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BARN OWL REPRODUCTION: PATTERNS AND VARIATION NEAR THE LIMIT OF THE SPECIES' DISTRIBUTION[1]

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Abstract. I studied reproduction of the Barn Owl (*Tyto alba*) in irrigated farmlands of northern Utah for 16 years documenting 391 nesting attempts. Most Barn Owls began nesting at one year of age and produced one brood per year. The owls rarely produced second broods or replaced failed first clutches. Complete first clutches averaged 7.17 eggs (n = 275). Replacement ($\bar{x}$ = 5.81, n = 16) and second clutches ($\bar{x}$ = 5.79, n = 19) were significantly smaller than first clutches, but first ($\bar{x}$ = 5.45) and second broods ($\bar{x}$ = 5.37) did not differ significantly. Replacement broods ($\bar{x}$ = 3.83) were significantly smaller than first. Of all nesting attempts 88% produced full clutches and 71% yielded at least one fledgling. Successful nests on average produced 5.09 fledglings per first brood, 4.94 per second brood, and 3.60 per replacement brood. Second attempts were more likely to produce fledglings than either first or replacement attempts. Sixty-three percent of all eggs laid hatched and 55% produced fledglings. Of eggs that hatched, 87% survived to fledging. March 13 was the mean date for initiation of egg laying and latest second clutches hatched on 4 October. Persistent snow cover and low winter temperatures significantly delayed onset of egg laying and reduced the number and success of breeding attempts. Clutch size, however, did not differ significantly among years or among nest sites.

Key words: Barn Owl; breeding age; breeding success; Tyto alba; *Utah; weather effects.*

INTRODUCTION

The Barn Owl (*Tyto alba*) has a higher biotic potential and more flexible reproduction than most other owls and ecologically similar birds. Barn Owls commonly breed at one year of age (Bunn and Warburton 1977, Colvin 1984), produce large clutches (Marti 1992), and often produce two and sometimes more broods per year (Lenton 1984, Schulz and Yasuda 1985, Baudvin 1979). Although usually considered monogamous, Barn Owls sometimes mate polygamously (Schönfeld and Girbig 1975, Colvin 1984, Epple 1985, Marti 1990). The species is also highly flexible in use of nest sites including many in human-dominated landscapes (Bunn et al. 1982, Marti 1992).

The Barn Owl is the most widespread of all owl species (Burton 1984) and extensive literature exists on its reproduction. However, this information has not been gathered evenly from the species' range, and two voids in knowledge about Barn Owl reproduction stand out: (1) the understanding of how a population's reproductive performance varies over an extended period, and (2) the understanding of environmental factors that influence reproductive performance in different parts of the species' broad distribution.

The northern boundary of Barn Owl breeding range in the intermountain western United States is approximately 150 km north of the Utah-Idaho boundary (Marti 1988a). This range limit is apparently the result of winter weather, especially the combination of cold temperatures and deep snow that increases the quantity of food needed and makes finding it difficult. Johnson (1974) found that Barn Owl plumage affords less effective insulation than would be expected for a bird of that size, and Piechocki (1960) reported that Barn Owls had less fat reserve than several other owl species. Evidence that these Barn Owl characteristics are involved in range limitation comes from reports of occasional heavy winter mortality in the northern United States and Europe (Dobinson and Richards 1964, Güttinger 1965, Frylestam 1972, Marti and Wagner 1985).

My objectives were to: (1) characterize the reproductive parameters of a Barn Owl population near the northern limit of the species' distribution, and (2) quantify the variance in reproductive parameters over time, and identify the primary environmental factors that cause this variation.

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STUDY AREA

The study area (500 km^2) is in a narrow (12–25 km wide) valley lying between the Wasatch Mountains and the Great Salt Lake in Box Elder, Weber, and Davis counties of northcentral Utah. This area was formerly shrub-steppe 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. The largest monthly portion of the 35 cm annual precipitation falls in April (Climatological Data Summary, National Climatic Center, Asheville, North Carolina).

Suitable nesting habitat for Barn Owls is limited; breeding populations occur only in lower valleys, primarily those with irrigated agriculture and nest sites in human structures. Breeding densities may be locally high in favorable years, but Barn Owl densities are low overall in this area. Barn Owls are known to nest in natural cliff sites adjacent to one end of the study area but essentially no natural nest sites suitable for Barn Owls occur on the study area. In fact, Barn Owls probably did not nest there prior to the availability of anthropogenic structures; barns, other open buildings, and haystacks provide suitable sites for owl nesting.

METHODS

Data were gathered from 1977 through 1992 from nest boxes that Barn Owls used for nesting and as winter roosts (Marti et al. 1979). Approximately 40 boxes located in abandoned concrete agricultural silos were available each year, and this number did not vary annually by more than three boxes except in the first year when only seven boxes were available. Density of boxes was not uniform throughout the study area, being dictated by location of silos (range 0.1–1.5 box/km^2). I visited boxes at least once per month year-round, and made additional visits as needed to ascertain timing of reproductive activities, 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. I cleaned the boxes annually to remove accumulations of broken pellets, prey remains, and fecal material.

Adult owls were caught in nest boxes year-round to determine their identity and age either from banding records or from molt characteristics (P. Bloom, pers. comm.). Egg-laying dates were determined either from direct observation or by backdating from date of hatching using 30 days as the incubation period (Marshall et al. 1986).

I used weather data from official weather stations within the study area (Climatological Data Summary, National Climatic Center, Asheville, North Carolina). Patterns of the weather variables thought most likely to strongly affect Barn Owl reproduction are shown in Figures 1 and 2. The two winter-weather variables—snow cover and ambient temperature—were highly correlated ($r_s = 0.86$, $P = 0.001$; Fig. 1).

All statistical analyses were performed using the Statistical Analysis System (SAS Inst. 1988). Key-factor analysis followed the method of Varley and Gradwell (1960): k-value = log(initial numbers) − log(survivors). The following mortality factors were calculated as follows.

Hatching failure:

$k1$ = log(number of eggs laid) − log(number of hatchlings).

Nestling mortality:

$k2$ = log(number of hatchlings) − log(number of fledglings).

Mortality outside the breeding season:

$k3$ = log(number of fledglings) − log(number of one-year-old breeders next year).

Total mortality (K) = $k1 + k2 + k3$.

RESULTS

GENERAL REPRODUCTIVE PATTERN

Barn Owls produced large clutches in northern Utah, bred early in life—usually only once in their life—and only rarely produced two broods per year. Occasionally females laid replacement clutches following the failure of a first clutch.

My results are based on 391 nesting attempts where at least one egg was laid. Comprehensive histories were known for 348 of these and most of the following analyses are based on that subsample.

Clutch size. Complete first clutches ($n = 275$) averaged 7.17 eggs (SD = 1.36) and ranged from 3–13 eggs (Table 1). Clutches were considered to be complete if incubation continued for at least two weeks after the last recorded egg was laid.

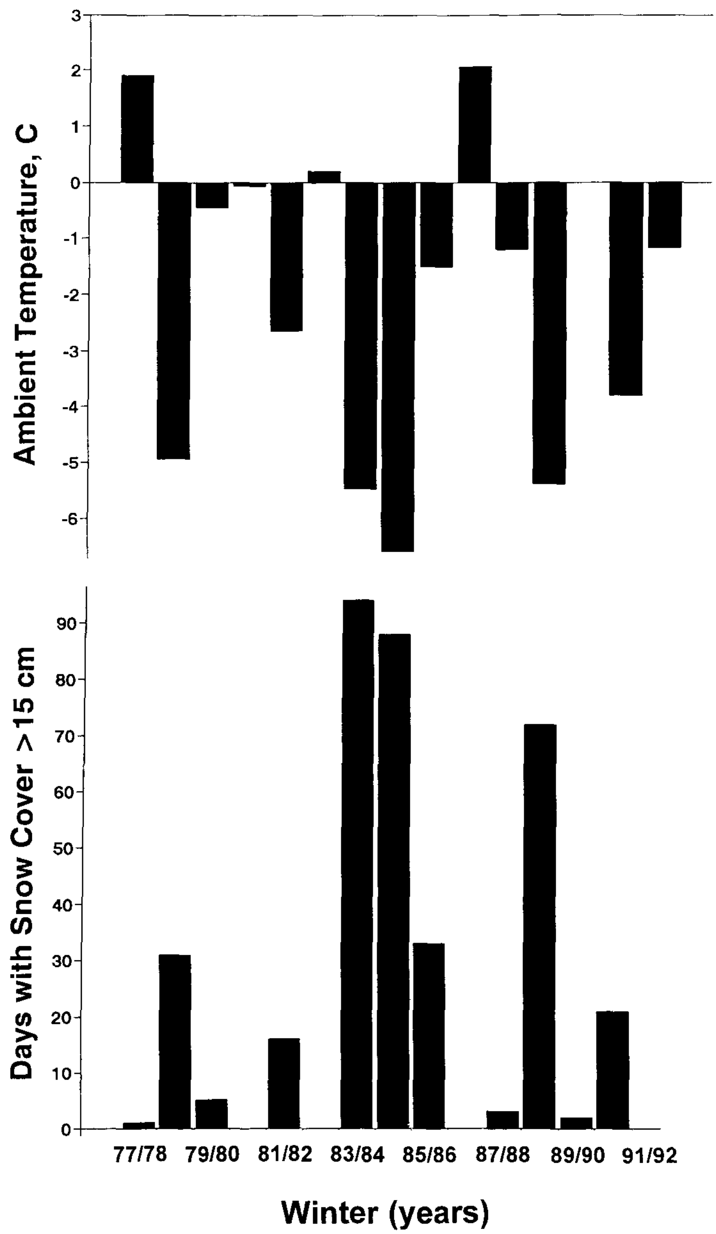

FIGURE 1. Annual variation of winter weather in northern Utah (air temperature = daily mean for December–February; snow cover = number days with snow on the ground, November–March).

First clutches were significantly larger than replacement clutches ($\bar{x}$ = 5.81, SD = 1.42, n = 16), both when all complete first and replacement clutches were compared (t = 3.87, df = 289, P = 0.0001) and when first and replacement clutches by the same females in the same years were compared ($\bar{x}$ = 1.41 fewer eggs in replacement than in first; paired-t = 3.40, df = 11, P = 0.006). Means of first clutches were also larger than second clutches ($\bar{x}$ = 5.79, SD = 1.23, n = 18; t = 4.30, df = 292, $P < 0.0001$), as was the difference between first and second clutches by the same females in a year ($\bar{x}$ = 1.39 fewer eggs in second than in first; paired-t = 3.03, df = 17, P = 0.007).

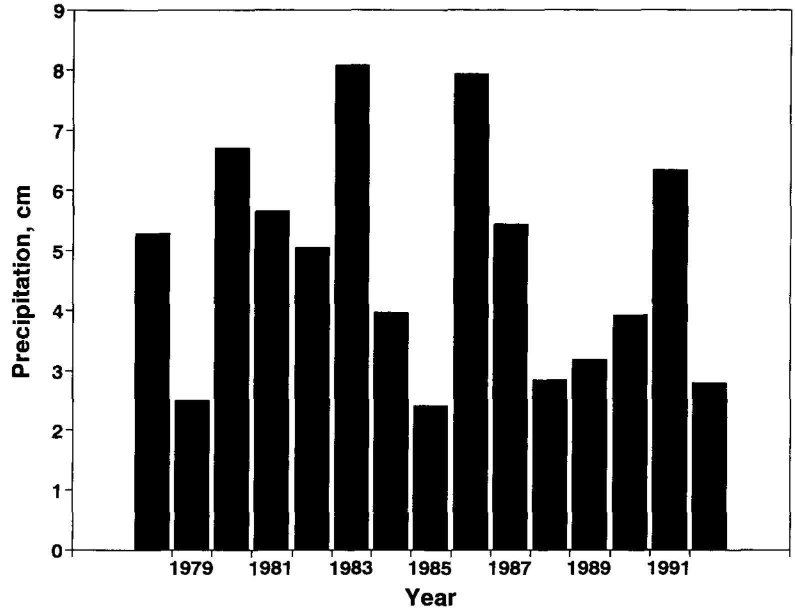

FIGURE 2. Annual variation in precipitation falling in spring in northern Utah (March–May).

Brood size. Mean numbers of eggs hatching in first (5.45, SD = 1.62) and second (5.37, SD = 1.67) clutches were not significantly different between all first and second broods ($t = 0.21$, df = 253, $P = 0.83$), nor between first and second broods of the same female in the same year (paired-$t = 0.36$, $P = 0.73$; mean difference = 0.18). Size of replacement broods ($\bar{x} = 3.83$, SD = 2.04) was, however, significantly smaller than that of first broods ($t = 3.32$, df = 246, $P = 0.001$).

Number of fledglings. Ninety-three percent of nest attempts reaching the nestling stage went on to produce fledglings (Table 2). No difference was discerned between the number of fledglings produced in first ($\bar{x} = 5.09$, SD = 1.70) and second broods ($\bar{x} = 4.94$, SD = 1.92) either when all first and second nesting attempts were compared ($t = 0.35$, df = 236, $P = 0.73$) or when fledgling numbers from first and second broods in the same year by the same females were paired (paired-$t = 0$, $P = 1.00$). Replacement broods produced significantly fewer fledglings ($\bar{x} = 3.60$, SD = 1.58) than did first broods ($t = 2.72$, $P = 0.007$).

Nest success. Eighty-eight percent of all nest attempts produced full clutches and 71% produced at least one fledgling. Second nesting attempts were proportionately more successful than both first and replacement attempts (Table 2). Eighty-six percent of nest attempts attaining full clutches reached the hatching stage and 80% of them yielded at least one fledgling (Table 2). Of the 52 nest attempts that failed, 75% did so before eggs hatched and 25% between hatching and fledging (Table 1). Cause of failure was seldom known but included a few cases of vandalism, and at least one case where the male was killed in a collision with a car. Nest failure from abandonment caused by my visits may have occurred at seven nests, but Taylor (1991) found that Barn

TABLE 1. Clutch size and outcome of complete first clutches of Barn Owls in northcentral Utah, 1977–1992.

		Percent failing[a]		
Clutch size	Number of clutches	Before hatching[b]	After hatching[c]	Total failures[b]
3	2	0	0	0
4	3	33.3	0	33.3
5	16	6.2	6.7	12.5
6	65	21.5	9.8	29.2
7	83	12.1	5.5	16.9
8	68	8.8	4.8	13.2
9	28	21.4	0	21.4
10	7	14.3	0	14.3
11	0	0	0	0
12	2	0	0	0
13	1	0	0	0

[a] Failing to hatch or fledge at least one young.
[b] Of 275 clutches.
[c] Of 236 broods.

TABLE 2. Success of Barn Owl nesting attempts in northcentral Utah.[a]

Type of nesting attempt[b]	All nest attempts: % producing full clutches	All nest attempts: % producing fledglings[c]	Nests that attained full clutches: % producing nestlings[c]	Nests that attained full clutches: % producing fledglings[c]	% of broods producing fledglings[c]
First (295)	93.2	74.6	85.8	80.0	93.2
Replacement (32)	50.0	31.2	83.3	62.5	83.3
Second (21)	90.5	85.7	100.0	94.7	94.7

[a] Where complete reproductive history was known.
[b] Sample size in parentheses.
[c] At least one.

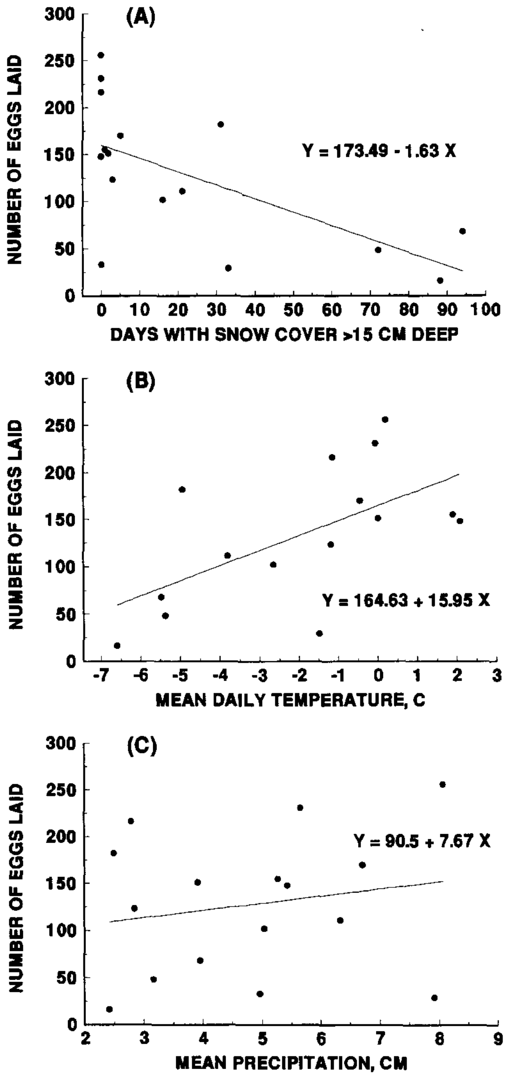

FIGURE 3. Relationship between the number of eggs laid in first clutches of Barn Owls and: A. number of days that ground was covered by snow (November–March; $r^2 = 0.56$, $F = 16.62$, $P = 0.001$), B. mean daily temperature (December–February; $r^2 = 0.36$, $F = 7.35$, $P = 0.02$), and C. mean spring precipitation (March–May; $r^2 = 0.04$, $F = 0.52$, $P = 0.48$).

Owl nests visited often by investigators did not differ in success from seldom-visited nests.

One or more eggs did not hatch in 75.2% of successful first clutches but only 23.4% of broods lost young between hatching and fledging. All eggs hatched and young survived to the fledging stage in 15.6% of successful first clutches; the largest clutch in which all eggs hatched and survived to fledging was nine. On average, 1.70 eggs (SD = 1.66) disappeared before hatching, and a mean of 0.49 young (SD = 0.91) died or disappeared between hatching and fledging in first broods. The loss of young after hatching was significantly less than the loss of eggs prior to hatching ($t = 9.54$, df = 217, $P < 0.00001$). Death of young shortly after fledging was impossible to quantify, but I documented deaths at this stage from electrocution, collision with automobiles, and predation by domestic dogs (*Canis familiaris.*)

Population egg history. Sixty-three percent of the 2,265 eggs laid hatched and 55% survived to fledgling age (see Table 3 for breakdown by type of clutch). Eighty-seven percent of hatchlings survived to fledging age. The total number of eggs laid in first clutches was significantly smaller in breeding seasons following winters with many days of snow cover and unusually cold temperatures, but showed no relationship to spring precipitation (Fig. 3).

TABLE 3. Fate of Barn Owl eggs in first, replacement, and second clutches in northern Utah.

Clutch type	Number of eggs	% of eggs that hatched	% of eggs that produced fledglings	% of nestlings that fledged
First	2,039	63.1	55.0	87.2
Replacement	111	41.4	32.4	78.3
Second	115	85.2	77.4	90.8

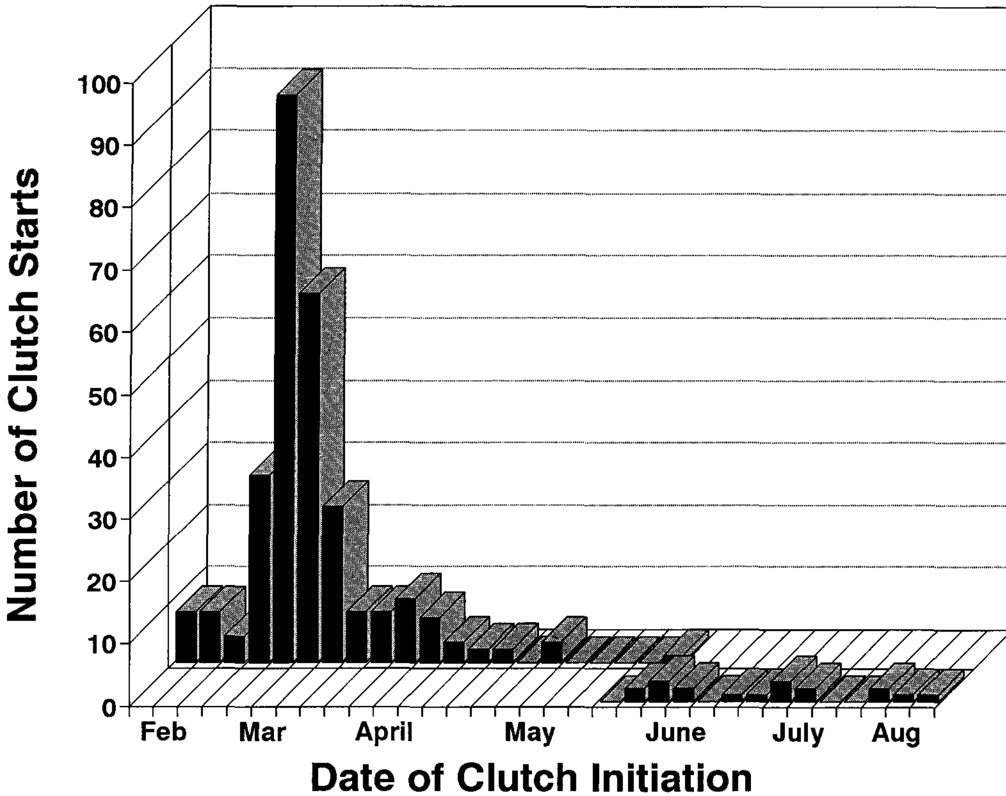

FIGURE 4. Dates of Barn Owl clutch initiation (16 years combined) in northern Utah (x-axis intervals are six days; back row = first clutches and front row = second clutches).

TABLE 4. Dates of Barn Owl reproductive events in northcentral Utah.

	Date of initiation											
	First clutches						Second clutches					
	Egg laying			Hatching			Egg laying			Hatching		
Year	Median	Mean	*n*	Median	Mean	*n*	Median	Mean	*n*	Median	Mean	*n*
1977	14 Mar	14 Mar	4	13 Apr	12 Apr	4	—	—	0	—	—	0
1978	9 Mar	8 Mar	21	8 Apr	8 Apr	19	—	—	0	—	—	0
1979	12 Mar	13 Mar	24	11 Apr	12 Apr	22	—	—	0	—	—	0
1980	7 Mar	12 Mar	26	8 Apr	12 Apr	21	9 Jun	—	1	8 Jul	—	1
1981	12 Mar	12 Mar	28	10 Apr	11 Apr	20	25 Jun	28 Jun	4	25 Jul	30 Jul	4
1982	19 Mar	30 Mar	16	19 Apr	30 Apr	9	—	—	0	—	—	0
1983	6 Mar	6 Mar	32	4 Apr	5 Apr	21	6 Aug	—	1	6 Sep	—	1
1984	4 Apr	5 Apr	10	1 May	7 May	8	5 Aug	—	0	1 Sep	—	1
1985	12 Apr	12 Apr	2	6 May	—	1	—	—	0	—	—	0
1986	8 Mar	9 Mar	3	11 Apr	11 Apr	3	—	—	0	—	—	0
1987	6 Mar	2 Mar	17	6 Apr	4 Apr	15	13 Jun	13 Jun	2	6 Jul	—	1
1988	10 Mar	12 Mar	18	11 Apr	17 Apr	17	—	—	0	—	—	0
1989	10 Mar	11 Mar	3	9 Apr	11 Apr	5	14 Jun	—	1	16 Jul	—	1
1990	10 Mar	22 Mar	21	9 Apr	22 Apr	19	19 Jul	29 Jul	6	17 Aug	27 Aug	4
1991	5 Mar	9 Mar	14	8 Apr	10 Apr	11	27 Jun	12 Jul	3	27 Aug	27 Aug	2
1992	4 Mar	6 Mar	28	3 Apr	6 Apr	25	29 Jun	29 Jun	2	—	—	0

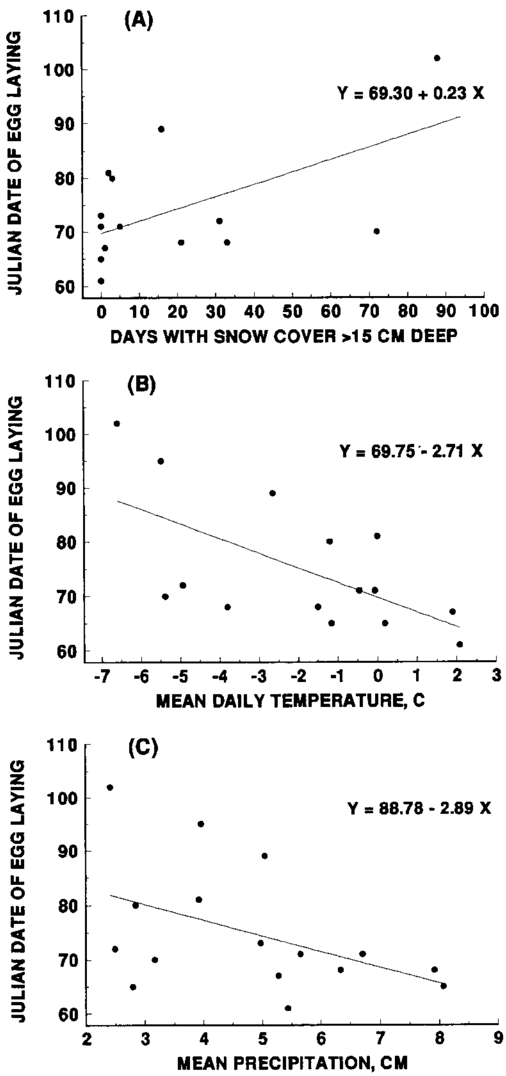

FIGURE 5. Relationship between mean Julian date that egg laying began by Barn Owls and: A. number of days that ground was covered by snow (November–March; $r^2 = 0.42$, $F = 9.56$, $P = 0.001$), B. mean daily temperature (December–February; $r^2 = 0.38$, $F = 8.05$, $P = 0.01$), and C. mean spring precipitation (March–May; $r^2 = 0.21$, $F = 3.74$, $P = 0.07$).

TIMING OF REPRODUCTIVE EVENTS

Initiation of first clutches. Barn Owls began laying eggs for first clutches on average on 13 March (SD = 15.9 days; $n = 16$ years), ranging between 9 February and 9 June (Fig. 4). Mean egg-laying dates for first clutches were significantly different among years (ANOVA, $F = 7.22$, $P = 0.0001$; Table 4). Severity of the preceding winter had a significant effect on the initiation of reproduction—the greater the number of days of deep snow cover and the lower the mean daily temperature in the preceding winter, the later the onset of egg laying (Fig. 5). Amount of spring precipitation was not related to timing of nest starts (Fig. 5).

Initiation of second clutches. Second clutches began on average on 11 July (SD = 26.3 days), ranging from 7 June to 17 August (Fig. 4), but mean dates for the initiation of second clutches did not vary significantly among years (ANOVA, $F = 2.10$, $P = 0.13$; Table 4). Over the 16 years, first clutches began hatching from 10 March to 8 July with an overall mean of 13 April (SD = 15.9 days). Differences among annual mean hatching dates were significant (ANOVA, $F = 1.79$, $P = 0.04$; Table 4). Second clutches began hatching on average on 11 August ranging from 6 July to 4 October, but these dates did not differ significantly among years (ANOVA, $F = 0.36$, $P = 0.90$; Table 4).

Fledging. Time of fledging (first flight) is hard to quantify in Barn Owls because juveniles return to the nest to roost for several weeks after fledging. Also, the large broods and asynchronous hatching may result in individuals of a brood fledging over a two-week or longer period.

PATTERNS OF REPRODUCTIVE VARIATION

Nesting attempts and success by year. First clutches initiated varied from 3–37 per year (Fig. 6) and successful first clutches (those that produced at least one fledgling) ranged from 1–25 per year. The number of days of deep snow cover in the previous winter was very important in determining the number of nesting attempts—winters with many days of deep snow cover were followed by breeding seasons with few nest attempts and low success (Fig. 7). Low winter temperatures were also associated with reduced number of nesting attempts and their success in the following nesting season (Fig. 8). The amount of precipitation falling in the spring, however, was not significantly related to either the number of nest attempts or their success (Fig. 9).

Clutch and brood size and number of fledglings. Variation in the size of first clutches both among years and among nest sites was exceptionally small. Several factors could potentially affect clutch size (condition of the adults following winter, food supply in the home range, ability of males to provide food for their mates, and date

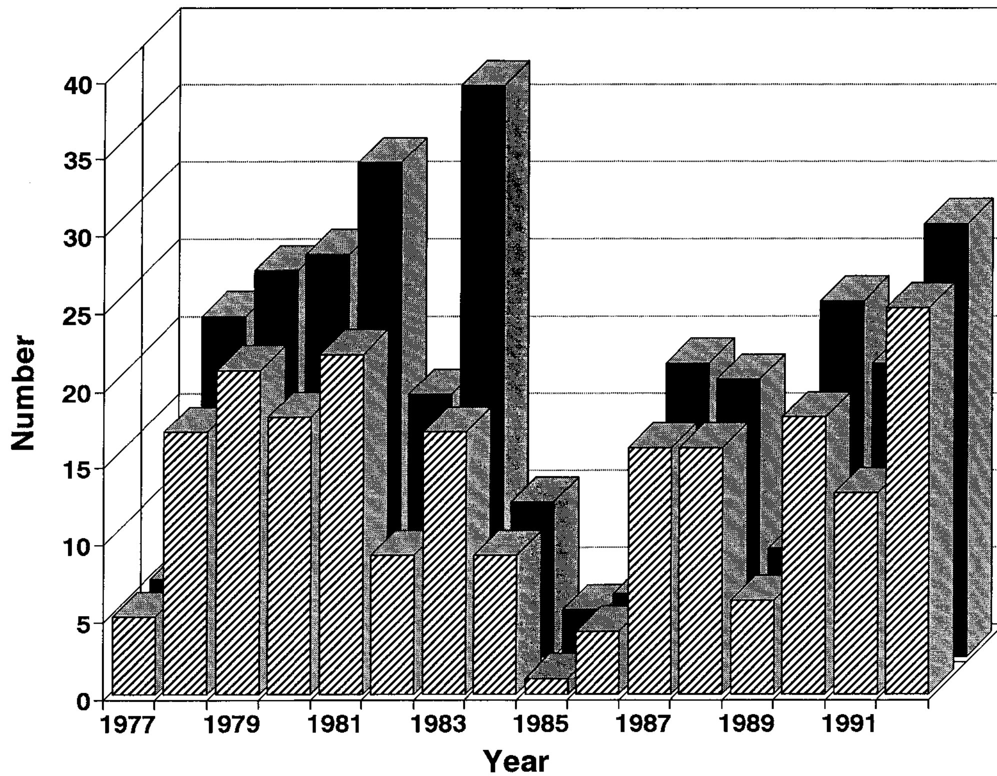

FIGURE 6. Number of Barn Owl nests (first clutches) initiated (back row) and number successful (front row) by year in northern Utah.

of egg laying), but most could not be addressed directly. Despite the strong effects of harsh winter conditions on the size of the breeding population and timing of reproduction, those conditions did not significantly affect clutch or brood size nor the mean number of young fledging/brood (Figs. 10 and 11). Neither did spring precipitation significantly affect those reproductive parameters (Fig. 12).

Under the assumption that nest sites used infrequently were avoided because they were inferior (e.g., because of lower prey densities) and thus should produce smaller clutches, I tested the mean clutch size at sites used less than 40% of the years they were available ($\bar{x}$ = 7.12, SD = 1.39) against the clutch size of sites used greater than 60% of the time ($\bar{x}$ = 7.19, SD = 1.40). These means were not significantly different (t = 0.21, P = 0.83). To remove possible genetic contribution to reproductive variation in these analyses, I used data for only one clutch from each female. Under the assumption that environmental conditions (severe winters) causing few breeding attempts to occur in a given year would also reduce the size of clutches, I compared the mean clutch in the quartile of years with the lowest number of breeding pairs ($\bar{x}$ = 7.12, SD = 1.32) and the mean in the quartile of years with the highest number of breeding pairs ($\bar{x}$ = 7.20, SD = 1.37); these means also were not significantly different (t = 0.22, P = 0.83). Further, using data from all 16 years and the 11 sites with complete first clutches in at least 50% of the years (Fig. 13), I found no evidence that clutch size varied significantly either among years (ANOVA, F = 0.88, P = 0.59) or among nest sites (ANOVA, F = 0.53, P = 0.86). Thus, clutch size was remarkably constant across a range of sites and weather variables.

The pattern of brood size (first broods) among years was only slightly different from the pattern of clutch size; the mean brood size in the quartile of years with the lowest number of breeding pairs ($\bar{x}$ = 6.12, SD = 1.31) was significantly greater

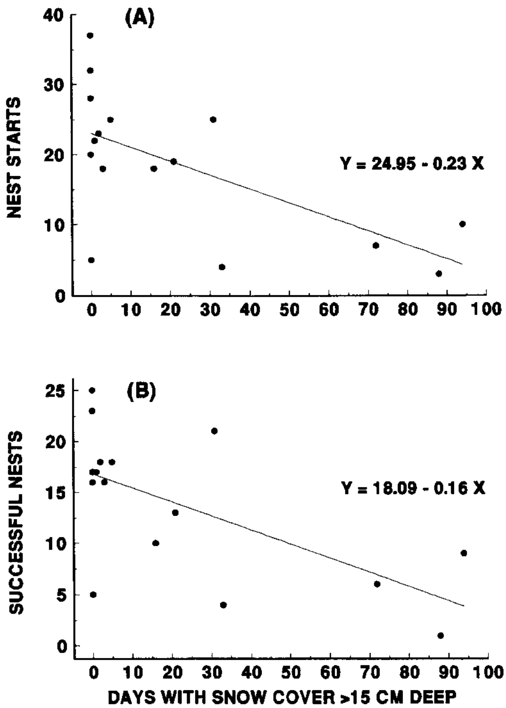

FIGURE 7. Relationship between number of days that ground was covered by snow (November–March) and: A. number of first Barn Owl nesting attempts (r^2 = 0.59, F = 18.41, P = 0.001), and B. number of successful Barn Owl nests (r^2 = 0.56, F = 16.68, P = 0.001).

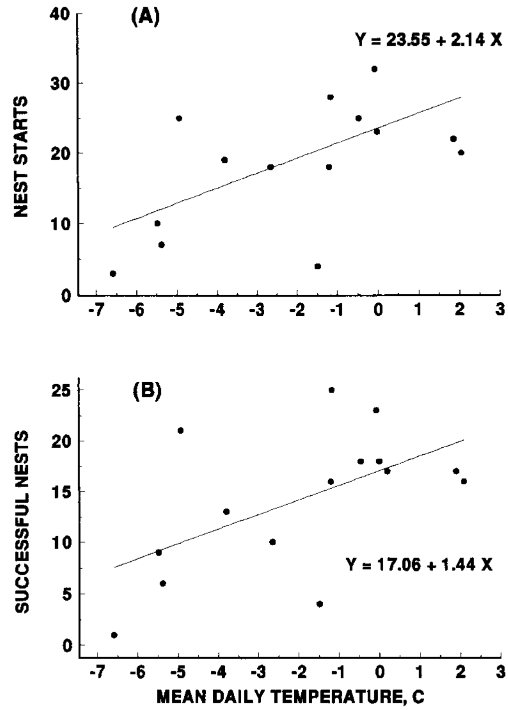

FIGURE 8. Relationship between mean daily winter temperature (December–February) and: A. number of first Barn Owl nesting attempts (r^2 = 0.35, F = 6.98, P = 0.02), and B. number of successful Barn Owl nests (r^2 = 0.32, F = 6.12, P = 0.03).

(t = 3.08, P = 0.003) than the mean of the years with the highest number of breeding pairs ($\bar{x}$ = 4.88, SD = 1.50). However, as in clutch size, the mean brood size at sites used less than 40% of the years available ($\bar{x}$ = 5.47, SD = 1.81) was not significantly different from that at sites used over 60% of the years available ($\bar{x}$ = 5.69, SD = 1.42; t = 0.58, P = 0.56). Likewise, brood size did not differ when the 11 most-used sites from all 16 years were compared either among years (ANOVA, F = 0.66, P = 0.81; Fig. 13) or among sites (ANOVA, F = 0.54, P = 0.86).

Mean numbers of fledglings per nest attempt (first broods) followed the same pattern as brood size. At infrequently used sites the mean number of fledglings ($\bar{x}$ = 5.25, SD = 1.98) did not differ from that at frequently used sites ($\bar{x}$ = 5.24, SD = 1.58; t = 0.02, P = 0.98) nor did the mean number of fledglings differ among all years (ANOVA, F = 0.85, P = 0.62; Fig. 13) or among sites (ANOVA, F = 0.59, P = 0.82). Significantly more young were fledged per brood in years of low breeding numbers ($\bar{x}$ = 5.94, SD = 1.39) than in years of high breeding numbers ($\bar{x}$ = 4.53, SD = 1.50; t = 3.41, P = 0.001).

Population-level productivity. The number of days of snow cover and mean daily winter temperature were significantly related to all measures of population-level reproductive success: harsh winters reduced the reproductive output the following year (Figs. 14 and 15). Spring precipitation, however, had no significant affect on reproduction (Fig. 16).

Also pivotal in terms of the annual population production was that the number of fledglings produced each year was significantly related to the number of breeding adults in the previous year (r^2 = 0.64, F = 22.74, P = 0.0004). However, the converse was not true; the number of fledglings in a year had no affect on the number of breeders the following year (r^2 = 0.0001, F = 0.001, P = 0.97).

Key-factor analysis. Figure 17 shows the mortality factors plotted against years. Nestling mortality ($k2$), was consistently lowest of the sub-

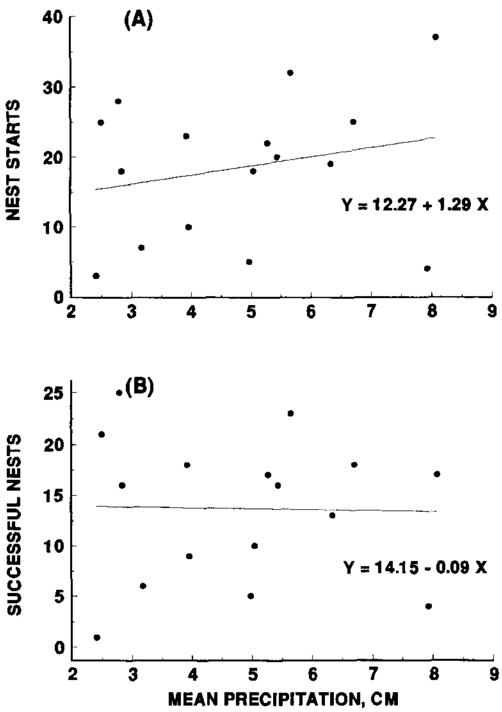

FIGURE 9. Relationship between mean spring precipitation (March–May) and: A. number of first Barn Owl nesting attempts ($r^2 = 0.05$, $F = 0.80$, $P = 0.38$), and B. number of successful Barn Owl nests ($r^2 = 0.001$, $F = 0.008$, $P = 0.93$).

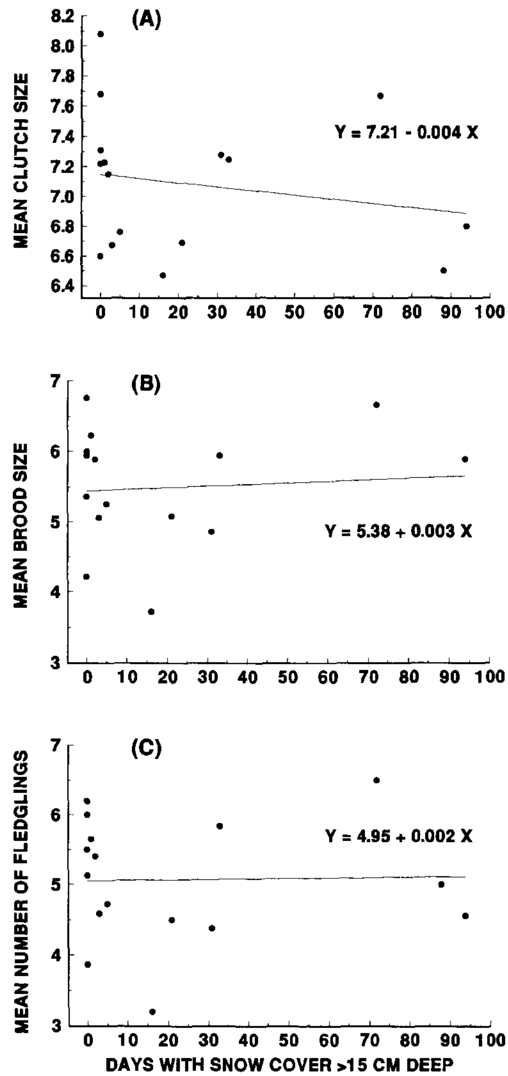

FIGURE 10. Relationship between the number of days that ground was covered by snow (November–March) and: A. mean Barn Owl clutch size ($r^2 = 0.07$, $F = 0.95$, $P = 0.35$), B. mean Barn Owl brood size ($r^2 = 0.01$, $F = 0.20$, $P = 0.66$), and C. mean number of Barn Owl fledglings ($r^2 = 0.007$, $F = 0.09$, $P = 0.77$).

mortalities, and mortality outside the nesting season ($k3$) was the highest, averaging 57% of the total mortality. Nestling mortality ($k2$), though, was the key factor—it most closely paralleled total mortality (regression coefficient of K on $k1 = 0.21$; K on $k2 = 0.65$; K on $k3 = 0.05$; [Podoler and Rogers 1975]). None of the submortality factors met the criterion for density dependence (Stubbs 1977; $k1$, $F = 0.37$, $P = 0.55$; $k2$, $F = 1.43$, $P = 0.25$; $k3$, $F = 0.52$, $P = 0.48$).

CORRELATES OF SECOND NESTING ATTEMPTS

Barn Owls have a relatively long period between egg laying and independence of young (120 days). Thus, in years when the initiation date of first clutches was early, more time would be available for the production of a second brood. I found that the number of first and second clutches within years was significantly correlated ($r = 0.52$, $P = 0.04$) suggesting that conditions that favor more first clutches also favor more second ones. However, the relationship between mean date of the beginning of first clutches and number of second clutches attempted in a year was not significant ($r = -0.16$, $P = 0.55$). To see if pairs that produced second broods started nesting earlier than other pairs, I compared their starting dates with the annual mean population starting dates. In 14 of the 20 cases where dates were known, pairs producing second clutches began their first

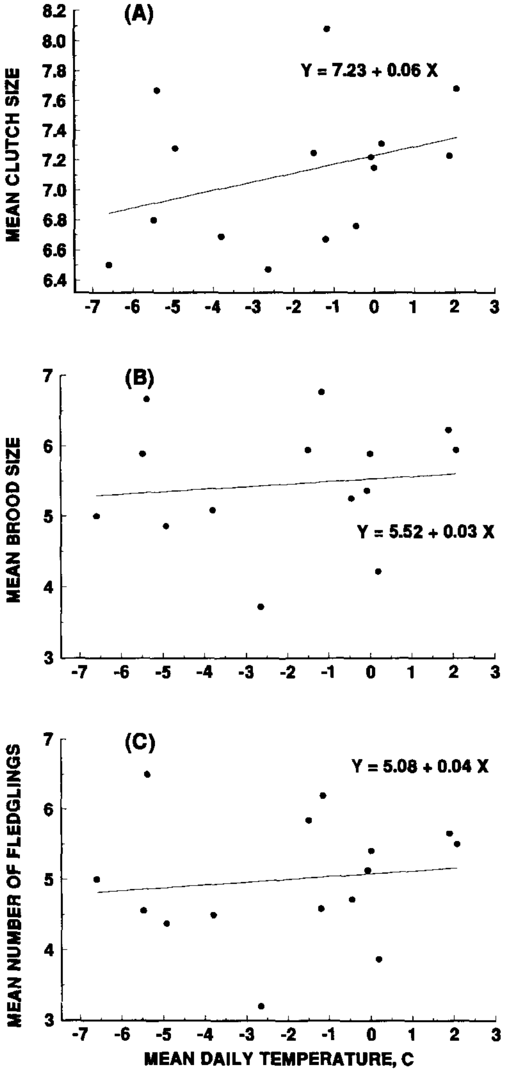

FIGURE 11. Relationship between mean daily winter temperature (December–February) and: A. mean Barn Owl clutch size ($r^2 = 0.12$, $F = 1.74$, $P = 0.21$), B. mean Barn Owl brood size ($r^2 = 0.01$, $F = 0.17$, $P = 0.69$), and C. mean number of Barn Owl fledglings ($r^2 = 0.01$, $F = 0.20$, $P = 0.66$).

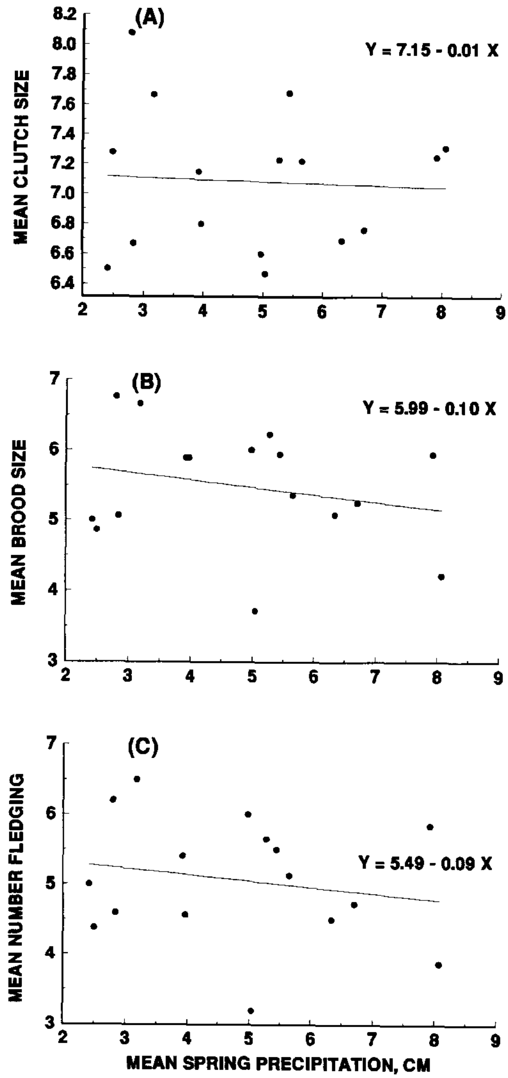

FIGURE 12. Relationship between mean spring precipitation (March–May) and: A. mean Barn Owl clutch size ($r^2 = 0.002$, $F = 0.04$, $P = 0.85$), B. mean Barn Owl brood size ($r^2 = 0.05$, $F = 0.79$, $P = 0.39$), and C. mean number of Barn Owl fledglings ($r^2 = 0.03$, $F = 0.49$, $P = 0.49$).

clutches before the mean date of the population for the year ($\bar{x} = 5.65$ days before the population mean; range = 28 days before the mean population date to six days after it). This suggests that earlier starting of the first clutch is a factor in determining whether a second will be produced, but the data were not sufficient to make statistical comparisons.

AGE AND SUCCESS OF BREEDERS

Of 248 known-age breeders, 94% began breeding at one year of age. Seven individuals were first known to breed at two years of age and five at three years, although I did not know for certain that these 12 had not bred in previous years. Three owls (two males and one female) actually bred (laid eggs) in the breeding season of their

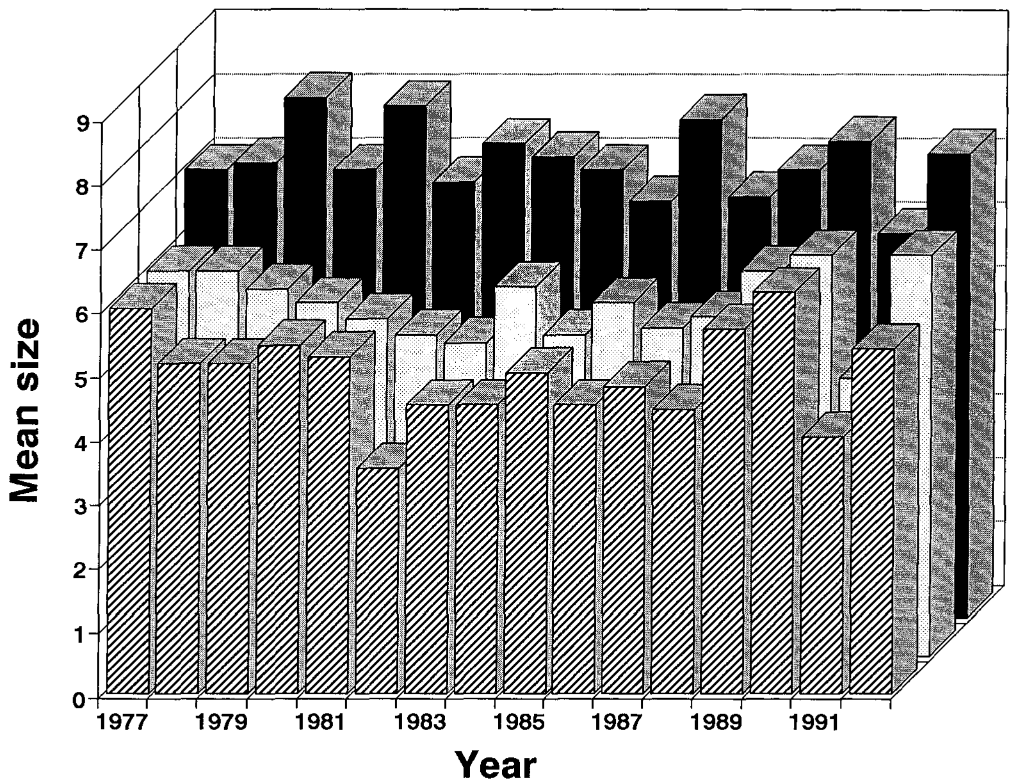

FIGURE 13. Mean clutch size (back row), brood size (middle row), and number of fledglings/brood (front row) for Barn Owls in northern Utah.

own birth (at 6–7 months of age) but all failed to raise young. Forty-five percent of the marked breeders failed to breed successfully (i.e., to raise at least one fledgling), and 79.0% of those that bred successfully did so in only one year (Table 5). Table 6 lists known-age breeders by year.

UNUSUAL REPRODUCTIVE EVENTS

Several observations, outside the normal pattern of Barn Owl reproduction, give further evidence of the plasticity of Barn Owl reproductive strategy. Four cases of polygyny were observed where two females nested simultaneously in the same site (Marti 1990), and several other trios were found at the same nest site. In seven such instances, two males were present, sometimes with all three birds in the same nest box. Only one of these biandrous trios produced eggs, but none was known to raise young. I documented two cases of divorce; in both cases both birds of a pair nested at different sites with new mates in the following year. Only three pairs were known to nest together for two years, although a number of pairs contained unmarked birds, making it impossible to determine mate persistence. Siblings from the same brood paired at a site 1.5 km from their natal site and raised two broods in the year following their birth.

TABLE 5. Number of years that banded Barn Owls were known to breed successfully.

Number of years	Owls breeding successfully	
	Number	Percent
0	112	44.8
1	109	43.6
2	19	7.6
3	6	2.4
4	1	0.4
5	1	0.4
6	1	0.4
7	1	0.4

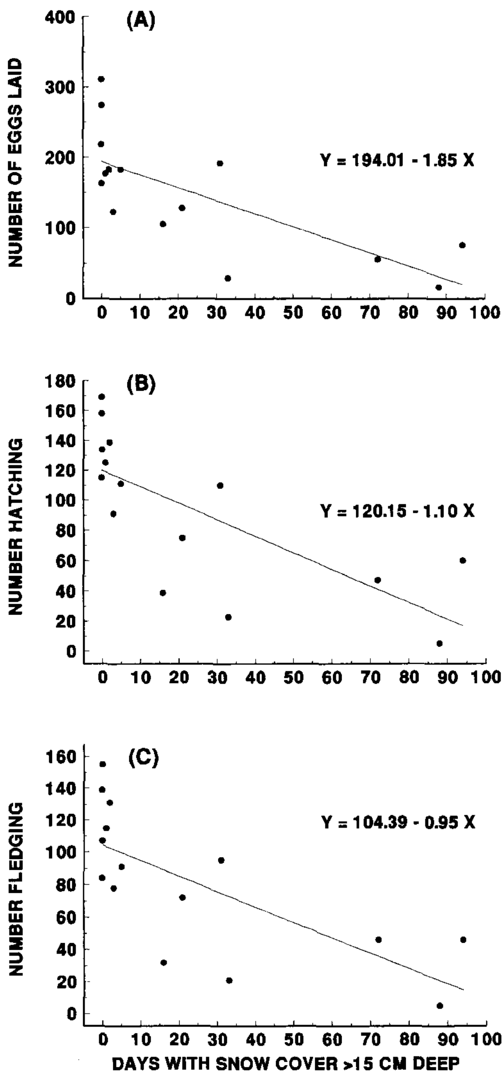

FIGURE 14. Relationship between number of days that ground was covered by snow (November–March) and: A. total annual number of eggs laid ($r^2 = 0.53$, $F = 14.64$, $P = 0.002$), B. total annual number of young hatching ($r^2 = 0.54$, $F = 15.02$, $P = 0.002$), and C. total annual number of young fledging ($r^2 = 0.51$, $F = 13.57$, $P = 0.003$) by Barn Owls.

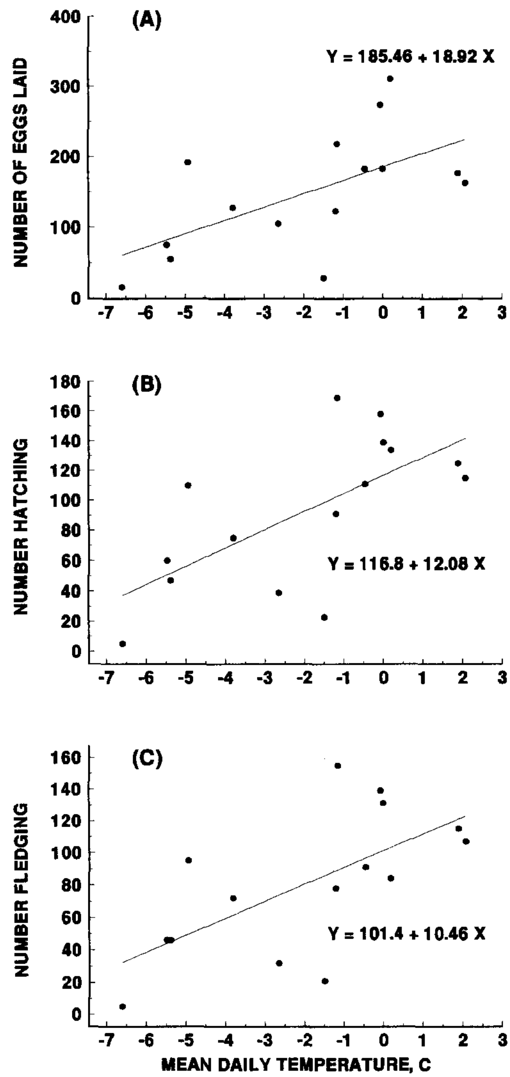

FIGURE 15. Relationship between mean daily winter temperature (December–February) and: A. total annual number of eggs ($r^2 = 0.37$, $F = 7.67$, $P = 0.02$), B. total annual number of young hatching ($r^2 = 0.43$, $F = 10.10$, $P = 0.007$), and C. total annual number of young fledging ($r^2 = 0.41$, $F = 9.14$, $P = 0.01$) by Barn Owls.

DISCUSSION

PATTERNS IN BARN OWL REPRODUCTION

Despite a considerable literature on Barn Owl reproduction, little is known about reproductive patterns and causes of reproductive variation in the species. Mikkola (1983) could not find a pattern for clutch size in European Barn Owls—clutch size did not decrease from north to south as it does in other European owls. Chanson et al. (1988) proposed that Barn Owl breeding dynamics occur on two scales: (1) local annual fluctuations perhaps in relation to rodent availability, and (2) between year and geographically widespread fluctuations, perhaps related to weather or owl density. Giraudoux et al. (1990) believed that reproductive fluctuations of Barn Owls in Europe were in synchrony but that fluc-

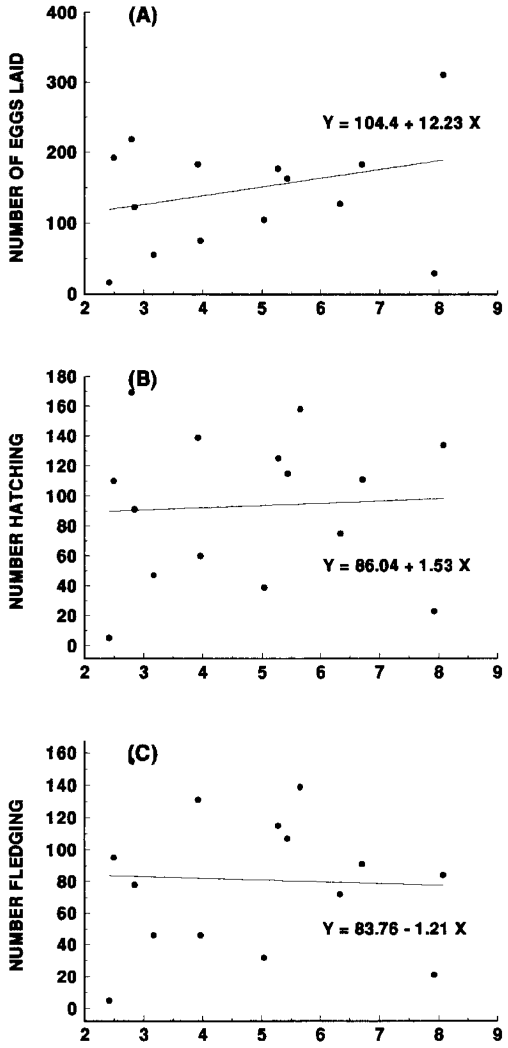

FIGURE 16. Relationship between mean spring precipitation (March–May) and: A. total annual number of eggs ($r^2 = 0.07$, $F = 1.06$, $P = 0.32$), B. total annual number of young hatching ($r^2 = 0.01$, $F = 0.04$, $P = 0.84$), and C. total annual number of young fledging ($r^2 = 0.002$, $F = 0.03$, $P = 0.86$) by Barn Owls.

tuations in rodent densities there were not. They held this opinion despite evidence from several investigators that linked variation in Barn Owl reproductive success to rodent availability (Otteni et al. 1972, Wilson et al. 1986, Taylor et al. 1992).

Barn Owls in northern Utah possessed a high reproductive potential because nearly all birds bred in their first year, produced uniformly large clutches, and, on occasion, raised two broods per

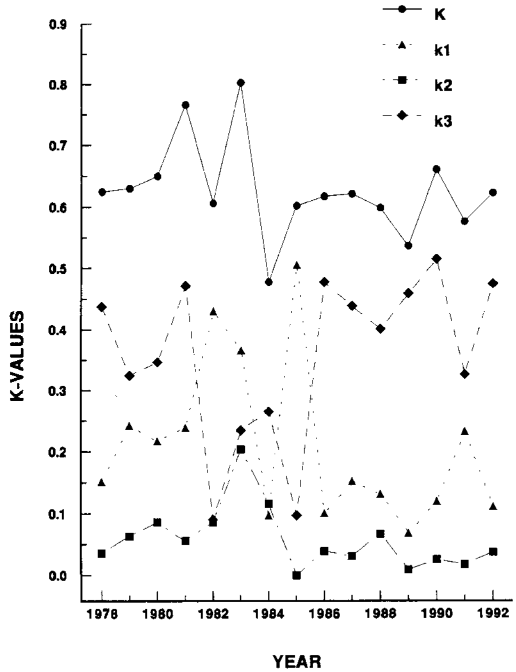

FIGURE 17. Key factor analysis of Barn Owl population data. $k1$ = hatching failure, $k2$ = nestling mortality, $k3$ = mortality outside the nesting season, K = total mortality.

year. Clutch size was remarkably constant from year to year and nest to nest, probably due to the homogeneity of the landscape and because agricultural irrigation caused predictable vegetative growth and prey populations.

Clutch size on my study area (7.17) was the highest reported for a Barn Owl population. Other studies found clutches averaging from as low as 2.9 in Surninam (Haverschmidt 1962) and 3.1 in the Galápagos Islands (De Groot 1983) to 4.7 in England (Bunn et al. 1982), 4.9 in Texas (Otteni et al. 1972), 5.5 in Maryland (Reese 1972), 6.0 in France (Baudvin 1975), 6.0 in Mali (Wilson et al. 1986), and 6.6 in Malaysia (Lenton 1984). Brood size in my population (5.45) was also larger than reported for other populations: 3.8 in Czechoslovakia (Pikula et al. 1984), 4.2 in Maryland (Klaas et al. 1978), 4.6 in Malaysia (Lenton 1984), 4.79 in Mali (Wilson et al. 1986). The mean number of fledglings on my area (5.09), was higher than those reported at other localities: 1.8 in Mali (Wilson et al. 1986), 3.5 in Czechoslovakia (Pikula et al. 1984), 3.8 in Maryland (Klaas et al. 1978).

Second broods were not common in northern

TABLE 6. Age of breeding Barn Owls by year.

Year	Total number of breeders	Number of known-age breeders		% of known-age breeders			
				One year old		> One year old	
		Male	Female	Male	Female	Male	Female
1977	8	0	0	—	—	—	—
1978	44	0	9	—	88.9	—	11.1
1979	50	9	17	100.0	76.5	0	23.5
1980	54	9	19	55.6	42.1	44.4	57.9
1981	66[a]	13	30[a]	61.5	50.0	38.5	50.0
1982	36	6	16	50.0	62.5	50.0	37.5
1983	65[a]	16[a]	30	62.5	70.0	37.5	30.0
1984	26	2	12	100.0	91.7	0	0.3
1985	4	1	1	100.0	100.0	0	0
1986	8	2	2	100.0	50.0	0	50.0
1987	43[b]	12	20	83.3	90.0	16.7	10.0
1988	35[b]	5	15[b]	100.0	73.3	0	26.7
1989	18	3	6	66.7	83.3	33.3	16.7
1990	44	9	20	88.9	85.0	11.1	15.0
1991	37[a]	7	12	71.4	58.3	28.6	41.7
1992	56	11	26	90.9	92.3	9.1	7.7

[a] Includes replacement mates.
[b] Includes extra females as polygynous mates.

Utah but they have been in some places (Baudvin 1979, Lenton 1984, Pikula et al. 1984). Even though I found that second clutches were significantly smaller than first, a higher percentage of them produced fledglings and the mean numbers of fledglings produced in first and second broods were not statistically different. Second nestings may have had a better rate of success because they were produced by more proficient breeders—those that had already managed to raise one brood. Despite the higher success of second broods, postfledging survival of young produced from them in Utah was likely low because second broods fledged late in the breeding season and had little time to perfect hunting skills before winter arrived. Of 59 birds I banded in second broods, only three (5.1%), all males, were known to survive their first winter and breed; eight others were found dead in their first winter. The remaining 48 individuals were never seen again after fledging, but it is likely that some of them dispersed off my study area. An even smaller proportion (3.3%) of nestlings banded in first broods were known to attempt breeding on my study area. However, first broods produced almost three orders of magnitude more fledglings than second broods, and added many more breeders to this population. In a population where most adults breed in only one season, producing two broods would be a good strategy—some pairs managed to raise as many as 15 young on my study area this way.

Reproductive success was high in northern Utah where 71% of nesting attempts produced at least one fledgling, but 84% of all successful nests lost at least one egg or young between laying and fledging. The most vulnerable stage of reproduction was incubation—75% of unsuccessful nests failed at that stage. Loss of eggs in successful nests was about 3.5 times greater than the loss of nestlings.

Highest annual loss of individuals from this northern Utah population occurred in winter. Part of this loss was due to weather-related causes (Marti and Wagner 1985), but it also consisted of the dispersal of immature birds out of the area (see review in Marti 1992). Loss of individuals by dispersal was offset by the immigration of owls into northern Utah from other populations. That such an immigration occurred was known because some breeding Barn Owls had been banded elsewhere and some were unbanded, also indicating that they were born in other populations.

Little is known about the age of first breeding in most Barn Owl populations. In Scotland first-year birds were never more than 40% of the breeding population (Taylor et al. 1992) whereas 100% of breeders were first-year birds during several years of my study and 94% of all known-age Barn Owls in Utah bred in their first year. The high annual population turnover in Utah probably is a factor in age of first breeding. Higher adult survival coupled with limited nest sites likely would reduce the chances for owls to nest in their first year.

CAUSE OF REPRODUCTIVE VARIATION

Winter weather caused great variation in reproductive performance in northern Utah by its influence on the number of nesting attempts, their success, and the time that first clutches began. Reproduction was most depressed following winters with concurrent periods of very cold temperatures and many continuous days of deep snow cover. The proximate cause of this depression was death of potential breeders. Even though Barn Owls can locate prey acoustically (Konishi 1973), snow can still interfere with prey capture. Snow depths too great for the owls to penetrate or a hard crust on the snow surface can make capturing sufficient prey a major problem. Limited accessibility of prey is compounded by cold temperatures requiring that owls use more energy to maintain body temperature. This combination can be fatal to Barn Owls (Marti and Wagner 1985). In Scotland, though, no relationship between the duration of winter snow cover and the number of breeding Barn Owls was detected (Taylor 1992). This anomaly might be resolved by examining differences in snow depths, snow consistency, and air temperatures between Utah and Scotland.

Several investigators reported that prey availability was a major factor regulating Barn Owl reproduction (Otteni et al. 1972, Wilson et al. 1986, Taylor et al. 1992). In northern Utah this did not seem to be the case. Owl diets there exhibited little year-to-year or place-to-place variation, and were consistently heavily dominated by voles (*Microtus* spp.; Marti 1988b). I had no direct vole population estimates, but where voles are major Barn Owl prey their relative proportion in Barn Owl diets is a good indicator of vole availability (Taylor et al. 1992). Additional support for the contention that Barn Owl prey populations in northern Utah were not a factor in reproductive variation came from an intensively studied vole population located 50 km from my study area (Negus et al. 1986). This population did not exhibit cyclic population density apparently because it occupied a climatically and vegetationally constant marsh. Irrigated agriculture land throughout my study area provided similarly constant vegetational conditions favorable to voles making it likely that vole populations were also stable there.

CONCLUSIONS

My results are important in showing that a Barn Owl population located near the northern limit of the species' range had a high reproductive rate and a very high population turnover. I also show that winter weather was a major factor in annual reproductive success. Additionally, these results are important for understanding one of the reasons—harsh winter weather—that limits the geographic distribution of the species. Similar long-term studies in climatically different parts of the Barn Owl's range are needed to understand the species' overall reproductive pattern.

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