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NESTING PHENOLOGY OF KITTLITZ'S MURRELET[1]

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Key words: Kittlitz's Murrelet; Brachyramphus brevirostris; *nesting; phenology; timing; Alaska; Russia.*

The Kittlitz's Murrelet (*Brachyramphus brevirostris*) is a small, solitarily nesting alcid that nests near the subarctic North Pacific and the more arctic Bering and Chukchi Seas (American Ornithologists' Union 1983). Because of its low nesting density and the extreme difficulty of finding its nests, it truly is one of the most poorly known species regularly breeding in North America; only 18 definite nests of this species have ever been located (Day et al. 1983, Naslund et al. 1994, Day 1995). Most of the little information that is available lists those few nests that have been found and summarizes the scattered data on characteristics of nest-sites and eggs (Day et al. 1983, Naslund et al. 1994, Piatt et al. 1994, Day 1995). This paper summarizes the available information on nesting phenology of this species and speculates on reasons for the observed patterns.

METHODS

I surveyed both published literature and unpublished information for data on the timing of particular aspects of nesting phenology of Kittlitz's Murrelets: eggs in oviducts, egg-laying dates, eggs in nests, hatching dates,

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chicks in nests, and juveniles at sea. I stratified these data into geographic regions of probably different nesting phenology: Southeastern Alaska, Southcoastal Alaska (the Northern Gulf of Alaska and Alaska Peninsula), Aleutian Islands/Okhotsk Sea, Bering Sea, and Chukchi Sea. I do not identify Alaska records as such and label the location of records from elsewhere. The nest described by Naslund et al. (1994) and Piatt et al. (1994) is what I call here the "Kachemak Bay nest."

RESULTS

EGGS IN OVIDUCTS AND EGG-LAYING DATES

In Southeastern Alaska, a female was collected with a fully-shelled egg (Museum of Comparative Zoology [MCZ] #320,028) at Icy Strait on 17 May 1913 by Kleinschmidt (R. A. Paynter, pers. comm.); although Kleinschmidt claimed that "every specimen" collected in this vicinity during the first two weeks of May had an egg (Thayer 1914), I have been unable to locate other, earlier specimen records than this one. The presence of a complete shell on this egg suggests that the egg would have been laid that night or the following day (17–18 May). A second record is from Glacier Bay on 12 June 1919 (Bailey 1927). The egg was "almost ready for the shell," suggesting that it would have been laid the following day or the day after that (13–14 June).

In Southcoastal Alaska, a fully-shelled egg was taken from "low in the reproductive tract" of a bird collected at Hinchinbrook Island on 27 May 1976 (Nysewander and Knudtson 1977). The presence of a complete shell and the egg's location suggests that the egg would have been laid that night or the following day (27–28 May). A second record is from Kodiak Island, where a female with a fully-formed egg was collected on 29 May 1913 (MCZ #9,497; Paynter, pers. comm.). This egg would have been laid that night or the following day (29–30 May).

In the Aleutian Islands/Okhotsk Sea, a female with a "mature" but unshelled egg was collected at Adak Island on 9 June 1970 (Byrd et al. 1974; G. V. Byrd, pers. comm.). This egg would have been laid the following day or the day after that (10–11 June). In addition, Murie (1959) collected a female with a post-ovulatory follicle at Attu Island on 8 (U.S. National Museum of Natural History [USNMNH] #366,515) or 9 (Murie 1959) June 1937; the egg probably had been laid within the previous few days (7–9 June).

No information is available on exact laying dates of Kittlitz's Murrelet eggs. This lack of information reflects the fact that all nests have been found accidentally, after eggs have been laid (Day et al. 1983, Day 1995).

EGGS IN NESTS

Eighteen eggs of Kittlitz's Murrelets have been found in nests throughout the species' nesting range. The only egg record from Southeastern Alaska is from the Humphrey Creek nest on 16 June 1979 (Fox and Hall 1982).

Of the six egg dates from Southcoastal Alaska, the earliest seasonal record is the Pavlof Volcano nest on 9 (MCZ #9,498; Paynter, pers. comm.) or 10 (Thayer 1914), June 1913 and the latest is the Frosty Peak nest on 22 July 1972 (Bailey 1973). Other records from this region are the Kachemak Bay nest on 13 June 1993 (Naslund et al. 1994, Piatt et al. 1994), the Harris Bay nest on 15–20 June 1976 (Day et al. 1983), the Windy River nest on 26 June 1977 (Day et al. 1983), and the Katmai National Monument nest in mid-July of an unknown year (Murie 1959), probably the 1920s or 1930s (Hubbard 1935).

Eggs have been found in only two nests from the Aleutian Islands/Okhotsk Sea. These records are the Atka Island nest on 13 July 1980 (Day et al. 1983) and the Shelikhova Bay, Russia, nest on 16 July 1963 (Kistchinskii 1965).

Of the seven egg dates from the Bering Sea, the earliest seasonal record is the Iron River nest on 10 June 1904 (Day et al. 1983), and the latest is the Hill Point nest on 19 July 1934 (Ford 1936). Other records are the Tin City nest on 16 June 1943 (Bailey 1948), the Goodnews Bay nest on 21 June 1933 (Day et al. 1983), the Tin Creek nest on 21 June 1973 (Day et al. 1983), the Tavuvnan Mountain, Russia, nest on 26 June 1990 (Smetanin 1992), and the Wales Mountain nest on 29 June 1935 (Ford 1936).

There are only two egg dates from the Chukchi Sea. These records are the Chukchi Sea nest on 28 June 1978 (Murphy et al. 1984) and the Angmakrog Mountain nest on 26 July 1960 (Thompson et al. 1966).

HATCHING DATES AND CHICKS IN NESTS

Only three hatching dates are available for this species. In Southcoastal Alaska, the Kachemak Bay nest hatched on 3 July 1993 (Naslund et al. 1994), and the egg in the Frosty Peak nest was pipped in two places when it was discovered on 22 July 1972; Bailey (1973) believed that it hatched on the same day. In the Chukchi Sea, the egg in the Angmakrog Mountain nest was fully intact when it was discovered on 26 July 1960 but fully hatched on 28 July (Thompson et al. 1966). I assume that it hatched on 27 July.

The two records of chicks in nests are from Southcoastal Alaska. From photographs, the chick in the Mt. Griggs nest on 2 July 1979 appeared to be ≈6 days old (Day 1995), suggesting hatching on ≈26 June. The chick in the Broken Mountain nest on 23 July 1986 appeared to be ≈6–10 days old (Day 1995), suggesting hatching on ≈13–17 July.

FLEDGING DATES AND JUVENILES AT SEA

The only exact fledging dates that have been determined are from Southcoastal Alaska. The chick in the Kachemak Bay nest fledged on 27 July 1993 (Naslund et al. 1994), and a juvenile on its way to the sea was found at Pederson Lagoon (in Aialik Bay) on 8 August 1980 (Day et al. 1983).

Determining exact fledging dates for this species is difficult, for most records of juveniles at sea probably do not refer to dates of first fledging but instead refer to the first date when investigators visited a particular location. In Southeastern Alaska, C. Estabrook found that "some" of ≈1,000 birds in Beardsley Channel of Glacier Bay were in "winter plumage" (= juveniles?) on 8 July 1974 (UAM, unpubl.), Walker (1922) collected several juveniles at Glacier Bay between 3 and 5 August 1921, and Bailey (1927) collected two juveniles there on 12 August 1919. Although the birds from Beardsley Channel may have been molting subadults (J. F. Piatt, unpubl.), forward-calculation from records

TABLE 1. Known or estimated dates of egg-laying, hatching, and fledging of the Kittlitz's Murrelet throughout its breeding range.

Region	Date of: Egg-laying	Hatching	Fledging
Southeastern Alaska	15 May–13–14 June	14 June–13–14 July	8 July–6–7 August
Southcoastal Alaska	22 May–17 June	22 June–17 July	15 July–10 August
Aleutian Islands/Okhotsk Sea	7–17 June	7–17 July	31 July–10 August
Bering Sea	≤9–20 June	≤9–20 July	≤2–13 August
Chukchi Sea	≤16–28 June	≤16–28 July	≤9–21 August

of eggs in oviducts also would place fledging at about this date (see below).

In Southcoastal Alaska, the chick in the Frosty Peak nest was gone when Bailey (1973) returned on 15 August 1972, suggesting either fledging at ≤24 days of age or predation of the nestling. In addition, D. Zwiefelhofer (pers. comm.) has recorded juveniles at Kodiak Island on 15 July 1986, 18 July 1989, 23 July 1985, 30 July 1987, 31 July 1993, and 3 August 1993 (two juveniles). In the Chukchi Sea, two "young" were collected at Wrangel Island, Russia, on 9 August 1960 (Velizhanin 1965 *in* Portenko 1972), and "first-year birds" were seen there on 31 August 1960 (Portenko 1972).

OVERALL NESTING PHENOLOGY

These records provide a sketchy outline of the basic nesting phenology of Kittlitz's Murrelet. I have used the incubation period for the similar Marbled Murrelet (*Brachyramphus marmoratus*) and the fledging period for Kittlitz's Murrelet in forward- and back-calculating from the above dates, to estimate when egg-laying, hatching, and fledging probably occurred. The incubation period for Kittlitz's Murrelet is not known, but I assume that it is similar to that for the Marbled Murrelet (≈30 days; Sealy 1974). The fledging period for the only Kittlitz's Murrelet nest that has been studied is 24 days (Naslund et al. 1994). Although further research may show that mean incubation and fledging periods for Kittlitz's Murrelet are slightly different from these values, the estimated egg-laying, hatching, and fledging dates that are calculated here will be off by only a few days at most.

Known or estimated egg-laying dates in Southeastern Alaska range between (1) the date back-calculated from the date of probably fledged juveniles at Glacier Bay (two days later for an egg in an oviduct at Icy Strait) and (2) the estimated date of laying of an egg in an oviduct at Glacier Bay (Table 1). In Southcoastal Alaska, dates range between (1) the date back-calculated from the date of a fledged juvenile at Kodiak Island and (2) the date back-calculated from the estimated hatching date for the Broken Mountain nest. In the Aleutian Islands/Okhotsk Sea, dates range between (1) the estimated date of laying from a post-ovulatory follicle at Attu Island and (2) the date back-calculated from the earliest possible hatching date (the next day) of the egg in the Shelikhova Bay nest. In the Bering Sea, dates range between (1) the earliest possible laying date (the previous day) of the egg in the Iron River nest and (2) the earliest possible hatching date (the next day) of the egg in the Hill Point nest. In the Chukchi Sea, dates range between (1) the date back-calculated from the date of fledged juveniles at Wrangel Island and (2) the date back-calculated from the hatching date at the Angmakrog Mountain nest. Egg-laying dates in some regions (e.g., Aleutian Islands/Okhotsk Sea) probably exceed the short periods known at this time.

DISCUSSION

Although the ranges of dates of nesting phenology are not exact for each region, nesting phenology clearly is earlier in southern populations than in northern populations of Kittlitz's Murrelets (Table 1). For example, the last egg-laying and the earliest hatching in Southeastern Alaska probably ends about the time the birds in the Chukchi Sea begin laying (around mid-June). At the other extreme, the first juveniles in Southeastern Alaska (≈8 July) fledge well before the first eggs in the Chukchi Sea hatch (≈16 July or earlier). This pattern is seen in many other species of Alaska seabirds, which nest considerably earlier in Southeastern or Southcoastal Alaska than they do in the Chukchi Sea, probably because of a negative relationship between sea-surface temperatures and timing of breeding in arctic birds (Birkhead and Harris 1985, Lloyd 1985, Murphy et al. 1991; but see data for Common Murres *Uria aalge* in Murphy and Schauer 1994).

The ranges of dates suggest that phenological variation in reproduction declines in more northern populations, from 30 days in Southeastern Alaska and 26 days in Southcoastal Alaska to ≥11 days in the Aleutian Islands, ≥12 days in the Bering Sea, and ≥12 days in the Chukchi Sea. The fact that the earliest known or estimated laying dates vary by 30 days but the latest laying dates vary by only 14 days at either end of the species' range suggests that renesting may be less important than phenological variability in affecting laying dates. In other words, birds nesting in more southern parts of the range have a wider "window of time" in which to nest than do birds nesting in more northern parts of it, but there apparently is a date beyond which birds everywhere cannot nest or renest successfully.

This decline in the "window of time" over which egg-laying occurs is an adaptation to arctic conditions and is also seen in arctic-nesting geese, which have both shorter breeding seasons and greater synchrony in nesting phenology than do more temperate populations and species (Newton 1977). In arctic-nesting geese, at least, the breeding season is shortened primarily as a result of a smaller spread of egg-laying dates (Newton 1977). There are two main reasons why the Kittlitz's Murrelets' nesting window is wider for southern populations than for northern ones: physical barriers to nesting in the northern part of the range and a greater diversity of nesting habitat in the southern part of the range.

The freezing of the surface of both the Chukchi Sea and nesting areas inland from it until May or June represents a physical barrier that prevents Kittlitz's Murrelets from being in that area and the ice-covered Bering Sea until around the beginning of egg-laying in Southeastern Alaska. There are, however, leads in the ice of the southern Chukchi by May in many years, allowing some Kittlitz's Murrelets to penetrate northward before the ice recedes (e.g., basic-plumaged birds in the ice at Wales, Alaska, on 28 April; Bailey 1948).

The diversity of nesting habitat also affects nesting phenology. For example, the range in elevations of nests in the southern part of the breeding range (Southeastern Alaska to the Okhotsk Sea) is 140–2,000 m (median = 840 m; n = 10), whereas the range in the northern part of the breeding range (Bering and Chukchi seas) is 270–430 m (median = 335 m; n = 4). (These estimates were calculated from data presented in Day et al. [1983], Piatt et al. [1994], and Day [1995], with the data for Wales Mountain and Tavuvnan Mountain being omitted.) With the exception of the East Amatuli Island nest at 140 m (Bailey 1976, Day et al. 1983), there is no overlap in nesting elevations between the two regions.

The Gulf of Alaska is bordered by mountains as much as 5,500 m high, and the shores of the Aleutian Islands and Okhotsk Sea may have mountains as high as 3,000 m. In contrast, much of the coastline of the northern Bering and Chukchi seas is only a few meters above sea level. Such a diversity in potential nesting sites in the southern part of the range would allow birds that are nesting at lower elevations to nest early, whereas those nesting at higher elevations would have to wait until later for nesting sites to become snow-free. This hypothesis is supported by the fact that three of the four highest-elevation nests of this species have faced in a southerly direction and the other faced easterly, suggesting the importance of solar warming in opening up high-elevation nesting sites (Day 1995).

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GEOGRAPHIC VARIATION IN SIZE OF FEMALE WILD ROCK DOVES[1]

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Key words: Size variation; external characters; replication; Eurasia; female Columba livia.

The Rock Dove (*Columba livia*) was domesticated around 5,000 years ago in the eastern Mediterranean region generally called the Near East (Levi 1974). Escapes of domestics from confinement for thousands of years have provided stocks that developed into feral populations. Feral pigeons now have characteristics of both wild and domestic ancestry, frequently live essentially as though they are wholly wild, and are capable of broadscale genetic introgression in wild colonies (Johnston et al. 1988, Johnston and Janiga 1995).

In western Europe, wild colonies are known to exist in the Outer Hebrides of Scotland and perhaps on the coastline of northern and western Ireland; in the Mediterranean basin, wild colonies are known from coastal Sardinia, northwestern Egypt, and perhaps Libya and montane sectors of the former Yugoslavia. Interior montane North Africa, the Near East, Afghanistan, Pakistan, northwestern montane India, southwestern China, Uzbekistan, and Russia probably have Rock Dove populations that are still isolated from feral pigeons, but recent information is fragmentary. No information exists on the degree to which wild Rock Doves are killed for food by humans living under high densities in politically and economically unstable regions, but the birds can be subjected to overharvesting when their nesting cliffs are discovered by people short of dietary protein.

For these reasons, as well as of the difficulties in travelling to some of the regions just noted, specimen samples of wild Rock Doves are not likely to be significantly augmented in the near future. An earlier report (Johnston 1992) on size variation was restricted to samples of male specimens, although a display of sexual size dimorphism over the characters employed was provided. Here I provide comparable data for females.

MATERIALS AND METHODS

Museum specimens of wild *C. livia* represent the following regions of Europe, Africa, and Asia: the Faeroes, Shetland, Orkney, Hebrides, Ireland, Italy, Crete, Turkey, north coastal Africa, Chad, Sudan, Egypt, the Near East, Iran, Afghanistan, Pakistan, and northwestern India (Table 1). As is true for males, no specimens from Russia, lowland India, and northwestern coastal Africa were examined. Most specimens were taken in the last half of the 19th century and the first two decades of the 20th, but a few came from the 1940s. Specimen localities were aggregated into 17 regional samples (Table 1). The specimens examined were from the British Museum of Natural History, Tring, England; Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany; and the National Museum of Natural History, Washington, D.C.

The size variables (Table 1) were wing length as maximum chord (using a metal ruler with an end stop), tarsus length, from the heel transversely to the last undivided frontal scute, bill length, from the tip to ceral-base feather growth, and bill width at the anterior edge of the external nares (using dial calipers for the last three).

Data were log-transformed and processed using the

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