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

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Author Contributions

Isabella B. R. Scheiber: Conceptualization; formal analysis; funding acquisition; methodology; project administration; supervision; verification; visualization; writing – original draft; writing – review and editing. **Annabel J. Slettenhaar:** Data curation; funding acquisition, investigation; software; visualization; writing – review and editing. **M. J. J. E. Loonen**: Resources; writing – review and editing. **Margje E. de Jong**: conceptualization; data curation; formal analysis; investigation; methodology; software; supervision; verification; visualization; writing – original draft; review and editing.

Abstract

In most Anseriformes (ducks, geese and swans) only females are known to incubate. The few exceptions where males have been described to incubate regularly are several species of swans (Cygninae) and whistling ducks (Dendrocygninae). Here we describe, unprecedented in any goose species, indicidents of male nest sitting in barnacle geese (*Branta leucopsis*) as a form of paternal care of nest attendance. Based on pictures from wildlife cameras we identified males, which sat 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 to this study. To attach transmitters, some geese were caught while defending their nests, thus we may have unintentionally selected bolder males which defended their nests more aggressively and were easier to catch. Nest sitting occurred relatively frequent, *i.e*. in 6/15 individuals. Our results show that males with collars were more likely to nest sit, but this does not deflect from the fact this behaviour is novel in geese. Nest sitting may even be more common as collared birds are more easily recognised, but also uncollared males have been observed to nest sit. We discuss several possible functions of this behaviour, *i.e.* against raiding of nests by aerial predators, thermal control of nest temperature, and intraspecific brood parasitism. At this time we cannot demonstrate a possible function, as chances of successful hatching were not increased in nests of males, which were nest sitting. At this time, we lack sample size for more in depth analyses. Lastly, we discuss whether 'male incubation' is misleading in the waterfowl literature, as it is truly justified for only two species, the black swan and black-bellied whistling duck.

Keywords:

Branta leucopsis, geese, waterfowl, paternal care, male incubation, incubation behaviour

1 INTRODUCTION

Nest defence by parents is considered a risky behaviour, as they may endure injury or even death when trying to ward off predators [1], thus the risk of clutch protection has to be gauged against its benefits [2]. 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 [3]. In most waterfowl species, *i.e.* swans, geese and ducks, however, only females incubate. Thus far, it was never observed in geese (Anserinae). Therefore, the purpose of this paper is threefold: First, we revive the term '*nest sitting*' [4] and describe it for the first time in geese, *i.e.* barnacle ganders (*Branta leucopsis*). Nest sitting refers to cases, where the non-incubating parent attends to or is present directly on the nest and differs from incubation, which entails the transfer of heat to the developing eggs [5]. Secondly, we will discuss possible functions of nest sitting in barnacle geese, and, finally, we question whether previously reported studies in waterfowl, which refer to 'male incubation', are actually misinterpreted.

Barnacle geese are an Arctic breeding species, well-known for nesting high on steep mountain cliffs and islets as a protection against predators [6]. Our study population breeds contemporaneously on islands with common eiders (*Somateria mollisma*), glaucous gulls (*Larus hyperboreus*), Arctic (*Stercorarius parasiticus*) and great skuas (*S. skua*), the latter three being the main avian predators of barnacle geese [7, 8]. Just as other geese (*e.g.* lesser snow goose, *Anser caerulescens caerulescens;* pink-footed goose, *A. brachyrhynchus;* Canada goose, *Branta canadensis),* barnacle geese, protect their nests against avian predators through a high rate of nest attendance [9-11] and active defence [1, 12-14].

Nests on islets seem relatively safe from terrestrial predators. Islets in the inner fjord, however, can stay connected with the mainland via ice-bridges when there is a late break-up of fjord ice. This allows Arctic foxes (*Vulpes lagopus*) not only to reach the islands, but may also confine them to stay there, once the ice breaks, at the time when the geese breed [15]. However, as the fjord ice has diminished in recent years [*e.g.* 16, 17], the risks of encountering foxes on the breeding islands has gone down [18]. Polar bears (*Ursus maritimus*), which are known to prey on eggs and goslings [19], have increased substantially in numbers [8, 20]. They now visit islands more and more during the breeding season to raid nests [8, 21, 22]. This results in complete nest failures in some years [8].

Barnacle geese are socially monogamous and biparental with precocial offspring where parental roles before and after hatching are clearly defined. Before hatching, males normally do not come straight up to the nest, but stay in close vicinity, maintaining contact with their

incubating mates visually and vocally [9, 23]. In case of an intruder coming close, most males actively protect and defend the nest and incubating female [1, 13].

Just as in all other geese, only females incubate. During nest construction, they develop thermosensitive brood patches, which guarantee an efficient heat transfer from the body to the egg [24]. Female geese actively pluck feathers, which they add as an insulating inner layer of nest lining. They then begin to lay one egg per day until a clutch is completed with a mean clutch size of about five eggs [25]. During this time, barnacle ganders closely guard their receptive mates [26]. Incubation in barnacle geese lasts for 25 days on average [27].

Incubation starts after the penultimate egg is laid [28]. 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 [29, 30]. In our study population, geese take five 20-min incubation recesses per day on average, yielding an incubation constancy of 93% [31]. Before leaving the nest, females use the down lining of the nest feathers to cover the eggs for insulation and/or hide them from predators. Common comprehension is that males either join their mates during incubation recesses, leaving the nest unattended, or stay behind close to the nest [32]. To the best of our knowledge, we now report, for the first time in geese, that some males nest sit, while females are away.

2 METHODS

Our study population resides on the west coast of Spitsbergen, the largest island of the Svalbard archipelago. In Kongsfjorden an established breeding colony nests on a group of several islets [15]. These islets are characterised by exposed ridges and flat stretches of tundra [7]. Two are monitored in detail; the larger main breeding islet, Storholmen (ca. 30 ha, 259 nests in 2021) and Prins Heinrichøya (ca. 3 ha, 29 nests in 2021) located offshore of the village Ny-Ålesund (78°55’N, 11°56’E), Svalbard, Norway.

Within the scope of a larger study on circadian and circannual rhythmicity, we fitted 24 adults (½ males, ½ females of established pairs) in 2020 with solar-powered GPS-GSM transmitters attached with neckbands (OrniTrack-NL40 3G, Ornitela, UAB, Lithuania) in order to locate geese during migrations and on the wintering grounds. Those 24 individuals were chosen following a suite of criteria, including that it would be desirable if both pair partners were marked with unique colour rings already (for details of criteria see supplemental material). 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', 33], or else during the annually performed mass captures of moulting geese, where considerable numbers of geese are funnelled into a trap ['moult catches', 34]. 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 trappability *sensu* STRANGE [35], as these males show high nest defence and risk-taking behaviour [1, 36]. 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. The neck collar allows a definite recognition of the pair partners on and close by the nest, even when colour rings are not visible. In the following we refer to colour ring codes, when we mention 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.* 37]. At each nest, we placed the camera, set in time-lapse mode, in one-metre distance of 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 ($\bar{x}$ days ± SD: 12 ± 6.1; for details see supplement, Table S1)

When scanning the photos, we noticed that in several instances males, rather than females, were sitting on the nest (Figure 1). In the goose data base, first sporadic notes of this behaviour stem from 2006 (M. E. de Jong & M. J. J. E. Loonen, pers. obs.). We thus decided to investigate this phenomenon further. In particular, we wanted to determine how often nest sitting of males occurred, whether only certain individuals did so, if male age played a role, and whether individuals, which performed nest sitting did so multiple times or only once. As successive photos in a series are contingent, we only counted male nest sitting bouts as independent if the female returned to the nest and incubated the clutch for a pronounced period of time. As occurrence of male nest sitting might have been a consequence of our selection of males [35], we also took the method of catching into account. Finally, we investigated if eggs, were more likely to hatch if males were nest sitting.

2.1 Statistical Analysis

Using the R programming environment [38], 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, (3) whether the method of catching, *i.e.* snare/net vs. moult catch, was correlated with male nest sitting, and (4) if male nest sitting was associated with hatching probability of the clutch, *i.e.* at least one egg hatched (for details on counts of the three queries see 2 x 2 contingency tables, supplement Table S2).

2.2 Ethics Approval Statement:

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).

3 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 [$n_{\text{males not nest sitting}} = 9$, $\bar{x}$ years ± SD: 8.33 ± 3.16; $n_{\text{males nest sitting}} = 6$, $\bar{x}$ years ± SD: 11.00 ± 3.1; $t_{(13)} = 1.612$, $p = 0.131$, Figure 2a)]. Of the six nest sitting males, two were observed on the nest only once (gZUN, oFIJ), whereas the others four males were observed multiple times (oFIA twice, oFIY and yBYI four times, oFZY five 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)]. The likelihood of males sitting on the nest was independent of whether they were caught near the nest during incubation or during the moult catches [Fisher's Exact Test: $p = 0.143$, $OR_{2\text{-sided}} = 0.00$ with 95% CI of [0.00, 3,53], Figure 2c)]. Whether males nest sat had no effect on whether eggs hatched or else 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)]. However, throughout this study sample size is small and these results should be taken with caution.

4 Discussion and Conclusion

4.1 Nest sitting in barnacle ganders – possible functions

To the best of our knowledge, this is the first confirmation of males sitting on nests in any goose species. Although we may have introduced a bias to catch predominantly bold individuals [35], this does not alter the fact that we have shown for the first time that some ganders perform this behaviour. We oppose to calling this behaviour 'male incubation', as termed repeatedly in the waterfowl literature [*e.g.* 39-42], because there is no active transfer

211 of heat from the male to the eggs as ganders do not form brood patches. Rather, we revive the
212 term 'nest sitting' [4] as the appropriate label. Before female geese start actual incubation,
213 they adopt a posture when on the nest, in which the brood patch is not brought into contact
214 with the eggs, so there is no effective heat transfer to start embryonic development [43]. This
215 behaviour may serve to shield the nest and eggs from *e.g.* predation, inclement weather and/or
216 intraspecific brood parasitism. We suggest that male nest sitting is equivalent to this posture
217 at times when the female is on incubation recesses. To date, we cannot provide a definite
218 explanation of why this behaviour occurs, as neither the age of males seems to play a role, nor
219 could we show an increase in hatching success of nests, where males nest sat. At this moment,
220 we lack sample size for other more in depth analyses, such as when nest sitting occurs over
221 the incubation period or if males compensate with nest sitting for females taking more
222 incubation recesses. In the following we suggest three possible, not mutually exclusive,
223 functions of male nest sitting, to initiate future studies not only in barnacle geese, but also
224 other species.
225 The primary cause of hatching failure in ground nesting waterfowl is predation [*e.g.* 11,
226 44], thus several different strategies are employed for nest protection. These range from high
227 nest attendance [11], selecting sites where nests can either be successfully concealed or are
228 difficult for predators to reach [45], breeding in close proximity to more aggressive species to
229 take advantage of their nest defence [46] to actively put predators to rout [11]. Barnacle geese
230 historically nested high up on steep rock faces, particularly suitable to avoid terrestrial
231 predators. There, however, food is scarce for incubating females [9]. Breeding islands off the
232 coast used to be fairly safe from polar bears and Arctic foxes, but this turns out to now also be
233 changing [15, 20]. Furthermore, breeding on islands forces geese to nest in close proximity to
234 their main aerial predators, thus nest sitting of barnacle ganders might function in shielding
235 the nest from them. This is backed by our choosing the most aggressive males when attaching
236 transmitters, which might be bold enough to attack predators actively. What needs to be
237 investigated, is whether males adjust their behaviour to certain environmental conditions, *i.e.*
238 through behavioural plasticity, or whether nest sitting confers fitness benefits as an adaptive
239 response to breeding on islands [47, 48]. In the future, attention should be paid to how often
240 nest sitting of males occurs, how long the incubation recesses of the female last, what the
241 predation pressure is, and at which stage during incubation the behaviour is performed.
242 Another possible function of nest sitting by males is to control the temperature in the nest.
243 To some extent, nest insulation can reduce both the degree of egg cooling when the female is
244 absent and the time spent to rewarm the eggs after she returns from an incubation recess [49].

Avoidance of egg cooling is particularly important for Arctic breeding birds, where the difference between optimal temperature for developing embryos (in geese: 37-38°C) and the average air temperature during incubation (Ny-Ålesund average air temperature 2021: June 2.6°C, July 5.5°C, Norwegian Meteorological Institute) is striking [50]. Thus, eggs should be covered more or less constantly. Indeed, Arctic geese adjust their incubation behaviour in response to prevailing weather conditions, such as wind velocity, air temperature and solar radiation [50, 51], remaining on the nest more continuously during inclement weather [51, 52]. Yet, egg cooling in the absence of the female might be overrated. In greater snow geese, egg temperature throughout incubation remained high with only slight drops during the frequent incubation recesses of females [43]. This might be, in part, ascribed to the female's covering the nest with down [49]. Even under unfavourable weather conditions, egg temperature drops during incubation recesses are probably nowhere near the minimal temperatures, which endanger an embryo's development or survival. Rather, this will only lengthen the incubation period until the eggs hatch [7, 53].

Overheating of unprotected eggs in the nest might become an issue in the Arctic in the future. Also in Ny-Ålesund temperature has risen steadily since the 1970s [*e.g.* 54]. During continuous incubation in climate control chambers, the critical temperature, at which no embryos will survive, is 40.5°C [53]. 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 in the Arctic. Yet, common guillemots (*Uria aalge*), a high-latitude seabird, already showed an increased probability of egg loss at higher temperatures in a colony in the Baltic Sea [55]. Whether nest sitting in barnacle ganders occurs predominantly on extremely warm or cold days could be subject to further investigations. In sum, whereas nest sitting of barnacle ganders undoubtedly will assist in 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 laying, another possible function might be to prevent intraspecific brood parasitism, which frequently occurs in barnacle geese [27]. When conspecific barnacle geese attempt to dump eggs, females apply one of three strategies. They either lay eggs in unguarded nests, leave parasitic eggs in close proximity to the nest for the host female to retrieve, or attempt to lay an egg into the nest despite vigorous defence by the host female. In contrast, males let those instances happen, behaving only mildly aggressive, if at all, towards the parasitic female [56]. The tameness of the male towards the parasitic female, when the host female is present, leads us to suggest that during egg laying his propensity to nest sit in the absence of his mate is probably low. We cannot

answer this question adequately, however, because we placed cameras not until the host female had started incubation, therefore lack photos from the laying period.

A question is whether nest sitting of barnacle ganders is a behaviour that has been overlooked in the past or is a response to a changing environment. Although adult males are slightly bigger than the females, barnacle geese are monomorphic. It is difficult to determine the sex of an individual, even if it is marked, as rings are not visible when a bird sits on the nest. It is comprehensible that a bird on the nest was assumed to be female, just as the literature suggests. The relatively frequent occurrence of male nest sitting, *i.e.* 40% in our limited number of individuals was unexpected to us. Even more, considering that we synergise many years of detailed observation of goose behaviour in various species, we feel confident that we are capable of distinguishing between the sexes convincingly.

4.2 'Male incubation' in waterfowl?

Found throughout the literature is the general assumption that in swans, and to some extent whistling ducks, deviate from the female only incubation pattern in waterfowl, as here 'males incubate' [39, 42, 57]. But are these males indeed incubating or is it a term that should be avoided, as is leads to a misconception when compared with species, where incubation is truly shared [3]?

In an early study, Hawkins already concluded that the well-developed male incubation behaviour in tundra swans (*Cygnus columbianus columbianus*.) protected against egg predation, provided some egg cooling benefits, but was not essential for successful embryo development [42]. This led Henson & Cooper to apply the term 'nest sitting' in the case of trumpeter swans *(C. buccinator*). They state that the behaviour was not 'as well developed as in tundra swans', because it was independent of predator presence or adverse weather conditions, despite males occasionally exhibiting some of the nest-settling motions characteristic of incubating females [4]. Our extensive search of the literature revealed that in most waterfowl, including three single observations in wood duck (*Aix sponsa*), mandarin duck (*A. galericulata*) and fulvous whistling duck [*Dendrocygna bicolor*, 40, 41, 58], males nest sit rather than incubate.

The two notable exceptions, for which the term incubation is warranted, are the black swan (*C. atratus*, BLSW) and black-bellied whistling duck (*D. autumnalis*, BBWD*)*. Whereas BLSW exhibit the Cygnidae typical long-term monogamy and biparental care, this is also true for BBWD, unusual for Anatidae, although in some species males participate in attending broods after hatching [59]. Besides male incubation, there are some features, which BLSW

313 and BBWD share. In both species, neither females nor males develop brood patches [60, 61],
314 thus either parent of each species can incubate in a similar manner. Also, both species are
315 known to re-nest after successful breeding attempts [39, 60, 62-64], whereas most other
316 waterfowl may attempt a second clutch only if the first one failed particularly during early
317 stages of incubation. We speculate that re-nesting might be the reason of both parents
318 incubating. Near constant incubation minimizes the time it takes for eggs to develop and
319 hatch, thereby possibly shortening the inter-clutch interval, but this would need to be tested in
320 mate removal experiments. In waterfowl with uniparental female care, mate removal did not
321 affect hatching success or body condition of the female [65, 66].
322 In conclusion, this is the first report in any goose species, where males expand paternal
323 duties beyond the established view, which during the breeding period is to protect the nest and
324 female in close vicinity of the nest. We have pictorial evidence that several individuals
325 displayed nest sitting behaviour. Although we may have unintentionally selected bolder
326 individuals, this should not divert from the fact that the behaviour exists. Both predation and
327 thermal risks are increased for eggs, which are not protected by parents, thus minimising
328 those risks are the main causes for successful hatching. In barnacle geese, we suggest nest
329 sitting of males to be a response to avian predator presence. We cannot exclude that
330 preventing egg cooling (and overheating) in the absence of the female may also play a role,
331 but consider this unlikely. Our final point is that in most waterfowl species, males do not
332 participate in incubation. Nest sitting is an unbiased term and should be used for cases, in
333 which no active warming of eggs has (yet) been demonstrated.

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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 and aluminium rings, and if they were fitted with a transmitter, the neck collar ID. Except two individuals, which were ringed as goslings (*), the minimum age is given ($\bar{x}$ age ± SD: males 9.4 ± 3.31; females 10.4 ± 4.46). Whether or not males sat on nests is also indicated.

Male colour ID	Male ID	Male neck collar ID	Age (years)	Male nest sitting	Female colour ID	Female ID	Female neck collar ID	Age (years)
oFYJ	CA46944	201913	16	yes	oFVD	CA46857		10
gZUN	CA45605	201915	9	yes	oFLC	CA45810		12
alur	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

FIGURE LEGENDS

Figure 1: An example of one barnacle gander nest sitting. Photos taken on June 18th, 2021 between 15:48 and 16:28. Panel A) Female oFVD without a neck collar is incubating. Panel B) The female left the nest. Panel C) Male alur with neck collar approaches the nest. Panel D) He sits on the nest with the neck collar clearly visible. Panel E) The female returns to the nest. Panel F) She resumes incubation. Temperature and time are shown in the lower right hand corner of each photo.

Figure 2: Features, which might influence nest sitting in barnacle ganders. a) Age did not affect the likelihood of male to nest sit (Student's *t*-test: $p > 0.05$). 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) The method of catching for transmitter deployment, either near the nest or the during moult catch, had no effect on nest sitting propensity of males (Fisher's Exact Test: $p > 0.05$). d) Whether eggs hatched or did not hatch was independent of males' nest sitting (Fisher's Exact Test: $p > 0.05$).

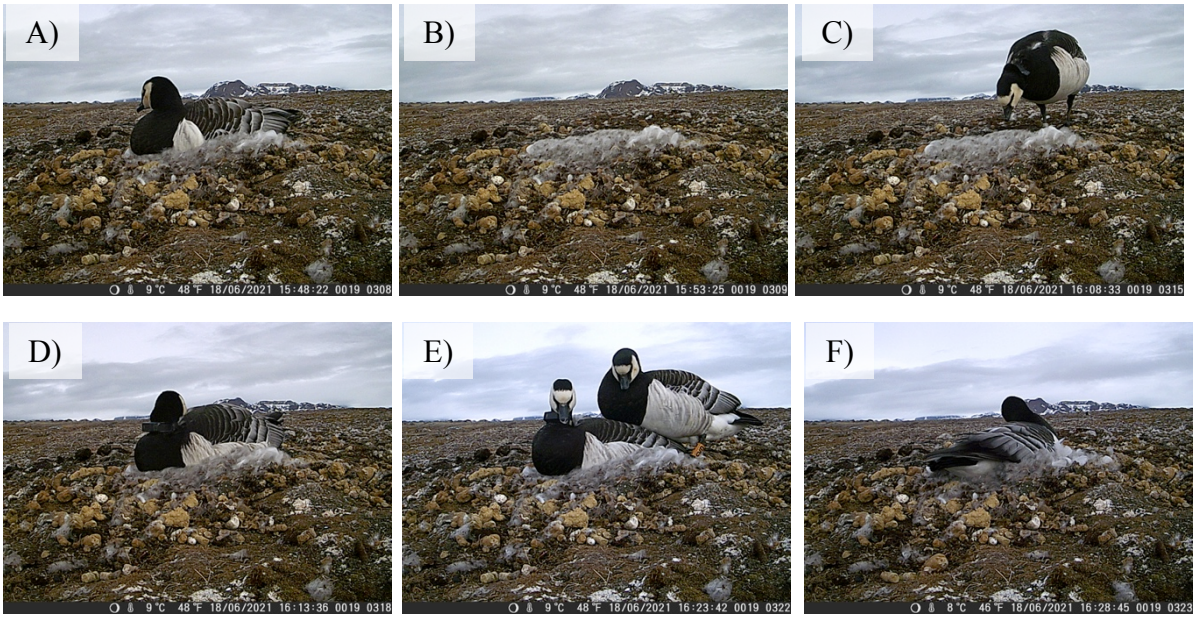

Figure 1

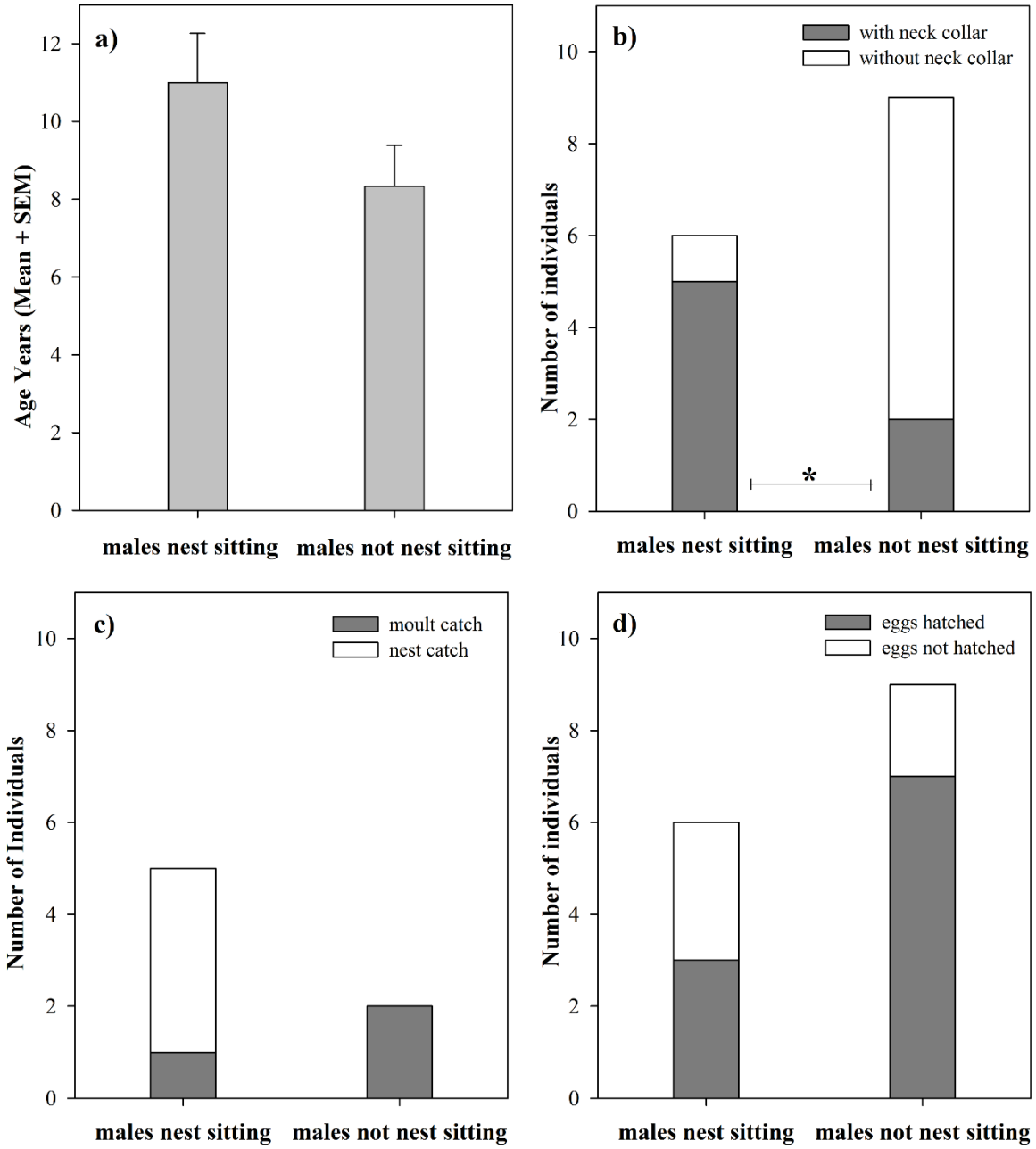
a)
Age Years (Mean + SEM)
0
2
4
6
8
10
12
males nest sitting
males not nest sitting
b)
with neck collar
without neck collar
Number of individuals
0
2
4
6
8
10
*
males nest sitting
males not nest sitting
c)
moult catch
nest catch
Number of Individuals
0
2
4
6
8
10
males nest sitting
males not nest sitting
d)
eggs hatched
eggs not hatched
Number of individuals
0
2
4
6
8
10
males nest sitting
males not nest sitting

Figure 2