

Double Brooding by the Northern Wheatear on Baffin Island

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ABSTRACT. Most Arctic-breeding passerines raise a single brood in a season, presumably because the short Arctic summer does not provide sufficient time to raise a second brood. Here we document the first cases of two broods being raised or attempted, after successful fledging of a first brood, in an Arctic-breeding population of Northern Wheatears *Oenanthe oenanthe*, at Iqaluit, Nunavut, Canada, in 2010 and 2011. In one case, the same pair was involved in raising both broods. In a second case, the female that raised the first brood was mated to a different male for her second brood. In a third case, it was not known whether the same male was involved in a female's attempt to raise two broods. The three females that attempted to raise two broods started their first clutches four to six days earlier than the estimated median date of laying first eggs and represented about 6% of all females in the study population. Potential constraints on raising two broods include not only the shortness of the summer season but also the nature and abundance of the food supply, trade-offs between the success of the first brood and that of the second brood, and effects of the one- and two-brood strategies on the survival and future reproductive output of the adults.

Key words: second brood, Northern Wheatear, *Oenanthe oenanthe*, Arctic passerine, life-history theory

RÉSUMÉ. La plupart des passereaux nicheurs de l'Arctique n'élèvent qu'une nichée par saison, vraisemblablement parce l'été est trop court dans l'Arctique, ce qui ne laisse pas de temps pour une deuxième nichée. Ici, nous décrivons les premiers cas pour lesquels deux nichées ont été élevées ou tentées d'être élevées, après le succès d'envol de la première nichée chez une population de traquets motteux (*Oenanthe oenanthe*) nichant dans l'Arctique, à Iqaluit, au Nunavut, Canada, en 2010 et en 2011. Dans un des cas, le même couple d'oiseaux a élevé les deux nichées. Dans un deuxième cas, la femelle qui a élevé la première nichée a eu sa deuxième nichée avec un autre mâle. Dans un troisième cas, nous ne savons pas si le mâle était le même pour les deux nichées. Les trois femelles qui ont essayé d'élever deux nichées ont fait leur première ponte de quatre à six jours plus tôt que la date médiane estimée de ponte des premiers œufs, ce qui a représenté environ 6 % de toutes les femelles à l'étude. Parmi les contraintes auxquelles font face les femelles qui tentent d'élever deux nichées, notons non seulement les courts étés, mais aussi la nature et l'abondance des approvisionnements alimentaires, les concessions mutuelles entre le succès de la première nichée et celui de la deuxième nichée, et les effets des stratégies d'une nichée ou de deux nichées sur la survie et l'efficacité de la reproduction future des adultes.

Mots clés : deuxième nichée, traquet motteux, *Oenanthe oenanthe*, passereau de l'Arctique, théorie du cycle biologique

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INTRODUCTION

Arctic-breeding passerines typically raise a single brood in a season, presumably because they are constrained by the shortness of the Arctic summer. Temperate species and populations, in contrast, often raise two or more broods. The Northern Wheatear is one of seven widespread small passerines that commonly breed at high latitudes north of the tree line in parts of the North American Arctic. Evidence of a second brood, after successful raising of the first, has not been documented unequivocally in four of those species: Horned Lark *Eremophila alpestris* (Beason,

1995), American Pipit *Anthus rubescens* (Hendricks and Verbeek, 2012), Lapland Longspur *Calcarius lapponicus* (Hussell and Montgomerie, 2002), and Snow Bunting *Plectrophenax nivalis* (Montgomerie and Lyon, 2011), although two cases of second broods produced by unmarked females were suspected in a seven-year study of Lapland Longspurs at 71.3° N in Alaska (Custer and Pitelka, 1977). There is also no strong evidence of regular double brooding in Arctic-breeding populations of two other species, the Hoary Redpoll *Acanthis hornemanni* and the Common Redpoll *A. flammea* (Knox and Lowther, 2000a, b), although redpolls were suspected to have raised more than one brood close

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to 60° N in western Alaska (Troy and Shields, 1979), and a second clutch was reported for the Common Redpoll north of 60° N in the Yamal Peninsula (Aleksieva, 1986, cited in Knox and Lowther, 2000a). It appears that both redpoll species normally raise only one brood at most Arctic and subarctic locations.

The Northern Wheatear is a species of Old World origin that breeds in open country and in cold and hot treeless habitats throughout Eurasia and south to about 30° N in North Africa and the Arabian Peninsula (Kren and Zoerb, 1997; Cramp, 1998). The breeding range of the nominate race *O. o. oenanthe* extends eastward into Alaska, Yukon, and the extreme western parts of the Northwest Territories in North America. A slightly larger race, *O. o. leucorhoa*, often called the “Greenland” Wheatear, breeds in Iceland, Greenland, and the eastern Canadian Arctic, including on Ellesmere and Baffin Islands, the Ungava Peninsula, and Labrador (Kren and Zoerb, 1997; Cramp, 1998). Evidence from banding and light-sensitive geolocators shows that Alaskan breeders migrate westward to wintering sites in East Africa, while the eastern Arctic and Greenland populations cross the Atlantic Ocean to winter in West Africa (Lyngs, 2003; Hussell, 2009; Bairlein et al., 2012).

Northern Wheatears often raise two broods in much of their range in the temperate zone, for example 10.0%–32.5% of pairs in a study in Germany (Buchmann, 2001), but normally raise only one brood in Iceland and Scandinavia (Cramp, 1998; Conder, 1989). Moreno (1989) reported that he found no second broods on the island of Öland (56.6° N) in southern Sweden, but indicated that he might have missed some because he left the study area too early (Juan Moreno, pers. comm. 2013). At Uppsala (60° N), Tomas Pärt (pers. comm. 2013) estimated that about 1%–5% of successful breeding attempts are followed by a second brood, and he suspects, from observation of late broods, that the proportion is higher on Öland. Nicholson (1930) suspected double brooding on the southwest coast of Greenland (64.7° N, 51.3° W) in 1928, but the evidence was inconclusive. Here we report evidence of Northern Wheatears raising second broods to the fledging stage at Iqaluit, Nunavut (63.8° N, 68.5° W), in 2010 and 2011.

METHODS

We studied breeding Northern Wheatears at Iqaluit, Baffin Island, Nunavut, over six summers (2007 to 2012) during the following periods: 25 June–14 July 2007; 25 June–27 July 2008; 16 June–8 August 2009; 18 June–12 August 2010; 24 June–14 August 2011; and 20 June–23 July 2012. At Iqaluit, Northern Wheatears nest in natural and artificial cavities that are usually inaccessible to humans. We trapped adult wheatears that were bringing food to their nestlings, using either spring-loaded nets baited with meal worms, set close to the cavity entrance or “walk-in” traps placed in the cavity entrance. Each captured adult was marked with a unique combination of a standard numbered

aluminum band and two or three coloured bands made of Darvic plastic (Avinet Inc., Dryden, New York). We visited known nest sites as frequently as possible to check on progress, which consisted of inspecting contents of accessible nests or, more often, recording other evidence as described below for inaccessible nests (based on Cramp, 1988; Conder, 1989; Kren and Zoerb, 1997; our own observations).

Females that are incubating eggs bring no food to the nest cavity. They stay in the cavity for varying lengths of time, but rarely for less than 15 minutes, then leave to feed for about 5–10 minutes. After the eggs hatch, both sexes bring food to the nestlings. When the nestlings are about 13 days old, they start to come to the entrance of the cavity to be fed. At this stage they frequently defecate at or near the cavity entrance, leaving visible signs of their presence and age. Nestlings leave the nest cavity at about 15 days and go individually to other nearby cavities, where they continue to be fed by their parents. At about 17 days, they are flying strongly. Confirmation that a brood was raised to the fledging stage was obtained by direct observations, by finding feces around the cavity entrance, or by seeing colour-banded adults attending fledglings.

Timing of clutch initiation was estimated by calculating backwards from the fledging date, hatch date (first observation of adults carrying food), or laying dates, or by estimating age from stage of growth (D.J.T. Hussell, unpubl. data). All acceptable estimates were probably accurate within ± 2 days. In the absence of contrary evidence, it was assumed that one egg was laid per day, that clutch size was seven (mean clutch or brood size at Iqaluit = 7.2, $n = 22$, D.J.T. Hussell, unpubl. data), that the incubation period (last egg to last hatch) was 13 days, that hatching spread was two days, and that fledging occurred 15 days after first hatch (Cramp, 1988; Conder, 1989; Kren and Zoerb, 1997; our own observations). We could detect a second brood only if (1) at least one of the adults was banded, (2) their first brood was known to have fledged, and (3) our observations continued late enough to find a second brood. The latter criterion limits us to using data from 2009, 2010, and 2011 to estimate the proportion of females or pairs having second broods.

Distances between nests were calculated from coordinates recorded at each nest site on a Garmin Etrex GPS unit.

RESULTS

Second Broods

Evidence of second broods (Table 1) is summarized below for two females in 2010 and one pair in 2011. In each case, the site of the first brood is named first. Designation of a male or a female with a capital letter (A, B, C) indicates that it was individually identifiable by its colour bands; B1 and B2 indicate first and second mates of female B.

Nests 2010-29 and 2010-36: Female A raised a first brood that fledged before 9 July. She attempted a second brood, 350 m WSW of the first site, but the attempt failed

TABLE 1. Observations providing evidence of double brooding by Northern Wheatears at Iqaluit. Males and females designated with a capital letter (A, B, C) were individually identifiable by their colour bands. Males B1 and B2 were two different males mated to female B. “Banded” birds with no capital letter designation were seen to be banded, but the colour combination was not determined.

Year-Nest No.	Brood	Date(s)	Observations
2010–29	1	3 July	Female was seen visiting with food.
		5 July	Female A was trapped.
		8 July	Female A came to the nest briefly. A male was singing nearby.
		9 July	Female A was seen nearby with fledglings.
		14 July	Female A was seen with at least five nearly independent fledglings. A male was present.
2010–36	2	11 July	A banded female was seen carrying nesting material. An unbanded male was present.
		13 July	Female A entered the nest cavity.
		15 July	Female was not seen. Male perched and sang briefly over the nest cavity.
		17 July	Male was chasing another male. Female A was foraging nearby but did not enter the cavity.
		21 July	Female A entered the nest cavity and stayed inside for at least 30 minutes.
		23 July–1 August	Incubation behaviour by Female A was observed on six dates.
		2–3 August	Female A and a male brought food.
		5 August	No activity. Presumably nest was taken by a predator or abandoned.
2010–30	1	3 July	Both male and female were seen visiting with food.
		5 July	Female B and Male B1 were trapped.
		9 July	Male B1 was trapped again. Female B behaviour indicated some fledglings were out of the nest.
2010–43	2	15 July	Female B was seen with an unbanded male near the site of nest 43 (found on 21 July).
		21 July	A banded female, attended by an unbanded male, entered the cavity and stayed at least 20 minutes.
		23 July	Female B was seen entering and leaving the nest cavity.
		25–29 July	Female B displayed incubation behaviour on four dates.
		1 August	Female B and unbanded male brought food.
		2 August	Female B and unbanded male entered. Male removed a fecal sac.
		3 August	Female B and male were trapped. Male B2 was colour banded. Both were in flight feather moult, the female having moulted primary 1 and the male, primaries 1–5.
		5–11 August	Female B and Male B2 visited the nest cavity on five dates.
2011–23	1	12 August	Final brief observation recorded adults still present near the nest site.
		27 June	An unbanded male was seen carrying food near the nest site found on 4 July.
		4 July	An unbanded male and a female brought food to the nest cavity.
		6 July	Both adults were observed carrying food to the nest site.
		7 July	Both adults carried food to the nest site.
		8 July	The female and male were trapped and colour-banded.
		9 July	Female C and Male C were present.
		10 July	Male C was seen carrying food; he fed fledglings in boulders below the nest site.
2011–49	2	11 July	Female C gave alarm calls below the nest site.
		15 July	Female C and a male were seen feeding fledglings near the site of nest 49, found on 5 August.
		31 July	Male C was near the site of nest 49, found on 5 August.
		5 August	Female C and Male C were seen carrying food to the nest cavity.
		8 August	At least five nestlings were visible. Female C and Male C were trapped. Both were in flight feather moult (female: primaries 1–3, male: primaries 1–6).
		9 August	An adult was observed nearby. At least three nestlings were visible.
13 August	Female C and Male C brought food. Nestlings were mobile in the cavity.		

when the nestlings were 3–5 days old. It is not known whether she was mated to the same male as for her first brood or to a different male.

Nests 2010-30 and 2010-43: Female B and male B1 raised a first brood that fledged around 9 July. She raised a second brood to at least 11 days old (on 12 August, when observations ceased) and was mated to a different male (B2) than for her first brood. The second brood site was 720 m NNW of the first brood site.

Nests 2011-23 and 2011-49: Female C and Male C raised a first brood that fledged on 9–10 July. The same pair raised a second brood at a site 120 m S of the first site; the brood was close to fledging when observations ceased on 13 August.

Time Constraints on Raising Second Broods

Among 82 nests whose clutch initiation dates could be estimated during the six years, 71 were started between

29 May and 27 June (median 11 June). The 11 clutches in a second group—which may have included late first broods, second attempts after an earlier failure, or second broods—were initiated between 3 and 14 July (median 9 July).

Initiation dates of first clutches for the three females that attempted second broods were estimated as 7, 5, and 7 June, respectively. In 2010 and 2012, some females initiated clutches up to seven days earlier than the three double-brooded females, but the latter were well ahead of the median date (11 June) for the early group of clutches documented in all years. Fledging dates and dates of initiation of second clutches, described below, indicate it is unlikely that females laying the first eggs of their first clutches later than 7 June would have time to raise a second brood successfully. Considering all clutches not known to be second broods, in all years, 32% (25/79) were estimated to have been initiated early enough (by 7 June) to allow time for a second brood.

The first broods of the three double-brooded females fledged (i.e., left the nest cavity) between 7 and 10 July.

These females were all estimated to have laid the first eggs in their second clutches on 14 July, indicating that the interval between fledging and starting a second clutch was 4–7 days. This figure is consistent with observations in Wales, where the average interval between fledging the first brood and laying the first egg of a second clutch was 5.7 days (Conder, 1989). No other clutches were estimated to have started later than those of the three double-brooded females; therefore, it is unlikely that second clutches started later than 14 July could be successful.

Summarizing, the evidence from the three double-brooded females indicates that for second broods to be raised successfully, the first clutch must be started before 8 June, the first brood fledged by 10 July, and the second clutch initiated no later than 14 July. Nevertheless, only three cases of double brooding were detected among the 20 first clutches (15%) that were estimated to have been started by 7 June in 2009–11.

Proportion of Females Attempting Second Broods

Even in the unlikely event that all 11 late clutches (recorded over the full six years) were genuine second broods, and assuming that all of the 71 early clutches were first clutches, no more than 15% (11/71) of females attempted second broods. The number of known second broods was three, providing a minimum estimate of 4% (3/79) of the number of first-brood females that attempted a second brood. This calculation suggests that the proportion of females raising second broods was in the range of 4% to 15%.

Using only nests from 2009, 2010, and 2011, when we stayed late enough to detect second broods, and combining data from the three years, we found that three of 52 females (6%) responsible for “early” clutches (started on or before 27 June) were known to have attempted a second brood, which is consistent with the estimate above that 4% to 15% of females attempted second broods.

DISCUSSION

As far as we are aware, these are the first confirmed records of double brooding in Arctic populations of Northern Wheatears or in any other Arctic-breeding passerines, with the possible exception of rare and geographically marginal cases in the Common Redpoll. However, double brooding is exceptional in wheatears at Iqaluit: we estimated that no more than 32% of pairs started their first broods early enough to allow them time for a second brood, and in 2009–11 we detected second broods in only 15% of those pairs that did start early enough.

An important environmental constraint on the ability of Arctic passerines to raise two broods is the time available to do so. To lengthen the breeding season, Northern Wheatears must either start earlier or continue later. The evidence indicates that wheatears lengthen the breeding

season mainly by continuing later, although only those making an early start to their first clutches are able to do so.

In addition to the short summer, other factors must also impose constraints on the ability of Arctic-breeding wheatears to have a second brood. At 56.6°N on the island of Öland in southern Sweden, only a small proportion of wheatears have second broods, despite starting their first clutches nearly a month earlier than wheatears at Iqaluit (median 13–15 May; Moreno, 1989). On Skokholm Island, Wales (51.6°N), the peak for starting first clutches was in the first 10 days of May, and 47% of pairs produced second clutches (Conder, 1989). In Germany at 49.7°N, where the median date for first brood clutches was 4 May, only 10%–32.5% had two broods (Buchmann, 2001). Evidently, many pairs at all sites did not have second broods, regardless of the latitude or the dates of starting first clutches. Nevertheless, a warming climate is likely to increase the incidence of second broods at Iqaluit and elsewhere.

Fledging from second broods at Iqaluit occurred in mid-August, leaving adults and young only about six weeks—at least two weeks less than the time available to most single broods and their parents—to prepare for the challenging migration across the Atlantic Ocean to their winter range in Africa. Following fledging, young wheatears moult their body plumage, while adults have a complete moult that includes all of the flight feathers. D.J.T. Hussell captured and examined both adult pairs raising second broods at nests 2010-43 and 2011-49, on 10 and 13 August, when nestlings were about 11 and 13 days old, respectively. Both males were in heavy moult, replacing primaries 1–6 and all rectrices, but they were bringing food regularly despite their obviously impaired flight performance. Both females had started moulting and were replacing primaries 1–3, but retained all of their old rectrices. Overlap of moult with caring for a brood must impose a considerable energetic stress on these adults that may reduce their survival (Murphy, 1996; Hemborg and Lundberg, 1998).

The decision to start a second brood after successfully raising a first brood must be governed by the relative genetic contribution to fitness of the two strategies. The benefits and costs of the two strategies may include trade-offs between the survival of the first brood and that of the second brood and between parental survival and the probability of future reproductive output (Hussell, 1983). Such trade-offs are not confined to Arctic-breeding species, but the short breeding season undoubtedly tends to favour a single-brood strategy in the Arctic.

Both foraging strategies and food availability could influence the ability of a species to raise a second brood successfully. Redpolls forage in trees (where present), shrubs, and other vegetation, as well as on the ground (Knox and Lowther, 2000a, b). There are no data on Common Redpoll nestling diets in North America, but in Scandinavia they consisted of a mix of animal items (mainly insects) and substantial numbers of seeds (Knox and Lowther, 2000a). This dietary pattern contrasts with that of most Arctic-breeding passerines, which are wholly dependent on animal foods

for provisioning their nestlings (Beason, 1995; Kren and Zoerb, 1997; Hussell and Montgomerie, 2002; Montgomerie and Lyon, 2011; Hendricks and Verbeek, 2012).

Horned Larks, American Pipits, Lapland Longspurs, and Snow Buntings all forage primarily by walking and picking food off the ground and vegetation, and nestling diets consist almost exclusively of insects and other invertebrates (Beason, 1995; Hussell and Montgomerie, 2002; Montgomerie and Lyon, 2011; Hendricks and Verbeek, 2012). Northern Wheatears have several foraging techniques, but in our experience they are primarily “perch and pounce” and “hop and peck” foragers (Conder, 1989). At Iqaluit, they often perch on boulders (or other structures, if available) and fly to the ground to seize their prey. There are no published data on nestling diets of Northern Wheatears in North America, but information from elsewhere indicates that they are almost entirely made up of animal material (Kren and Zoerb, 1997). Our observations at Iqaluit indicate that spiders, beetles, other adult insects, and caterpillars are important items in nestling diets. D.J.T. Hussell has seen small berries (probably *Empetrum nigrum*) carried to one nest, but this food choice appears to be rare. It is possible that the wheatear’s foraging technique, including its perhaps superior ability to catch fast-moving spiders and beetles, may place less constraint on its ability to raise second broods than exists for species that are more dependent on large emergences of relatively small adult insects.

Although much remains to be learned about the demography of Arctic-breeding passerines, it is reasonable to hypothesize that survival, both of adults between breeding seasons and of young from fledge to first breeding, is lower for Northern Wheatears from the eastern North American breeding population than for other Arctic-breeding passerines whose migrations are less demanding. Other benefits of their migration strategy, such as a high reproductive output, high survival on the winter range, or both, must compensate for the potentially negative effects of a long and hazardous migration. Our observations indicate that large broods and high fledging success are the norm at Iqaluit. The mean clutch or brood size we observed in wheatears was 7.2 ($n = 22$), compared to 5.5 for Snow Buntings ($n = 45$) and 4.5 for Lapland Longspurs ($n = 27$) (Hussell, 1972, D.J.T. Hussell, unpubl. data), and young were fledged from 82% of 95 wheatear nests with known outcome in 2009–12 (D.J.T. Hussell, unpubl. data). The ability to raise a second brood will add to reproductive output, but it could have adverse consequences for the adults involved if it reduces their chances of migrating successfully and returning to breed again. Wheatears must make the most of the current reproductive opportunity if they have low probabilities of surviving and returning the next year, regardless of whether they raise a second brood that could interfere with their subsequent moult and migration.

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