

Where to settle in a rapidly expanding bird colony: a case study on colony expansion in High Arctic breeding geese

Helen B. Anderson · Jesper Madsen · Sarah J. Woodin · René van der Wal

Received: 18 July 2014 / Revised: 3 November 2014 / Accepted: 3 November 2014 / Published online: 14 November 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract As colonies fill up with more individuals, areas of preferred nesting habitat can become scarce. Individuals attracted to the colony by the presence of conspecifics may then occupy nest sites with different habitat characteristics to that of established breeders and, as a result, experience lower nesting success. We studied a rapidly growing colony of Svalbard pink-footed geese *Anser brachyrhynchus* to determine any such changes in nest site characteristics and nesting success of newly used nest locations. Svalbard pink-footed geese are a long-lived migratory species that breeds during the short Arctic summer and whose population has doubled since the early 2000s to c. 80,000. From 2003 to 2012, nest numbers increased over fivefold, from 49 to 226, with the majority (range 57–82 %) established within 30 m of another nest (total range 1–164 m). Most nests, particularly during the early stages of colony growth, shared common features associated with better protection against predation and closer proximity

to food resources; two factors thought key in the evolution of colony formation. As nest numbers within the colony increased, new nests occupied locations where visibility from the nest was restricted and foraging areas were further away. Despite these changes in nest site characteristics, the nesting success of geese using new sites was not lower than that of birds using older nests. Hence, we propose that nesting in dense aggregations may offset any effects of suboptimal nest site characteristics on nesting success via the presence of more adults and the resultant increased vigilance towards predators.

Keywords Nest site characteristics · Nesting success · Clustering · Coloniality · Geese

Introduction

Since there are thought to be fitness costs for individuals nesting in dense aggregations (Wittenberger and Hunt 1985; Møller 1987), a number of hypotheses have been proposed to explain the evolution of colony formation (Wittenberger and Hunt 1985; Brown et al. 1990; Anderson and Hodum 1993). The two key factors (and therefore main benefits of colonial nesting) are hypothesised to be reduced predation risk and ready access to food resources (Wittenberger and Hunt 1985; Barta and Szép 1995). Such benefits may be attributable to physical characteristics of the habitat where nest sites are situated within the colony. For instance, some individuals cluster closer to foraging grounds (Daunt et al. 2002) and/or nest in areas that provide increased security from predators (Harris et al. 1997).

Although individuals are predicted to settle within a colony where the habitat is most suitable, i.e. areas that provide the best chance of reproductive success (Fretwell and Lucas 1969), the physical characteristics of the habitat that provide the best nesting sites are rarely distributed uniformly across

Communicated by J. A. Graves

H. B. Anderson (✉) · S. J. Woodin · R. van der Wal
School of Biological Sciences, University of Aberdeen,
Aberdeen AB24 3UU, UK
e-mail: helen.anderson@uit.no

S. J. Woodin
e-mail: s.woodin@abdn.ac.uk

R. van der Wal
e-mail: r.vanderwal@abdn.ac.uk

J. Madsen
Department of Bioscience, Arctic Research Centre, Aarhus
University, Grenåveg 14, DK-8410 Kalø, Denmark
e-mail: jm@bios.au.dk

Present Address:

H. B. Anderson
Department of Arctic and Marine Biology, Faculty of Biosciences,
Fisheries and Economics, University of Tromsø, NO-9037 Tromsø,
Norway

the landscape. Therefore, it is likely that the most suitable sites for nesting are preferentially occupied and subsequently become scarce as the numbers of individuals in the colony increases. As a result, the nest site characteristics of new sites are liable to differ from that of older sites, potentially resulting in lower nesting success for those breeders occupying new sites (Ens et al. 1992; Stokes and Boersma 2000 and references therein; Kokko et al. 2004).

A suitable species with which to study these processes of changing nest site characteristics and nesting success of new recruits is the Svalbard pink-footed goose *Anser brachyrhynchus*. These long-lived and long-distance migratory birds are a semi-gregarious ground-nesting species which, like most Arctic breeding geese, are thought to express colony site fidelity (Cooke et al. 1975; Mehlum 1998). Furthermore, the population has almost doubled to c. 80,000 individuals since 2000 (Madsen and Williams 2012). These factors, combined with the rapid expansion in numbers of individuals using a known colony, make this an ideal species with which to study colony expansion. Hence, we determined if changes in nest site characteristics and reproductive success occurred in a rapidly growing colony of pink-footed geese. We predicted that as nest numbers within the colony increased, the characteristics associated with new nests would differ from those of older nests. As a consequence of this change in nest site characteristics, we also predicted that new nests would be less successful than that of older nests.

Materials and methods

Study area and study population

The pink-footed goose colony studied covered an area of 0.76 km² on the exposed, vegetated southwest facing tundra slopes of Sassendalen (79° 20' N; Fig. 1), one of the main pink-footed goose breeding areas in Svalbard (Jepsen et al. 2002). Vegetation within the valley is classed within the middle Arctic tundra zone, with dry ridges, characterised by *Cassiope tetragona* and *Dryas octopetala* dwarf shrub vegetation, particularly prevalent on tundra slopes (Elvebakk 1997) and fen, marsh and moss tundra vegetation found where freshwater accumulates (Vanderpuye et al. 2002).

Pink-footed geese initiate nesting towards the end of May, as soon as snowmelt allows access to nest sites (Madsen et al. 2007). The female incubates for 26–27 days, while the male remains close to the nest (Løvenskiold 1964; Inglis 1977). When both adults are present they are generally able to guard the nest against Arctic foxes *Vulpes lagopus* and avian predators, such as glaucous gulls *Larus hyperboreus* and Arctic skuas *Stercorarius parasiticus* (Inglis 1977; Madsen et al. 2007). However, if the female leaves the nest (usually to feed), the male will follow her, leaving the eggs exposed to potential

predation by both foxes and avian predators (Løvenskiold 1964; Nyholm 1965; Inglis 1977). Arctic foxes can kill geese (Prestrud 1992), particularly solitary incubating geese (Inglis 1977; Frafjord 1990), which may occur if the male moves too far away from the nest to feed.

Reproductive parameters

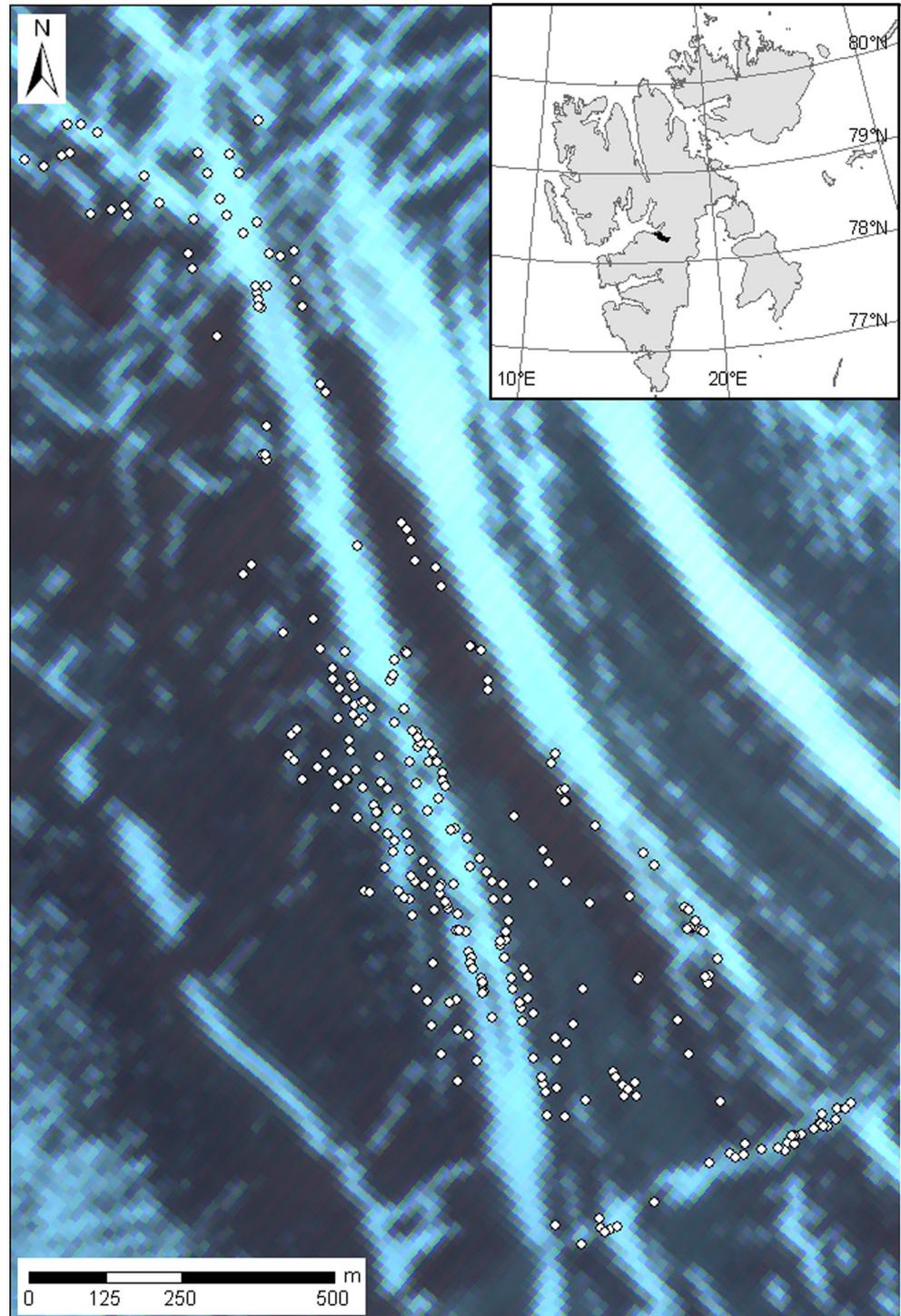
To determine both nest numbers and nesting success of pink-footed geese, systematic searches for nests were undertaken for 7 years (2003–2006 and 2010–2012; no searches were conducted from 2007 to 2009 due to financial constraints). Searches followed a predetermined protocol and were conducted by a team of observers over the same fixed area in every year to ensure consistency in the coverage of the landscape and took place as soon as possible after hatching. We systematically searched for nests by working in pairs and walking in straight line transects (spaced at 5-m intervals) across the tundra slopes. The coordinates of every nest found were recorded and stored in a handheld GPS (Garmin GPS60), and each nest was labelled with a unique number written on a stone and placed unobtrusively next to the nest. Checking the ID number of a used nest, and its coordinates with that of nests identified in previous survey years allowed us to check how many nests recorded in previous years had been missed. This resulted in a detection probability of 93–94 %, which compares favourably with those proposed by Johnson and Shaffer (1990) for colonial breeding species. Thus, this approach is unlikely to have influenced the outcomes of our research.

We determined nesting success after hatching, rather than regular checking of each individual nest during the incubation period, because the pink-footed goose is particularly shy of humans, with nest losses after human disturbance known to be over one third (Madsen et al. 2009). Nests were easily identified by the presence of a bowl-shaped depression in the ground surrounded by a prominent vegetated rim. Nests were classified as having been used during the current breeding season if fresh down feathers were found within the nest bowl, and fresh droppings were present in the nest vicinity. Empty nests, nests containing eggshells with no membranes and eggs with clear indications of gull peck marks or fox tooth marks on eggs were recorded as having been abandoned/predated. Successful nests were those where membranes were still present within the eggshell remains (Davis et al. 1998; Madsen et al. 2007; Prop et al. 2013). A nest was considered to have been successful if at least one egg hatched.

Snow cover

Since the pattern of persistent snow lie can be a major landscape component controlling access to breeding areas and hence dictate where nests can be established (Cotter 1999;

Fig. 1 ASTER satellite image showing the spatial extent of persistent snow lie patterns across the pink-footed goose colony at Sassendalen, Svalbard (image from 28 May 2004). Locations of all nests recorded in the period 2003–2012 are indicated by symbols. *Inset map* shows the location of Sassendalen in *black*



Madsen et al. 2007; Smith et al. 2010), we used an ASTER satellite image (resolution 15 m) from 28 May 2004 to determine the spatial distribution of annually persistent snow patches in the colony during late May (the beginning of the pink-footed goose nesting period; Madsen et al. 2007). From this image, we produced a three-class snow coverage map (snow, no snow, snow edge) which enabled a snow class to be

assigned to each nest location within the colony and hence determine where nests were located in relation to snow cover. Suitable low-cloud cover high-resolution (m scale) satellite images were not available for years other than 2004. However, we are confident that the spatial distribution of snow lie in the colony in other years of the study resembled that found in 2004. This is because although the overall extent of snow

cover varies between years (Jensen et al. 2014), the pattern of persistent snow lie is annually consistent, i.e. snow always lies in the same predictable places every year (verified through the visual inspection of oblique photographs taken during late May in 2003–2005 and pers. obs. by JM and RvdW). Atmospheric correction was not needed as cloud cover over the lower right quadrant of the image where the colony was situated was low (8 %), and there was no observable reduction in image clarity. Snow cover classification was completed on a subset of the satellite image covering the Sassendalen area using visually interpreted training points and a maximum likelihood classification which evaluated attributes of each pixel in the image to assign it to a snow class. No fewer than 100 pixels were used to define each snow class.

Characteristics of nest sites

To define the characteristics of each nest site, we recorded data on a number of different variables (elevation, slope, visibility from the nest, distance to foraging areas and size thereof), which have been predicted to be of importance to nesting geese (Løvenskiold 1964; Madsen et al. 2007; Wisz et al. 2008). The elevations of nest site locations were recorded as metres above sea level (masl), as indicated by GPS. Although nests were always established on areas of flat and horizontal substrate, such as ledges, rocky outcrops and promontories, the slope of the underlying terrain varied throughout the colony. This underlying slope was estimated using a compass and is hereafter referred to as ‘slope’. The dominant plant community in which each nest was located was recorded as *D. octopetala*, *C. tetragona*, *Carex* spp., *Poa* spp., moss, rocks or bare ground.

To determine how far geese had to travel from their nest to find food, the distance from each individual nest to the nearest area of suitable goose forage vegetation (see below), in any direction, was measured using a range finder (Nikon Forestry 550, range 10–500 m). Sizes of the nearest foraging areas were also recorded, with the minimum size suitable for use as goose foraging set at 2 m × 2 m (patches smaller than this were very rapidly denuded of vegetation and therefore not regarded as a meaningful resource for incubating geese). Foraging areas were wet marshes with standing water, containing the vascular plants *Dupontia* spp., *Eriophorum scheuchzeri*, *Equisetum arvense* and *Bistorta vivipara*, with the ground cover of vegetation dominated by moss species. The previous use of such areas was confirmed by the presence of fresh goose droppings and/or disturbance of the vegetation and by visual observations of feeding geese during the nesting period.

To establish an index of the field of view that a pair of nesting geese had while incubating, the distances from the nest to the nearest visual obstruction (caused by changes in the terrain, e.g. boulders, rocky outcrops, etc.) in the four cardinal

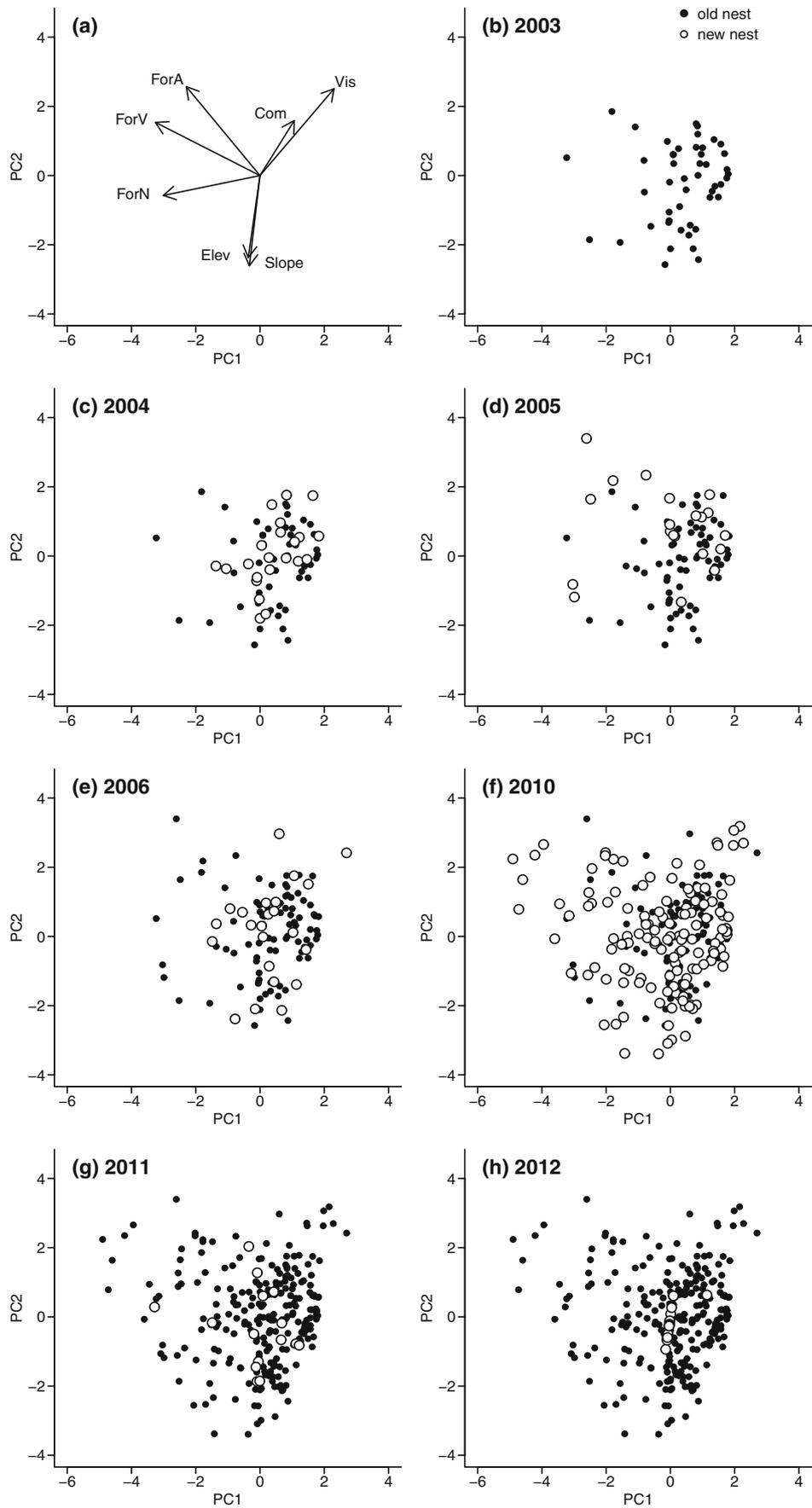
Fig. 2 PCA ordination diagrams of habitat characteristics measured in association with pink-footed goose nest establishment in Sassendalen, Svalbard between 2003–2006 and 2010–2012. Habitat characteristics are shown as arrows in **a** with *Com* plant community, *Vis* visibility from the nest, *Slope* slope, *Elev* elevation, *ForN* distance to nearest forage area, *ForV* distance to nearest visible forage area and *ForA* size of nearest forage area; **b** to **h** ordination diagrams with *hollow symbols* for new nests and *filled symbols* for old nests

directions were recorded either using the range finder or, for distances shorter than 10 m, by eye. These distances were subsequently used to calculate the area of an ellipse ($\text{area} = \pi \times A \times B$, where A equals half the major axis and B half the minor axis) which gave a single measurement, in square kilometres, of an area of visibility around a nest, centred at the individual nest. All distances were measured at a height approximately equivalent to that of an incubating goose sitting on the nest (30–40 cm).

Statistical analysis

All statistical analyses were carried out using R v3.0.2 (R Core Team 2012). The first set of analyses determined which nest site characteristics of new nests changed as the number of nests in the colony increased. As a first step, we used principal component analysis (PCA) to reveal which nest site characteristics explained most of the variation in the data. Within the PCA, variables representing the characteristics of nest sites were normalised before analysis to ensure unit variance and to allow a correlation matrix to be generated. Next, the formal assessments of relationships suggested in the PCA were conducted using generalised linear models (GLMs). Since nest site characteristics (elevation, slope, visibility from the nest, distance to foraging areas and size thereof) were continuous variables with potential zero values, we used the package *tweedie* (Dunn 2014). This allowed us to use GLMs with gamma distributions to determine changes in nest site characteristics of new nests with increasing nest numbers within the colony.

Pearson’s chi-squared analyses were used to determine associations between patches of snow lie and i) nest locations and ii) plant communities in which nests were located. Snow cover classes and nest locations were derived from the three-class snow map generated in ArcGIS and spatial maps of nest locations. To determine how closely individuals nested to each other as the colony increased in size, nearest neighbour distances for each year (2003–2006 and 2010–2012) were calculated in ArcGIS (version 9.3 ESRI Inc 1999–2008). Nearest neighbour ratios were calculated by comparing the observed nest distribution in any one year to that of a randomly generated distribution of nests, where values less than 1 indicate clustering



and values equal to 1 indicate a random distribution. To determine if the randomly generated and actual nest distributions differed in any one year, we compared the means using z tests.

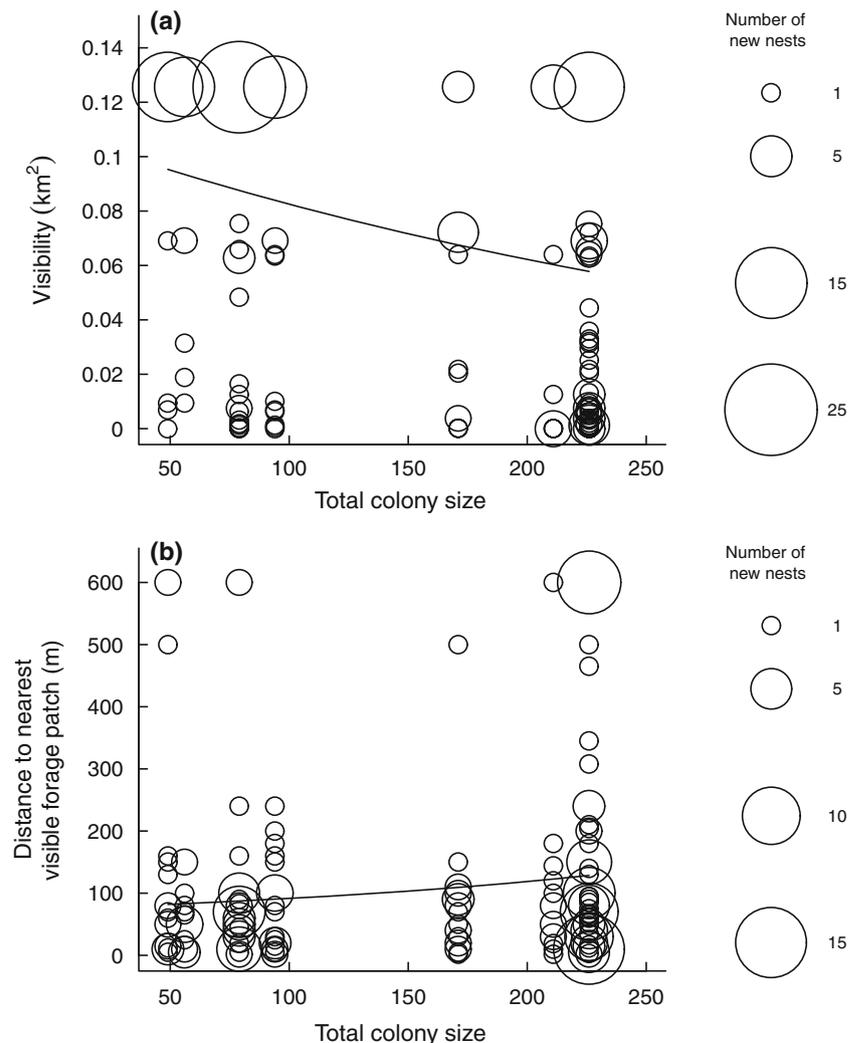
Moving on to explore which nest site characteristics influenced the nesting success of new nests in the colony, we employed a further PCA to help identify which nest site characteristics influenced nesting success. Formal assessment of relationships between nest site characteristics and nesting success of new nests, suggested in the PCA, was then analysed in a GLM with binomial distribution and logit link function to determine changes in the nesting success of new nests with changes in nest site characteristics. To eliminate any potential bias due to the prior breeding experience of individuals (see Forslund and Larsson 1992), data for new nests only were used. Since the numbers of new nests in any one year was too low to allow meaningful analysis to be conducted for individual years, we combined all the data for first-year nests together.

Results

Nest establishment

The initial PCA, which explored nest site characteristics associated with the establishment of new nests, identified that the characteristics which were most strongly correlated with PC1 were the index of all-round visibility from the nest ($r=0.55$), distance to the nearest forage area ($r=-0.51$) and its size ($r=0.58$; Fig. 2a). Distance to visible forage ($r=0.50$) and slope ($r=-0.40$) were correlated with PC2 (Fig. 2a) and plant community ($r=-0.81$) with PC3. Many nests in the colony occupied the same core ordination space, characterised by a plant community at the nest dominated by *D. octopetala*, high visibility from the nest, relatively steep underlying slopes, low elevations and large forage areas that were located near nests (Fig. 2b–h). However, as time progressed and colony size increased, some new nests were established in parts of the ordination space most closely associated with low visibility

Fig. 3 Relationships between the number of new nests in a pink-footed goose colony and **a** visibility from the nest and **b** distance to the nearest visible area of forage. The different number of new nests associated with an individual measure of visibility from the nest or distance to the nearest visible area of forage are shown as *different circle sizes* with *fitted lines* from the GLM analyses displayed



from the nest (Fig. 2e–g), greater distances to smaller foraging areas (Fig. 2d, f, g), higher elevations (Fig. 2f), shallower underlying slopes (Fig. 2e, f) and vegetation types such as *C. tetragona*. In the PCA, axes 1, 2 and 3 combined explained a total of 63 % of the variation in the data (PC1=25 %, PC2=24 %, PC3=14 %).

Formal analysis confirmed that as total nest numbers within this colony increased from 49 to 226, average visibility from new nests decreased by more than a third from 0.096 to 0.058 km² ($t_{239}=4.12$, $p<0.001$; Fig. 3a). For new nests, the distances to the nearest visible patch of forage vegetation increased by just over 50 %, from 82 to 127 m ($t_{248}=2.02$, $p=0.04$; Fig. 3b), and the elevation of new nests increased from 35 to 48 masl ($t_{271}=2.65$, $p=0.009$). We did not find any significant relationships between nest establishment and slope ($t_{258}=1.81$, $p=0.07$) or forage patch size ($t_{227}=0.52$, $p=0.6$).

There was strong evidence that new nests were established near existing nests (p values <0.001 ; Table 1), generally within 30 m. Of the 276 nests to which we could assign a snow class, significantly more (61 %, $n=168$) were established at the snow edge than expected ($\chi^2_2=96.1$, $p<0.001$; Fig. 1). We also found that 86 % of nests ($n=190$) where the underlying vegetation type was recorded (total=226) were located in *D. octopetala* vegetation, significantly more than expected ($\chi^2_2=95.7$, $p<0.001$), with the remaining 11 % ($n=23$) in patches of *C. tetragona* and 3 % ($n=7$) in areas dominated by other vegetation types, rocks or bare earth.

Nesting success

Although the second ordination, which explored nest site characteristics and nesting success of new nests, indicated a slight separation between successful and unsuccessful nests in some years (Fig. 4), there were no clear patterns to indicate

strong relationships between any of the characteristics of nest sites and the success of new nests. The absence of such relationships was confirmed by formal analysis (slope: $z=1.39$, $p=0.12$; elevation: $z=0.96$, $p=0.34$; distance to forage: $z=0.59$, $p=0.56$; forage area size: $z=1.49$, $p=0.14$; visibility from nest: $z=0.77$, $p=0.44$). Thus, factors other than nest site characteristics likely influenced the nesting success of new nests.

Discussion

This study has captured the changing dynamics of individual nest site characteristics during a period of rapid colony growth at one of the main pink-footed goose breeding areas in Svalbard. The majority of nests, particularly those established when the colony was smaller, shared a number of core characteristics which were associated with good visibility from the nest (as a proxy of reduced predation risk) and ready access to food resources; two factors which have been proposed as key drivers in the evolution of colony formation (Wittenberger and Hunt 1985; Barta and Szép 1995). Nest site characteristics of new nests changed as the colony filled up, but such changes appeared to have no measurable impact on nesting performance.

High Arctic breeding species often encounter extensive spring snow cover that can restrict access to breeding areas (McLaren and Alliston 1985). However, in those years when snow cover is more extensive, geese delay nesting until this transient snow melts to reveal their nest site (Madsen et al. 2007). Since we found a strong positive association between the edge of persistent snow patches and nest sites and *D. octopetala* and nest sites, it may be that geese use the

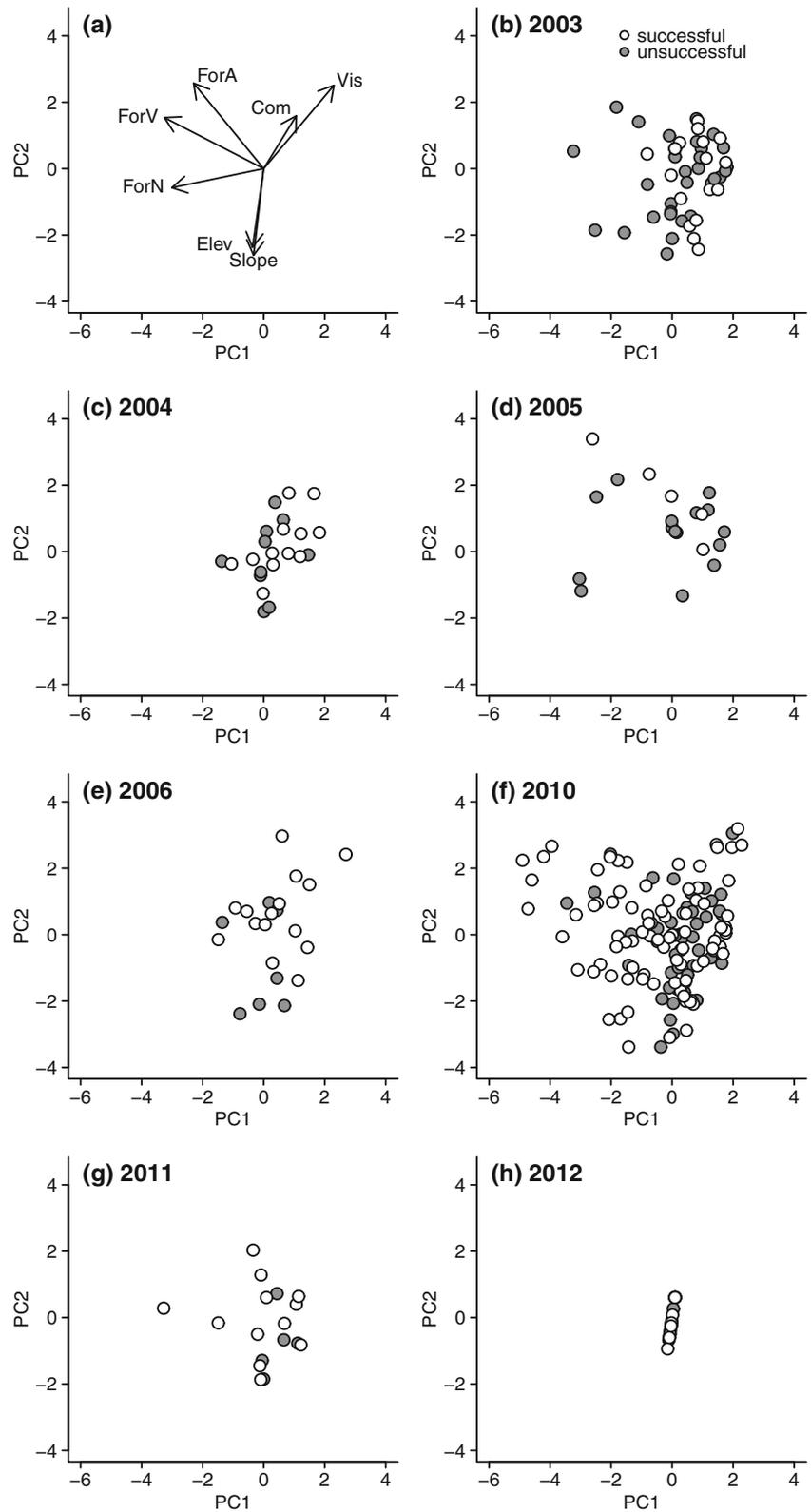
Table 1 Colony size, number of nests within 30 m of a neighbour, nest density and clustering information for the pink-footed goose colony studied at Sassendalen in Svalbard between 2003 and 2012

Year	Colony size (nest numbers)	Number of nests within 30 m of a neighbour n (%)	Nest density (km ⁻²)	Nearest neighbour ratio ^a	Test statistics for nest distributions ^b (z value, p value)
2003	79	48 (61)	104	0.71	-4.33, <0.001
2004	56	35 (62)	74	0.74	-3.55, <0.001
2005	49	28 (57)	65	0.94	-0.74, 0.46
2006	94	63 (67)	124	0.78	-3.97, <0.001
2010	226	174 (77)	294	0.75	-6.31, <0.001
2011	211	173 (82)	278	0.73	-7.17, <0.001
2012	171	139 (81)	225	0.71	-8.21, <0.001

^a The nearest neighbour ratio is the observed nest distribution compared to an expected random distribution of nests. Values less than 1 indicate clustering, values equal to 1 indicate a random distribution and values greater than 1 indicate dispersion

^b The test statistics for nest distributions are the results of z tests comparing the means of a random generated nest distribution with the actual nest distribution

Fig. 4 PCA ordination diagrams of habitat characteristics measured in association with the pink-footed goose nesting success in Sassendalen, Svalbard between 2003–2006 and 2010–2012. Habitat characteristics are shown as *arrows* in **a** with *Com* plant community, *Vis* visibility from the nest, *Slope* slope, *Elev* elevation, *ForN* distance to nearest forage area, *ForV* distance to nearest visible forage area and *ForA* size of nearest forage area. In any one year, successful nests are shown as *hollow symbols* and unsuccessful nests as *filled symbols*



snow edge as an indicator of suitable nesting habitat. For instance, the edge of these persistent snow patches occurred at the junctions of exposed steep ridges and horizontal, flatter

parts of the tundra. Wisz et al. (2008) predicted that nests would be preferentially established on the edge of such steeper slopes, and we hypothesise that pink-footed geese establish

their nests along exposed ridge edges and within patches of *D. octopetala* vegetation because winds blow the snow away from these areas before other parts of the landscape, such as areas vegetated with *C. tetragona*, which is characteristic of deeper winter snow cover (Mallik et al. 2011). Such locations also had very good all-round visibility, allowing the approach of predators to be easily observed. This may aid in nest defence and explain why long-lived pink-footed geese, similar to Emperor geese *Chen canagica* and Cackling geese *Branta hutchinsii minima* (Petersen 1990), prefer to nest in more open areas, as it helps maximise adult survival and lifetime reproductive output. With pink-footed geese, most egg losses occur when the nest is left unattended by adults moving away to feed rather than due to adult geese being forced off the nest by predators (Inglis 1977; Madsen et al. 1998). Hence, nesting close to food resources, particularly where the nest is visible while feeding, would be beneficial as adults can quickly return to the nest if approaching predators are spotted. Thus, good visibility from the nest and easily accessible food resources may be crucial in avoiding nest predation and may explain why many pink-footed goose nests are established in areas where food availability is good. Close proximity of food resources may also indicate why a large colony has been established at this location in Sassendalen, as it is situated on the ridges that overlook the widest extent of wetland vegetation in the valley.

This colony grew primarily by infilling rather than by expansion across a larger area of the tundra, with clustering of nests in every year with the exception of 2005 when nest numbers were lowest. Clustered nest distributions can arise due to lack of suitable nesting habitat, forcing individuals to occupy new nest locations in very close proximity to neighbours. Kinship processes, whereby the offspring of adults already nesting within a colony return to establish their nests close to that of relatives, may also promote a clustered nest distribution, e.g. the formation of clusters of continuous territories by red grouse *Lagopus lagopus scoticus* kin (Piertney et al. 1999; MacColl et al. 2000). Since nests were established across areas of differing nest site characteristics and the majority of nests in this colony were established at very short nearest neighbour distances, it is unlikely that habitat availability has limited nest establishment here, and hints that many of the adults breeding in this colony were tolerated and may therefore be kin. Particularly, since pink-footed geese are known to display antagonistic behaviour towards conspecifics which intrude close to the nest (Inglis 1977), and lower rates of aggressive disputes with neighbours that are kin compared to those that are not closely related have been observed in other species that form kin structures during nesting (Watson et al. 1994). Indeed, since kinship and natal philopatry are important factors in colony formation and growth in barnacle geese *Branta leucopsis* (van der Jeugd et al. 2002), greater white-fronted geese *Anser albifrons frontalis* (Fowler et al. 2004) and lesser snow geese *Chen caerulescens caerulescens*

(Cooch et al. 1993), it seems highly likely that kinship processes also play an important role in the colony dynamics of pink-footed geese and have helped to shape the growth and structure of this colony.

With increasing nest numbers in the colony, new nests began to be established upslope from older nests and in locations that had reduced all-round visibility and were situated further away from food patches. Despite this change in the underlying characteristics of nest sites, we did not find evidence to support the prediction that new nests would experience reduced nesting success. This is perhaps surprising as reduced breeding success has been reported in highly colonial species such as the common guillemot when colony size increased and nest site quality declined (Kokko et al. 2004). However, the reproductive success of barnacle geese has been shown to respond positively to increasing nest aggregation density (Karagicheva et al. 2011). Thus, since one of the foremost suggested benefits of colonial breeding is reduced predation risk (Wittenberger and Hunt 1985; Anderson and Hodum 1993), nesting in a larger colony on the open tundra may thus reduce predation for wildfowl because the vigilance of many neighbours aids in detecting and repelling predators.

The predicted expansion of pink-footed geese across the Svalbard archipelago due to climatic warming in the region (Jensen et al. 2008) suggests that open tundra colonies are likely to continue to grow (Wisz et al. 2008). Although locations covering a range of different characteristics are used for nesting, the relative abundance of food resources on the open tundra and the potential protection afforded by nesting close to conspecifics may help to buffer the effects of predation and therefore reduce any potential negative effects of habitat on nesting success for the majority of colonial nesting pink-footed geese. These findings appear to support the theories that protection against predators and good access to food resources are key benefits to colonial nesting, with kinship processes a possible strong driver behind the observed pattern of spatial dynamics of nest distribution in this rapidly expanding colony.

Acknowledgments Juliet Blum, Malcolm Parsons and Troels Hastrup are thanked for their contributions to data collection in the field. We are indebted to Christiaane Hübner for her considerable help before, during and after fieldwork. The Norwegian Polar Institute supplied the vital logistic support and the Governor of Svalbard allowed access to Sassendalen.

Ethical standards This study complied with the laws of Norway, and all permissions required for this work were granted by the Governor of Svalbard.

References

Anderson DJ, Hodum PJ (1993) Predator behaviour favors clumped nesting in an oceanic seabird. *Ecology* 78:2462–2464

- Barta Z, Szép T (1995) Frequency-dependent selection on information-transfer strategies at breeding colonies: a simulation study. *Behav Ecol* 6:308–310
- Brown CR, Stutchbury BJ, Walsh PD (1990) Choice of colony size in birds. *Trends Ecol Evol* 5:398–403
- Cooch EG, Jeffries RL, Rockwell RF, Cooke F (1993) Environmental change and the cost of philopatry: an example in the lesser snow goose. *Oecologia* 93:128–138
- Cooke F, MacInnes CD, Prevett JP (1975) Gene flow between breeding populations of lesser snow geese. *Auk* 92:493–510
- Cotter RC (1999) The reproductive biology of rock ptarmigan (*Lagopus mutus*) in the central Canadian arctic. *Arctic* 52:23–32
- Daunt F, Benvenuti S, Harris MP, Dall'Antonia L, Elston DA, Wanless S (2002) Foraging strategies of the black-legged kittiwake *Rissa tridactyla* at a North Sea colony: evidence for a maximum foraging range. *Mar Ecol Prog Ser* 245:239–247
- Davis JB, Kaminski RM, Stephens SE (1998) Wood duck eggshell membranes predict duckling numbers. *Wildl Soc B* 26:299–301
- Dunn PK (2014) tweedie: Tweedie exponential family models. R package version 2.2.1, <http://r-project.org/package=tweedie>
- Elvebakk A (1997) Tundra diversity and ecological characteristics of Svalbard. In: Wielgolaski FE (ed) *Ecosystems of the world 3: polar and alpine tundra*. Elsevier, Amsterdam, pp 347–359
- Ens BJ, Kersten M, Brenninkmeijer A, Hulscher JB (1992) Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *J Anim Ecol* 61:703–715
- Forslund P, Larsson K (1992) Age-related reproductive success in the barnacle goose. *J Anim Ecol* 61:195–204
- Fowler AC, Eadie JM, Ely CR (2004) Relatedness and nesting dispersion within breeding populations of greater white-fronted geese. *Condor* 106:600–607
- Frafjord K (1990) A study of the pink-footed goose in Gipsdalen, Svalbard, during the pre-breeding and early breeding periods. In: Severinsen T, Hansson R (eds) *Environmental Atlas Gipsdalen, Svalbard, vol III, Reports on the Fauna of Gipsdalen*. Norsk Polarintitutt, Oslo, pp 1–18
- Fretwell SD, Lucas HL (1969) On territorial behaviour and other factors influencing habitat distribution in birds. Part 1 theoretical development. *Acta Biotheor* 1:16–36
- Harris MP, Wanless S, Barton TR, Elston DA (1997) Nest site characteristics, duration of use and breeding success in the Guillemot *Uria aalge*. *Ibis* 139:468–476
- Inglis IR (1977) The breeding behaviour of the pink-footed goose: behavioural correlates of nesting success. *Anim Behav* 25:747–764
- Jensen RA, Madsen J, O'Connell M, Wisz MS, Tømmervik H, Mehlum F (2008) Prediction of the distribution of Arctic-nesting pink-footed geese under a warmer climate scenario. *Global Chang Biol* 14:1–10
- Jensen GH, Madsen J, Johnson FA, Tamstorf M (2014) Snow conditions as an estimator of the breeding output in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biol* 37:1–14
- Jepsen JU, Eide NE, Prestrud P, Jacobsen LB (2002) The importance of prey distribution in habitat use by arctic foxes (*Alopex lagopus*). *Can J Zool* 80:418–429
- Johnson DH, Shaffer TL (1990) Estimating nest success: when Mayfield wins. *Auk* 107:595–600
- Karagicheva J, Rakhimberdiev E, Dobrynin D, Saveliev A, Rozenfeld S, Pokrovskaya O, Stahl J, Prop J, Litvin K (2011) Individual inter-annual nest-site relocation behaviour drives dynamics of a recently established Barnacle Goose *Branta leucopsis* colony in sub-arctic Russia. *Ibis* 153:622–626
- Kokko H, Harris MP, Wanless S (2004) Competition of breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. *J Anim Ecol* 73:367–376
- Løvenskiöld HL (1964) Avifauna Svalbardensis. *Nor Polarinst Skr* 129:125–134
- MacColl ADC, Piertney SB, Moss R, Lambin X (2000) Spatial arrangement of kin affects recruitment success in young male red grouse. *Oikos* 90:261–270
- Madsen J, Williams JH (2012) International species management plan for the Svalbard pink-footed goose *Anser brachyrhynchus*. AWEA 48:1–51
- Madsen J, Bregnballe T, Frikke J, Kristensen JB (1998) Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard light-bellied brent geese *Branta bernicla hrota*. In: Mehlum F, Black JM, Madsen J (eds) *Research on arctic geese, Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 1997*. Norsk Polarintitutt, Oslo, pp 221–234
- Madsen J, Tamstorf M, Klaassen M, Eide N, Glahder C, Rigét F, Nyegaard H, Cottaar F (2007) Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed geese *Anser brachyrhynchus*. *Polar Biol* 30:1363–1372
- Madsen J, Tombre I, Eide NE (2009) Effects of disturbance on geese in Svalbard: implications for regulating increasing tourism. *Polar Res* 28:376–389
- Mallik AU, Wdowiak JV, Cooper EJ (2011) Growth and reproductive responses of *Cassiope tetragona*, a circumpolar evergreen shrub, to experimentally delayed snowmelt. *Arct Antarct Alp Res* 43:404–409
- McLaren MA, Alliston G (1985) Effects of snow and ice on waterfowl distribution in the central Canadian arctic islands. *Arctic* 38:43–52
- Mehlum F (1998) Areas in Svalbard important for geese during the pre-breeding, breeding and post-breeding periods. In: Mehlum F, Black JM, Madsen J (eds) *Research on arctic geese, Proceedings of the Svalbard Goose Symposium, Oslo, Norway, 1997*. Norsk Polarintitutt, Oslo, pp 41–55
- Møller AP (1987) Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. *Anim Behav* 35:819–832
- Nyholm ES (1965) Ecological observations on the geese of Spitsbergen. *Ann Zool Fenn* 2:197–207
- Petersen MR (1990) Nest-site selection by emperor geese and cackling Canada geese. *Wilson Bull* 102:413–426
- Piertney SB, MacColl ADC, Lambin X, Moss R, Dallas JF (1999) Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). *Biol J Linn Soc* 68:317–331
- Prestrud P (1992) Food habitats and observations of the hunting behaviour of arctic foxes, *Alopex lagopus*, in Svalbard. *Can Field Nat* 106:225–236
- Prop J, Oudman T, van Spanje TM, Wolters EH (2013) Patterns of predation of pink-footed goose nests by polar bear. *Omis Nor* 36:38–46
- R Core Team (2012). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Smith PA, Gilchrist HG, Forbes MR, Martin JL, Allard K (2010) Inter-annual variation in the breeding chronology of arctic shorebirds: effects of weather, snow melt and predators. *J Avian Biol* 41:292–304
- Stokes DL, Boersma PD (2000) Nesting density and reproductive success in a colonial seabird, the Magellanic penguin. *Ecology* 81:2878–2891
- van der Jeugd HP, van der Veen IT, Larsson K (2002) Kin clustering in barnacle geese: familiarity or phenotype matching? *Behav Ecol* 13:786–790
- Vanderpuye AW, Elvebakk A, Nilsen L (2002) Plant communities along environmental gradients of high-arctic mires in Sassendalen, Svalbard. *J Veg Sci* 13:875–884
- Watson A, Moss R, Parr R, Mountford MD, Rothery P (1994) Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. *J Anim Ecol* 63:39–50
- Wisz MS, Tamstorf MP, Madsen J, Jespersen M (2008) Where might the western Svalbard tundra be vulnerable to pink-footed goose (*Anser brachyrhynchus*) population expansion? *Divers Distrib* 14:26–37
- Wittenberger JF, Hunt GL (1985) The adaptive significance of coloniality in birds. In: Famer DS, King JR, Parkes KC (eds) *Avian biology* 8. Academic, London, pp 1–78