# Snowy Owl (*Nyctea scandiaca*) Reproduction in Relation to Lemming Population Cycles on Wrangel Island

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*Abstract.*—Data on Snowy Owl (*Nyctea scandiaca*) reproduction on Wrangel Island were collected for six seasons from a total of 423 nests. Nest densities ranged from 0.15 to 0.40 nests/km $^2$. Mean clutch size for all 6 years was 6.5 (from 5.3 to 8.4) being significantly higher during low lemming season (7.17) (N = 29) than for peak lemming season (6.0, $p < 0.001$). Clutch size correlated with weather conditions, females' age, and lemming numbers. Number of young fledged per nest was the highest during peak lemming numbers. Bigamous units occurred only during medium, high, and peak lemming numbers. Nestling mortality was due to lack of food.

Snowy Owl (*Nyctea scandiaca*) biology has been studied in different parts of its circumpolar range, including Wrangel Island (Litvin and Baranyuk 1989, Robinson and Becker 1986, Taylor 1974). However, few long-term studies on this species have been conducted (Pitelka et al. 1955a,b), and even those did not investigate the whole variety of Snowy Owl population parameters. Watson (1957) suggested that Snowy Owl nest density, clutch size, and reproductive success may differ in different areas even under high lemming population numbers. In most of the previously published articles on Snowy Owl biology, the relationship between the number of nests and clutch size, and lemming numbers is mentioned but without describing the mechanisms of this correlation (Cramp 1985, Johnsgard 1988, Krechmar and Dorogoi 1981, Litvin and Baranyuk 1989, Parmelle 1992, Robinson and Becker 1986, Voous 1988).

This paper presents data on Snowy Owl reproduction on Wrangel Island collected from a permanent study plot (45 km $^2$) and on routes (3,000 km) for six seasons, 1990-1995, during which lemming numbers ranged from depression to peak.

Objectives of the study were:

1. To determine factors responsible for the density of Snowy Owl reproductive settlements.
2. To investigate relationships between variations in Snowy Owl clutch size and survival of young, and various environmental parameters, including lemming numbers.
3. To estimate the reproductive contribution of females of different age.
4. To investigate occurrence of polygyny in Snowy Owls during different phases of population cycle, and reproductive success in family units of bigamous males.

## STUDY AREA

Wrangel Island is situated in the Chukchi Sea 140 km north of Chukotka peninsula between 70°-71°N and 179°W - 177°E. It is the only large land mass in the eastern sector of the Asian Arctic. The island is 7,670 km $^2$ in size, 4,700 km $^2$ of which are mountain masses with the highest top of 1,095 m above sea level, surrounded from north and south by open tundra. The climate is rather continental (Svatkov 1970), with average annual temperature below zero (Celsius) and a warm period not longer than 2 months. All types of major arctic landscapes are represented here (Petrovskyi 1967). Two lemming species—the hooted lemming (*Dicrostonix vinogradovi*) and common lemming (*Lemmus sibiricus*)—are the main Snowy Owl prey on the island (Dorogoi 1987).

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*The study plot of 45 km $^2$ was situated in the very center of the island in the upper reaches of the Neizvestnaya River (Unknown River). It included part of the river valley with numerous tributaries and bordered on the west by Pervaya Mountain (first mountain, 503 m) and on the east by the watershed and upper reaches of the Krasnyi Flag River (Red Flag River). Such features as rugged landscape with hilltops up to 200-350 m, differences in substrate composition, in timing of snow melt, and in wetting of the territory cause formation of a great variety of ecotopes. In terms of floristic classification, the study plot reflects the special sub-zonal type with mixed characteristics of typical northern tundras and arctic tundras (Yurtcev et al. 1989).*

## *METHODS AND MATERIALS*

*Observations were carried out in the spring-summer seasons (from May to September) of 1990-1995, during a total of 22.5 months. The length of each observation period varied from 3 to 5 months depending on environmental conditions of the year. Characteristics of the spring conditions and lemming populations are given in table 1. Lemming numbers were estimated by the number of lemming under-snow nests, freshly cleaned den entries and number of lemming carcasses at Snowy Owl nests. Lemming nest and den survey routes crossed all types of habitats and slope exposures, and had a counting strip width of 10 m.*

*I observed Snowy Owls from blinds positioned within nesting territories, on routes conducted by snowmobiles in various parts of the island during snow-cover periods, or by foot and ATV during snow-free times. Within the study plot all Snowy Owls and their nests were counted, and each nest was visited periodically during the field season. Routes in other parts of the island were conducted from one to three times each. The locations of all nests were mapped. I recorded the sex and age class of birds, based on distribution, size, and density of dark dots on the plumage (Josephson 1980). I determined boundaries of owl reproductive territories by farthest points of male landings (not only on perches) and by territorial displays (Taylor 1973). All territories were mapped. I observed the growth of owl nestlings in all families within the study area; nestlings were provided with temporary individual colored marks and regularly weighed. In 1992-1994, I marked 25 nestlings from 11 different broods with colored patagial-tags. Reproductive success was estimated by the number of nestlings observed to fledge. Total time of observations was 3,700 hours, total length of routes was 3,000 km. During six seasons I examined a total of 423 nests, including 79 in the study plot and its nearest vicinity. The history of 75 nests was known from the beginning to the end of the breeding season.*

## *RESULTS*

### *Timing of Egg Laying*

*Snowy Owls do not stay on Wrangel Island over winter. Only single birds were rarely recorded on the island during winter in years of very high lemming numbers (Ovsyanikov and Menyushina 1986). The arrival of large numbers of owls to the island begins by mid-May and lasts from 1 to 3 weeks. Weather conditions, timing of snow melt and floods, to which the beginning of the owls' breeding season is related, vary considerably (table 1). Nevertheless, whatever the weather conditions are, the*

*Table 1.—Characteristics of spring conditions and lemming populations on Wrangel Island.*

| **Year** | **Spring** | **Beginning of flood**[1] | **End of snow melting** | **Lemming number** | **Phase of lemming population** |
|---|---|---|---|---|---|
| | | *dd.mm* | *dd.mm* | | |
| 1989 | ? | ? | ? | ? | Depression |
| 1990 | Very early | 15.05 | 28.05 | Low | Beginning of growth . |
| 1991 | Normal | 25.05 | 10.06 | Low | *L.s.*decrease, *D.v.*growth[2] |
| 1992 | Normal | 22.05 | 10.06 | Low | Growth |
| 1993 | Normal | 22.05 | 10.06 | Medium | Growth |
| 1994 | Late | 07.06 | 20.06 | High | Peak |
| 1995 | Very late | 12.06 | 25.06 | Med-High | Decrease |
| 1996 | ? | ? | ? | ? | Depression |

[1] Dates of flood beginning on Neizvestnaya river.
2 *L.s.* = *Lemmus sibiricus*, *D.v.* = *Dicrostonix vinogradovi*.

majority of Snowy Owls (80.5 percent, n = 142) begin egg laying and incubation within a short period from 15 to 31 May. In late springs, the period when first egg laying and incubation begins is 2-3 times longer than under normal spring conditions—27-30 days against 7-11 days respectively.

### Lemming Population Estimation

The number of lemming under-snow winter nests and freshly cleaned den entries positively correlated with each other (r = 0.8861, P = 0.0187). Therefore, these parameters are considered relative indicators of the intensity of lemming under-snow reproduction that determines rodent abundance in the subsequent summer (table 2). For the hoofed lemming, numbers of lemming under-snow nests and cleaned den entries positively correlated with hoofed lemming carcasses at owl nests (r = 0.9188, P = 0.0096 and r = 0.9910, P = 0.0001, respectively). For the common lemming, only the number of under-snow nests positively correlated with the number of common lemming carcasses at owl nests (r = 0.7965, p = 0.0544), whereas den number did not correlate (r = 0.5053, p = 0.3065).

### Snowy Owl Nest Density

Snowy Owl population on Wrangel Island fluctuates between years, and has a dynamic spatial and demographic structure (Litvin and Baranyuk 1989, Menyushina and Ovsyanikov 1991). Owl numbers recorded during route surveys across the island ranged from 0.11 to 0.7 birds per km. In the beginning of a breeding season adult birds ready for reproduction arrive first (April-May). Immature owls and adult non-breeders arrive later (June-July). Owl numbers within the study plot positively correlated with owl numbers recorded during route surveys in other parts of the island (r = +0.8363, P = 0.038, fig. 1). However, owl nest densities within the study plot did not positively correlate with the number of owls observed on routes in other parts of the island (r = 0.3663, P = 0.4803). This can be explained by the fact that the spatial distribution of owls in different areas of the island is not equal, being determined by landscape features and food availability (Menyushina and Ovsyanikov 1991). In other words, even when owl numbers are low, the majority of breeding birds are concentrated within the most favorable nesting habitats, whereas spatial patterns of non-breeders are more opportunistic.

Owls nested every year except years of lemming population depression (1989, 1996). Study plot nest densities ranged from 0.15 to 0.4 nests per km$^2$ (table 3). Nest densities did not positively correlate with the numbers of lemming under-snow nests per hectare (combined data for both species, r = 0.5166, P = 0.2940), nor with the numbers of cleaned dens per hectare (r = 0.1941, P = 0.7125). However, the density of successful nests was positively correlated with lemming numbers (r = 0.8939, P = 0.016). Increased nest density within the study plot was observed during years when the proportion of older females in the breeding population was lower (r = -0.8504, P = 0.0319), and during late spring seasons (r = 0.8020, P = 0.0549). Usually, younger owls and later arriving birds, while choosing a nesting spot, orient themselves on already settled owls. This is evident from the spatial structure of the settlement of breeding owls and from the dates

Table 2.—Data on lemming nests, dens and carcasses at Snowy Owl (*Nyctea scandiaca*) nest sites on Wrangel Island.

| Year | LWN | N of ha | LCD | N of ha | LC at owl nests | Number of visits to owl nests |
|---|---|---|---|---|---|---|
| | *per ha* | | *per ha* | | *D.v./L.s* | |
| 1990 | 5.1 | 14 | 2.1 | 14 | 17/15 | 51 |
| 1991 | 6.4 | 17 | — | — | 32/4 | 49 |
| 1992 | 5.2 | 17 | 2.0 | 17 | 28/5 | 64 |
| 1993 | 9.3 | 17 | 11.0 | 11 | 35/8 | 75 |
| 1994 | 20.2 | 15.5 | 69.0 | 12 | 159/31 | 145 |
| 1995 | 15.4 | 14 | 14.6 | 14 | 58/46 | 136 |

LWN = number of lemming under-snow nests, LCD = number of cleaned dens, LC = lemming carcasses, *D.v.* = *Dicrostonix vinogradovi*, *L.s.* = *Lemmus sibiricus*, N of ha = area (ha) surveyed..

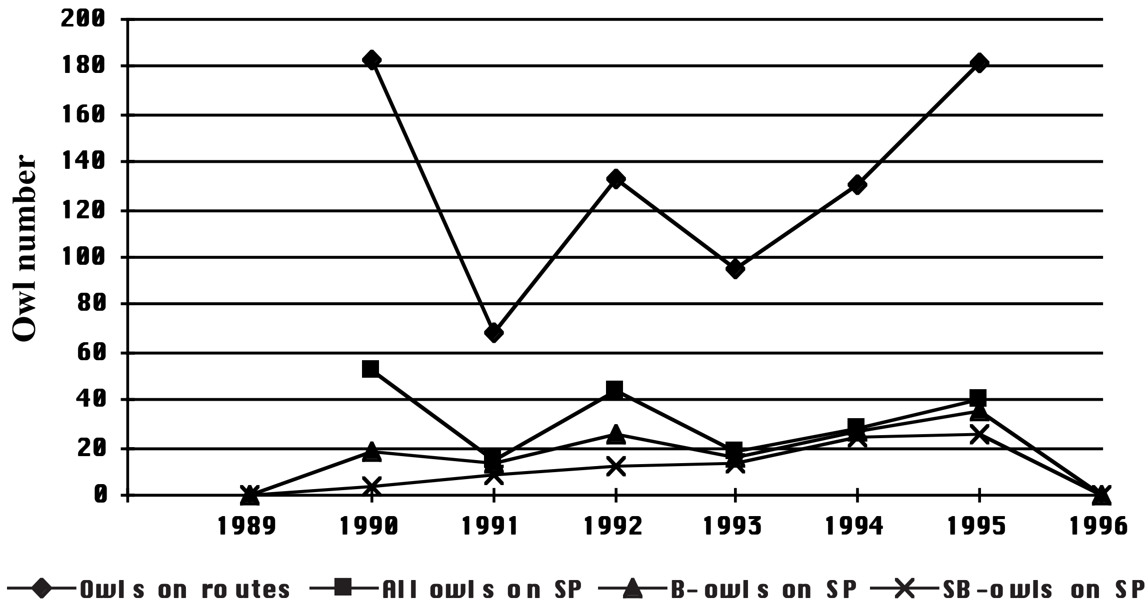


*Figure 1.—Dynamics of Snowy Owl (Nyctea scandiaca) numbers on survey routes and in the study plot (SP-study plot, B-breeding, SB- successfully breeding) on Wrangel Island.*

*Table 3.—Snowy Owl (Nyctea scandiaca) nest density, mean distance between nests, and mean nesting territory size on Wrangel Island.*

| Year | Lemming trend | Lemming number | Owl nest density | Mean nest distance | Range | Territory size | Range |
|---|---|---|---|---|---|---|---|
| | | | *Number\km²* | *km* | | *km²* | |
| 1989 | Depression | | ? | 0 | ? | ? | ? |
| 1990 | Growth | Low | 0.2 | 1.84 | 1.2-3.0 | 2.4 | 1.3-4.0 |
| 1991 | Growth | Low | 0.15 | 2.8 | 1.1-5.2 | 3.6 | 2.6-4.5 |
| 1992 | Growth | Low | 0.28 | 1.5 | 1.1-2.0 | 1.9 | 1.1-2.5 |
| 1993 | Growth | Medium | 0.2 | 2.17 | 1.2-3.2 | 2.3 | 2.0-2.6 |
| 1994 | Peak | High | 0.26 | 1.21 | 0.35-2.2 | 1.46 | 0.7-2.5 |
| 1995 | Decrease | Med-High | 0.4 | 1.46 | 0.3-2.4 | 2.48 | 1.5-6.7 |
| 1996 | Depression | | ? | ? | ? | ? | ? |

*of egg laying. Later arriving birds prefer to settle for nesting close to already incubating owls (within 1-2 km), thus increasing the nest density.*

*The process of breeding settlement formation is, to a great extent, directed by the intensity of the "signal field" [Definition of the term "signal field" is used here in accordance to the concept of N.P. Naumov (1973)] within the owl breeding habitats—by number and distribution of permanent perches and old nest sites. For instance, 81 percent (61 of 75) of all study plot nests were situated in old nest sites.*

*The density of 0.4 nests per km² was a maximum possible nesting density for Wrangel Island, at least for area samples up to 40-50 km². Under such high density many territorial conflicts between breeding owls occurred. As a result, one nest had been abandoned by the beginning of the incubation period. Nest densities for smaller area samples (10 km²) can be even higher—up to 0.7 nests per km². Under such conditions one male was killed during the settling period, perhaps in territorial combat.*

### Clutch Size

Mean clutch size for all research years was 6.5 ± 0.1SE (n = 292). Study plot mean clutch size for all 6 years did not differ from that in other parts of the island (table 4). Therefore, data collected from the study plot is representative for the entire population. Mean clutch sizes for each season in the study plot ranged from 5.8 ± 0.47 SE (n = 18) to 8.4 ± 0.52 SE (n = 7) and were not positively correlated with lemming numbers (r = -0.5990, P = 0.2089) or with owl nest densities (r = -0.6273, P = 0.1824). Mean clutch size during low lemming seasons (7.21 ± 0.15 SE, n = 67) was significantly higher than for peak lemming season (6.0 ± 0.17 SE, n = 48, P = 0.001). Mean clutch size was influenced by a number of factors, in addition to lemmings, such as weather, time of egg laying, females' age, and previous winter conditions.

Mean clutch size in early spring seasons was significantly higher than in late spring seasons (M1 = 8.03, N = 36, M2 = 5.59, N = 39, P = 0.0001). In this calculation, in addition to my own data, I included data collected by the staff of the nature reserve prior to my research.

In all seasons, mean size of clutches with first eggs laid during the period from 15 to 20 May was significantly higher than for clutches with first eggs laid in the period from 26 May to 05 June (M1 = 7.19, N = 16, M2 = 5.89, N = 26, P = 0.003).

For young females, mean clutch size was larger than for middle-age (M1 = 5.52, N = 25, M2 = 6.34, N = 41, P = 0.001) and old females (M1 = 5.52, N = 25, M2 = 6.91, N = 52, P = 0.028) (Josephson 1980).

Although data on Snowy Owl wintering ecology in this region is lacking, wintering conditions appear to influence Snowy Owl clutch size. For example, the winter of 1992-1993 in Chukotka was extremely severe with frequent long blizzards. During the following summer of 1993, when other season characteristics were favorable for normal clutch size, I recorded the lowest clutch size for the entire 6 year period (table 4). Moreover, in the summer, breeding males were unusually passive during both settling and nesting periods. Only 44 percent of all males in that season demonstrated active nest defense and not one of them risked attacking a human intruder.

Male activity also influenced clutch size, perhaps due to successful competition for better nesting territories. During 3 years with low lemming numbers, mean clutch size for nesting males was higher than for non-nesting males (M1 = 7.79, N = 14, M2 = 6.64, N = 14, P = 0.026).

### Polygamy

I observed five cases (6.5 percent of all family units observed) of polygamy in the study plot, only during medium, medium-high, and peak lemming numbers. Bigamous families were formed in the absence of male partners on suitable nesting territories (N = 3) and as a result of territorial conflicts (N = 2) in one of which the second male was killed. Hatching in nests of one bigamous family occurred within only 1 day of each other. In all other cases second females started egg laying 10-14 days later than first females. Mean distance between first and second nests in bigamous units

Table 4.—Variations of Snowy Owl (Nyctea scandiaca) clutch and brood sizes in study plot on Wrangal Island.

| Year | WI mean clutch size (±SE) | N | SP mean clutch size (±SE) | N | Range | Mean brood size (±SE) | N | Range |
|---|---|---|---|---|---|---|---|---|
| 1990 | 6.37 | 10 | 6.78±0.4 | 9 | 5-9 | 0.33±0.23 | 9 | 0-2 |
| 1991 | 8.33 | 21 | 8.43±0.29 | 7 | 8-10 | 1.71±0.52 | 7 | 0-3 |
| 1992 | 6.45 | 18 | 6.71±0.3 | 13 | 4-9 | 1.78±0.49 | 9 | 0-3 |
| 1993 | 5.79 | 55 | 5.78±0.4 | 9 | 5-8 | 2.57±0.72 | 7 | 0-5 |
| 1994 | 6.01 | 32 | 6.19±0.33 | 14 | 3-8 | 5.50±0.29 | 14 | 4-7 |
| 1995 | 5.50 | 13 | 5.80±0.25 | 18 | 4-8 | 3.62±0.47 | 13 | 0-6 |

WI- Wrangel Island, SP - study plot.

was 0.85 km (SE = 0.13, range 0.35-1.1 km, N = 5). In all cases, males quit feeding and defending one of the nests or broods before the young fledged. In three cases, the male remained with the first female, in two the male remained with the second. Both nests in bigamous units fledged young only during the peak lemming year. From 10 nests in bigamous families 2 (20 per cent) were abandoned by males during incubation. In monogamous families only 9 percent of nests (3 from 35) were abandoned.

Mean clutch and brood sizes in bigamous units did not differ significantly for first and second females (M1 = 5.0 $\pm$ 0.01SE, M2 = 5.80 $\pm$ 0.37SE, N = 5, P = 0.066 for clutch sizes and M1 = 3.75 $\pm$ 0.57SE, M2 = 3.00 $\pm$ 0.89SE, N = 4, P = 0.524, for brood sizes respectively).

Mean clutch size in bigamous and monogamous families did not differ significantly (M1 = 5.40 $\pm$ 0.78SE, N = 10, M2 = 6.07 $\pm$ 0.81SE, N = 35, P = 0.092). However, general reproductive success in bigamous units was lower than in monogamous pairs. Mean fledgling brood size in bigamous units was lower than in monogamous families (M1 = 3.375 $\pm$ 0.63SE, N = 8, M2 = 4.687 $\pm$ 0.51SE, N = 32, P = 0.038).

Number of fledglings in bigamous units ranged from 3 to 9 (M = 5.40 $\pm$ 1.29SE, N = 5). Average number of fledglings per adult male in bigamous and monogamous families did not differ significantly (M1 = 5.40 $\pm$ 1.29SE, N = 5 and M2 = 4.69 $\pm$ 0.51SE, N = 32, t = 1.115, P = 0.273).

## Reproductive Success

Reproductive success was defined as the percentage of fledglings from all hatched nestlings of the brood. From 1990-1995, reproductive success varied from 5 to 96 per cent (table 5). Lemming abundance was the major factor affecting owl reproductive success. Successful nest density and mean brood size was positively correlated with lemming numbers (r = 0.8213, P = 0.045 and r = 0.9581, P = 0.0026, respectively). Mean brood size ranged from 0.33 (SE = 0.23) to 5.50 (SE = 0.29) on different phases of the population cycle (table 4). Mean brood size in 1990—the first year after lemming depression—differed significantly from two following seasons of low lemming populations (P = 0.004). A sharp increase in brood size was recorded in the peak lemming season of 1994, when it differed significantly from seasons of medium, 1993 (P = 0.0001) and medium-high, 1995 (P = 0.001) lemming numbers.

All other factors had an insignificant influence on owl reproductive success. Egg or nestling loss was caused by embryo mortality (2.3 percent of eggs, N = 11), failure of egg fertilization (2.3 per cent of eggs, N = 11), egg freezing caused by reindeer or musk-oxen grazing in the vicinity of owl nests (1.6 per cent of eggs, N = 8), aggressiveness by Snow Geese (Chen caerulescens) (towards Snowy Owls whose nests were surrounded by goose nests (1.1 percent of eggs, N = 5) (see Menyushina and Ovsyanikov 1989), and arctic fox predation (1.5 percent of nestlings, N = 6) (see Menyushina 1995). From 50 to 70 per cent of all eliminated nestlings died during the first 10 days after hatching due to lack of food. I did not observe cannibalism in Snowy Owls in the form of weak nestling killing, however, already dead nestlings were utilized by the female for feeding surviving ones. In one case, a female cached the carcass of her dead nestling for 2 days before feeding it to the other young. Cold wet weather also influenced nestling survival; during the lemming peak of 1994, under good feeding conditions, 4 per cent of all nestlings (N = 3) were lost due to adverse weather.

Table 5.—*Reproductive success of Snowy Owls (Nyctea scandiaca) on the study plot, Wrangel Island.*

| Year | Nest N | Aborted nests(%) | Eggs | Lost eggs (%) | Nestling N | Fledgling N (%) |
|---|---|---|---|---|---|---|
| 1990 | 9 | 39 (30) | 61 | 5 (8) | 56 | 3 (5) |
| 1991 | 7 | 0 | 68 | 5 (7) | 63 | 11 (17) |
| 1992 | 13 | 5 (38) | 94 | 24 (26) | 70 | 17 (24) |
| 1993 | 9 | 1 (11) | 54 | 7 (12) | 47 | 18 (38) |
| 1994 | 12 | 0 | 94 | 11 (11) | 83 | 80 (96) |
| 1995 | 18 | 3 (16) | 104 | 14 (13) | 90 | 68 (76) |

*Reproductive Investment of Females of Different Age Classes*

Female age was identified by details of plumage in May-June, before active molting. Three age categories were distinguished—young adults, middle-aged adults, and old females. During seasons of low and medium lemming numbers, 30-40 percent of nesting females ceased incubation. Young adult females successfully reproduced only during medium, medium-high, and peak lemming numbers, whereas old and middle-aged females reproduced during all seasons except the lemming depression. Old females comprised the base of reproductive population during the two first seasons following the lemming depression (fig. 2). In 1992, under low lemming numbers, 67 per cent of young females abandoned their nests during incubation. Mean brood size did not differ significantly for females of different age categories (for young—M1 = 3,75 ± 0.51SE, N = 12, for middle age—M2 = 2.72 ± 0.78SE, N = 25, for old—M3 = 3.32 ± 0.49SE, N = 28; for M1-M2 P = 0.087, for M1-M3 P = 0.337, for M2-M3 P = 0.586).

*Sex Ratio*

Sex of fledglings was identified by the shape and size of dark spots on their wing and tail feathers (Josephson 1980). Females prevailed among older chicks in most broods, due to female fledgling survival being higher under low lemming numbers (fig. 3). The most complete data on sex ratio in fledglings was collected during the peak lemming season, when almost all nestlings survived. During that year, the fledgling sex ratio was 1M:1.56F (N = 71). During seasons with medium lemming numbers, the proportion of males and females in broods was equal. For all six seasons, the sex ratio among fledglings was 1M:1.3F (N = 178). The sex ratio of adult owls was 1.3M:1F (N = 820)—opposite of sex ratio in fledglings. Males prevailed among adults in all seasons. This may indicate a higher mortality of juvenile females during the time of dispersal and their first winter. Female Snowy Owls are heavier than males—weight differences become apparent in young owls at 5-6 weeks of age (males: M = 1301g ± 31.2SE, N = 34; females: M = 1625g ± 38.2SE, N = 37; P = 0.001). This difference may result in young female owls being more vulnerable to food shortages during dispersal.

DISCUSSION AND CONCLUSION

Snowy Owl nest densities on Wrangel Island during my study were similar to data from other parts of its nesting range. On Baffin Island, owls had densities of 0.3 nests per km$^2$ (for 30 km$^2$ plot) and 0.47 nests per km$^2$ (for 12.8 km$^2$ plot) (Watson 1957). Nest densities in Greenland were 0.28 nests per km$^2$ (for 50 km$^2$ plot), and 0.7 nests per km$^2$ on Bylot Island (Cordier et al. 1990). For Bathurst Island, Taylor (1974) reported 0.17 nests per km$^2$ (for 84.5 km$^2$ plot). On Wrangel Island I observed relatively high and stable nest densities within the study plot on all phases of the population cycle, except lemming depression. This may be explained by three features of the island. First,

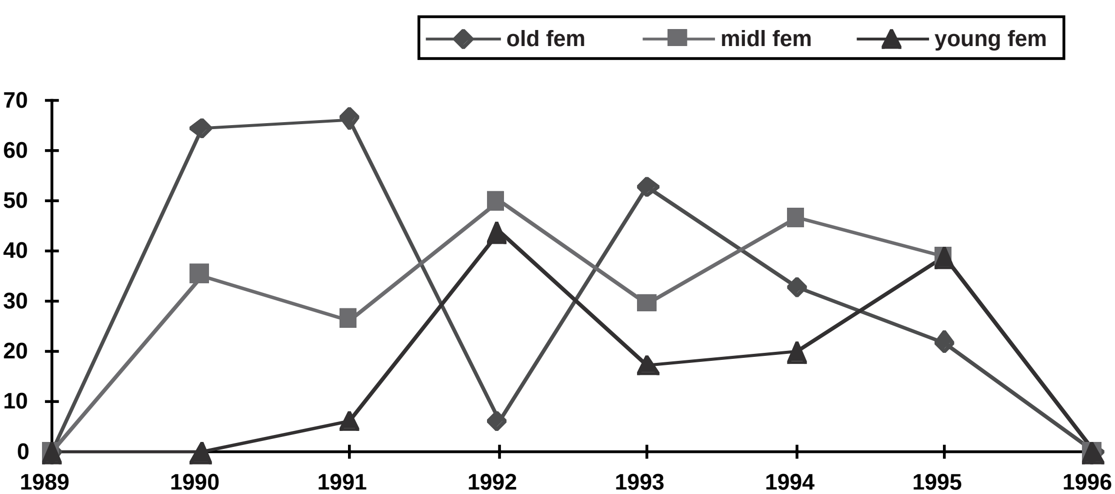


Figure 2.—Relative number of nesting female Snowy Owls (Nyctia scandiaca) of different age (N = 130) on Wrangel Island.

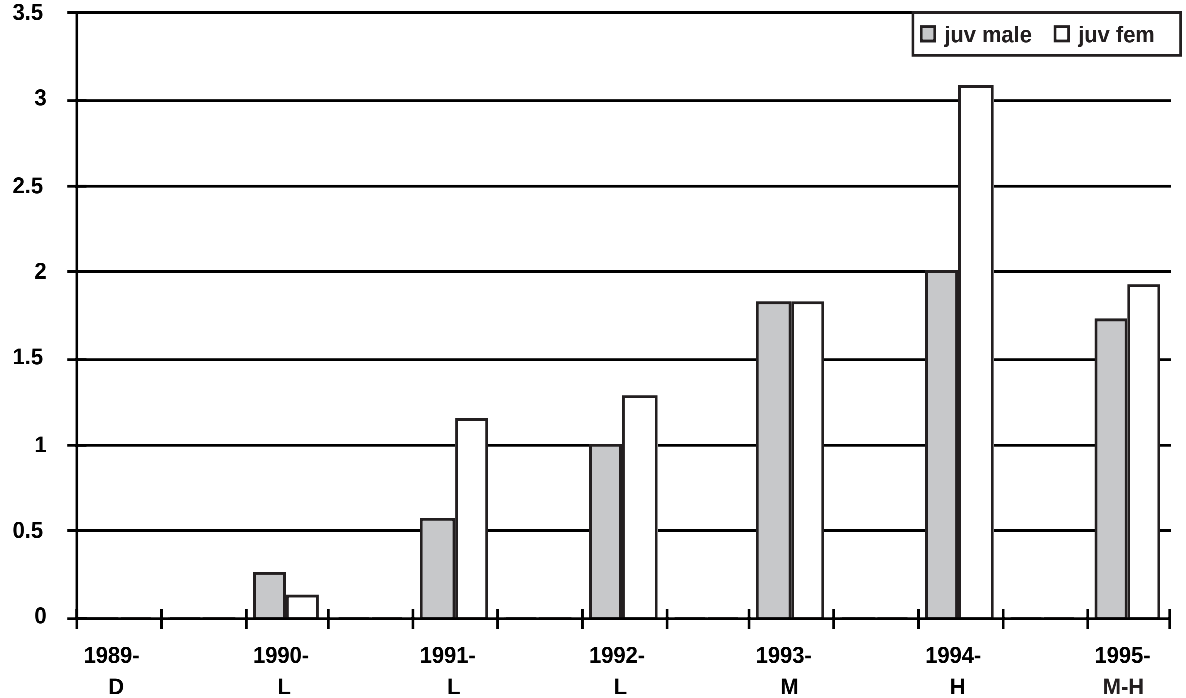


*Figure 3.—Average number of male and female Snowy Owls (Nyctia scandiaca) fedglings per brood, on Wrangel Island.*

*the island is on the northernmost edge of the owl's nesting area in this region. Therefore, there may be owl accumulation effect—birds arriving in spring cannot disperse farther north-, east-, or westward and have to settle on the island even if lemming numbers are not high enough to maintain the entire breeding population. Second, the island is large enough to represent a variety of suitable breeding habitats. Third, lemming cycles on Wrangel Island are longer than in other areas of the Arctic, with a peak-to-peak period from 5 to 7 years (Chernyavskyi and Tkachev 1982, Krebs 1993). Thus, the whole of Wrangel Island should be considered as a high quality owl breeding area. At the same time, owl nest density at the beginning of the breeding season does not indicate the lemming population number. Only successful nest densities positively correlated with lemming numbers, thereby indicating their population stage.*

*The lack of correlation between owl nest density and clutch size to lemming numbers, may perhaps, reflect the association of the owls' egg laying activity to lemming surface activity at the onset of the owls' breeding season. On Wrangel Island, most Snowy Owl group*

*Table 6.—Time of flood and percent of breeding Snowy Owls (Nyctia scandiaca) (N = 127 pairs) on Wrangel Island.*

| **5 day-periods (dd-dd.mm)** | **1990 flood-15.05** | **1991 flood-25.05** | **1992 flood-22.05.** | **1993 flood-22.05.** | **1994 flood-07.06.** | **1995 flood-12.06.** |
|---|---|---|---|---|---|---|
| 15-20.05. | 55.6 | 10 | 7.7 | 27.8 | 13.3 | 24.2 |
| 21-25.05 | 22.2 | 60 | 53.8 | 33.3 | 20 | 27.2 |
| 26-31.05 | 11.1 | 20 | 38.5 | 27.8 | 0[1] | 24.2 |
| 01-05.06 | 11.1 | 10 | 0 | 5.6 | 40 | 18.2 |
| 06-10.06 | 0 | 0 | 0 | 0 | 13.3 | 3 |
| 11-15.06 | 0 | 0 | 0 | 0 | 13.3 | 0 |
| 16-20.06 | 0 | 0 | 0 | 5.6 | 0 | 3 |

[1] Snow storm.

*copulation is related to the beginning of snow melt (table 6). At that time, most of the land is still covered by snow. Direct observations indicated that owl activity was determined by lemming availability, rather than by absolute number of lemmings within the nesting territory. High levels of lemming surface activity at the onset of breeding is caused not only by high absolute number of rodents, but by snow melting patterns which determines the proportion of snow-free ground and intensity of flood. Starting reproduction under (temporarily) favorable feeding conditions later in summer, Snowy Owls would not have enough prey to raise broods. Due to this factor, owls ready for nesting first settle on slopes with large snow-free areas. Usually, these are slopes of southern exposure with no or little snow accumulation during winter.*

*Usually, not all of the factors that determine owl clutch size—lemming availability in spring, weather, time of egg laying, female age, and previous winter conditions—are favorable within the same season. Such a situation never happened during my study. However, such a situation occurred in 1981. This coincidence resulted in an outbreak of owl breeding with outstandingly high clutch size (M = 9.71 ± 0.45 SE), which was significantly larger than in all other seasons including other lemming peak years (P = 0.001 compared to peak lemming seasons).*

*Polygamy in Snowy Owls was reported for Baffin Island (Watson 1957), Hardangervidda, Norway (Cramp 1985) and the Shetland Islands (Robinson and Becker 1986). On Wrangel Island I observed polygamy in Snowy Owls not only during peak lemming numbers, but also during seasons of high and medium lemming populations. My results, however, indicate that polygamy in Snowy Owls cannot be considered a reproductive advantage for the species. For females, occurrence of bigamous units resulted in a decrease in reproductive success. For males, formation of bigamous units may be considered a reproductive strategy aimed to maximize reproductive potential under peak lemming years.*

*The Snowy Owl's breeding strategy may be characterized as a program to lay the maximum amount of eggs at any opportunity. Laying of as many eggs as possible, in combination with very fast nestling growth (Watson 1957), is considered a species adaptation for badly predictable feeding conditions and a very restricted time frame for reproduction. Final reproductive success, however, depends on summer lemming numbers and is fully realized only during peak lemming years.*

*The major factor affecting nestling mortality is food limitation. My observations revealed that arctic fox predation has no serious impact on Snowy Owl reproduction on Wrangel Island at any season. This finding refutes an opposing statement of K. Litvin (Litvin and Ovsyanikov 1990) which was made based on irregular examinations of a few owl nests until mid-July only.*

*The fact that old females can reproduce in all years except lemming depressions may be explained by their better spring condition which results from their hunting and surviving experience (Parmelee 1992). It was shown that the percent of successful hunting in winter was higher for old females than for juveniles (Boxall 1979). Sharp increases of reproductive investment in the owl population during peak lemming years is due to involvement of young females successfully reproducing, whereas reproduction of old females supports the population continuously.*

*The sex ratio among adult owls and fledglings was reversed. I suggest that the prevalence of females among fledglings may be an adaptation to neutralize higher juvenile female mortality during their first winter to maintain a sex ratio in adult owls closer to 1:1.*

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