

Changing environmental conditions and structure of a breeding population of the threatened Lesser White-fronted Goose (*Anser erythropus* L.)

Juha A. Markkola* & Risto T. Karvonen

Juha Markkola Department of Ecology and Genetics, Faculty of Science, University of Oulu. P.O.Box 3000, FI-90014 University of Oulu, Finland. * Corresponding author's e-mail: jmarkkol@gmail.com

Risto Karvonen, Järvitie 34, FI-36110 Ruutana, Finland

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Migratory birds breeding at high latitudes face challenges in relation to timing of breeding vs. annual weather, climate change, and predator abundance. Hunting pressure along migration routes and wintering quarters forms an additional challenge. We studied population structure and interaction with environmental factors in a small population of threatened Lesser White-fronted Geese *Anser erythropus*, living in sub-arctic zone in Lapland in 1989–1996. Thereafter the population disappeared. The population comprised 2–15 breeding pairs plus 0–12 non-breeders, which left in June to moult elsewhere. 30 broods were observed (0–8 annually) with an average number of 2.9 goslings. Of the 3 satellite tagged plus 7 ringed geese at least 3 were shot and altogether 4 killed during the first year. Only 2 were seen alive next year or later. Laying started on average 4 June (21 May–13 June) and hatching took place 2 July (21 June–10 July) with an intra-seasonal clutch size decline. Variation in nesting initiation was not explained by local phenology, but instead by the date of staging peak in the last pre-breeding staging area 600 km south. Reproduction was affected negatively by cold spells and positively by the sum of daily effective temperatures by 5 July. Vole populations were low and a real cycle missing. No effect of reindeer abundance or human presence on reproduction could be found.



1. Introduction

Most Northern Hemisphere goose populations have grown significantly since World War II thanks to hunting regulation and increased access to high-quality food on farmland made available to the geese in winter (Cooke *et al.* 1995, Madsen *et al.* 1999). Exceptions include the Red-breasted Goose (*Branta ruficollis*), the Lesser White-fronted Goose (*Anser erythropus*), the Emperor Goose (*Anser canagicus*), the Swan Goose (*Anser*

cygnoides) and a number of other East Asian goose populations (IUCN 2018), and since the 1990's, the Taiga Bean Goose (*Anser fabalis fabalis*) (Marjakangas *et al.* 2015). The reasons for these declines are diverse and differ between populations, but over-harvesting and deterioration in the quality and extent of staging and wintering habitats are among the most common causes.

The Lesser White-fronted Goose (hereafter LWfG) breeds from Fennoscandia in the west to north-eastern Siberia between the northernmost

taiga and tundra ecoregions (Cramp & Simmons 1977). It is classified as globally vulnerable, and the world population was recently estimated as 24,000–40,000 individuals (IUCN 2018). Extensive surveys of NW and N Kazakhstan in autumn 2016 (Cuthbert *et al.* 2018) revealed as many as 34,250 (28,500–40,100) LWfG, at the most important staging areas for the western main population (NW Russia–Central Siberia). Together with the c. 10,000–20,000 birds of the Eastern Palearctic population (Yakutia–East Siberia) which winter in China (Wang *et al.* 2012, Wang 2019), the estimated world population is c. 40,000–50,000. Finally, the most endangered of the subpopulations breeds in the Nordic countries, where a population of *ca.* 10,000 individuals (Merikallio 1915) declined to 20 breeding pairs (Aarvak *et al.* 2009). Low mtDNA diversity and significantly different haplotype frequencies in Fennoscandian LWfG subpopulation warrant it to be considered as an own management unit (Ruokonen *et al.* 2004).

It has been considered that the most important causes for the declines in these populations are hunting and habitat loss on the staging and wintering areas (Jones *et al.* 2008). However, cyclic fluctuations in vole density contribute to delayed fluctuations in predator density, which have been shown to affect reproduction success in many arctic birds (e.g., Summers & Underhill 1986, Syroechkovskiy *et al.* 1991, Angerbjörn *et al.* 2001, Nolet *et al.* 2013). Synchronised years of high avian breeding success across species in rodent peak years, contrasting low reproductive success when these small mammals are scarce has been explained under by the hypothesis that predators in the latter years seek alternative prey (e.g., Lack 1954, Bêty *et al.* 2001), shifting to bird eggs and chicks when their primary prey is scarce (although predators may also respond to low mammal densities by migration, Reiter 2006).

Goose breeding success can also be affected by tail- and headwinds during the spring migration (Ebbinge 1989; Syroechkovskiy *et al.* 1991), while food quality and abundance as well as weather, can influence breeding success on the nesting grounds (Baranyuk & Litvin 1989). Low temperatures and late snow-melt may cause large numbers of geese to abandon their breeding attempts in such years (Barry 1962, Gauthier *et al.*

1996, Skinner *et al.* 1998, Bêty *et al.* 2001). Arctic geese are somewhat buffered against local conditions, since they gather energy reserves during their wintering and spring staging (Ebbinge *et al.* 1982; Davies & Cooke 1983). Females of some species lay and incubate a clutch relying largely on body stores accumulated prior to arrival to nesting areas (Thompson & Raveling 1987), while others like the LWfG use considerable time in feeding in breeding areas (own observations).

Conservation efforts to safeguard small and declining population of LWfG began in Sweden, Finland and Norway in 1970s and 1980s based on local initiatives, later supported by WWF, Bird-Life International, since 1995 by IWRB (later Wetlands International) and latterly by the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA). The LWfG has also been the subject of three completed EU Life projects.

Work undertaken has included population studies, improving conservation legislation and hunting regulations in extensive areas of Eurasia, management of migration staging and wintering habitats, and compilation of national and international action plans (Jones *et al.* 2008, Tolvanen *et al.* 2009, 2015, Vougioukalou *et al.* 2017). The long-term investment of conservation effort seems recently to have turned the tiny Fennoscandian population from declining population trends to growth. In Greece, where the majority of the Fennoscandian population winters, their numbers increased from 53 to 144 between 2011 and 2016 (AEWA 2017, Demertzi *et al.* 2017), and on the Bothnian Bay coast, Finland from a minimum of 6 in 2004 to 124 in 2017 (R. Karvonen & J. Markkola unpubl.).

The study we report here relates to the discoveries from large-scale field surveys started in 1984 by the LWfG working group of WWF Finland (Tolvanen *et al.* 2015, Ympäristöministeriö 2009). These surveys found a breeding population of LWfG in Finnish Lapland in 1989, which we monitored and studied until the geese disappeared in 1998, although surveys were continued annually in the former breeding areas during 1999–2002, 2005–2009 and again in 2012, 2015, 2016 and 2018 (Supplementary material Table 1).

The aim of this study was to try to assess the most important ecological and environmental fac-

tors potentially affecting the reproduction success of LWfG in a small population. We hypothesized that the breeding success and population size of LWfG could be related to (i) the pattern of alternative prey dynamics shown by local predator populations, (ii) annual variation in weather conditions and phenology, and (iii) disturbance caused by reindeer herding and human activities. Knowledge of these factors and how they affect the geese is important when managing conservation interventions for such an endangered species in the most effective way.

2. Material and methods

2.1. Study area

The data were collected in subarctic Finnish Lapland c. 69° 30'–70° N in an area of 250 km² in 1989–1996 (and 1997–2002, 2005–2009, 2012, 2015, 2016 and 2018 with no breeding, Supplementary material, Table 1). The area is oroarctic, tundra-like with gently sloping terrain and low mountains, covered in treeless heat, subject to heavy grazing pressure by domestic reindeer, with numerous mires including rich fens and many lakes and ponds. Birch (*Betula pubescens ssp. tortuosa*) grow in sheltered, southerly exposed steeper slopes, and along the tops of eskers and hills in the southernmost and less elevated parts of the area.

The thermal spring (defined by daily mean temperatures between 0°C and 10°C, Ilmatieteen laitos 2019) began during 11–26 April in 1989–1994, but as late as 16–18 May in 1995–1996. Most snow disappeared during the first half of June. Large lakes were free of ice on average 14 (7–28) June.

2.2. Goose surveys

The survey area was initially chosen based on historical observations prior to 1988, which included four sightings from 1972 onwards, one of 6 individuals, and an obscure description that “people have seen LWfG in the wilderness in summer 1978”, and two observations of 1–2 LWfG in 1986 and 1988, some of which indicated breeding. In 1988, we found 6 LWfG in a minor part of the total

area surveyed and we confirmed breeding the next year.

The entire area was surveyed systematically from 1989 onwards until the population disappeared in 1997 and in many years later in the hope of establishing recolonization (Supplementary material Table 1).

We mapped breeding pairs and other LWfG during late May–June and scanned broods and moulting geese without goslings in July–August. Nesting pairs were widely scattered, associated with the shores of lakes or far from lakes on treeless heaths. After hatching, they moved their broods to ponds and lakes, sometimes rivers and often aggregated into larger family groups. In early summer, practically all ponds, shores of lakes, rivers and brooks and bogs and fens were scanned with binoculars and spotting scopes from hillsides and other good viewing points. The effort invested depended on landscape heterogeneity: in complex topography, one observer walked 37 km over three days to complete an inventory of 25 km². More even areas could be covered by walking 20 km per 25 km². Early summer surveys required 23–30 days plus additional time used in special studies (e.g., trapping voles).

During clear weather, surveys were mostly carried out at night (because the sun is over horizon 24 h per day) to avoid heat haze that hampers searching for birds with a telescope, while in cloudy conditions surveys could take place in any time.

Observed LWfG were classified into adult pairs, males or females, unsexed adults, 2nd calendar-year birds or unaged (Table 1) based on the criteria described in Øien *et al.* (1999). Birds were also classified as breeders or non-breeders according to their behavior. Near the nest, LWfG (usually only males) gave alarm displays in response to predators or human observers. Early season pairs often grazed in early melting fens. Laying females could be identified by their extreme rounded abdomen profiles. LWfG females take feeding breaks during incubation, when they can be observed flying to grazing sites with their mates. In good feeding areas, breeding LWfG form groups with other breeders and immatures (2–3 calendar-year birds) and may associate with Bean Geese (*Anser fabalis*).

To avoid disturbance and increased nest preda-

Table 1. Population history of LWfG in numbers during 1988–1997 in the study area. See details in Material and Methods.

Year	Males adults	Females birds	Unsexed birds	2cy	Unaged	Indiv tot max	Ind final estimate	Potential breed pairs
1988	1	1	2	0	6	8	8	?
1989	9	5	10	0	0	24	23	12
1990	12	8	13	6	0	39	35	10
1991	13	9	16	6	1	45	41	15
1992	13	13	3	3	1	33	33	15
1993	9	5	0	1	0	15	15	9
1994	7	2	6	0	0	15	15	9
1995	1	0	1	0	0	2	1	2
1996	2	0	3	0	0	5	5	2
1997	0	0	1	0	0	1	1	0
Mean 89–96	–	–	–	–	–	–	–	9.3

Year	Pairs with breed effort min	Molt ad without goslings	Broods seen	Addit brood tracks	Broods max	Goslings tot	Goslings per brood	Pull per pair
1988	–	–	–	–	–	–	–	–
1989	12	0	8	0	8	31	3.99	2.58
1990	10	a1,a1	6	3	9	16	2.67	1.60
1991	15	a4,a2	7	4	11	19	2.71	1.27
1992	9	a1,a2	3	1	4	6	2.00	0.40
1993	5	0	0	0	0	0	–	0.00
1994	5	a2	4	0	4	9	2.25	1.00
1995	2	0	2	0	2	7	3.50	3.50
1996	0	0	0	0	0	0	–	0.00
1997	0	–	0	0	0	0	–	–
Mean 89–96	7.3	1.4	3.8	1.0	4.8	11.0	2.93	1.29

tion, we did not search for nests, but measured subsequent reproductive success according to numbers of goslings later produced. In Table 1 “Max count” is the possible maximum number of all >1cy LWfG individuals in a given year and “Final estimate” our estimate of the most probable total number present. “Potential breeding pairs” were counted according to adult pairs seen, alarming or guarding males (or rarely single females) and half of all unsexed adults (+ 1 if the total number was odd). “Min pairs” represents the (minimum) number of pairs or single individuals behaving as breeders. In Table 1, “Moulting ads without goslings”, a1 is one bird in one group, a4 means 4 birds in one group etc. “Add brood tracks” signifies additional broods whose footprints and faeces were detected in areas where other broods detected by scanning could not have visited, because the distance to the nearest seen brood was long (≥ 3 km) and there was no water connection between

the observation points. “Max broods” is the sum of scanned broods and additional broods according to tracks. Gosling number was related to scanned broods (“goslings per brood” in Table 1) and potentially breeding pairs (“Pull per pair”). Although we sometimes had a “guestimate” of the number of goslings in “add broods” according to footprints, we did not include these in the total number of goslings.

After hatching, broods moved to near-by ponds and lakes, and sometimes rivers. During day-time, broods stayed near the shoreline, but at night, broods could be seen swimming, or the head and neck of the watching parent (typically male) could be picked out at a distance. Broods were scanned from elevated vantage points on hillsides using a telescope. After watching 0.5–1 hours without observation the observer visited the shore to search for footprints and moulted feathers or hiding broods.

The size of goslings was assigned to 7 size classes (1/10, 1/4, 1/3, 1/2, 2/3, 3/4, 5/6 of adult size, based on breast-to-tail length) in relation to accompanying adults. Age was estimated using a growth curve constructed on the principles presented by Cooch *et al.* (1999). In the case of LWfG, age 0 days = body size 1/10 and age 38 days = 3/4, i.e., body size at fledgling (Markkola *et al.* 1998). For the first weeks, the correlation was linear, becoming asymptotic later, but we mainly used the linear part; the average inaccuracy of this classification is ± 3 days per class.

Hatching date was back-calculated by subtracting the age (midpoint of the age class) of the brood from the date of the scanning event (Supplementary material Table 2). To calculate laying dates, we assumed an incubation period of 26 days and daily laying interval (Markkola *et al.* 1998). We assessed seasonal clutch size variation in laying and hatching.

Two males were satellite-tagged and ringed (4 August 1994, 30 July 1995), while their mates and the 6 goslings (1 + 5) from these two broods were ringed with metal and collar color rings only during the moult of parents and before fledging of chicks. In 1994, we used a Telonics satellite transmitter (PTT) with the duty cycle of 6 h on / 96 off, and in 1995 a Toyocom PTT with the duty cycle 8 h on / 168 off and Argos research satellite services (Argos, Inc. 1992).

Satellite tracking revealed a previously unknown autumn staging place of the study population in Varangerfjord, on the Norwegian coast in 1994, so this area was surveyed in 1995–2008, 2013 and 2017–2019 (Supplementary material Table 3). A spring staging place of a small number of LWfG probably belonging to the study population was found in the Teno-Tana River valley originally in the 1980's and surveyed in 1998–1999 and 2001–2019 (Supplementary material Table 1). We surveyed this area to confirm whether the studied breeding population really had gone extinct or just shifted their distribution.

2.3. Effect of environmental variables

We wished to test a range of hypotheses as follows. The reproductive success of LWfG is high in rodent (variable 1) peak years, when a concurrent

high breeding density of birds like waders, the Willow Grouse and the Lapland Bunting (2) offers alternative prey for the main nest predator, the Red Fox (3). The success is further promoted by early and warm summers (4–8), and limited by large raptors (9), reindeer (10), other goose species (11) and human disturbance (12). Annual values of all variables are listed in Supplementary material Table 4.

The variables included in the hypothesis were calculated as follows:

- 1) Abundance of alternative prey for goose nest predators (mainly the Red Fox), was first estimated as the biomass of small mammals caught in standardised snap-traps (g / km^2). We used 160 traps per day and night annually. In years without trapping (1989–1991), abundance of mammals was estimated translating the number of their predators to mammal densities and biomass. The R^2 of small mammal biomass vs. predator density was 0.586 (as also found by in Korpimäki 1984, 0.598). Because of the wide confidence limits associated with these estimates, rather than use inaccurate density estimates, we divided seasons into poor (1) or very poor (0) rodent years.
- 2) Egg biomass. Bird densities (pairs / km^2) were measured using the line transect census method (Järvinen & Väisänen 1976; Järvinen *et al.* 1991) and converted to egg biomass (g / km^2), using clutch size and egg biomass data by Cramp *et al.* (1983, 1984, 1985, 1988, 1994). Of the approximately 75 species observed, seven were most numerous, Lapland Bunting (*Calcarius lapponicus*), Meadow Pipit (*Anthus pratensis*), Golden Plover (*Pluvialis apricaria*), Willow Grouse (*Lagopus lagopus*), Ruff (*Calidris pugnax*), Long-tailed Skua (*Stercorarius longicaudus*) and Long-tailed Duck (*Clangula hyemalis*) (Supplementary material Table 5). These seven species plus Rock Ptarmigan (*Lagopus muta*), a quite large and numerous species with large clutches, were included in the next step of estimating their breeding density (pairs / km^2) and egg biomass. In a test year (1993), these eight species contributed 83% of all breeding birds and an even larger proportion of egg biomass.

For 1989, when we failed to census Meadow Pipits and Lapland Buntings, we used the average densities from the rest of the study period.

- 3) Abundance of the supposed main LWfG nest predator, the Red Fox (individuals / survey km).
- 4) Staging phenology in terms of date (of May) when the peak staging of LWfG occurred on the Bothnian Bay coast (Markkola 2010).
- 5) The sum of effective temperatures (daily average degrees above +5°C, Ilmatieteen laitos 1989–1996) by 5 July (3 days after the average hatching date, table 3). This sum by 27 May and 10 June were also used to correlate phenology and breeding schedule.
- 6) Timing of ice melting in the same large lake annually. Day in June when ice disappeared.
- 7) Cold spells. Occurrence (yes or no) of cold spells (period of frost and heavy snowfall) in June.
- 8) Birch phenology. Emergence (budding, opening) of mountain birch leaves in the same forest near the base camp (date in June).
- 9) Abundance of avian goose predators. Raptor densities (pairs / km²) including White-tailed Eagle (*Haliaeetus albicilla*), Golden Eagle (*Aquila chrysaetos*) and Gyr Falcon (*Falco rusticolus*) measured using the line transect census method (Järvinen & Väisänen 1976; Järvinen *et al.* 1991; Väisänen *et al.* 1998).
- 10) Abundance of reindeer by 5 July (reindeer units / observing km; adult = 1, calf = 1 / 3 unit, sum of daily moving averages).
- 11) Abundance of Bean Goose (*Anser fabalis*), a potential competitor (e.g., Kristiansen & Jarret 2002) was measured by similar methods as LWfG.
- 12) Human disturbance. Intensity of human interference caused by hikers, herdsman (presence in man-days according to a hiking cabin guest book located in the area and assuming that one visitor stayed one day) and ourselves.

2.4. Statistical analyses

Phenological variables (staging peak date, May average temperatures, beginning of thermal summer, sum of effective temperatures at Kevo,) were associated with onset of breeding using Pearson correlation analysis. To test seasonal clutch size

variation we used generalized linear mixed models (function “*glmer*” in package “*lme4*”, R Development Core Team 2016), where number of goslings in broods was the response variable and date of the laying of the first egg the explanatory variable. The dates were year-standardized determining the average as zero and the standard deviation to be 1. Possible variation in gosling numbers between years was considered by assigning year as a random variable. As the response variable was a count variable, we assumed a Poisson distribution for the dependent variable. Broods with known age ($n = 26$, Supplementary material Table 2) were used as sample units.

The phenological and ecological factors affecting gosling production of LWfG (measured as the number of goslings per brood) were studied using linear mixed model analysis by function *gamlss* (package “*gamlss*”, R Development Core Team 2016), with negative binomial error distribution (*NBII*) as this fitted better than Poisson distribution. The number of goslings in a brood was the response variable, phenological and ecological factors were explanatory variables and the year of observation a random variable. Sample unit was a brood, also including those “broods” with 0 goslings, i.e., potentially breeding pairs with no goslings (Supplementary material Table 4, column “LWfG pair #”) were included in sample units. The sample size was 74 for broods and phenological and ecological factors (the latter two having 8 different values).

Some explaining factors correlated with each other, and thus *VIF*-analyses were applied to test multicollinearity among them. The problematic variables (*VIF* > 2) were dropped from the further analyses. These included biomass of parent prey (of foxes) birds, biomass of parents plus eggs and biomass of all alternative prey (birds, eggs, small mammals).

3. Results

3.1. Lesser White-fronted Goose population history in the study area

The highest numbers of breeding pairs and the highest breeding success were observed in the beginning of the period, in 1991 and 1989, respec-

Table 2. Number of goslings in scanned broods.

N of goslings in broods	Number of broods						Total
	1989	1990	1991	1992	1994	1995	
1	–	1	1	2	2	–	6
2	–	2	3	–	–	1	6
3	2	1	1	–	1	–	5
4	5	2	1	1	1	–	10
5	1	–	1	–	–	1	3
Total	8	6	7	3	4	2	30

Table 3. Laying initiation and hatching of the Lesser white-fronted Goose in 1989–1995. Dates indicate annual initiation and hatching of the average, the first and the last clutches.

	1989	1990	1991	1992	1994	1995	All
Laying initiation							
Mean	Jun 5	Jun 11	Jun 2	Jun 5	May 30	May 24	Jun 4
First	Jun 2	Jun 10	May 28	Jun 3	May 27	May 21	May 21
Last	Jun 7	Jun 13	Jun 9	Jun 8	Jun 1	May 27	Jun 13
Hatching							
Mean	Jul 5	Jul 10	Jul 1	Jul 3	Jun 27	Jun 26	Jul 2
First	Jul 3	Jul 10	Jun 27	Jul 2	Jun 23	Jun 21	Jun 21
Last	Jul 6	Jul 10	Jul 8	Jul 5	Jun 30	Jun 24	Jul 10
N =	6	4	6	4	4	2	26

tively (Table 1). The average density of breeding pairs in the 250 km² study area in 1989–1996 was 0.03 (0.01–0.06) pairs / km².

In most years, moulting adult LWfG without nestlings were observed in the study area (Table 1). These had probably lost their nest or chicks late in the season. Fennoscandian LWfG abandoning a breeding attempt early in the season seem to migrate to moult as far east as to Taimyr Peninsula, Central Siberia, Russia (Øien *et al.* 2009). All immature LWfG disappeared from the study area and were never seen after 14 June. The number of moulting adults without goslings was 1.4 (0–6) per year. The average number of broods seen was 3.8 (0–8) and that of unseen broods (based on track counts) 1.0 (0–4) per year.

Only one nest was found before hatching (three hatched ones later) by accident in 4th June 1990 and contained 4 eggs. Of pairs showing breeding

behaviour in early summer, 27–67% (33–90% if unseen broods revealed by tracks are included) bred successfully in years with a moderate number of birds present. The proportion of successful breeding was 0–100% annually, and the mean 43.1% (51%). The total number of goslings produced was 0–31, on average 11 per year, although this does not include the number of unseen broods. The mean annual number of goslings per brood was 2.93 (2.0–3.99) for all years. Altogether 30 broods and 88 goslings were seen (Table 1, 2).

No broods were found in 1993 and 1996. In 1993 no LWfG were seen during July–August and most of them left the area to moult elsewhere. Fresh tracks of 3–4 LWfG were found 19 July 1993, and these probably moulted in this area. In 1997, only a single male was observed. However, in the autumnal staging place revealed by satellite tracking in 1994 at Varangerfjord, Norway, 10–50

Table 4. The correlations between timing of breeding (estimated onset of egg-laying) and local phenological variables and staging time in 1989–1996 ($n = 6$). The significances were revised using Bonferroni correction.

Phenological variable	First egg of season r (p)	Average 1 st egg r (p)
May Temperature	0.387 (1.000)	0.428 (1.000)
Effective Temperature sum 27.5.	0.014 (1.000)	0.054 (1.000)
Effective Temperature sum 10.6.	0.014 (1.000)	0.001 (1.000)
Beginning of Thermal spring	-0.852 (0.031)*	-0.873 (0.023)*
Peak staging at Bothnian Bay	0.833 (0.038)*	0.891 (0.017)*

LWfG were still seen annually 1995–1999, among them 5–18 goslings. In 2000–2008 and 2013 the LWfG were absent also here, but two individuals were again seen in 2017 and one in 2018 (Ruokolainen *et al.* 1999, Tolvanen 2000, Kaartinen 2001, Kaartinen & Pynnönen 2004, Sulkava *et al.* 2009, Supplementary material Table 3).

3.2. Timing of reproduction

In the six study years with successful breeding, the estimated first egg laying date was on average 4 June (21 May–13 June \pm 3 days), and hatching took place 2–3 July (21 June–10 July \pm 3 days) (Table 3). The local phenological variables (May

average temperatures, sum of effective temperatures by 27 May and 10 June) did not correlate with timing of breeding (all $p > 0.05$, Table 4), i.e., LWfG seemed to start breeding independently of local weather conditions. In contrast to predictions, timing of breeding was negatively correlated with the beginning of the thermal spring (Table 4), although this is likely a statistical artifact. The timing of breeding correlated positively only with timing of LWfG spring migration staging on Bothian Bay coast (Table 4). The number of goslings was lower in late breeders as indicated by an intra-seasonal decline in gosling numbers: (estimate for timing = -0.259 , $z = -2.006$, $p = 0.0449$, Fig. 1).

Table 5. Phenological and ecological factors affecting the per-brood gosling production of LWfG, as revealed by linear mixed model analysis by using function GAMLSS (in program R), with negative binomial error distribution (NBII). Number of breeding pairs was included as a controlling variable of decreasing population size. All explanatory variables were standardized (Mean = 0, sd = 1, indicated with “z”). Small mammal abundance was estimated as high or moderate (1) or low (0).

Variables included	Estimate	Std.Error	t-value	Pr(> t)
Intercept	-0.1411	0.2160	-0.653	0.5157
zTemperature Sum (by 5 July)	0.6912	0.1721	4.018	0.0001 ***
zCold Spell in June (0/1)	-0.6482	0.2660	-2.437	0.0174 *
zBreeding pairs	-0.2596	0.2084	-1.246	0.2169
Explanatory variables excluded				
zSmall mammal abundance (0/1)	-0.0270	0.2296	-0.118	0.9066
zBean Goose abundance	-0.1185	0.2061	-0.575	0.5674
zBirch phenology	-0.3937	0.3506	-1.123	0.2653
zEgg biomass	0.0762	0.1603	0.475	0.6360
zTiming of ice melting	-0.4434	0.3226	-1.374	0.1737
zRaptor abundance	0.4169	0.5061	0.824	0.4130
zFox abundance	0.1693	0.3011	0.562	0.5758
zReindeer disturbance	0.8031	0.9556	0.840	0.4036
zStaging phenology	-0.0241	0.2063	-0.117	0.9074
zHuman disturbance	-0.0961	0.2348	-0.409	0.6836

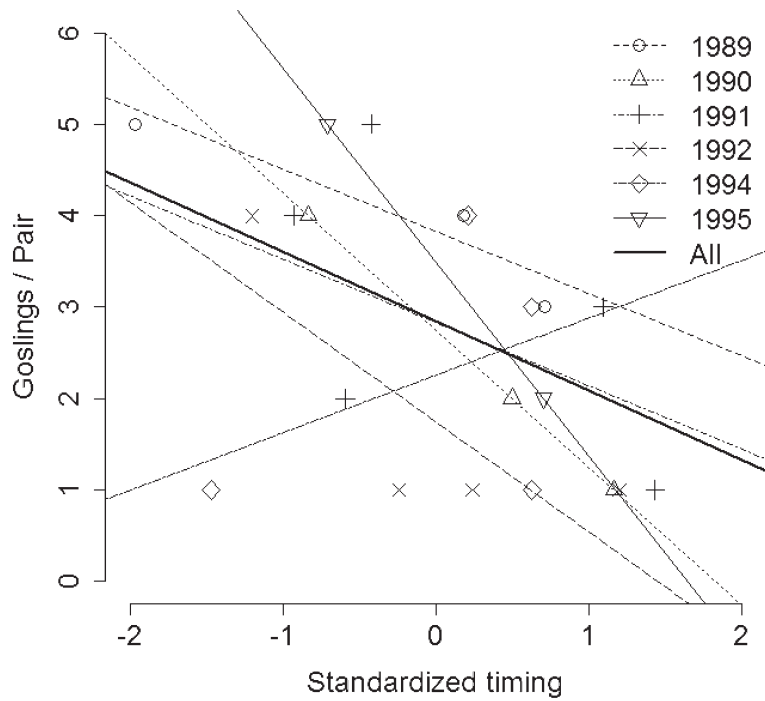


Fig. 1. Seasonal decline in the gosling production of the Lesser White-fronted Goose in 1989–1995. Estimated egg laying dates were year-standardized (Mean = 0, SD = 1). N = 6.

3.3. Phenology and reproductive success

LWfG reproduction rate was strongly affected by the effective temperature sum by 5 July (zTemperature Sum in Table 5) and occurrence of cold spells in June (Table 5, Fig. 2, 3). The higher the temperature sum, the greater the reproductive success. Very poor reproduction rate occurred in years with cold spells (as in 1992 and 1996). Population size as a covariate did not significantly explain the variation in gosling production per pair when temperature sum and cold spell (0 / 1) were included in the model (Table 5).

The mean May and June temperatures and their sum for the time period as well as their deviation from the average in 1963–2014 at Kevo (Ilmatieteen laitos 2015) are presented in Supplementary material Table 6. The average sum (May + June temperature) of the whole period was 13.3 °C. Six out of eight of the study years were below it – and the two following years 1997, 1998, too.

The year 1996 was the third coldest and 1993 the sixth coldest of all. The good reproduction year 1989 was the second warmest and the warm fore-summer of the year 1992, which was interrupted by a cold spell, was the seventh warmest in 52

years. Timing of staging on Bothnian Bay coast had no effect on reproductive output (zStaging phenology in Table 5).

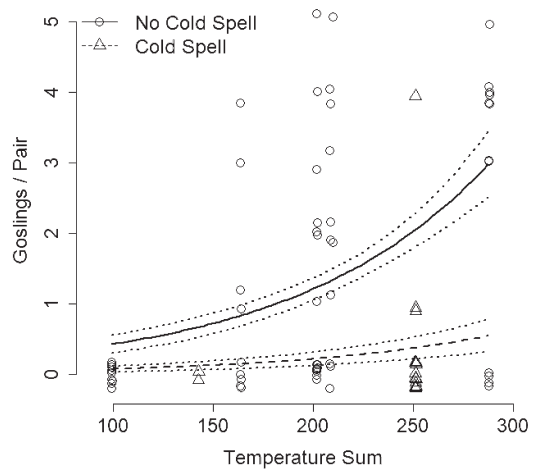


Fig. 2. The effects of effective temperature sum (to 5 July) and occurrence of cold spells in June on Lesser White-fronted Goose gosling production. Dotted lines represent ± SE. For statistics, see Table 5.

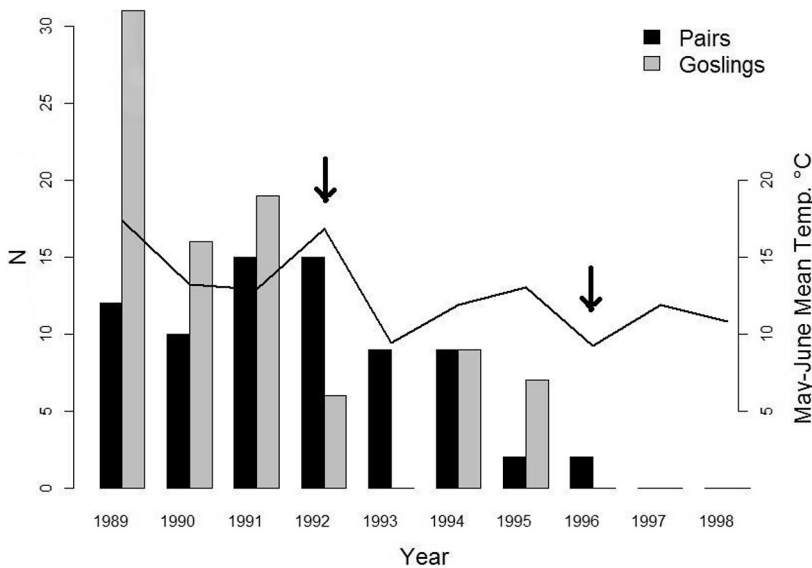


Fig. 3. Number of potentially breeding pairs, goslings and sum of average May + June temperatures in 1989–1998. Timing of cold spells in June is indicated with arrows.

3.4. Predators

Avian predators occurred in low densities and had no significant effect on LWfG gosling production ($zRaptor$, Table 5). During the first 5 years 1989–1993, the abundance of Red Foxes seemed to have a strong negative correlation with the number of goslings calculated as absolute or relative (goslings' number related to pairs indicating breeding) numbers ($r = -0.96$ and -0.94 , both $p < 0.01$). However, the overall pattern remained non-significant ($zFox$ abundance, Table 5) as the following three years disrupted the pattern. Most foxes were non-breeders and seemed to follow reindeer flocks to the area in early summer. The numbers of reindeer and foxes did not, however, correlate significantly ($r = 0.430$, $p = 0.287$, $n = 8$).

3.5. Other factors potentially affecting reproduction rate

The number of reindeer varied strongly in the study area, but was unrelated to LWfG reproduction ($zReindeer$ disturbance in Table 5). Human presence had no significant effect, either ($zHuman$ disturbance in Table 5). We expected that the abundance of small mammals could be related to predation and thus reproduction rate of LWfG. However, there was no significant relationship of small mammal numbers to LWfG reproduction

($zSmall\ mammal\ abundance$ in Table 5). All trapped species, Grey-sided Vole (*Myodes rufocanus*, 63% of individuals), Northern Red-backed Vole (*M. rutilus*, 27%) and Common Shrew (*Sorex araneus*, 10%) were extremely sparse and the total biomass of them was throughout the entire study period only 0–3.2 kg / km². Similarly the biomass of bird eggs ($zEgg\ biomass$ in Table 5) was not related to LWfG breeding success.

3.6. Observations of mortality during migration and wintering

Satellite locations, ringing-recoveries and re-sightings of LWfG tagged in the study area were received from N coast of Norway, NW Russia, Kazakhstan and the Azov Sea area in S Russia, but not from sites along what is now recognized as the western fly-way, i.e., Fennoscandia-Hungary-Greece (Lahti & Markkola 1995; Anonymous 1998; Lorentsen *et. al* 1998, Tolvanen *et al.* 2009). Of the 10 ringed and tagged individuals, at least three were shot and four killed during the following year (Table 6). The transmitter of the male tagged in 1995 stopped functioning at the same time as its two goslings were shot in Kazakhstan, so in all likelihood was probably also shot. This and those individuals known to have been killed comprise half of all tagged individuals. Three of the remaining geese were never seen subse-

Table 6. First year survival and mortality observations of LWfG tagged in 1994 and 1995.

1 year after tagging	1994			1995			All
	Ad male	Ad female	Gosling	Ad male	Ad female	Gosling	
Reported shot	–	–	1	–	–	2	3
Killed by a bird of prey	1	–	–	–	–	–	1
Probably shot	–	–	–	1	–	–	1
Fate not known	–	1	–	–	–	2	3
Seen alive next year or later	–	–	–	–	1	1	2
All	1	1	1	1	1	5	10

quently. Only two others were definitely seen later, an adult female ringed in 1995 (many times during 1996–1999, Tolvanen 2000, Supplementary material Table 3) and its gosling. These observations underline the very heavy hunting pressure on LWfG along its migration routes in the 1990s.

4. Discussion

At the time of its discovery, the numbers of breeding Lesser White-fronted Geese in our study were the most known in Fennoscandia. In 1989, when *ca* 12 pairs were seen and at least 8 of them were confirmed to breed, counts at spring-time staging sites indicated that the total number of LWfG breeding in Norway, Finland and Sweden – excluding the reintroduced stock in Sweden was only 30 pairs (e.g., Markkola 1992).

The average brood size (2.93) of these geese was comparable to 3.1 reported from Porsanger Fjord, N Norway in 1994–2008 (Aarvak & Øien 2009). Similar brood sizes have been reported from the main autumn staging area of the European-Central Siberian population in NW Kazakhstan: 2.8 goslings per brood ($n = 22$) in October 1999, when shooting was still legal (Tolvanen *et al.* 2009). At Dongting Lake, China, the main wintering quarter of the East Asian population, the average brood size in early February 1999 was 2.9 ($n = 154$) (Markkola *et al.* 2000). In Norway, the average brood size increased from 3.04 to 3.37, when red fox culling took place (2008–2016) in breeding areas (Aarvak *et al.* 2017).

The number of goslings per potentially breeding pairs was 1.29 in our material vs. 1.48 at

Porsangerfjord in 1994–2008 (Aarvak & Øien 2009). The figures were 1.55 before and 1.57 during culling, when years 1998–2016 were included (Marolla *et al.* 2019). In our study area, 40.5% of potentially breeding pairs reproduced compared with 46.1% before and 47.3% after fox culling in Norway. The authors, however, emphasize that the increase after fox culling may be a consequence of phase differences in rodent cycles (Aarvak *et al.* 2017). Indeed, in the more comprehensive study the proportion of breeding pairs did not increase during culling (0.49 vs. 0.47) (Marolla *et al.* 2019).

Reproduction decreased towards the end of our study period before the population disappeared. However, the drop in reproductive rate is unlikely to be the only factor to explain the disappearance of these geese, because the sudden drop in adult numbers happened between 1994 and 1995, likely due to high mortality (most likely hunting) during migration and in winter. Did the LWfG respond to deterioration of environmental conditions by dispersal to breed elsewhere? Poor breeding success may have triggered this movement elsewhere. Goose breeding groups are held together by site fidelity and social bonding, but once conditions change, the decision to disperse may potentially result in dispersal of the entire breeding group. This, in addition to high mortality, might explain the sudden drop in numbers.

Indeed, many LWfG were seen in autumn on the Norwegian coast until 1999 (Supplementary material Table 3). As revealed by satellite locations in 1994, the studied LWfG population moved to Varangerfjord after breeding before autumn migration (e.g., Lahti & Markkola 1995, Tolvanen *et al.*

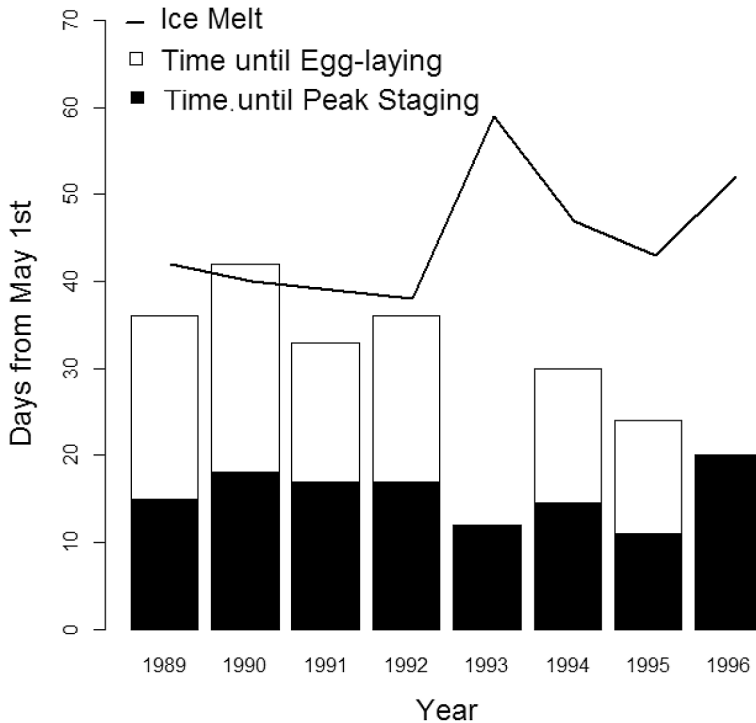


Fig. 4. Timing of maximum numbers of Lesser White-fronted Geese on Bothnian Bay coast during spring staging, mean initiation of egg laying and ice melt in the breeding area.

al. 1998). By the time that area was surveyed for the first time in 1995, LWfG in our study area had already declined drastically (to two breeding pairs). Despite this, up to 50 LWfG were seen together in the fjord, including the brood tagged in the study area three weeks earlier (Supplementary material Table 3). In 1996, when no breeding birds were seen in Finland 13 LWfG were present at Varangerfjord, among them the “Finnish” female again with the only brood. In 1997, 40–49 LWfG were seen, among them the same female and its 2 goslings. In 1998, 15 adults and 6 goslings were seen. In 1999, 10 LWfG were seen, but later none despite surveys in 2000–2008, 2013 and 2017–2019 (Supplementary material Table 3).

It seems that LWfG that had formerly occupied the Finnish breeding area moved to breed closer to the coast following declining reproduction in 1989–1995 and the late summers of 1996–1999, but in 2000 they had also disappeared from Varangerfjord. It seems likely that 11–15 probably breeding pairs (i.e., the same number that bred in the study area in good years), were present at Varangerfjord in 1995 and 1997 but only 4 in 1996, 7–8 in 1998 and only 3 or less in 1999. The

number of goslings per pair declined from 2.4 of 1995 to 0.8–1.33 in later years (data not shown). The pattern was the same as on Finnish side: decline in reproductive success, followed by disappearance.

One explanation could be the possible use of the more eastern, longer and more dangerous migration route via Russia and Kazakhstan by this eastern sub-population, as the more western Norwegian population survived. Indeed, all of the few distant recoveries and satellite locations of tagged birds support this: these came from Kazakhstan and Azov Sea, i.e., along the eastern fly-way (Anonymous 1998). Later, tracking and ringing recoveries showed that successful breeders from the remaining western population migrate straight through Eastern Europe to Greece, but unsuccessful birds move eastwards to moult in Siberia and in autumn via Kazakhstan to Greece (Øien *et al.* 2009).

Low effective temperatures and cold spells led to poor reproduction. Similarly, reproduction of Greenland White-fronted Goose (*Anser albifrons flavirostris*) was positively correlated with summer temperatures up to 1990’s (Boyd 1982,

Zöckler & Lysenko 2000, Boyd & Fox 2008), but later increased spring temperatures led to increased precipitation, which delayed snow melt and decreased reproduction (Boyd & Fox 2008). Conditions in our study area became colder during the study (Supplementary material Table 6) and the time difference between the staging peak of spring migration and onset of nesting grew longer. Similarly, the delay between migration staging peak and ice melting of lakes in breeding areas increased (Fig. 4). Most probably several successive cold springs represented stochastic variation in contrast to the general trend of global warming (IPCC 2014). Although warming has been demonstrated e.g., by Kivinen *et al.* (2017) in Northern Fennoscandia, there are surprisingly large temporal and regional differences in relation to the impact of phenology even between quite near-by areas, so for instance, Marolla *et al.* (2019) did not find any effect of phenology on LWfG reproduction success.

Increased predation pressure or at least presence of foxes might also explain the drop in reproductive success, though no significant effect was found. We assume the Red Fox to be the main nest predator based on intensive antipredator behavior that it elicits in LWfG. Subsequent studies have shown that culling of Red Fox allows more adult LWfG, including unsuccessful breeders who have lost their chicks during later phases of the brood rearing period, to moult in the breeding area. As a result, they choose to take the shorter and safer western autumn migration route instead of moving to Central Siberia to moult (Øien & Aarvak 2009, Tolvanen *et al.* 2009; Aarvak *et al.* 2017, Marolla *et al.* 2019).

The lack of a positive effect of abundance of alternative prey on LWfG reproduction rate was not expected and differed from the situation further west in Finnmark, Norway 1998–2016 (Marolla *et al.* 2019), but is understandable because of the constant low abundance of rodents in our area. At Kilpisjärvi, NW Finnish Lapland, the biomass of the commonest rodent, Grey-sided Vole, can be 200 kg / km² in peak years, while Root Vole (*Microtus oeconomus*) reaches 100 kg / km², and even the Northern Red-backed Vole 10 kg / km² (Tast *et al.* 2010). The biomass of the latter alone is three times higher than we estimated for all small mammals in the “peak” year of 1990 (3.2 kg /

km²). At Kilpisjärvi, rodent cycles had an effect on wader reproduction in 2005–2015 (Lehikoinen *et al.* 2016), while the recent faltering of lemming cycles has been connected to climate change (Ims *et al.* 2008, Nolet *et al.* 2013).

In the current core breeding area of the Fennoscandian LWfG in Norway, the total number of LWfG goslings and the number of young produced per pair fluctuated clearly in synchrony with vole cycles in 1994–2016, even when the duration of cycle phases was unstable (Aarvak *et al.* 2017, Marolla *et al.* 2019). By contrast, Kausrud *et al.* (2008) showed that winter weather and snow conditions accounted for lemmings (*Lemmus lemmus*) population dynamics in an alpine southern Norwegian core habitat 1970–1997, and predicted there observed absence of rodent peak years after 1994.

The Caribou (*Rangifer tarandus*) is listed as a nest predator of Lesser Snow Goose (*Anser caerulescens caerulescens*) at la Prouse Bay, Canada (Cooke *et al.* 1995). We found no correlation between abundance of reindeer and LWfG reproduction, but an indirect connection may exist. The area is heavily grazed by domestic reindeer and this can be seen in the form of a lack of willows, absence of new Mountain Birch sprouts after the *Epirrita autumnata* mass occurrences, trampled shore sedge zones, *etc.*, that are less striking on the other side of the reindeer fence dividing herding units. Overgrazing of vegetation and possible (constant) silica defense (Soininen 2012) by the vegetation or succession to more silica-rich plants may have been a factor that caused the constant low phase of rodent cycles. As geese also need good-quality nutrition during the brood rearing period and moult to compensate for losses of egg-laying and incubation, to renew feathers and for goslings to grow, it is possible that their diet preferences overlap with those of reindeer and / or they suffer from the decreased nutritional value of the vegetation. Ims & Henden (2012) reported adverse effects of grazing on passerines in Norway.

The potential depredation by reindeer and non-breeding Red Foxes following them could be masked by the effect of temperatures, as the sum of effective temperatures by 7 July correlated positively both with the reproduction rate of LWfG and gathering of reindeer (and foxes) to the study area. In Norway (Marolla *et al.* 2019) an increase in number of reindeer carcasses correlated nega-

tively with LWfG breeding success, which was explained by increased winter survival of meso-carnivores during rodent troughs.

The few breeding groups of LWfG in Nordic countries form a metapopulation structure. Compared with typical metapopulation models e.g., in insects (Hanski & Gilpin 1997), with scattered suitable habitat patches, the decreased breeding groups of geese are remnant patches of former, more numerous subpopulations. Suitable habitats may be well available, but mostly inhabited. Breeding groups are held together by social behaviour, natal philopatry of females and side fidelity of breeders, but after reaching a threshold in numbers and / or density, the fidelity can break down. After the disappearance of the breeding population studied here, only one was known to exist in Nordic countries by the 2010's. Fortunately, the population has started to grow and new local populations have been established during the latest few years (Aarvak *et al.* 2016, 2017). LWfG have also been observed near our study area both in spring and, after an absence of 17 years, also in autumn (Supplementary material Table 1, 3).

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Uhanalaisen kiljuhanhen populaatorakenne ja ympäristönmuutokset Tunturi-Lapissa

Pohjoisten muuttolintujen kannan kehitys riippuu mm. pesimäpaikkojen petoeläinten ja pikkunisäkkäiden runsausvaihteluista, pesinnän optimaalisesta ajoituksesta, johon ilmastonmuutos tuo uusia sopeutumisongelmia sekä muuttolevähdyks- ja talvehtimisalueiden metsästyksestä ja ruokailupaik- kojen kunnosta.

Uhanalaisia kiljuhanhia *Anser erythropus* tutkittiin Tunturi-Lapin pesimäkeskittymässä 1989–1996, kunnes esiintymä hävisi. Seurantaan kuuluivat pesivien kiljuhanhien parimäärän, nuorten pesimättömien ja pesinnässä epäonnistuneiden las- kenta sekä poikastuotanto ja poikastuotantoon mahdollisesti vaikuttavat ympäristötekijät. Alueella pesi 2–15 kiljuhanhiparia, ja siellä tavattiin kesän alussa vuosittain 0–12 nuorta pesimätöntä kiljuhanhea. Alkukesän suurin yksilömäärä, 41, tavattiin vuonna 1991. Poikueita nähtiin yhteensä 30 (vuosittain 0–8), ja niissä oli keskimäärin 2.9 poikasta / poikue.

Yhteensä 10 kiljuhanhea rengastettiin tai valjastettiin satelliittilähettimellä. Niistä ainakin 3 ammuttiin ja yhteensä 4 kuoli ensimmäisen vuo- den aikana. Vain kaksi havaittiin seuraavina vuosi- na. Muninta alkoi keskimäärin 4.6. (21.5.–13.6), ja poikaset kuoriutuivat 2.7. (21.6.–10.7). Pesyeen havaittiin pienenevän pesinnän aloituksen siirtyessä myöhäisemmäksi. Aloituspäivälle ei löytynyt selitystä paikallisfenologiasta, mutta se korreloi merkitsevästi 600 kilometriä etelämpänä Peräme- ren rannikolla sijaitsevan levähdysalueen pää- muuton ajankohdan kanssa. Takatalvilla oli negatiivinen ja tehoisan lämpötilan summalla 5. heinä- kuuta asti laskettuna positiivinen vaikutus lisääntymistulokseen. Myyräpopulaatiot olivat koko tut- kimusjakson äärimmäisen heikot, sykliisyys puut- tui. Porojen tai ihmisten ei havaittu vaikuttaneen pesimätulokseen.

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Online supplementary material

Supplementary Table 1.

Lesser White-fronted Goose observations in and near the study area 1997–2019.

Supplementary Table 2.

Broods of which size and age of goslings was determined, clutch size, estimated age, hatching date, duration of laying and incubation and date of the 1st egg.

Supplementary Table 3.

LWfG at Varangerfjord area, Norway in autumn 2005–2017. The staging place was found during the first satellite telemetry effort in 1994.

Supplementary Table 4.

Lesser White-fronted Goose pairs, number of goslings in broods and environmental variables in 1989–1996.

Supplementary Table 5.

Densities of breeding birds classified into avian goose predators, small mammal abundance indicators and alternative fox prey species.

Supplementary Table 6.

May and June daily mean temperatures and their sum at Kevo 1963–2014 and their deviation from the average.

Supplementary Fig 1. (cf. Fig. 1.)

Seasonal decline in the gosling production of the Lesser White-fronted Goose in 1989–1995.