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Reactions of a colonial seabird species to controlled gunshot disturbance experiments

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Gunshots are a worldwide source of anthropogenic disturbance, and knowledge about the potential effect on wildlife is central for conservation and sustainable management of affected species. This study contributes novel insight of the response behaviour and effect of gunshot disturbance on one of the most culturally important seabird species of the Arctic, the thick-billed murre (Brünnich's guillemot, *Uria lomvia*). We studied effects of gunshot disturbance at breeding colonies to explore the distance where effects started, the difference in the behavioural response between presumed disturbed colonies (e.g. by traffic and hunting) and largely undisturbed colonies, and among plots with varying seabird densities. We carried out two different types of controlled gunshot experiments – one measuring the distance at which murres first reacted to gunshots (flight initiation distance, 'FID') and one measuring the proportion of murres remaining in the colony during and after repeated gunshots (20 gunshots within 78 min). FID varied from 0.5 to 5 km. The proportion of murres remaining in the plot after the repeated gunshots ranged from 0.44 to 0.8. Mainly murres not attending offspring took off when disturbed by gunshots, but occasionally also birds incubating their egg or brooding their chick took off. We found that density of seabirds (murres and black-legged kittiwakes *Rissa tridactyla*) at the plot area scale was the best explaining factor for FID, and to some extent also for the effect of repeated gunshots, both for disturbed and undisturbed colonies. Murres in denser colonies reacted earlier (had larger FIDs) and somewhat more strongly (higher proportions fleeing) to gunshots than murres in less densely populated colonies. FID clearly showed that the current legislation in Greenland regulating gunshots near breeding colonies is insufficient. We provide some recommendations for improved management of a popular game species under pressure.

Keywords: flight initiation distance, gunshot disturbance, seabird colonies, thick-billed murre, *Uria lomvia*, wildlife

Anthropogenic disturbances on wildlife, caused by activities such as farming, construction, transport, wildlife tourism and outdoor recreation, is a worldwide and increasing issue (Burton 1998, Buckley 2004, Green et al. 2005, Davenport and Davenport 2006, Stankowich 2008). In some areas, hunting (recreational and/or subsistence) is a noteworthy activity in otherwise remote areas (Dahl 1989, Milner-Gulland and Bennett 2003, Sharp and Wollscheid 2009). However, the disturbance effects of gunshots on wildlife are rarely investigated (Stankowich 2008, Livezey et al. 2016). With this paper we aim to contribute to the limited knowledge about the effect of gunshot disturbances with an experimental approach.

Disturbance of wild animals is, depending on the disturbance level, known to cause increased vigilance, habitat loss, reduced fitness and/or lower breeding success due to increased stress, energetic costs, predation of offspring or loss of offspring when fleeing (Olsson and Gabrielsen 1990, Creel et al. 2002, Beale and Monaghan 2004, Rodríguez-Prieto and Fernández-Juricic 2005, Lundquist et al. 2013). Animals can habituate or show increased tolerance to repeated disturbances (Nisbet 2000, Diego-Rasilla 2003, Stankowich and Blumstein 2005, Walker et al. 2006), but in contrast disturbance can also lead to sensitization (Stankowich 2008, Rankin et al. 2009, Blumstein 2014). This means that the response to disturbances can differ among individuals of the same species due to previous experiences (Stankowich and Blumstein 2005, Ellenberg et al. 2009, Ellenberg et al. 2012, Villanueva et al. 2012, Pichegru et al. 2016).

Cliff-breeding colonial-seabirds, such as the thick-billed murres *Uria lomvia* (hereafter 'murres'), are particularly vulnerable to repeated disturbances, because they aggregate in large numbers and are very faithful to their breeding sites (Gaston et al. 1994, Gaston and Hipfner 2000, Coulson 2002, Bejder et al. 2009). This species is highly abundant with a circumpolar distribution (Gaston and Hipfner

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2000, Irons et al. 2008), but is declining in several regions of the North Atlantic (Descamps et al. 2013, Merkel et al. 2014, Fauchald et al. 2015, Frederiksen et al. 2016). Climate-related oceanographic changes at the wintering areas have been associated with population declines in Svalbard (Descamps et al. 2013), and Frederiksen et al. (2016) reported a strong connection between wintering areas and population status of several Atlantic breeding populations. Hunting in the wintering areas off Greenland and Canada is also a contributing factor to the population decline (Frederiksen et al. 2019). However, local factors during the breeding season, such as disturbances, may contribute to some of the contrasting trends observed for different breeding colonies of murres in Greenland – 13 of 19 colonies are declining; the remaining six colonies are stable or increasing (Merkel et al. 2014).

Although never quantitatively measured, it is well known that some murre colonies in Greenland were extensively disturbed in the past by anthropogenic factors, such as hunting, boat traffic, aerial traffic, and by purposefully using guns and other loud noises to initiate fleeing from the colony. Passenger ships and locals regularly used this latter activity, so that they could view the spectacular phenomenon of many birds fleeing the colony simultaneously (Chardine and Mendelhall 1998, Gilchrist 1999, Merkel et al. 1999).

Despite a declining number of families that depend on hunting for subsistence, hunting remains an important source of sustenance for many, as well as a popular recreation activity, now involving larger and faster motor boats (Dahl 1989, Rasmussen 2005, Boertmann et al. 2013, Boertmann and Mosbech 2017). Seal hunting from open boats at sea is one of the most common forms of hunting throughout the year (Boertmann et al. 2013, Boertmann and Mosbech 2017), and, for the summer months of June, July and August, about 25 000–50 000 seals are reported shot every year (2006–2015, PILU/Piniarneq database, June 2017). Furthermore, researchers have witnessed several incidents of illegal bird hunting at or near seabird colonies in Greenland during the field season (Labansen et al unpubl.). In one extreme case in 1998, researchers observed seven hunting episodes over a period of 12 days, involving a minimum of 284 gunshots (Merkel et al. 1999). By Greenland law, murre colonies are protected by a no-shooting zone that was 5 km from the colony from 1958 (Anonymous 1958) until 2009 and was reduced to 1 km in 2009 (Anonymous 2009). However, it is unknown how well the no-shooting zones are respected. In some areas, colonies closest to settlements and boating routes have the largest population declines (Boertmann 2001).

According to the optimal escape theory, potential prey will counterbalance the risks and costs of fleeing from predators during an encounter with a predator (Ydenberg and Dill 1986), and we can control several factors that affect the risk and cost of fleeing (e.g. species, season, life stage and distance to cover) when studying disturbance response behaviours in murre colonies at a specific breeding stage. However, density, or group size in a specific area, is an important factor that can vary among and within colonies. Group size can decrease the fleeing distance (distance from which individuals decide to flee from an approaching predator) due to the diluted predation risk of each individual (Cresswell and Quinn 2011), and the decreased likelihood of predator success with multiple targets (the confusion effect) (Milinski 1984, Parrish 1993, Jeschke and Tollrian 2007). Conversely, group size can cause an increased fleeing distance due to an increased probability of detecting predators and from the increased probability of more vigilant individuals being present in the group (Ydenberg and Dill 1986, Lima 1995, Stankowich and Coss 2006, Stankowich 2008, Braimoh et al. 2018).

We carried out controlled experiments in murre colonies; 1) to investigate the distance at which birds first reacted to approaching gunshots – the so-called flight initiation distance (FID), and 2) to study the response to repeated gunshots, imitating an at-sea hunting situation in Greenland (Merkel et al. 1999, Boertmann et al. 2013, Boertmann and Mosbech 2017). The experiments were carried out in multiple colonies to allow comparison of behavioural responses between disturbed/declining and undisturbed/stable colonies, and in multiple plots within colonies to investigate the importance of group size and colony structure. Based on the FID results of the approaching gunshot experiment, we evaluated whether colonies are sufficiently protected by a no-shooting zone of 1 km. The repeated gunshot experiment illustrates effects of hunting near murre colonies and we discuss possible long-term effects.

Methods

Study species and colonies

Murres breed in dense colonies on narrow ledges along steep coastal cliff sides. In Greenland, murres often breed in mixed colonies with black-legged kittiwakes *Rissa tridactyla* and some are homogenous colonies of only murres. Murre colonies can also include one or more of the following species northern fulmar *Fulmarus glacialis*, glaucous gull *Larus hyperboreus*, razorbill *Alca torda* and other alcids. However, these latter species are typically less numerous and generally found in the periphery of the main murre nesting areas. The female lays one egg directly on the cliff ledge and both parents take turns attending (incubating and rearing) the egg/chick (Gaston and Hipfner 2000). The Greenland colonies, including the study colonies vary significantly in size and structure – some consist of relatively uniform cliff sides with continuously occupied breeding ledges, others have a patchy distribution, while others consist of sub-colonies separated by barren cliffs or distributed within an archipelago (Table 1, Fig. 1).

Data were collected in 2015 (four colonies) and 2017 (three colonies) from a total of six colonies, of which four colonies had declining breeding populations (Apparsuit in Northern Upernavik, Kingittoq in Southern Upernavik, Innaq in Disko Bay and Sermilinnguaq in the Maniitsoq area) and two had populations that were stable or slightly increasing (Kitsissut in the Qaanaaq area and Kippaku in Northern Upernavik – Table 1, Fig. 2) (Falk and Kampp 1997, Merkel et al. 2014). The disturbance level of colonies was roughly categorized as high or low based on accessibility. The sub-colonies of Kitsissut, placed on an archipelago about 50 km from the nearest coast of the sparsely inhabited Qaanaaq area, have a very low disturbance level (Burnham and

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Table 1. Colony characteristic and latitude of thick-billed murre colonies in Greenland where gunshot experiments were carried out in 2015 and/or 2017. Colony size represents the number of individuals counted on photos in 2015 or 2017 (Greenland Institute of Natural Resources, unpubl.), population trend since the late-nineties is shown as stable (→) or declining (↓) (Merkel et al. 2014), and disturbance level was categorized as low or high. The type of experiment is indicated by AGS (approaching gunshot study) or RGS (repeated gunshot study) with date (and year) of the experiment(s) indicated. Colonies are sorted according to latitude from north to south.

Colony	Colony description	Size (year)	Trend	Disturbance level	Study type	Date(s) (year)
Kitsissut	12 sub colonies of varying size and density on three islands in an archipelago 50 km from the mainland. Murre-only colonies. Latitude 76°44′.	9100 (2015)	→	Low	AGS RGS	Aug 2, 8 Aug 7, 8 (2015)
Apparsuit	18 sub colonies of varying size and density, some murre-only some with kittiwakes, along tall coastline of 7 km along S–SW side of large island. Latitude 73°48′.	50 500 (2017)	↓	High	AGS RGS AGS	Jul 23 (2015) Jul 23 (2017)
Kippaku	More or less continuous along 0.5 km coastline on N–NE side of small island mixed with kittiwakes. Latitude 73°43′.	21 400 (2017)	→	Low	AGS RGS	Jul 21, 25 Jul 21 (2015)
Kingittoq	Patchy distribution along tall coastline of 0.6 km on peninsula mixed with kittiwakes. Latitude 72°40′.	2450 (2017)	↓	High	AGS	Jul 11 (2017)
Innaq	Patchily distributed in two main areas of respectively 0.8 and 0.2 km within a bay and mixed with kittiwakes. Latitude 69°48′.	1000 (2015)	↓	High	AGS RGS	Jul 12 Jul 12 (2015)
Sermilinnguaq	Patchily distributed along coast of 0.6 km along north coast of small fjord, mixed with kittiwakes. Latitude 65°40′.	4600 (2017)	↓	High	AGS	Jul 17 (2017)

Burnham 2010). The remaining colonies are within boating distance of nearby settlements and are all, to some extent, exposed to anthropogenic disturbances. However, the disturbance level at Kippaku is assumed to be relatively low. Kippaku is only about 7 km from the much larger Apparsuit; however, it is somewhat shielded by Apparsuit because the latter is much closer to the boating route.

Data collection was, to a large degree, coordinated with monitoring work or other research projects, due to the high costs of doing fieldwork in the Arctic (Mallory et al. 2018). In some colonies, it was possible to stay and work for a longer period (Innaq, Kippaku and Kitsissut), whereas others were more sporadically visited due to safety and to logistical concerns (Apparsuit, Kingittoq and Sermilinnguaq). The experiments were carried out during the chick rearing period, when most eggs had hatched, which varied from mid-July to early August (Table 1) depending on latitude (Falk and Kampp 2001).

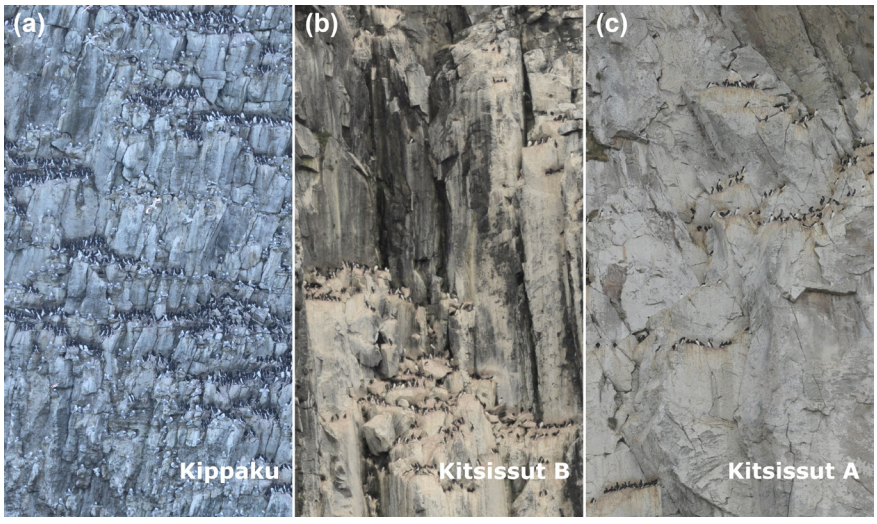


Figure 1. Examples of thick-billed murre breeding colonies of varying density and structure in Greenland: (a) high density area continuously occupied with breeding ledges of thick-billed murre mixed with black-legged kittiwake, (b) partly continuous and partly patchy structure of breeding murres of medium density, (c) patchy distribution of breeding ledges in low density area.

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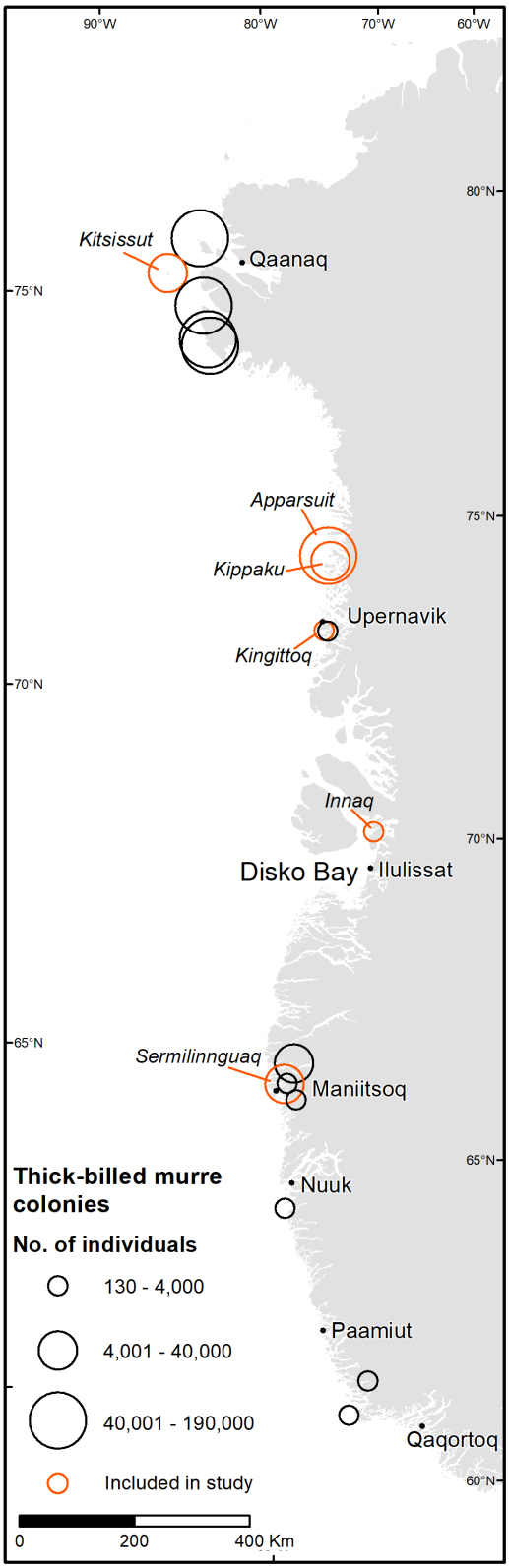


Figure 2. Location and population size of thick-billed murre breeding colonies in West Greenland based on the most recent surveys (2014–2017, Greenland Institute of Natural Resources, unpubl.). Colonies of this study are highlighted with orange. Nearest main town (black dots) for areas with murre colonies are shown.

In the approaching gunshot experiment, a mix of video recordings and direct observation were used to monitor murre reaction (alertness and fleeing) and in the repeated gunshot scenario, video recordings were used to determine the proportion of murres leaving after each gunshot (see later description on the use of cameras). The plots varied in size and were limited to sites where it was possible to mount cameras to record a suitable amount of murres (> 60 murres). For one colony, Apparsuit, this meant that breeding densities at the plots were less dense than typical for this colony. Density of birds at the plots was defined as the number of murres and black-legged kittiwakes (hereafter 'kittiwake') on the cliff within an area of about 75 × 75 m, with the plot as the centre point. The number of birds and the size of the area was determined from high quality photographs taken for colony census purposes, either within the same year of the experiments (4 of the 6 colonies) or within two years of the experiment (Kippaku and Apparsuit B). The size of the area was extrapolated from the pixel height of an upright standing murre assuming the average height of a murre to be about 30 cm from head to tail when standing in a typical upright pose with the ventral side towards the cliff (assessed from taxidermy mounts of murres).

Camera setup

Video cameras (Panasonic HC-W850 and/or JVC GZ-EX515BE) were placed so that they covered a plot with about 70–400 adult murres within a distance of about 30–200 m; this allowed us to identify chicks on most of the recordings (not at Apparsuit B and Kitsissut B+). Two different plots were filmed during the experiments at Kitsissut, Kippaku and Innaq.

The cameras were started at least 15 min (and preferably an hour or more) before initiation of disturbance experiments and continued 13–536 min after the disturbances were stopped. This varied due to the very different conditions at every plot, both in terms of the physical characteristic of the respective colonies (i.e. accessibility of the plots) and the weather conditions at the time of the experiments.

At Innaq and Kippaku, a video plot from each colony were overlapped significantly with time-lapse photo plots established for monitoring purposes (Huffeldt and Merkel 2013). Data from these plots, originating from the same field season, made it possible for us to identify active breeding sites in the overlapping area at the time of the repeated gunshot experiment (see later description of the repeated gunshot experiment) (Greenland Institute of Natural Resources, unpubl.).

Gunshot experiments

Murre response was observed while conducting two types of controlled gunshot experiments: 1) the approaching gunshot experiment, and 2) the repeated gunshot experiment at a fixed distance (approx. 500 m). On three occasions, the repeated gunshot experiment was carried out shortly after the approaching gunshot experiment, but first allowing birds to return to the plots (Innaq, Apparsuit and Kitsissut).

A caliber .222 Remington bolt-action rifle (CZ527, 1:14″), with ammunition from Sellier and Bellot (FMJ, 50 g)

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was used for the experiments. The caliber .222 is a common choice of weapon for the hunting of most seals (NAMMCO 2004). The smaller and less powerful .22 magnum and .17 are also common; more powerful weapons are used for larger seals and other mammals (up to .30-06) (NAMMCO 2004). Shotguns are the primary choice for seabird hunting (e.g. 12 gauge). The noise level of these kinds of recreational weapons has been measured to range from about 140 dB (.22 LR) to 164 dB (.30-06) dB, depending on location of measuring device relative to the weapon, ammunition type, weapon model and location, among other factors (Flamme et al. 2009, Meinke et al. 2014). The .222 is a caliber between the least and the most powerful types mentioned. The experiments were conducted in calm weather with no or little wind, because noise impacts are greatly influenced by conditions like wind speed, wind direction, humidity and landscape (Pater et al. 2009). The shooter was in contact with an observer via VHF radios during the disturbance event. The observer at the colony, was located well away from the birds so that they were not disturbed by the observer. The gunshots were directed towards the colony and plot(s), with an upward shooting angle of about 45 degrees, making sure not to compromise the safety of people or birds.

Approaching gunshot experiment

This experiment was carried out from a boat. The first gunshot was fired at a distance of at least 7 km (measured using a Garmin GPS with a waypoint near the relevant plot(s)) – well away from the detection range of birds at the colony. The colony was approached by the boat with the shooter at max. 3 knots when nearing the colony – well below the speed that might elicit responses from the birds due to boating (personal experience and following general guidelines for boating near seabirds colonies in Greenland, Anonymous 2019). The propulsion of the boat was briefly halted while a single gunshot was fired by the shooter towards the colony at the following distances: 6, 5, 4, 3, 2, 1.5, 1 and 0.5 km – or until flight initiation of murres from the plot(s) (i.e. the FID) was detected by the observer, in which case the observer signalled the shooter to stop.

For each gunshot, the following were recorded: wind speed and direction, time of the gunshot and the effect of the shot (reaction of murre (alertness and flight initiation) and kittiwake (flight initiation)) in the colony in general and reactions within the plot.

At Apparsuit and Kitsissut the experiment was repeated within the same colony but in different sub-colonies. At Kippaku it was repeated at the same location due to fog during the first experiment. At Sermilinnguaq and Kingittoq, the approaching gunshot experiment was conducted without video cameras, and the reaction of murre and kittiwake within defined focus areas were observed from a boat.

Repeated gunshots experiment

At a consistent distance of approx. 500 m from the plot(s), four series of five gunshots were fired at an interval of 10 min between each series with 3 min between gunshots within a series (20 gunshots over 79 min in total). With no prior experience, it was assumed that all plots would show fly-outs at a distance of about 500 m and show the effect of hunting activities near murre colonies. The shooting was performed from a boat, except at Kitsissut where the topography of the island allowed for doing this on land while facing the colony at a similar distance. Time and general reactions in the colony were noted for each shot. The results from one plot at Kitsissut was excluded due to adverse wind conditions.

The number of murres present at the plots before and after each shot in the repeated gunshot experiment were counted on screenshots from the video recordings using ImageJ (Vers. 1.51j, <https://imagej.nih.gov/ij/> – a public domain image processing software program (Schneider et al. 2012)). When the video footage was of sufficient quality, it was noted when any chicks or eggs were left alone by an attending parent bird. The number of birds in the plot before the first, and after the last, gunshot was counted at least three times (usually more than five times) at 3–10 min intervals, depending on how long the plot was filmed. If filmed for more than an hour before/after the gunshot sequence, then birds were counted every 20–60 min.

For murre it is not possible to distinguish males from females or breeders from non-breeders, and non-breeders in addition to failed breeders are inclined to hang out in the colony, behaving much like breeding birds (Gaston and Hipfner 2000). However, based on attendance patterns, a technique using time-lapse photography and digital image analysis was developed by Merkel et al. (2016) that identifies breeding sites and non-breeding sites and distinguishes between successful and unsuccessful breeding sites. Breeding sites at the Kippaku and Innaq plots that were overlapped with the time-lapse photo plots were individually observed on the video recordings to identify the reaction of the attending bird to every gunshot. The reaction of these birds was categorized as either staying at a site or leaving the site and it was noted whether the site was attended again before the next gunshot. Any egg or chick that was lost, or otherwise relocated, during the disturbance event was noted.

Data analysis

Regression analyses were carried out in the software R ver. 3.6.1 (<www.r-project.org>) using the 'lm' function and were used in the analysis of both experiment types; in the approaching gunshot experiment to test for the relationship between bird density and FID, and in the repeated gunshot experiment, to test for relationship between bird density and regression coefficients, where the latter was used as a measure of reaction strength. When testing for differences between categorical parameters, low sample size was accounted for by using the Mann–Whitney U test according to Fowler and Cohen (1990). Graphs were made with Microsoft Excel (Office 365) and by using the *ggplot2* package in R (Wickham 2016).

Results

Approaching gunshot experiment

Data were obtained from 11 plots of which the two from Kippaku were repeated resulting in 13 data points. Overall, the distance that birds first reacted with alertness ranged from 1 to 5 km and FID ranged from 0.5 to 5 km (Table 2,

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Table 2. Alertness distance (A) and flight initiation distance (FID) for thick-billed murre exposed to approaching gunshots from a cal. .222 rifle at 6 breeding colonies in West Greenland. The colonies were classified as with a high (H) or low (L) disturbance level, colony structure as patchy (p) or continuous (c) and densities of murre and black-legged kittiwake (BLK) of the area (75 × 75 m) surrounding and including the plots/center of observations. Wind direction, relative to the shooting direction, is indicated as headwind (h), crosswinds (c) or tailwind (t). The plots are sorted by descending FID.

			Bird density (75 × 75 m)			Distance of bird reaction (km)		
						Within plot		Outside plot
Colony, plot*	Disturbance	Structure	Murres	BLK	Wind (m s^{-1})	A	FID	FID[¤]
Kippaku, C	L	c	4533	3178	0	4	4	5
Kippaku, E	L	c	5672	3625	0	4	3	5
Kippaku, E [(f)]	L	c	5672	3625	0–1 c	3	3	5
Kippaku, C [(f)]	L	c	4533	3178	0–1 c	3	–	5
Kingittoq	H	c/p	758	940	0	4	3	(5)
Kitsissut, B+ [(w)]	L	c/p	868	0	0–3 t/c	2	2	2
Sermilinnguaq	H	p	1154	1292	1–2 h/c	2	2	–
Apparsuit, B	H	p	633	1	0	3	1.5	–
Innaq, A	H	p	114	277	0–1 h/c	2	1.5	(5)
Innaq, H	H	p	185	1547	0–1 h/c	2	1.5	(5)
Apparsuit, Q	H	p	286	425	0	1	< 1	3
Kitsissut, A [(f)]	L	P	415	0	0–1 h	3	0.5	–
Kitsissut, C	L	p	192	0	0–3 t/c	1.5	0.5	0.5

* Experiments carried out in sub-optimal conditions due to wind [(w)] or fog [(f)].
[¤] FID for BLK in brackets.

Supplementary material Video A1 (<https://youtu.be/C9Y41HZr_zo>)). Kippaku showed lower FIDs during the first experiment when conditions were foggy (Table 2). In the following analyses the results from the second experiment for Kippaku was used.

The difference in median FID between plots from high (median = 1.5 km) and low (median = 2 km) disturbance level colonies was not significant (Mann–Whitney U test: $U = 13$; $p > 0.05$; $n1 = 6$; $n2 = 5$). Rather, a visual inspection of the data implied a relationship between colony structure and density of the observed area and the reaction distance – the FID in particular (Table 2); plots with an FID of 1.5 km or less were characterized by being in areas of relatively small and isolated groups of birds with a density of less than 700 murres per 5625 m^2 (75 × 75 m), and plots with an FID of more than 2 km were situated within denser and relatively large breeding areas (Table 2).

A regression analysis showed that the FID not only was related to the number of murres, but also the number of kittiwakes within the defined surroundings (75 × 75 m) of the plots. Both murre density and the combined density of murres and kittiwakes showed a linear relationship with murre FID; however, the combined density explained a larger proportion of the variation in FID (murre density, lm: $F(1,9) = 14.78$, $p < 0.004$, $R^2 = 0.6215$; combined density, lm: $F(1,9) = 23.42$, $p < 0.001$, $R^2 = 0.7224$; Fig. 3).

Repeated gunshots experiment

Data were obtained from 9 plots (Table 3). The proportion of birds leaving the plots at any gunshot ranged from 0 (Kitsissut C) to 0.38 (Kitsissut A) relative to the initial number of birds (before the first gunshot). The number of birds remaining in the plot after each gunshot decreased markedly

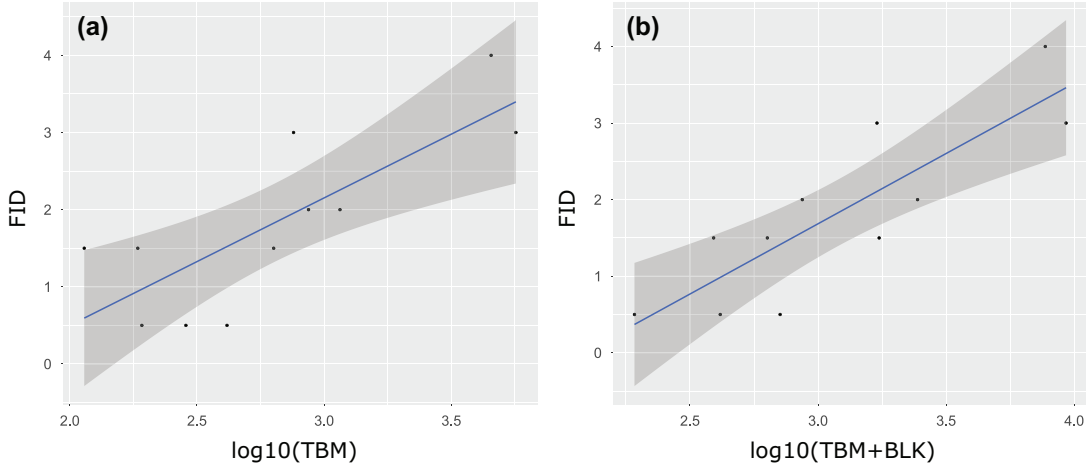


Figure 3. Flight initiation distance (FID) of approaching gunshots in relation to density of birds (a – thick-billed murre (TBM), b – thick-billed murre and black-legged kittiwake (BLK)) in 11 plots from 6 breeding colonies of thick-billed murre in West Greenland. The density was defined as the number of birds within a 75 × 75 m area, containing and surrounding the observed plot/focus area.

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Table 3. Escape response to repeated gunshots at four colonies of thick-billed murre (TBM) in Greenland, 2015. Initial number of TBM in video plots of varying size before a repeated gunshot (gs) experiment of 20 gs fired at 500 m, and the proportion of TBM remaining in the plots at the last gs. The regression coefficient represents the blue regression line in Fig. 4 and describes the development and significance (·) of the proportion of TBMs remaining in the plot over the course of the gs experiment. Density of birds indicates the number of TBM and black-legged kittiwakes combined, within an area of 75 × 75 m surrounding the plots. The range in number of observed eggs/chicks that were abandoned at each gs and the number of times abandonments occurred during the gs series is indicated. The quality of each video footage was categorized as low (l), medium (m) or high (h). The plots are sorted with ascending proportion of birds at last gunshot relative to the initial number of TBM.

Colony, plot	Initial no. of TBM	Proportion remaining after last gs	Regression coefficient (×10³)	Density of birds	No. of egg/chicks abandoned; freq. of occurrence	Quality (l, m, h)
Kitsissut, A	98	0.44	−2.23··	415	1–5; 15	m
Kippaku, E	210	0.49	−2.25···	9297	1–2; 8	m
Kippaku, C	**415**	**0.51**	−2.35···	7711	**2–19; 20**	**h**
Innaq, H	96	0.53	−0.98··	1732	1; 1	m
Kitsissut, B	69	0.55	−1.83···	868	1–2; 14	h
Kitsissut, B+	175*	0.67	–	868	–	l
Apparsuit, B	106	0.76	0.26	634	–	l
Kitsissut, C	147	0.78	−0.56	192	0	m
Innaq, A	**111**	**0.80**	−0.96···	391	**1; 1**	**h**

Bold: Plots overlapping with time-lapse photographic monitoring plots (Fig. 5).
* Number of murres before the effect of the flight initiation study (3 shots before the repeated gs experiment started).

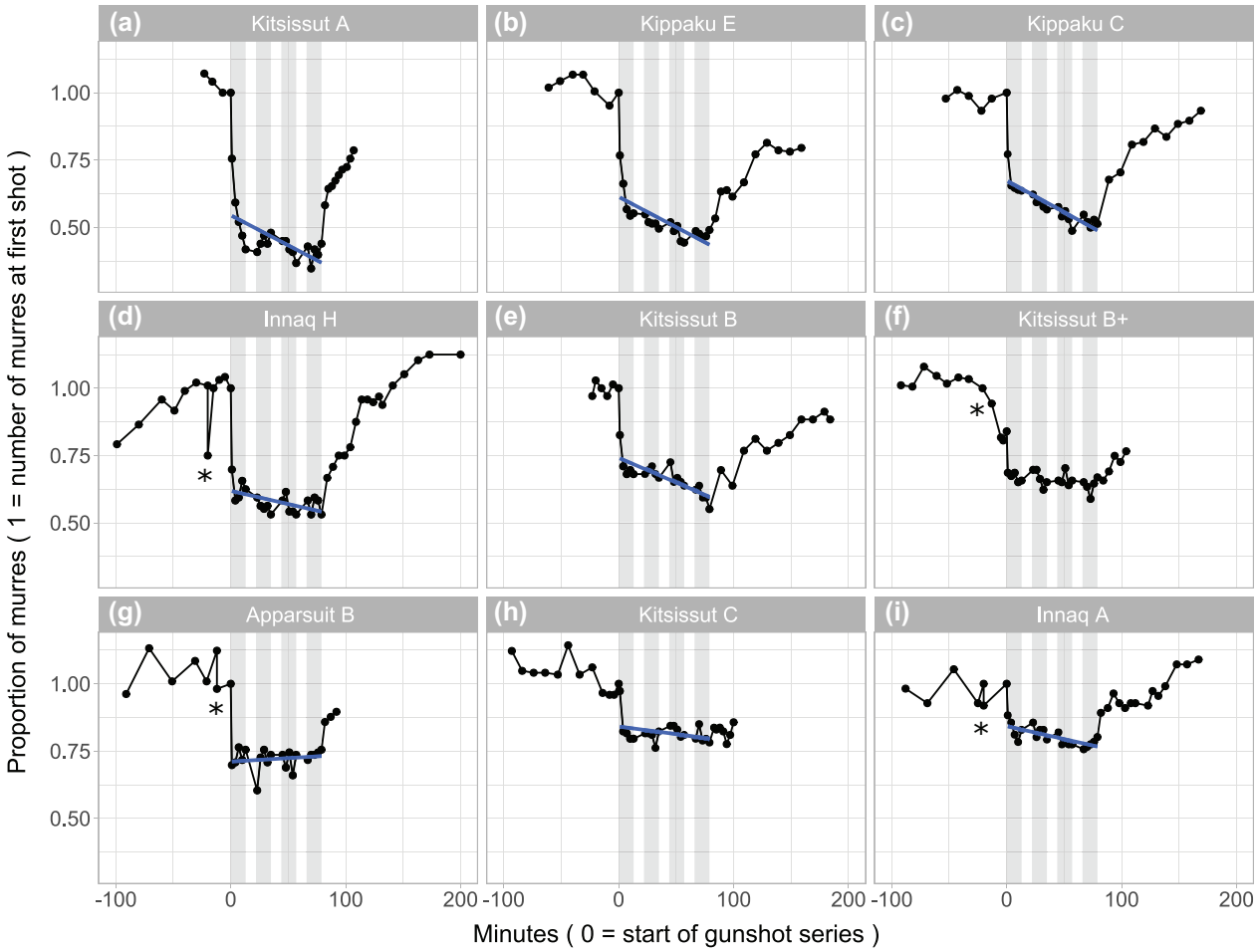


Figure 4. Proportion of thick-billed murres remaining on the ledges at nine different video plots before, during and after a repeated gunshot disturbance experiment of 20 gunshots. The shaded areas indicate the four series of five gunshots with three minutes intervals, showing the proportion of murres just after each gunshot relative to the initial number of murres. Innaq A+H, Apparsuit B and Kitsissut B+ were following an approaching gunshot study and exhibited fly-outs at respectively 1, 1 and 3 gunshots (*) prior to the gunshot series. The number of birds before the three gunshots at Kitsissut B+ are considered as the initial number of birds. The regression lines (blue) are based on the proportion of birds remaining in the plot after each gunshot. The plots are sorted with ascending proportion of murres at last gunshot, see Table 3.

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during the first series of five gunshots (Fig. 4). Hereafter, the pattern more or less stabilized at some plots (Apparsuit B, Kitsissut C and Innaq A) at a proportion of about 0.75 or more, whereas the numbers kept decreasing at the remaining plots to somewhere between 0.4 and 0.7 of the initial number of murres (Fig. 4, Table 3).

The repeated gunshot experiment occurred after, and was potentially influenced by, an approaching gunshot experiment in four of the plots (Fig. 4d, f, g and i). At Innaq and Apparsuit a single gunshot caused flight initiations 20 and 12 min prior to the start of the experiment, respectively (both at a distance of 1.5 km), but the number of birds at the three plots went back to previous levels before the gunshot series were initiated. Kitsissut B+ was influenced by three gunshots prior to the repeated gunshot experiment, and, in this case, the count immediately before these three gunshots (21 min before the repeated gunshot experiment) was considered the initial number of murres (Table 3, Fig. 4f). Thus, Kitsissut B+ was not included in the following regression analyses.

Regression analyses of the proportion of birds remaining in a plot after each gunshot showed that high-density plots typically had a regression coefficient that was much lower, i.e. with a steeper negative slope, indicating a stronger reaction, than the low-density plots (Table 3, Fig. 4). However, there was no significant relationship between regression coefficient and bird density (lm: $F(1,6)=2.942$, $p=0.13$, $R^2=0.329$). Similarly, median regression coefficients overlapped between plots of disturbed and un-disturbed colonies (Mann–Whitney U-test: $U=2$; $p > 0.05$; $n1=3$; $n2=5$). Furthermore, median regression coefficients were similar between plots that were observed after an approaching gunshot experiment and plots that were not preceded by such an experiment (Mann–Whitney U-test: $U=3$; $p > 0.05$; $n1=4$; $n2=4$).

The only two plots that were filmed long enough to reach 100% of pre-disturbance levels were the Innaq plots A and H, which had a duration of 69 and 62 minutes, after the last gunshot was fired, respectively. After 14 (plot A) and 35 (plot H) minutes they had reached 95% of pre-disturbance levels. The plots at Kitsissut B and Kippaku C reached 90% of the initial numbers after 100 and 90 min, respectively. Kippaku E appeared to stabilize between 77 and 81% after 40–80 min (Fig. 4). The recording times after the last gunshot for the remaining plots (13–28 min) were not sufficient to determine a return rate (Fig. 4).

Reaction among attending breeders

Without data on breeders/non-breeders for most of the plots, it was not possible to estimate the proportion of breeders leaving after gunshots, but it was, to some degree, possible to observe chicks left alone, indicating a minimum number of attending breeders leaving their offspring. The observed plots showed a noticeable variation in the range of this response – from none to 19 attending breeders leaving their nest sites, and some repeatedly (Table 3). The two time-lapse photo plots at Kippaku and Innaq, in which all breeding sites were identified, represented two extremes. An increasing proportion of attending breeders at the Kippaku C plot left their offspring during the repeated gunshots, and an increasing proportion of these did not return to the plot before the next gunshot (Fig. 5). The number of times the same nest site was abandoned by the attending bird ranged from 1 to 13. In contrast, only a single chick was left alone on one occasion at the Innaq A plot (Fig. 5).

Four of the 114 nest sites identified within the video plot at Kippaku, were classified as failed on the date of the repeated gunshot experiment, based on the time-lapse overlay analyses

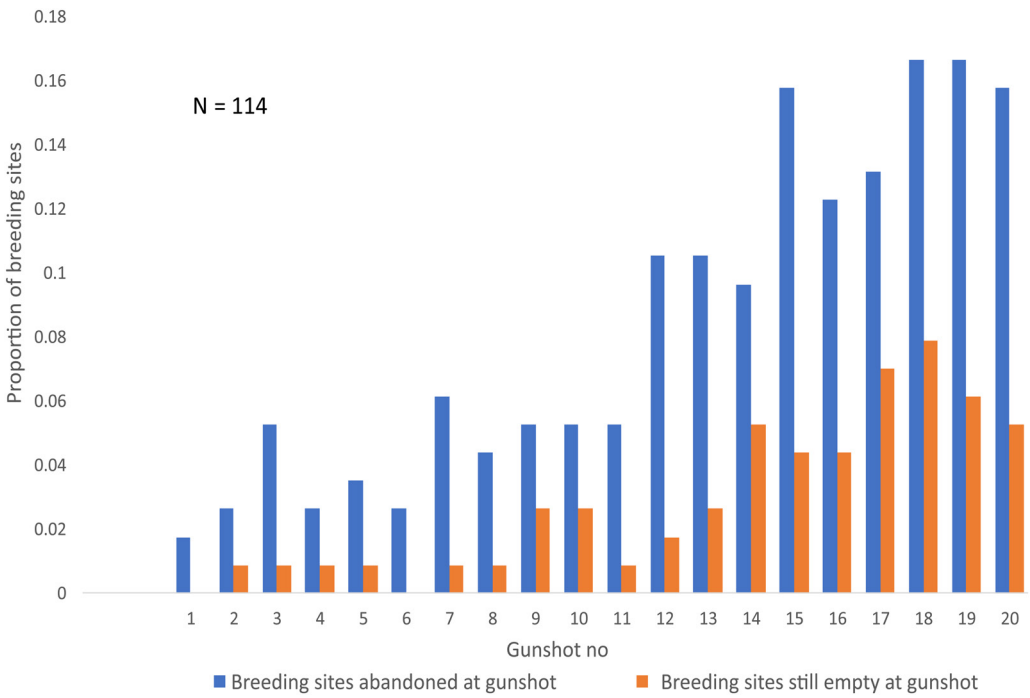


Figure 5. Proportion of 114 breeding sites abandoned by attending thick-billed murres (blue bars) as a reaction to a series of 20 gunshots during a repeated gunshot disturbance study at Kippaku, and the proportion of sites still unattended at each gunshot since the preceding gunshot (orange bars).

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(Greenland Institute of Natural Resources, unpubl.). However, only one of the failures was verified as a direct result of the experiment, because video footage captured a chick falling off the cliff at the second gunshot. Two other chicks that were dislodged at some point during the experiment, managed to return to their respective nest sites. In addition, one egg outside the plot was observed falling off the cliff.

Discussion

This study is the first to document effects of gunshot disturbances on colonially breeding birds – both in terms of approaching gunshots and effects of repeated disturbances. The results indicate that murres in larger, more densely populated colonies react to disturbances at greater distances and with a larger proportion of birds fleeing. Thereby, murres in dense colonies are at larger risk of acute reproductive failure from gunshot disturbances, than murres breeding in smaller and more sparsely populated colonies. It was not possible to document a clear link between response behaviour and presumed experience with disturbances in the declining murre colonies. However, the results from the repeated gunshot experiment were less conclusive than the approaching gunshot experiment, and experience with gunshot disturbances could be a contributing factor to the observed variation in response behaviour.

Given the usually remote character of seabird breeding locations, it is difficult to know the extent of the problem from gunshot disturbances caused by illegal seabird hunting, nearby seal hunting, or similar. However, it is our experience that these kinds of incidents occur to a lesser extent today compared to 20 years ago (Merkel et al. 1999). The murres from our six study-colonies probably share similar flyways and winter quarters, which would suggest similar experience with hunting exposure outside the breeding season (Frederiksen et al. 2016). Additionally, this species is adapted to naturally occurring noisy events at the colonies from ice breakup, collapsing icebergs and rock falls, the first two being relatively harmless, while the latter force them to leave their nest sites rapidly or risk death. However, given the varying distances to settlements and boating routes, they most likely have been exposed to different levels of anthropogenic disturbance and sounds of gunfire during the breeding season.

Generally, behavioural responses to disturbances should be interpreted with caution because the same behaviour can be an expression of both robustness and vulnerability (Gill et al. 2001). For example, the lack of a reaction can indicate lack of stress, but it can also indicate a freeze response or limited possibilities to react. Hence, behavioural tolerance does not necessarily equal physiological tolerance. Physiological responses (like heart rate and stress hormone levels) would be more objective measures of the response of individual birds to human disturbance (Tarlow and Blumstein 2007, Ellenberg et al. 2013); although these are not always feasible to perform. From a population perspective, however, leaving a chick or egg behind on the ledge is a more significant measure.

Approaching gunshots

Generally, group size of a prey species can influence the FID in both directions. Larger groups either allow a closer approach of the predator, due to a larger perception of safety, or the opposite, due to earlier detection of potential danger and the larger probability of more timid individuals in the group (Ydenberg and Dill 1986, Stankowich and Blumstein 2005, Stankowich and Coss 2006). In our case, the gunshot noise was most likely detected at similar distances among the plots, and the FID was more likely dependent on murres assessing whether the risk of staying exceeded the cost of fleeing during an increasingly threatening situation. Timid individuals would make this decision sooner than more tolerant individuals, and flight of timid individuals can initiate fleeing by the rest of the group (Stankowich and Coss 2006, Stankowich 2008). Another possible factor contributing to a larger FID in high density areas could be the swarming effect, where individuals in a swarm gain protection from predation due to the confusion effect (Milinski 1984, Jeschke and Tollrian 2007). Birds in high density areas would gain more protection during a fly-out when leaving the cliff within a swarm than birds in low density areas. Lastly, murres in low density areas have an increased risk of avian predation of offspring and, therefore, a larger incitement to stay at the breeding site (Gilchrist 1999). These density dependent effects are supported by the number of kittiwakes that contribute to the positive correlation between bird density and FID. Also, the sub-colony of Apparsuit Q had a very small FID, whereas murres from the nearby, larger and denser sub-colony were observed to fly off at a noticeably greater distance.

In accordance with existing knowledge (Laursen et al. 2005, Pater et al. 2009, Dehnhard et al. 2019), weather conditions, more specifically wind and fog, also appeared to have an influence on the FID in our study. Kippaku, where the approaching gunshot experiment was repeated due to fog, showed a lower FID during foggy conditions than during calm and clear weather (Table 2). Similarly, the FID for Kitsissut A was relatively low considering the density of birds, which could be explained by the foggy conditions during the experiment. Wind and fog can change the transmission of noise and might weaken the perception of danger (Stankowich and Blumstein 2005).

FID is a relatively easy and widely used measure of fearfulness, but it is also a measurement that is influenced by many factors than can be difficult to control for (Stankowich and Blumstein 2005, Tarlow and Blumstein 2007). This made any conclusion on the significance of former gunshot experience on FID difficult, especially with the limited sample size. Nonetheless, the large variation observed in FID advocates for considering some degree of buffer distances when establishing no-shooting zones based on limited data (Livezey et al. 2016).

Repeated gunshots

Unlike the approaching gunshot experiment, the repeated gunshot experiment provided information on the fraction of murres fleeing, and to some extent also the type of murres fleeing (attending/non-attending). This presented better opportunities to explore colony-specific differences in effects of and tolerance to gunshot disturbances. The duration of the repeated gunshot setup was likely longer than a typical marine mammal or bird hunting situation near colonies of cliff-nesting seabirds. However, the experiment was within

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the range (duration and number of gunshots) of what has been observed in the field (Merkel et al. 1999). In addition, the results showed that most of the birds fleeing, fled during the first series of five gunshots, which represent a disturbance level (in number of gunshots) that is likely to occur in most hunting scenarios for marine mammals or seabirds from small open boats in Greenland. A similar mechanism has been observed from an experiment on murre response to drones, where most of the flushing was associated with the initial start up of the rotors by non-breeding birds (Brisson-Curadeau et al. 2017).

At first glance the results from the repeated gunshot experiment appeared to be explained by density, similar to the approaching gunshot experiment (Table 3, Fig. 4). However, this was not supported by the regression analysis. The low-density plot of Kitsissut A displayed a relatively strong negative regression coefficient (-2.23×10^3) and a relatively low proportion of birds remaining in the plot at last gunshot. Furthermore, Innaq H was in the low end of the proportion of birds remaining after the last gunshot, indicating a strong reaction. However, the regression coefficient indicated a relatively gradual slope (-0.98×10^3), indicating a weak reaction (Table 3). This low-density murre plot had a high density of kittiwakes (Table 2), that did not seem to influence the FID (murre FID = 1.5 km, kittiwake FID = 5 km), but the high density of kittiwakes might have influenced the reaction to repeated gunshots. The deviating characteristics of Kitsissut A and Innaq H may indicate that other factors than density explain some of the observed variation. Kitsissut was representing a stable/undisturbed colony, and the birds could have reacted more strongly to the repeated gunshot disturbances due to less experience with gunshots. Also, the reaction pattern with a more gradual regression slope at Innaq, a declining/disturbed colony, could be influenced by more tolerance to gunshot disturbances.

It is difficult to say whether this difference in behaviour could be a result of birds being more tolerant due to experience with disturbances, or whether the difference is a consequence of more timid individuals already being selected out of this population and thus the remaining birds were more tolerant. Another explanation could be that declining colonies (whether from over-harvesting, climate change, human disturbances or a combination thereof) will have more areas of lower murre density, and, therefore, murres in declining colonies will be less influenced by surrounding birds, which may be reinforced by more motivation to stay at the colony due to risks from avian predation (Gilchrist 1999). This would cause birds at declining colonies to be less reactive due to density alone, irrespective of experience with disturbances. The difference between Innaq A and Kippaku C – the two time-lapse monitoring plots – illustrates how contrasting the reaction pattern can be between a highly reduced and an intact colony. It is difficult to tell whether the difference is due to Innaq being reduced in numbers owing to a general and prolonged negative population trend or due to experience with, and hence increased tolerance to, disturbances – or a combination of both. Our limited sample size makes any inference on this issue difficult and further studies would be needed to make any conclusions on this matter.

The fraction of attending breeders and the fraction of non-breeders in a plot, of which we lacked data, was also likely to influence our results, especially if varying among plots. The number of non-attending breeders and non-breeders varies throughout the day affecting the density of murres, usually in a colony-specific diurnal pattern (Gaston and Hipfner 2000, Merkel et al. 2007, Mosbech et al. 2009, Huffeldt and Merkel 2013). Depending on time of the day, our results could have been affected by this. Attending breeders, unlike non-breeders and non-attending mates, are highly motivated to stay with their offspring during a disturbance event, and to return quickly if they flee, due to the risk of hyperthermia and predation to their egg or chick. This motivation is likely even higher in low density areas because of the higher risk of predation, as mentioned earlier (Gilchrist 1999). The unwillingness to flee may be reinforced by a limited swarming effect by other fleeing birds at these low density colonies. This is supported by the pronounced difference between Kippaku C and Innaq A in the number of attending breeders leaving their site (Table 3). Optimally, the experiments should have been carried out at a time of the day when the conditions were similar at all the plots (e.g. average level of murres present). However, even if we had data for diurnal pattern for all our colonies, we were often restricted to windows of favourable weather regardless of time of day.

Because the two plots at Innaq were recorded for the longest time after the last gunshot, they were, unsurprisingly, the only two plots returning to 100% of the initial numbers. Interestingly, these two plots also reached both 95% and 90% levels relatively quickly compared to plots from other colonies that were recorded for a similar duration. This could, to some degree, support the hypotheses that these plots showed a higher level of tolerance due to more experience with disturbances, were composed of more robust birds, or a combination of the two.

Reproductive implications

Ultimately, disturbances at breeding colonies can affect colony size directly through loss of eggs and chicks and indirectly through lowered fitness and breeding propensity of adults. A minimum of one chick and two eggs were lost as a direct consequence of the repeated gunshot experiment events – all the observed cases were from the two stable colonies (Kippaku and Kitsissut). Likewise, the time-lapse data from Kippaku showed a marked increase in breeding failures at the date of the disturbance experiment. However, the failures detected with the time-lapse camera method could have occurred before the experiment, because failures are not recorded by the time-lapse method until the absence of birds coincide with a picture being taken, and only one of the breeding failures was confirmed from the video recordings. Nevertheless, the observed losses of eggs and chick confirm previous knowledge about this type of disturbance causing significant fly-outs, although with relatively small immediate consequences for the breeding success in our study. That said, the loss of offspring might have been larger, if the experiment had been carried out during the incubation period. According to parental investment theory, nest defence should increase as the breeding season progresses (Forbes et al. 1994). Also, as murres do not build nests and lay their egg directly on the cliff (Gaston and Hipfner 2000), eggs are more easily lost than chicks due to eggs' propensity to roll off the ledges.

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Apart from the effect of lost offspring on colony size, there is also a potential long-term effect of repeated gunshots on adult fitness. At Kippaku, it was clear that the number of eggs and chicks being left alone increased gradually with the number of repetitions (Fig. 5). In the most extreme case, the same chick was abandoned 13 times over the course of the experiments. The repeated escape behaviour has direct fitness implications for the breeding bird, especially for an auk species like the thick-billed murre, that has the highest wing loading among flying birds (Elliott et al. 2013). This may partly explain why some Greenland colonies are stable while others, including nearby colonies, are declining (Merkel et al. 2014). In a longer-term perspective, repeated disturbances may also influence site fidelity or future breeding propensity (Lima 2009). Although, both are normally considered high for auk species (Gaston and Hipfner 2000), such a mechanism could potentially lead to low recruitment and a bias towards selection by individuals more tolerant to disturbances.

Management recommendations

Most of the observed FID (11 of 13) and all but one alert distance were longer than the no-shooting zone of 1 km outlined in the current Greenland legislation on the protection of cliff-nesting seabirds (Anon 2019). Disturbance effects from a sound source are very weather dependent (Pater et al. 2009), as our results also have shown; however, shotguns and the larger rifles are more powerful than the caliber .222 used in our experiments, and FIDs are likely to be larger for those calibre firearms compared to those found in our study. Evidently, this study provides a basis for specifying a larger no-shooting zone than the existing no-shooting zone.

Several different methods have been used elsewhere to decide on minimal approach distances for birds, including mean FID, mean FID with a standard deviation added, alert distance and distance of which 95% of birds became alert (Livezey et al. 2016). A minimum shooting distance based on our results could be 5 km if FID is considered a sufficient measure. Some studies have shown physiological effect of disturbances before clear behavioural responses, and this would suggest a zone wider than the FID is necessary to reduce effects by gunshots (Ellenberg et al. 2012). Given the relatively small sample size of this study, it is plausible that some colonies have a larger reaction distance than observed and a safer no-shooting zone would be 1.5 × FID (7.5 km). However, deciding on a meaningful zone can be complicated because a zone too wide could result in a lack of understanding and acceptance of the no-shooting zones by residents (Falk and Kampp 2001). Based on this study, showing that birds in dense areas react at longer distances than birds in less dense areas, the decision makers could consider a differentiated no-shooting zone depending on colony size, as density usually is correlated with colony size. However, it is important to keep in mind that small colonies often are declining colonies that are vulnerable to other pressures.

Larger no-shooting buffer zones should not necessarily lead to changed accessibility for the general public to cliff-nesting seabird colonies. On the contrary, recreational access to wildlife (for tourism or local recreational purposes) can increase awareness and encourage conservation (Gill 2007), provided that no harmful disturbances are caused (Reiertsen et al. 2018). The simple presence of tourists or local recreationists can help limit events of individuals pursuing illegal hunting or other types of severe disturbances at or near seabird colonies. Legal enforcement is difficult and demand many resources in remote areas, and the encouragement of non-disturbing access to cliff-nesting seabird colonies could be considered as a potential conservation tool.

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Permits – All procedures were in accordance with GINR ethical standards and the field work was conducted under permission provided by the Government of Greenland.

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