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FSH 464 Final Paper

17 March 2019

Arctic tern (*Sterna paradisaea*) behavior and reproductive success as an indicator of a changing global climate

**Introduction**

Many animals depend on environmental cues to know when it is the best time for their species to undergo a migration annually (Møller et al. 2010). For some animals, this migration may be as small as a few hundred meters to go from one type of habitat to another, but this is not the case for the Arctic Tern (*Sterna paradisaea*). This bird species is notable for holding the title of the longest annual migration that takes place on Earth; these birds fly over 80,000 km a year to leave their breeding grounds in the Arctic circle to spend the austral summer in various regions across the Antarctic (Egevang et al. 2010). Unlike most other species on Earth, these birds are dependent on resources from nearly every latitude at some point during their lifetimes, and this makes their populations highly susceptible to being impacted by climate change (Egevang et al. 2010). As the Arctic continues to warm at an exponential rate, these birds are being studied increasingly often due to their potential to be an indicator of the health of our oceans globally (Egevang et al. 2010). It is crucial to investigate the recent changes in Arctic tern behavior that have been linked to a warming climate alongside recent trends in reproductive success in order to gain a better understanding of what the outlook is for this species in the future.

**Overview of Arctic tern migration**

Life in the Arctic can be energetically costly, but the strategy of traveling across the world in order to reap the benefits of productive spring waters also seems very demanding. Fortunately, Arctic terns have physiological adaptations that make this long flight possible (Barrett et al. 2016). Arctic terns are extremely light birds, weighing in at about 100 g (Barrett et al. 2016). Their wings are quite long and slender, which saves the birds from having to spend a lot of energy flapping at low speeds (Barrett et al. 2016). Instead, they are able to glide with the winds, while expending little energy. In fact, the wind is accountable for 60% of the variation in the ground speed of the terns (Barrett et al. 2016). The distance that these birds travel in a lifetime is equivalent to three journeys to the moon and back, so being highly adapted for long flights is an essential for these birds (Runge et al. 2015).

Although Arctic terns all make the journey from the Arctic circle to the Antarctic, there are many possible routes that the birds may take from point A to point B (Egevang et al. 2010). It has been observed that two birds from the same colony may take two drastically different routes to reach the same wintering grounds (Egevang et al. 2010). For instance, birds from colonies in Greenland and Iceland were tracked flying either along the western coast of Africa or the eastern coast of South America in order to reach a similar region of the Weddell Sea in Antarctica (Egevang et al. 2010). During this long-distance migration, wind is important not only for minimizing energy expenditure as described above, but also for influencing tern arrival time at breeding or wintering grounds (Egevang et al. 2010). The winds can also be used to account for differences in tern arrival to their breeding or wintering grounds; if headwinds are strong, the arrival of the birds will be delayed (Barrett et al. 2016). Conversely, tailwinds will advance the arrival of the birds (Barrett et al. 2016). Climate change is increasing the strength of southwesterly winds, and this is predicted to cause Arctic terns to arrive earlier than usual in the Northern Hemisphere before breeding (Barrett et al. 2016).

In 2013, a study conducted by Fijn et al. investigated if Arctic terns from different northern populations became mixed once they reached the Antarctic or if they remained separate (Fijn et al. 2013). The movements of terns from colonies in Greenland, Iceland, and the United States were traced with geolocators that were attached to seven birds who were captured in 2011 and recaptured in 2012 (Fijn et al. 2013). It was discovered that birds from the three different regions all spent the majority of the non-breeding period intermixed in the same region of Wilkes Land, Antarctica (Fijn et al. 2013). The terns tended to stay in regions where there are large glaciers that have high rates of flow into the sea, such as east of Prydz Bay in the Amery Basin (Fijn et al. 2013). All of the birds from this study migrated to Wilkes Land, Antarctica, however, it is known that Arctic terns have circumpolar distributions in the Arctic during the breeding season and in the Antarctic during the non-breeding season; although the birds from the colonies who were monitored migrated to Wilkes Land, birds from other northern populations will migrate to other regions of Antarctica during the non-breeding season (Fijn et al. 2013).

**Taking advantage of global nutrients**

Even though many different routes are taken from the Arctic to the Antarctic, there is usually one thing in common; the migratory stopover regions that the terns rely on tend to be regions of major coastal upwelling (McKnight et al. 2013). When there is upwelling, this means that water from deep in the ocean is forced to the surface, and this water tends to be high in nutrients that promote the growth of plankton and other organisms at the base of the food chain which, in turn, allows for increasingly larger organisms to thrive (McKnight et al. 2013). Egevang et al. (2010) conducted a study in order to examine the preferred stopover locations of the terns from two breeding populations in Greenland and Iceland during their migrations to find out what oceanographic qualities were preferred and necessary for their journey. A similar study was conducted by McKnight et al. (2013), except the terns in this study were from colonies in Alaska. Both of these studies noted that the birds needed to utilize areas of high biological productivity during these extremely long migrations (Egevang et al. 2010; McKnight et al. 2013). The Alaskan terns utilized stopover regions within the California current, the North and South Humboldt currents, and the Patagonian shelf, all of which are high in upwelling (Egevang et al. 2010; McKnight et al. 2013). It is critical to protect regions that the birds use during every stage of their migrations because the birds stop in locations where they have historically had success foraging (McKnight et al. 2013). Arctic terns are highly specialized to feed on certain kinds of prey that are abundant in the poles; if Arctic terns cannot access stopover locations where they have historically been able to find suitable prey, they my face starvation due to their specialized foraging tactics (McKnight et al. 2013).

A significant disturbance to one stopover location could make migrations between the poles impossible for Arctic terns if they are not able to forage enough to maintain energy for their long flight (McKnight et al. 2013). Unfortunately, there are many significant threats to the stopover sites that the birds depend on (Runge et al. 2015). Many of the areas that the terns travel through are located adjacent to the coastlines of various countries, and some countries have more protective regulations about what can be done to the environment than others (Runge et al. 2015). A study conducted by Runge et al. (2015) examined the migration routes of 1451 species of migratory birds and found that only 9% of the species were traveling through migration routes that were adequately protected during every stage of their journeys. Consequently, over half of these 1451 species have experienced a significant population decline in the past 30 years (Runge et al. 2015). Common threats to the habitats that these migratory birds rely on during their journeys are habitat loss, hunting, degradation due to pollutants, and changing conditions due to climate change that are making foraging more difficult (Runge et al. 2015).

The Arctic tern is highly specialized to collect the prey species that are highly abundant near their northern breeding colonies, and small seabird species are more vulnerable to starvation than large seabirds because they must consume food more often due to their small body size (Monaghan et al. 1989). Therefore, changes to the abundance of prey species that the Arctic terns typically prey upon near the colonies could be detrimental to Arctic tern survival due to their specialized feeding strategy (Monaghan et al. 1989). Arctic terns feed by plunge-diving or by surface-dipping to collect small fish or large zooplankton (Egevang et al. 2010). This drastic migration between the hemispheres allows for these birds to take advantage of the productivity of the polar waters during the spring, and Arctic terns are known to rely on Antarctic krill blooms once they complete their southbound migration (Egevang et al. 2010). It is essential for the terns to receive adequate nutrients during their migration not only to have enough energy for flight, but also to ensure that they have enough energy to raise their chicks (Scopel et al. 2018).

Birds such as Arctic terns who feed on the ocean’s surface are particularly susceptible to reproductive decline if the environment experiences changes that alter the oceanographic conditions of the region (Scopel et al. 2018). Arctic terns feed on invertebrates or small vertebrates who live near the surface of the water, and if the changing climate alters the winds there may be less upwelling, leading to less primary productivity and potential bottom-up changes to the ecosystem (McKnight et al. 2013). Arctic terns have historically been the first seabirds to experience a decline in breeding success in North America when there is a change that negatively impacts their feeding conditions (Scopel et al. 2018). In a study conducted by Scopel et al. (2018), a metapopulation of Arctic terns in the Gulf of Maine were monitored in order to examine how the quality of prey influenced the breeding success of the colony. During the breeding season, it is essential for both parents to receive adequate nutrients from the environment or the breeding attempt may be abandoned after the chick has hatched (Scopel et al. 2018). Early in the breeding season is the most important time for the terns to have a high supply of nutrients because this is when the chick is growing the fastest (Scopel et al. 2018). For the colony observed in this study, the highest quality prey available was Atlantic herring, but the parents would feed on lower-quality invertebrates for prey if herring was not available (Scopel et al. 2018). When fed a diet of entirely invertebrate prey, Arctic tern chicks will not experience a net loss of mass but Common tern (*Sterna hirundo*) will (Scopel et al. 2018). This difference highlights how the Arctic terns are better adapted to utilize nutrients in the harsh arctic environments than the less specialized Common tern, although there is still a significant risk of chick abandonment if there are not enough nutrients available to support both the chick and the parents (Scopel et al. 2018).

**Patterns of reproductive success & timing**

Arctic terns rely on the ocean for food throughout their migration, so their reproductive success each year can serve as an important bioindicator of the health of the global environment (Scopel et al. 2018). Reproductive success reveals if the parents were able to obtain enough energy from their environment in order to maintain their own health as well as raise a chick (Suddaby et al. 1997). If food becomes too scarce, the parents will have to expend a high amount of energy in order to forage and they may not have enough energy to either feed a chick or produce viable eggs (Suddaby et al. 1997). Arctic tern eggs consist of 16% of the body mass of an average adult tern, and laying an egg is a significant energetic cost to the mother (Suddaby et al. 1997). In a study conducted by Suddaby et al. (1997) in Shetland, the relationship between food supply and reproductive success was analyzed. In this region, the terns feed primarily on sandeels and there are few alternative prey species, but sandeels are also preyed upon by various species of gulls, whose populations have been increasing in this region (Suddaby et al. 1997). The increased prevalence of gulls in the Arctic terns’ feeding ground has made is necessary for the terns to spend more energy on foraging for sandeels than they needed to previously (Suddaby et al. 1997). If this extra energy that is being spent on foraging does not result in the gain of sufficient nutrients to raise young, there is predicted to be a population decline in the Arctic terns due to increased nonbreeding, chick abandonment, emigration, and mortality of adults due to starvation (Suddaby et al. 1997). During the course of this study, the Arctic tern colonies being studied in Shetland had six consecutive years of nearly complete breeding failure (Suddaby et al. 1997). This failure occurred because many chicks were abandoned and starved after they hatched; when food supply does not remain constant during the breeding season, the females may initially have enough nutrients to lay eggs but then must reduce the size of the brood if there is not enough food available to feed every chick (Suddaby et al. 1997). Additionally, gulls also preyed upon the tern eggs which led to a further reduction of tern reproductive success (Suddaby et al. 1997). It is unknown how Artic tern populations will respond in the long term due to the new foraging challenges and increased gull predation, but the current trends have been suggesting significant population declines (Suddaby et al. 1997).

In order to analyze how the reproductive period and stressors of Arctic terns is changing, it is critical to understand the normal parameters of Arctic tern reproduction. Typically, Arctic terns will breed for the first time when they are 2 to 4 years old, and the terns arrive to the breeding grounds somewhere in the Northern hemisphere between March and May, and egg laying occurs in either April or July (Møller et al. 2006B). The terns will nest in locations with high ground, which will help protect the eggs because it will be more difficult for many predators to invade the colony (Egevang et al. 2010). Arctic terns, along with most species of seabirds, have high site fidelity to their natal breeding colonies (Devlin et al. 2008). Devlin et al. (2018) observed breeding colony fidelity in Arctic terns in the Gulf of Maine, and this study found that the average rate of breeding colony fidelity for Arctic terns was between 0.993 and 0.968, depending on the specific colony. Therefore, it is essential for the sites that these terns rely on each year to be protected from changes due to climate, increased predation, and human activity (Devlin et al. 2008). If small areas where high numbers of terns return each year are protected, this could make a significant impact on improving trends of reproductive success for the species (Devlin et al. 2008).

Each year, Arctic terns depend on environmental cues to know when it is the proper time to breed (Egevang et al. 2010)). A study conducted by Møller et al. (2010) over a 38-year period found that the changes in the breeding season of Arctic terns is directly correlated with the average temperature during spring. As the spring reaches a warmer temperature at an earlier point each year, this makes it possible for the terns to reproduce earlier and, hence, increases the duration of the breeding season (Møller et al. 2010). In this study, over 20 species of seabirds from Denmark were included in the data analysis (Møller et al. 2010). As the climate became warmer, the duration of the breeding season increased by 0.43 days per year for multi-brooded species and decreased by 0.44 days per year for species with only one brood (Møller et al. 2010). Arctic terns are multi-brooded species, so it is hypothesized that the duration of their breeding season will continue to increase as temperatures become warmer (Møller et al. 2010). Another novel finding of this study is that the date when the breeding season ends appears to remain constant throughout the study, but the day that breeding started became progressively earlier (Møller et al. 2010). This advancement in the start of the breeding season will cause increased stress on the parents because there may be less of the desired prey during the new time interval when breeding is now occurring, which could lead to a reduction in brood size post-hatching (Suddaby et al. 1997).

Additionally, changes in climate specific to the North Atlantic Ocean are also altering the start of the breeding season (Møller et al. 2006A). A study conducted by Møller et al. on Arctic tern colonies in Denmark revealed that the day that marked the halfway point of the breeding season has advanced 18 days over the 70 years of data analyzed for this study (Møller et al. 2006A). This change in breeding season onset could be explained by the increased average temperature of the region in April and May, which also leads to an increase in the North Atlantic Oscillation (NAO) index (Møller et al. 2006A). The NAO index is a measure of the difference of the atmospheric pressure at sea level in the North Atlantic Ocean, and a high NAO index indicates a high atmospheric pressure in the region (Møller et al. 2006A). Another study conducted by Møller et al. (2006B) during the same year also concluded that Arctic tern breeding dispersal is also affected by the NAO. An increase in dispersal distance can increase the rate that genes are spread between metapopulations of Arctic terns (Møller et al. 2006B). As the distance between where the bird was born to where it will breed increases, terns may interact with birds who have a different genetic composition than the terns within the dispersing tern’s original colony, leading to higher genetic diversity of the offspring (Møller et al. 2006B). Currently, it is unknown if the observed trends in breeding dispersal will allow for terns to become more or less adapted to changes in climate caused by the NAO (Møller et al. 2006B).

**Changes in prey abundance & potential consequences**

Changes in climate are not only causing changes in the behavior and abundance of Arctic terns, but also the species that they prey upon for food, which in turn has an effect on reproductive success (Williams et al. 1990). When chicks first hatch, they are extremely sensitive to variations in the rate at which they are receiving food; if there is low food availability for a portion of the brooding period, this will significantly impact chick growth, development, and survival (Williams et al. 1990). In a study conducted by Williams et al. (1990), the effects of climate change on the prey availability of Gentoo penguins (*Pygoscelis papua*) was monitored as the parents returned from sea to feed their chicks. The contents of the adult birds’ stomachs were examined as a way to estimate food availability for the offspring (Williams et al. 1990). It was concluded that in years of poor food availability, the average weight of surviving chicks increased because the lightest chicks would not be able to survive; thus, in more productive years with a higher abundance of prey species the mean fledge weight decreased because the heavy and light chicks were able to survive equally well (Williams et al. 1990). Although this research was conducted on Gentoo penguins and not Arctic terns, the authors stated that they believe that the trends observed could also apply to other species of seabirds who have prolonged chick-rearing periods as well (Williams et al. 1990).

The reproductive success of Arctic terns has been linked to the abundance of key prey species, so it is crucial to understand potential changes in species that the Arctic terns rely on in order to understand why changes in Arctic tern populations are occurring (Williams et al. 1990). During the nonbreeding season when the Arctic terns are in the Southern Hemisphere, they feed primarily on Antarctic krill (*Euphasia superba*) (Ross et al. 2000). This species is not only an important food source for Arctic terns, but also for many other Antarctic marine vertebrates such as crabeater seals (*Lobodon carcinophagus*), humpback whales (*Megaptera novaeangliae*), and many species of penguins (Williams et al. 1990). A study conducted by Ross et al. (2000) found that the growth rates of Antarctic krill in the austral spring and summer was related to both food quantity and quality. Measurements of chlorophyll a concentration were taken in order to represent food quantity, and food quality was represented by the biomass and composition of phytoplankton communities (Ross et al. 2000). If chlorophyll a concentration does not reach a certain threshold, this means that there are not sufficient nutrients available for maximum growth of Antarctic krill (Ross et al. 2000). Before this study was conducted, it was unknown if levels of Antarctic krill productivity were more strongly affected by diet or temperature; now, there is evidence that points to the food quality of the Antarctic krill having a stronger effect on their productivity than temperature (Ross et al. 2000). As the spring becomes warmer increasingly earlier each year and the ice recedes earlier, the juvenile Antarctic krill will shift from their habitat under the ice to the open-water and will need to graze in order to survive (Ross et al. 2000). If there is less time in the year where the Antarctic krill have ice cover, they will have to graze for a longer period of time and will deplete their food supply faster, which could lead to a decline in Antarctic krill population, followed by a decline in Antarctic vertebrate species who are reliant on Antarctic krill for food such as the Arctic tern (Ross et al. 2000).

Additionally, sandeels are an important resource that Arctic marine vertebrates must complete for when they are in in the Northern hemisphere during the breeding season, so their population abundance is connected to Arctic tern reproductive success as well (Monaghan et al. 1989). Two populations of Arctic terns were monitored in Shetland and Coquet island in the 1980s by Monaghan et al. (1989), and some important differences between these colonies were observed for the first time. The foraging performance, adult body condition, and reproductive success of Arctic terns was significantly higher on Coquet island than in Shetland (Monaghan et al. 1989). In Shetland, there was a higher prevalence of kleptoparasites, such as gulls, who would steal sandeels from the terns, which led to high rates of foraging with small amounts of energy gained in return (Monaghan et al. 1989). There were no differences observed in the mean clutch or egg size in each colony, but the majority of the chicks in Shetland grew slowly and died during their first week of life, which was not the case on Coquet island (Monaghan et al. 1989). This difference is believed to be occurring because in Shetland, the Arctic terns had difficulty finding sandeels that were between 4-8 cm long, which is the ideal size for feeding to Arctic tern chicks (Monaghan et al. 1989). Sandeels larger than this were difficult for the small Arctic terns to catch or deliver to their young (Furness et al. 2000). A study by Furness et a. (2000) conducted an analysis on seabird vulnerability to a decline in breeding success of 25 species in the Arctic and subarctic who relied on sandeels as a food source. Unsurprisingly, the Arctic tern was deemed the most vulnerable to changes in breeding success due to the terns’ small size, high cost of foraging per unit time, short foraging range, lack of spare time in daily budget, and low ability to switch diet (Furness et al. 2000). The findings of this study were significant because sandeels are the most heavily targeted species by fisheries in the North Sea, yet many Arctic terns are not able to catch enough sandeels that they need in order to raise their young (Furness et al. 2000; Monaghan et al. 1989). Perhaps there is a need for stronger legislation to protect highly susceptible species such as the Arctic terns from experiencing population decline that is accelerated by human activity (Furness et al. 2000).

**Response to these changes & potential future research**

 Arctic tern populations are experiencing declines on a global scale, and this is a significant matter because these birds are sensitive bioindicators revealing changes in our climate that are altering the way ecosystems are functioning (Diamond et a. 2003). The mean date of Arctic tern arrival to their breeding grounds has already been observed to begin increasingly earlier each year, leading to an extension of the breeding period (Barrett et al. 2016). This extension of breeding period could be followed with a mismatch between the breeding season and abundance of necessary prey to feed offspring, leading to increases in chick abandonment and a decline in reproductive success (Diamond et a. 2003; Møller et al. 2006A). As a small, highly-specialized seabird who is required to spend a relatively high amount of energy feeding often, Arctic terns are especially vulnerable to reductions in population size if their prey becomes less abundant due to a lack of alternative prey species (Furness et al. 2000).

 In order to protect the Arctic tern from further population decline, it is critical to decrease the energy that they spend on foraging during the breeding season in order to reduce rates of chick abandonment (Diamond et a. 2003; McKnight et al. 2013). Species such as the sandeel and Antarctic krill should be monitored due to their importance as a food source to many Arctic and Antarctic vertebrate species (Ross et al. 2000, Furness et al. 2000). Also, because of the high site fidelity that is displayed by the birds, it is important to have increased protection and monitoring of their breeding grounds to discourage predators from consuming chicks from the nest sites in order to increase the rates of reproductive success (Devlin et al. 2008). Additionally, it is crucial to protect the areas that the Arctic terns rely on during their annual migrations so that they can receive adequate nutrients at their stopover locations (Runge et al. 2015). If Arctic terns are facing significant threats during one part of their journey across the earth, this could impact their ability to reach their breeding or wintering grounds, so they will not be able to take advantage of the productivity blooms to feed their chicks (Runge et al. 2015). These birds travel across many international borders, so the protection of migratory bird’s pathways is a shared responsibility that must be coordinated between various countries who monitor different types of habitats over various seasons (Runge et al. 2015).

 The most important change that humans can make in order to save the Arctic terns is to pass stronger legislation that will fight climate change at a global scale (Runge et al. 2015). Additionally, action must be takes on a smaller scale to reduce habitat degradation and pollution across stopover sites that may be utilized by the Arctic terns during their migrations, and this may lead to rebounds in prey species who have experienced population declines in these areas (McKnight et al. 2013; Runge et al. 2015). These birds, along with numerous other Arctic species, are altering their migratory and reproductive behavior as the Arctic becomes warmer increasingly earlier each year; the long-term effect that this will have on populations is unknown, but downward trends have already been observed (Møller et al. 2006A; Scopel et al. 2018). The Arctic tern is a figurative “canary in a coal mine” revealing the effects of global climate change, and it is crucial for humans to listen to the message that these birds are telling us before it is too late.

 In the future, it would be interesting to conduct additional research on the migration patterns on the terns as geolocators become smaller and more affordable. Geolocator research on Arctic terns is relatively new due to the recent reduction in size and cost of the machinery. In the past, it would have been difficult to track the movements of such small birds due to the weight of geolocators (Egevang et al. 2010). Older designs would have been too heavy and would have had a significant negative impact on the aerodynamics of the terns (Egevang et al. 2010). This technology could be used to conduct studies with larger sample sizes on birds from more colonies in order to observe further differences in migration patterns. It appeared that significantly more research had been conducted on Atlantic Arctic terns rather than the Pacific populations, so additional data on Pacific Arctic tern reproductive success and migration patterns could be useful when making legislative decisions about climate change or habitat protection because it will reveal more areas that the birds rely on which should be protected and monitored (McKnight et al. 2013). Arctic terns could also be a valuable tool for oceanography research because they are dependent on the ocean throughout their lifespans, which is relatively long for a marine organism (McKnight et al. 2013). Trackers could be used not only to monitor the location of these birds but also salinity, currents, and nutrients in the water in their stopover sites (McKnight et al. 2013). Lastly, it is important to monitor trends in seabird reproductive success alongside data collected from fisheries that harvest common prey species of the Arctic terns to examine if there are any trends that may be leading to an acceleration in population decline (Monaghan et al. 1989; Furness et al. 2000).

Literature Cited

Barrett RT (2016) Upwind or downwind: the spring arrival of Arctic Terns *Sterna paradisaea* at Troms, north Norway. T&F S Syst Contr 31(1): 23-29

# Devlin CM, Diamond AW, Kress SW, Scott Hall C, Welch L (2008) Breeding dispersal and survival of Arctic terns (*Sterna Paradisaea*) nesting in the Gulf of Maine. The Auk 125 (4):850-858

Diamond AW, Devlin CM (2003) Seabirds as indicators of changes in marine ecosystems: ecological monitoring on Machias Seal island. Environ Monit Assess 88:153-175

Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. P Natl Acad Sci USA 107(5):2078-2081

Fijn RC, Hiemstra D, Phillips RA, van der Winden J (2013) Arctic Terns *Sterna paradisaea* from the Netherlands Migrate Record Distances Across Three Oceas to Wilkes Land, East Antarctica. Ardea 101(1): 3-12

Furness RW, Tasker ML (2000) Sea bird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. Mar Ecol Prog Ser 202: 253-264

McKnightA, Allyn AJ, Duffy DC, Irons DB (2013) ‘Stepping stone’ pattern in Pacific Arctic tern migration reveals the importance of upwelling areas. Mar Ecol Prog Ser 491: 253-264

Møller AP, Flensted-Jensen E, Mardal W (2006B) Dispersal and climate change: a case study of the Arctic tern *Sterna paradisaea*. Glob Change Biol 12: 2005-2013

Møller AP, Flensted-Jensen E, Klarborg K, Mardal W, Nielsen JT (2010) Climate change affects the duration of the reproductive season in birds. J Anim Ecol 79: 777-784

Møller AP, Flensted-Jensen E, Mardal W (2006A) Rapidly advancing laying date in a seabird and the changing advantage of early reproduction. J Anim Ecol 75: 657-665

Monaghan P, Uttley JD, Burns MD, Thaine C, Blackwood J (1989) The relationship between food supply, reproductive effort and breeding success in Arctic terns (*Sterna Paradisaea*) J Anim Ecol 58(1): 261-274

Runge CA, Watson JEM, Butchart SHM, Hanson JO, Possingham HP, Fulle RA (2015) Protected areas and global conservation of migratory birds. Science 350(6265): 1255-1258

# Ross RM, Quetin LB, Baker KS, Vernet M, Smith RC (2000) Growth limitation in young *Euphasia superba* under field conditions. Limnol Oceanogr 45(1): 31-43

Scopel LC, Diamond AW (2018) Predation and food-weather interactions drive colony collapse in a managed metapopulation of Arctic Terns (*Sterna paradisaea*). Can J Zool 96:13-22

Suddaby D, Ratcliffe N (1997) The Effects of Fluctuating Food Availability on Breeding Arctic Terns (*Sterna paradisaea*). The Auk 114 (3): 524-530

Williams TD, Croxall JP (1990) Is chick fledging weight a good index of food availability in seabird populations? Oikos 59(3): 414-416