Dads on duty:
First account of nest sitting in Barnacle ganders

Isabella B.R. Scheiber[1,*], Annabel J. Slettenhaar[2,3], Maarten J.J.E. Loonen[3] & Margje E. de Jong[1,3]

Scheiber I.B.R., Slettenhaar A.J., Loonen M.J.J.E. & de Jong M.E. 2025. Dads on duty: First account of nest sitting in Barnacle ganders. Ardea 113: 45–52. doi:10.5253/arde.2024.a21

In most Anseriformes (ducks, geese and swans) only females are known to incubate. Here we describe incidents of male nest sitting in Barnacle Geese *Branta leucopsis* as a form of paternal care. Based on pictures from wildlife cameras, we identified males sitting on their nests when their mates took incubation recesses. Wildlife cameras were placed at nests of which either the male or female was fitted with a GPS neck collar in the year prior, which aided with identifying individual birds on the nest. To attach transmitters, some geese were caught while defending their nests, thus we may have unintentionally selected bolder males as they defended their nests more aggressively and were easier to catch. Nest sitting occurred relatively frequently, i.e. in 6 out of 15 individuals. Our results show that males with collars were more likely to nest sit than males without a collar. We discuss several possible functions of this behaviour: protection against aerial predators, thermal control of nest temperature and protection against intraspecific brood parasitism. At this time, we cannot confirm the function of this behaviour, as the chances of successful hatching were not increased in broods with nest-sitting males, and we lack the necessary sample size for more in depth analyses. Lastly, we argue that 'male incubation' is misleading in the waterfowl literature, as it is truly justified for only two species, the Black Swan *Cygnus atratus* and Black-Bellied Whistling Duck *Dendrocygna autumnalis*.

Key words: *Branta leucopsis*, geese, waterfowl, paternal care, male incubation, incubation behaviour

[1]Dept. of Behavioral and Cognitive Biology, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria;
[2]Faculty of Biosciences and Aquaculture, Nord University, Kongens Gate 42, 7713 Steinkjer, Norway;
[3]Arctic Centre, Aweg 30, 9718 CW Groningen, The Netherlands;
*corresponding author (isabella.scheiber@univie.ac.at)

Nest defence by parents is considered a risky behaviour, as they may endure injury or even death when trying to ward off predators (de Jong *et al.* 2021, Samelius & Alisauskas 2006). Furthermore, nest defence also bears energetic costs (Caro 2005, Thys *et al.* 2019) thus the risk of clutch protection must be gauged against its benefits (Ringelman & Stupaczuk 2013). In birds, there is large variation in how much males and females contribute to parental care and in more than half of all species, males participate in incubation (Deeming & Reynolds 2015). In most waterfowl species, i.e. swans, geese and ducks, however, only females incubate. For Barnacle Geese *Branta leucopsis* breeding on Svalbard anecdotal evidence indicates that males sometimes sit on the nest (from now on referred to as 'nest sitting'). In this study we dive further into this behaviour.

The Barnacle Goose is an Arctic breeding species, renowned for nesting high on steep mountain cliffs and islets (Mitchell *et al.* 1998). They often breed on islands with Glaucous Gulls *Larus hyperboreus*, Arctic Skuas *Stercorarius parasiticus* and Great Skuas *S. skua*, which are the main avian predators of Barnacle Geese eggs and/or adults (Tombre & Erikstad 1996, Prop *et al.* 2015). Similar to other geese, such as the Lesser Snow

Goose *Anser c. caerulescens*, Pink-footed Goose *A. brachyrhynchus* and Canada Goose *B. canadensis*, Barnacle Geese protect their eggs against avian predators through a high rate of nest attendance (Prop *et al.* 1984, Samelius & Alisauskas 2001, Schreven *et al.* 2021) and active defence (Dittami *et al.* 1979, Clermont *et al.* 2019, de Jong *et al.* 2021, Speelman *et al.* 2022).

Just as in all other geese, only Barnacle females are known to incubate. During nest construction, geese develop thermosensitive brood patches, which guarantee an efficient heat transfer from the body to the egg (Jones 1971). During this time, ganders closely guard their receptive mates (Lamprecht 1989). Males stay in close vicinity of the nest, maintaining contact with their incubating mates visually and vocally (Prop *et al.* 1984). If an intruder comes close to the nest, most males actively protect and defend the nest and incubating female (Speelman *et al.* 2022).

Incubation starts after the penultimate egg is laid (Hübner *et al.* 2002) and lasts for 25 days on average (Black *et al.* 2014). Females only take brief incubation recesses for feeding and preening, as each time they leave the nest, the eggs are at risk of dropping below an optimal temperature, possibly overheating, or being discovered by a predator (Alsos *et al.* 1998, Ahmad & Li 2023). Before leaving the nest, females often use the down lining of the nest to cover the eggs for insulation and/or hide them from predators. It is commonly understood that males either join their mates during incubation recesses, leaving the nest unattended, or stay behind close to the nest (Owen & Wells 1979).

Here we report on several cases of Barnacle ganders nest sitting while females are away. The first sporadic notes of this behaviour stem from 1979 in a Barnacle Goose colony on Nordenskiöldkysten (J. Prop pers. comm.) and 2006 in our Kongsfjorden study colony database (M.J.J.E. Loonen pers. obs.). This type of behaviour was also mentioned anecdotally in a study on Pink-footed Geese breeding in Iceland, which described a few males “crouching over the eggs” for up three minutes when their female left (Inglis 1977). We decided to investigate this phenomenon further and provide the first scientific account of nest sitting in any goose species, although we cannot exclude the possibility that reports of this behaviour may have been disseminated outside peer-reviewed publications. We wanted to determine how often nest sitting of males occurred, if male age played a role, and whether individuals performing nest sitting did so multiple times or only once. Finally, we investigated whether eggs were more likely to hatch if males were nest sitting.

Table 1. Identities of 15 focal pairs, whose nests were monitored with wildlife cameras in 2021. For each individual, we provide codes of unique colour (o = orange, g = green, y = yellow, plus a three-letter code) and metal (CA#) rings, and if they were fitted with a transmitter, the neck collar ID. One male (metal only) lost its colour ring, but we identified it by reading the inscription on its metal ring. Except for two individuals, which were ringed as goslings (*), the minimum age is given, calculated from the time the geese were originally ringed as adults (mean males: 9.4 ± 3.31 y (±SD), females: 10.4 ± 4.46 y). Whether or not males sat on nests is also indicated.

Male colour ID	Male ID	Male neck collar ID	Age (y)	Male nest sitting	Female colour ID	Female ID	Female neck collar ID	Age (y)
oFYJ	CA46944	201913	16	yes	oFVD	CA46857		10
gZUN	CA45605	201915	9	yes	oFLC	CA45810		12
metal only	CA47072	201917	8	no	yBSV	CA45997		4
oFZY	CA46942	201918	10	yes	gSNF	CA36931		19
oFIJ	CA45800	201924	12	yes	yBHJ	CA45891		5
oFIA	CA45795	201930	12	yes	gLDC	CA41238		14
yBID	CA46840	201932	7	no	yBIB	CA44228		14
oFZX	CA46941		10	no	gTTL	CA41113	201912	16*
yBYI	CA45746		7	yes	yAUF	CA45744	201919	7
yAXY	CA45703		8	no	yBHY	CA46848	201925	5*
gLHX			2	no	yAVV	CA45736	201926	7
yAZT	CA45715		8	no	oFXV	CA45632	201927	10
yAXC	CA45942		8	no	yAPH	CA45929	201931	8
gTCZ	CA46957		10	no	yAXV	CA45701	201934	8
yBYX	CA41397		14	no	yBYV	CA41400	201935	14

METHODS

Our study population resides on the west coast of Spitsbergen, the largest island of the Norwegian Svalbard archipelago. In Kongsfjorden an established breeding colony nests on a group of several islets (Tombre *et al.* 1998). These islets are characterised by exposed ridges and flat stretches of tundra (Tombre & Erikstad 1996). Two are monitored in detail: the larger main breeding islet, Storholmen (c. 30 ha, 259 nests in 2021) and Prins Heinrichøya (c. 3 ha, 29 nests in 2021) located offshore of the village Ny-Ålesund (78°55'N, 11°56'E).

Within the scope of a larger study on circadian and circannual rhythmicity (de Jong *et al.* in press) we fitted 24 adults (12 males and 12 females of established pairs) in 2020 with solar-powered GPS-GSM transmitters attached with neckbands (OrniTrack-NL40 3G, Ornitela, UAB, Lithuania). Except for two geese, which were ringed as goslings, the individual age was back calculated from the time geese were originally colour marked as adults; thus, ages given in Table 1 are conservative. Individuals were chosen following a suite of criteria (for details see Supplementary Material), including that it would be desirable if both the male and female of a pair were already marked with colour rings. The neck collar allowed definite recognition of the identity of birds on and close by the nest, even when colour rings were not visible. Sexing of all individuals was performed when birds were originally ringed with metal and colour rings by examining the cloaca for the presence of intromittent penises. To attach transmitters, geese were caught in the vicinity of the nest either by hand, with a small hand-net, or a fishing rod with an attached nylon snare ('nest catches'; Fenstad *et al.* 2017), or else during the annually performed mass captures of moulting geese, where considerable numbers of geese are funnelled into a trap ('moult catches'; Loonen *et al.* 1997). Only males, which remained close to the nest when a human observer approached, could be caught by hand, using the fishing rod or hand-net. We are aware that these methods might comprise a bias in trapability sensu STRANGE, an acronym highlighting several possible sources of sampling biases (Webster & Rutz 2020), as these males show high nest defence and risk-taking behaviour (de Jong *et al.* unpubl. data). From here on we consider them 'bold'.

In 2021, we were able to locate 15 nests of the initial 24 pairs, where either the male (n = 7) or female (n = 8) was fitted with a transmitter in the previous year. During transmitter attachment, four males were caught at the nest, while three were caught during the moult catch. In the following we refer to unique colour ring codes when mentioning certain individuals.

Near the 15 nests, we set up wildlife cameras (Usogood TC30 Trail Camera) to get a more detailed picture of behaviours of males and females during incubation. Cameras were used in the past and do not seem to disturb the geese (e.g. de Jong *et al.* 2019). At each nest, we placed the camera, set in time-lapse mode, at a one-metre distance from the nest to monitor primarily the behaviour of the incubating female. Cameras took two pictures every five minutes to detect any movement of the geese. The time in which cameras provided reliable pictures varied between nests (mean: 12 ± 6.1 d (± SD; Table S1; de Jong *et al.* in press), thus we captured part of the incubation period. When scanning the photos, we noticed that in several instances males, rather than females, were sitting on the nest (Figure 1). As successive photos in a series are contingent, we only counted male nest sitting bouts as independent whenever the female returned and sat on the nest.

Statistical Analysis

Using the R programming environment (R Core Team 2021), we (1) applied a Student's t-test to determine whether male age influenced the propensity to nest sit. We applied Fisher's Exact Tests and give odds ratios and their 95% confidence intervals to determine (2) if males, which sat on the nest, were more likely to have been fitted with transmitters and (3) if male nest sitting was associated with hatching probability of the clutch, i.e. at least one egg hatched (for details on counts see 2 × 2 contingency tables, Table S2). The sample size pertaining to the method of catching (nest catch vs. moult catch) was very small and showed clear separation, because all males that were caught at the nest showed nest sitting (Hauck & Donner 1977). Due to the challenges this poses for statistical testing, we opted to refrain from a formal statistical analysis in this case.

RESULTS

Observations of the 15 nests where cameras were placed revealed that six males sat on the nest, whereas nine did not (Table 1). Age of males had no effect on nest sitting (not nest sitting: mean = 8.33 ± 3.16 year (±SD), nest sitting: mean = 11.00 ± 3.1 year; t_{13} = 1.612, P = 0.131; Figure 2A). Of the six nest sitting males, three were observed on the nest only once (gZUN, oFIJ, oFIA), whereas the other three males were observed multiple times (oFYJ and yBYI four times, oFZY six times). Males with neck collars were more likely to sit on nests than males without (Fisher's Exact Test: $P = 0.041$, $OR_{2\text{-sided}} = 13.59$ with 95% CI of 0.86–934.01; Figure 2B). Among males caught near the nest, 100% were observed sitting on nests ($n = 4$), compared to 33.3% of males caught during moult (one on nest, two not on nest; Figure 2C). Whether males nest sat had no effect on whether eggs hatched or were abandoned/depredated (Fisher's Exact Test: $P = 0.329$, $OR_{2\text{-sided}} = 0.3$ with 95% CI of 0.02–4.30; Figure 2D. See Table S2 for 2 × 2 contingency tables). All but one male (oFIA), which started to nest sit shortly after the eggs hatched (Figure S1), sat on the nest during incubation. Males took on average 12 ± 17 min (±SD, range: 0–42 min) after the female left before they started nest sitting and they on average stayed for 39 ± 21 min (range: 12–70 min). This corresponds to about 60 ± 27% (range: 16–88%) of the time the female was on incubation recess. After males terminated nest sitting, it took approximately 17 ± 13 min (range: 3–32 min) for the female to return to the nest (Table S3). Based on examinations of four nests, where we had at least three days of camera observations, the percentage of female nest recesses with male nest sitting varied greatly between individuals (mean ± SD: 20.0 ± 21.0%, range: 1.0– 43.0%; Table S4). However, throughout this study sample size is small, and these results should be taken with caution.

DISCUSSION

Nest sitting in Barnacle ganders: possible functions
To the best of our knowledge, this is the first scientific account of males sitting on nests in any goose species. Although we may have introduced a bias in catching predominantly bold individuals (Webster & Rutz 2020), this does not alter the fact that some ganders perform this behaviour. We oppose to calling this behaviour 'male incubation', as termed repeatedly in the waterfowl literature (e.g. Rollin 1957, Bruggers 1979, Hawkins 1986, Brugger & Taborsky 1994), because there cannot be active transfer of heat from the male to the eggs as ganders do not form brood patches. Thus, we revive the term 'nest sitting' (Henson & Cooper 1992) as the appropriate label. We identified from the photos that male posture on the nest was somewhat different from the female posture during incubation, in that males sat higher than females, not in the nest bowl but rather on top of the nest (compare panels A and D in Figure 1). Female ducks and geese sometimes adopt

Figure 1. An example of one Barnacle gander nest sitting. Photos taken on 18 June 2021, between 15:48 and 16:28. (A) The female without a neck collar, fitted with the individual orange colour ring oFVD, is incubating. (B) The female left the nest. (C) Male oFYJ (ring lost during breeding) with neck collar approaches the nest. (D) He sits on the nest with the neck collar clearly visible. (E) The female (with the colour ring partially visible) returns to the nest. (F) She resumes incubation. Temperature, date and time are shown in the lower right-hand corner of each photo.

such a posture not only before actual incubation starts, but also during incubation (Lorenz 1991, Poussart *et al.* 2000, Hartman *et al.* 2023) to shield the nest and eggs from e.g. predation, inclement weather and/or intra-specific brood parasitism. We propose that male nest sitting has equivalent functions in the absence of the female. To date, we cannot provide an explanation of why this behaviour occurs, as neither the age of males seems to play a role, nor could we show an increase in hatching success of nests where males nest sat. At this moment we lack a large enough sample for more in-depth analyses, such as when nest sitting occurs across the nesting period or to what extent males may compensate for more or longer incubation recesses of their mates. Furthermore, it should also be investigated in-depth, whether males adjust their behaviour in response to certain environmental conditions, such as nest density and location, and whether nest sitting confers fitness benefits (Mery & Burns 2010, Madsen *et al.* 2019). In the following we suggest three possible, not mutually exclusive, functions of male nest sitting to initiate future studies not only in Barnacle Geese, but also other goose species.

The primary cause of hatching failure in ground nesting waterfowl is predation, thus various strategies are employed for nest protection (Schranck 1972, Samelius & Alisauskas 2001, Quinn *et al* 2003, Peterson *et al.* 2022). Geese often nest near their main aerial predators. By not leaving the nest unattended when the females are away, the nest sitting of Barnacle ganders might function in shielding the nest. This is in keeping with our experience of being able to catch the most aggressive males when attaching transmitters, those who might be bold enough to attack predators actively. In the future, attention should be paid to how often nest sitting occurs, how long the incubation recesses of the female last, what the predation pressure is, and at which stage during incubation the behaviour is performed, to gain a deeper understanding of male nest sitting as one form of predator protection.

Another possible function of nest sitting by males is to control the temperature in the nest. To some extent, nest insulation can reduce both the degree of egg cooling when the female is absent and the time spent to rewarm the eggs after she returns from an incubation recess (Thompson & Raveling 1988). Indeed, Arctic geese adjust their incubation behaviour in response to prevailing weather conditions (Harvey 1971, Poussart *et al.* 2001, Elkins 2004). Yet, egg cooling in the absence of the female might be overestimated, as even under unfavourable weather conditions egg temperature drops during incubation recesses are not large enough to endanger an embryo's development or survival (Poussart *et al.* 2000). It is worth noting that over-heating of unprotected eggs in the nest might become an issue in the Arctic in the future. Even if Barnacle nests are exposed to direct sun, they probably will, at present, not reach this temperature limit long enough for embryos to die. Yet, Common Guillemots *Uria aalge* already showed an increased probability of egg loss at higher temperatures in a high-latitude colony in the Baltic Sea (Olin *et al.* 2024). Taken together, although nest sitting of Barnacle ganders might assist in the temperature control of eggs in the nest, we suggest it to only play a minor role, at least here and now.

If male nest sitting occurs during the period of egg

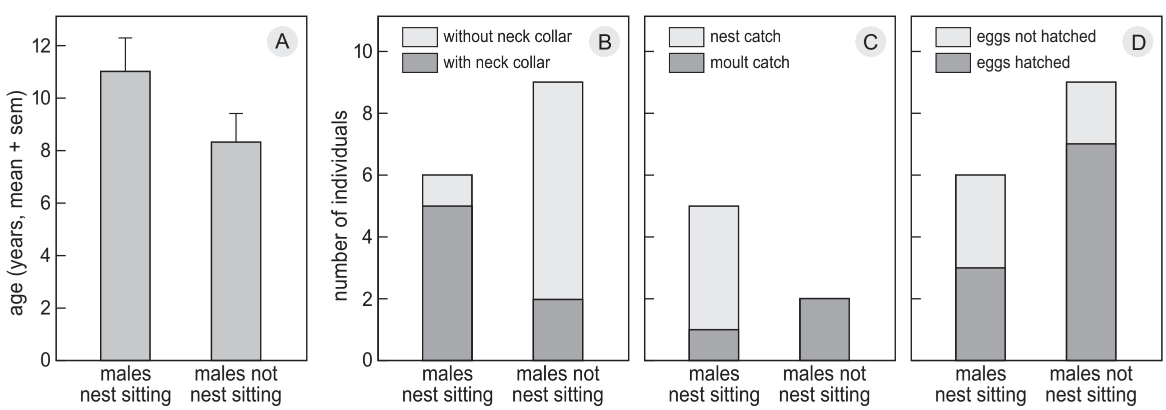

Figure 2. Features which might influence nest sitting in Barnacle ganders. (A) Age did not affect the likelihood of males to nest sit (Student's *t*-test: $P > 0.05$, whiskers represent SEM). (B) Males which were fitted with a neck collar, were more likely to nest sit than males without (Fisher's Exact Test: $P = 0.041$). (C) Among males caught near the nest, 100% were observed to nest sit, while only 33.3% of males caught during moult did so. (D) Whether eggs hatched or did not hatch was independent of males' nest sitting (Fisher's Exact Test: $P > 0.05$).

laying, another possible function might be to prevent intraspecific brood parasitism, which frequently occurs in Barnacle Geese (Black *et al.* 2014). We cannot answer this question adequately, however, because we placed cameras once the host female had started incubation, therefore lack information from the laying period.

'Male incubation' in waterfowl?
In the literature only swans *Cygnus* spp., and to some extent whistling ducks *Dendrocygna* spp. are described to deviate from the female-only incubation pattern in waterfowl, as here male incubation occurs (Hawkins 1986, Scott 1977, Brugger & Taborsky 1994,). But are these males indeed incubating or is it a term that should be avoided, as it leads to a misconception when compared with species where incubation is truly shared (Deeming & Reynolds 2015)?

Hawkins already concluded that male incubation in Tundra Swans *Cygnus c. columbianus* was not essential for successful embryo development (Hawkins 1986) but protected against egg predation and provided some egg cooling benefits. This led Henson & Cooper (1992) to apply the term 'nest sitting' in Trumpeter Swans *C. buccinator*, as here males are occasionally exhibiting some of the nest-settling motions characteristic of incubating females, independent of predator presence or adverse weather conditions. Our extensive search of the literature revealed that in most cases in which male incubation was described (e.g. Rollin 1957, Flickinger 1975, Bruggers 1979), they nest sit rather than incubate.

The two notable exceptions, for which the term incubation is warranted, are the Black Swan *Cygnus atratus* and Black-bellied Whistling-duck *Dendrogygna autumnalis*. Where the Black Swan exhibits the typical long-term monogamy and biparental care of swans, this is true also for the Black-bellied Whistling-duck, a feature atypical for ducks. Some other features which the two species share are that neither females nor males develop brood patches (Skutch 1976, Bolen & Smith 1979), thus either parent is equally fit to incubate, and that both species may re-nest after successful breeding attempts (Delnicki 1973, Bolen & Smith 1979, Brugger & Taborsky 1994, James *et al.* 2012, Coleman 2014). Most other waterfowl attempt a second clutch only if the first one failed. Black Swan and Black-bellied Whistling-duck might be able to re-nest because both parents incubate. Near constant incubation minimizes the time of egg development and hatching, thereby shortening the inter-clutch interval (James *et al.* 2012).

Conclusion
To sum up, this is the first scientific report in any goose species, where males expand paternal duties beyond the established view, namely that during the breeding period they only protect the nest and female in close vicinity of the nest. We have pictorial evidence that several Barnacle ganders nest sat in the absence of their mates. Both predation and thermal risks are increased for eggs which are not protected by parents. In Barnacle Geese, we suggest the nest sitting of males to be a response to avian predator presence. We cannot exclude that preventing egg cooling in the absence of the female may also play a role but consider this unlikely. Our final point is that in most waterfowl species, males do not participate in incubation. Nest sitting is an unbiased term and should be used for cases in which no active warming of eggs has (yet) been demonstrated.

ACKNOWLEDGEMENTS

We are grateful to Børge Moe (Norwegian Institute for Nature Research, NINA) as the project administrator of AJS' field grant, the staff of the French-German Arctic Research Base at Ny-Ålesund, chiefly Bettina Haupt (station leader AWI 2020/21) and Kings Bay AS, Ny-Ålesund for logistic support. We thank Jouke Prop for sharing his unpublished observations and Kees Schreven for directing our attention to the one dated reference, where nest sitting in ganders was briefly alluded to. Comments by two anonymous reviewers and Thomas Lameris from the editorial board of Ardea helped to improve an earlier version of this manuscript. Funding was provided by the Austrian Science Fund (P32216 to IBRS) and an Arctic Field Grant (The Research Council of Norway) in collaboration with NINA (ES676286, to AJS). The study conforms to Directive 2010/63/EU and was conducted under FOTS ID 23358 from the Norwegian Animal Research Authority and approved by the Governor of Svalbard (RIS ID 11237). The data that support the findings of this study are provided within the article and corresponding supplementary material.

REFERENCES

Ahmad I.M. & Li D. 2023. More than a simple egg: Underlying mechanisms of cold tolerance in avian embryos. Avian Res. 14: 100104.

Alsos I.G., Elvebakk A. & Gabrielsen G.W. 1998. Vegetation exploitation by barnacle geese *Branta leucopsis* during incubation on Svalbard. Polar Res. 17: 1–14.

Black J.M., Prop J. & Larsson K. 2014. The Barnacle Goose. Bloomsbury Publishing, London, UK.

Bolen E.G. & Smith E.N. 1979. Notes on the incubation behavior of black-bellied whistling ducks. Prairie Nat. 11: 119–123.

Brugger C. & Taborsky M. 1994. Male incubation and its effect on reproductive success in the black swan, *Cygnus atratus*. Ethology 96: 138–146.

Bruggers R.L. 1979. Nesting patterns of captive mandarin ducks. Wildfowl 30: 45–54.

Caro T.M. 2005. Antipredator defenses in birds and mammals. University of Chicago Press, Chicago, USA.

Clermont J., Réale D. & Giroux J.-F. 2019. Similarity in nest defense intensity in Canada goose pairs. Behav. Ecol. Sociobiol. 73: 108.

Coleman J.T. 2014. Breeding biology of the black swan *Cygnus atratus* in southeast Queensland, Australia. Wildfowl 64: 217–230.

de Jong M.E., Nicolaus M., Fokkema R.W. & Loonen M.J.J.E. 2021. State dependence explains individual variation in nest defence behaviour in a long-lived bird. J. Anim. Ecol. 90: 809–819.

de Jong M.E., Wetherbee R. & Loonen M.J.J.E. 2019. Effects of fleas on nest success of Arctic barnacle geese: Experimentally testing the mechanism. J. Avian Biol. 50: e01944.

de Jong M.E., Slettenhaar A.J., Fokkema R.W., Leh M., Verhoeven M.A., Griffin L., Millesi E., Moe B., Barnreiter E., Loonen M.J.J.E. & Scheiber I.B.R. In press. Diel rhythmicity of activity and corticosterone metabolites in Arctic barnacle geese during breeding. Behav. Ecol.

Deeming D.C. & Reynolds S.J. 2015. Nests, eggs, and incubation: New ideas about avian reproduction. Oxford University Press, Oxford, UK.

Delnicki D.E. 1973. Renesting, incubation behavior, and compound clutches of the black-bellied tree duck in southern Texas, MSc, Texas Tech University, Lubbock, TX, USA.

Dittami J.P., Kennedy S. & Thomforde C. 1979. Observations on barnacle goose breeding, *Branta leucopsis*, in Spitsbergen 1975. J. Ornithol. 120: 188–195.

Elkins N. 2004. Breeding: Incubation. In: Elkins N. (ed.) Weather and bird behaviour. T. & A.D. Poyser, London, UK, pp. 101–104.

Fenstad A.A., Bustnes J., Lierhagen S., Gabrielsen K.M., Öst M., Jaatinen K., Hannssen S.A., Moe B., Jenssen B.M. & Krøkje Å. 2017. Blood and feather concentrations of toxic elements in a Baltic and an Arctic seabird population. Mar. Pollut. Bull. 114: 1152–1158.

Flickinger E.L. 1975. Incubation by a male fulvous tree duck. Wilson Bull. 87: 106–107.

Hartman C.A., Ackerman J.T., Peterson S.H., Fettig B., Casazza M. & Herzog M.P. 2023. Nest attendance, incubation constancy, and onset of incubation in dabbling ducks. PLOS One 18: e0286151.

Harvey J.M. 1971. Factors affecting blue goose nesting success. Can. J. Zool. 49: 223–234.

Hauck W.W. & Donner A. 1977. Wald's test as applied to hypotheses in logit analysis. JASA 72: 851–853.

Hawkins L.L. 1986. Nesting behaviour of male and female whistling swans and implications of male incubation. Wildfowl 37: 5–27.

Henson P. & Cooper J.A. 1992. Division of labour in breeding trumpeter swans *Cygnus buccinator*. Wildfowl 43: 40–48.

Hübner C.E., Tombre I.M. & Erikstad K.E. 2002. Adaptive aspects of intraclutch egg-size variation in the high Arctic barnacle goose (*Branta leucopsis*). Can. J. Zool. 80: 1180– 1188.

Inglis I.R. 1977. The breeding behaviour of the pink-footed goose: Behavioural correlates of nesting success. Anim. Behav. 25: 747–764.

James J.D., Thompson J.E. & Ballard B.M. 2012. Evidence of double brooding by black-bellied whistling-ducks. Wilson J. Ornithol. 124: 183–185.

Jones R.E. 1971. The incubation patch of birds. Biol. Rev. 46: 315–339.

Lamprecht J. 1989. Mate guarding in geese: Awaiting female receptivity, protection of paternity or support of female feeding. In: Rasa A.E., Vogel C. & Voland E. (eds) The sociobiology of sexual and reproductive strategies. Springer Science and Business Media, Dordrecht, NL.

Loonen M.J.J.E., Oosterbeek K. & Drent R.H. 1997. Variation in growth of young and adult size barnacle geese *Branta leucopsis*: Evidence for density dependence. Ardea 85: 177–192.

Lorenz K. 1991. Here I am – where are you? Hartcourt Brace Jovanovich, New York, NY, USA.

Madsen J., Jaspers C., Frikke J., Gundersen O.M., Nolet B.A., Nolet K., Schreven K.H.T., Sonne C. & de Vries P.P. 2019. A gloomy future for light-bellied brent geese in Tusenøyane, Svalbard, under a changing predator regime. Polar Res. 38: 3393.

Mery F. & Burns J.G. 2010. Behavioural plasticity: An interaction between evolution and experience. Evol. Ecol. 24: 571–583.

Mitchell C., Black J.M. & Evans M. 1998. Breeding success of cliff-nesting and island-nesting barnacle geese in Svalbard. Norsk Polar. Skrift. 200: 141–146.

Olin A.B., Dück L., Berglund P.A., Karlsson E., Bohm M., Olsson O. & Hentati-Sundberg J. 2024. Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. Mar. Ecol. Prog. Ser. 737: 147–160.

Owen M. & Wells R.L. 1979. Territorial behaviour in breeding geese – A re-examination of Ryder's hypothesis. Wildfowl 30: 20–26.

Peterson S.H., Ackerman J.T., Keating M.P., Schacter C.R., Hartman C.A., Casazza M.L. & Herzog M.P. 2022. Predator movements in relation to habitat features reveal vulnerability of duck nests to predation. Ecol. Evol. 12: e9329.

Poussart C., Larochelle J. & Gauthier G. 2000. The thermal regime of eggs during laying and incubation in greater snow geese. Condor 102: 292–300.

Poussart C., Gauthier G. & Jacques L. 2001. Incubation behaviour of greater snow geese in relation to weather conditions. Can. J. Zool. 79: 671–678.

Prop J. *et al.* & Moe B. 2015. Climate change and the increasing impact of polar bears on bird populations. Front. Ecol. Evol. 3: 33.

Quinn J.L., Prop J., Kokorev Y. & Black J.M. 2003. Predator protection or similar habitat selection in red-breasted goose nesting associations: Extremes along a continuum. Anim. Behav. 65: 297–307.

R Core Team 2021. R: A language and environment for statistical computing, 1.13 ed. R Foundation for Statistical Computing, Vienna, Austria.

Ringelman K.M. & Stupaczuk M.J. 2013. Dabbling ducks increase nest defense after partial clutch loss. Condor 115: 290–297.

Rollin N. 1957. Incubation by drake wood duck in eclipse plumage. Condor 59: 263–265.

Samelius G. & Alisauskas R.T. 2001. Deterring arctic fox predation: The role of parental nest attendance by lesser snow geese. Can. J. Zool. 79: 861–866.

Samelius G. & Alisauskas R.T. 2006. Sex-biased costs in nest defence behaviours by lesser snow geese (*Chen caerulescens*): Consequences of parental roles. Behav. Ecol. Sociobiol. 59: 805–810.
Schranck B.W. 1972. Waterfowl nest cover and some predation relationships. J. Wildl. Manag. 36: 182.
Schreven K.H.T., Stolz C., Madsen J. & Nolet B.A. 2021. Nesting attempts and success of Arctic-breeding geese can be derived with high precision from accelerometry and GPS-tracking. Anim. Biotelem. 9: 25.
Scott D. 1977. Breeding behaviour of wild whistling swans. Wildfowl 28: 101–106.
Skutch A.F. 1976. Parent birds and their young. University of Texas Press.
Speelman F.J.D., Hammers M., Komdeur J. & Loonen M.J.J.E. 2022. Nest defence behaviour is similar between pair members but only male behaviour predicts nest survival in barnacle geese. J. Avian Biol. 2022: e02982.
Thompson S.C. & Raveling D.G. 1988. Nest insulation and incubation constancy of Arctic geese. Wildfowl 39: 124–132.
Thys B., Lambreghts Y., Pinxten R. & Eens M. 2019. Nest defence behavioural reaction norms: Testing life-history and parental investment theory predictions. R. Soc. Open Sci. 6: 182180.
Tombre I.M. & Erikstad E. 1996. An experimental study of incubation effort in high-Arctic barnacle geese. J. Anim. Ecol. 65: 325–331.
Tombre I.M., Mehlum F. & Loonen M.J.J.E. 1998. The Kongsfjorden colony of barnacle geese: Nest distribution and the use of breeding islands 1980–1997. Norsk Polar. Inst. Skrift. 200: 57–65.
Webster M.M. & Rutz C. 2020. How STRANGE are your study animals? Nature 582: 337–340.

SAMENVATTING

Van de meeste Anseriformes (eenden, ganzen en zwanen) is bekend dat alleen de vrouwtjes broeden. Hier beschrijven we, op basis van foto's van wildcamera's, een aantal gevallen van mannelijke Brandganzen *Branta leucopsis* die op het nest gingen zitten tijdens broedpauzes van hun partner. We plaatsten de wildcamera's in Kongsfjorden, Spitsbergen, bij nesten waarvan het mannetje of vrouwtje het jaar daarvoor een GPS-halsband had gekregen, wat hielp bij het identificeren van individuele vogels op het nest. Om de halsbanden aan te leggen werden sommige ganzen gevangen terwijl ze hun nest verdedigden, waardoor we mogelijk onbedoeld dappere mannetjes selecteerden die hun nest agressiever verdedigden en zo gemakkelijker te vangen waren. 'Nestzitten' kwam relatief vaak voor, namelijk bij zes van de 15 mannetjes. Onze resultaten laten zien dat mannetjes met halsbanden vaker 'nestzitten' dan mannetjes zonder halsband. We bespreken verschillende mogelijke functies van dit gedrag, zoals het tegengaan van nestroof door luchtpredatoren, voorkomen van intraspecifiek broedparasitisme en het op peil houden van de nesttemperatuur. We vonden geen bewijs dat de kans op succesvol uitkomen hoger was voor nesten van 'nestzittende' mannetjes en onze steekproef was niet voldoende groot genoeg voor meer diepgaande analyses. Ons onderzoek laat echter zien dat de rol van mannetjes Brandganzen in de zorg voor het nest uitgebreider kan zijn dan alleen op wacht staan.

Corresponding editor: Thomas Lameris
Received 16 September 2024; accepted 16 December 2024

Supplementary Material is available online
www.ardeajournal.nl/supplement/s113-045-052.pdf

SUPPLEMENTARY MATERIAL

Criteria for attachment of transmitters to selected focal individuals:

1) Minimum age of three years
2) Both pair partners with uniquely coded colour rings desirable
3) Observed in Ny-Ålesund in two consecutive years to ensure that they went throug at least one complete annual cycle
4) Preferably with known nest site locations
5) Found in and/or close to the village after hatching of young
6) Good health as judged by their physique and plumage condition

Table S1. Details of wildlife camera placement at 15 Barnacle Goose nests in 2021. For each individual we provide codes of colour rings, GPS transmitter ID and sex. Abbreviations of nest locations on islets in Kongsfjorden (see also Figure 1): SH: Storholmen, PH: Prins Heinrichøya, JH: Juttaholmen, OH: Observasjonsholmen, MH: Midtholmen. Date and time when cameras were placed and the number of days during which they provided reliable pictures of observations of males and females on the nest are provided. Nest fate indicates whether eggs hatched (H), nests were abandoned (A) or depredated (P).

Nest Nr.	Goose Colour ID (Transmitter Nr.)	Sex	Nest Location	Camera placed (Date, Time)	Number of days with at least one observation	Nest fate
1	oFYJ (201913)	M	SH	18/06 02:55	3	A/P?
2	gZUN (201915)	M	JH	25/06 14:04	1	P
3	metal only (201917)	M	SH	18/06 03:05	14	H
4	oFZY (201918)	M	SH	18/06 01:48	4	A
5	oFIJ (201924)	M	SH	18/06 01:17	15	H
6	oFIA (201930)	M	SH	18/06 02:10	19	H
7	yBID (201932)	M	SH	18/06 02:17	18	H
8	gTTL (201912)	F	SH	18/06 03:22	15	H
9	yAUF (201919)	F	SH	18/06 02:30	13	H
10	yBHY (201925)	F	SH	18/06 02:41	16	H
11	yAVV (201926)	F	MH	25/06 15:26	12	H
12	oFXV (201927)	F	OH	25/06 14:52	14	H
13	yAPH (201931)	F	JH	25/06 14:14	3	P
14	yAXV (201934)	F	PH	09/06 15:22	15	A/P?
15	yBYV (201935)	F	SH	18/06 01:05	18	H

Table S2. 2 × 2 contingency tables of males, which were or were not sitting on nests and whether they were (A) fitted with neck collars, (B) caught during moult or at the nest and (C) if eggs hatched or not.

		Male sitting on nest	Male not sitting on nest	Total
A	Male with neck collar	5	2	7
	Male without neck collar	1	7	8
	Total	6	9	15
B	Moult catch	1	2	3
	Nest catch	4	0	4
	Total	5	2	7
C	Eggs hatched	3	7	10
	Eggs did not hatch	3	2	5
	Total	6	9	15

Table S3. Individual observations of male nest sitting behaviour in decimal time (min): the duration of time that males were on the nest, length of the female recess bout, percentage of time the male spent on the nest in the absence of the female and the duration of time until the male nest sat after the female left, as well as the duration of time it took the female to resume incubation after the male left. For males, which nest sat multiple times, individual means are also provided (in italics). *Observation for one male, oFIA, was excluded, because he sat on the nest only after eggs hatched. His mate, gLDC, stayed in the vicinity of the nest with the newly hatched goslings, returning to the nest repeatedly (see Figure S1).

	Duration male on the nest	Female recess bout length	time male nest sitting (%)	Duration from female leaving to start male nest sitting	Duration from male leaving until female returns
oFYJ	15.15	35.35	42.86	20.20	0.00
oFYJ	60.57	60.57	100	0.00	0.00
oFYJ	10.10	141.32	7.15	0.00	131.22
oFYJ	70.67	75.72	93.33	5.05	0.00
Mean (oFYJ)	*39.12*	*78.24*	*60.84*	*6.31*	*32.81*
yBYI	05.04	30.28	16.73	10.08	15.13
yBYI	25.25	30.30	83.33	5.05	0.00
yBYI	10.10	10.10	100	0.00	0.00
yBYI	10.10	25.25	40	10.10	0.00
Mean (yBYI)	*12.62*	*23.98*	*60.02*	*6.31*	*3.78*
oFZY	20.20	171.63	11.77	55.53	5.05
oFZY	90.85	323.00	28.13	10.10	0.00
oFZY	15.15	176.63	8.58	131.2	30.28
oFZY	40.37	212.00	19.04	10.08	75.72
oFZY	65.63	312.98	20.07	30.30	5.05
oFZY	5.05	80.77	6.25	15.15	60.57
Mean (oFZY)	*39.54*	*212.83*	*15.79*	*42.06*	*29.45*
gZUN	35.00	40.00	87.50	0.00	5.00
oFIJ	70.68	100.93	70.03	5.03	15.13
*oFIA	N/A	N/A	N/A	N/A	N/A

Table S4. Percentage of female nest recesses with male nest sitting during incubation. We give the number of recesses females took and the number of nest sitting events of the males as well as the number of days during which the wildlife cameras were functioning. Two individuals, denoted in italics, were excluded when calculating percentages. For male gZUN the camera worked reliably for one day only, and male oFIA was excluded because he sat on the nest only after eggs hatched.

Nest sitting males	Number of female recesses	Number of male nest sitting	Number of nest recesses with male nest sitting (%)	Number of days when cameras were functioning
oFYJ (201913)	12	4	33.33	3
yBYI (mate yAUF w/ transmitter 201919)	98	4	4.08	13
oFZY (201918)	14	6	42.86	4
gZUN (201915)	*1*	*1*	*100*	*1*
oFIJ (201924)	98	1	1.02	15
**oFIA (201930)*	*N/A*	*N/A*	*N/A*	*19*

Figure S1. Male oFIA began nest sitting shortly after all eggs hatched. His mate gLDC stayed in close vicinity to the nest with the newly hatched three goslings. Photo taken from the wildlife camera.