

Original Research

Behavioural Responses of Moulting Barnacle Geese to Experimental Helicopter Noise and a Predator

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Abstract

The response of animals to anthropogenic noise can be aggravated by lack of familiarity with its auditory pattern and also by nervousness characteristic of particular phases of their life cycle. Both conditions apply in the Arctic where human activity is highly localised and field operations, being largely restricted to summer, coincide with the period when animals produce and nurse offspring and, in the case of some birds, are rendered flightless by wing moult. We measured behavioural responses in moulting barnacle geese (*Branta leucopsis*) in Svalbard to a low flying helicopter and compared these with their responses to the presence of Arctic fox (*Vulpes lagopus*). The pattern of the responses of the birds was independent of stimulus type but the radius of the effect (response distances) was small (≈ 50 m) for foxes but large (> 3 km) for the helicopter. The geese displayed remarkable auditory discrimination: they responded to the sound of the helicopter at 3.2 km even though engine sound level exceeded background only at ≤ 2 km from source. We attribute their sensitivity to the fact that fundamental frequencies of calls and absolute auditory sensitivities of Anatidae fall close to the peak noise energy output of small helicopters. The specific instantaneous time and energy costs of the responses observed here were very small. Simple time and energy models indicate that the impact of these natural (fox) and anthropogenic (helicopter) disturbances is likely to depend chiefly on their frequency of occurrence.

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INTRODUCTION

Anthropogenic noise affects free-living wild animals across a wide range of taxa and noise reduction is a recognised priority in environmental conservation (Rabin *et al.* 2003; Kight and Swaddle 2011; Ortega 2012; Francis and Barber 2013; Morley *et al.* 2014). Exposure to anthropogenic noise ranges from chronic (continuous or near continuous) to acute (isolated and infrequent). The former is typical of the urban environment and industrial locations (e.g., Warren *et al.* 2006; Barber *et al.* 2010; Halfwerk *et al.* 2011) while the latter is a feature of physically remote sites where, because the frequency of noise events is low, their effect may quite literally be startling (e.g., Harrington and Veitch 1991).

The response of animals to anthropogenic noise is likely to be aggravated at remote sites (i) by their lack of familiarity with its auditory pattern, and (ii) by increased susceptibility to unfamiliar stimuli owing to nervousness characteristic of the phase of the life cycle when noise generally occurs. Both conditions apply in the Arctic. First, the overall density of humans is low and localised and the overwhelming majority of animals, which live beyond the immediate vicinity of settlements and field operations, have neither much experience of anthropogenic noise nor any possibility of becoming accustomed to it. Second, many field operations (e.g., industry, scientific research, tourism) are restricted to summer and therefore coincide with the period when animals produce and nurse their offspring, during which they show increased vigilance (Williams *et al.* 1994; Toigo 1999) and wariness (evidenced by increased flight initiation distances: e.g., Clutton-Brock and Guinness 1975; Kahlert 2006).

The situation for geese, which are the subject of this paper, is complicated by their annual moult when, for 25 to 30 days in July-August, the birds are unable to fly. While in this state, their principle response to perceived threat of attack is to move onto water. So important is this that birds migrate to specific moulting sites characterised typically by fresh water ponds with adjacent good grazing (Christensen 1967; Meltofte 1976; Owen and Ogilvie 1979; Aarvak and Øien 2003). Consistent with this, moulting geese are apparently highly sensitive to disturbance: barnacle geese (*Branta leucopsis*) are reported to respond to the sound of helicopters up to 10 km although in most cases the response distance is in the order of 2–4 km (Madsen 1984; Mosbech and Glahder 1991). To our knowledge, these observations have never been experimentally confirmed. Here we report the response

of moulting barnacle geese to helicopter engine noise in experimental trials and to Arctic fox (*Vulpes lagopus*) at a site in Svalbard, and discuss our observations in relation to auditory discrimination in birds.

STUDY AREA

Geese were studied at freshwater tundra ponds in Stormyra ('the Great Marsh'; 77° 54' N, 15° 36' E) at the mouth of Reindalen, Svalbard (Figure 1). The area consists of low lying (<25 m above sea level [a.s.l.]) tundra wetland with little relief (Bye and Hansson 1991; Sonesson 1994; Spjelkavik 1994). Stormyra is used by a large variety of wetland birds in summer (Brekke 1990; Bye and Hansson 1991; Jacobsen 1994). Seven main ponds at Stormyra ranged in size from 0.01 to 0.5 km².

MATERIAL AND METHODS

Study design

This study was part of an analysis of the potential impact of a road linking the settlements of Longyearbyen (78°13'N, 15°38'E) and Svea (77°54'N, 16°44'E) in Svalbard. The road, which was in fact never built, would have included a section of some 20 km running across Reindalen, one of the largest ice-free valleys in Svalbard which then, as now, contained no permanent infrastructure. The purpose of the road would have been to transport coal miners and coal mining equipment between the 2 settlements. Hence, we set out not to test the responses of geese in Reindalen to helicopter overflights *per se* but, instead, to use a helicopter to mimic the passage of a heavy vehicle (lorry or bus; see McClure *et al.* 2013). Consequently, we arranged for our helicopter to fly low and slowly along the route of the intended road rather than high and fast in the manner of regular helicopter traffic.

Fieldwork

Studies were carried out July 25–29, 1994 based at a small hut due east of Stormyra (Figure 1). The hut, erected decades ago, commanded a good view of all ponds except Pond 7 which, however, was not used by geese during our stay. The shortest distance between the hut and Ponds 1–6 ranged from 390 to 600 m.

Field parties of 2 persons (July 25) and 1 person (July 28) were dropped by helicopter 6 km northeast of Stormyra and

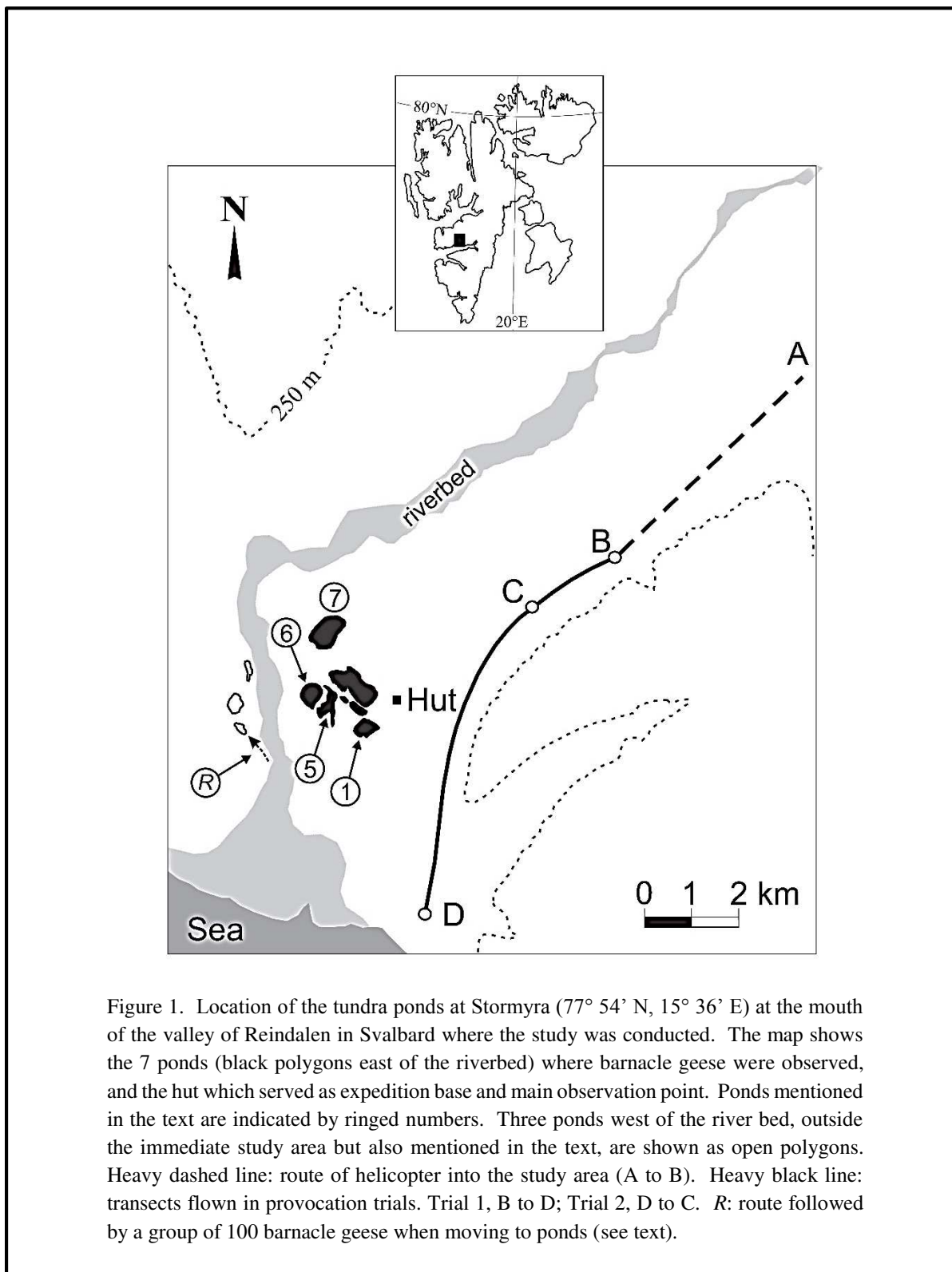


Figure 1. Location of the tundra ponds at Stormyra ($77^{\circ} 54' N$, $15^{\circ} 36' E$) at the mouth of the valley of Reindalen in Svalbard where the study was conducted. The map shows the 7 ponds (black polygons east of the riverbed) where barnacle geese were observed, and the hut which served as expedition base and main observation point. Ponds mentioned in the text are indicated by ringed numbers. Three ponds west of the river bed, outside the immediate study area but also mentioned in the text, are shown as open polygons. Heavy dashed line: route of helicopter into the study area (A to B). Heavy black line: transects flown in provocation trials. Trial 1, B to D; Trial 2, D to C. R: route followed by a group of 100 barnacle geese when moving to ponds (see text).

walked to the hut from there. The helicopter approached the dropping point from the northeast, flying the last 5 km of its approach 2 m above ground level (a.g.l.). Human activity around the hut was kept to a minimum throughout fieldwork. All helicopter activity within a radius of 8 km of Stormyra was forbidden from 19 to 29 July inclusive.

Weather data

Weather data were extracted from the records of the Norwegian Meteorological Institute (<http://www.eklima.no>). For Stormyra, we used data collected 25 km away at Sveagruva (station number 99760; 77° 53' N, 16° 43' E). For the sound test (below), we used data collected 9 km away at Svalbard Lufthavn (station number 99840; 78° 15' N, 15° 30' E).

Counts

Barnacle geese, present in the study area every day, were counted on July 28. Two observers, each sitting a point approximately 25 m a.s.l. behind the hut, repeated independent counts with 20–45x telescopes, 20x60 binoculars, and handheld trip counters until both achieved the same score.

Behaviour

Control

All barnacle geese on or near ponds were observed continuously in 15-min scan samples for 12 h (07:00 – 19:00 GMT) on July 27 and 28, and from 07:00 – 15:00 on July 29. All birds on the water (OTW) and on land, in zones 0 – 10 m and >10 m from the water's edge, were counted at each scan.

Provocation trials

Two provocation trials were carried out on July 29. A helicopter (AS 350B Ecureuil carrying 1 pilot and 1 observer) flew along the path of the proposed road at 30 knots (56 km·h⁻¹) and at 2 m a.g.l.

Trial 1 (start 12:45 GMT) – Observations were made on 1 group of barnacle geese ($n = 160$) which was on land between Ponds 5 and 6 at the start of the trial. This group was approximately 1,500 m from the observers. The helicopter started its engine and took off from a point approximately 6.5 km northeast from the geese (point B in Figure 1). It was not visible from Stormyra at this stage owing to low relief along the flight path. The pilot first reported being able to see the ponds when the shortest straight-line distance between the helicopter and the geese was approximately 3.7 km. From this point the helicopter remained visible to the geese up to and after it landed approximately 4 km south of the ponds (point D in Figure 1) when its engine was switched off.

Trial 2 (start 13:53 GMT) – Observations were made on all the barnacle geese in the study area. These were aggregated in a single group at or on Pond 6 at the start of trial; the majority of birds ($n = 631$) were on land while the remaining 178 were OTW. The engine was started and the helicopter took off and returned in a similar manner along the same route (transect D – C in Figure 1) before landing when, again, its engine was immediately switched off.

Two observers sitting on elevated ground behind the hut recorded the behaviour of the geese for 6 h prior to the first provocation trial using 15-min scan samples. During both trials, each observer watched his allotted geese continuously through a telescope and noted any changes in the behaviour of the birds. As soon as a change of any kind was observed, a message was transmitted to the helicopter pilot using a portable VHF radio. The pilot, in turn, noted the position of the machine at that instant using a GPS navigation device. The shortest straight-line distance between the helicopter and the geese (d) at each reported instant was subsequently calculated to the nearest given second (30 m) using these data. Weather during trial consisted of unbroken cloud cover at 1,000 m a.s.l.; temperature, 10° C; and local wind speed, 0 m·s⁻¹.

Sound test

The sound generated by and propagated over tundra from the helicopter was measured on July 31 in the valley of Adventdalen (78° 12' N, 15° 50' E). The machine, carrying 1 pilot and 1 passenger, flew 2 m a.g.l. at 30 knots along a 10-km straight course marked at 1-km intervals. The test site (<25 m a.s.l.) consisted of flat mixed grass and moss tundra and mudflats. The recording instrument (Brüel and Kjær Impulse Precision Sound Level Meter, Type 2204, with a Condenser Microphone Cartridge, Type 4145, calibrated with a Brüel and Kjær Acoustic Calibrator, Type 4230) was mounted on a tripod standing unprotected at a point exactly half-way along the course. The helicopter started 5 km from the recording instrument, passed it at 20 m (horizontal distance) and continued for 5 km beyond it (Pass 1) before turning around and returning along the same route (Pass 2). As each marker was passed, the pilot radioed a message to the ground team who noted the instantaneous sound pressure level. The recording instrument was rotated 180° when the helicopter passed so that the microphone always pointed directly at it. Sound pressure level (dB-lin) was expressed as a function of distance to helicopter. There was 7/8 cloud cover at 100 m a.g.l. during the trial; temperature, 6° C; wind, 6.2 m·s⁻¹, blew parallel to the flight path. Pass 1 was flown into the wind; Pass 2 was flown with a tail wind.

RESULTS

Number and distribution of birds

We counted 809 barnacle geese, including 15-20 chicks, on Stormyra. The birds were normally divided into 2 to 4 groups scattered on or near the ponds. These groups were temporary associations of tens to hundreds of individuals that divided and amalgamated at intervals throughout the day. The birds were still moulting: just 2 birds were observed flying on 2 occasions during 30 h of observation and covered only 10 – 15 m each time.

Behaviour

Background

Barnacle geese remained on or near the southernmost 6 of the 7 ponds at Stormyra throughout the study (Figure 1). The majority of birds were on land most of the time. Thus, there were birds on land in every 1 of 121 15-min observations made prior to the trials. The proportion of birds on land at each observation ranged from 40.2 to 100% of the population (median 93.81%, quartile range 81.5 – 99.1%, $n = 809$; Figure 2).

The birds on land spent time grazing, resting or preening close to the water's edge. Birds were recorded >10 m from the edge of any pond in just 8 (6.6%) of 121 15-min observations, involving between 10 (1.2%) and 150 (18.5%) animals each time. No birds at Stormyra were ever seen >50 m from water.

Response to foxes and other non-helicopter provocations

The proportion of birds OTW increased substantially on 14 occasions, 10 of which were explained by events (Figure 2). Thus, on 4 occasions birds entered water while moving from the vicinity of 1 pond to the vicinity of another. These movements were apparently spontaneous and unprovoked. Each time an entire group of geese walked calmly down to a particular pond, entered it, swam purposefully across it in an extended line and exited the water at another point.

On 3 occasions, a single fox ran straight towards a group of geese. The birds ceased their current activity and moved OTW when the fox arrived \approx 50 m from them. The fox then scampered backwards and forwards along the edge of the pond, stopping once or twice to look at the birds before running out of the study area. The fox was present <10 min each time. On each occasion, the geese on Stormyra were dispersed around 1 or more ponds and only those nearest the fox reacted visibly to its presence. Each time the birds which responded, all plainly aware of the fox, walked calmly down to the water and swam gently away from the shore and then dispersed and paddled quietly about—some no more than 4 – 5 m from the intruder—before returning onto land within 15 min of the fox's departure.

On 1 occasion, our 2-man dome tent, which had been set up on elevated ground behind the hut for use as a hide, was wrenched up by a strong wind and blown past the geese causing about 260 (32%) of them to enter the water and swim out onto a pond. Remaining disturbances were the result of helicopter provocation (below).

Responses to helicopter

Trial 1 – The pilot first reported being able to see the ponds at $d = 3.7$ km at which point the observers at Stormyra also first heard the machine. The first behavioural response to the approaching helicopter was observed at $d = 3.2$ km when 10 geese lifted their heads and craned their necks. At $d = 2.7$ km, approximately one third of the birds, representing that part of the focal group closest to the helicopter, began to waddle rapidly towards Pond 6. Shortly afterwards, the rest of the group began to waddle rapidly, and at $d = 2.5$ km, all the birds were OTW at Pond 6. The helicopter landed, and its engine was switched off at $d = 4.8$ km (point D in Figure 1). The sequence of events, with split times, is given in Appendix 1.

Six minutes after the helicopter landed, all the birds in the focal group ($n = 160$) began to swim calmly from the edge to the middle of Pond 6 where they joined another group ($n = 649$) which swam out from the northwest side of the pond. The combined group of 809 birds swam northeast across the pond, and 3 min later (i.e., 9 min after the helicopter had landed), some birds left the pond and walked ashore. Ten min later, 159 birds came ashore and immediately began to graze. Four min later (i.e., 23 min after the helicopter had landed), all the barnacle geese were ashore, and 5 min later they were all either resting or grazing calmly. Ten minutes later, approximately 300 birds suddenly waddled rapidly down and swam out onto the pond. Nothing was observed that might have provoked this response. Approximately half of these birds were back on land within 15 min.

Incidental to the observations at Stormyra, a group of approximately 100 barnacle geese, observed on the west bank of the river close to the sea ($d = 5$ km), set off waddling rapidly northwest along the river bank (*R* in Figure 1). The birds continued in this manner for 20 min after which 80 of them entered the water and swam out onto 1 of 3 ponds on the west bank (Figure 1). The remaining 20 birds arrived 4 min later, and 2 min after that (21 min after the helicopter had landed), all 100 birds were grazing at the waters' edge. The sequence of events, with split times, is given in Appendix 2.

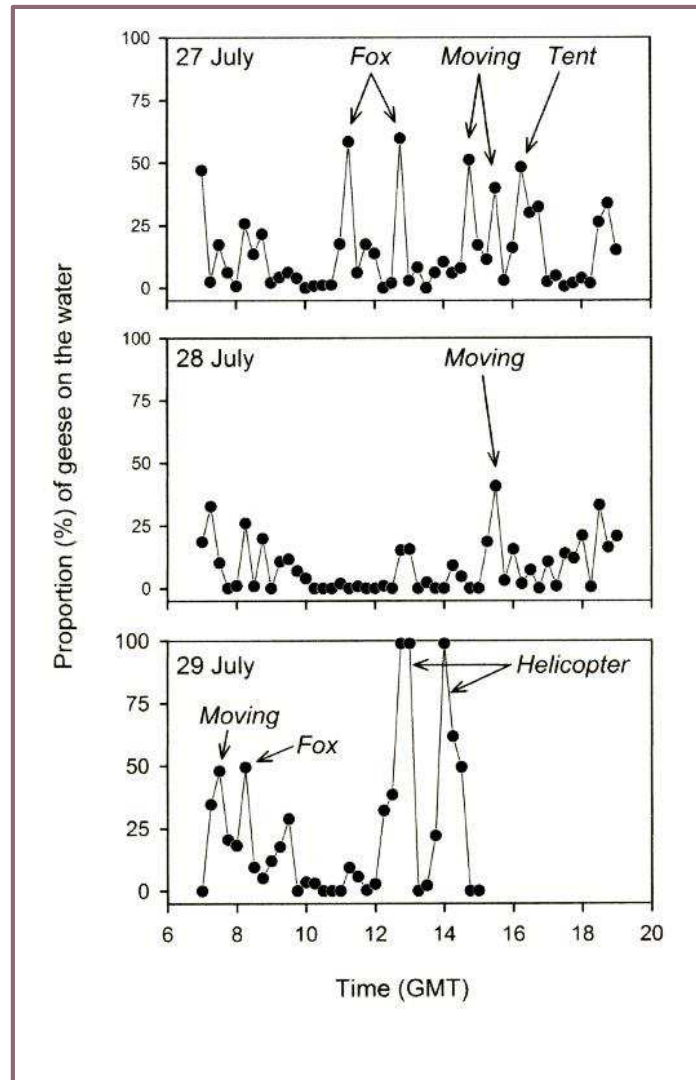


Figure 2. Time series of the proportion (%; $n = 809$) of barnacle geese on the ponds at Stormyra during 2 x 12 h periods of observation (July 27-28), 1 x 6 h period of observation before and during 2 helicopter provocation trials (July 29). Data from 15-min scan samples. Several rapid increases in the proportion of geese on the water were accounted for in terms of stimuli indicated within the figure: 'Fox' – An Arctic fox entered the study area, ran towards some of the geese and then departed; 'Moving' – a number of geese moved from 1 grazing site to another by entering and swimming across a pond; 'Tent' – our tent was wrenched up by a strong wind and blown past the geese; 'Helicopter' – experimental provocation trials (see text).

Trial 2 – Approximately half of the combined group of 809 barnacle geese responded instantly to the sound of start-up of the engine of the helicopter that was parked at $d = 5.2$ km (point D in Figure 1). These birds waddled rapidly down and swam out onto Pond 6. The remaining birds soon followed and the entire group was OTW at $d = 4.7$ km. The birds formed a single group in the middle of the pond. The group was loosely packed at $d = 3.8$ km but tightly packed at $d = 3.1$ km. After 8 min flying time, the helicopter landed at $d = 5$ km (Point C in Figure 1) where it was out-of-sight of the geese and its engine was switched off. The birds continued to paddle about in a single packed group. The first birds came ashore after 8 min and about 300 birds were on land 6 min after that. All birds were on land after a further 9 min (i.e., 23 min after the helicopter had landed).

Most of the birds calmly performed routine activities (grazing, resting, walking) but some seemed nervous and alert. Six min later, all 809 suddenly rushed down to the water and about half of them swam out a little way from land and paddled calmly about. We observed nothing that might have provoked this response. Fifteen min later, all the birds were engaged in routine activity on land. The sequence of events, with split times, is given in Appendix 3.

Sound test

The helicopter was clearly audible to the observers from 4 km both when approaching and when receding. Sound pressure exceeded maximum background (70 dB-lin) at ≤ 1 km into the wind, and ≤ 2 km with a following wind, and reached maximum level (95 dB-lin) at 20 m (Figure 3).

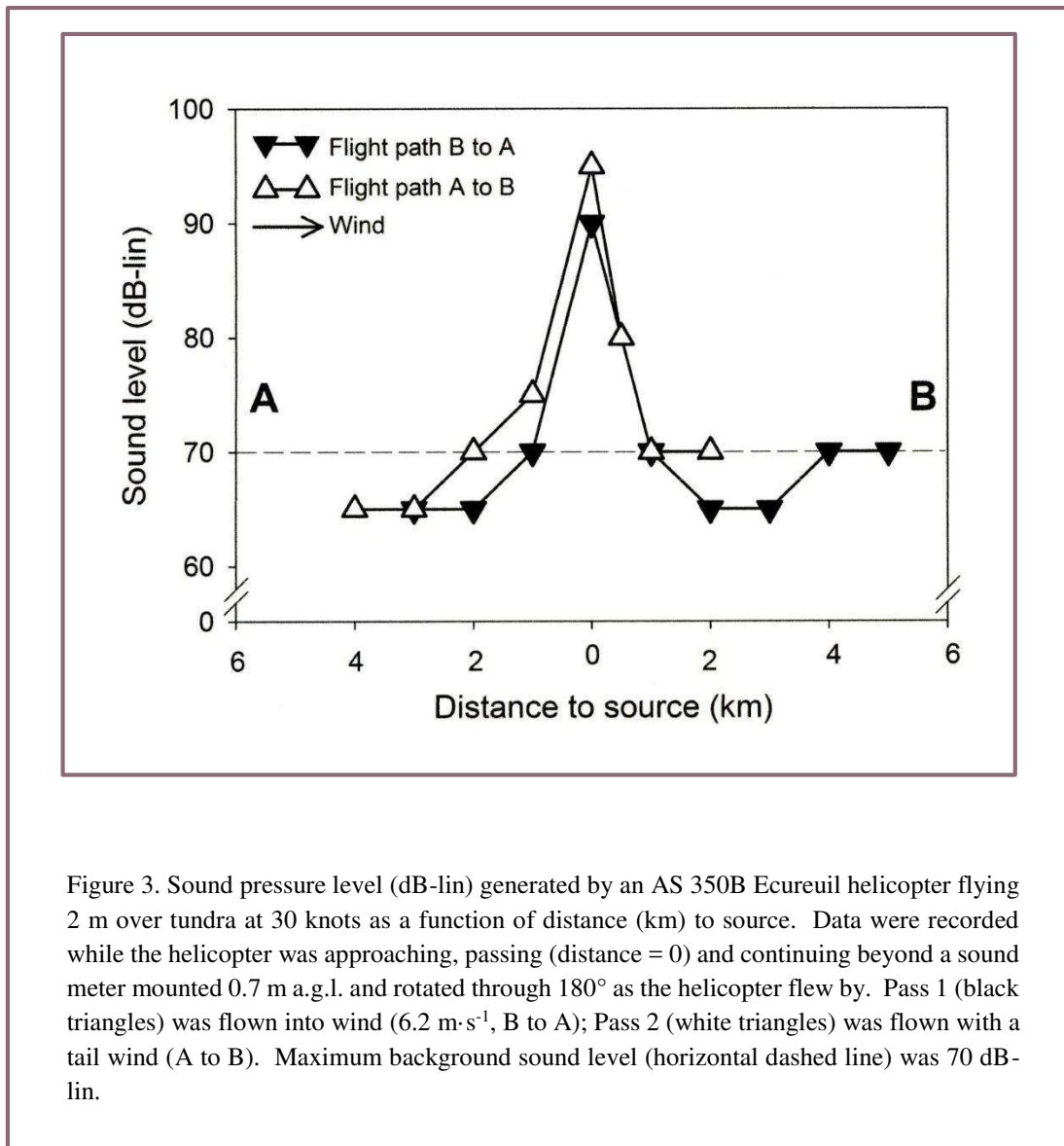


Figure 3. Sound pressure level (dB-lin) generated by an AS 350B Ecureuil helicopter flying 2 m over tundra at 30 knots as a function of distance (km) to source. Data were recorded while the helicopter was approaching, passing (distance = 0) and continuing beyond a sound meter mounted 0.7 m a.g.l. and rotated through 180° as the helicopter flew by. Pass 1 (black triangles) was flown into wind (6.2 m s⁻¹, B to A); Pass 2 (white triangles) was flown with a tail wind (A to B). Maximum background sound level (horizontal dashed line) was 70 dB-lin.

DISCUSSION

The pattern of geese responses to disturbance was independent of stimulus type. The birds were confronted by both natural and artificial stimuli. Foxes were a natural visual stimulus. The flying tent was an artificial visual stimulus. The helicopter represented artificial stimuli in 3 categories—auditory alone, auditory and visual without spatial displacement (i.e., helicopter on the ground with engine running), and auditory and visual with spatial displacement (i.e., helicopter flying). Geese responded to all these stimuli by stopping their current activity, waddling by the shortest route to the nearest pond, entering and swimming about on it before emerging and resuming their former activity on land. There was no difference in this respect between their responses to the sound of a distant helicopter or the sight of a tangible threat (an Arctic fox) at close quarters.

There were, by contrast, clear quantitative differences between birds' responses to different types of stimulus. Thus, the duration of responses following encounters with foxes were shorter (≤ 15 min) than following provocation by a helicopter (median duration = 35 min, range 14 – 52 min; Appendix 1-3). Second, the prevalence of responses in geese to the presence of a fox was substantially lower (between 50 and 60% of birds moved onto water) than the prevalence of their responses to a helicopter (100% each time; Figure 2). This, however, is potentially misleading. It may indeed be, as the numbers suggest, that geese find unfamiliar sound from an initially invisible source more disturbing than the unrestricted view of a familiar predator at close range but there was clearly also a spatial component to the effect. Thus, the geese were dispersed around the ponds prior to the arrival of each fox and only those birds nearest the intruder reacted visibly to its presence. The chief difference between their response to a fox and to our helicopter was the radius of the effect (and, hence, the prevalence of the response), evidenced by response distances of ≈ 50 m for the former and $> 3,000$ m for the latter, rather than the behaviour of the birds that actually responded (i.e., the intensity of the response).

This study provides insight into the notion that reaction distance (helicopter-geese) is positively correlated with engine size and, hence, noise level. The reaction distance observed here in response to a 350B Ecureuil (engine 546 kW; reaction distance 3.2 km, Appendix 1) is close to the value of 2.6 km observed in barnacle geese in response to a Bell 206 helicopter (engine 310 kW; Mosbech and Glahder 1991) but substantially less than in barnacles exposed to a Bell 212 helicopter (engine 1,342 kW; reaction distance ≈ 10 km; Mosbech and Glahder 1991). The perceived noise

level (PNL) for a Bell 206 passing 150 m overhead at 114 kts is 88 dB compared to 98 dB for a Bell 212 (True and Rickley 1977; no data are available for the 350B Ecureuil but the PNL for this machine, like its engine size, presumably falls between these values). Thus, geese obviously have acute hearing and detect a louder signal at longer range. Our data suggest that they have remarkable auditory discrimination as well. The extraordinary ability of birds, like humans and other animals, to recognize communication (i.e., familiar) sound over background noise (the 'cocktail-party effect'; Wiley and Richards, 1982) is well known (e.g., Aubin and Jouventin 1998; Pohl *et al.* 2015). The barnacle geese, however, were evidently able to discriminate very low levels of *unfamiliar* sound. Under our experimental protocol, engine sound level only exceeded background up to 2 km from source (Figure 3) while the observers heard it and birds reacted to it at 2.4 and 3.2 km, respectively (Appendix 1). Most studies of hearing and sound production in birds have used songbirds (e.g., Dooling 2004). We are unaware of any study of sound production or hearing in barnacle geese but Canada geese (*Branta canadensis*) have fundamental frequencies at 0.131, 0.385 and 0.510 kHz in their calls (Johnsgard 1971). Moreover, many birds hear best at frequencies between 1 and 5 kHz, with absolute sensitivity < 10 dB at ≈ 2 -3 kHz (Dooling *et al.* 2000; Dooling 2004). Unfortunately, no sound spectrum is available for the AS 350B Ecureuil helicopter but most sound energy for 5 other small helicopters falls in the range 0.1-1 kHz (True and Rickley 1977). It follows that helicopter noise peaks at frequencies close to those at which birds hear best. Geese can probably also detect a small helicopter visually at 3 km, especially if it is brightly coloured and moving, but it is unlikely that they derive much spatial information at this distance and we will not, therefore, speculate about the extent to which the birds' response to auditory stimulus may have been enhanced by a visual stimulus.

Short-term effects of animal disturbance include reduced energy intake, owing to lost feeding time, and increased energy expenditure, owing to their fleeing (e.g., Miller *et al.* 1994). Response specific rates of loss of feeding time and increase in energy expenditure were very small in this study. There were 2 reasons for this. First, the birds remained remarkably calm throughout. On the single occasion that they packed in a tight aggregation in the middle of a pond (Appendix 3), they displayed no vigorous signs of alarm, neither squawking nor flapping their wings. This contrasts with moulting pink-footed geese (*Anser brachyrhynchus*) in Greenland that reacted to a helicopter by 'running' to water at $d = 10$ km on which they aggregated 'in panic' at $d = 4$ km (Madsen 1984), a behaviour presumably involving high

expenditure of energy. Second, the time and energy costs of the responses of the birds at Stormyra were evidently small. Thus, undisturbed, non-breeding barnacle geese spend $\approx 46\%$ of their time grazing during the moulting period (Madsen and Mortensen 1985). For birds that are active around the clock during the continuous daylight of the Arctic summer (Dittami *et al.* 1979; Daan and Aschoff 1981), this is equivalent to $\approx 662 \text{ min} \cdot 24 \text{ h}^{-1}$. On this basis, a response of median duration (35 min; Appendix 1-3) would therefore represent a potential loss of $\approx 6\%$ of grazing time per 24 h. Such a loss would be significant only if the birds were unable to compensate for any ensuing reduction in food intake. Failure to compensate, however, seems unlikely in a species in which intradiel variation in grazing time is as much as $\approx 20\%$ of the mean (Ebbinge *et al.* 1975). We conclude that the loss of grazing time during 1 response of median duration is unlikely to have much, if any, biological significance for the birds.

The response specific cost of disturbance in terms of increased energy expenditure would also have been small. Birds on Stormyra were rarely $>10 \text{ m}$ from the waters' edge and used $<1 \text{ min}$ to reach water each time they were disturbed. The increment in the birds' daily energy expenditure (DEE) due to walking during disturbance must therefore have been almost negligible. The same is true of the incremental cost of swimming: the birds paddled about slowly and their oxygen consumption ($\dot{V}O_2$) would therefore barely have risen above resting (Nolet *et al.* 1992). The 1 exception to this was the case of the birds outside the immediate study area that were $>1 \text{ km}$ from the nearest pond when disturbed. These birds waddled rapidly for $\leq 24 \text{ min}$ to reach water. This single response represents an increase of 48% of mean daily (24 h) walking time of undisturbed birds in Greenland ($\approx 50 \text{ min} \cdot 24 \text{ h}^{-1}$; Madsen and Mortensen 1985) and, assuming that DEE_{walking} barnacle geese is approximately the same as in pink-footed geese ($\approx 3.1\%$ DEE; Madsen 1984), such an increment would generate an increase in energy consumption of $\approx 1.5\%$ DEE. This is a conservative estimate. The birds appeared to be moving as fast as they could and, given that the $\dot{V}O_2$ of barnacle geese walking at speed ($0.88 \text{ m} \cdot \text{s}^{-1}$) is 64% greater than at slow walk ($0.44 \text{ m} \cdot \text{s}^{-1}$; Nolet *et al.* 1992), the energy cost of the observed response may have been as much as 2.5% DEE.

We draw 2 conclusions. First, the spatial distribution of birds and, specifically, the distance from birds to water onto which they may move to escape perceived danger, is evidently a major determinant of the instantaneous energy cost of their response. Second, the specific instantaneous time and energy costs of the responses to both the natural (fox) and anthropogenic (helicopter) disturbances to which

the birds on Stormyra were exposed were small and the impact of such disturbances will therefore depend chiefly on the frequency of their occurrence.

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Appendix 1. Time course of helicopter provocation. Trial 1: a group of barnacle geese ($n = 160$) on Stormyra.

Time (GMT)	Distance geese - helicopter (d , km)	Observations	Time from first reaction (min)
12:42	6.0	Helicopter takes off.	
12:45	3.7	Helicopter pilot can see the ponds at Stormyra for the first time. Observers at Stormyra can hear the helicopter; distance observers – helicopter = 2.4 km.	
12:45	3.2	Ten geese crane their necks.	0
12:46	2.7	Geese nearest the helicopter ($n \approx 50$) begin to waddle towards Pond 6.	<1
12:46	2.5	All geese ($n = 160$) on Pond 6. Helicopter at its closest point to the geese during this trial.	1
12:50	5.0	Helicopter lands. Engine switched off.	8
12:58		All geese swim calmly towards the middle of Pond 6 and combine with another group of barnacle geese ($n = 649$) swimming across from the NW side of the pond. The combined flock of 809 geese (i.e., all the barnacle geese at Stormyra) swims calmly NE across the pond.	13
13:01		The first barnacle goose walks ashore on the NE side of Pond 6.	16
13:11		The combined group divides in two. One group ($n = 158$) walks ashore and begins to graze.	26
13:15		All geese, in 2 groups ($n = 158$ and $n = 649$), on land close to Pond 6.	30
13:20		All geese now either calmly grazing or resting.	35
13:30		Approximately 300 birds from the large group waddle down and swim out on to Pond 6.	
13:45		178 geese still swimming about on Pond 6. Observations end.	

Appendix 2. Time course of helicopter provocation. Trial 1: a group of barnacle geese ($n \approx 100$) on the west bank of the river beyond Stormyra.

Time (GMT)	Distance geese - helicopter (d , km)	Observations	Time from first reaction (min)
12:42	≈ 10.0	Helicopter takes off.	
12:45		All geese start waddling rapidly NW along the riverbank towards ponds on the W bank of the river beyond Stormyra.	
12:50	6.0	Helicopter lands. Engine switched off.	5
13:05		The majority ($n \approx 80$) arrive at and swims out on to a pond. The remaining 20 birds are still waddling rapidly NW.	20
13:09		The remaining 20 birds arrive at the same pond and swim out on to it.	24
13:11		All birds grazing on land. Observations end.	26

Appendix 3. Time course of helicopter provocation. Trial 2: all barnacle geese ($n = 809$) on Stormyra.

Time (GMT)	Distance geese -helicopter (d , km)	Observations	Time from first reaction (min)
13:53	5.2	Helicopter engine starts. Approximately half the birds waddle down and swim out on to Pond 6.	0
13:53	4.7	All geese on Pond 6.	<1
13:54	3.8	All geese in 1 moderately tightly packed group Pond 6.	1
13:55	3.1	All geese in 1 tightly packed group on Pond 6.	2
14:01	5.0	Helicopter lands. Geese have swum SW to the middle of Pond 6. Most now resting in a tightly packed group but some birds have turned back.	8
14:09		The first birds come ashore.	17
14:15		Approximately 300 birds now ashore.	23
14:24		All birds on land in a single, tightly packed group and either grazing, walking about or resting. Some birds seem nervous.	31
14:30		All birds waddle rapidly down to the water's edge and approximately half swim out on to the pond. No obvious cause for this response.	37
14:45		All birds on land in a single, tightly packed group and either grazing or walking about. Observations end.	52