate of the seasonal decline in clutch size indicates that inexperienced females differ from experienced birds in their reaction to the causal relationship between laying date and clutch size. Besides theoretical interest, this observation also has practical applications. First, care should be taken in planning surplus-feeding experiments so that inexperienced and experienced breeders are separated. Second, this difference should be considered when date-related changes in clutch size and brood size are analyzed.

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