Aspects of the breeding biology of Bewick's Swans *Cygnus columbianus bewickii* nesting in high densities in the Chaun River delta, Chukotka, east Russia

DIANA SOLOVYEVA[1]* & SERGEY VARTANYAN[2]

[1]Institute of Biological Problems of the North Far East Branch, Russian Academy of Sciences, 18 Portovaya St., Magadan, 685000, Russia.
[2]North-East Interdisciplinary Scientific Research Institute n. a. N. A. Shilo, Far East Branch, Russian Academy of Sciences, 16 Portovaya St., Magadan, Russia.
*Correspondence author. E-mail: diana_solovyova@mail.ru

Abstract

The breeding biology of Bewick's Swans *Cygnus columbianus bewickii* nesting on Ayopechan Island in the Chaun River delta, Chukotka, northeast Russia was monitored from 2002–2013 inclusive, which coincided with a marked increase in the number of swans in the Eastern Population. A total of 535 nests were located during the study, and nest density, clutch size, egg dimensions, earliest hatch dates and nest success (*i.e.* whether at least one egg hatched) were recorded. Average nest density was 2.07 ± 0.25 nests/km^2 (range = 0.98–3.33 nests/km^2) and nest density appeared to increase over the study period, although the trend was not statistically significant. The minimum distance between two swan nests was 82 m, and average clutch size was 3.60 eggs (s.d. = 1.05; range = 1–7 eggs, *n* = 410 clutches). Nest success, recorded in 2009–2013, ranged from 32.2–72.2% and averaged 46.5%. Weather variables, such as the date on which temperatures rose above zero, the timing of snow melt, late May and early June temperatures, and a general (integrated) measure of spring weather conditions, were not significantly associated with nest density. Mean clutch size decreased during the study, through there being a decreasing proportion of large clutches of 5 and 6 eggs. Results are discussed in relation to a separate study of the breeding biology of Bewick's Swans in the Northwest European Population, which increased in numbers between the mid 1970s and the mid 1990s but is currently in decline.

Key words: Bewick's Swan, breeding biology, Chaun River delta, Chukotka, clutch size, *Cygnus bewickii,* nest density, nest success.

Long-term data on the breeding biology of the Bewick's Swan *Cygnus colombianus bewickii* have been reported for birds nesting on the Bolshezemel'skaya and

Malozemel'skaya Tundras and the Yugorskiy Peninsula (Mineev 1987, 1991, 2003), on Vaygach Island (Syroechkovsky *et al.* 2002; Syroechkovsky 2013) and in the Nenetskiy National Nature Reserve (*zapovednik*) (Shchadilov *et al.* 1998, 2002; Rees 2006), all in the western part of arctic Russia. These study areas had high densities of territorial and breeding Bewick's Swans during the late 20th century; nest density varied among sites and years but peaked at 1.40 nests/km^2 on the Malozemel'skaya Tundra and 1.60 nests/km^2 in the area around Khabuicka in the Nenetskiy *zapovednik* (Mineev 1991; Rees 2006). The observations made in European Russia from the early 1970s to 2000 coincided with an increase in the Northwest European Bewick's Swan Population until the mid-1990s, after which numbers declined (Rees & Beekman 2010). Ringing and satellite-tracking studies indicate that the Northwest European Population breeds in western Russia (Beekman *et al.* 2002; Rees 1991, 2006) and thus the studies were carried out on an increasing population, which was possibly reaching saturation level.

Bewick's Swans breeding in the Chaun River delta, Chukotka, in the eastern part of the range, were studied in 1971–1989 (summarised in Krechmar *et al.* 1991; Krechmar & Kondratiev 2006). The delta of the Chaun River was thought to be an important breeding area for Bewick's Swans from the Eastern Population, which migrate to winter in China, Japan and Korea, although the maximum nesting densities there in the second half of the 20th century (0.25 nests/km^2, Krechmar & Kondratiev 1986; Rees 2006) did not approach values similar to those recorded in the western part of Russia. Some of the Bewick's Swans breeding in the Chaun Delta in the late 1970s and early 1980s were found to winter in Japan (Kondratiev 1984). There was a significant increase in the number of Bewick's Swans wintering in Japan during the 1990s (Albertsen & Kanazawa 2002), and more recently there was no discernible trend for Bewick's Swans reported wintering in China (which vary substantially in number between years) in the early 2000s (Cong *et al.* 2011a,b). By 2007, the Eastern Population was estimated to number 92,000–110,000 birds, compared with 21,500 swans reported in the Northwest European Population in 2005 (Wetlands International 2012). Unfortunately, information is lacking for the period during which the Eastern Population was increasing (*c.* 1990–2001). Our study commenced in 2002, by which time population levels were considered relatively high.

An increase in bird abundance is generally to be welcomed, particularly when the species is one of conservation concern. The Chukotian-breeding population of the endangered Lesser White-fronted Geese *Anser erythropus* has increased recently, as have numbers of Bewick's Swans in the same area (Solovyeva & Vartanyan 2011). The Bewick's Swan and its habitats have long received protection through both national and international legislation, and the species was listed under The Red Data Book of the Russian Federation (2001). Amongst large herbivorous birds, such as the Anserini, however, increasing density can affect species interactions and their food supply on the breeding grounds. Over-grazing by the Lesser Snow Goose *Anser* *caerulescens caerulescens* has been found to damage tundra habitats in arctic Canada (Batt 1997), and local increases in abundance have long been thought to affect Barnacle Geese *Branta leucopsis* in some of the breeding areas on Spitsbergen (Drent *et al.* 1998), and the Greater White-fronted Goose *Anser albifrons* nesting on Kolguev Island, Russia (Zainagutdinova *et al.* 2011). The paper by Drent *et al.* (1998) found a density-dependent reduction in all reproductive parameters, namely: breeding propensity, nest success and the number of fledged young per pair. Decreasing production of young has also been reported for the increasing Greater White-fronted Goose population wintering in Europe (Mooij 2005).

This paper describes observations of the breeding biology of Bewick's Swans nesting in the Chaun River delta, at a time when numbers in the Eastern Population, and thus also local nest densities, are thought to be high. Results are considered in relation to similar observations made in the same area during the 1970s and 1980s, and also in comparison to those for swans breeding in western parts of the range during the late 20th century.

Methods

Study area

Ayopechan Island (68°50'N, 170°30'E; covering 91 km^2 and with a maximal elevation of 5–6 m a.s.l.; Fig. 1) is the largest island within the delta formed at the confluence of the Chun, Puchveem and Palyavaam Rivers, where they enter Chaun Bay in the East-Siberian Sea. The island was formed by alluvial and coastal marine sediments 3,000–4,000 years ago, with the highest points situated on the south and southeast parts of the island. Well-developed peat bog, thermokarst lakes and alas depressions (*i.e.* shallow temporary lakes formed by freeze-thaw cycles) constitute the main habitat types in areas of higher ground. A coastal strip of maritime marshes is regularly flooded by the sea. The island contains many lakes and ponds which are of different size (up to 2 km^2) and depth (but all are shallower than 5 m). Lakes of small and medium size, with indented shorelines and several islands, are typical of the area. Drained lake beds, covered with grassy meadows, also cover a significant portion of the island. Ayopechan Island is regularly flooded by wind-induced tides and the water in most of the lakes is brackish. A well-developed network of brackish channels is located on the north side of the island. Sub-arctic grass tundra is the predominated vegetation type with Hare's-tail Cottongrass *Eriophorum vaginatum*, several species of sedges *Carex* sp. and willow *Salix* sp., Arctic Dwarf Birch *Betula nana exilis*, and mosses dominating the plant community (Krechmar *et al.* 1991). The southern part of Ayopechan Island is covered by Shrubby Alder *Duschekia fruticosa* and willow bushes, while the northern part represents maritime tundra on salt marshes. Shallow parts of lakes were overgrown with horsetails *Equisetum* sp., mare's tail *Hippurus* sp., Arctic Marsh Grass *Arctophila fulva* and Pallas' Buttercup *Ranunculus pallasii*.

The coastal climate is typical of the Siberian arctic, strongly influenced by Atlantic cyclones during the summer. The

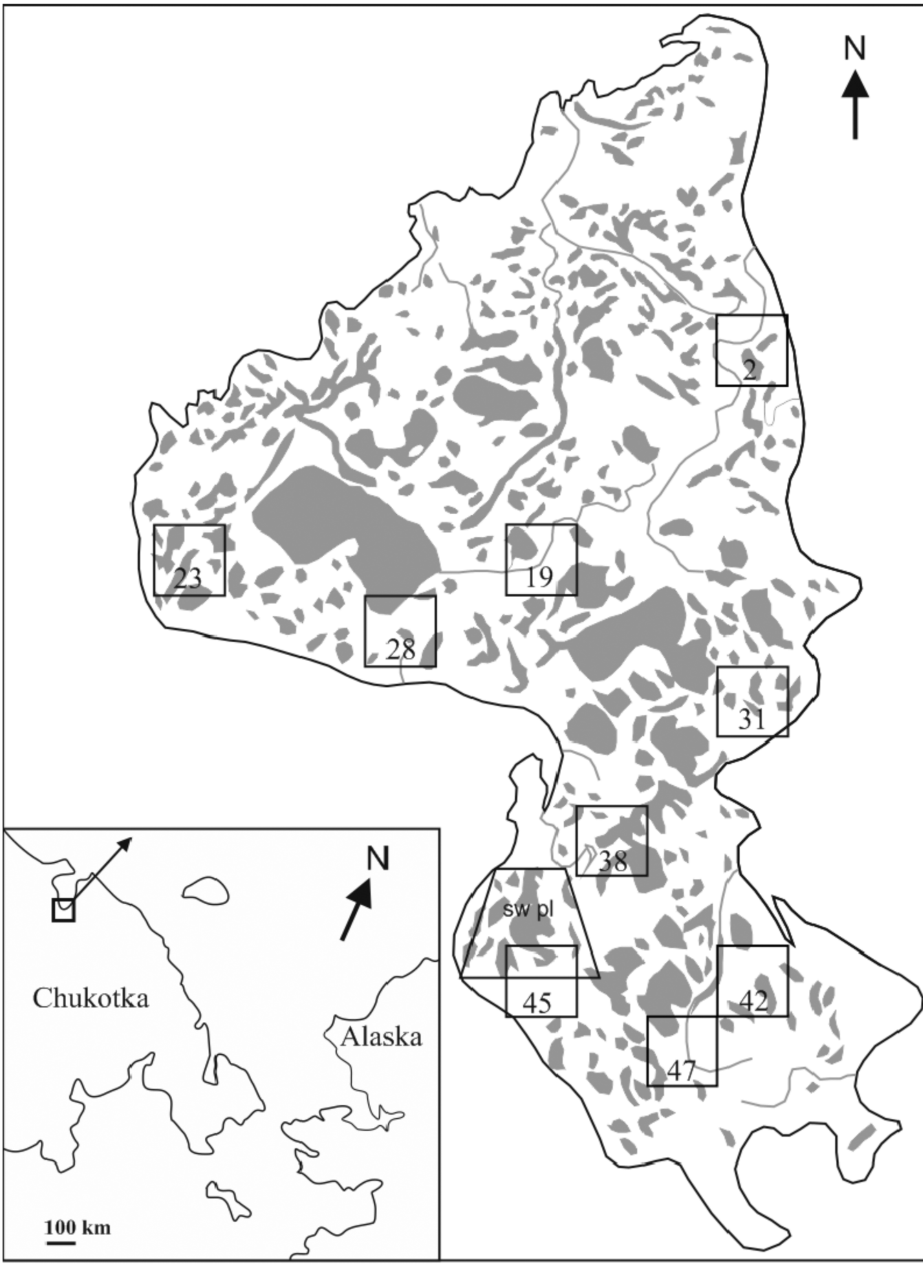

Figure 1. Map of Ayopechan Island, Chaun Delta. Nine 1 km^2 nest plots are shown and identified by their number codes according to a Spectacled Eider nest plot grid. The quadrilateral swan plot of 3.06 km^2 is shown and marked as **"sw pl"**.

coldest month is January (mean temperature = –34°C) and the warmest is July (12°C). Average temperatures recorded for the last 10 days of May and the first 10 days of June, and durations of frost-free season over the study period, are given in Table 1. Duration of the frost-free season, measured as the number of days between the date of the last frost in spring (when temperatures are consistently above zero) and the date of the first frost in autumn, indicates the period of vegetation growth during the summer months.

The Chaun Delta, and Ayopechan Island in particular, is an important breeding area for several waterfowl species in addition to the Bewick's Swan, notably for Long-tailed Duck *Clangula hyemalis* and Spectacled Eider *Somateria fischeri*. Other breeding waterfowl, such as Greater White-fronted Goose, Northern Pintail *Anas acuta*, Greater Scaup *Aythia marila* and King Eider *S. spectabilis* were less abundant, with densities of < 0.1 nests/km^2. Predators of eggs and chicks included the Arctic Fox *Alopex lagopus* (five dens on the island, 1–3 of them active per season), Red Fox *Vulpes vulpes* (one den used irregularly) and nesting Glaucous Gulls *Larus hyperboreus* and Vega Gulls *L. vegae*. Tundra birds of prey (Falconiformes) and owls (Strigiformes) were irregular summer visitors and did not reproduce on the island. About 500 people live at Rytkuchi, the only settlement in Chaun Delta. The village is situated *c.* 4 km inland from the east coast and its economy is based mainly on Reindeer *Rangifer tarandus* herding.

Data collection

The Bewick's Swan study was undertaken during fieldwork on Spectacled Eider in the Chaun Delta. Fifty-one eider nest plots, each of 1 km^2, were set up for this project, equally distributed across Ayopechan Island except for the northern maritime part and the southern shrub-tundra area. There was little additional effort invested in surveying swan nests in the years 2002–2010, except for establishing and monitoring a Bewick's Swan nest search plot, 3.06 km^2 in size (area "sw pl" on Fig. 1). In 2011–2013, the focus of the fieldwork shifted to monitoring bird communities in the Chaun Delta in relation to climate change and anthropogenic factors, which included searching for and locating all "large" bird nests (*i.e.* for all nesting species excepting shorebirds and passerines) within nine of our previous 51 eider plots (Fig. 1). Bewick's Swan nesting density therefore was estimated for the "sw pl" area during 2002–2010 (except in 2008) and for nine 1 km^2 plots (9 km^2 in total) in 2011–2013. In 2002–2010 (excepting 2008), a single search by 3–4 people for all swan nests was made in late June–early July each year, searching the swan plot during a 9–10 h day and mapping all swan nests, both active and predated. In 2011–2013, two people each searched one of the nine "large bird" plots each day; no searches of the "sw pl" area occurred after 2010. At each of the nine plots from 2011 onwards the first search was made in mid-June, the second 10 days later, and subsequent surveys aimed to located lately-built nests and to follow the fate of eggs in previously found nests. Only nests recorded on the plots were used to calculate the density of breeding pairs each year.

In addition to observations made at the swan nest plot, swan nests were also located

Table 1. Spring weather characteristics measured at the Chaun Delta, Siberia, each year during the study period (2002–2013). Years with a late spring (*n* = 3) are shaded in dark grey; years with "normal" spring (*n* = 6) are unshaded; years with an early spring (*n* = 3) are shaded in light grey. dd = data deficient.

Year	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013
Days from 1 January when mean daily temperatures first remain above 0°C	138	137	141	143	140	134	136	129	138	142	137	145
Days from 1 January when snow cover was completely melted	153	155	155	147	154	145	155	140	152	159	147	148
Duration of frost-free season (days)	74	57	dd	97	74	115	85	70	112	85	68	82
Daily average temperature: 20–31 May	4.27	0.42	1.33	0.92	3.47	3.91	1.18	2.74	1.53	–0.35	1.85	–2.04
Daily average temperature: 1–10 June	6.27	7.69	9.81	7.50	4.57	8.33	1.50	4.47	7.55	4.55	7.86	5.45

Table 2. Nest abundance, density and the earliest hatch dates (dd.mm) amongst Bewick's Swans nesting on Ayopechan Island, Chaun Delta, Siberia, in 2002–2013. dd = data deficient.

	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	Total/ average
No. of nests located	16	20	27	43	5	58	23	43	65	48	100	92	535
Nest density, nests/km^2	1.96	2.94	0.98	1.31	1.31	0.98	dd	2.61	2.61	2.00	3.33	2.78	2.07
Earliest hatch date	29.06	04.07	dd	06.07	dd	07.07	06.07	29.06	04.07	11.07	28.06	03.07	03.07

during searches for eider nests at all the eider plots from 2002–2013 inclusive. Fieldworkers were asked to report swan clutch sizes for these less regularly located nests, but as swan monitoring was not an aim of the eider study, whether they did so was at the discretion of the observer. Information therefore was missed for many swan nests, but the data collected are still considered representative for estimating annual variation in clutch size. Only complete clutches (*i.e.* those found after the onset of incubation, determined either by floating eggs in water (Westerkov 1950) or from a known hatch date) were included in the clutch size analyses; partial nest depredation was not measured, and thus the observed clutch size could be an underestimate due to the partial depredation of eggs. In 2009–2013 the teams were asked to report on all hatching success by reporting the presence of egg membranes at the nest. Nests without membranes and eggs were considered as depredated. Clutches where at least one young hatched were classed as having been successful. In 2011–2013, hatching success was documented for all clutches found on the nine "large bird" plots. Swan eggs were measured with calipers to the nearest 0.1 mm in 2011–2013. The date on which the first birds hatched each year ("earliest hatch date") was determined by recording when swan broods were first seen on the tundra (in which case hatch date was taken as the date on which the cygnets were first observed minus one day) or in the nests. We used seven Reconyx camera-traps to record the outcome of swan nesting activity in 2013. Cameras were set up in 5–8 m from the nests. The behaviour of nesting pairs was recorded for 24 different nesting pairs in 2013, with behaviour grouped somewhat subjectively into three categories: (1) aggressive to observer, (2) escaped when humans at a distance of 300 m ("shy"), and (3) intermediate behaviour (*e.g.* hiding behind the nest).

Weather data

Weather data, including daily temperatures and the timing of the snow melt, were obtained from the nearest weather station, Chaun, 8 km from the centre of the island (www.rp.5.ru). The onset of warmer (above zero) temperatures was estimated as the earliest date after which average temperatures remained above zero for at least three consecutive days (subsequent days with negative temperatures during summer weren't considered). Spring weather conditions were classified as either: 1 = warm (2002, 2007 and 2009), 2 = normal (all other years), or 3 = cold (2008, 2011 and 2013), on the basis of their overall characteristics (Table 1), depending on the date of onset of warmer weather (*i.e.* temperatures above zero), the date of complete melt of the snow cover and the average temperature from 20–31 May and into June. This method for describing spring weather conditions has been used in other Bewick's Swan studies (Syroechkovsky *et al.* 2002; Syroechkovsky 2013), and is used here to permit comparisons with observations made elsewhere in the swans' breeding range. Duration of the frost-free season was not analysed as an explanatory variable because it is relevant to fledging success, rather than to the early stages of the breeding season considered in this paper, but is included in Table 1 to provide an overview of weather conditions in the study area during the 2002–2013 breeding seasons.

Data analysis

The associations between spring weather conditions and biological parameters were analysed using statistic functions in Excel software. Overall nesting period was *c.* 37 days (*e.g.* sum of a 7-day laying period for a clutch of 4 eggs and a 30-day incubation period, Rees 2006). The total number of eggs laid by Bewick's Swans on Ayopechan Island each year was estimated by multiplying the average clutch size by nest density and by the area of the island (91 km^2). Partial loss of clutches was not controlled for in this calculation.

Results

Nest density

A total of 535 Bewick's Swan nests was located on Ayopechan Island over the 2002–2013 study period. The number of nests under observation varied among years because of different attention paid to swans in each year. Nest densities also varied among years and averaged 2.07 nests/km^2 (s.d. = 0.61, range = 0.98–3.33 nests/km^2) in 2002–2013 (Table 2, Fig. 2). In 2011–2013, when densities were recorded for 73 nests across nine plots, annual variation in nesting density in these plots was non-significant (ANOVA: $F_{2,24} = 2.13$; $P = 0.14$, n.s.). Nest densities looked bimodal, with high densities in 2003, lower numbers in 2004–2007, and relatively high densities again during 2009–2013. Minimal distances between swan nests on Ayopechan Island were recorded in 2012, the three lowest being 82 m, 84 m and 110 m apart. The minimum distance between nests in 2003 was 231 m; this parameter was not recorded in other years.

Clutch and egg sizes

Average Bewick's Swan clutch size was 3.60 eggs (s.d. = 1.05, n = 410 clutches) during 2002–2013. The frequency of different clutch sizes across years is illustrated in Table 3, together with the annual average and median values. The decrease in average clutch size over the years (Fig. 2) did not reach statistical significance (linear regression: $F_{1,9} = 4.42$, $P = 0.065$, n.s.). Unusually, a clutch of 7 eggs was found in 2003, and a second clutch of 7 eggs was reported by local people in 2005 (A. Kashina, pers. comm.). Clutches of 6 eggs were found in 5 years of our 11-year study and only in 2002–2010 (Table 3; Fig. 3). We found that the proportion of large clutches of 5 or more eggs and of 6 or more eggs also declined during the study (linear regression: $F_{1,10} = 7.20$, $P = 0.03$ and $F_{1,10} = 9.62$, $P = 0.01$, respectively; Fig. 3). Despite the common opinion among local people that the Bewick's Swans never incubate a clutch of 1 egg, incubation of single egg clutches was often reported (Table 3). In the cases where nest histories had been monitored, these were found to be clutches where some eggs had been taken by predators (see nest success and hatch dates for details of nest predation).

Egg dimensions recorded in 2011–2013 are given in Table 4 together with historical sizes from the same site. Small sample size in 1988–89 (n = 22 eggs) did not permit

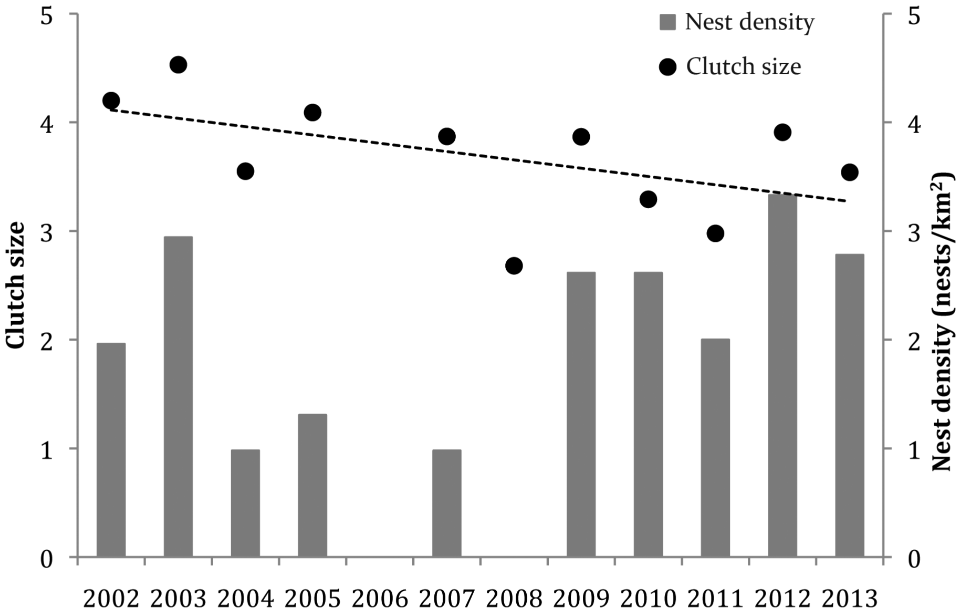

Figure 2. Between year changes in the nest density and mean clutch size of the Bewick's Swan nesting on Ayopechan Island, Chaun Delta, in 2002–2012. Nest density trend (not significant) is represented by the dotted line; clutch size trend (not significant) is represented by the dashed line.

comparisons with the egg size data recorded more recently. A sample size of 104 eggs for the years 1975–1977 and 1980–1984 was similar to our sample sizes; however, neither s.d. nor s.e. values for the egg size measures were given for this time period in Krechmar *et al.* (1991), and the data therefore again could not be compared statistically. In considering the extreme measures, the largest ranges both for egg length (85.1–116.9 mm) and for egg diameter (61.4–78.7 mm) were recorded in 2012. An abortive egg with no yolk was reported once in a Bewick's Swan nest in 2011: it measured 66.1 × 48.2 mm in size. About 1,538 eggs were encountered during the 2002–2013 study (Table 3), so the proportion of abortive eggs was very low in this population, at 0.07%.

Nesting success

Nesting success ranged between 32.2–72.2% in the years 2009–2013 and averaged 46.5% (Table 5). We observed Arctic Foxes successfully depredating clutches in all years, and a dead adult swan was found in an active Red Fox den in 2008. Significant predation of eggs by gulls *Larus* sp. was reported. Seven camera-traps recorded the outcome of Bewick's Swan nesting attempts in 2013. Of these, the clutches hatched in two nests, three were depredated by Arctic Fox and two were depredated by an unknown predator, most likely by gulls (the predation was not recorded on camera). Bewick's Swan pairs showed a variety of reactions to the observer: some strongly defended their

Table 3. Clutch sizes recorded for Bewick's Swan nesting on Ayopechan Island, Chaun Delta, Siberia, in 2002–2005 and 2007–2013.

Years	No. of clutches of each clutch size							No. of nests	Average clutch size (± s.d.)	Median clutch size
	1	2	3	4	5	6	7			
2002	0	0	0	3	8	2	0	13	4.92 (0.41)	5
2003	1	2	1	6	4	2	1	17	4.18 (2.40)	4
2004	0	3	7	6	4	0	0	20	3.55 (1.00)	3.5
2005	1	1	4	17	9	2	0	34	4.12 (1.02)	4
2007	1	5	6	16	10	0	0	38	3.76 (1.16)	4
2008	0	9	11	2	0	0	0	22	2.68 (0.42)	3
2009	2	1	6	12	8	1	0	30	3.87 (1.36)	4
2010	0	8	23	13	3	1	0	48	3.29 (0.81)	3
2011	4	7	21	12	1	0	0	45	2.98 (0.89)	3
2012	2	4	18	40	24	0	0	88	3.91 (0.87)	4
2013	1	6	24	27	9	0	0	67	3.54 (0.89)	4

nests, even threatening the observer (Fig. 4) while others escaped from the nest when the observer approached to within 300 m. The latter always left a nest uncovered, didn't return to the nest for several hours, and their nests were subjected to gull depredation. Intermediate behaviour, which fell between these two extremes, involved female swans hiding behind the nest and leaving only when the observer approached to within 10–20 m. Such females returned to their nests soon after the observer left the vicinity of the nest. This last type of behaviour has also been described for Bewick's Swans in other areas (Krechmar & Kondratiev 2006; Rees 2006; our observations in the Lena Delta, Siberia), whereas their active protection of nests from humans is known only from studies on the Chaun Delta in 1988–1989 and in the 2000s (A. Kondratiev, pers. comm.) and from observations on the Kolyma Delta in the 2000s (http://ibpc.ysn.ru/?page_id=386). In 2013, for 24 nesting pairs, in which behaviour at the nest was reported, three pairs were aggressive to observers, eight pairs were "shy" and thirteen pairs showed intermediate behaviour.

Nesting chronology

Bewick's Swans were first observed in the study area on average on 13 May (range = 10–17 May) in 2011–2013, earlier than the mean arrival date of 27 May recorded in 1971–1984 (range = 20 May – 2 June; Krechmar *et al.* 1991). The onset

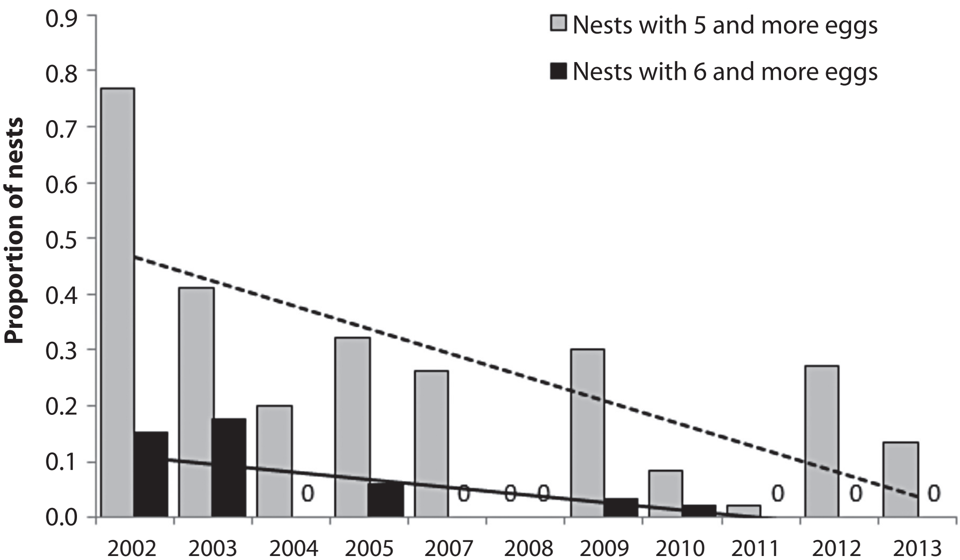

Figure 3. Between year changes in the proportion of large clutches in Bewick's Swan nesting on Ayopechan Island, Chaun Delta, 2002–2012. Clutches with 5 or more eggs and clutches with 6 or more eggs are considered as separate rows, although 6+ clutches are included in 5+ clutch row. Trend of 5+ clutch proportion is shown by dash line; trend of 6+ clutch proportion is shown by solid line.

of egg-laying occurred between 29 May and 8 June in 1975–1977 and 1980–1984 (Krechmar & Kondratiev 2006) and between 23 May and 4 June in 2002–2013.

Daily field observations made by the team on Ayopechan Island enabled us to record the dates on which the earliest Bewick's Swan broods first appeared on the tundra each year (except in 2004 and 2006), and the estimated earliest hatch dates ranged from 28 June (in 2012) to 11 July (in 2011) (Table 2).

Influence of weather characteristics

Most measures of spring weather conditions each year (*i.e.* the date of consistently above zero temperatures, snow melt date and temperatures in late May and early June) did not correlate significantly with nesting density, clutch size and hatch date (Table 6). Average clutch size increased with average temperature during 1–10 June (when most clutches were initiated), but this was not statistically significant (Spearman Rank correlation: $r_{10} = 0.445$, n.s., Table 6). Clutch size varied according to the spring classification, however, with larger clutches laid during early springs (mean ± s.d. = 3.99 ± 1.12) than in normal springs (3.79 ± 1.04) or late springs (3.22 ± 0.94) (ANOVA: $F_{2,419} = 18.15$, $P < 0.001$), and average clutch size also varied according to whether the spring was early, normal or late each year (Spearman Rank correlation: $r_{10} = 0.662$, $P < 0.05$, Table 6). Although

Table 4. Historic and recent mean egg size measurements recorded for Bewick's Swans nesting on Ayopechan Island, Chaun Delta, Siberia between 1975 and 2013, in comparison with those for Bewick's Swans from Northwest European Population nesting at Khabuicka, Nenetskiy *zapovednik*, Archangelsk Okrug. (1) = Krechmar *et al.* 1991; (2) = Krechmar & Kondratiev 2006; (3) = Rees 2006; n/a = not available. Egg size measurements are in mm in each case.

Parameter/Year	**2011**	**2012**	**2013**	**1975–1977 and 1980–1984(1)**	**1988–89(2)**	**Khabuicka(3)**
Average egg length	103.78	104.20	105.09	104.6	107.1	102.7
(± s.d.)	(4.24)	(5.13)	(3.91)	(n/a)	(2.91)	(n/a)
Maximal egg length	114.1	116.9	113.5	113.8	111.5	117.4
Minimal egg length	96.6	85.1	95.6	93.5	100.5	89
Average egg diameter	66.74	67.51	67.04	67.7	67.9	66.4
(± s.d.)	(1.44)	(2.38)	(1.82)	(n/a)	(2.02)	(n/a)
Maximal egg diameter	69.9	78.7	70.4	70	71.1	72
Minimal egg diameter	60.5	61.4	63.2	63.3	63	60.5
Sample size (no. of eggs)	72	102	44	104	22	342

nesting chronology (expressed as the date on which the first broods were seen to have hatched) appeared to increase with the snow melt date, and also to be earlier in springs where the weather conditions were classed as early, these associations were not statistically significant (n.s., Table 6).

Discussion

Before this study, the highest reported average nest density of the Bewick's Swan was 1.1 nests/km^2 (peak density = 1.6 nests/km^2), reported from Zakhar'in Bereg near the Pechora Delta, northeast Russia, and at the time this was considered one of the highest throughout the entire range (Rees 2006). During 2002–2013, nest density in Chaun Delta averaged 2.07 nests/km^2 with peak densities of 3.3 nests/km^2, *i.e.* twice that of Zakhar'in Bereg and ten times higher than that reported at the same site in the 1970s and 1980s (0.2 nests/km^2 Krechmar *et al.* 1991). There was tentative evidence for an increase in Bewick's Swan nesting density during the study, though the trend would be better described as bimodal, and the increase was not significant. A break in monitoring occurred here between 1984 and 2002 and thus the increase in nest density throughout this time period was not fully documented.

Table 5. Proportion of clutches where at least one egg hatched, for Bewick's Swan nesting on Ayopechan Island, Chaun Delta, Siberia in 2009–2013.

Year	2009	2010	2011	2012	2013	Average
Nest success (≥ 1 egg hatched)	0.353	0.333	0.722	0.595	0.322	0.465
No. nests where nest success was known (*n*)	17	15	18	41	62	

Despite the Bewick's Swans' territorial behaviour, birds were found breeding in close proximity to each other on the Chaun Delta in the year of highest nest densities (2012). An increase in nest density in the Chaun Delta between the 1970s and 2010s corresponds with the reported growth in numbers wintering in Japan over this period, which increased from < 2,000 birds in the 1970s to > 30,000 birds by 2000 (Albertsen & Kanazawa 2002; see also Kondratiev 1984 for confirmation that at least some swans breeding on the Chaun Delta winter in Japan), representing a ten-fold increase on

Figure 4. Bewick's Swan actively protecting a nest from an observer, June 2013. (Photograph by A. Krechmar).

Table 6. Spearman rank correlations for weather conditions in relation to clutch size, nest density and the earliest hatch date amongst Bewick's Swans nesting on Ayopechan Island, Chaun Delta, Siberia, 2002–2013. Significant correlations (n = 10, P < 0.05) are highlighted in grey.

Weather variable	Clutch size	Nest density	Earliest hatch date
Days after 1 January when above zero temperatures commenced	–0.113	–0.133	0.186
Days after 1 January when snow had fully melted	–0.345	–0.056	0.407
Daily average temperature for 20–31 May	0.394	–0.360	–0.342
Daily average temperature for 1–10 June	0.376	–0.192	–0.092
Integrated spring characteristic	–0.662	0.303	0.340

both breeding and wintering grounds. Given the discovery of a large Chinese-wintering population in recent years (Cong *et al.* 2011a) a new ringing programme would help to establish contemporary migratory ties within the Eastern Bewick's Swan Population.

Recent warming has been especially pronounced in the Bering sector of the Russian arctic, resulting in unprecedented conditions for nesting birds which may have contributed to the dramatic increase in the Bewick's Swan in this area. Warm climate and the associated verdant vegetation were known to enable Bewick's Swan to extend their breeding range as far north as Zhokhov Island (76°N), in the New Siberian Archipelago, during the Holocene period 8,500 years ago (Makeev *et al* 2003). The median date for the onset of above-zero temperatures in spring has shifted from 1 June in 1975–1984 to 20 May in 2002–2013, and the median date of snow melt likewise advanced from 15 June to 2 June over the same period (Kondratiev 1979; Krechmar *et al.* 1991). The duration of the frost-free season has almost doubled from 35–60 days in the 1950s–1970s (Krechmar & Kondratiev 2006) to an average of 83.5 days during 2002–2013 (Table 1). We suggest these dramatic changes in the duration of the frost-free season, and a resulting increase in plant biomass production, may provide favourable conditions for breeding herbivorous swans (Rustad *et al.* 2001).

It seems reasonable to attribute variation in Bewick's Swan nest density, clutch size and nesting phenology to weather conditions within each nesting season, and several attempts have been made to this in different parts of the swans' breeding range (see summary in Rees 2006; Syroechkovsky 2013). We found that nest density in 2002–2013 was not correlated to any weather characteristics, but this period was relatively warm throughout. During a study on Vaygach Island, Syroechkovsky and co-workers found that Bewick's Swan nesting density was strongly associated with spring weather conditions, with reduced breeding propensity in cold springs (Syroechkovsky *et al.* 2002; Syroechkovsky 2013). This was for swans breeding in the high Arctic (latitude of the middle point of the Vaygach Island is 70°00'N, compared with 68°50'N at our study site), however, and during a run of relatively cold springs in 1986–1997. We suggest that the recent prevailing weather conditions were favourable for breeding even during the colder years, and that this could explain why nest density was independent of any weather variables.

Clutch size was influenced by spring weather conditions, with larger clutches laid in relatively warm "early" springs. Warmer June temperatures have previously been shown to be correlated with higher breeding productivity in arctic waterfowl (Barry 1962; Summers & Underhill 1987), but the mean annual clutch size did not vary significantly with June temperatures during the present study. No nests with 6 eggs were recorded during 2012, despite the large sample of nests checked and June temperatures being warmer than in 2003, when the highest proportion of very large clutches (*i.e.* with 6 or 7 eggs) was reported. The decline in the proportion of large clutches could be the first indication of density dependence on the island, perhaps as a consequence of overexploitation of local food resources at a critical period. With increasing nest density, female swans may have been unable to obtain sufficient reserves to produce clutches of 6 or more eggs in more recent years. During the earlier studies of A.Y. Kondratiev in 1975–1977 and 1980–1984, one clutch of 6 eggs was reported amongst 118 clutches (0.85%, Krechmar *et al.* 1991) compared to 2–17% in early years of this study. The unusual clutch of 7 eggs in 2003 could be a result of the food supply in that year, but we cannot exclude the possibility that this was one or more eggs dumped in another swan's clutch, the product of more than one female. The possibility of nest parasitism is difficult to reconcile with the Bewick's Swans' territorial behaviour, but it may be possible amongst closely related females, and has been demonstrated elsewhere (Syroechkovsky 2003). The minimal distance between nests (82 m) was also much lower than found in previous studies, for instance in comparison with 860 m reported on Vaygach Island (Syroechkovsky *et al* 2002).

There was a marked difference in clutch sizes between the Northwest European and the Eastern Bewick's Swan Populations, with a higher average clutch size of 3.6 eggs (range = 1–7 eggs; annual mean clutch size = 2.7–4.9 eggs) in the present study than the 3.4 eggs (range = 1–6; annual mean clutch size = 2.6–3.9 eggs) recorded at Khabuicka during 1991–2000, at a time when numbers in the Northwest European Bewick's Swan Population were peaking (Rees 2006). Bewick's Swan clutch size may be related to the latitude of the breeding site (Rees 2006), but Khabuicka in the Nenetskiy *zapovednik* is at a similar latitude to the Chaun Delta (N 68°15'). There was no obvious difference in the egg dimensions recorded for the Eastern and Northwest European Populations, although eggs from Chaun Delta appeared to be slightly larger. Thus, it seems that the Bewick's Swans in the Chaun Delta not only nested at higher densities than those at Khabuicka (average = 2.07 nests/km^2 and 1.1 nests/km^2 respectively), but also had larger clutches, perhaps reflecting higher quality breeding habitats for the species in the two study areas.

The average nesting success of 46.5% (range = 32.2–72.2%) recorded in this study was lower than the 67.2 % (range = 20–94%) reported on Vaygach Island (Syroechkovsky *et al* 2002). Annual nest success was not fully documented at Khabuicka but it averaged at least 54.9% during 1992–2000 (Rees 2006). Whether nesting density influences nest protection behaviour by Bewick's Swans is unclear. Following the findings of Drent *et al.* (1998) we suggest that low nesting success in this study may reflect density-dependent regulation of swans breeding at what seems to be a prime site, though the level of human activity in the region may also be a contributing factor. Some 33.3% of pairs in 2013 left the nest in response to human activity, rather than actively defending their clutch or hiding nearby, and egg depredation by gulls was recorded primarily amongst these "shy" pairs. Illegal shooting by villagers during the breeding season has been reported in the Chaun Delta, making nest protection dangerous for swans. Nevertheless, in contrast to this behaviour, at 12.5% of nests at least one pair member showed aggression to observers in 2013. All three nests with aggressive swans were situated close to the Chaun Biostation (average distance from these three nests to the station was 883 m, range = 490–1,500 m), and a territorial swan is also known to have nested near the Biostation in 1988–1989. The average distance from the station to "shy" swan nests was 5,233 m and to "intermediate" swan nests was 5,543 m in 2013, and none of these birds nested close to the Biostation. It therefore seems that the more territorial swans may have become habituated to the presence of researchers, who do not present any real danger to birds.

Overall, we consider that conditions in the Chaun Delta have become increasingly conducive as a breeding area for Bewick's Swans and that it has become a "swan paradise" in recent years. As the swans' feeding behaviour and food supply in the Chaun Delta have not been studied to date, we are unable to assess the extent to which the increasing density of nesting pairs observed in 2002–2013 can continue without affecting their food resources on the island and thus increase intra-specific competition for food. The Northwest European Population of the Bewick's Swan started to decline from 1996 onwards, after nesting density in at least one important breeding area had peaked (Rees 2006). It remains to be seen if the same pattern occurs for swans in the Eastern Population, possibly as a result of local density dependence regulation of one or more breeding parameters, such as nesting density, clutch size and fledging success.

Acknowledgments

We thank our field assistants in 2002 to 2013 whose hard work made this publication possible. The various transportation and logistic support (including helicopter flights to the remote study area) was kindly provided by Chukotka Mining and Geological Company (Kupol) of Kinross Gold Corporation in 2010–2013 and we express our great thanks to the managers. The Spectacled Eider study was financially supported by the U.S. Fish and Wildlife Service, Alaska, during all years of the research. The bird community monitoring project was funded by the Beringia Programme of the Wildlife Conservation Society in 2011–2013. Advice on statistical analysis was kindly provided by Eileen Rees from the Wildfowl and Wetlands Trust and by Anthony Fox from Aarhus University. Special thanks to Eileen Rees, Tony Fox and to two anonymous referees for helpful comments on an earlier draft of the text.

References

Albertsen, J.O. & Kanazawa, Y. 2002. Numbers and ecology of swans wintering in Japan. *Waterbirds* 25 (Special Publication No. 1): 74–85.

Batt, B.D. (ed.). 1997. *Arctic Ecosystems in Peril: Report of the Arctic Goose Habitat Working Group*. Arctic Joint Venture Special Publication, U.S. Fish & Wildlife Service, Washington, D.C., USA and Canadian Wildlife Service, Ottawa, Ontario, Canada.

Barry, T.W. 1962. Effects of late seasons on Atlantic Brant reproduction. *Journal of Wildlife Management* 26: 19–26.

Beekman J.H., Nolet, B.A. & Klaassen, M. 2002. Skipping swans: fuelling rates and wind conditions determine differential use of migratory stopover sites of Bewick's Swans *Cygnus bewickii*. *In* C. Both & T. Piersma (eds.), The avian calendar: exploring biological hurdles in the annual cycle. Proceedings 3rd Conference European Ornithologists' Union, Groningen, August 2001. *Ardea* 90 (Special Issue): 437–460.

Cong, P, Cao, L., Fox, A.D., Barter, M., Rees, E.C., Jiang, Y., Ji, W., Zhu, W. & Song, G. 2011a. Changes in Tundra Swan *Cygnus columbianus bewickii* distribution and abundance in the Yangtze River floodplain. *Bird Conservation International* 21: 260–65.

Cong, P.H., Rees, E.C., Sun, M.M., Zhao, M., Cao, L., Barter, M. & Fox, A.D. 2011b. A comparison of behaviour and habitat use by Bewick's Swans *Cygnus columbianus bewickii* at wintering sites in China and Europe: preliminary observations. *Wildfowl* 61: 52–73.

Danilov-Danil'an, V.I. (ed.). 2001. *Red Data Book of Russian Federation (Animals)*. AST Astrel', Moscow, Russia. [In Russian.]

Drent, R.H., Black, J.M., Loonen, M.J.J.E. & Prop, J. 1998. Barnacle geese *Branta leucopsis* on Nordenskiöldkysten, western Spitsbergen – in thirty years from colonisation to saturation. *In* F. Mehlum, J.M. Black & J. Madsen (eds.), Research on Arctic Geese, Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 23–26 September 1997. *Norsk Polarinstitutt Skrifter* 200: 105–114.

Kondratiev, A.Ya. 1984. Migrations of the East-Siberian Tundra Swans (*Cygnus bewickii jankovskii*) and their wintering in Japan. *Zool. Journal* 63 (2): 1835–1847. [In Russian with English summary.]

Kondratiev, A.Ya. 1979. Seasonal events in bird life in Chaun Lowland. *In* A.V. Krechmar & F.B. Chernyavsky (eds.), *Birds of the North-East Asia*, pp. 95–105. Academy of Sciences of the USSR (Far East Branch), Vladivostok, Russia. [In Russian.]

Krechmar, A.V., Andreev, A.V. & Kondratiev, A.Ya. 1991. *Birds of Northern plains*. Nauka Publishing House Leningrad, Russia. [In Russian with English summary.]

Krechmar, A.V. & Kondratiev, A.Ya. 1986. Comparative and ecological analysis of Bewick's and Whooper Swan nesting biology. *In* A.V. Andreev & A.V. Krechmar (eds.), *Experimental methods and results of their application in northern bird studies*, pp. 34–58. Academy of Sciences of the USSR (Far East Branch), Vladivostock, Russia. [In Russian.]

Krechmar, A.V. & Kondratiev, A.V. 2006. *Waterfowl Birds of North-east Asia*. NESC FEB RAS, Magadan, Russia. [In Russian with English summary.]

Makeev, V.M., Ponomareva, D.P., Pitulko, V.V., Chernova, G.M. & Solovyeva, D.V. 2003. Vegetation and Climate of the New Siberian Islands for the Past 15,000 Years. *Arctic, Antarctic and Alpine Research* 35(1): 56–66.

Mineev, Yu.N. 1987. *Waterfowl of the Bolshezemelskaya tundra: Fauna and Ecology*. Nauka, Leningrad, Russia. [In Russian.]

Mineev, Yu.N. 1991. Distribution and numbers of Bewick's Swans *Cygnus bewickii* in the European Northeast of the USSR. *In* J. Sears & P.J. Bacon (eds.), Proceedings of the Third International Swan Symposium, Oxford 1989. *Wildfowl* (Special Supplement No. 1): 62–67.

Mineev, Yu.N. 2003. *Waterfowl of the East European tundra*. Ural Branch of Russian Academy of Science, Ekaterinburg, Russia. [In Russian.]

Mooij, J.H. 2005. Protection and use of waterbirds in the European Union. *Beitr. Jagd- und Wildforschung* 30: 49–76.

Rees, E.C. 1991. Distribution within the USSR of Bewick's Swans *Cygnus columbianus bewickii* marked in Britain. *In* J. Sears & P.J. Bacon (eds.), Proceedings of the Third International Swan Symposium, Oxford 1989. *Wildfowl* (Special Supplement No. 1): 209–213.

Rees, E. 2006. *Bewick's Swan*. T. & A.D. Poyser, London, UK.

Rees, E.C. & Beekman, J.H. 2010. Northwest European Bewick's Swans: a population in decline. *British Birds* 103: 640–650.

Rustad L.E., Campbell J.L., Marion G.M., Norby R.J., Mitchell M.J. & Gurevitch A. J. 2001. A meta analysis of the response of soil respiration, net nitrogen mineralization and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126: 543–562.

Shchadilov, Y.M., Belousova, A.V., Rees, E.C. & Bowler, J.M. 1998. Long-term study of the nesting success in the Bewick's Swans in the coastal tundra in the Nenetskiy Autonomous Okrug. *Casarca* 4: 217–228.

Shchadilov, Y.M., Rees, E.C., Belousova, A.V. & Bowler, J.M. 2002. Annual variation in the proportion of Bewick's Swans and Whooper Swans breeding in northern European Russia. *Waterbirds* 25 (Special Publication No. 1): 86–94.

Solovieva D. & Vartanyan, S. 2011. Lesser White-Fronted Goose *Anser erythropus*: good news about the breeding population in west Chukotka, Russia. *Wildfowl* 61: 108–118.

Summers, R.W. & Underhill, L.G. 1987. Factors related to breeding production of Brent Geese and waders on the Taimyr Peninsula. *Bird Study* 34: 161–171.

Syroechkovsky, E.V., Litvin, K.E. & Gurtovaya, E.N. 2002. Nesting ecology of Bewick's Swans on Vaygach Island, Russia. *Waterbirds* 25 (Special Publication No. 1): 221–226.

Syroechkovsky, E.V. 2003. On possible egg dumping in the Bewick's Swans. *Casarca* 9: 43–52. [In Russian with English summary.]

Syroechkovsky, E.V. 2013. *The Mechanisms of Adaptation of Anserini to the Arctic Environment*. KMK Scientific Press, Moscow, Russia. [In Russian with English summary.]

Westerkov, K. 1950. Methods for determining the age of game bird eggs. *Journal of Wildlife Management* 54: 627–628.

Wetlands International 2012. *Waterbird Population Estimates. Fifth edition*. Wetlands International, Wageningen, the Netherlands.

Zainagutdinova, E.M., Kondratiev, A.V. & Krukkenberg, H. 2011. *Greater White-fronted Goose on the Kolguev Island: Biology in Reproductive Period*. Lambert Academic Publishing, Saarbrucken, Germany. [In Russian with English summary.]

Photograph: Bewick's Swan nesting habitat in Chuckotka, Russia, by Gleb Danilov.

