Living child-free: proposal for density-dependent regulation in Bewick's Swans *Cygnus columbianus bewickii*

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Abstract

Density-dependent population regulation in the Bewick's Swan *Cygnus columbianus bewickii* can be assessed from aspects of its productivity including breeding propensity, nest density and clutch size, and also from nest and brood protective behaviour. Bewick's Swans breeding on the delta of the Chaun River in western Chukotka, Russia, winter in Japan and migrate along Sakhalin Island and the Kolyma River in spring. The flyway population increased > 20-fold from 2,000 to 45,000 individuals between the late 1980s and 2002, and a period of smooth decline or stabilisation was reported thereafter. We collected data on nesting Bewick's Swans in 2002–2018 on Ayopechan Island in the Chaun Delta. There was a negative association between nest density and the number of swans counted in Japan during the January prior to the breeding season ($R = -0.623$, $n = 16$, $P < 0.01$), providing evidence for density-dependent population regulation. A mean of 7.9% of all nests were "built without laying" in 2014–2018. Annual mean clutch size declined significantly by 1.15 eggs, or 23.4% of the initial annual mean, during the study period ($F_{1,14} = 8.89$, $P < 0.01$); year and an integrated spring characteristic (scored from 1 to 3) were the parameters with the greatest influence on clutch size. Nest success was highest (0.92) in aggressive pairs, lower in pairs with "normal" behaviour (0.55), and lowest (0.15) in "shy" pairs; these differences in nest success between three behavioural categories were statistically significant ($F_{2,12} = 10.11$, $P = 0.003$). We conclude that the Bewick's Swan breeding population on the Chaun Delta, and probably along the flyway population's breeding range, is regulated by reduced breeding propensity, with declining clutch sizes and low nest success resulting from the behaviour of nesting pairs.

Key words: behaviour, Bewick's Swan, *Cygnus columbianus bewickii,* Chaun Delta, Chukotka, clutch size, density-dependent regulation, nest density.

Animal populations can regulate their size, returning the population to its equilibrium (Ratikainen *et al.* 2007). Populations of migratory birds may experience density dependence in more than one location or time period, and the ideal study of population regulation should consider all stages of the annual cycle; however, this is difficult to achieve in practice for many migratory species. In swans *Cygnus* sp., which are long-lived birds with high fidelity to their breeding territories, the most efficient way of regulating overabundant local populations is through the regulation of the survival rate of adult birds rather than the regulation of productivity (Ellis & Elphick 2007; Hindman & Tjaden 2014; Wood *et al.* 2013). However, autoregulation of adult mortality is not typical for wild birds and the simplest mechanism of autoregulation in local populations is through the regulation of productivity (Koons *et al.* 2014). Such regulation may occur via: 1) breeding propensity, 2) regulation of clutch size, or 3) nest and brood protective behaviour. Alternatively, there may be pronounced bottle-necks in the annual cycle where the population is regulated via direct mortality of adults and/or juveniles.

Bewick's Swans *Cygnus columbianus bewickii* breeding on the Chaun Delta in western Chukotka, Russia, winter on Honshu Island in Japan and have a migration route that is the shortest among suitable routes between these two locations (Kondratiev 1984; Kamiya & Ozaki 2002). Swans wintering in Japan breed along the coast of eastern Asia from the Indigirka Delta in the west (150°E) to Koluchin Bay in the east (175°W; Kistchinskiy *et al.* 1975; A. Antonov & I. Bysikatova, pers. comm.). Numbers of Bewick's Swans wintering in Japan have increased dramatically from 2,000 to 45,000 individuals between the late 1980s and 2002, with a slight decline/stabilisation in numbers reported thereafter (Albertsen & Kanazawa 2002; Ministry of the Environment of Japan 2018). The breeding population in the optimal subarctic habitats of the Kolyma Delta doubled between 1984 and 1995, while numbers breeding on the arctic tundra between the River Alazeya and River Kon'kovaya increased by 13.6-fold (Degtyarev 2010), and a similar 15-fold increase was reported on the Chaun Delta breeding grounds over the same time period (Solovyeva & Vartanyan 2014). An increase in Bewick's Swans migrating along the Kolyma River in spring was reported between 1966 and 1980, indicating that population growth had actually commenced sometime before the 1980s, at the time when it was recognised in Japan (Degtyarev 2010 after Labutin & Degtyarev 1983; Albertsen & Kanazawa 2002). Reasons proposed for the population growth include: (i) supplementary feeding of swans in Japan, together with an increase in waste gain on combine-harvesting rice fields in Japan since 1975 (Shimada & Mizota 2011); (ii) increased vegetation productivity and a doubling of the duration of the frost-free period on the breeding grounds (Solovyeva & Vartanyan 2014); and (iii) reduced competition for food on the breeding grounds following a decline in Reindeer *Rangifer tarandus* numbers (Degtyarev 2010). Autumn warming and vegetation productivity increased along the Kolyma River between 1991 and 2013 (Sinel'nikova & Pakhomov 2015), which has probably improved the swans' survival rates during their autumn migration, and in spring they feed on berries (*e.g.* Lingonberry *Vaccinium vitis-idaea* and Crowberry *Empetrum nigrum*) left-over from the previous summer in the Chaun Delta (our observations). Food resources therefore seem to be generally favourable for the swans during their entire annual cycle. Numbers wintering in Japan stabilised between 2004 and the present time, when the winter food supply also plateaued (Shimada & Mizota 2011).

This paper tests the hypotheses that breeding propensity depends on population size and that it is less dependent on weather conditions on the breeding grounds. It also aims to analyse how protective behaviour may affect the swans' reproductive success. In particular, it assesses whether internal population regulation acts on the breeding grounds of the Chaun Delta, through density-dependent nesting resulting in a variation in breeding propensity, a decline in clutch size and a lack of nest protective behaviour.

Methods

Data collection

We collected the data on Bewick's Swans nesting on Ayopechan Island in the Chaun Delta during 2002–2018. Bewick's Swan habitat on Ayopechan Island, along with the nest plot search methods and the nest information recorded, are described in detail in an earlier publication (Solovyeva & Vartanayan 2014). In summary, nine 1 km^2 plots for "large" birds were searched by two observers each summer in 2011–2018, except for 2017 when five plots were used. Nests located inside each of the plot areas were mapped, and clutch size, nest age and swan behaviour were recorded. In 2013–2018 we observed the behaviour of nesting swans and classed them as: (i) "aggressive" to the observer, (ii) "shy" (for birds displaced on seeing the observer at a distance), or (iii) "normal" birds, which were intermediate individuals that initially hid behind the nest and escaped as the observer approached to within 10–20 m.

Swan nests have a pronounced indent in the nest material underneath each egg, which can be seen even in cases where eggs were removed within a few days before the observation. Feathers are also found in nests in which eggs have been laid. In 2014–2018 we used these features to distinguish between nests where laying occurred from those where no eggs were laid. These latter nests were classified as "built without laying". Fresh nest constructions were readily distinguished from the flat low constructions of previous years in that they also included new vegetation. Nests built without a clutch subsequently being laid were considered in estimates of nest density and hatching success. Only complete clutches (*i.e.* those found after the onset of incubation based either on water tests (Westerkov 1950) or with known first laying or hatch dates) were included in the clutch size analyses; partial nest depredation is not considered in this paper, and thus the observed clutch size could be an underestimate due to the partial depredation of eggs. Clutches where at least one young hatched were classed as having been successful. In 2011–2018, hatching success was documented for all clutches found on the nine "large bird" plots (five plots in

2017). Before 2011, hatching success was estimated for the years in which the outcome for ≥ 10 nests were documented, which were in 2005, 2007, 2009 and 2010. Production (P) for the study area was calculated as P = clutch size*nest density*nest success*100 km^2. We set up Reconyx camera-traps at distances of 5–7 m from active swan nests; 3–7 nests were monitored annually, from laying or early incubation until hatching, in 2013–2018. Cameras recorded images at 1 min intervals, and a motion sensor was activated to record movements around nests. We visited nests with cameras at 6-day intervals to change the memory card.

Weather data (including temperatures) measured 8 times a day, and also the timing of the snow melt, were obtained from the nearest weather station at Rytkuchi, which is 8 km from the centre of Ayopechan Island (www.rp.5.ru). Rodent abundance was ranked from 0 (almost absent) to 4 (over-abundant and present every day; Ehrich *et al.* in press) in early June each year, based on visual observations of voles and lemmings during searches for bird nests and around the field station. Apparent nest success was the proportion of successful nests out of the total number of nests for which hatching success was known.

National mid-winter counts of swans in Japan were carried out in mid-January as a part of "Annual Census on Waterfowl (Anatidae) Population" by the Ministry of the Environment of Japan (Albertsen & Kanazawa 2002). Observers were from birdwatching groups, hunting organisations and local government officers with different skills in identification and counting. The number of sites counted as part of the census reached 8,939 in January 2018.

Data analyses

Spring weather conditions were integrated and classified as either: 1 = warm (2002, 2006, 2007, 2009 and 2016), 2 = normal (all other years), or 3 = cold (2008, 2011, 2014 and 2018), on the basis on their overall characteristics, such as snow melt date, positive temperature date and mean temperatures in late May – early June (see also Solovyeva & Vartanyan 2014). The year was considered as "warm" when the dates of snow melt and positive temperatures fell within the first third of the range (among all years) and the sum of positive temperatures between 20 May and 10 June exceed 100°C. Mean temperatures were calculated for 20–31 May and 1–10 June each year. The snow melt date was considered as the date when the snow plot became completely snow-free at the weather station (Table 1).

Using multivariate regression, we tested for a linear relationship between the total number of Bewick's Swans in Japan in January and the observed nest density on the Chaun Delta in the following summer. The model was fitted using maximum likelihood accounting for year and the following weather variables: mean temperature on 20–31 May, mean temperature on 1–10 June, snow melt date (as the number of days from 1 May) and the integrated spring characteristic. Using GLMs, we modelled annual mean clutch size and apparent nest success in a similar manner. Variables potentially explaining clutch size included year and all weather variables. We modelled apparent nest success, taking year, rodent abundance,

Table 1. Mean nest density (ND), mean clutch size (CS), apparent nest success (NS) and productivity (P) for Bewick's Swans, together with estimated rodent abundance in ordinal abundance classes (RA), the mid-January number of Bewick's Swans in Japan derived from national counts of waterbird numbers during 2002–2018 (WN), and the following weather variables: mean temperature for 20–31 May (20_31); mean temperature for 1–10 June (1_10), date of complete snow melt from 1 May (SM), and integrated spring characteristics (SC) on the Chaun Delta, Chukotka, Russia. dd = data deficit.

Year	ND	CS	NS	P	WN	20_31	1_10	SM	SC	RA
2002	1.961	4.92	dd	dd	34,455	4.27	6.27	35	1	1
2003	2.941	4.18	dd	dd	38,983	0.42	7.69	36	2	3
2004	0.980	3.55	dd	dd	45,283	1.33	9.81	35	2	4
2005	1.307	4.12	0.50	269	44,804	0.92	7.50	28	2	0
2006	1.307	dd	dd	dd	40,619	3.50	4.60	27	1	0
2007	0.980	3.76	0.55	dd	42,648	3.91	8.33	26	1	1
2008	dd	2.68	dd	dd	40,485	1.18	1.50	36	3	0
2009	2.614	3.87	0.35	354	39,965	2.74	4.47	29	1	1
2010	2.614	3.29	0.31	284	36,809	1.53	7.55	32	2	0
2011	2.000	2.98	0.72	429	36,810	–0.35	4.55	39	3	0
2012	3.330	3.91	0.60	781	32,946	1.85	7.86	27	2	0
2013	2.778	3.54	0.40	394	39,825	–2.00	5.50	28	2	1
2014	2.333	2.76	0.09	32	37,154	–2.99	2.20	42	3	0
2015	2.222	3.29	0.25	183	35,122	0.45	3.07	35	2	0
2016	1.444	3.50	0.26	76	38,617	3.92	9.94	24	1	1
2017	1.600	3.72	0.60	357	35,596	0.13	7.63	30	2	1
2018	1.555	2.79	0.53	239	42,620	–1.27	1.01	41	3	0

spring characteristics, nest density and mid-January population size as variates. We selected models based on an information-theoretic approach (Burnham & Anderson 2002) using Akaike's Information Criterion corrected for small sample size (AIC_c). We used the software Statistica 10.0, together with the 'mixlm' package in Program R (Liland 2018; R Development Core Team 2018), for the analyses.

Results

Nest density

A total of 759 nests of Bewick's Swan were recorded on the Chaun Delta between 2002 and 2018. The nest density averaged 2.00 nests/km^2 and ranged between 0.98 and 3.33 nests/km^2 in 2002–2018 with the exception of 2008 when nest density was not recorded (Table 1). Hence data from 2002–2007 and 2009–2018 were used to examine variation in nest density. Our best approximating model of nest density included population size in Japan in mid-January of the same year (WN = Winter Numbers); the second model included the population in Japan and mean temperatures in 20–31 May (Table 2). We found little support for other models of nest density that included year, winter numbers in Japan and all other weather variables. Bewick's Swan nest density on the Chaun Delta was lower in the years in which higher numbers of swans were counted in Japan in the January preceding the breeding season ($F_{1,14}$ = 8.89, P < 0.01) (Fig. 1). The regression of production against the deviation of the winter population between the previous and following January was not statistically significant ($F_{1,9}$ = 2.09, P = 0.19).

A phenomenon of nest building without the subsequent laying of eggs was observed in recent years between 2014–2018. A mean 7.9% of all nests were nests "built without laying", accounting for 9.4% in 2014, 18.1% in 2016, 4.0% in 2017 and 0.0% in both

Table 2. Top models used to assess variation in nest density (2002–2007 and 2009–2018) and clutch size (2002–2005 and 2007–2018) for Bewick's Swans nesting on the Chaun Delta, Chukotka, Russia. The best supported model is indicated in bold. For each parameter the null model is presented for comparison.

Parameter	Models[a]	K[b]	AIC_c[c]	δAIC_c	R^2_{adj}
Nest density	**WN**	**2**	**34.214**	**0.000**	**0.345**
	WN, 20_31	3	35.307	1.092	0.398
	Year, WN, 20_31	4	37.573	3.358	0.428
	Null (intercept only)	1	39.005	4.790	0.000
	Year, WN, 20_31, 1_10, SM, SC	7	54.914	20.700	0.377
Clutch size	**Year, SC**	**3**	**20.317**	**0.000**	**0.651**
	Year	2	28.922	8.605	0.303
	Null (intercept only)	1	32.726	12.409	0.000
	Year, 20_31,1_10, SM, SC	6	34.861	14.545	0.595
Nest success	**Null (intercept only)**	**1**	**–2.369**	**0.000**	**0.000**
	Year, WN, ND, SC, RA	6	31.459	33.828	0.000

[a]Model parameter abbreviations are given in the heading to the Table 1.
[b]K = number of parameters in model (including the intercept).
[c]The best approximating model has the lowest Akaike's Information Criterion (AIC_c).

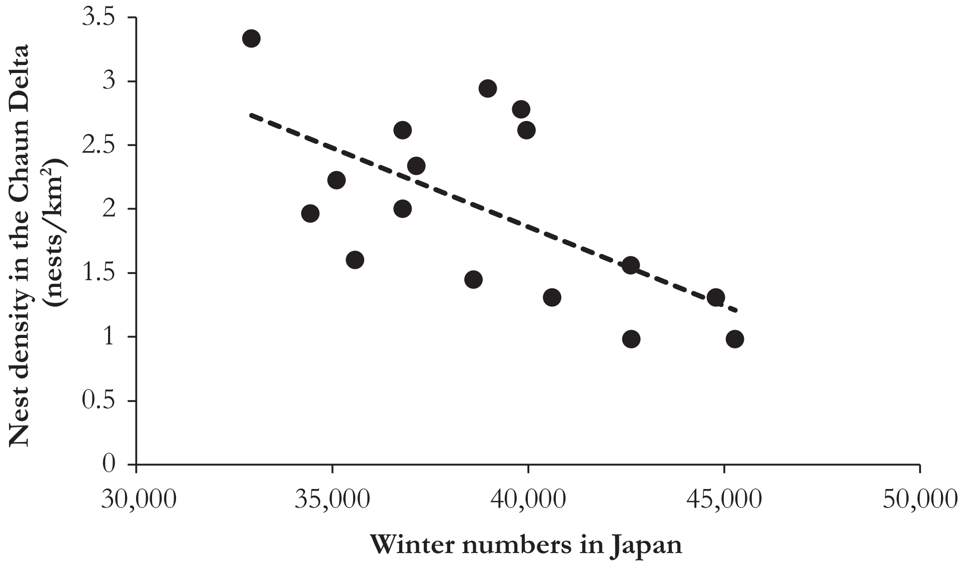

Figure 1. Nest density of Bewick's Swans on the Chaun Delta (nests/km^2) plotted *versus* the mid-January number of Bewick's Swans in Japan, derived from national counts (WN) during 2002–2018. The negative regression was found to be significant ($F_{1,14}$ = 8.89, P < 0.01; Y = 6.8007–0.0001*X), whilst the regression line intercepts the X axis at the mid-January number of 68,000 individuals.

2015 and 2018. In 2016 one pair of swans, whose territory was established at the field station thus facilitating daily observations of the birds, built three nests but did not lay eggs in any of them. In the same year another pair built two nests only 1 m from each other and also laid no eggs. Exclusion of these nests from our dataset would reduce the effective nest density, however, and so we have included them in our analysis.

Clutch size

We included data from 572 complete clutches to examine variation in clutch size in 2002–2005 and 2007–2018. Among models, year and integrated spring characteristics (SC) were the most influential parameters of clutch size (Table 2). We found less support for a model that included year alone, whilst there was little support for the model that included year, mean temperature on 20–31 of May, mean temperature on 1–10 June, spring characteristic and snow melt date (Table 2). Annual mean clutch size declined significantly by 1.15 eggs, or 23.4% of the initial annual mean, over the study period (R = –0.699, P = 0.003; Fig. 2). Besides the annual decline, clutch sizes were found to be low in the springs of 2008, 2011, 2014 and 2018, which were considered to be "cold" springs (Fig. 2).

Nest success and nest protective behaviour

Mean (± s.e.) apparent nest success averaged 0.42 ± 0.04 and ranged between 0.09 and

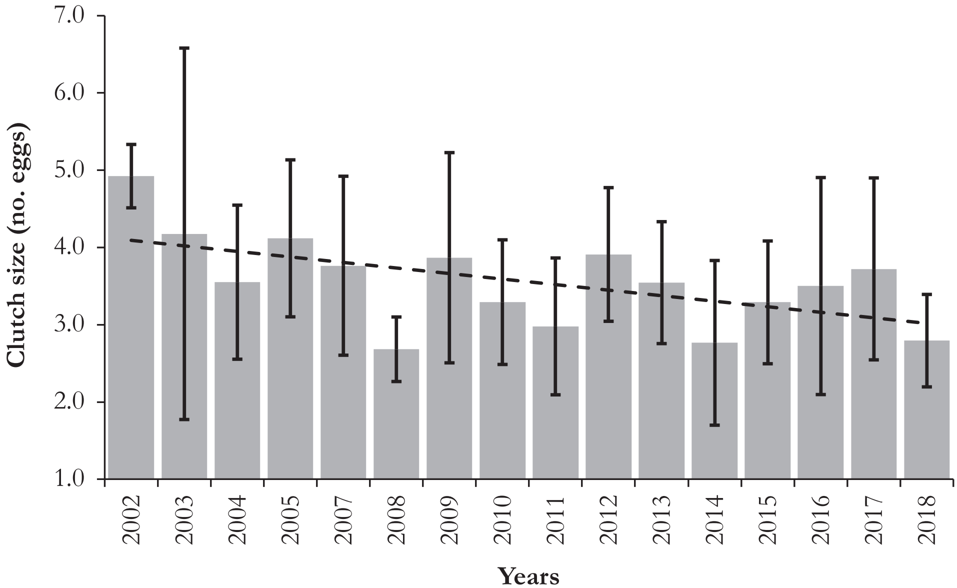

Figure 2. Annual mean (± s.d.) clutch size for Bewick's Swans on the Chaun Delta, Chukotka, Russia. The decline in clutch size with years was statistically significant (R = –0.699; P = 0.003).

0.72 for Bewick's Swans on the Chaun Delta in 2005, 2007 and 2009–2018 (Table 1). We found no support for any model of apparent nest success (Table 2). Nest success was highest in "aggressive" pairs (0.92), lower in pairs with "normal" behaviour (0.55), and was the lowest (0.15) in "shy" pairs, which escaped from humans approaching their nest from a distance and did not return for a long time (Table 3). From 73 pairs in which behaviours were recorded, 53% showed normal behaviour and 23% were shy and aggressive. Aggressive pairs successfully protected their nests from Arctic Foxes *Alopex lagopus* and camera-trap images showed that they lost only to a Wolverine *Gulo gulo*. Nests of "shy" pairs were predated mainly by gulls by *Larus* sp. and skuas *Stercorarius* sp. and the predation rate could have been affected by our visits to the plots, *i.e.* increased due to the shy swans escaping from the visitor.

Discussion

During this study the proportion of pairs that skipped reproduction, which would have been helpful to estimate breeding propensity, was not recorded. Annually 300–500 non- or failed-breeding Bewick's Swans were observed moulting in the Chaun Delta, yet it was unclear how many of these birds were local and how many had undertaken moult migrations to the delta. Among 18 birds captured during their moult on the Chaun Delta in 2016–2017 and equipped with GPS/GSM trackers, 17 returned to the Chaun Delta for the next summer; the remaining individual, a year-old

Table 3. Proportion and nest success of Bewick's Swan pairs with different nest protection behaviours (2013–2018), on the Chaun Delta, Chukotka, Russia. Differences in nest success between the three behavioural categories were statistically significant (one-way ANOVA; $F_{2,12} = 10.11$; $P = 0.003$).

Parameter	**Shy**		**Normal**		**Aggressive**	
	Mean	**(s.e.)**	**Mean**	**(s.e.)**	**Mean**	**(s.e)**
Proportion of swans showing behaviour	0.239	(0.021)	0.529	(0.007)	0.232	(0.007)
Apparent nest success	0.15	(0.04)	0.55	(0.07)	0.92	(0.04)

swan, dispersed to the lower Kolyma River. Thus site fidelity in the adult swans tagged was 100% and natal site fidelity was 80% (with 4 out of 5 young returning to the Chaun Delta at an age of one year old; L. Cao and D. Solovyeva *in litt.*). During the breeding period, all surviving adult swans returned to the Chaun Delta, where they could either breed or not breed. Nest density was negatively related to numbers in the total flyway population, based on the best fit model which included mid-January counts in Japan as the single most important factor affecting nest density on the Chaun Delta. In animals a certain nutritional threshold must be achieved in order to maintain full reproductive function (Nelson *et al.* 1992). In large-bodied herbivorous birds, density-dependent nutritional deficiencies of pre-breeding females affect production of young (Ross *et al.* 2017). We suggest that intraspecific competition for food at spring staging areas, such as Piltun Bay on the northern part of Sahkalin Island and/or the Kolyma River lowlands, served as a bottleneck for the reproduction of swans in this region. Seemingly the entire flyway population could be regulated in the same way, with lower productivity in the years of high winter numbers and increased productivity when the population has dropped, as found for the Northwest European Bewick's Swan population (Wood *et al.* 2016). Early spring temperatures also featured into the model of nest density, probably reflecting the effect of local spring conditions for swans arriving on their breeding grounds (Table 2).

The Chaun Delta produced between 32 and 781 newly-hatched cygnets per year in 2005–2018 (see Table 1 for Production). Relative to the entire flyway, the low numbers of cygnets produced here, reduced lately by unknown juvenile mortality, did not affect the total wintering population: regression of production *vs.* deviation of winter population between the previous and following January was not significant. Trends in the productivity of the entire flyway population are mostly unknown and a small segment such as the Chaun Delta cannot provide a complete

Table 4. Nest densities of Bewick's Swans across East Asia. * = *C. c. bewickii* x *C. c. columbianus* hybrid pairs.

Location	**Years**	**Size of study area (km^2)**	**Mean nest density (nests/km^2)**	**References**
Chaun Delta	1975–77 & 1980–84	200	0.20	Krechmar & Kondratiev 1986
Kolyma Delta	1984–1985	50	0.20	Krechmar *et al.* 1991
Kolyma Delta	1996	20	0.50	Andreev *et al.* 2015
Lena Delta	1993–2000	120	0.08	D. Solovyeva *in litt.*
Ekvyvatap River mouth, north Chukotka	2011	25	0.24*	Arkhipov *et al.* 2013
Ayon Island	2015	50	0.33	Solovyeva 2016
Chaun Delta	2002–2018	100	2.00	This study
Pevek city environs	2018	20	0.40	O. Prokopenko *in litt.*

picture, even though this site supports the highest known nest density in eastern Russia (Table 4). The latest data available on the nest density from the Kolyma Delta is from 1996, when the flyway population was beginning to increase (Andreev *et al.* 2015). We predict that the nest density at suitable habitats on the Kolyma Delta should be close the density observed on the Chaun Delta. Among the sites listed in Table 4, the Lena Delta belongs to a different flyway population of Bewick's Swan, the China-wintering population (L. Cao, A. Antonov and D. Solovyeva *in litt.*), whilst all other sites are used by birds thought to winter primarily in Japan. In recent years, high nest densities were reported elsewhere where Japanese birds breed: at the eastern margin of the Bewick's Swans' breeding range on the Ekvyvatap River mouth (179°W) where it overlaps with the Whistling Swan *C. columbianus columbianus* on the arctic tundra of Ayon Island (69.4°N), and in the anthropogenic landscape near the city of Pevek (69.5°N) where swan nesting was not reported prior to 2007 (Tomkovich 2007). We assume that the breeding habitats of the Japanese flyway population have been saturated with swans in the last decade, and so we suggest that the observed phenomena of swans building nests without laying eggs is an unusual behavioural response to high population numbers. This behaviour could be a result of conflict between reproduction instinct and either: 1) poor female body condition upon arrival at the breeding site, or 2) a reaction to overabundant conspecifics via direct visual contacts. It was described for rodents that an "*increase of local density was accompanied by the increase of* *glucocorticoids in blood of mature and immature individuals of both sexes that argues for the important role of hypothalamic-pituitary-adrenal axis in density dependent regulation*" (Novikov *et al.* 2012). It is unclear if this type of autoregulation acts in birds; however, we suggest this possibility. Clutch size varied independently of winter numbers and nest density and steadily declined over the years of our study, dropping further in seasons with cold springs (Table 2, Fig. 2). A similar decline in clutch size was found for a population of Lesser Snow Geese *Chen caerulescens caerulescens* at La Perouse Bay, Manitoba, Canada; however, clutch size was "*negatively correlated with the size of both the breeding colony and the total flyway population, both of which have increased significantly*" (Cooch *et al.* 1989). The decreased production of young of the Mute Swan *C. olor* in Finland was attributed to density-dependent effects on reproduction (Nummi & Saari 2003).

We lacked information about swan nest success and overall production during the years of rapid population growth in 2001–2004; however, those years were the last years in which significant fluctuations in rodent abundance were still evident on the Chaun Delta and we were able to estimate rodents to an abundance class of 3 or 4 out of a maximum of 4 (Table 1; Ehrich *et al.* in press). In later years rodent cycles declined to the lowest levels of abundance recorded. Rodents, and lemmings *Lemmus* sp. and *Dicrostonyx* sp. in particular, are well known for their population cycles creating boom and bust dynamics, which influence the whole vertebrate tundra food web including herbivorous waterfowl (Ims & Fuglei 2005; Nolet *et al.* 2013). However, in our study area swan nest success was not related to any tested variables including weather, swan population size, year, and rodent abundance.

Nest attendance behaviour in large white birds in open tundra is a function of the careful balance between the risk of nest predation for such a conspicuous bird and the needs of the parent to survive. The behaviour of a breeding pair of swans, or of one individual within a pair, in terms of aggressiveness can explain the relative success of their nest. In our study we found that differences in nest success were significantly associated with three behavioural categories. Evolutionary history has led to differences in the nest defence strategies for individuals within a population, such that individual swans could be defined as aggressive, normal or shy, and each of these different behavioural strategies could be the most successful in different ecological situations. Aggressive behaviour towards nest intruders such as Arctic Foxes and avian predators, resulting in higher nest success (productivity = 0.92 for pairs classed as aggressive in our study), is possible in the absence of larger predators such as wolverines, wolves and bears, and when people do not intend to harm the swan. Shy swans are most successful when predators are large and humans shoot at them during summer (*e.g.* subsistence hunting by indigenous people), while birds with normal behaviour may be most successful at an intermediate combination of these ecological scenarios. The high proportion of aggressive swans in our study area (23%), especially around the Chaun Field station, resulted from human protection and rare visits of wolverines; furthermore, wolves and bears were never reported on Ayopechan Island. In contrast to this, the one case of an aggressive swan known to have been killed, presumably by a Wolf *Canis lupus*, was on Ayon Island, a site with a high density of Brown Bears *Ursus arctos* and wolves (D. Solovyeva & S. Vartanyan, pers. obs.). The mean of the annual average nest success recorded for our study area of 0.42 ± 0.04 (range = 0.09–0.72; nest density = 2.0 nests/ km^2) was lower than the nest success reported from any other location: 0.61 ± 0.84 (range = 0.2–0.94; nest density 0.22 nests/ km^2) on Vaygach Island (Syroechkovsky 2013) and 0.55 for a nest density of 1.1 nests/km^2 on the Pechora delta (Rees 2006). The survival of the adults themselves seems to be more important for swans than the protection of their clutch (23% of shy pairs) at high population levels. A linear model of nest success against nest density for all three sites reached the X-axis at a nest density of 5 nests/km^2; however, it is difficult to draw firm conclusions from only three data points, so data from more study areas or including annual rather than averaged data for different sites is required for a more rigorous analysis.

We conclude that Bewick's Swans breeding in our study area on the Chaun Delta and potentially more widely are regulated by a reduced breeding propensity, with a decline in clutch size and low nesting success also associated with the behaviour of nesting pairs. These findings, and the relatively stable numbers recorded wintering in Japan during the 21st century, suggest that the sub-population breeding in Chukotka and wintering in Japan may be at equilibrium. Better information on movements of individual swans between breeding and wintering areas to identify sub-populations, on breeding parameters for swans from other parts of the Russian Arctic, and on trends in numbers for the whole of the Eastern Bewick's Swan population (*i.e.* coordination of counts of swans wintering in Japan, China and South Korea), however, are required to provide a full understanding of the dynamics and conservation status of Bewick's Swans in the East Asian flyway.

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Photograph: Bewick's Swan with newly-hatched cygnet, by Ben Sad.

