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Life strategy of the Arctic tern

Ph.D. Thesis

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Life strategy of the Arctic tern (*Sterna paradisaea*)

Ph.D. Thesis

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Annotation

This thesis is focused on the life strategy of the Arctic tern (*Sterna paradisaea*) and covers topics such as breeding biology, antipredation behaviour, human impact, and migration behaviour. The first study uncovers the mystery of the Arctic tern migration and focuses on the ecology of the remarkable journey concerning environmental factors such as wind conditions and food opportunities along the way. The second study compares the reaction of breeding Arctic terns to human disruption at two localities differing in terns experience with humans and discusses the potential habituation abilities of terns to human disturbances. The third study continues with the issue of human disturbance and discusses the correlation between disturbances, not only by humans but also by predators, and behaviour reactions in two *Sterna* species (the Arctic tern, the Antarctic tern – *Sterna vitatta*). The last study is focused on the abilities of predator recognition by Arctic terns with respect to various predators. Moreover, the study addresses the question of predator unfamiliarity and its consequences for behavioural response.

Declaration:

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

České Budějovice, 16.7.2024 Tereza Hromádková

Affiliation

Thesis was created at the Faculty of Science, University of South Bohemia in České Budějovice

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Confirmation of author´s contribution to articles

RNDr. Václav Pavel, Ph.D., as a co-author of the article nr. I, fully agree with the above-mentioned contribution of Tereza Hromádková to the article.

In Dobruška

RNDr. Václav Pavel, Ph.D.

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In Olomouc

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The Arctic

> *Arkticós* is an ancient Greek word meaning ‘the land to the North’ and is related to the celestial constellation of the Great Bear that is visible only in the Northern Hemisphere.
>
> CAFF (2013a)

The Arctic region is a vast area which constitutes the northernmost part of the Earth and consists of an ocean surrounded by land. There are several definitions of this area and its boundaries. The easiest delimitation of this region is by means of the Arctic circle. The Arctic circle, 66° 33’ 44’’ N, is the southernmost latitude in the Northern Hemisphere where the sun does not set and, more importantly, does not rise above the horizon for 24 hours (resulting in a half year of dark/light at the pole). Other delimitation of the Arctic region are reached either by use of the 10°C July isotherm (the area where the average temperature of July is below 10°C), or by the Arctic tree line boundary (the northernmost latitude where trees can grow) (Danell 2021). But delimitations can also be found which are based on conservation approaches such as the Arctic CAFF boundary (CAFF = The Conservation of Arctic Flora and Fauna) or the delimitation used in Arctic shipping (the so-called the Polar code; IMO 2016).

Regardless of the definition/delimitation, the Arctic region is an area characterised by extreme environmental conditions. The climate is diverse, but the annual average summer temperature mostly does not exceed 10°C and winter temperatures can drop to -60°C in some places (regions of Siberia). A major part of the land in the Arctic is permanently frozen with snow or ice coverage for most of the year resulting in a very short vegetation and reproduction period. For example, the suitable time for birds to breed lasts 2½-3 months in the Arctic while it is 3-4 months in temperate regions (Danell 2021). Based on (very limited) vegetational coverage, the Arctic region can be divided into three zones, or regions – the High Arctic, Low Arctic, and subarctic (Team CAVM 2003). The High Arctic is covered exclusively by plants growing close to the ground such as lichens, mosses, or tundra herbs. Further south in the Low and subarctic, there is a higher diversity of plant species along with an increase in the size and abundance of plants (Aleksandrova 1980).

The Arctic region offers a broad pallet of marine and terrestrial habitats – mountains, cliffs, tundra, wetlands, lakes, temporal ponds, shallow ocean shelves, deep ocean, ice shelves, floating icebergs, and glaciers – that provide a home for around 21,000 species of plants and animals including fungi and lichens (CAFF 2013a). Most of the species are highly cold adapted, however, their distribution is not even. Closer to the North Pole, the amount of species generally declines (e.g. Willig et al. 2003). The Arctic region comprises around 2% of mammals, 2% of birds, 1% of freshwater, 2.2% of saltwater, and 7.7% of cartilaginous fish of the global species diversity respectively (five amphibians and one reptile are also included). The diversity of vascular plants (also including recognised subspecies) reaches around 1%, arctic lichens about 10%, and fungi around 4% of the global species diversity respectively (CAFF 2013a). Arctic invertebrate (marine, freshwater, and terrestrial) species are estimated to number several thousand with proper information about their distribution and biology lacking.

Birds in the Arctic

> *"The life conditions are usually so severe that the slightest aggravation, the least alteration from the normal, will result in widespread hunger or wholesale destruction of entire populations."*
>
> (Salomonsen 1972)

The avian community in the Arctic is rather low in species richness and the estimated number of species differs according to the delimitation of the borders of the area. Estimates range from 70 (Dunbar 1968) through 90 (Thomas et al. 2008) to over 200 bird species (CAFF 2013b). However, there are groups such as seabirds and shorebirds that peak in abundance in subpolar waters or Arctic tundra. By far the largest diversity is found in the order Charadriiformes with representatives from the families Stercorariidae, Laridae, Alcidae, Scolopacidae, and Charadriidae (del Hoyo et al. 1996). Well known in the Arctic is also the order Gaviiformes as all representatives breed there (Järvinen and Väisänen 1978). Representatives of the orders Procelariiformes, Anseriformes (del Hoyo et al. 1992), Galliformes (del Hoyo et al. 1994), and Passeriformes also breed in the Arctic region.

Only a few birds could be called true Arctic species, i.e. remaining in the Arctic through the whole annual cycle. Among them terrestrial birds are represented by the willow and rock ptarmigan (*Lagopus lagopus* and *Lagopus muta* respectively), snowy owl (*Bubo scandiacus*), common raven (*Corvus corax*), gyrfalcon (*Falco rusticolus*), and Arctic redpoll (*Acanthis hornemmani*). Regarding the marine group the black guillemot (*Cephus grylle*), ivory gull (*Pagophila eburnea*), and thick-billed murre (*Uria lomvia*) are notable. However, the majority of Arctic species (93%) from all bird taxa have adapted their life strategies and annually migrate from the Arctic to milder climates (CAFF 2013b).

The widespread dispersal of birds links Arctic breeding grounds with wintering areas all around the globe. Some move to lower boreal and temperate latitudes (e.g. waterfowl, auks, or gulls), some migrate to the tropics (e.g. phalaropes – *Phalaropus sp.*), and others as far as sub-Antarctic or Antarctic regions (e.g. skuas or Arctic tern – *Sterna paradisaea*). Birds migrating from close breeding grounds share similar flyways resulting in major migration routes navigating through or around of all the continents.

Birds spend only a small amount of time each year within their Arctic breeding grounds. This has its pros and cons. Birds coming to breed in the Arctic benefit from a huge seasonal eruption of food availability both in marine and terrestrial biomes. Additionally, long days (continuous daylight) offer unlimited possibilities for feeding and provide relative safety from predation for diurnal birds. Predation generally decreases toward the poles (McKinnon et al. 2010), however, Kubelka et al. (2018) showed that ongoing changes in global climate can lead to shifts in predator-prey interactions and birds breeding in the Arctic may have recently experienced increasing predation pressure (but see

Bulla et al. 2019; Kubelka et al. 2019). It has been documented that even polar bears (*Ursus marinus*), specialized marine predators of seals, have shifted their attention to eggs and their predation rate of bird nests has increased in many Arctic places (e.g. Rockwell et al. 2011; Stempniewicz et al. 2014). Climate change affects not only species distribution and food web dynamics but could also lead to an increase in diseases and pathogens (e.g. Root et al. 2003; Kutz et al. 2005; Pilfold et al. 2021) in the relatively pristine environment of the Arctic.

Short breeding seasons and harsh climatic conditions are some of the disadvantages of breeding in the Arctic. These disadvantages are gaining importance with respect to global warming. Birds have to cope with the proper timing of reproduction (Winkler et al. 2002). On the one hand, late ice break-up can lead to a reduced availability in suitable breeding places and feeding areas with consequences for overall reproduction (Martin and Wiebe 2004). On the other hand, earlier ice break-up or snowmelt can allow an earlier initiation of the growing season and consequently an earlier initiation of the breeding season. Fjelldal et al. (2020) documented an increase in the earlier beginning of breeding by young barnacle geese (*Branta leucopsis*) as a result of advanced spring onset. Also in other waterbird species, the ability to adjust clutch initiation date was observed with respect to annual variation in thawing days (Solovyeva et al. 2022). In that respect, the proper timing of arrival by migratory birds at breeding grounds is crucial.

The Arctic tern

General and breeding biology

> *"…**takatakiaq** in Inutitut…this word mimics their calls."*
>
> Henri et al. (2020)

Arctic tern belongs to the genus *Sterna* and the family Laridae. Arctic terns are mid-sized birds weighing about 110 g with aerodynamically shaped bodies, long and pointed wings, and a great predisposition for dynamic and acrobatic flight. Arctic terns are characterized by the presence of a black upper side of the head, a greyish back, and a deeply forked tail with long outer rectrices feathers (Fig. 1). Their bills and legs are bright red during the breeding season but out of the breeding season their bills and legs are darkly coloured. (del Hoyo et al. 1996). Both sexes look alike and distinguishing between males and females needs either an observation of courtship behaviour or proper morphometric measurements supplemented with DNA testing (Devlin et al. 2004). The breeding distribution of Arctic terns is circumpolar and covering areas from the Arctic (maximal latitude 83.11°N) through the subarctic to the temperate zone as far south as northern France (Brittany) or the northern USA (Massachusetts, minimal latitude 41.24°N; BirdLife International 2018; Tobias et al. 2022). Arctic terns are strictly migratory birds connecting northern breeding grounds with wintering areas in the Antarctic and sub-Antarctic regions.

Arctic terns are monogamous birds with very high fidelity to breeding grounds, however, long-distance

Fig. 1 The Arctic tern (*Sterna paradisaea*) sitting on the ice. *Photo:* Václav Pavel

dispersal (tens of kilometres) may occur in the years after hatching (called natal dispersal). Breeding dispersal (of breeding-age adults) occurs predominantly within neighbouring colonies in the same region (Brindley et al. 1999; Møller et al. 2006; Devlin et al. 2008). Arctic terns first breed when 2-4 years old. After performing courtship displays (flights, postures, ritual feeding), adults establish pairs and choose a site for the nest. Their pair bonds last from year to year, however, divorces have been reported, especially of young birds (Busse 1983; Redfern 2021). There is evidence that the pair bonds of Arctic terns are reestablished every year as they perform migration separately and even overwinter at different sites (personal observation; Redfern 2021).

Arctic terns breed on deglaciated sites close to the seashore in colonies amounting from tens to hundreds of nests; though solitary nesting birds can be found as well (del Hoyo et al. 1996). Nests are small depressions primarily in gravel or sand, filled with local vegetation if available. The clutch size ranges from 1 to 3 eggs (e.g. Eklund 1944; Egevang and Frederiksen 2011; Burnham et al. 2017; Mallory et al. 2017; Fig. 2). Incubation lasts for 21-23 days (Chapdelaine et al. 1985; Kovacs and Lydersen 2006; Mallory et al. 2017) and both partners are involved in incubation (in most tern species the females spend more time caring for the eggs and chicks compared to the males; Cabot and Nisbet 2013).

Threats and predators

> *“A Jaeger chasing one of the Terns. The latter was quickly joined by five of its companions with the result that the tables were quickly turned, and the Jaeger was glad to call off the hunt. ”*
>
> Gibson (1922)

As mentioned above, breeding in the Arctic is very challenging for the Arctic tern, as the daily mean temperatures do not exceed 10° C (Ambrožová and Láska 2017; Mallory et al. 2017) which leads to subsequent increased requirements for egg thermo-regulation over a breeding season (Piersma et al. 2003) with possible negative consequences for hatching and breeding success. Additionally, severe climatic conditions like strong winds, heavy rains or snow storms can strongly affect breeding success, and in extreme cases they can make nesting impossible in some years (Bunin and Boates 1994; Robinson et al. 2002). The overall breeding success of Arctic terns is highly colony- and year-dependent (Schreiber and Kissling 2005; Mallory et al. 2017) with, alternatively, complete breeding failure mostly due to weather conditions (as mentioned above) or predation (Levermann and Tøttrup 2007; Egevang and Frederiksen 2011; Burnham et al. 2017), or very high probability of success (Monaghan et al. 1989; Mallory et al. 2017; personal observation).

On the other hand, the adult probability of survival is very high, ranging between 70 and 96 % (Devlin et al. 2008; Mallory et al. 2018; Petersen et al. 2020). Death in adult Arctic terns is most often caused by disease, old age, or unfavourable weather conditions. Adult terns have few effective predators. Falcons (e.g. peregrine falcon – *Falco peregrinus*, merlin – *Falco columbarius*, and gyrfalcon; Hawksley 1957) are specialized aerial predators but also some large gulls (e.g. great-black backed gull – *Larus marinus*, herring gull – *Larus argentatus*), common ravens (Chapdelaine et al. 1985; Henri et al. 2020), and American minks (*Neogale vison*; Craik 1995) can occasionally catch an incubating bird. It is no surprise that an

Fig. 2 Nest with hatching eggs on Svalbard. *Photo:* Tereza Hromádková

Arctic tern of 34 years of age was once recaptured in North America.

On the contrary, eggs, hatchlings, and fledglings have a wider variety of possible predators with egg predation being considered the main cause of nesting failure in ground nesting and colonial birds such as terns (Lack 1968). Mammalian predators like the American mink, Arctic fox (*Vulpes lagopus*), or polar bear are usually very effective and can cause complete breeding failure and abandonment of a colony site by adults (Stempniewicz and Jezierski 1987; Craik 1995; Levermann and Tøttrup 2007; Wojczulanis-Jakubas et al. 2008; Egevang and Frederiksen 2011; Burnham et al. 2017). The most common bird predators are large gulls (great black-backed gull, herring gull, or glaucous gull – *Larus hyperboreus*), jaegers (great skua – *Stercorarius skua* or parasitic jaeger – *Stercorarius parasiticu*s), or common ravens. However, waterfowl may also represent a threat to eggs e.g. common eiders (*Somateria mollissima*), specialized in eating benthic molluscs, represent a threat to tern nests, as they frequently breed at the same colony site as Arctic terns, and being protective of their own nests may occasionaly crush tern eggs (Burnham et al. 2017, personal observation). In the Bay of Fundy in Canada, semi-domestic mallards (*Anas platyrhynchos*) intentionally predated on eggs and newly hatched chicks (Hawksley 1957). But mallards are not the only domesticated animal to have an impact on the breeding success of Arctic terns. It is documented that dogs could also have an impact by eating tern eggs (Hawksley 1957; Burton and Thurston 1959; Drury 1960).

Antipredator behaviour

“The predators in the area are limited to five vertebrate species: Glaucous Gull (Larus hyperboreus), Arctic Skua (Stercorarius parasiticus), Arctic fox (Alopex lagopus), Greenland Dog and Man.”

Burton and Thurston (1959)

Defending a nest with eggs/hatchlings or juveniles is a critical aspect of parental care. However, this defence comes with both benefits and costs. The nest content itself is defenceless; therefore, parental behaviour may importantly increase the survival probability of eggs and chicks. Birds in general can show two forms of defence against predators – passive or active. Passive defence includes behaviour that ensure not being found and escaping. Active defence covers a whole spectrum of reactions from calls to direct attacks in the extreme case (review Caro 2005). Terns are very effective in defending their colonies against any intruder and can express a wide variety of active defence (Drury 1960; Mallory et al. 2010). Active defence on the one hand helps to increase the survival probability of offspring, but on the other hand, it also consumes a lot of energy and can lead to the injury or death of parents e.g. when trying to distract or attack the intruder/predator (Brunton 1986).

Does the intruder pose a threat? If so, then to whom – to an adult or to eggs/offspring? The first step for parents in keeping the expense of antipredator behaviour as low as possible is to correctly identify the threat and react accordingly (Suzuki 2011; Mahr et al. 2015; Strnadová et al. 2018). To recognise and categorize a predator, birds in most cases make use of so-called ‘key features’ (stimuli which start an instinctive reaction; Lorenz 1937) and then adjust the type and the strength of the reaction (e.g. Beránková et al. 2014; Fuchs et al. 2019). The resulting reaction may thus differ in line with encountering predators of adults, predators of eggs, or harmless species. Clode et al. (2000) showed that common (*Sterna hirundo*) and Arctic terns perform more aggressive defence against a potential predator of eggs (stuffed rabbit – *Oryctolagus cuniculus*) than against a potential predator of adults (stuffed American mink). The study Špička (2022) found that Arctic terns vigorously attacked (with physical contact) a gull dummy, which posed a threat to the nest. However, at the same time, authors did not find a significant difference between attacks on a gull dummy and on a dummy of a harmless duck (common eider) suggesting that bird responses are driven also by the experience of individual birds.

The experience of birds also plays a role in the recognition of familiar and unfamiliar predators and the ability to react accordingly to the current situation (van Heezik et al. 1999; Greggor et al. 2019). Carthey and Blumstein (2018) reviewed eight basic hypotheses about predator-prey interactions and what would happen in the case of a prey species losing a predator and either an unfamiliar/new predator being introduced or the familiar/old one reintroduced. Understanding predator-prey interactions is crucial, especially in our rapidly changing world. Ongoing changes will have consequences for variation in species distribution (IPCC 2023) which can lead to the introduction of a new species to habitats where local fauna is not adapted to that species. Such introduction plays an important role, especially on isolated islands where birds tend to change their behaviour and morphological characteristics (e.g. flightless kakapo parrot) and become more vulnerable to habitat changes and invasions (Clout and Merton 1998). The Polar regions represent areas particularly sensitive to changes as they face the most pronounced global warming effects with significant consequences for ecosystem structure and species distribution ranges (IPCC 2023). Red foxes (*Vulpes vulpes*) are for example establishing viable populations in many Arctic localities resulting in the displacement of Arctic foxes and an accompanying change in the food web dynamic (Gallant et al. 2020). All these ongoing changes can bring new challenges for local fauna including Arctic terns. New competitors and predators can arise.

> *“…the intruder seemed always to be seeking a chick unless fleeing from terns that sometimes attacked so vigorously that they pulled or knocked out feathers.”*
>
> Hatch (1970)

The antipredation reaction of colonial birds species includes a variety of response such as alarm/warning calls, flyovers with or without faecal bombing, or even diving upon an intruder with or without striking (e.g. Burger et al. 1993). The final behavioural reaction is the result of the interplay of many factors. The stage of incubation belongs to one of the most pronounced factors affecting parental behaviour. The *brood value hypothesis* predicts that parental defence in birds becomes more vigorous with increasing investment in the nest (e.g. Andersson et al. 1980; Onnebrink and Curio 1991). From the time when the first egg is laid antipredator behaviour gains in intensity with the most intense reaction around hatching time (Shealer and Burger 1992; Whittam 1997). However, Whittam (1997) observed that breeding terns responded more to corvids at the beginning of incubation, whereas they responded more to gulls later in the breeding season. Adult terns thus properly evaluated that gulls pose a greater threat to hatchlings and reacted appropriately (Whittam 1997; Whittam and Leonard 2000). Another factor with a big impact on the strength of the antipredation response is the distance between the threat and the nest/chicks. The Terns' reaction became more vigorous to gulls that were performing hunting flight (zig-zag flight over the colony) than to gulls flying over 20 m above the colony (so-called overflight; Hatch 1970) and escalated if a gull landed in the colony (Nisbet 1973; Whittam 1997; Whittam and Leonard 2000). The most vigorous attacks occur in adults from the closest nest to the threat (Drury 1960).

Terns vs. humans

"Previous to our decision to make the nest count, three of the Greenlanders in our party had gone to the island and collected 146 eggs…Eggs are something of a delicacy in Greenland, and the collection was made for food…the freshness or the developmental stage of the embryo apparently did not influence the Greenlanders. All the eggs were boiled and eaten with relish."

Eklund (1944)

Humans are very specific predators of Arctic terns. In several studies, there are records of people, whether intentionally or unintentionally, destroying tern nests (Eklund 1944; Hawksley 1957; Burton and Thurston 1959; Henri et al. 2020). An Inuit community from northern Québec (Kuujjuaraapik community) in Canada even developed a very close relationship between Arctic terns through their style of life. On the one hand, indigenous people harvest terns eggs (considering them a delicacy), but on the other hand, Arctic terns serve them as indicators of environmental conditions and together with a deep knowledge of tern ecology as a basis for the seasonal calendar (Fig. 3; Henri et al. 2020). However, harvesting or destroying the nests is now seen in only sporadic and extreme cases.

The human impact on the overall breeding biology of birds is both more pronounced and more studied. Birds are sensitive to human disturbance and their reaction to it shows similar patterns to their reaction to natural predators (Frid and Dill 2002). Human disturbance includes activities such as walking by, jogging, birdwatching, sunbathing, driving with vehicles, fishing, or aeroplane flyovers. Immediate behavioural reaction ranges from increased vigilance, flushing (Rodgers Jr and Smith 1995; Yorio and Quintana

1996), calling, and/or changes in daily activities. In more severe cases terns react with reduced breeding success or decreased population numbers (Burger et al. 1995; Peter et al. 2008).

A good tool in the conservation approaches of breeding seabirds is flight-initiation distance (= the distance at which birds flee an approaching intruder, FID; e.g. Rodgers Jr and Smith 1995; Carney and Sydeman 1999; Tarlow and Blumstein 2007). Even though FID is highly dependent on a large variety of variables (such as species, area, or disturbance; Rodgers Jr and Smith 1995; Mallory 2016; Althouse et al. 2019) many studies use FID as an indicator of the tolerance of birds to human disturbance (e.g. Lin et al. 2012). Urban populations tend to have a shorter FID and tend to be more tolerant to human presence than rural populations (e.g. Møller 2008; Mikula et al. 2023).

Similarly, studies conducted at different places have documented a remarkable tolerance to human disturbance in several tern species. For instance, bridled terns (*Onychoprion anaethetus*) in Western Australia, which expanded/started breeding in areas under continuous disturbance (Dunlop and Jenkins 1994; Dunlop 1996; Gyuris 2003), and multiple populations of common tern, have become highly tolerant to human activity after long-term coexistence with humans (Nisbet 2000; Jennings 2012). Data from polar areas yielded a mixed picture. The presence of people close to Arctic tern colonies has resulted in a decrease in predation attempts by gulls (Hawksley 1957), but contrary to that severe impacts of human activities on nesting success and colony tenacity have been reported, for example in Antarctic terns breeding in the neighbourhood of polar stations (Kaiser et al. 1988, Peter et al. 2008, 2013).

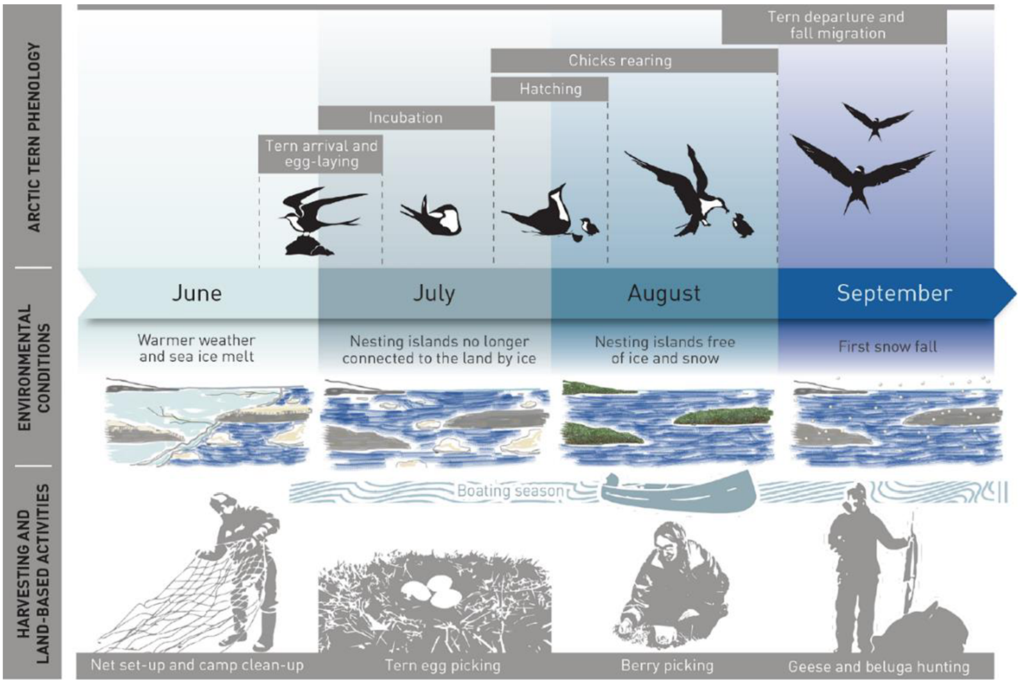


Fig. 3 Arctic tern (*Sterna paradisaea*) phenology calendar presenting how the life of indigenous people is connected with nature (see Henri et al. 2020)

However, studies focusing on the long-term fitness consequences of the coexistence of terns breeding in the Arctic with humans are lacking

Migration

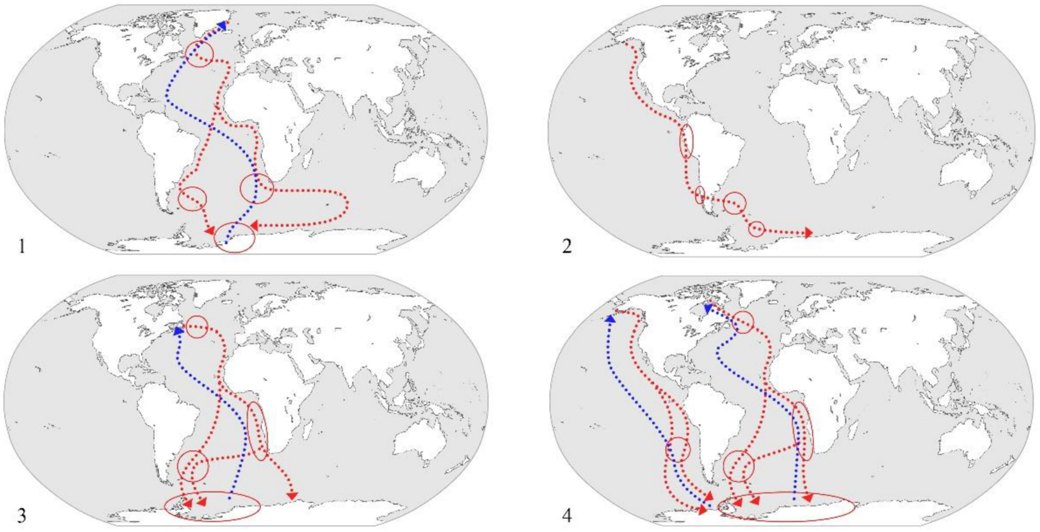
> *"The one that each year gets away, hovers Like a humming-bird above the waves, pinpoints Its prey, and dives. Patiently, I wait to see It rise with a sandeel in its beak, but am Distracted by her laughter, trapped by a smile. Looking back, a millisecond too late, the Arctic tern has moved south, ten thousand miles away."*
>
> Migrating tern by Meade (1995)

The flight abilities of Arctic terns have attracted attention for decades. In the past, observations were limited to ring recoveries and visual or later radar observations with incomplete results that could not fully describe their breathtaking migration. Nevertheless, the first attempt at describing one of the longest animal migrations outlined that tern southbound flight follows two flyways depending on the position of breeding grounds. Birds from the west coast of North America and the eastern part of Siberia follow the west coast of the American continent. Whereas terns from the east coast of North America, Greenland, northern Europe, and the west coast of northern Siberia follow the west European and later west African coast (rarely crossing the Atlantic Ocean at the equator to the east South American coast). All flyways result in wintering areas around Antarctica (Austin 1928; Kullenberg 1947; Storr 1958; Radford 1961; Salomonsen 1967). The northbound route remained a mystery until the arrival of new tracking technologies that allowed a detailed description of migration routes not only of Arctic terns.

The development of new tracking technologies, especially lighter locator devices (so-called geolocators - small devices which determine the position based on ambient sunlight) opened space for a better understanding of migration movement in general. Studies of Arctic terns confirmed the pathways of southbound migration and uncovered the mystery of northbound migration (Egevang et al. 2010; Fijn et al. 2013; McKnight et al. 2013). Terns leaving Antarctica follow the west coast of Africa where later, around the equator, their paths may divide. Some of them continue north through the eastern part of the Atlantic. Whereas others fly through the western part of the Atlantic, the shape of their path resembling the letter S (Fig. 4). According to Wong et al. (2021) and the U.S. Fish and Wildlife Service (unpublished data) Arctic terns performed high route fidelity during two years of tracking.

Every year Arctic terns undertake a 70,000 km long journey (average; Egevang et al. 2010; Fijn et al. 2013) to wintering areas in Antarctica and back to their breeding grounds. The longest migration was measured at about 103,000 km and was performed by Arctic terns from the area of the Onega Peninsula in the White Sea (64°56′42″ N, 36°44′20″ E; Volkov et al. 2017) making it one of the longest migrations among animals.

A) North America group (including Greenland)



B) European and west Siberia group

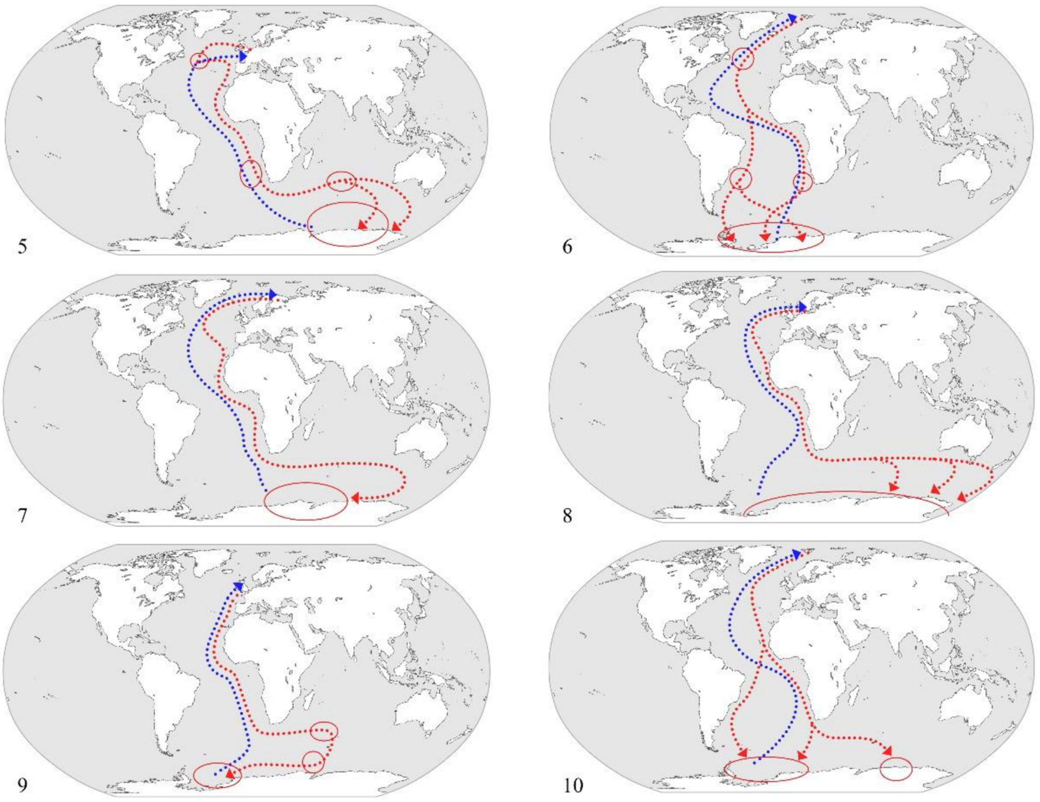


Fig. 4 Grouped migration routes of Arctic tern (*Sterna paradisaea*) based on breeding grounds: A) North America group including Greenland and B) European and West Siberia group. Red – autumn/southbound migration, blue – spring/northbound migration. Important stopover sites and wintering areas around Antarctica are marked with red circles. Maps were made based on tracking results from studies: 1) Egevang et al. (2010), 2) McKnight et al. (2013) 3) (U.S. Fish and Wildlife Service, unpublished data), 4) Wong et al. (2021), 5) Fijn et al. (2013), 6) van Oosten (2014), 7) Volkov et al. (2017), 8) Alerstam et al. (2019), 9) Redfern and Bevan (2020a), 10) Hromádková et al. (2020).

"After 110 days since leaving the colony and having migrated 29 700 km…the terns reached Antarctic waters."

Fijn et al. (2013)

All birds (young ones included) are involved in migration, however, Arctic tern juveniles were seen not to fly as far south as Antarctica but overwinter also in South Africa or South America (Radford 1961; Salomonsen 1967). On the way, terns fly in small flocks amounting to around 25 pairs or fewer (Gudmundsson et al. 1992). The flight may be performed at altitudes greater than 1,000 m a.s.l. (Gudmundsson et al. 2002; Duffy et al. 2013).

Migration is influenced by many factors beginning with the position of the breeding grounds itself (Gilg et al. 2013; Davis et al. 2016). Generally, breeding grounds at higher latitudes mean later departure to wintering areas (mostly because of the late onset of the summer season; e.g. Conklin et al. 2010). Similarly, terns with breeding grounds at lower latitudes reach their breeding locations earlier than conspecifics from northern latitudes (Egevang et al. 2010; Fijn et al. 2013; Loring et al. 2017; Volkov et al. 2017; Alerstam et al. 2019; Wong et al. 2021). Environmental factors are more pronounced regarding their influence on migration behaviour. Salomonsen (1967) summarized the key factors that shape the long-distance flight of Arctic terns and suggested the main determinants of the migration pattern: food availability and distribution, prevailing wind patterns, and moulting strategy.

The *optimal migration theory* suggests that birds lower their migration duration to a minimum and simultaneously minimize the energy expenditure (Alerstam 2011). Arctic terns use flapping flight in their migration, which generally comprises flight bouts interrupted by stopovers. Birds adjust their time spent on stopover sites according to resource availability (Thorup et al. 2017). However, stopover sites are not distributed evenly across flyways. Important feeding areas for Arctic terns during southbound migration have been described in several studies (U.S. Fish and Wildlife Service unpublished data; Egevang et al. 2010; Duffy et al. 2013; Fijn et al. 2013; McKnight et al. 2013; Alerstam et al. 2019; Wong et al. 2021) and cover the following locations: the North Atlantic, the Benguela current, subtropical water in the Indian Ocean, and Falkland current (see Fig. 4). All these places are characterized as marine productivity hotspots with high ocean productivity and play an important role as refuelling areas during seabirds movements/migration (Raymond et al. 2010; Boertmann 2011; Frederiksen et al. 2012; Gilg et al. 2013; Davies et al. 2021).

Similarly, the wintering area around Antarctica offers a burst of sea productivity with the most productive waters in the Weddell Sea (e.g. Jennings Jr et al. 1984; Vernet et al. 2019). Simultaneously, the Weddell Sea is also a place where Arctic terns gather before beginning their northbound migration (Salomonsen 1967; Alerstam et al. 2019). It has been shown that northbound migration has been more affected by prevailing winds and wind support than by time spent on stopover sites. Terns performed more feeding activity and stayed longer at stopover sites during the autumn migration than during the spring migration (McKnight et al. 2013; Wong et al. 2022). These findings indicate that Arctic terns when flying to Antarctica need to refuel more energy after the breeding season compared to the spring migration to breeding grounds.

> *"The increased likelihood of encountering heavy winds may deter terns from taking the southern route."*
>
> Duffy et al. (2013)

Prevailing winds can play an important role in route decisions (Liechti 2006; Duffy et al. 2013) as strong headwinds may cause high energy expenditures and tailwinds can lead to higher flight speed and energy savings. Thus, seabirds adapt their migration path according to profitable winds (e.g. shearwaters; Felicísimo et al. 2008; González-Solís et al. 2009; Raymond et al. 2010), including Arctic terns (e.g. Egevang et al. 2010; Hensz 2015). The flight speed in Arctic terns differs between the two migration directions with the highest speed during northbound migration (see Table 1). A faster spring migration speed can also be found in other migratory birds (Henningsson et al. 2009; Karlsson et al. 2012).

A review of recent studies indicates that Arctic terns choose the path according places with high ocean productivity when flying to wintering areas (McKnight et al. 2013; Hensz 2015), however, wind conditions may play its role too (Hensz 2015; Skyllas et al. 2023). The northbound migration is on the contrary affected mainly by the general wind conditions and prevailing winds (Skyllas et al. 2023), while ocean productivity does not play a significant part in flyway decisions (Hensz 2015). The final migration route pattern of Arctic terns (Fig. 4) is shared with other trans-equatorial migrants such as long-tailed skua (*Stercorarius longicaudus*; Gilg et al. 2013), Sabine's gull (*Xema sabini*; Davis et al. 2016), and others (e.g. Guilford et al. 2009; Harrison et al. 2022).

Migration behaviour could be also sex-biassed (e.g. timing differences; Briedis et al. 2019) or influenced by body conditions (e.g. weight; Duijns et al. 2017). Male Arctic terns tend to be larger and heavier than females (see Devlin et al. 2004). Based on that, Wong et al. (2022) predicted that larger terns (according to the total head length) would choose shorter migration paths to wintering areas compared to smaller birds. However, more studies are needed to assess the influence of individual conditions on migration behaviour in Arctic terns.

When thinking about factors influencing the migration behaviour of birds we cannot omit the pronounced ongoing changes on the global scale (IPCC 2023). Birds take advantage of profitable winds when on migration, however, Skyllas et al. (2023) and Morten et al. (2023) have shown that wind conditions are subject to future changes and terns will have to cope with and adapt to changing conditions on route. Similarly, important seabird hot spots, characterized by high ocean productivity, are undergoing changes too. For example, there is a decline in the abundance of

Table 1 Summary table of the migration phenology of Arctic terns from previous studies.

Migration phenology	**General**			**Southbound/autumn migration**			
	Breeding site	Number of tagged birds	Recaptured	Departure from breeding site^2	Duration of southbound migration (days)^2	Distance travelled on southbound migration (km)^2	Travel speed on southbound migration (km/day)^2
Egavang at al. (2010)	Grenland (Sand Island) 74°43' N, 20°27' W	50	10	August (not dated)	93 (69–103)	34 600 (28 800–38 500)	330 (280–390)
	Iceland (Flatley Island) 65°22' N, 22°55' W	20	1		80		
Fijn et al. (2013)	The Netherlands (Delfzijl and Eemshaven) 53°19-27' N, 6°49-56' E	7	7 (5*)	1–7 Jul	110 (± 9 SD)	29 700 (± 2700 SD)	420 ± 24
McKnight et al. (2013)	USA (Harriman Fjord, Alaska) 61°00' N, 148°20' W	20	6	24 Jul–15 Aug	112 (104–116)	NA	NA
Volkov et al. (2017)	White Sea (Onega Peninsula) 64°56' N, 36°44' E	20	7	1 Aug	104 (94–115)	44 993 (33 696–54 568)	432 (345–549)
Alerstam et al. (2019)	Sweden (Landöskärgården) 56°00' N, 14°30' E	47	10 (8*)	15 Jul (7–28 Jul)	115	25 840	277
Redfern and Bevan (2020a, b)	The United Kingdom (Farne Islands) 55°37' N, 1°39' W	53	47	17 Jul–10 Aug	NA	NA	NA
Wong et al. (2021) Wong et al. (2022)	USA (Alpine, Alaska) 70°21' N, 151°01' W	23	9 (8*)	12 Aug (6–15 Aug)	88 (82–93)	33 806 (± 2839 SD)	NA
	Canada (four locations**)	100	61 (45*)	4 Aug–5 Sep	68–116		
U.S. Fish and Wildlife Service (unpublished data)	USA (Gulf of Main) 43°53' N, 69°07' W	30	16 (14*)	5 Aug (18 Jul–2 Sep)	93 (33–126)	30 246 (19 219–39 826)	339 (233–582)

* number of working geolocators

** four locations in Canada: Country Island (45°03' N, 61°19' W), East Bay (64°00' N, 82°04' W), Karrak Lake (67°15' N, 100°15' W), Nasaruvaalik Island (75°49' N, 96°18' W)

[1] mean ± SD

[2] mean (min-max) - unless otherwise mentioned

Table 1 – Continued – Summary table of the migration phenology of Arctic terns from previous studies.

Migration phenology	Wintering region				Northbound/spring migration					Total distance travelled on migration (km)^2
	Arrival in wintering region^2	Time spent in wintering region (days)^2	Coordinates of wintering region	Distance travelled within winter site (km)^2	Departure from wintering region^2	Arrival to breeding site^2	Duration of northbound migration (days)^2	Distance travelled on northbound migration (km)^2	Travel speed on northbound migration (km/day)^2	
Egavang at al. (2010)	24 Nov (25 Oct–30 Nov) 5 Nov	149 (139–173) 151	0°–61° E south of 58° S	10 900 (2 700–21 600)	16 Apr (12–19 Apr) 3 Apr	late May/early June (not dated)	40 (36–46) 41	25 700 (21 400–34 900)	520 (390–670)	70 900 (59 500–81 600)
Fijn et al. (2013)	12 Nov (mediate date)	128 (± 10 SD)	25°–150° E	23 600 (± 3160 SD)	21 Mar (mediate date)	25 Apr (mediate date)	34 (25–45)	19 000 (± 2600 SD)	610 ± 120	90 000 (86 100–91 000)
McKnight et al. (2013)	15–26 Nov	NA	Weddell Sea	NA	NA	1 May (one bird data)	NA	NA	NA	NA
Volkov et al. (2017)	14 Nov (4–24 Nov)	128 (105–150)	90°–10° E (Wilkes Land)	10 272 (2 636–19 251)	21 Mar (5 Mar–9 Apr)	20 May	61 (41–76)	29 098 (24 736–34 745)	488 (332–603)	84 300 (66 497–103 645)
Alerstam et al. (2019)	7 Nov	126	45° W–207° E (153° W)	7 890 (5 450–10 990)	Mid–Mar	26 Apr (24–30 Apr)	44	17 170	367	50 900 (45 330–59 520)
Redfern and Bevan (2020a,b)	7 Nov (20 Oct–5 Dec)	139	22° W–111° E	NA	26 Mar (23 Feb–12 Apr)	28 Apr–22 May	NA	NA	NA	NA
Wong et al. (2021) **Wong et al. (2022)**	8 Nov (2–15 Nov) 1–25 Nov	147 (138–157) 133–174	160° W–60° W 60° W–70° E	NA	4 Apr (29 May–11 Apr) 2–26 Apr	26 May (22 May–1 Jun) 5 May–14 Jun	52 (41–64) 21–58	22 906 (± 3473 SD)	NA	NA
U.S. Fish and Wildlife Service (unpublished data)	5 Nov (5 Sep–26 Nov)	153 (114–218)	NA	16 614 (9 834–33 046)	7 Apr (30 Mar–16 Apr)	NA	30 (24–39)	22 512 (19 515–26 689)	760 (593–883)	NA

[*] number of working geolocators

[**] four locations in Canada: Country Island (45°03' N, 61°19' W), East Bay (64°00' N, 82°04' W), Karrak Lake (67°15' N, 100°15' W), Nasaruvaalik Island (75°49' N, 96°18' W)

[1] mean ± SD

[2] mean (min-max) - unless otherwise mentioned

zooplankton (Edwards et al. 2021) and a projected decline in net primary productivity (Morten et al. 2023) in the North Atlantic that is well-known as a refuelling location for many seabird species including Arctic terns (e.g. Egevang et al. 2010; Boertmann 2011). Terns wintering in the Antarctic region are associated with the Antarctic pack-ice zone (Redfern and Bevan 2020b) where the important part of the tern's diet is at higher abundances (e.g. Antarctic krill – *Euphausia superba*; Brierley et al. 2002). However, the projected decline in habitat loss connected with other factors (e.g. predation; Hill et al. 2013) impacting krill abundance could have significant consequences for over-wintering tern populations. Since Arctic terns live for decades and migrate across the globe every year, their future in the light of global changes remains to be studied.

Aims and scope of the thesis

"Unfortunately, we had ringed and put a geolocator on both a female and a male from one nest. They both returned to Longyearbyen and are now breeding together 5 metres from the previous year's nest. However, they spent the summer in different locations in Antarctica, they did not fly together, and they even chose different flyways."

Hromádková, personal observation

This thesis is focused on the life strategy of the Arctic tern breeding under the harsh climatic conditions of the northern tundra. Studies were performed mainly on the population of terns from the Svalbard archipelago (78.22°N 15.65°E).

Our main aim in the **Chapter 1** was to uncover the basic incubation behaviour of Arctic terns under the harsh climatic conditions of the northern tundra concerning the worldwide increasing activity of people. We predicted that Arctic terns would respond to increased human disturbance by decreased overall nest attentiveness (increasing frequency of incubation breaks and restlessness on the nest) and that the response will show similar patterns as behavioural response to predator disturbance in closely related *Sterna* species (the Antarctic tern *Sterna vittata*) on the Antarctic peninsula. Studies covering the effect of human disturbance on the incubation behaviour of terns is well studied, but works from the Polar regions are mostly lacking.

In the **Chapter 2** we continued to focus on the impact of humans on terns breeding behaviour. Humans are often perceived as predators by birds and perform various antipredation behaviour. The flight initiation distance is one of many studied aspects and it is well known that flight initiation distances are generally shorter within urban birds than rural ones. The latency of return (return time to the nest after disturbance) could be comparable with the flight initiation distances, however, it is more indicative of the degree of risk to the egg and parental investment in the brood. Our aim was to assess the effect of human to a latency of return by studying two populations of terns differing in experience with humans. We tested the null hypothesis that terns will show equal latencies of return after disturbance by humans.

After more conservative studies, we moved our attention from human impact to more naturally occurring predator-prey interactions in the **Chapter 3**. We used Arctic terns as a model species to test several hypotheses summarizing primary knowledge about predator discrimination. Our aim was to compare the ability to recognize and properly react to a possible threat of an isolated island population of Arctic terns on Svalbard where the number of possible predators was low to that in the lower latitudes of northern Norway. In order to achieve this task, we presented different types of predators (specialized in predating eggs or adults respectively) to incubating adult terns with respect to their present distribution range. The prediction was that Arctic terns breeding on Svalbard would react to unknown predators that do not occur on Svalbard (raven and falcon) according to three hypotheses reviewed by Carthey and Blumstein (2018): (i) the *multipredator hypothesis* is based on the prediction that antipredator behaviour is genetically conserved and prey will retain the ability to recognise and react appropriately even after a predator´s extinction (Blumstein 2006), (ii) the *archetype hypothesis* is based on so-called archetypes and predicting that prey would be able to recognise and react to unfamiliar predators according to shared characteristics (Cox and Lima 2006), and (iii) the *relaxed selection hypothesis* presumes that if costs for retaining antipredator behaviour are high, prey will potentially lose their recognition/discrimination abilities (Lahti et al. 2009). The proper recognition followed by the appropriate reaction to a potential threat is an important ability for most animals. We predicted that Arctic terns would show equal antipredator reaction to a predator species regardless of nest location.

To fully uncover the life strategy of Arctic terns we also focused on migration behaviour in the **Chapter 4**. Migrating birds adapt their flyways according to a food availability and prevailing wind conditions. However, significant gaps remain in our knowledge about the ecology of remarkable migration behaviour of Arctic terns. Our main concern in this study was how the migration strategy of terns is adapted to prevailing wind conditions and refuelling possibilities along the path. To achieve our task, we deployed archival data loggers (geolocators) to 30 breeding arctic terns on Svalbard.

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Chapter 1

Incubation behaviour of Arctic (*Sterna paradisaea*) and Antarctic (*Sterna vittata*) terns under disturbance by humans and predators

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Abstract

The activity of people increased worldwide and has become an important source of disturbance to nesting birds even in a pristine environment of the polar regions. In this study, we focused on the correlation between disturbances and incubation behaviour of two Sterna species. By video surveillance of nests on low-disturbance and high-disturbance sites we evaluated (i) whether the incubation behaviour of Arctic terns *Sterna paradisaea* in Svalbard differed between various levels of mostly anthropogenic (passing people) disturbances and (ii) whether the incubation behaviour of Antarctic terns *Sterna vittata* on the Antarctic Peninsula differed between various levels of mostly natural (predators) disturbances. We analysed whole-day continuous recordings (median length > 24 h) of 72 nests from four study sites. Incubation behaviour at high-disturbance sites was characterized by lower nest attentiveness, shorter on-bouts, and recurrent interruptions, while off-bout length remained mostly unchanged. The total time spent sleeping and average sleep-bout length were shorter, while the frequency of visual inspection of the surroundings was higher at high-disturbance sites. In all, the responses of incubating terns to human disturbance did not exceed those induced by native predators. The behavioural responses, as measured by the direction and size of effects, were remarkably consistent for both species, representing the two polar regions with different natural predation risks as well as a different history of human impacts. Unless there are specific long-term costs associated with human disturbance, that we cannot evaluate here, the coexistence of people and breeding terns might be sustainable even in the polar regions.

Keywords: Antarctic Peninsula, anthropogenic disturbance, incubation behaviour, incubation rhythm, predator disturbance, Svalbard

Introduction

Environments where the presence of people is a relatively new factor offer unique opportunity to study the initial stages of interaction between humans and wildlife. The polar regions are a prime example of a pristine environment that have only recently become easily accessible to mass tourism. The steadily increasing number of visitors (Antarctic Treaty Consultative Meeting (44th : 2022 : Berlin) 2022) has already many harmful consequences for local ecosystems, including bird fauna (Tin et al. 2009; Coetzee and Chown 2016). Even in the absence of human disturbance, birds have to breed in extreme climatic conditions with limited chance for re-nesting due to short breeding season.

In this study, we focus on the impact of disturbance on incubation behaviour of two closely related tern (*Sterna*) species representing the two polar regions, the Arctic tern (*Sterna paradisaea*) and its southern close relative, the Antarctic tern (*Sterna vittata*). Both species breed in colonies on deglaciated sites close to the coast (del Hoyo et al. 1996). Their breeding is strongly affected by climatic conditions and predation pressure; which may even make nesting impossible in some years (Bunin and Boates 1994; Schulz and Gales 2004). Thus the nesting success is generally low and highly colony and year dependent (Jablonski 1995; Milius 2000; Tree and Klages 2004; Schreiber and Kissling 2005; Weidinger and Pavel 2013a; Mallory et al. 2017).

Terns are known for their aggressive behaviour towards any intruder into their colonies including people (Cramp 1985; Marchant et al. 2006). In the case of terns, people often play a role of eggs predators (Feare et al. 2007; Henri et al. 2020) and at the same time, they do not present serious risk for adults. The effect of human disturbance on the breeding biology of terns is generally well studied, but mainly in locations with milder climate (Burger et al. 1995; Yorio and Quintana 1996; Gyuris 2003; Jennings 2012), whereas, studies from the polar regions, where the co-existence of breeding terns and humans is a novel situation, are almost lacking. Nevertheless, available results suggest that breeding Antarctic terns are sensitive to human disturbance, as shown by reduced breeding success and desertion of breeding colonies (Kaiser et al. 1988; Peter et al. 2008, 2013). Additionally, human disturbances are likely to be additive to natural mortality caused by harsh climate, so the consequences of disturbance are likely to be more severe in the polar regions. In all cases, when birds leave the nest, regardless of the source of disturbance, they are interrupting the continuity of incubation with potentially harmful consequences for nesting success such as causing the eggs to cool down (Deeming 2002) or leading to elevated predation (Götmark 1992).

We studied the incubation behaviour of the two tern species by means of continuous video surveillance of their nests at multiple locations. Here, we evaluated (1) whether the incubation behaviour of Arctic terns differed between two sites with high/low level of human disturbance in Svalbard; (2) whether the incubation behaviour of Antarctic terns differed between two sites with high/low level of predator disturbance in the region of the Antarctic Peninsula; (3) whether the incubation behaviour of Antarctic terns was influenced by the number of locally breeding avian nest predators within the high-disturbance site; and (4) whether the behavioural responses show similar patterns across both tern species and different sources of disturbance. We predicted that terns would respond to either source of disturbance by increased restlessness on the nest and by increasing frequency of breaks in incubation, thus decreasing overall nest attentiveness.

Methods

Fieldwork

Arctic terns were studied at two sites on Svalbard archipelago, Norway (Online Resource 1a). We made a 24-hour observation on both sites where we recorded and noted all movements (animals and humans) in and around colonies. For every movement we recorded a reaction of the colony. Based on the observation, we classified both sites as low vs. high disturbance. The low-disturbance site was represented by small, isolated island Retrettøya (78.65°N, 16.91°E), studied in 2012 and 2014 (hereafter RET12 and RET14, respectively). The breeding colony of about 250 pairs was situated on Retrettøya island (approximately 2 ha) in front of Nordenskiöld glacier in Adolfbukta bay with the closest human settlement about 12 km away (Pyramiden, up to 10 inhabitants). Small groups of scientists/tourists up to 10 people visit the island irregularly during the breeding season (1-2 visits per week). Terrestrial predators – the polar bear (*Ursus maritimus*) visited the island only for a period of four days during the 14-day observation period in July 2014, the Arctic fox (*Vulpes lagopus*) was never seen on the island during observation periods in 2012 and 2014. Aerial predators – the glaucous gull (*Larus hyperboreus*) was the most common aerial predator on the island – were seen flying over the colony every day, the parasitic jaeger (*Stercorarius parasiticus*) and the great skua (*Stercorarius skua*) visited the island occasionally, the long-tailed jaeger (*Stercorarius longicaudus*) was never seen there.

The high-disturbance site was represented by the area within and around the town of Longyearbyen (78.22°N, 15.64°E, approximately 2500 inhabitants), studied in 2014 (LYR14). Arctic terns bred there (between 80-100 pairs) directly among houses and 20 m next to a campsite. The area is characterized by all-day presence of walking people, car traffic (as shown in a short video footage, Online Resource 2) and permanent occurrence of predators. In 2014, glaucous gulls were the most common aerial predators at Longyearbyen – they were seen flying over and resting close to tern colonies every day (terns are known to react less strongly to overflying than to hunting gulls, Whittam and Leonard 2000), at least two pairs of a parasitic jaeger bred in town and an Arctic fox was seen a few times within the town but not directly in the colony. Altogether, the two Svalbard sites differed markedly in the level of human disturbance, while disturbance by predators was present at both sites (Table 1).

Antarctic terns were studied at two sites in the region of the Antarctic Peninsula (Online Resource 1b), during austral summer 2010/2011 (Weidinger and Pavel 2013a). The low-disturbance site was represented by an area within 700 m around the Argentinian polar station Marambio on Seymour Island (64.24°S, 56.63°W; SEY10/11). Terns bred in loose colony on steep slopes separated by an edge of a plateau from the station and the airport runway, which was situated on the top plateau. Station crew members did not

Table 1 Comparison of disturbance regimes and video records among study sites of Antarctic (*Sterna vittata*) and Arctic (*Sterna paradisaea*) terns

Species	Site	Disturbance		Date of study	Nests	Video record per nest (h)		
		Predators	Humans			Median	1stQ	3rdQ
Antarctic tern	ROS10/11	High (~100)	Low (individuals)	4.-22.1.2011	17	24.15	24.03	24.68
Antarctic tern	SEY10/11	Low (individuals)	Low (individuals)	23.-30.12.2010	10	24.32	22.57	24.93
Arctic tern	LYR14	High (~100)	High (hundreds)	17.-23.7.2014	14	24.20	24.05	24.43
Arctic tern	RET12	High (~50)	Low (individuals)	6.-13.7.2012	15	24.68	24.25	24.98
Arctic tern	RET14	High (~50)	Low (individuals)	9.-15.7.2014	16	24.28	24.22	24.38

Disturbance is characterized by the low/high division of sites with an approximate quantification in parenthesis: number of human approaches to the colonies/nests for 24 h period or the number of avian predator individuals breeding/occurring adjacent to the colony

leave the top plateau and thus did not enter the tern breeding sites, and visits of avian predators to breeding area were rare during the study period (only one registered skua overflight). The nearest southern black-backed gulls (*Larus dominicanus*) nested 1 km away and foraged along the coastline, while the nearest south polar skua (*Stercorarius maccormicki*) nests were more than 7 km away close to the Adélie penguin (*Pygoscelis adeliae*) colony. Thus, the predator and direct human disturbance was minimal in this area.

The high-disturbance site was represented by the northern part of James Ross Island (63.80°S, 57.88°W; ROS10/11). The nests under study were located in loose colonies (hyper colony) 500 m – 10 km from the Czech Johan Gregor Mendel Station (summer station for up to 20 people, no other human settlement in the area), yet the disturbance was not confined to station surroundings as pedestrians (researchers from the station) crossed the entire area on a regular basis but avoided close passes to known bird nests/colonies. While the southern black-backed gulls bred only along the coastline, the south polar skuas bred on the whole area (44 known occupied nests). As a proxy of local disturbance by predators, we counted the number of breeding skua pairs whose nests were located within a 1.5 km radius around the each focal Antarctic tern nest. This value of radius was chosen as it yielded an approximately even distribution of skua numbers (number of tern nests with 0-6 skua pairs was: 2,4,2,4,2,2,1). Within a 1 km radius, there were mostly no breeding skuas (0-2 pairs), while within a 3 km radius there were always several breeding skuas (3-16 pairs). Altogether, the two Antarctic study sites differed markedly in the level of predator disturbance, while the low human disturbance, though of different type (passing researchers in ROS10/11 vs. human disturbance connected to the operation at the runway in SEY10/11), was present at both sites (Table 1).

At each study site, we video recorded whole-day samples of incubation behaviour. Some recordings were interrupted due to inclement weather or system malfunction, some recordings were prolonged due accessibility constraints. Included in the analysis were 72 recordings, of which 56 lasted 23–25 h, five recordings were shorter (min = 18 h) and 11 recordings were longer (max = 28 h). Nevertheless, median length was very similar and > 24 h across all sites

(Table 1) and the diel distribution of the missing/excessive recording hours was independent of the site disturbance category. Video systems consisted of a camera (35 × 40 mm) with IR illumination, a portable digital video recorder (Yoko RYK-9107), and a 12V battery. The recorder was housed in a camouflaged plastic box (125 × 95 × 50 mm) and connected to the camera by a 5-m cable. The camera was placed among two or three stones 0.5–2 m from a nest, depending on terrain configuration. The resulting accumulation of stones did not protrude in any way above the naturally uneven surface of the terrain. All other parts (box, battery, cables) were also covered by stones or soil. We set the recorders to work continually with a frequency of 10 fps at 640 × 480-pixel resolution. Deployment of one video system by two people took up to 15 min after which time observers moved away to allow the birds to resume incubation. We did not record any change of behaviour of breeding tern or their predators after camera installation. According to the camera records, terns returned to the nest not later than the average length of off-bouts recorded during the whole day. Cameras were deployed to nests depending on availability of video systems (two video sets in Antarctica, four video sets in Svalbard) and time constraints. Of the available nests, we selected those with complete clutches (2 eggs) with no signs of commenced hatching; one-egg clutches were included only if repeated nest visits confirmed the end of laying (mean clutch size was as follows: RET12 = 1.89 (n = 37), RET14 = 1.89 (n = 76), LYR14 = 1.83 (n = 88), ROS10/11 = 1.16 (n = 43), SEY10/11 = 1.23 (n = 111); see Weidinger and Pavel (2013a) for further data from ROS and SEY sites). By floating the eggs (Westerskov 1950) we found the same mean stage of incubation on the sites RET14 and LYR14. Due to short time window to collect data, the incubation stage was not evaluated in Antarctic sites. Cameras were distributed approximately evenly across the whole colony in order to minimize the time spent at any particular group of nests. General field protocol of nest monitoring was similar for both tern species (as described in Weidinger and Pavel (2013a)).

Data Analyses

Video records were analysed always by the same person per species, with some overlap to standardize the protocol (the person processing the data from Svalbard used some of the previously processed data from Antarctica to calibrate their own skills). Moreover, the main emphasis in this work is on the comparisons within the species. Not absolute values but standardized effects are compared between species. The following primary data were extracted from video records: time of start/end of uninterrupted incubation bout (delimited by times of sitting on the eggs and leaving the nest); time of start/end of sleeping bouts (sleeping period was defined as a posture with a bill under wing – as shown in a short video footage in Online Resource 3; Amlaner Jr and Ball 1983); a number of scans (< 10 s lasting interruption of sleep bout when bird scanned surrounding); the mode of departure from the nest (quick take-off vs. slowly walking away – as shown in a short video footage Online Resource 4). Because both tern species are sexually monomorphic and the birds under study were not individually marked, we considered each arrival and uninterrupted stay within the camera field of view as a different individual. From these primary data we derived the following incubation variables for each nest (all data are given in Online Resource 5): attentiveness – the proportion of the total time the eggs were incubated (calculated as a ratio of [mean on-bout/(mean on-bout + mean off-bout length)] for given nest); on-bout length – mean length of incubation bouts (in minutes); off-bout length – mean length of the interval between consecutive incubation bouts when the eggs were not incubated (in minutes); off-bout frequency per hour – number of off-bout sessions of incubating individuals per hour per nest; time spent sleeping – the proportion of the total incubation time spent in sleeping position; sleep-bout length – mean length of the sleeping bout (in minutes); scans per minute – mean number of scans per minute of sleeping time; the portion of take-off – the proportion of quick take-offs from all nest departures. Descriptive statistics of the incubation behaviour for each of the studied localities are given in Online Resource 6.

Data analyses were conducted in R version 4.1.1. (R Core Team 2021). We compared incubation behaviour between high-disturbance and low-disturbance sites by means of one-way ANOVA, separately for the two tern species. Visual examination of the data revealed departures from normality and heterogeneity of variances for most incubation variables. We first checked validity of all outlying data points and kept them in the analysis (we also preformed analyses without outlying data, see below). Because data transformation did not solve these problems and because ANOVA is quite robust in this respect, we analysed all variables untransformed (Knief and Forstmeier 2021) and validated our conclusions in two other ways (see below). Our intention here was to use the same simple method (two sample comparison) for both tern species to assure direct comparability of effect sizes between species and with other studies. Because we had three nest samples for the Arctic tern, we first conducted pair-wise comparisons among all three samples (Tukey HSD post hoc test) to see if the differences between years within the RET site were smaller than differences between RET and LYR sites. No significant differences were found between RET12 and RET14. However, RET12 differed significantly from LYR14 in five out of eight variables and RET14 differed significantly from LYR14 in four out of eight variables (see Online Resource 7). Based on this, we pooled two yearly samples from the RET and used this pooled sample in all subsequent analyses. We estimated raw effects size as the difference between site means, as well as standardized effect size (Hedges' d – unbiased; Nakagawa and Cuthill 2007: equations 3, 14, 17 applicable to simple two-sample comparisons based on t-statistic) to allow for comparison among variables and species.

To check for an effect of outlying data points on the results of the between-locality comparison, we reran all univariate analyses with a reduced data set where some data (nests) were excluded. A nest was excluded from an analysis of particular variable if two conditions were met: (i) the value was detected as an outlier within its own site and (ii) the outlier was outside the range of values found in the compared site. This has been examined graphically using boxplots. This procedure effectively made the between-site comparisons more conservative and in most cases also removed the problem with heteroscedasticity. As the most conservative check of the validity of between-site comparisons we repeated the analyses using nonparametric Wilcoxon test based on ranked data.

Apart from between-site comparisons we also calculated correlations (Spearman's coefficient) between incubation variables and the number of breeding skuas within 1.5 km radius around individual Antarctic tern nests at the ROS site. Although the correlation coefficient itself is a standardized effect, we rescaled correlations (Nakagawa and Cuthill 2007: equation 26) to compare effects sizes between correlation and ANOVA analyses.

Our emphasis in all analyses was on detecting patterns in the data, rather than on formal statistical testing. Hence further, we present results as raw or standardized effects with 0.95 CIs, while traditional tests are provided as Supplementary information.

Results

Incubation behaviour differed markedly between sites in both tern species (ROS10/11 vs. SEY10/11, LYR14 vs. RET12 + RET14; Fig. 1, Table 2), while comparatively low differences were found between years within the RET site in the Arctic tern (Fig. 1, Online Resource 7). Hence, we pooled data from RET for all subsequent analyses.

Between-site comparison of incubation variables yielded mostly similar results for the Antarctic and the Arctic tern. Incubation behaviour at low-disturbance sites (SEY10/11 and RET12+14) was characterized by significantly (as indicated by 0.95 CI non-overlapping zero effect) higher attentiveness, longer on-bouts, lower frequency of off-bouts, a higher proportion of time spent sleeping, longer sleep-bouts and lower frequency of scans. Off-bouts were only nonsignificantly shorter at low-disturbance site in the Antarctic tern (SEY10/11), while little effect was found in the Arctic tern (RET12+14). The only marked difference between species was found in the proportion of take-offs, which was markedly lower in a low-disturbance site in the Antarctic tern (SEY10/11) but differed little in the Arctic tern (RET12+14). Rescaling the raw effects (Table 3) revealed a consistent pattern of standardized effects in both tern species and all incubation variables except the proportion of take-offs (Fig. 2). Between-site comparisons based on the reduced data set (without outliers, Fig. 1) led to essentially the same conclusions as analyses of the full data set, in terms of statistical significance of the observed differences (Online Resource 8, Online Resource 9), raw effect size (Online Resource 10) as well as standardized effect size (Online Resource 11). Results based on parametric analyses were further corroborated by nonparametric rank-based tests.

Within-site correlations between incubation parameters and the number of breeding skuas within 1.5 km radius around individual Antarctic tern nests ($n = 17$) at the high-disturbance site (ROS10/11) were low to moderate (see Online Resource 12). Standardized effects calculated from the within-site correlations were of the same direction as those based on between-site comparison (all variables), yet mostly smaller (except for on-bout length) and formally nonsignificant (0.95 CI overlapping zero), except for on-bout and sleep-bout lengths (Fig. 3).

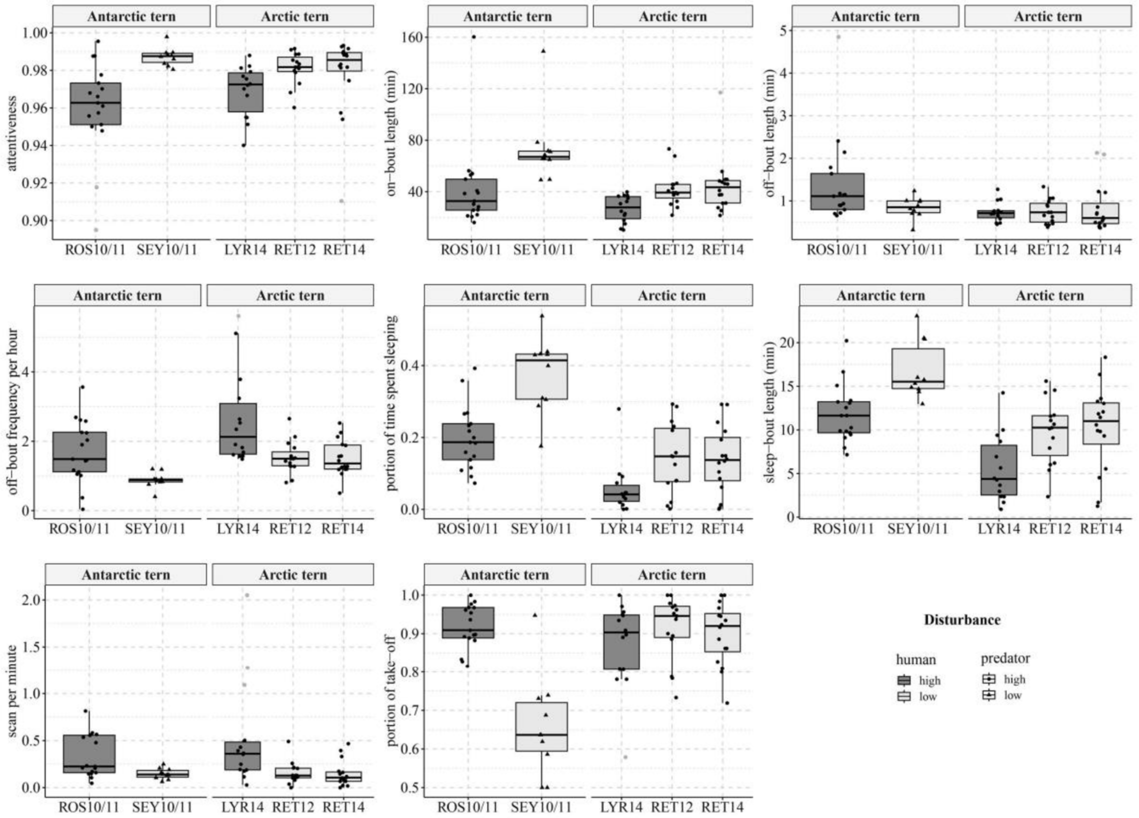

Fig. 1 Incubation behaviour of Antarctic (*Sterna vittata*) and Arctic (*Sterna paradisaea*) terns under different levels and types of disturbance. More disturbed (dark grey) vs. less disturbed (light grey) sites by humans and more disturbed (circles) vs. less disturbed (triangles) sites by predators. Shown is median, interquartile range (box), non-outlier range (vertical lines), and individual data values (points). Data excluded from validation analysis are shown in light grey

Table 2 A summary of incubation behaviour (mean ± SD) of Antarctic (*Sterna vittata*) and Arctic terns (*Sterna paradisaea*) at each site

	Antarctic tern		Arctic tern	
Variable	ROS10/11 (*n*=17)	SEY10/11 (*n*=10)	LYR14 (*n*=14)	RET12+14 (*n*=31)
Attentiveness	0.96±0.02	0.99±0.00	0.97±0.01	0.98±0.02
On-bout length (min)	42.04±33.04	73.34±28.18	26.60±10.26	43.31±18.03
Off-bout length (min)	1.40±1.03	0.84±0.25	0.74±0.23	0.79±0.45
Off-bout frequency per hour	1.71±0.90	0.88±0.22	2.64±1.35	1.52±0.48
Portion of time spent sleeping	0.20±0.09	0.37±0.10	0.06±0.07	0.14±0.09
Sleep-bout length (min)	11.82±3.32	16.80±3.31	5.55±3.84	9.99±4.25
Scan per minute	0.34±0.23	0.15±0.06	0.53±0.56	0.15±0.12
Portion of take-off	0.92±0.06	0.66±0.13	0.87±0.11	0.91±0.08

Table 3 The effect of disturbance on incubation behaviour of Antarctic (*Sterna vittata*) and Arctic (*Sterna paradisaea*) terns expressed as the raw difference (with 0.95 CI) between sample means.

	Antarctic tern (SEY10/11 vs. ROS10/11)			Arctic tern (RET12+14 vs. LYR14)		
Variable	diff	0.95 CI		diff	0.95 CI	
attentiveness	0,03	0,01	0,04	0,01	0,00	0,02
on-bout length (min)	31,30	6,41	56,18	16,71	8,14	25,28
off-bout length (min)	-0,55	-1,10	-0,01	0,05	-0,16	0,25
off-bout frequency per hour	-0,83	-1,31	-0,35	-1,11	-1,91	-0,32
portion of time spent sleeping	0,18	0,09	0,26	0,08	0,03	0,13
sleep-bout length (min)	4,98	2,22	7,75	4,44	1,82	7,06
scan per minute	-0,19	-0,31	-0,07	-0,38	-0,71	-0,05
portion of take-off	-0,26	-0,36	-0,16	0,03	-0,04	0,10

Positive effect indicates a higher trait value in relatively less disturbed sites vs. more disturbed ones

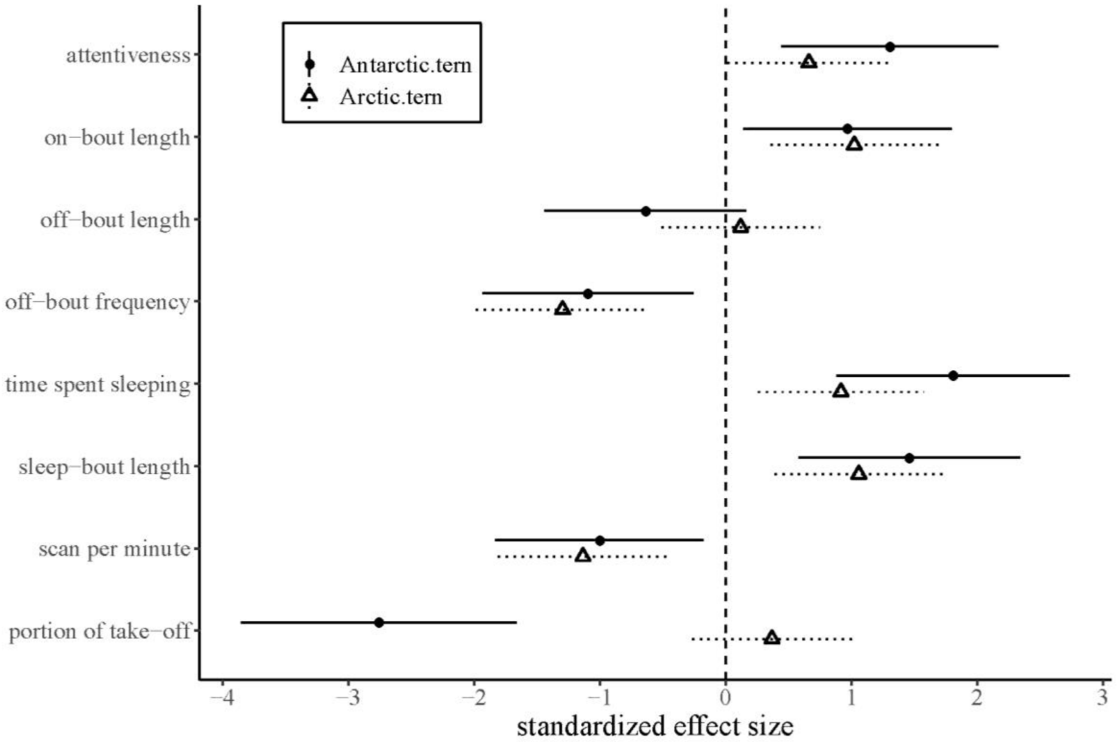

Fig. 2 The effect of disturbance on incubation behaviour of Antarctic (solid circles, solid line, *Sterna vittata*) and Arctic (triangles, dotted line, *Sterna paradisaea*) terns expressed as standardized effect size (Hedges´ d, with 0.95 CI). Positive effect indicates a higher trait value in relatively less disturbed sites vs. more disturbed ones. Effects on the original scale are shown in Table 3

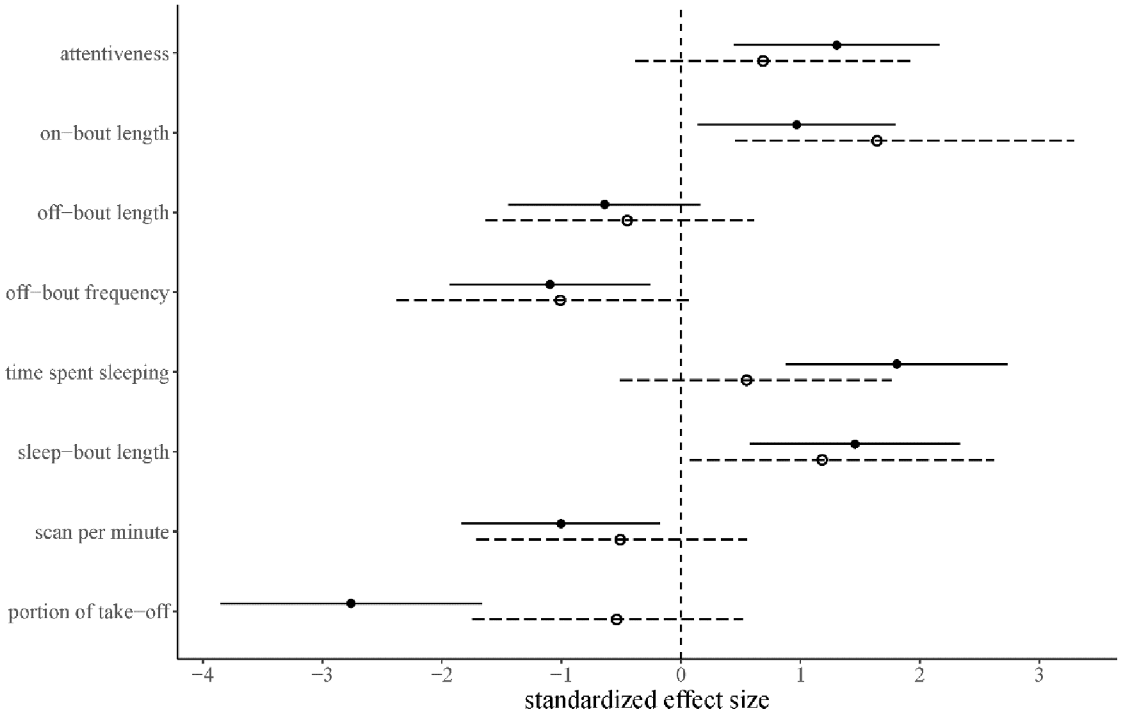

Fig. 3 The effect of disturbance on incubation behaviour of Antarctic terns (*Sterna vittata*) expressed as standardized effect size (with 0.95 CI). Effects were calculated either from the difference between sample means for the less disturbed site vs. more disturbed one (SEY10/11 vs. ROS10/11; solid circles, solid line) or from correlation with the level of disturbance within the more disturbed site (ROS10/11, open circles, dashed line). Positive effect indicates a higher trait value under lower disturbance

Discussion

We showed that the incubation behaviour of both tern species differed consistently between low-disturbance and high-disturbance sites. Generally, incubation behaviour at high-disturbance sites was characterized by lower attentiveness and increased restlessness on the nest. Lower attentiveness was due to shorter on-bouts, and concurrently, an increased frequency of off-bouts. This in turn was likely a consequence of recurrent interruptions of incubation bouts by external disturbance, either anthropogenic (passing people) or natural (predators).

In the present study, we could not fully separate the effects of human and predator disturbances, yet the similarity of behaviour responses between study sites is remarkable.

Regarding predation effect, tern incubation behaviour was affected at the study site under permanent predation risk (the Antarctic tern: ROS) compared to study site with very low level of predation risk (the Antarctic tern: SEY) but not at the site experiencing episodic, though heavy predation (the Arctic tern: RET12 vs. RET14) by the polar bear. The role of permanent predation risk was further supported by the observed variation among individual nests within the high-predation study site (the Antarctic tern: ROS), where tern incubation behaviour correlated with the number of locally breeding skuas in the same direction as shown in between-site comparison.

Regarding the effect of human disturbance, tern incubation behaviour was clearly affected at the study site with permanent presence of passing people close to the nests (the Arctic tern: LYR vs. RET), while any such effect at the two Antarctic study sites, if present, was likely obscured by the concurrent effect of predator disturbance. However, severe impacts of human activities on nesting success and colony tenacity, have been reported in the Antarctic terns at other sites (Kaiser et al. 1988; Peter et al. 2008, 2013; Braun et al. 2014).

Terns at disturbed sites spend more time off the nest, yet the average off-bout length remained mostly unchanged (the Arctic tern), or it was only slightly longer (the Antarctic tern). The comparatively fixed mean length of off-bouts suggests that birds in highly disturbed sites have to become more tolerant to disturbances than those breeding in less disturbed sites. Indeed, an experimental study of the return time to the nest after simulated disturbance by people showed that Arctic terns in the high-disturbance site (LYR) returned to their nests significantly faster than terns in the low-disturbance site (RET) (Syrová et al. 2020). Similarly, shorebirds (order Charadriiformes) intentionally disturbed by people returned to the nest faster and even increased nest attentiveness in the more disturbed site (Baudains and Lloyd 2007). Taken together, these results indicate that birds in sites with permanent anthropogenic disturbance can be more tolerant to human presence and alter their incubation behaviour, to prevent eggs from cooling down by retaining the continuity of incubation (Baudains and Lloyd 2007).

Terns in high-disturbance sites not only decreased overall nest attentiveness but also increased their overall restlessness/vigilance when on the nest. Firstly, the time spent sleeping and average sleep-bout length was shorter in high-disturbance sites. This corresponds with the findings of higher vigilance and less time devoted to resting under human disturbances in gentoo penguins (*Pygoscelis papua*, Holmes et al. 2006). In birds in general, species that sleep in more risky environments spend less time in the relatively vulnerable state of sleep (Rattenborg et al. 2017; Diehl et al. 2020). Furthermore, the frequency of scans – head movements with opened eyes performed during short interruptions of sleep bouts – was also on average higher in high-disturbance sites. This finding corresponds well with results based on different metrics of vigilant behaviour (e.g., frequency/time spent having their eyes opened; Lendrem 1983, 1984). In all, the above findings suggest that terns in high-disturbance sites perceived the permanently high risk of threat and adjusted their behaviour accordingly, even if they were not forced to leave the nest.

The notable exception from the consistency of reactions to disturbance between the two tern species (the polar regions) is the proportion of take-offs, which was markedly higher in the high-disturbance site in the Antarctic tern but differed little between sites in the Arctic tern. In absolute terms, the proportion of take-offs was lowest at the low-disturbance Antarctic site (SEY10/11), characterized by low (avian) predator pressure. On the other hand, the proportion of take-offs was comparatively high and similar across all three other study sites (Fig. 1), characterized in common by the high numbers and/or frequent occurrence of avian predators (Table 1). Flying away directly from the nest, as opposed to slowly walking away, might reduce the chance of disclosing the undefendable nest to aerial predators. Indeed, an artificial nest experiment conducted at the high-predation Antarctic site (ROS) showed that unattended eggs can benefit from crypsis (Weidinger and Pavel 2013b).

Apart from partial confounding between the different sources of disturbances at our study sites, the external validity of this study may be further limited by the lack of replicated study sites within species. For example O'Reilly and Wingfield (2001) described possible reduction of sensitivity to a stress of breeding shorebirds in extreme environments by lower responses to induced stress stimuli in high-Arctic sites compare to low-Arctic sites. In our study, we thus could not account for the contribution of site-specific effects to the observed patterns. Nevertheless, two pieces of evidence suggest that the inferred effects on incubation behaviour are real. Firstly, the direction and size of effects were remarkably consistent for both tern species. These two species represent the two polar regions characterized by different natural predation risks as well as different history of anthropogenic disturbance. Terns in Svalbard were not only historically exposed to mammalian predators, but also have longer historical experience with people and had more time to habituate to them. Secondly, in the Antarctic tern the direction and size of between-site effects were in agreement with those observed within the high-predation site.

In all, our findings suggest that even under harsh climatic conditions of the polar regions, various components of incubation behaviour represent plastic traits that could be adjusted within the physiological constraints imposed by the low ambient temperature. Terns breeding in high-disturbance sites responded to permanently increased risk of threat by decreasing overall nest attentiveness and increasing restlessness on the nest. Available evidence suggests that the direction and rate of these behavioural responses was similar in both tern species, regardless of the prevailing source of disturbance. This means that the response to moderate human disturbance in the polar regions, as reflected in incubation behaviour, did not exceed that induced by native predators. This implies that coexistence of terns with people might be sustainable even in the polar environment, where anthropogenic disturbance is a comparatively novel and still infrequent factor. However, as we measured only immediate behavioural response, more studies are needed to assess whether there are any specific long-term costs associated with human-caused vs. natural predator disturbances. Finally, because behavioural responses to various disturbances are context-dependent, our conclusions have to be validated by replicated studies in other locations.

Supplementary Information: The online version contains supplementary material available at https://doi.org/10.1007/s00300-023-03199-5.

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Author contributionst: TH collected data in Svalbard 2014 and participated on the manuscript preparation and data analysis. KW conceived and designed the study, collected data on Antarctic Peninsula 2010/2011 and participated on the manuscript preparation and data analysis. VP participated on study-design preparation, collected data on Antarctic Peninsula 2010/2011 and in Svalbard 2012+2014 and participated on the manuscript preparation.

Data availability: All data supporting the findings of this study are available within the paper and its Supplementary Information materials.

Declarations

Conflicts of interest: Authors declare no conflict of interests.

Ethical approval: The work in Antarctica was conducted under permission from the Ministry of Environment; all field procedures comply with the current laws of the Czech Republic. The work in Svalbard was conducted according to Norwegian law and the study was a part of a large project “Czechpolar – Czech polar stations: construction and logistic expenses (czechpolar)” registered in Research in Svalbard database (ID 5069).

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Chapter 2

Responses of nesting Arctic terns (*Sterna paradisaea*) to disturbance by humans

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Abstract

Nesting birds often respond to human disturbance as to a predatory act. In the case of the high Arctic, the disturbance of incubating birds may bring further complications due to egg cooling. In addition, it is assumed that birds in the high Arctic are not shy and do not respond to human presence fearfully. We tested how quickly the Arctic terns (*Sterna paradisaea*) nesting in two colonies in Svalbard return to the nest after human disturbance. One colony was situated inside a town where the terns were regularly harassed by human presence. The second colony was on a glacial foreland where breeding terns have limited experience with humans. We found that terns without frequent experience with humans returned to the nest about 5 min after disturbance, while urban terns habituated to human presence returned within a few tens of seconds. The urban terns in this way likely solve the risk of spending too much time off the nest, which could lead under the conditions of the high Arctic to the stopping of embryogenesis. Terns from a remote colony do not show lower hatching success of their eggs than the urban ones, however, incubation and the whole population of terns could be threatened when there is more frequent disturbance by researchers or tourists.

Keywords Antipredation behavior, Arctic tern, Human impact, Nesting behavior, Svalbard

Introduction

Breeding is a crucial period in the life of birds, especially in relation to the threat of predation. Adult animals can decide between a 'fight or flight' strategy when encountering a predator, but eggs and nestlings can usually rely only on their crypsis or defense from parents (Curio et al. 1969; Clutton-Brock 1991; Stearns 1992). Both antipredation strategies of the parent birds might have pros and cons (see Caro 2005 for review). If parents decide to be passive and not to defend the nest, relying on the nests' crypsis, the parents minimize the threat to themselves and save energy, but they may expose the nest to the predator. If they decide to actively defend the nest, they may chase the predator away, but they risk being attacked and spend a lot of energy at the same time (Collias and Collias 1978; Dale et al. 1996; Scheuerlein et al. 2001).

Humans often act as predators of bird nests, or rather are often considered as predators by the breeding birds (e.g., Burger and Gochfeld 1988; Beale and Monaghan 2004; Smith-Castro and Rodewald 2010). Responses to humans may be different, including physical attacks (e.g., chinstrap penguins, *Pygoscelis antarcticus* – Vińuela et al. 1995; Eurasian kestrel, *Falco tinnunculus* – Carrillo and Aparicio 2001), alarm calling (e.g., Leavesley and Magrath 2005; Magrath et al. 2010), and injury pretending (e.g., zenaida dove, *Zenaida aurita* – Burger et al. 1989; lesser golden plover, *Pluvialis dominica dominica* – Byrkjedal 1989), but the most common response is flight. Therefore, one of the main measured behavioral response of birds to human presence at the nest is the flight-initiation distance (Blumstein 2003; Blumstein et al. 2003; Albrecht and Klvaňa 2004). Nevertheless, birds fleeing from the nest face a trade-off between safety for themselves and the threat to nest. Moreover, during their absence at the nest, the eggs and small chicks lack the thermal protection from the incubating parent, which may threaten successful nesting (e.g., Gillett et al. 1975; Piatt et al. 1990; Lord et al. 2001).

Each antipredation behavior may be affected by a set of variables, summarized within the 'Optimal theory' (McNamara and Houston 1986; Clark 1994). Differences in investments to nest defense might be caused by varying environmental and social contexts as well as by the condition, sex, and age of the defending parents (Gill et al. 2001; Beale and Monaghan 2004; Abolins-Abols and Ketterson 2017), different types of predators (Patterson et al. 1980; Brunton 1986; Sordahl 1990; King 1999; Strnad et al. 2012; Němec and Fuchs 2014), breeding stage (eggs vs. nestlings; Kruuk 1964; Lemmetyinen 1972; Shedd 1982; Becker 1984; Knight and Temple 1986; Pavel 2006; Strnadová et al. 2018), age of nestlings (Patterson et al. 1980; Curio and Regelmann 1985; Montgomerie and Weatherhead 1988; Redondo and Carranza 1989; Dale et al. 1996; Pavel and Bureš 2001; Pavel 2006; Lima 2009), and, in the case of colonially nesting birds, also by the colony size (Regelmann and Curio 1986; Wiklund and Andersson 1994; Krams et al. 2009) and position of the nest within the colony (Kruuk 1964; Krebs and Davies 1993). Moreover, the reaction to predator might be influenced also by the previous predatory and disturbance events (Fontaine and Martin 2006; Holm and Laursen 2009; Němec et al. 2015).

The familiarity of breeding birds with humans and the risk of being predated by them is also an important factor affecting their antipredation responses. Urban populations of birds have consistently shorter flight initiation distances than their rural counterparts (Møller 2008; Møller et al. 2013). Knight (1984) and Knight et al. (1987) showed that ravens and crows perform the most aggressive nest-defense behavior in areas of low persecution by humans even though the ravens were in an area of low human density and the crows were in an area of high human density. Other study systems suggest that the effect of human presence and persecution to birds decreases with increasing latitude, e.g., birds breeding in Finland and Sweden show lower flight initiation distances than in Spain (Díaz et al. 2013). On the other hand, the willingness of parental risk taking during nest defense in meadow pipits (*Anthus pratensis*) is higher in Norway than in Central Europe (Pavel et al. 2000). The question is to what extent can be these examples generalize to the situation of isolated populations in high Arctic, where the human disturbance is a novel and still relatively scarce phenomenon.

In the current study, we examined the impact of human presence on the behavior of nesting Arctic terns (*Sterna paradisaea*) in Svalbard. The Arctic tern is a colonially nesting bird known for its vigorous mobbing behavior used not only against bird predators, but also ground predators and even against humans (Burger and Gochfeld 1991; Clode et al. 2000). According to IUCN, Arctic tern is globally considered as decreasing (BirdLife International 2018), though detailed information is notoriously lacking. The main effects identified to be responsible for this decrease are predation (Nordström et al. 2002), egging (Gilchrist and Robertson 1999), and food shortage (Schreiber and Kissling 2005; Vigfúsdóttir 2012; Frederiksen et al. 2013; Vigfúsdóttir et al. 2013). According to the IUCN, the other important threatening factor is yachting and other leisure activities, which have led to a significant increase in disturbance of breeding terns (BirdLife International 2018).

In our study, we focused on the threat of human presence on the incubation behavior of Arctic terns in Svalbard. Nesting in the Arctic is very challenging due to severe weather conditions with daily mean temperatures lower than 10 °C during the breeding season (June–July) in Svalbard (Ambrožová and Láska 2017), which places higher demands on the parents in terms of thermo-regulation during incubation and foraging over breeding season in high latitudes (Piersma et al. 2003). Therefore, as a measure of the risk for the eggs in a nest, we decided to measure the latency of parents to return to the nest after being expelled by a human approaching the nest as a proxy of parental investment in the brood. In such an experimental design, the actual threat has already passed, and the parents should calm down and return to the nest as soon as possible to provide heat to the eggs. On the contrary, returning too early means that parents may expose themselves to the threat. Such risk-taking behavior was measured, e.g., by Dale et al. (1996) on pied flycatcher (*Ficedula hypoleuca*) as the time elapsed until the first parent returned to nest after the presence of a predator near the nest. At the same time, the acute necessity to quickly return to the nest could be in conflict with the generally low fear responses of breeding birds to humans in the high Arctic.

We studied the nest-defense behavior of the Svalbard population of Arctic tern in two colonies differing significantly in the presence of humans and disturbance. This allowed us to test the null hypothesis that terns breeding within the town and in the wild show equal latencies of return to the nest after human disturbance.

Material and methods

Study area

We selected two Arctic tern colonies in Svalbard (the main island Spitsbergen). One colony with 50–60 pairs on the area of 500 m2 was affected by the presence of humans, being situated within Svalbard´s main settlement, Longyearbyen (GPS: N78° 13.283´ E15° 35.868´; Fig. 1), where the colony is scattered between houses with only few meters to the closest building, road, or pathway. Humans encounter tern nests on a regular basis within this colony. Sometimes, eggs are accidentally damaged by a pedestrian.

The second colony with approximately 200 pairs on the area of 500 m2 is situated on a glacial foreland on Retrettøya Island in Adolfbukta (GPS: N78° 39.368´ E16° 54.819´, Fig. 1). There is one occasionally inhabited Cottage (approximately 10 people for 2 days twice a month) approximately 1800 m from the colony. The permanent human settlement is a polar station 12 km distant (oversea distance). Human visits at this locality are only sporadic (up to 10 persons per week during the breeding season, from June to August). During our stays at the locality, we met only once two canoeists, therefore, our visits were the main disturbance during recording the birds.

Experiments were conducted at the stage when Arctic terns incubate their eggs, in July 2015 and 2016, usually in the afternoon (16:39 ± 3:06, $n = 66$). Our previous research (Hromádková and Pavel personal observation), in which temperature data were collected from Arctic tern colonies at both these localities, showed that there is no difference in the mean daily air

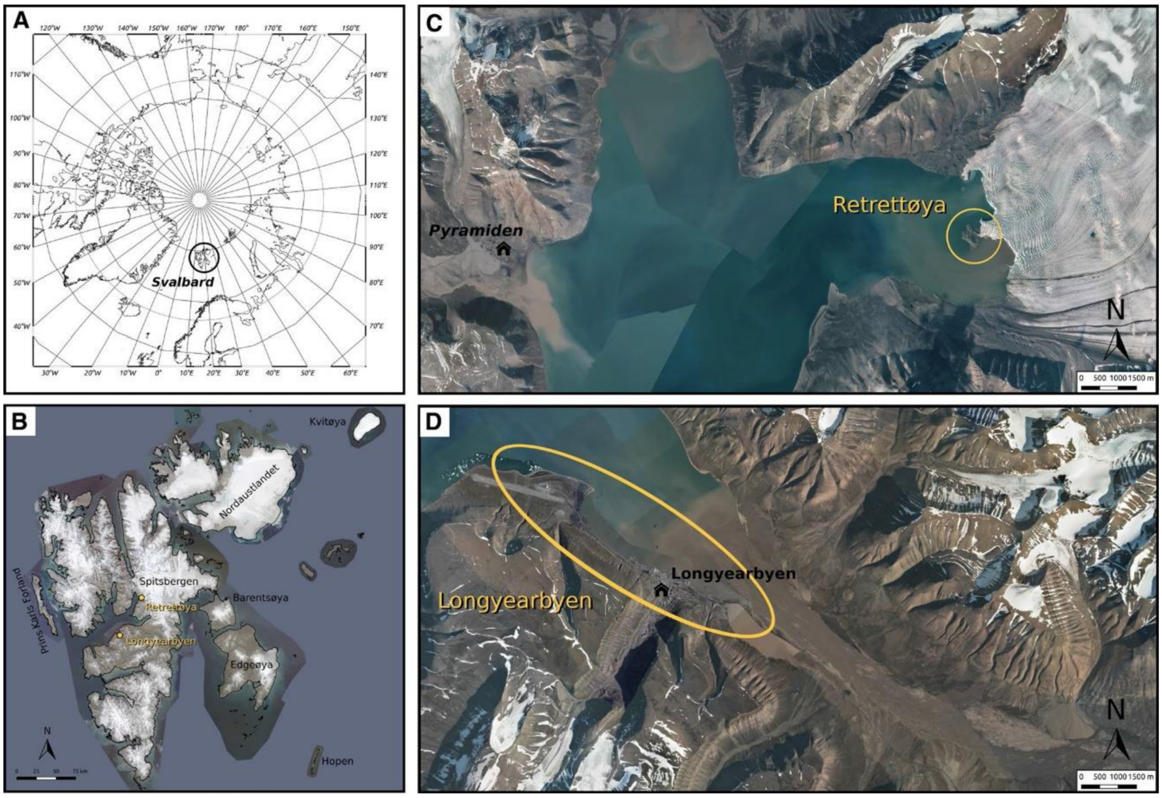

Fig. 1 Map of study locations. **a** Svalbard archipelago in the Arctic; **b** Svalbard archipelago with both studied colonies; **c** Colony Retrettøya; **d** Colony Longyearbyen

temperature between the study colonies (Fig. 2). Generally, the weather conditions were similar (and mild) during the days when we conducted the trials (wind speed: 2.95 ± 1.36 m/s; sum of precipitation: 0.01 ± 0.05 mm; temperature: 8.28 ± 1.58 °C; for detail information see Online Resource 1).

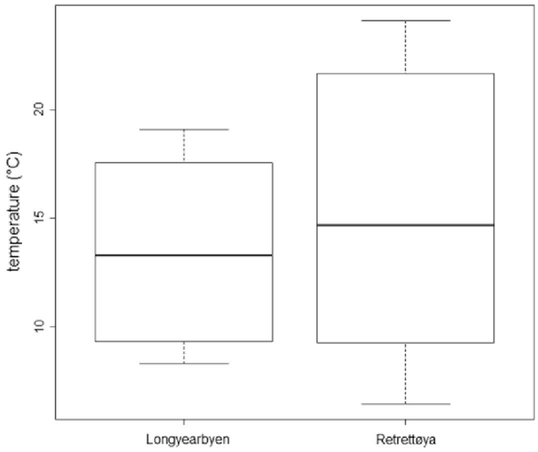

Fig. 2 Mean daily air temperature (°C) at the borders of Arctic tern (*Sterna paradisaea*) nests on two studied colonies in Retrettøya and Longyearbyen (Hromádková and Pavel, personal observation)

Study species

The Arctic tern is a medium-sized seabird of the family Sternidae without sexual dimorphism. The birds breed in either solitary nests to colonies of up to 500 pairs in Svalbard, on coast or islands, near the water (Burton and Thurston 1957; Lemmetyinen 1972; personal observation). Breeding is usually highly synchronized among pairs within a colony (although in poor season the synchronization can be broken down). In spite of the fact that Arctic terns undertake one of nature's longest migrations (from the Arctic to Antarctica and back – more than 70 thousand kilometers each year – Egevang et al. 2010; Fijn et al. 2013; Volkov et al. 2017; Hromádková et al. in press), they return to the same colony each year (Perrins 2003; Devlin et al. 2008). The nest is usuallyrepresented by a depression in the ground where terns lay one to three mottled and camouflaged eggs depending on food availability (Kilpi et al. 1992; Monaghan et al. 1992; Suddaby and Ratcliffe 1997).

Terns defend their nests and young very aggressively. They can attack humans and large predators, usually striking the top or back of the head and defecating. Although it is too small to cause serious injury to an animal of a human's size, it can efficiently repel many birds and mammalian predators (Cramp 1985).

Experimental design

We searched for nests within each colony and subsequently conducted the experiments at nests with a finished, already incubated clutch, before the chicks hatched. We assessed the approximate beginning of incubation using the egg floating test (measured in weeks: 1.91 ± 0.77, n = 66). The experimental method consisted first of an observer placing a video camera facing a tested tern's nest. The observer then went away from the nest to a distance of at least 30 m and waited till parents were habituated to the presence of the camera and the observer and sat on the eggs. After that, the human intruder (MS in 2015 and TH in 2016) went towards the nest, stopping directly above the nest, and then went back to the original distance of 30 m. The intruder walked slowly without any conspicuous behavior and movements. The reaction of the terns was recorded on the camera. We measured the time till the parent sat back on its nest (following Dale et al. 1996). The observation was ended after the parent bird either sat on the nest or after 15 min.

If the parent did not return within 15 min, the latency was recorded as 900 s.

Each nest was recorded only once. For each trial, we noted the colony identity (Longyearbyen and Retrettøya), nest GPS location, number of eggs in the nest, stage of incubation (days), number of neighbors within 20 m, and date of experiment.

Statistical analyses

The response variable was the latency of getting back to the nest after a disturbance (measured as time in seconds). To meet the demands of normal distribution, these data were transformed by logarithmic transformation [log(latency)]. Firstly, we compared the logtransformed latency of getting back to the nest after disturbance between the experiments conducted at the Longyearbyen in 2015 and 2016. We showed that there is no difference ($F_{1,31} = 2.82$, $p = 0.10$) and therefore, we decided to lump these data together. We ran a linear mixed effect model (LMM) to assess the effect of the predictor variables (command lmer in R package lme4; Bates et al. 2015) with colony size as a random factor.

The model included two categorical predictor variables, colony identity and the number of eggs (values 'one' and 'two'). There were also three continuous predictor variables: stage of incubation (days), date, and number of neighbors within 20 m from the tested nest. The effect of particular predictors was assessed during stepwise forward selection using likelihood ratio test (*Chi*-square) to compare subsequent models.

Results

We recorded the reaction of parents for 33 nests in each colony for a total of 66 nests tested (Longyearbyen 23 + Retrettøya 33 in 2015 and Longyearbyen 10 in 2016, for more details see Online Resource 1).

We found a strong difference in the reaction of the terns between our two studied colonies. Terns in Longyearbyen returned to the nest faster after a disturbance than the birds in Retrettøya (Linear model, $F_{1,59} = 146.67$, $p < 0.01$, Fig. 3).

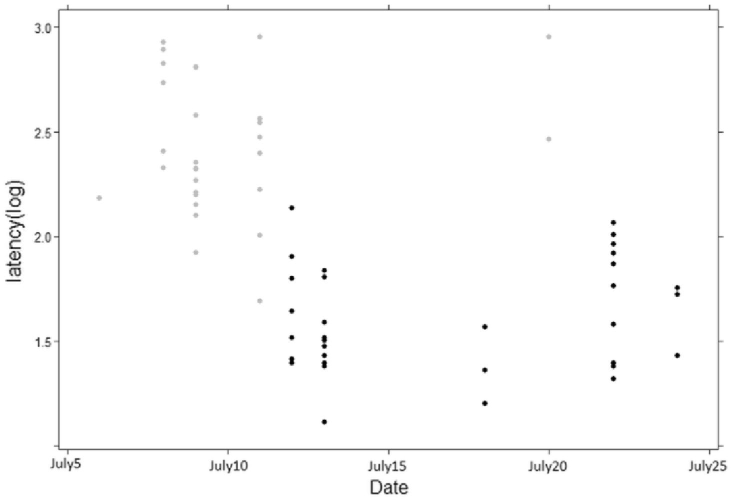

Fig. 3 Latency of the parent Arctic tern (*Sterna paradisaea*) to return to the nest after being disturbed by a human (measured in seconds, log transformed) in the course of the season starting with the day of the first trial conducted. Seasons 2015 and 2016 were lumped together. Black dots refer to the Longyearbyen colony and gray dots to the Retrettøya colony

Table 1 Effect of particular predictor variables on the latency of return to the nest after human disturbance (Linear model)

	AIC	BIC	*Chi* value	*df*	*Pr* (>Chisq)
Intercept	45.590	52.159			
Colony identity	**37.12**	**45.88**	**10.47**	**1**	**<0.01**
Stage of incubation	39.59	52.73	1.53	2	0.47
Number of eggs	41.53	56.85	0.06	1	0.80
Date of experiment	**40.31**	**73.15**	**17.23**	**8**	**<0.05**
Number of neighbors within 20 m	40.00	75.03	2.31	1	0.13

Bold indicate variables with significant effect

We also found a weak effect of the date when the experiment was conducted (Table 1); terns returned to the nest faster with increasing date of the experiment (later in the breeding season; Fig. 4). Other factors (stage of incubation, number of eggs, stage of incubation, and number of neighbors within 20 m) had no effect (Table 1).

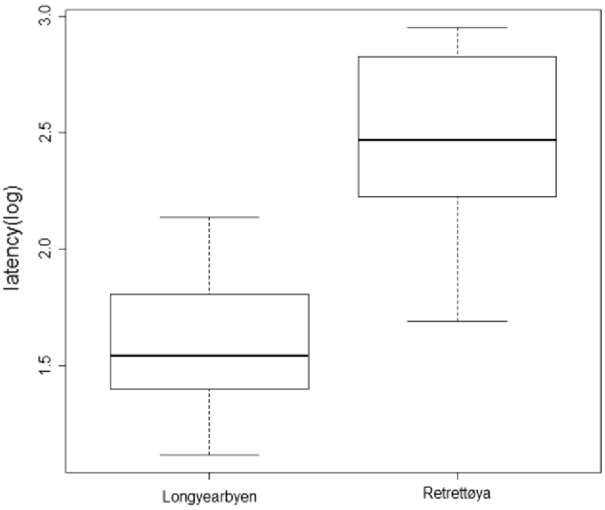

Fig. 4 Latency of the parent Arctic tern (*Sterna paradisaea*) to return to the nest after being disturbed by a human (measured in seconds, log transformed) in two colonies (Retrettøya and Longyearbyen)

Discussion

We found that terns from the colony within the human settlement returned to the nest significantly faster than terns breeding in pristine habitat at the edge of glacier. This difference is most probably caused by the habituation of the urban terns to human presence. Numerous studies have investigated the habituation of human presence in nesting behavior, e.g., Vennesland (2009) showed that breeding Great blue herons (*Ardea herodias*) reduced their behavior response by decreasing the response distance and habituated to the repeated approach of people, similarly Pfeiffer and Peter (2004) showed that south polar skuas (*Catharacta maccormicki*) are able to reduce aggressiveness in frequently visited areas. Moreover, Beale and Monaghan (2004) showed a habituation effect in nest occupancy patterns of the ruddy turnstone (*Arenaria interpres*), where young birds were forced into traditionally more disturbed areas. Burger and Gochfeld (1991) studied parameters correlated with flush distance of 138 species in India. They found that the flush distance is lower as the number and activities of near-by people are higher. On the other hand, ducks (*Anas platyrhynchos*) generally increase flushing distances in response to repeated human visits to the nest, most probably because these birds increasingly perceive a risk to themselves from the predator repeatedly approaching (Albrecht and Klvaňa 2004). Pfeiffer and Peter (2006) showed same increase of activity and nest defense in southern giant petrel (*Macronectes giganteus*), brown skua (*Catharacta antarctica lonnbergi*), and south polar skua (*Catharacta maccormicki*) in irregularly and unpredictably disturbed areas.

Nevertheless, crows and ravens show a lower rate of antipredation behavior when people persecute them, despite the level of urbanization of their locality (Knight 1984; Knight et al. 1987). This suggests that these birds might be more sensitive to a real disturbance than to simple human presence and urbanization level.

Breeding in human settlement confronts the terns with people approaching the tern nests on regular basis, which forces the parents to leave the nest too often. The parents needed to solve the trade-off between staying at the nest or leaving too early after the disturbance and exposing their eggs. Birds in the Arctic cannot afford to leave the nest for a too long period since there is a high risk of cooling. There were some studies showing that eggs of Arctic birds may survive cooling below 10 °C for many hours (Norton 1972; Roby and Ricklefs 1984); nevertheless, the embryos develop slowly (reviewed in Webb 1987) and there are high energy demands on the incubating parents (Tulp et al. 2012). It has been repeatedly shown that Arctic birds have almost 100% attentiveness on the nests with both parents incubating (e.g., Cresswell et al. 2003; Martin and Wiebe 2004; Bulla et al. 2014). As a consequence, the urban terns learned to overcome their natural fear of people and return to the nest quickly.

The terns from the colony without human presence returned to the nest approximately 5 min after a disturbance, which is ten times longer than the time needed by the terns from the colony in the main settlement. It is obvious that they are not used to such a disturbance and, since it is not common, they are not forced to return to the nest quickly to prevent the risk of their eggs cooling.

Food supply may be another, alternative explanation of the observed difference in the terns' behavior between the two studied colonies. Terns hunting near the glacier might have significantly richer food sources (krill, small fish – Lydersen et al. 2014), which may substantially affect their investment in offspring. Animals feeding in particularly rich habitats may be able to afford more of an interruption in the breeding behavior during a disturbance than those in poor feeding areas where individuals must devote all their available time to breeding (Gill et al. 2001). On the other hand, Beale and Monaghan (2004) showed that individuals in good conditions are less sensitive to disturbance. Anyway, we have no exact data on the foraging ground location of both studied localities. Based on personal observation, a significant portion of birds forages at the shores within several hundreds of meters from the colony; nevertheless, there may be local, more distant, and rich food sources, exploited by both colonies, which remain undiscovered.

Another possible explanation might be the generally higher predation pressure in colony Longyearbyen. It was well documented that birds living in more urbanized habitats suffer higher predation pressure (Jokimäki and Huhta 2000; Thorington and Bowman 2003; Jokimäki et al. 2005; López-Flores et al. 2009; Rivera-López and MacGregor-Fors 2016). Nevertheless, Svalbard is rather an exception in this case. Cats are forbidden in the town and dogs are kept in pens, so the higher predation pressure might be expected rather in the foreland of the glacier where polar bears and Arctic foxes are more common. On the other hand, the most common predators of tern nests are gulls and skuas, which occur at both localities. We have data of hatching success from both localities (Hromádková et al. personal observation), which can be to some extent understood as a proxy of predation pressure, and we showed no difference between both tested localities.

The weather conditions (temperatures and especially winds) are another factor affecting the nest attentiveness in Arctic birds (Bulla et al. 2015). Nevertheless, both our localities do not differ substantially in any measured weather conditions, at least during the days when the trials were conducted (Fig. 2, Online Resource 1). We can therefore suggest that the effect of weather on our results is low. Anyway, if the temperature near the glacier would be significantly lower than temperatures in the town (which one could expect), there would be higher pressure on the terns to return faster to their nests in the Retrettøya colony (as shown for other bird species – Larson 1960; Gramza 1967; Regelmann and Curio 1983), which is the very opposite of our results.

However, terns in the Retrettøya colony do not have a significantly lower degree of hatching success than terns in the Longyearbyen colony (Hromádková et al. personal observation). This suggests that there is no direct effect of the time spent incubating on the embryogenesis. In our study, we found a significant effect of date in the season when the experiment was conducted, in that terns returned to the nest faster at the end of the nesting season than at the beginning. This effect supports the reproductive value hypothesis (Patterson et al. 1980; Redondo 1989; Redondo and Carranza 1989; Viblanc et al. 2016), which posits that, with older clutches, parents have already a high amount invested and thus will continue to make further investments, e.g., nest defense. However, in our case, this effect was just a by-product of the fact that there was high synchronization of breeding between terns in both studied colonies. Terns in the Longyearbyen colony nested later in the season and, because their latencies were significantly lower than in the Retrettøya colony, the effect of date was pronounced as well (Fig. 4). However, there was no significant date effect in the case of the stage of incubation (i.e., age of clutch). It is obvious that behavior such as coming back to the nest does not reflect the existing level of parent investment in the clutch. This can be caused by the fact that all our experiments were conducted in the incubation stage. The variability in parental investment during the early stage of breeding is usually too low to affect the antipredation behavior of parents (see e.g., Strnadová et al. 2018).

The Arctic tern colonies in our two studied locations importantly differed in the number of breeding pairs. Both colonies were covering approximately equal area (around 500 m2); nevertheless, the colony in Longyearbyen housed approximately four times less nests (50 vs. 200). This suggests that the Longyearbyen colony was of much lower density, which could importantly affect the behavior of incubating birds when disturbed. Several studies showed that colonially breeding birds tend to respond more intensively to equal threat, when the colony is bigger. Burger and Gochfeld (1988) showed that, in general, the flush distance of Common ostrich (*Struthio camelus*) is negatively correlated with nest density, while the number of birds attacking the predator was positively correlated with nest density. In general, this suggests that birds feel safer in denser and larger colonies, with more neighbors to come to their aid. Anyway, there was no significant effect of the number of neighboring nests, i.e., the colony density on the latency of the return of incubating birds. The reason why we were not able to show this effect may reside in the fact that the variability of the densities was equally distributed within both colonies and the effect of this factor was far weaker than the difference between both colonies.

Conclusion

Terns breeding within human settlement returned to their nests more quickly than those breeding pristine environment. At the same time, the level of disturbance did not affect egg survival at these two colonies. Terns are able to adapt their incubation behavior to different disturbance levels to meet the optimal incubation performance and to overcome disturbances that may affect the survival of the clutch.

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Chapter 3

Predator-prey interactions in the high-Arctic: the loss of antipredator behaviour

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Manuscript

Abstract

Isolated populations often lose their ability to respond appropriately to predation threat, despite this ability being believed to be evolutionarily conserved. Only predator-free populations are supposed to lose their antipredator behaviour and recognition ability. We compared the ability of nesting Arctic terns (*Sterna paradisaea*) in the remote Svalbard archipelago and continental Europe to recognize and respond appropriately to various avian predators. We presented the dummies of predators occurring only on the European mainland (raven – *Corvus corax*, falcon – *Falco peregrinus*) and on both localities (black-backed gull – *Larus marinus*). Svalbard terns showed strong aggression toward the gull, while incubating their eggs in the presence of all other stimuli. Mainland terns showed equal response to the gull as those on Svalbard and showed a high level of fear in the presence of the raven and the falcon. Our results suggest that unfamiliarity with a predator may result in a rapid decrease in antipredator behaviour, despite other predators still being present. The isolated tern population has lost the ability to recognize predators based on general characteristics (curved beak, long clawed talons), which is particularly surprising when compared to theoretical models presuming that if the population faces some predators their ability to recognize them persists.

***Keywords*:** antipredator behaviour, Arctic, predator recognition, isolated population, predator-free system, birds

Introduction

Correctly recognizing a potential threat and reacting accordingly is an essential ability for most animals. Not reacting to predator can have serious consequences, while responding to a harmless species is a waste of energy [1]. Numerous studies have shown that birds have the ability to distinguish potential predators from a harmless species [2–5] and that they are even able to identify the level and type of threat that particular predators represent and react accordingly [3].

On the other hand, there are numerous examples of populations which have lost their ability to recognize predators. The trend not to respond to predators can often be seen in populations or species which are freed from predatory pressure, typically on isolated islands. The effect of so-called island syndrome on multiple aspects of the behavioural ecology of species has recently been recognized as an understudied phenomenon [6,7] despite the fact that it has the potential to show evolutionary principles in detail and in real time.

Several hypotheses summarizing primary knowledge about predator discrimination have been proposed [8]. The *multipredator hypothesis* predicts that prey will retain the ability to recognise and react appropriately to a predator even after the predator´s extinction. This hypothesis is based on the assumption that antipredator behaviour is genetically bonded and conserved and that it is highly disadvantageous not to respond to other still present predators [9]. The *archetypes hypothesis* predicts that prey are able to recognize and react to unfamiliar predators based on shared characteristics, so-called archetypes [10]. The third hypothesis, *relaxed selection*, predicts that prey will potentially lose their recognition/discrimination abilities, especially when there are some costs in retaining this behaviour [11].

We studied the predator-prey interactions of an isolated island population of birds in the high-Arctic. The Arctic region is one of the last untouched habitats, where many threats may have come into play only recently, or may emerge in the future [12]. Multiple invasive species responsible for driving multiple isolated island bird populations and species to extinction have spread within recent centuries all over the world [13]. Changes driven by climate, the alteration of habitats due to anthropogenetic activity, and the associated increased food availability are leading to the establishment of new animal population at new localities [14–16], which can be followed by the introduction of invasive species with potential harmful consequences for local fauna [16,17]. The Arctic thus represents an optimal ecosystem in which to study changes in threat recognition in prey species.

We focused on the ability of the Arctic tern (*Sterna paradisaea*) to recognize and appropriately respond to the threat represented by various predators. We used this species as a model as it performs a very vigorous and easy-to-read antipredator behaviour during nest defence [18,19]. We compared the behavioural responses of the terns at two localities differing importantly in the array of predators present. The first was Svalbard, a remote archipelago in the high-Arctic (more than 600 km north of the nearest continent). These islands are so remote that they house only a limited array of Arctic species compared to the Eurasian mainland, but still preserve some predators. We may thus presume that this population of terns is still capable of antipredatory behaviour and predator recognition even towards unfamiliar predators. The second study locality was on the European mainland (northern Norway, Varanger peninsula), where a much broader variety of bird species including predators can be encountered and are thus supposed to display complex antipredator behaviour.

We presented the dummies of several predatory and non-predatory species at the tern nests and observed the antipredator behaviour of the parents. We selected avian predators of nests (black-backed gull – *Larus marinus*; raven – *Corvus corax*) and adult terns (falcon – *Falco peregrinus*). The gulls occur at both locations, while the raven and falcon do not occur on Svalbard. We compared this behaviour with responses to human intruders – as humans themselves may act as a predator (both intentionally and unintentionally; [20,21]); the harmless eider duck (*Somateria mollissima*), and a piece of wood as baseline stimuli.

We expected, as a result of either the multipredator hypothesis or archetypes hypothesis, that Arctic terns on Svalbard would show equal antipredator behaviour in the presence of a predator species not occurring on Svalbard as Arctic terns on the European mainland.

Material and methods

Study species

Arctic terns are long-lived birds breeding in large colonies; though solitary nests can be found as well [22]. They have a circumpolar distribution, with breeding grounds extending from the temperate to the Arctic region [23]. They lay 1 to 3 eggs and both parents incubate. Incubation lasts 21 days on average [24,25]. The incubation success of Arctic terns is highly colony and year-dependent [24,26] with the potential loss of the breeding season due to heavy predation pressure [27,28]. They are very well known for their aggressive behaviour near their nesting grounds, chasing away intruders by means of physical attacks including defecation [18,19].

Study area

The study was carried out on two locations differing in the presence of studied predators. The first location was on the south-east coast of the Varanger peninsula, Norway (70.11°N 30.19°E), between the towns of Vadsø and Vardø. Arctic terns nest here in scattered colonies along the coast. But, solitary nesting terns were also found. The second location was in the vicinity of the town of Longyearbyen, Svalbard (78.22°N, 15.64°E). The terns here were breeding in the vicinity of the administrative town Longyearbyen and formed small colonies consisting of 20 pairs, though solitary nests were found as well.

At both sites, especially solitary nests and nests on the edge of the colony were observed for the purposes of our study, to prevent large numbers of birds from engaging in simultaneous antipredator behaviour. The Varanger and Svalbard localites differed in the number of potential predators (of both eggs and adults; see below). Both localities are inhabited by humans, the Svalbard locality encompasses breeding grounds within the human settlement, where terns and humans encounter each other on a daily basis, while encounters with humans are scarcer on Varanger.

Predator monitoring

To establish a list of potential predators, we utilized two methods – a review of the European Bird Breeding Atlas (grid no. 36WVC1 and grid no. 33XWG1; [29]) and our own field data collection (linear transect). According to both approaches, the most common bird nest predators of terns at the Varanger locality are herring gulls (*Larus argentatus*), lesser black-backed gulls (*Larus fuscus*), great black-backed gulls, Arctic and long-tailed skuas (*Stercorarius parasiticus* and *longicaudus*), and common ravens. There are several breeding pairs of gyrfalcons (*Falco rusticolus*) and peregrine falcons, representing the predators threatening especially adult terns. In the Longyearbyen area, the most common tern nest predators are glaucous gulls (*Larus hyperboreus*) together with both skuas and, sporadically, great black-backed gulls. There are no raptors, owls, or corvids present there.

Stimuli

As a stimulus to test the reaction of the Arctic terns to potential threat, we chose dummies of species that pose a threat to adults, to nests, and harmless stimuli. Altogether, there were four dummies prepared from textile and painted with acrylic paint (Fig. 1; see [30] for justifying this method): great black-backed gull – a predator of eggs and chicks present at both localities; peregrine falcon – a potential predator of adult terns, familiar to the Varanger population only; common raven – a predator of eggs and chicks present on Varanger only; common eider – a harmless duck occurring at both localities. A sitting human figure was introduced to the tern nest to establish whether it was perceived as a threat. Lastly, as a baseline stimulus controlling for the natural behaviour of terns, we placed a 40 cm long piece of wood.

Experimental design

First, after our arrival to the study area, we searched for nests and the position of every nest was noted in GPS. We assessed the stage of incubation by floating the eggs (see 31). We conducted experiments only in nests with whole clutches to prevent parental desertion. The stimulus was carried to the nest covered with a black cloth and placed two metres away from the nest. The dummy (as well as the human figure) always faced towards the nest. At the same time an observer took up a spot 20-30 metres away from the nest, so that they had a good view of the nest and its surrounding, but did not affect the behaviour of the parents. The observer was equipped with binoculars and a recording device (video camera). The dummy remained covered by the cloth until the parent terns calmed down and sat

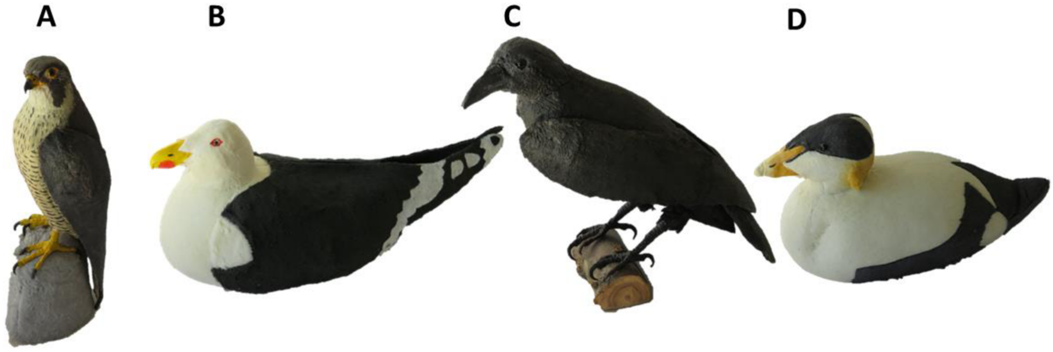

Fig. 1 Textile dummies presented at nests of Arctic terns (*Sterna paradisaea*): A) peregrine falcon (*Falco peregrinus*), B) great black-backed gull (*Larus marinus*), C) common raven (*Corvus corax*), D) common eider (*Somateria mollissima*).

back on the nest to incubate the eggs. If the parents did not calm down within 10 minutes, we continued with the experiment anyway. The experiment started when the dummy was uncovered by pulling the cloth down with a string (the cloth was completely removed from the nesting area). Exposure of one dummy lasted ten minutes and the observer recorded all behaviours performed by the nesting pair. After ten minutes, the dummy was taken from the nest covered in a cloth. The observer was never the one who carried the dummy to or from the nest. All stimuli were presented in randomised order at each nest (with human as the last). We scheduled one-hour breaks between stimuli in order to let the terns calm down and incubate.

Statistical analyses

We tested the reaction of 13 pairs of Arctic terns at the Varanger location and 12 pairs at the Longyearbyen location. As we focused on solitary nests at the edge of colonies, we were able to evaluate only the reaction of one focal pair that belonged to the experimental nest, even though there might be more terns present during the experiment. The Arctic terns were not individually marked; however, the parents' behaviour was always more active than that of other terns and we were able to spot these two most active individuals on the video recording. Nonetheless, we included the total number of all terns present during the experiment in subsequent data analyses (see below) to control for the effect of socially induced stronger antipredator behaviour.

We recorded eight behavioural responses in the tested terns: 1) the number of close attacks executed during the experiment (the attack was recorded when the tern flew towards the stimulus to a close proximity – 30 cm and less, which might have been associated with physical contact and/or defecation); 2) the number of distant attacks counted when the tern flew toward the dummy, decreased its height, but did not approach the dummy to a distance of less than 30 cm; 3) the number of flyovers (i.e. inspection flights above/over stimulus without apparent decrease in flight height); 4) the number of flights outside of the stimulus position (one flight determined by a change in direction); 5) the total distance flown during the entire experiment (in metres); 6) the total time spent at a distance less than 15 metres from the stimulus (in seconds); 7) the total time spent at distance greater than 15 metres from the stimulus (in seconds); 8) the total time spent sitting on the nest incubating (in seconds).

To obtain a composite behavioural response, we utilized the principal component analysis (PCA). This multivariate approach enabled us 1) to show the correlation of behavioural responses, 2) to normalize and standardize the response data and 3) to obtain canonical response variables describing the antipredator behaviour. This analysis was always carried out using Canoco 5 software [32].

The variability in the canonical response variables of two PCA axes (following Gaussian distribution) was explained using a linear mixed effect model (command lmm in R package lme4) with the bird ID nested in the nest ID (random slope model) coded as a random factor. We included the latency (in seconds) until the focal birds calmed down after being disturbed by the experimenter installing the stimulus at their nest as a covariate in both models to control for individual variability in the overall bird sensitivity to disturbance. We included three predictor variables in each model: interaction of the stimulus type (gull, falcon, raven, eider, human, a piece of wood) and locality (Varanger, Svalbard), the order of the experiment (first to sixth, coded as categorical variable), and the number of birds involved in the antipredator behaviour during the experiment (coded as continuous variable). We used stepwise forward selection, and we compared particular models using the likelihood ratio test (Chi squared test). To compare the categorical predictors values, we used a Tukey HSD post hoc test (z test, command glht in R package multcomp) with Tukey correction for multiple comparisons.

Results

The multivariate PCA analyses showed the first two canonical axes to explain the high portion of data variability (48 % and 28 % respectively). The first axis was loaded by the time spent incubating in positive values (loading coefficient 0.54) and by active nest defence, hereafter referred to as aggression (flown meters – 0.94, time spent close – 0.93, flyovers – 0.79, distant attacks – 0.63) in negative values (Fig. 2). The second canonical axis was loaded by the time spent incubating (0.70) in positive values and time spent away from the locality, hereafter referred to as fear (0.91), in negative values (Fig. 2).

First canonical axis

In subsequent analysis, we showed that the variability in scores of the first canonical axis is significantly affected by the interaction of stimulus and locality (LMM, Chi = 11.392, $p << 0.001$). We showed no effect for either the latency of the birds to calm down (LMM, Chi = 1.023, $p = 0.569$), the order of the experiments (LMM, Chi = 1.413, $p = 0.220$), or the number of terns present during the experiment (LMM, Chi = 3.115, $p = 0.093$).

Post hoc analyses showed that Svalbard terns showed less aggression to falcon (post hoc Tukey HSD test, $t = 4.186$, $p < 0.01$), raven (post hoc Tukey HSD test, $t = 4.087$, $p < 0.01$), and eider (post hoc Tukey HSD test, $t = 3.803$, $p < 0.01$) than Varanger terns. Responses to gull (post hoc Tukey HSD test, $t = 1.196$, $p = 0.99$), human (post hoc Tukey HSD test, $t = 0.672$, $p = 0.99$), and a piece of wood (post hoc Tukey HSD test, $t = 2.700$, $p = 0.23$) did not differ between both localities (Fig. 3A).

Within the Svalbard population, the terns showed the most aggressive responses to gull, differing significantly from responses to a piece of wood (post hoc Tukey HSD test, $t = 5.641$, $p < 0.001$), eider (post hoc Tukey HSD test, $t = 3.227$, $p < 0.05$), falcon (post hoc Tukey HSD test, $t = 4.748$, $p < 0.001$), and raven (post hoc Tukey HSD test, $t = 5.702$, $p < 0.001$). Aggression towards gull and human did not differ in the Svalbard tern population (post hoc Tukey HSD test, $t = 1.992$, $p = 0.695$).

Within the Varanger population, the terns showed most aggressive responses to gull, falcon and eider, all three differing significantly from the responses to a piece of wood (post hoc Tukey HSD test, $t = 5.254$, $p < 0.001$; $t = 3.363$, $p < 0.05$; $t = 4.556$, $p < 0.001$ respectively).

Second canonical axis

We showed that the variability in scores of the second canonical axis PCA

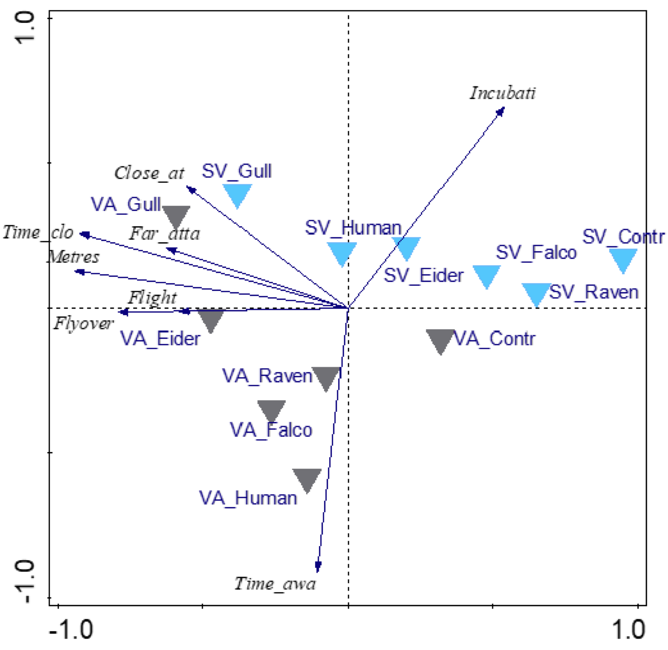

Fig. 2 – The multivariate analysis of behaviour of Arctic terns on the Varanger peninsula in continental Norway (grey, VA), and on the remote archipelago of Svalbard (blue, SV): Incubati – time spent incubating at the nest, Close_at – number of close attacks closer than 30 cm, Far_atta – number of attacks further away than 30 cm, Flyover – number of flyovers, Flight – number of flights outside of stimulus position, Metres – total distance flown during the experiment, Time_clo – time spent within 15 m off dummy/nest, Time_awa – time spent outside a range of 15 metres from the nest/dummy. Gull – *Larus marinus*, Falco – *Falco peregrinus*, Raven – *Corvus corax*, Eider – *Somateria mollissima*, Human – human figure, Contr – piece of wood.

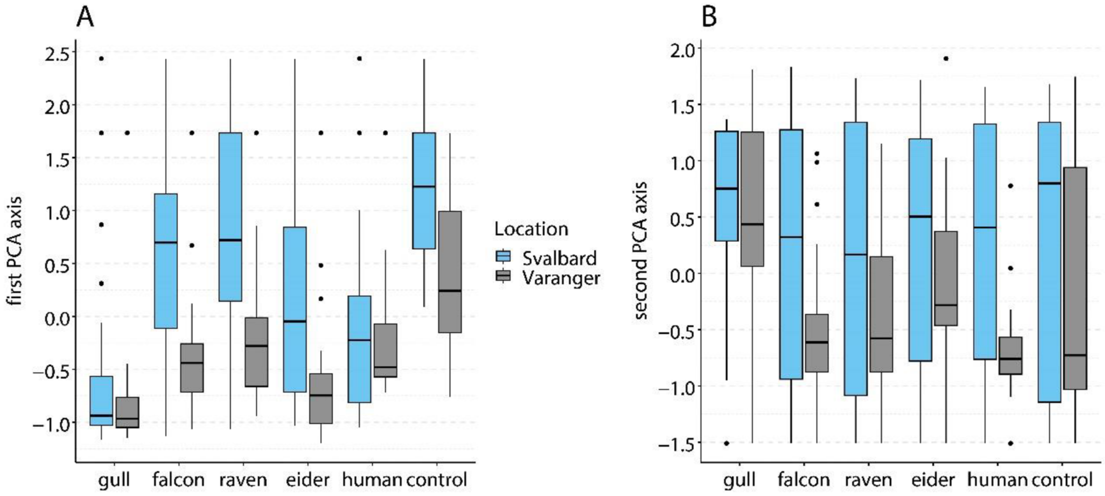

Fig. 3 – Effect of presented stimuli on both localities on the variability in scores of: **A)** the first canonical PCA axis and **B)** the second canonical PCA axis. Gull – *Larus marinus*, falcon – *Falco peregrinus*, raven – *Corvus corax,* eider – *Somateria mollissima*, human – human figure, control – a piece of wood. Shown is median and dots representing outliers.

is significantly affected by the interaction of stimulus and locality (LMM, Chi = 4.331, $p << 0.001$). We showed no effect for the latency of the birds to calm down (LMM, Chi = 0.125, $p = 0.869$), the order of the experiments (LMM, Chi = 0.588, $p = 0.710$), nor the number of terns present during the experiment (LMM, Chi = 2.059, $p = 0.125$).

Post hoc analyses showed that Varanger terns showed more fear towards the human figure (post hoc Tukey HSD test, $t = 3.970$, $p < 0.01$) than Svalbard terns. Human figure on Varanger also elicited more fear than gull (post hoc Tukey HSD test, $t = 4.697$, $p << 0.001$). Falcon also elicited more fear than gull on Varanger (post hoc Tukey HSD test, $t = 3.477$, $p < 0.05$). All other biologically relevant pairwise comparisons of tern responses were not significantly different (post hoc Tukey HSD test, t values below 2.9, p values above 0.15; Fig. 3B).

Discussion

The Arctic terns from Svalbard showed less intense antipredator behaviour to the dummies of the falcon and the raven (i.e. to predator species that do not occur in Svalbard) than the terns from continental Europe. The Svalbard terns were willing to incubate for most of the time of the presentation of these two dummies and their responses did not significantly differ from the reaction to the eider dummy and a piece of wood. On the contrary, the gull dummy elicited a very strong response in the Svalbard terns, including attacks (even hitting the dummy) and the terns flew a significantly greater number of metres than in the presence of other dummies.

Our results showed that the Svalbard terns did not recognise the falcon and the raven as potential threats and showed almost zero antipredator behaviour towards them, while the Varanger terns reacted with cautious behaviour and kept a distance from these two dummies. This is in contrast to the *multipredator hypothesis* [9] presuming that the ability to recognise predators is genetically based and, thus, the Svalbard terns should be able to recognise and react accordingly even to unfamiliar predators, because Svalbard is not a completely predator free locality. There are gulls and jaegers as avian predators posing a threat to eggs and hatchlings [29]. We showed that Svalbard terns actively defend their nests from gulls; meaning they have not lost their antipredator behaviour; however, they have lost their ability to recognize unfamiliar predators as a threat.

Recognising predators based on shared characteristics is a known phenomenon across many bird species [3]. The shared characteristics, so-called archetypes, of bird predators are typically a curved beak, long clawed talons, and bright eyes. The *archetypes hypothesis* predicts that a prey species will be able to recognize predators and react accordingly thanks to archetypes even after the predator has become extinct and a new one has been introduced [10]. However, Svalbard terns showed no behavioural responses to the presented raven and falcon dummies.

This is particularly surprising in the case of the falcon, which possessed all of the predatory features and elicited fear responses in the Varanger terns. The presence of a curved beak, conspicuous eyes and talons with claws has been shown several times to be crucial in predator/threat recognition [3]. When these traits (at least some of them) were removed or replaced with harmless ones, the predator was not treated as a threat [33]. Contrary to the *archetype hypothesis* [10], or similarly formulated hypotheses of prototype or exemplar [34]; these features did not secure generalization of a familiar threat to the unfamiliar falcon dummy in Svalbard terns.

Results from the European mainland showed that terns definitely recognized the falcon and raven as a threat and usually performed vigilant behaviour in their presence. Arctic terns are known for their impressive migration roaming over the globe [35,36]. During this transequatorial migration they mingle with many other bird species at diverse places in the world [37,38], and it is likely that along the coasts of Europe, Americas, or Africa, an encounter with similar species to the falcon and raven can occur. Obviously, these encounters do not importantly affect their attitude to such stimuli. However, we usually recorded a significant variability in Svalbard tern responses to most stimuli, including the unfamiliar ones (Fig. 2), suggesting that individual experience may play its part in the behaviour. If some of the terns had experienced a falcon attack on the African coast some years before, its response to our falcon dummy may have been affected by this single event.

Results from our study suggest that the *relaxed selection hypothesis* could be best applied to the case of the terns from Svalbard. This hypothesis predicts that the importance of a particular trait in predator recognition may slowly diminish if there is no selection for that particular trait [11]. In our case, it means that the ability to recognise the falcon according to its hooked beak will be lost if the ability to recognize a falcon is no longer advantageous and it is costly to maintain such ability. Responding to a non-predator could be potentially highly expensive for Svalbard terns. Any form of antipredator behaviour (attacks, vigilance of fleeing) takes away time from important activities such as incubating eggs, which can result in the cooling of eggs due to discontinuous incubation [24]. This is particularly important on Svalbard (even more so than on Varanger), where the ambient temperatures may be very low even during the tern breeding season [39].

The strength of the effect of the relaxed selection hypothesis relies importantly on the level of isolation of the population. We have no genetic data on the Svalbard tern population allowing us to assess the timing and level of isolation from other populations. Svalbard was firstly deglaciated and thus available for seabirds nesting around 15 100 – 14 200 years ago [40]. At the same time, Arctic terns show a very high level of fidelity to their breeding grounds [41], which suggests a likely very long isolation of the tern population on Svalbard.

Terns are a good example of a species where learning and forgetting even genetically conserved behaviours may be likely. Terns are social animals, especially during the breeding period [42], which may importantly emphasize social learning about predators. It has been confirmed that social animals learn faster about threats compared to those living solitarily [43]. For solitary animals a lack of reaction to a predator can lead to death. In social animals, learning may work through witnessing another member of the flock being predated or through alarm calls [44]. We may thus presume that for socially living birds (flocks, colonies) the punishment for forgetting the predator is not that high as they can later learn faster after the predator returns [45]. The latter is crucial when considering invasive species.

The experiments at the Varanger locality showed the high ability of terns to categorize predators. The gull's extreme threat to the nest content elicited vigorous attacks, while the falcon’s threat to the adults usually elicited flying away from the nesting locality. This is in concordance with other studies showing different attitudes to nest and adult predators [46–48].

Quite surprising is the response to the raven, which represents a threat to the egg and chicks of terns similar to that of the gull [48]. One possible explanation for the fear rather than the mobbing response to ravens may be low experience with ravens as nest predators; nevertheless, they were quite common at the Varanger locality (pers. obs.) and ravens were also shown to predate bird nests on the coastline [49]. Moreover, a similar difference in the responses of terns to gulls and ravens was detected in the North American population [48]. We may thus conclude that ravens and gulls are not perceived as equally threatening predators and that different antipredator strategies are, thus, utilised in their presence.

We were also able to detect differences in the responses of the Varanger and Svalbard terns to the human figure sitting at the nest. The terns at Varanger usually showed fear responses, flew away from the colony and waited until the figure disappeared. On the contrary, on Svalbard, the terns showed very variable response, some attacked the human figure, some incubated their eggs, and some flew away. We presume that the difference between the two localities is not a result of the isolation of the Svalbard population. The reactions rather reflect actual experience with humans at the tested localities, as has been shown before [50]. On Svalbard, we tested a colony breeding at the edge of a human settlement, some nests were even located in between houses and the birds experienced pedestrian passing by their nests on a regular daily basis. On the contrary, on Varanger, the colonies are further from the closest human settlements, and human intruders are quite seldom seen within the colonies (anglers or birdwatchers). This suggests that terns are able to flexibly adapt to actual experience with humans and respond accordingly. Nevertheless, further experiments are needed to test this presumption.

Lastly, we were able to observe some antipredator behaviour even towards the eider dummy; which we intended to present as a harmless stimulus. On both locations, but more pronounced at the Varanger locality, terns showed arousal at the presence of the eider at their nest, eventually attacked the dummy, and flying around it. This suggests that they do not perceive the eider as a harmless species. The reason may reside in its size as it is quite a big and clumsy bird species (at least when walking on the ground), and it may accidentally step on the nest and trample the eggs. Another possibility is that eider may intentionally destroy the tern eggs by eating them, which has already been recorded in mallards [51] as well as eiders [27; personal observation).

Conclusion

We showed that despite the fact that Arctic terns on Svalbard still face some predators and are able to perform antipredator behaviour, they have lost their ability to recognize predatory species not inhabiting Svalbard as a threat. The reason is very likely the long-lasting isolation of the philopatric Svalbard tern population, while retaining the antipredator responses to unfamiliar predators unfavoured the terns via egg cooling in the extreme arctic weather. The specific features common to most predators, such as a hooked beak and claws, are ignored, suggesting that the theories of recognition processes do not play their part here. We propose that the potential for evolutionary recalling of the antipredator responses to these unfamiliar species may be quite easy in terns, as they are colonial breeders with vigorous antipredator behaviour, which both importantly enhances the learning process. In the light of a possible future invasion (natural or human-induced) by some predatory species in this remote pristine ecosystem, the Arctic tern is likely to act as a naïve prey, may suffer from predation by this new exotic predator, but would eventually quickly learn to respond to it appropriately.

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Author contributions: JŠ - Conceptualization, Data curation, Writing–original draft, Writing–review & editing, Formal analysis, Visualization; TH – Funding, Conceptualization, Data curation, Writing–original draft, Writing–review & editing, Visualization; LH - Data curation; MS: Conceptualization, Data curation, Writing–review & editing; RF – Conceptualization, Writing–review & editing; PV – Conceptualization, Formal analysis, Writing–review & editing. All authors have read the final version of the manuscript.

Conflict of interest: The authors claim no conflict of interest.

Ethical approval: All applicable international, national and institutional guidelines for the care and use of animals were followed. This research adhered to the ASAB/ABS guidelines for the use of animals in research and complied with the current laws of Norway (including Svalbard). The project was registered in the Research in Svalbard Database (RiS ID 11061) and granted by the Svalbard authorities (Sysselmesteren på Svalbard). The terns were tested in their natural environment with minimum disturbance and experienced natural levels of stress.

Data accessibility: All data associated with this manuscript are available via the Dryad repository.

Declaration of AI use: We have not used AI-assisted technologies in creating this article.

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Chapter 4

Seasonally specific responses to wind patterns and ocean productivity facilitate the longest animal migration on Earth

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Abstract

Migratory strategies of animals are broadly defined by species' eco-evolutionary dynamics, while behavioural plasticity according to the immediate environmental conditions en route is crucial for energy efficiency and survival. The Arctic tern *Sterna paradisaea* is known for its remarkable migration capacity, as it performs the longest migration known by any animal. Yet, little is known about the ecology of this record-breaking journey. Here, we tested how individual migration strategies of Arctic terns are adapted to wind conditions and fuelling opportunities along the way. To this end, we deployed geolocators on adult birds at their breeding sites in Svalbard, Norway. Our results confirm fundamental predictions of optimal migration theory: Arctic terns tailor their migration routes to profit from (1) tailwind support during the movement phase and (2) food-rich ocean areas during the stopover phase. We also found evidence for seasonally distinct migration strategies: terns prioritize fuelling in areas of high ocean productivity during the southbound autumn migration and rapid movement relying on strong tailwind support during the northbound spring migration. Travel speed in spring was 1.5 times higher compared to autumn, corresponding to an increase in experienced wind support. Furthermore, with their pole-to-pole migration, Arctic terns experience approximately 80% of all annual daylight on Earth (the most by any animal), easing their strictly diurnal foraging behaviour. However, our results indicate that during migration daylight duration is not a limiting factor. These findings provide strong evidence for the importance of interaction between migrants and the environment in facilitating the longest animal migration on Earth.

Keywords: Arctic tern, *Sterna paradisaea*, daylength, geolocator, global wind systems, longdistance migration, migration phenology, migration strategy, ocean productivity

Introduction

Bird migration usually comprises an interchange of an active flying phase, when energy is consumed, and a stationary stopover phase, when fuel is restored by food intake (Alerstam & Lindström 1990, Hedenström & Alerstam 1998). This is especially true for flapping migrants (e.g. waders and songbirds) that fuel their flight by burning energy, as opposed to soaring migrants (e.g. raptors and albatrosses) that often take advantage of thermals or topography induced air uplifts, to cover large distances with minimal energy expenditure. For flapping flyers, this means that, while on migration, extended time needs to be spent at stopover sites refuelling and storing energy reserves to power the upcoming flight bouts (Hedenström & Alerstam 1997). Because the rate of energy expenditure during the flight phase is usually much higher than the rate of fuel deposition on stopovers, visiting high-quality stopover areas en route is of high importance for efficient and successful migration (Alerstam 2011). One of the main ways to reduce the expenditure of stored energy during flapping flight is to exploit prevailing wind regimes and adjust migration routes to take a full advantage of wind assistance for covering large distances rapidly (Kranstauber et al. 2015). Thus, maximizing fuelling rates on stopovers and minimizing energy expenditure during the flight bouts are the 2 key aspects of migration energetics for species that use powered flight for their migration (Alerstam 2003).

The overall migration duration of birds is largely dependent on fuelling rates (Lindström 2003), while tailwind support can significantly facilitate faster travelling during the movement phase

Geolocator tagged Arctic term *Sterna paradisaea* at a breeding site in Svalbard, Norway.

Photo: *Martins Briedis*

(Green 2004). Daylength regime (day:night ratio) has also been suggested to have considerable effect on the total migration duration of diurnally foraging species because of limited daylight hours available for fuelling (Bauchinger & Klaassen 2005). As the season progresses and migrants move across latitudes, they experience changes in the daylength regime, which can slow down or speed up their migration depending on the time of the year, latitude and species' activity cycle (nocturnal vs. diurnal migrants and nocturnal vs. diurnal foragers). For most species, migration should be shorter (and faster) when daylength is longer and there is more time for fuelling (Kvist & Lindström 2000, Bauchinger & Klaassen 2005).

All these aspects should be especially important for trans-equatorial migrants that cover long distances between their breeding and non-breeding areas. On the extreme range of the migration distance spectrum is the Arctic tern *Sterna paradisaea* that annually migrates over 50 000 km between the breeding areas in the Arctic and the non-breeding areas in Antarctica (Storr 1958, Egevang et al. 2010). Despite a recent surge in tracking studies on Arctic terns (Egevang et al. 2010, Fijn et al. 2013, McKnight et al. 2013, Volkov et al. 2017, Alerstam et al. 2019), significant gaps remain in our understanding about the ecology of this recordbreaking migration. To travel such vast distances across all climatic zones, exploitation of environmental settings for efficient travel may be crucial, as the seemingly favourable shortest route may not be optimal. By arching migration corridors according to the tailwind support and further fine-tuning the routes to pass through areas of high ocean productivity, migrants can sustain the energy-demanding flight phase by stopping over and refuelling at sites where food resources are abundant. Furthermore, while residing at the breeding and non-breeding sites, Arctic terns are exposed to 24 h daylight, enabling flexible interchange between foraging and resting time. In contrast, during migration terns are exposed to shifts between day and night as they pass through intermediate latitudes. Because Arctic terns are strictly diurnal foragers (McKnight et al. 2013), feeding and refuelling during migration are limited to the available daylight hours. This may force terns to feed during the day and travel at night if rapid and short-duration migration is advantageous.

In this study, we used geolocator tracking to, first, describe migration patterns and non-breeding areas of the Arctic terns breeding in the high Arctic (Svalbard, Norway) at the northern limits of the species' distribution range (BirdLife International 2018). Second, we tested how individual migration routes and stopover sites are adapted to take advantage of wind support and food availability en route. We hypothesized that the longest animal migration on Earth is facilitated by wind assistance during the flight phase and abundance of food resources during the refuelling stopover phase, which is further eased by extended daylength hours throughout the journey. Hence, we predicted that (1) the chosen migration routes of the tracked Arctic terns will be adapted so that the birds benefit from tailwind support during both southbound and northbound migrations; (2) the stopover sites of the terns will be located in areas of higher ocean productivity compared to passage areas (McKnight et al. 2013); (3) the terns will time their migration to cross the Equator near the equinoxes, enabling longer foraging hours in both hemispheres (Alerstam 2003).

Materials and methods

Field work

Our study site was located in Longyearbyen on the island of Spitsbergen, Svalbard archipelago (78° 14’ N, 15° 39’ E). We captured 30 breeding individuals during late stages of egg incubation between 8 and 14 July 2017, using tent spring traps placed on their nests. All captured birds were marked with unique colour ring combinations and equipped with multi-sensor archival data loggers (geolocators; model Intigeo-W65A9-SEA, Migrate Technology) that were fixed to the colour rings. Geolocators were set to sample ambient light intensity every minute and store maximal values at 5 min intervals. Temperature was sampled every 5 min, storing maximal and minimal values at 4 h intervals; immersion and conductivity measures were sampled every 30 s, storing the sum of samples scored as wet and maximal conductivity every 4 h.

The geolocators including colour rings weighed 1.06 ± 0.05 g (SD), which never exceeded 1.2% of the body mass of the tagged birds (106.2 ± 7.6 g, n = 30). Sex of all tagged individuals was determined molecularly using a droplet of blood taken from the brachial vein (Griffiths et al. 1998, Fridolfsson & Ellegren 1999, Ležalová-Piálková 2011), as the accuracy of sexing Arctic terns in the field is typically lower than 74% (Fletcher & Hamer 2003, Devlin et al. 2004).

In the following season between 27 June and 12 July 2018, we managed to recapture 16 birds with geolocators (53%) at the same breeding colony. At least 7 more of the previously tagged birds were sighted in the breeding colony (total return rate = 77%), but we failed to recapture them. This was mainly due to high predation rate of the nests in this season by Arctic fox *Vulpes lagopus* leading to frequent relocation or disappearance of the individuals whose nests were depredated.

Body mass of the tagged individuals was higher upon recapture and removal of the geolocators compared to the time of deployment a year earlier (2017: 104.6 ± 8 g [n = 16], mean capture date = 10 July; 2018: 110.9 ± 7.6 g, mean capture date = 4 July; paired t-test: $t_{14} = -2.691$, p = 0.018; data met the assumption of normality and homogeneity of variances based on a Shapiro-Wilk normality test and an F-test, respectively). Thus, geolocators apparently did not have a negative effect on the body condition of the tagged individuals (Brlík et al. 2020).

Data analyses

Geolocator tracking

All data analyses were done in R version 3.5.1 (R Core Team 2018). To calculate the geographic positions of the terns, we first log-transformed light intensity recordings from the retrieved geolocators to derive sunrise and sunset times (twilight events) using the 'preprocessLight' function in the R-package 'TwGeos'. Further, we used the R-package 'FLightR' to estimate geographic locations of the tracked individuals (Rakhimberdiev et al. 2017). During both breeding and non-breeding periods, tracked Arctic terns were exposed to 24 h daylight, thus making it problematic to use these stationary periods for calibrating the light data. Sunsets and sunrises were recorded only during migration periods and during an approximately 2 mo long period before the spring migration when the birds were at an unknown location at the non-breeding sites. Within the latter period, we identified extended periods when birds were stationary before the spring migration by visually inspecting recorded sunrise and sunset times. We then used the 'find. stationary. location' function to estimate the geographic location of this unknown site and used it for calibration.

Further, we followed standard analysis procedures in 'FLightR' as outlined by Lisovski et al. (2020). 'FLightR' uses a template fit method to compute a spatial likelihood surface for each twilight event. A posterior distribution of the likeliest migration path and its credible intervals are then derived via particle filtering. Because the conductivity (salinity) recording on all of our geolocators indicated that whenever geolocators were immersed, birds were in saltwater, we set 0 probability for birds occurring in areas that were further than 50 km away from the shoreline. For 1 track (BH004, see Fig. S1e in the Supplement at www. int-res. com/ articles/ suppl/ m638 p001 supp. pdf), the imposed spatial mask led to a failure of the particle filter; therefore, the analyses for this geolocator were run without a spatial mask. Finally, we used the 'stationary.migration.summary' function to determine stationary periods that were longer than 6 twilight events (3 d) and arrival/departure dates from them. For this, we defined 20% as the minimum probability of movement.

Using high-frequency data, McKnight et al. (2013) showed that Arctic terns typically do not rest on water, as only a small fraction of time (0.5 ± 0.22 h d−1 at most in August) is spent floating. Thus, immersion recordings should approximately reflect the daily rate of feeding dives. Based on this, we used the cumulative daily count of the number of times the geolocator was immersed in water as a proxy for estimating the feeding rate across the annual cycle.

We used ANOVA to test if there were differences in migration parameters (migration timing, speed, distance, feeding rate, etc.) between males and females. We used Bartlett's test of homogeneity of variances and a Shapiro-Wilk normality test to test homogeneity of variance and assumption of normality, respectively. In 3 migration parameters (onset of spring migration, migration distance in autumn and migration speed in autumn), homogeneity of variances and assumption of normality were not met, and in 1 migration parameter (total migration distance), only the assumption of normality was not met. Thus, we filtered outlying values from these 4 migration parameters. After excluding outlying values, total migration distance and migration speed in autumn met both assumptions. For onset of spring migration and migration distance in autumn, we used the nonparametric Wilcoxon rank sum test. Since no differences were found in any of the tested migration parameters, we pooled data of both sexes for all further analyses. Travel speed (km d−1) is defined here as the total distance travelled divided by the total number of days spent on migration in each migration season.

Ocean productivity

We used ocean productivity data to compare if stopover sites of terns were located in areas with potentially higher food resource abundance as compared to passage areas (migration corridors). We defined polygons for stationary sites in a radius of 2° around the median location of the stationary sites earlier established by the ‘stationary.migration.summary’ function. Migration corridors were defined as lines connecting twice-daily positions within the migration periods with 1° wide buffer around them and excluding stationary sites. We downloaded gridded (0.167° grid) weekly ocean productivity data from the Ocean Productivity website of the Oregon State University (www.science.oregonstate.edu/ocean.productivity/; Behrenfeld & Falkow ski 1997) and extracted productivity values for all grid cells within the defined stationary areas and migration corridors corresponding to the specific weeks. Grid cells that did not contain productivity data were omitted from the analyses. Because ocean productivity data were positively skewed, we transformed the values using the natural logarithm.

Wind support

To evaluate the role of wind assistance in facilitating the migration, we obtained wind data from the European Centre for Midrange Weather Forecast (ECMWF; https://www.ecmwf.int/). Wind data were averaged across the full migration period of the tracked terns (autumn 2017: 24 Aug-27 Nov, spring 2018: 31 Mar-6 Jun) for each 4×4° grid across the area between 85° N−85° S and 80° W−35° E. Because Arctic terns typically migrate at low altitudes near the water surface (Gudmundsson et al. 1992, Hedenström & Åkesson 2016) we used wind measurements at the surface level. We then used the ‘NCEP.Airspeed’ function from the R-package ‘RNCEP’ (Kemp et al. 2012) to calculate wind support for each movement segment (twice-daily positions and movement direction between them) along the migration routes of the tracked individuals.

Daylength

We used the light recording data from the geolocators to estimate the total amount of daylight hours experienced by individual terns throughout the annual cycle. Further, we calculated daylight duration at various latitudes across the year using the Rpackage ‘suncalc’ (Thieurmel & Elmarhraoui 2019). Daylight duration was calculated as the time between civil dawn and civil dusk when the geometric centre of the Sun is 6° below the horizon, which approximately matches light recording sensitivity of the geolocators’ light sensor.

Results

Migration and non-breeding areas

Terns departed their breeding site in Svalbard in late August–early September (Box 1) and migrated to a stopover area in the north Atlantic. Further, 9 individuals followed the west coast of Africa with later stopovers in the southeast Atlantic, while 7 individuals followed the east coast of South America with stopover sites in the southwest Atlantic (Fig. 1a). Interestingly, 2 individuals (BH011 and BH024, both females) made a loop at the beginning of the southbound migration and returned to Svalbard in early October before continuing their southward movement into tropical latitudes (Fig. S1i,p). Migration parameters are summarized in Box 1.

At the end of the southbound migration, all tracked individuals crossed the Antarctic Circle, entering the 24 h daylight zone; thus, location data from late November until early to mid-February are not available. Between February and April, non-breeding sites of all but 1 bird were located in the Weddell Sea (Box 1, Fig. 2). The outlier individual travelled to the Indian Ocean, residing at ca. 100° E longitude. Another individual crossed the Drake Passage between Antarctica and South America in late March, thus entering the Pacific Ocean before commencing the northbound migration. Overall, the terns were highly mobile during the non-breeding period covering several thousand km and residing at multiple sites during their 4–5 mo long non-breeding period in Antarctica (Box 1). Throughout the non-breeding period, all birds were exposed daily to sub-zero temperatures (Figs. S1 & S2).

Box 1. Summary data (mean and range) of key migration and non-breeding period parameters of 16 geolocator tracked Arctic terns from a breeding colony in Longyearbyen, Svalbard

Autumn migration	
Start date	3 Sep (24 Aug–11 Sep)
Crossing Equator	4 Oct (23 Sep–22 Oct)
End date	19 Nov (5–27 Nov)
Total migration duration (d)	78 (68–93)
Migration distance (km)	22900 (19500–34800)
Travel speed (km d^{-1})	294 (258–420)
Non-breeding period	
Wintering latitude	South of 63° S
Wintering longitude	55° W–94° E
No. days at non-breeding site	137 (127–153)
Movement distance (km)	10812 (5279–19480)
Spring migration	
Start date	5 Apr (31 Mar–16 Apr)
Crossing Equator	26 Apr (17 Apr–11 May)
End date	30 May (23 May–6 Jun)
Total migration duration (d)	54 (39–64)
Migration distance (km)	24800 (19600–29700)
Travel speed (km d^{-1})	435 (334–518)
Total track length (km)	58500 (50200–78500)
Total daylight hours	6985 (6750–7232)

Terns started the northbound migration in early April (Box 1), following an S-shaped migration pattern through the Atlantic (Fig. 1b). Longer stopover periods were scarce until the end of the migration period, when the birds arrived in the northern Atlantic residing at the same stopover region as at the beginning of the southbound migration. During this stopover period, the terns increased their feeding rate more than 2-fold (as implied by the number of times the birds were recorded being in water) as compared to the rest of the annual cycle (Fig. 3). Travel speed for all individuals was higher during the northbound migration compared to the southbound migration (paired *t*-test: $t_{15} = -9.56$, $p < 0.001$; Box 1), and birds arrived back at the breeding colony in late May–early June, having completed an average round trip migration distance of 58 500 km (range: 50 200–78 500 km; Box 1).

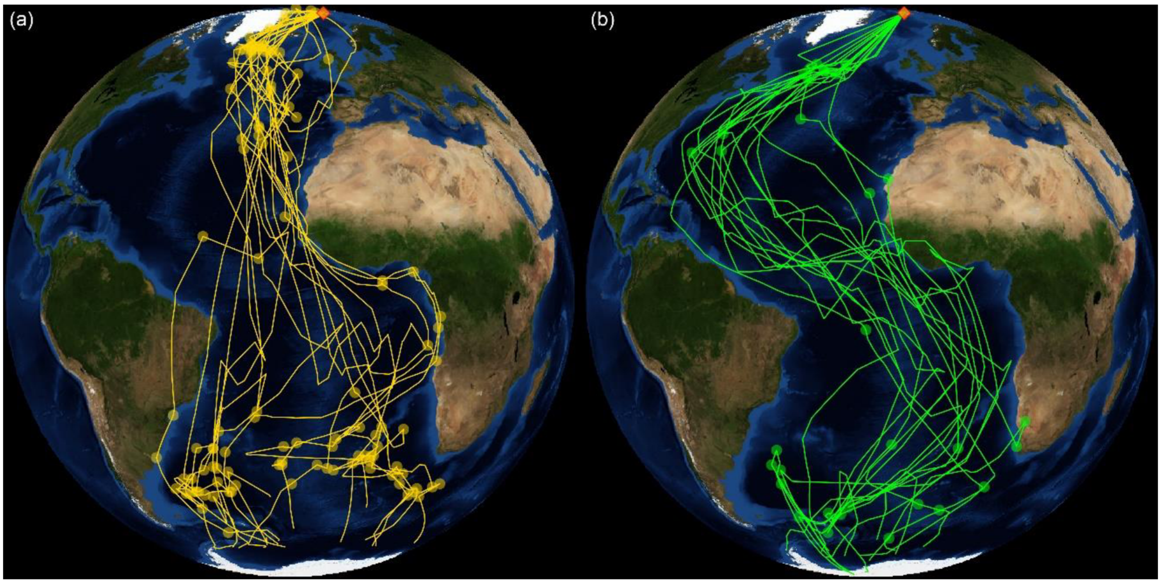

Fig. 1. Migration routes and stopover areas of 16 geolocator-tracked Arctic terns during (a) southbound and (b) northbound migration. Breeding site in Longyearbyen, Svalbard, is marked with an orange diamond, stopover sites longer than 3 d are marked with dots. Background map source: Blue Marble Next Generation, https:// visibleearth. nasa. gov/ collection/ 1484/ blue-marble

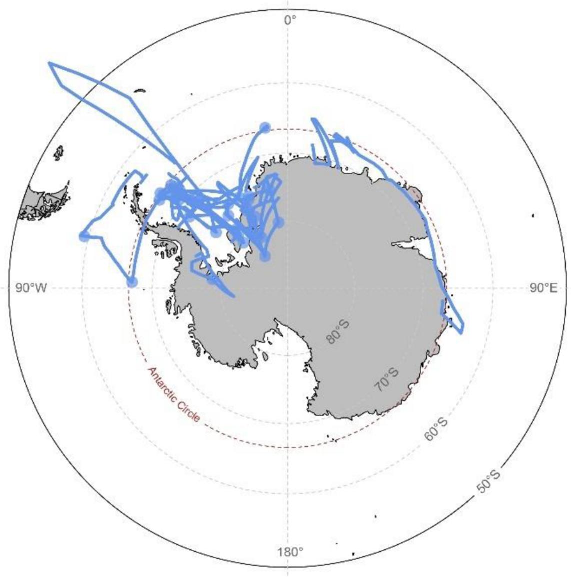

Fig. 2. Non-breeding areas (February–April) of 16 geolocator-tracked Arctic terns. Stationary sites where birds remained for at least 7 d are marked with dots; lines show movements within the non-breeding areas. Location data from late November (after the southbound migration) until early-mid February are not available due to 24 h daylight as all birds resided south of the Antarctic Circle

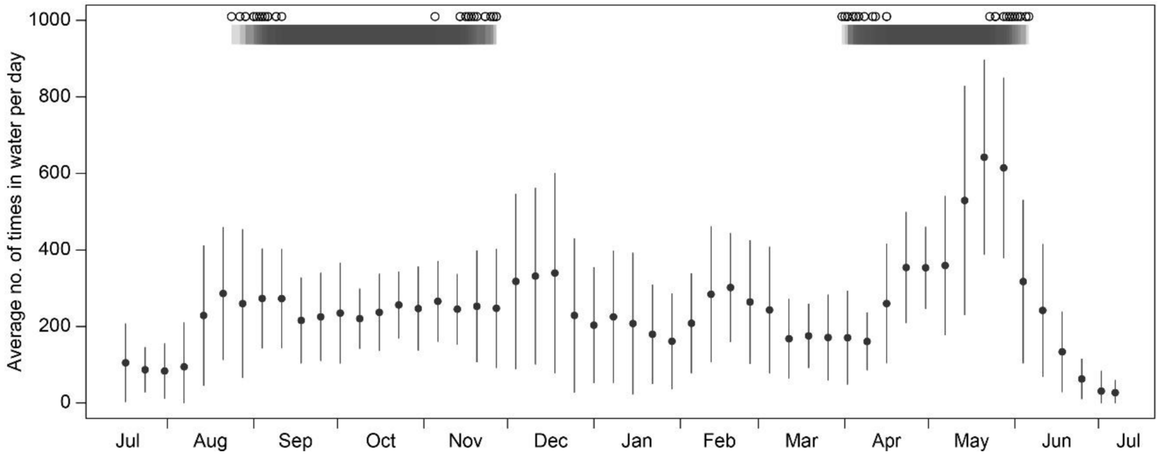

Fig. 3. Weekly average (± SD) number of times per day when geolocators were submerged in water during the annual cycle. Migration periods are marked with grey bars on top (higher colour intensity corresponds to overlapping migration periods of more individuals) and individual timings of start and end of migration are indicated by open circles

Migration routes and wind support

In both seasons, terns on average benefited from tailwind support along their chosen migration routes (Figs 4 & 5). During the southbound migration, terns on average experienced 0.4 ± 0.6 m s^{-1} (SD) tailwind support, while during the northbound migration the experienced tailwind support was substantially stronger, averaging 2.2 ± 1.2 m s^{-1} (paired *t*-test: $t_{15} = -5.34$, $p < 0.001$; Fig. 5). Testing for the wind support on reversed migration routes (travelling along the spring routes in autumn and autumn routes in spring) revealed that terns would experience significantly more headwinds in both migration seasons (southbound migration: −2.1 ± 0.8 m s^{-1}, paired *t*-test: $t_{15} = 8.36$, $p < 0.001$; northbound migration: −0.2 ± 0.7 m s^{-1}, paired *t*-test: $t_{15} = 6.81$, $p < 0.001$; Fig. 5).

After excluding the 2 outlying individuals that made a loop at the beginning of the autumn migration and had exceptionally high travel speeds, there was no relationship between wind support and individual southbound travel speed ($\beta = -0.72 \pm 7.38$, $F_{1,12} < 0.01$, $r^2 = 0.01$, $p = 0.924$), while there was a positive relationship between the experienced wind support and individual northbound travel speeds ($\beta = 28.89 \pm 9.33$, $F_{1,14} = 9.6$, $r^2 = 0.41$, $p = 0.008$).

Stopover areas and ocean productivity

While on migration, terns spent on average 32 ± 7.9 d (SD) on stopover sites during the southbound migration and 10 ± 7 d during the northbound migration. Stopover sites of the tracked terns were located in areas where ocean productivity was higher (mean ± SD; 6.28 ± 0.43 ln[mg C m^{-2} d^{-1}]) as compared to migration corridors (6.03 ± 0.39 ln[mg C m^{-2} d^{-1}]; paired *t*-test: $t_{18} = 3.87$, $p = 0.001$; Fig. 6). Weekly locations of stopover areas and migration corridors with the underlying ocean productivity maps can be found in Fig. S3.

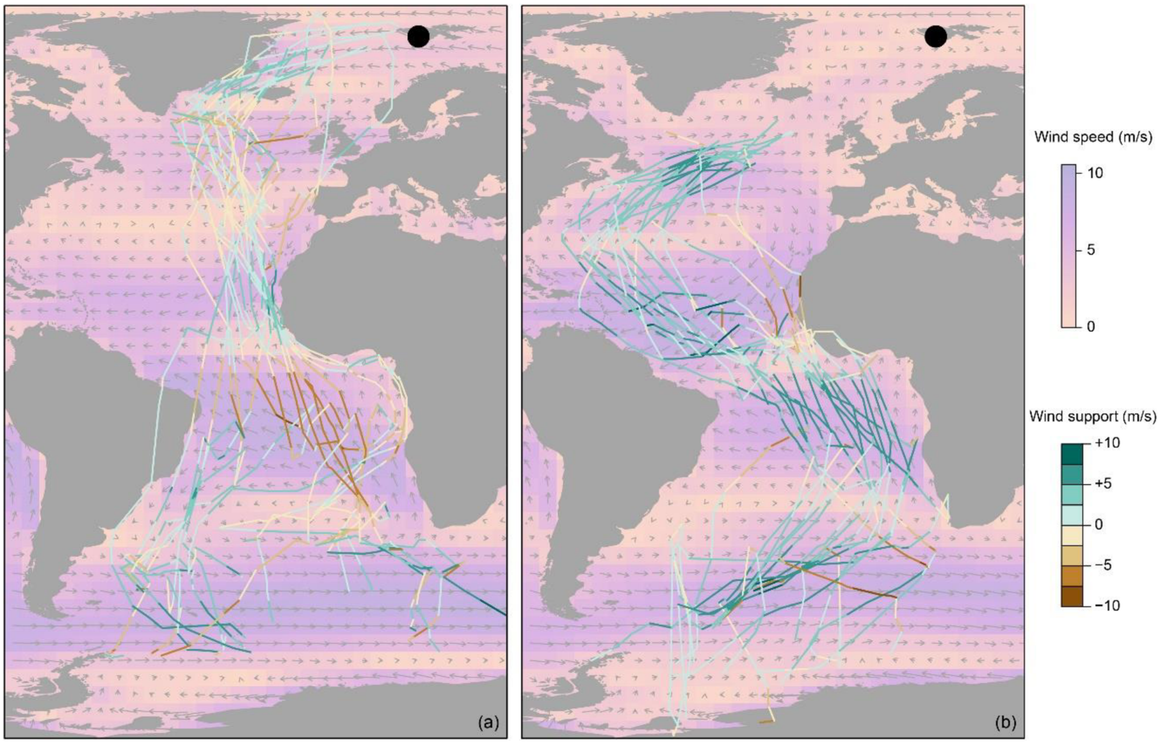

Fig. 4. Wind support along the migration routes of 16 geolocator-tracked Arctic terns during (a) southbound and (b) northbound migration. Lines show the most likely migration paths coloured according to the wind support in each segment (brown: headwind, turquoise: tailwind). Directions of arrows indicate gridded wind directions and background heatmap shows wind speed; both are averaged across the migration period of the tracked Arctic terns. Breeding site in Longyearbyen, Svalbard, is marked with a black dot

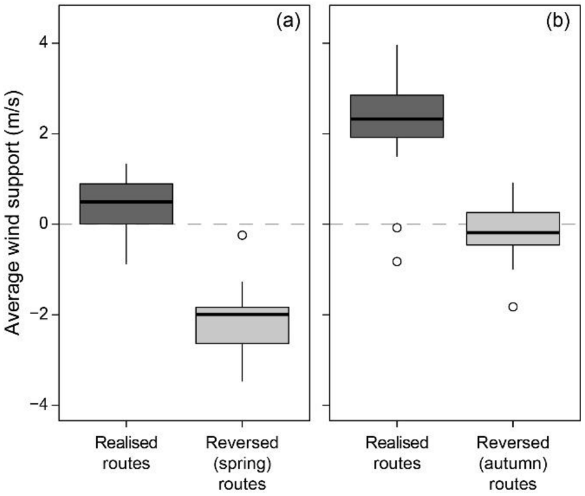

Fig. 5. Average wind support across the entire migration route for 16 geolocator-tracked Arctic terns during (a) southbound and (b) northbound migration. Wind support along the realised migration routes is shown in dark grey and reversed routes (spring routes in autumn and vice versa) are shown in light grey. Box plots show median values with interquartile ranges (IQR; boxes), whiskers extend to 1.5× the IQR, outliers are given as open circles

Migration timing and daylight hours

In both seasons and particularly in spring, terns on average crossed the Equator significantly later than the equinoxes (autumn average: +12 ± 8 d (SD), *t*-test: $t_{15} = 6.402$, $p < 0.001$, spring average: +38 ± 6 d; *t*-test: $t_{15} = 23.334$, $p < 0.001$; Fig. 7). Despite the low synchronisation between crossing the Equator and equinoxes, birds still on average experienced 6985 ± 123 h (SD) of daylight during the annual cycle, which corresponds to 79.7% of all available daylight on Earth per year (365 days × 24 h = 8760 h).

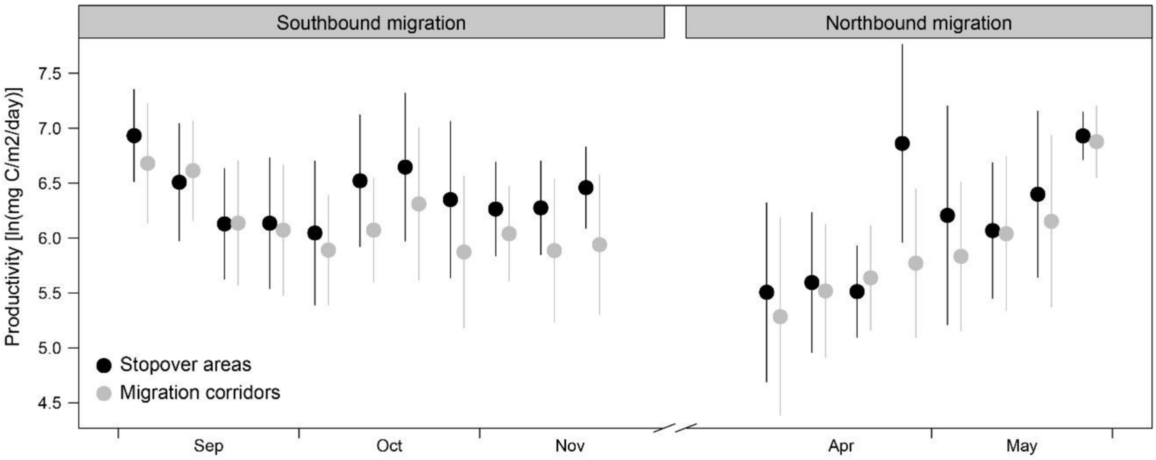

Fig. 6. Weekly ocean productivity at stopover areas (black circles) and migration corridors (grey circles) of Arctic terns during the southbound and northbound migration. Data are mean ± SD

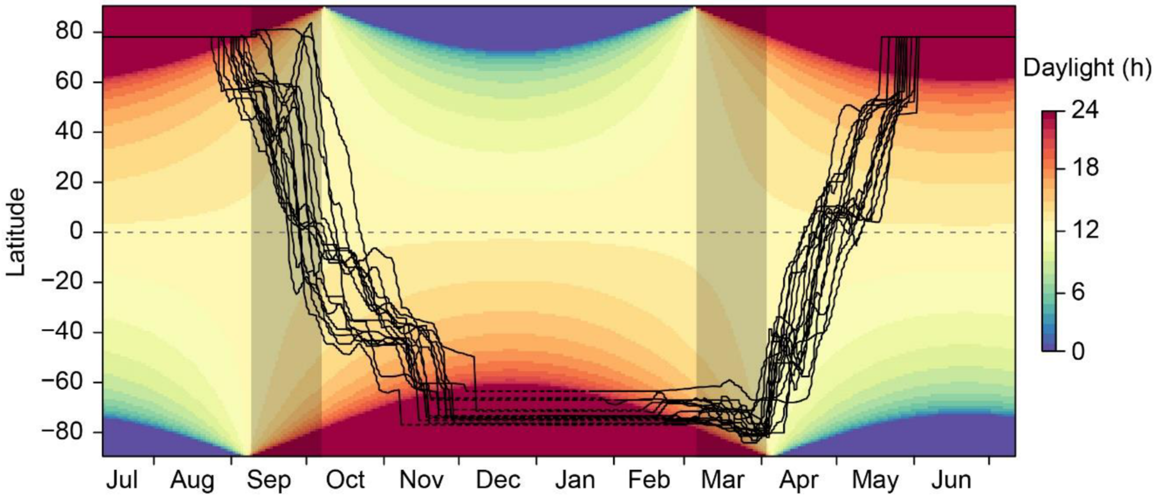

Fig. 7. Latitude and experienced daylight duration as a function of time across the annual cycle indicating the underlying phenological patterns of 16 individually tracked Artic terns. The dashed parts of the black lines indicate the nonbreeding period when birds were exposed to 24 h polar day making latitude estimates impracticable. Grey dashed line marks the Equator and shaded areas indicate periods 2 wk on either side of the equinoxes. Daylight duration was calculated as the time between civil dawn and civil dusk when the geometric centre of the sun is 6° below the horizon

Discussion

In this study, we show that Arctic terns breeding at 78° N in Svalbard migrate to non-breeding sites south of 63° S in the Weddell Sea covering up to 80 000 km on their round-trip journeys. This impressive migration is facilitated by tailwind support along the chosen migration routes in spring, and food-rich stopover areas for refuelling. Despite the low synchronisation between Equator crossing and equinoxes, which would allow for maximizing the experienced daylight (and thus, the amount of time when birds can forage), the tracked terns still experienced ca. 80% of all available daylight hours on the Earth per year, which is the most by any animal in the world. These findings suggest that the amount of time when the birds can feed is not the limiting factor during migration, but terns rather shift between seasonally specific exploitation of tailwind support (in spring) and ocean areas of high food abundance (particularly in autumn) to facilitate their remarkable migration.

Migration, non-breeding areas and population comparison

In our study, we did not find differences in migration patterns between males and females, corresponding to earlier studies on trans-Equatorial migratory seabirds (Shaffer et al. 2006, Guilford et al. 2009, Magnusdottir et al. 2012, Mosbech et al. 2012). Arctic terns from Svalbard migrated to their non-breeding areas in Antarctica via 2 distinct routes following either the west coast of Africa or the east coast of South America; both of these routes are known from earlier studies (González-Solís et al. 2007, Guilford et al. 2009, Egevang et al. 2010, Fijn et al. 2013, Volkov et al. 2017, Alerstam et al. 2019). Similarly, the Weddell Sea, where most of our tracked terns over-wintered, has previously been established as a prime non-breeding area for Arctic terns breeding across various longitudes in the northern hemisphere (Egevang et al. 2010, Fijn et al. 2013, McKnight et al. 2013, Volkov et al. 2017).

Terns from our study site on average departed from Svalbard on 3 September, which is from 1 to 2 mo later than previously shown in studies from more southerly breeding areas (Table S1; Egevang et al. 2010, Fijn et al. 2013, Loring et al. 2017, Volkov et al. 2017, Alerstam et al. 2019, Redfern & Bevan 2020a). The late departure date of our tracked individuals corresponds with later departure of other species from northern latitudes (Butler et al. 1998, Gilg et al. 2013, Davis et al. 2016). As a general pattern, migratory birds breeding at higher latitudes depart from their breeding areas later than their southern conspecifics, owing to the later onset of the breeding season at high latitudes (Conklin et al. 2010, Briedis et al. 2016). Similarly, our tracked terns arrived at the breeding sites later than their conspecifics breeding at more southern latitudes (Egevang et al. 2010, Fijn et al. 2013, Loring et al. 2017, Volkov et al. 2017, Alerstam et al. 2019, Redfern & Bevan 2020a). Such population-level differences in migration timing can lead to significant variation in migration strategies, as different populations face different environmental conditions en route (González-Solís et al. 2009, Sittler et al. 2011, Hanssen et al. 2016). In the case of Arctic terns, Alerstam et al. (2019) suggested that population-specific migration strategies are driven by intraspecific competition and different costs of migration. Subsequently, between-population differences in migration timing lead to population-specific wintering sites. Comparative assessment across populations corresponds with this hypothesis, as terns from Svalbard arrive in Antarctica relatively late compared to other populations and over-winter almost exclusively in the Weddell Sea. Breeding populations from lower latitudes arrive in Antarctica relatively earlier and often over-winter further east in the Indian Ocean (e.g. Alerstam et al. 2019, Redfern & Bevan 2020b).

We found that terns increased their feeding rate before arrival at the breeding site in spring (Fig. 3). At least 2 potential explanations for this may be brought forward: (1) behavioural changes regarding increased floating on water. However, using high-frequency data, McKnight et al. (2013) showed that Arctic terns spend only a small fraction of time floating on water, deeming this an unlikely explanation. (2) Birds increased their feeding frequency before arrival at the breeding site. Earlier studies confirmed Arctic terns as income breeders (species that primarily use local resources for egg production; Drent & Daan 1980, Hobson et al. 2000, Mallory et al. 2017); thus, this increase in feeding rate should not be attributed to resource deposition for future egg production. Moreover, we found that both sexes increased their feeding rate, further ruling out this behaviour as part of the capital breeding strategy. Another explanation for the observed changes in feeding rate may be attributed to changing conditions in food availability. When food is abundant, birds may require less time for feeding (e.g. at the breeding sites), while when food is scarce it may require more effort and time to feed. However, ocean productivity data indicate high food availability at the place and time when the birds showed increased feeding rate, implying that food availability may not be the main driver behind the observed pattern. A more likely explanation may be preparation against the forthcoming reduction in feeding time due to courtship behaviour and incubation. This explanation is also supported by the reduced number of times when the birds were in water after their arrival at the breeding sites, suggesting that birds could at least partially be using previously stored reserves for body maintenance during egg incubation. Moreover, body mass of the tagged individuals captured during incubation showed a decline of 0.75 g d^{-1} over the capturing period, further supporting this premise.

Migration patterns and the environment

Our findings suggest that the terns benefit from using a looped migration strategy where southbound and northbound migration routes do not overlap. By adapting the migration routes to the prevailing wind patterns across the Atlantic Ocean, Arctic terns take advantage of tailwind support en route. During the autumn migration, wind support along the 2 main autumn migration flyways – southeastern and southwestern Atlantic – is essentially different. The overall net wind support during the autumn migration was negligible, and individuals migrating through the southeastern Atlantic generally experienced more headwinds. Following this flyway may have a trade-off between relying on wind support and fuelling at food-rich stopovers, as ocean productivity in the southeastern Atlantic during this time of year is higher compared to the southwestern Atlantic (i.e. the coasts of Brazil; Fig. S3a–k).

Wind support was particularly pronounced during the northbound migration when strong tailwinds likely contributed to the exceptionally fast travel speed of terns: a 1.5-fold increase compared to travel speed during the southbound migration (Fig. 4, Box 1; sensu Kemp et al. 2010). Similar increases in seasonal travel speed have also been found in other seabirds (Felicísimo et al. 2008, González-Solís et al. 2009). In contrast, Hensz (2015) did not find wind to be a significant predictor for travel speed during either southbound or northbound migration of Arctic terns. Wind exploitation might also be used in combination with a fly-and-forage strategy (Strandberg & Alerstam 2007) to further increase travel speed. A fly-and-forage migration strategy is advantageous when an individual carries enough energy reserves from the non-breeding grounds and does not need to frequently refuel at stopovers (Strandberg & Alerstam 2007).

Stopover use, however, seems to play a more important role in route choice during the southbound migration. Tracked birds navigated between stopover sites of high ocean productivity with migration corridors passing over areas of lower productivity (Fig. 6 & Fig. S3). Such patterns in Arctic terns were first documented by McKnight et al. (2013) as birds from Alaska migrated along the west coast of the Americas. Similar patterns were described in a study where terns were tracked from Greenland and Iceland (Hensz 2015). During both migration periods, one of the main stopover areas of our tracked birds corresponded with the well-known refuelling area for migrating seabirds in the North Atlantic (Catry et al. 2011, Sittler et al. 2011, Gilg et al. 2013), also known as the North Atlantic drift province (Longhurst 2010). According to Bourne & Casement (1996), Arctic terns are present in the area from late April until late October, with a distinct peak in August. This time window corresponds with breeding site departure dates of terns from lower (Egevang et al. 2010, Fijn et al. 2013, Loring et al. 2017, Volkov et al. 2017) and higher latitudes (our study; Box 1).

Because terns are exclusively diurnal foragers (McKnight et al. 2013), we predicted that they will time their migration to cross the Equator close to the autumnal and vernal equinoxes, thus experiencing the longest foraging hours (Alerstam 2003). However, during both migration seasons, terns crossed the Equator significantly later than the equinoxes, suggesting that available daylength is not a limiting factor during migration. The large variation we observed in Equator crossing dates of the tracked terns suggests that crossing time is rather flexible. Furthermore, on southbound migration, Arctic terns from a breeding site in Sweden crossed the Equator almost 2 mo earlier than terns in our study (Alerstam et al. 2019; Table S1). Such population differences indicate that the timing of crossing the Equator on a population level is mainly influenced by the timing of departure from breeding sites rather than by environmental conditions.

Collectively, our findings suggest that the slower southbound migration is food-rich stopovers, whereas the faster spring migration is adapted to take advantage of the prevailing wind patterns to facilitate a shorter migration duration. Disentangling the influence of environmental drivers behind seasonal migration strategies of Arctic terns brings us a step closer to understanding the ecology of the world's longest animal migration. Our results provide a means to better understand the delicate relationship between seasonal migration strategies of birds and variation in environmental conditions, which may be disrupted by the ongoing global climate change.

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Summary

Thesis conclusions and future perspectives

Tereza Hromádková

In order to achieve our aim in **Chapter 1**, we used continuous video surveillance of incubating Arctic and Antarctic terns (Svalbard archipelago and the Antarctic peninsula respectively) and evaluated whether the incubation behaviour was affected and at which direction by higher level of human (the Arctic tern) or predator disturbance (the Antarctic tern). The conclusion of the study showed that the behavioural response of Arctic terns in Svalbard shared a similar direction and did not exceed the reaction of Antarctic terns induced by native predators on the Antarctic peninsula.

Results from this study add important details to the understanding of the possible impact of human presence on incubation behaviour. From an environmental protection point of view, such results imply that the increasing number of people coming to polar regions (including Svalbard) might be sustainable for Arctic terns (with proper regulations protecting breeding colonies).

The latency (the return time to the nest) in **Chapter 2** was different in two populations of Arctic terns from Svalbard. The population breeding within human settlement returned significantly faster to incubation after induced human disturbances than the population with scarce human experience. Such results supported the idea from **Chapter 1** that Arctic terns are able to adjust their breeding behaviour and potentially adapt to human disturbances.

However, both mentioned studies measured only immediate behaviour reaction to disturbance, more replicated studies are needed to evaluate whether there are any long-term costs (e.g. lower breeding success, higher mortality of eggs/hatchling, higher level of stress hormones) associated with human activities in close proximity of terns' nests/colonies.

Contrary to our predictions that Arctic terns will show equal antipredator behaviour regardless of nesting location (**Chapter 3**), results showed a significant difference in the response of breeding terns on Svalbard compared to those in northern Norway. The Svalbard terns remained to incubate in the presence of predators that do not occur there (raven, falcon). In the meantime, the Norway terns performed cautious behaviour when a raven or falcon were presented. These results are quite surprising and support neither the *multipredator* nor the *archetype hypothesis* but rather point to the *relaxed selection hypothesis*. Svalbard terns had lost their ability to recognize the falcon and the raven as predators. In the context of unfavourable environmental conditions (e.g. cold temperatures) these results are very likely. Reaction to non-threatening stimuli can lead to a potential loss of eggs due to cooling.

The understanding of predator-prey interactions is gaining in importance in respect to ongoing global changes. To be able to protect locations and/or species from potentially destructive new/old interactions a deeper understanding of the life strategy of birds is needed. In regard to that, further studies of more Arctic terns' populations would be necessary, also with respect to their highly social life.

We deployed 30 geolocators to breeding Arctic terns on Svalbard (**Chapter 4**). The following year, we managed to recapture 16 of them and we followed their all-year migration. The results confirmed the optimal migration theory in that the terns used the winds in their favours (significantly more during the northbound flight) and utilized areas with high ocean productivity to refuel (significantly more on the southbound migration). They also showed specific patterns of migration based on the season (longer autumn migration, faster spring migration).

Such results indicate a strong bond between environmental factors and migration patterns and show a great need for further studies of the interaction between migrants and the changing environment.

Arctic terns prove to be a good model species not only to study migration behaviour but also other aspects of bird life. Thanks to their remarkable migration abilities they offer a unique opportunity to study the dissemination of diseases, parasites, bacteria, or antibiotic resistance through their migration journey. Their circumpolar distribution offers an opportunity to study the behavioural reactions to new/old threats that can (re)emerge as a result of global climate change, and human pressure to the last pristine environments, along with the risks of invasive species at a huge variety of locations and under different circumstances. The Arctic tern definitely deserves our attention.

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