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Annual and large-scale variation in breeding output of Greylag geese *Anser anser* in Iceland

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Capsule Large-scale variation in breeding output of Greylag geese *Anser anser* is negligible across Iceland but detectable variation is likely related to spring temperature.

Aims To identify large-scale spatial and annual variation in breeding parameters to support sustainable utilization and conservation of Greylag geese that are a quarry species in Iceland and the UK.

Methods In 2012 and 2013, a total of 360 Greylag nests were visited across Iceland and timing of breeding, egg sizes and clutch sizes were measured. In addition, 888 Greylag families were surveyed in the same period to estimate large-scale variation in brood sizes.

Results Timing of nest initiation varied significantly between parts of the country and nesting started on average on 30 April in West and South Iceland, but considerably later in cooler parts of Iceland, North Iceland (10 May) and East Iceland (20 May). In 2012, clutch sizes were similar between areas but in 2013, East Iceland had a smaller mean clutch size than South and West Iceland. Overall, mean clutch sizes ranged from four to six eggs. Mean brood size varied from three to five goslings per pair between regions, where East Iceland was found to have the smallest brood size on average while West and North Iceland had the largest brood sizes. Brood size was the most variable parameter between years.

Conclusion Regional variation in timing of nest initiation and clutch size across Iceland suggests that variation in these parameters is related to ambient temperatures and this is supported by comparison of data from Iceland and other countries. The South and West parts of Iceland are the warmest and this study suggests that conditions for early breeding may be most favourable there. A more long-term study of the links between demography and environmental parameters is needed for sustainable management of the Greylag population.

Agricultural changes have had a great effect on many bird populations during the last few decades. Recent changes in agricultural policy have led to extensive areas of largely uniform, intensely managed areas of grassland and cereals (Rabbinge & van Diepen 2000). These changes, which started around 1960, have increased the carrying capacity of agricultural landscapes for grazing birds and the larger terrestrial herbivorous migratory wildfowl, such as swans and geese, have benefitted greatly and have been increasing in population size the last few decades (Madsen *et al.* 1999, Abraham *et al.* 2005, Fox *et al.* 2005). Geese take advantage of both cultivated land and natural wetlands but some of the highest food intake rates are on cultivated land (Therkildsen & Madsen 2000, Bos *et al.* 2004, Fox *et al.* 2005, Jónsson & Afton 2006, Van der Graaf *et al.* 2006, Klok *et al.* 2010). Even though geese are generally site-faithful in most years, they are known to change habitat use under altered environmental conditions (Jónsson *et al.* 2014).

It is likely that the conversion of natural habitats to agricultural land has been the dominant factor in the increase in goose numbers the last 50 years (Madsen

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et al. 1999). This has led to increasing conflicts with farmers but has also improved knowledge on the abundance and population sizes of wildfowl over longer time periods (Fox *et al.* 2010). Many geese are also quarry species and considerable interests lie in the continuation and stability of populations. To ensure sustainable utilization of animal populations, the crucial factors that limit population size must be monitored and a detailed understanding of demographic rates must be obtained (Caughley & Sinclair 1994, Sutherland 2001).

Adult survival of geese on the wintering grounds is mostly influenced by availability of suitable farmland (Gill 1996, Abraham *et al.* 2005, Swann *et al.* 2005, Alisauskas *et al.* 2011, Jónsson *et al.* 2014). On the nesting grounds the limitation of breeding success is usually the most important driver of population changes (besides hunting) but it is mostly influenced by availability of suitable habitat (Jensen *et al.* 2014). Several common correlates to fitness can be useful for estimating variation in habitat quality and reproductive output. The number of eggs shows a correlation to the physical condition of geese and ducks (Ankney & MacInnes 1978, Erikstad *et al.* 1993, Öst *et al.* 2008, Gladbach *et al.* 2010). Mean egg volume and total clutch volume can also increase with female body condition and females in better body condition hatch eggs earlier (Gladbach *et al.* 2010). Clutch volume and clutch size may therefore be a good indicator of physical condition of breeding geese. Clutch size decreases with later nesting in many species of birds (Christians 2002, Arnold *et al.* 2004, Claassen *et al.* 2014) and the life expectancy of offspring is often negatively related to hatching date in wildfowl (Bolton 1991, Traylor & Alisauskas 2006, Gladbach *et al.* 2010). An early start of incubation is often positively related to fitness in birds because those individuals that lay eggs first are generally those that are in the best physical condition, lay the largest clutches and have the best nesting success (Erikstad *et al.* 1993, Arnold *et al.* 2004, Bêty *et al.* 2004). Offspring that hatch earlier in spring have often a better life expectancy but this is often connected to food availability and how mature the offspring are at the time of autumn migration (Poussart *et al.* 2000, Prop *et al.* 2003, Durant *et al.* 2004, Frederiksen *et al.* 2004a).

The Greylag goose *Anser anser*, called simply the Greylag from now on, is the most common breeding goose across the lowlands of Iceland, i.e. terrain below 200 metres above sea-level, where the breeding distribution shows a strong association with waterways and wetlands (Gunnarsson *et al.* 2008). The Icelandic population overwinters mostly in Britain and returns to the breeding grounds in Iceland early in March and April (Swann *et al.* 2005, Gunnarsson & Tómasson 2011). Variation in parameters which relate to breeding output is however unknown but this information is needed for successful management and conservation. Greylags have been regularly counted in autumn in Britain since the early 1950s and they have increased from 20 000–30 000 birds in the 1950s to c.a. 100 000 in the early 1990s. In the later 1990s the Greylag population stopped increasing and declined until 2000 when the population was estimated at 80 000 individuals, which is about 20% decrease in population size. Bag statistics show that hunters in Iceland shoot on average about 40 000 Greylags per year (average of hunting statistics 2000–2010, The Environment Agency of Iceland 2014). Despite the extensive hunting, the Greylag population has been slowly increasing and was estimated at approximately 105 000 individuals in late autumn after hunting in Iceland in the 2012 census (Madsen *et al.* 1999, Frederiksen *et al.* 2004b, Mitchell 2013, Wildfowl & Wildlife Trust 2014). Furthermore, it is estimated that in Great Britain about 15 000–20 000 Greylags are hunted every year (Hart & Harradine 2003). Since 2000 there has been a considerable increase in cereal agriculture in Iceland, which coincides with the increasing size of the Greylag population (Statistics Iceland 2014). It is therefore possible that this change in agricultural practices is connected to the recent growth of the Greylag population. Frederiksen *et al.* (2004b) suggested that the population size was underestimated in the census on the winter grounds in Great Britain, which could explain how the population was doing well despite the intensive hunting. It is also likely that strong density dependence is operating which allows the population to compensate for the high hunting pressure or that it would be increasing in the absence of hunting (cf. Sutherland 2001).

We assessed variations in the breeding output of Greylags across Iceland over two years. The aim was to produce a large-scale comparison of parameters that relate to breeding output (timing of breeding, clutch size, reproductive investment and brood size) to produce a baseline for Greylag reproductive parameters and to better inform management efforts for this heavily hunted population.

METHODS

Study areas

Fieldwork was conducted during the spring and summers of 2012–2013. Study areas were chosen across the country to capture possible large-scale variation in breeding parameters (Fig. 1). The study comprised two phases: nest survey and gosling survey.

Each study area was visited in both years on a period from the first of May to the first of June. Sampling in each area spanned 2–3 days on average and the first area visited was West Iceland, then South and East and lastly the North. Major rivers and wetlands in each area were searched to locate breeding colonies and sample nests. Most nests were located in small islands in rivers but in West Iceland nests were found in islands in the Breiðafjörður bay (Fig. 1).

Greylag flocks were surveyed during a three-month period (June–August). Each area was covered at least once each month during the survey period. Brood surveys were conducted on a larger scale than the nest search because post-laying geese disperse from nesting colonies, often over large areas. The search was conducted by driving parallel to major rivers and selected lakes in the catchment area, or along the coastline, as in the case of Breiðafjörður. Frequent stops were made and the area surveyed for geese with binoculars and spotting scopes.

The surveyed areas (Fig. 1) in South Iceland ranged from the banks of River Ölfusá to River Eystri Rangá.

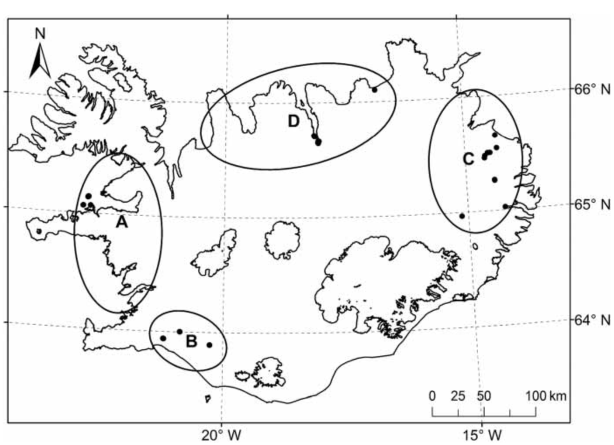

Figure 1. Location of study areas and nest sampling locations. The ellipses show the areas where surveys of broods were performed. West Iceland (A), South Iceland (B), East Iceland (C) and North Iceland (D).The large non-sampled area in the southeast of Iceland is dominated by sparsely vegetated glacial sand plains. Locations of nests that were sampled are marked with circles.

The surveyed area for West Iceland was extended south and we included the area from Borgarfjörður Fjord to Kollafjörður Fjord. For North Iceland the surveyed area ranged from River Vatndalsá and east to Lake Víkingavatn. The East Iceland surveyed area ranged from the River Jökulsá á Brú to River Lagarfljót.

Measures of productivity

Greylag clutch size, egg size (maximum length and width), clutch volume (total volume of eggs per nest) and estimated start of incubation were measured for each nest. To minimize disturbance, risk of desertion and cooling of eggs, the observation time at each nest and colony was kept as short as possible. When measurements at each nest were completed, the eggs were covered with down to minimize the risk of predation and to reduce heat loss. Stage of incubation was estimated by egg flotation (Westerskov 1950) and first day of incubation back-calculated with the equation (Walter & Rusch 1997):

$$\text{Days from start of incubation} = \text{incubation stage} \times 4.67 - 2.33.$$

We subtracted days from start of incubation from the sampling date to calculate the estimated start of incubation, in ordinal days. To calculate egg volume the following equation was used (Westerskov 1950):

$$\text{Volume (cm}^3) = 0.5.7 \times \text{length} \times \text{width}^2.$$

Clutch volume was then found by combining the total volume of eggs in each nest.

In 2012, measurements for North Iceland included only clutch size and start of incubation and in 2013 only clutch size was recorded for East Iceland (Table 1).

Brood sizes were estimated in monthly visits from the first week of June to the first week of September each year. Some Greylag families may have been sampled multiple times when areas were re-visited but this is hard to measure and avoid. Each time Greylags were sighted, the number of all Greylags, with and without goslings, were recorded. From those surveys the average brood sizes could be compared between areas and years. Brood size was the number of goslings with each pair or individual adult Greylag over the course of each sampling period, averaged over areas and years. Large mixed groups of Greylags were regularly observed (100–300 individuals) in specific sites. These groups

Table 1. Numbers of Greylag goose nests, eggs, pairs with goslings and goslings monitored in each area in each year of the study.

	2012				2013			
Area	Nests	Eggs	Pairs with goslings	Goslings	Nests	Eggs	Pairs with goslings	Goslings
West Iceland	39	175	93	454	23	120	102	395
South Iceland	82	275	143	538	52	256	134	432
East Iceland	30	124	152	467	67	255	158	478
North Iceland	26	111	18	70	41	186	88	371

In North Iceland in 2012 we only measured number of eggs and in East Iceland in 2013 we only measured number of eggs and start of incubation.

consisted of moulting non-breeding Greylags as well as breeding Greylags with goslings. Spotting scopes were used to divide groups of goslings into families when possible, by separation within the flock and/or size. Disturbance by the observer usually scattered the flocks which headed for the nearest open water, making identification of families more manageable. When family identification was not possible the goslings were counted but not included in the brood size estimates. The sample size of Greylag families differed somewhat between areas and years because different areas varied in their suitability for geese and brood surveys were affected by weather reducing visibility in some surveys.

Data analysis

Variation in breeding parameters between years and between parts of Iceland was compared by generalized linear models (GLM) and ANOVA. Data within areas were pooled. We used Tukey's honest significant difference as a post-ANOVA test to help distinguish differences between areas in the ANOVA. Year and area were explanatory variables. Statistical analyses were performed in R 2.15.2 (R Core Team 2013).

RESULTS

In the two years of sampling a total of 360 Greylag nests and 888 Greylag broods were sampled across Iceland (Table 1). Overall, the average clutch size was 4.7 (sd = 1.76, range 1–10) (Fig. 2a). Average egg length was 84.0 mm (sd = 3.37, range 54.1–94.2 mm). Average egg width was 57.7 mm (sd = 1.77, range 49.3–62.1 mm). The average clutch volume was 658 cm^3 (sd = 236.92, range 123.4–1369.0 cm^3). The overall average start of incubation was on day 124 (4 May) (sd = 10.64, individual nests ranged 100–157 (10 April–6 June)). Overall average brood size was 3.6 and ranged from 1–12 goslings/pair.

In 2013, fewer nests were found in South and West Iceland when re-visiting study areas from the previous year (Table 1). Clutch size was sampled in all four regions and both years (Supplementary Online Tables S1 & S2) and varied between areas and was independent of year (Table 2). Clutch size was smaller in East Iceland than both South and West Iceland, with North Iceland intermediate to the South/West and East Iceland (Fig. 2a). Annual clutch size, with all areas pooled, varied little between years and annual egg length and width were similar between years (Table 2). Clutch size within areas increased slightly in West Iceland between years (Table 2).

Length and width of eggs were measured in South, West and East Iceland in 2012 and in South, West and North Iceland in 2013 (Supplementary Online Tables S1 & S2). Comparison between years was therefore only possible in South and West Iceland. Both length and width of eggs varied between years but annual variation was dependent on area (i.e. the Area*Year interaction significant) (Table 2). Egg length increased in West Iceland between years but was similar between years in South Iceland (Table 2). Width of eggs was slightly smaller in South Iceland in 2013 but was similar between years in West Iceland (Table 2).

Clutch volume was calculated from length and width measurements of eggs and comparison between years was only possible between South and West Iceland (Supplementary Online Tables S1 & S2). Clutch volume was similar between areas (Fig. 2c, Table 2). Clutch volume increased between years in West Iceland but was similar in South Iceland (Table 2).

Eggs were floated in South, West and East Iceland both years but only in 2013 in North Iceland (Supplementary Online Tables S1 & S2). Estimated start of incubation differed between areas independent

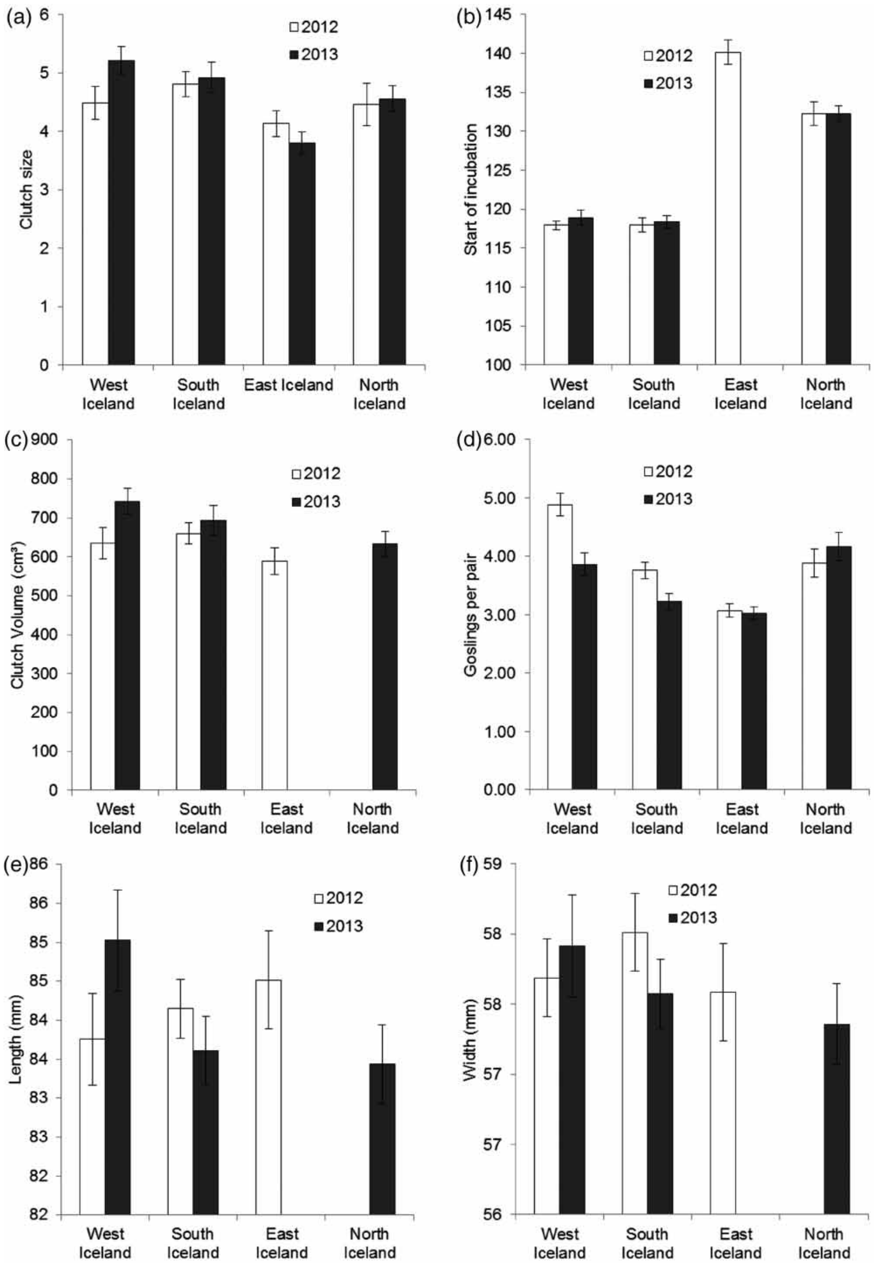

Figure 2. Annual and between area variation in mean (±se) (a) clutch size, (b) estimated start of incubation, (c) clutch volume, (d) brood size, (e) length of eggs and (f) width of eggs. White columns indicate values for 2012 and black columns indicate values for 2013. East Iceland lacks data in b, c, e and f for 2013 and was therefore not included. See Fig. 1 for research area locations and details and Table 1 for *n* values.

of year (Table 2). In West and South Iceland incubation started on average on 30 April (Fig. 2b), in North Iceland on average on 10 May and in East Iceland on average on 20 May (Fig. 2b). Estimated start of incubation did not vary within areas between years (Table 2).

Brood sizes differed greatly between areas, depending on year (Table 2). Mean brood size varied from three to five goslings per pair between areas, and brood size was smallest in East Iceland on average (Fig. 2d) while brood size was largest in West and North Iceland. The largest brood size in 2012 was in West Iceland but was smaller in 2013 and similar to that in North Iceland (Fig. 2d). Mean brood size was the only parameter that showed significant annual difference, with smaller brood sizes in 2013 than in 2012 (Table 2). Brood size

Table 2. Results of ANOVA and GLM models of yearly (df = 1) and between area (df = 3) variation in components of productivity of Greylag Geese in Iceland, between 2012 and 2013.

		F	P		Parameter est.	SE	t Value	Pr(>|t|)	
Clutch size	Area	6.1	<0.001	(Intercept)	1.3	0.054	24.9	<0.001	***
	Year	0.1	0.73	W. Iceland	0.2	0.066	3.2	0.001	**
	Area*Year	1.1	0.33	N. Iceland	0.1	0.065	2.1	0.034	*
				S. Iceland	0.2	0.056	4.1	<0.001	***
				Year	0.0	0.042	0.9	0.35	
Length	Area	3.6	0.014	(Intercept)	17.3	7.0	2.5	0.013	*
	Year	1.6	0.2	W. Iceland	−43.0	11.7	−3.7	<0.001	***
	Area*Year	13.4	<0.001	N. Iceland	−0.007	0.0058	−1.1	0.26	
				S. Iceland	−0.004	0.0043	−1.0	0.31	
				Year	−0.006	0.0035	−1.8	0.065	.
				W. Iceland:Year	0.02	0.0058	3.7	<0.001	***
				N. Iceland:Year	NA	NA	NA	NA	
				S. Iceland:Year	NA	NA	NA	NA	
Width	Area	2.7	0.043	(Intercept)	8.8	4.3	2.0	0.042	*
	Year	1.6	0.2	W. Iceland	0.004	0.0034	1.3	0.20	
	Area*Year	4.6	0.032	N. Iceland	−0.002	0.0042	−0.4	0.70	
				S. Iceland	0.004	0.0032	1.2	0.22	
				Year	−0.002	0.0021	−1.1	0.27	
Clutch volume	Area	1.2	0.3	(Intercept)	−171.9	108.5	−1.6	0.11	
	Year	1.2	0.3	W. Iceland	0.1	0.089	1.2	0.25	
	Area*Year	0.8	0.36	N. Iceland	−0.02	0.11	−0.2	0.88	
				S. Iceland	0.09	0.085	1.1	0.28	
				Year	0.09	0.054	1.6	0.10	
Est. Start of incubation	Area	133.6	<0.001	(Intercept)	4.9	0.0090	546.7	<0.001	***
	Year	0.3	0.62	W. Iceland	−0.2	0.012	−14.2	<0.001	***
	Area*Year	0.3	0.77	N. Iceland	−0.06	0.012	−4.8	<0.001	***
				S. Iceland	−0.2	0.011	−16.0	<0.001	***
				Year	0.002	0.0072	0.2	0.82	
Brood size	Area	22.6	<0.001	(Intercept)	32.2	138.3	0.2	0.82	
	Year	5.3	0.022	W. Iceland	440.5	185.4	2.4	0.018	*
	Area*Year	3.6	0.014	N. Iceland	−170.5	280.4	−0.6	0.54	
				S. Iceland	279.9	189.2	1.5	0.14	
				Year	−0.02	0.069	−0.2	0.82	
				W. Iceland:Year	−0.2	0.092	−2.4	0.018	*
				N. Iceland:Year	0.08	0.14	0.6	0.54	
				S. Iceland:Year	−0.1	0.094	−1.5	0.14	

Significance levels: <0.001 '***', <0.01 '**', <0.05 '*', <0.1 '.'

was smaller in West and South Iceland in 2013 while North and East Iceland were similar between years (Table 2).

DISCUSSION

Out of six parameters that were measured we found a significant difference between areas in three (clutch size, start of incubation and brood size) and one between years (brood size). Clutch size differed between areas because East Iceland had fewer eggs than the South and West Iceland. We found that breeding started earliest in South and West Iceland, with nearly identical start of incubation, then North Iceland and finally East Iceland. The South and West study areas were almost identical in most parameters although West Iceland showed a bit more variation in parameters between years. East Iceland seemed to have consistently smaller clutches and brood sizes than the other areas and the latest start of incubation. In general there was little annual difference in mean annual values except for brood size, which was smaller in 2013.

Clutch size averaged 4.7 eggs and was similar between years which, with the small differences in clutch volume, suggest that conditions for most adults were sufficiently good for egg production in both years, despite a cold spring in 2013. The average clutch size of the Icelandic population is slightly smaller than in neighbouring countries. The feral Greylag population in the UK is known to have clutch sizes from 2 to 9 eggs (mean 5.9). In Scania, in southern Sweden, the average clutch size is 5.36 eggs, with a mean post-hatch brood size of 4.60 and 3.14 at fledging. In Norway the clutch size varies from an average of 5.32 in Rogaland County in the south to 4.20 in Finnmark County in northern Norway (Madsen *et al.* 1999). A positive relationship is found between mean April temperatures in these areas and their respective clutch sizes ($R^2 = 0.71$, df = 10, $P = 0.009$, Pearson product-moment correlation coefficient; Fig. 3). A colder climate results in a lower amount of energy available for egg production, possibly because plant growth rates are inversely related to temperatures on the spring staging grounds.

In 2013 we found fewer nests in South and West Iceland than in 2012 when we visited the same locations. It is well known for some ducks and other long-lived species to skip breeding or abandon the nest right after laying eggs if conditions are unfavourable and survival is potentially poor (Coulson 1984). We do not know if this was only annual variation, a result of a colder spring in 2013 than in 2012 or a result of our sampling the previous year. However, it is highly unlikely that the sampling had different effect in the South and West Iceland than in the North and East. A possible explanation for this annual difference is that in years with less favourable conditions, only the high-quality individuals lay eggs and those in poor condition skip breeding (Oro *et al.* 2013). We suggest that this explains why there were fewer nests in 2013 but little change in clutch size or clutch volume.

We saw a considerable difference in the start of incubation between parts of the country and this difference was consistent over both years. This difference may be linked to variation in temperature in the different parts of the country (Einarsson 1984). Spring temperature shows a similar trend as the start of incubation for the different areas (Fig. 4). This may suggest that spring temperature influences breeding phenology, possibly through timing of vegetation growth and body condition of females (Summers & Underhill 1987, Gladbach *et al.* 2010).

Brood sizes were smaller in all areas in 2013 except for North Iceland, but the difference might be explained by the smaller sample size of 2012. Mean brood size was smaller in East Iceland than in the other areas. Brood

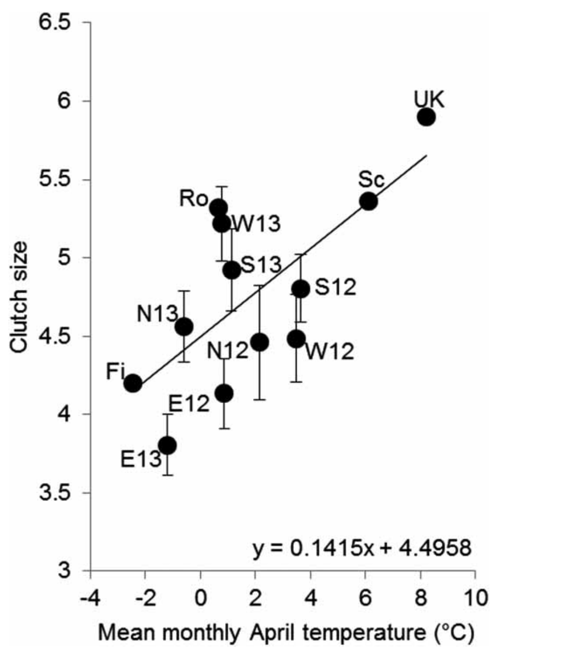

Figure 3. The relationship between average clutch size and mean monthly temperature in April for Iceland and several European localities. Localities are shown with following abbreviations: Ro = Rogaland (Norway), Fi = Finnmark (Norway), UK = Mid England (UK) and Sc = Scania (Sweden). Clutch size data for Rogaland, Finnmark, Mid England and Scania obtained from Madsen *et al.* 1999). Clutch size data for Iceland split into South (S), West (W), East (E) and North Iceland (N) and years are indicated by 12 (2012) and 13 (2013). Error bars show standard error. Meteorological data obtained from closest weather station to corresponding research area (Icelandic Meteorological Office 2014, Norwegian Meteorological Institute 2014a, 2014b, 2014c, 2014d).

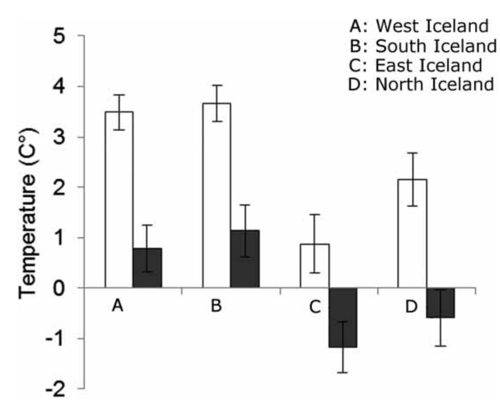

Figure 4. Annual and between area variation in mean temperature (±se) in April for the two sample years. West Iceland (A), South Iceland (B), East Iceland (C) and North Iceland (D). White columns represent 2012 and dark 2013. Meteorological data from closest weather station to corresponding research area (Icelandic Meteteorological Office 2014). Weather stations used were Stykkishólmur (West Iceland), Hella (South Iceland), Egilsstaðir (East Iceland) and Akureyri (North Iceland).

size was smaller in South and West Iceland in 2013 than the previous year, and there might be a possible link between the decrease in gosling survival and the lower temperature of that year. Temperature affects many factors, for instance length of the growing season for plants (Walker *et al.* 2006), and it is possible that the delayed start of incubation and the shorter growth season have a negative effect on the life expectancy of goslings. Lower brood size in East Iceland might be caused by a range of factors, including predation (Young 1972, Summers & Underhill 1987, Ebbinge 1989, Hersteinsson & Macdonald 1996), weather and temperature difference (Einarsson 1984, Summers & Underhill 1987, Sedinger 1992), and food availability (Mainguy *et al.* 2006) but the relative contributions of each factor are unknown.

The earlier start of incubation in South and West Iceland is likely to give the goslings a considerable advantage because they have longer time to develop and grow. The milder climate in South and West Iceland (Einarsson 1984) causes snow to melt sooner and furthermore provides plants with a longer growth season, which could benefit Greylags in the area. We therefore suggest that South and West Iceland generally have more favourable breeding conditions, at least in most years. South Iceland has the largest surface area dedicated to farmland in the country (National Land Survey of Iceland 2009) and is therefore highly important for pre- and post-breeding Greylags as well as non-breeding adults. This study mainly investigated the differences in breeding output between areas in Iceland. However, areas with breeding Greylags are more common in the East and Northeast, which is probably due to variation in availability of suitable habitat types around the country (Gunnarsson *et al.* 2008). So even though breeding conditions seem more favourable in the South and West, areas in the East and North are very important in the overall production of Greylags across Iceland. Conversely, since the weather conditions in the spring months differed between the two years, we suggest that these birds are robust regarding spring temperatures because we found little variation between years in clutch size and clutch volume. Furthermore, if the birds arrive in sufficient body condition, their success may be independent of spring conditions (Reed 1973, Raveling 1979 Summers & Underhill 1987, Madsen *et al.* 2007).

In Iceland, the most likely threat to the Greylag habitat are changes in land-use patterns in lowland areas, for instance an increase in commercial afforestation, increasing pressure on bodies of water (for instance through building of summerhouses and fish farming), increased traffic due to recreation, and increased amount of farming in the species' nesting habitats (Gunnarsson *et al.* 2006, 2008). This study is a significant step towards a better understanding of breeding output of Greylag geese in Iceland. For sustainable hunting and conservation of the Greylag population, a long-term study is needed that would also account for long-term changes in temperature and weather conditions during the spring. Such a monitoring programme could be based on the methods and study areas presented here. A large-scale marking programme where the success of individual geese breeding in different habitats and across Iceland, followed over more years, would add significantly to our understanding of the large-scale demographic processes which are needed to develop a successful management strategy for this population.

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SUPPLEMENTAL DATA

Supplementary online Tables S1 & S2 (locations, measured components and number of nests sampled) can be accessed at 10.1080/00063657.2015.1034655.

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