

Direct and indirect climate change effects on shorebirds in the Arctic

An analysis of the potential population dynamics and life history changes



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Abstract

Global warming causes many changes in the Arctic and therefore alter living conditions of the Arctic fauna. Part of this fauna are the migratory shorebirds who breed in the Arctic. Currently these shorebirds suffer from severe population declines. To get more insight into the decline, this essay focuses on the direct and indirect effects of climate change on the population dynamics and life history characteristics of migratory shorebirds in the Arctic. From the analysis, negative effects on shorebird populations are expected in the long term by potential mismatches with arthropods lifecycles and the increased predation pressure, because predators, although they decline in number, switch to alternative prey such as shorebirds. Yet, direct climate effects of warmer and longer summer periods, the short term higher activity and the increased number of lifecycles of arthropods during summer and life history adaptations of shorebirds might compensate for negative effects or might positively affect shorebird population dynamics. However, climate change effects are more complex because life history adaptations of different climate effects might counteract each other. Moreover life history adaptations might have a feedback on the species interactions themselves. Finally population dynamics are also influenced by changing conditions on other parts of their migratory flyway, invasion from other species from the south and interference of humans. Thereby, shorebirds species differ in their reaction on climate change which is also related to location. Therefore this essay can be used as a guideline to find out which factors are influencing a single species and together with research on changes during their whole migratory flyway more insights into population dynamics and potential adaptive abilities of shorebirds can be obtained.

Pictures of the front page:

- Polar bear: *Ljeto polarnog medvjeda*. [Picture online] Available on: <http://maxtv.tportal.hr/tvpreporuke/58710/Ljeto-polarnog-medvjeda.html> > [Accessed at January 26th, 2016].
- Arctic fox: Yúfera, I. (2016). *Canada: Nunavut 2, picture 5*. [Picture online] Available on: <http://www.iyufera.com/index.php#mi=2&pt=1&pi=10000&s=4&p=15&a=0&at=0> > [Accessed at January 26th, 2016]
- Red knot: Vyn, G. (2015). *Red knot (Calidris canutus rogersi) brooding newly hatched chicks at the nest. Chukotka, Russia. June*. [Picture online] Available on: <http://gerritvyn.photoshelter.com/image/I00006rxWeL9i5jl> > [Accessed at January 26th, 2016]
- Long-tailed jaeger: Small, B.E. *Brian small North American bird photography: Long-tailed jaeger (Stercorarius longicaudus), Seward Peninsula, AK, June*. [Picture online] Available on: http://www.briansmallphoto.com/long-tailed_jaeger.html > [Accessed at January 26th, 2016]
- Arctic wasp: Hoyer, R.C. (2011). *Arctic wasp – Trichiosoma triangulum, Kougarok Road 72 miles N of Nome, Seward Peninsula County, Alaska, USA, June 6, 2011*. [Picture online] Available on: <http://bugguide.net/node/view/532177/bgimage> > [Accessed at January 26th, 2016]

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Introduction

Global warming has a severe impact on the fauna of the Arctic, where climate changes faster than anywhere in the world (IPCC, 2014). Rapidly rising temperatures have been recorded all across the Arctic (Tingley & Huybers, 2013) and result in a strong transformation of the tundra. One of the most important changes is said to be the coverage of the snow. In winter the snow coverage becomes more variable resulting in more or less snow fall during different years and on different locations (Gilg *et al.*, 2012; IPCC, 2014). The snow coverage also becomes more variable during the winter, because the freeze and thaw periods increase in number due to higher winter temperatures (Callaghan *et al.*, 2005). In most years the snow melts nowadays earlier in spring and it returns later in autumn with some variation between the years (Grabowski *et al.*, 2013). This means that the short Arctic summer period (Liebezeit *et al.*, 2014) is extending. Thereby the Arctic summer is expected to be ice free in the future, as a result of the decline in the quantity and thickness of the sea ice (Rothrock *et al.*, 1999; IPCC, 2014). Apart from the changes in snow and ice, the amount of days with extreme weather events such as heavy rain and more severe wind will increase (Rowntree, 1997; IPCC, 2014). Although the amount of precipitation increases, the soil becomes drier and the permafrost retreats (Rowntree, 1997; IPCC, 2014). All these changes make the Arctic a less extreme environment with a different dynamic. These changes are likely to affect the living circumstances of the fauna of the Arctic.

These faunal species include the 50 species of migratory shorebirds, which migrate from different locations across the globe to the Arctic to breed (figure 1) (Moltofte *et al.*, 2007a). Breeding on the Arctic is beneficial, because of a lower predation risk and beneficial arthropod food peaks during the summer (Tulp & Schekkerman, 2008). The surface dwelling arthropods are especially important for the precocial shorebird chicks who feed on them under supervision of their parents (Tulp & Schekkerman, 2008). However, global warming is changing the timing of the spring season unequally across the globe. Because of this unequal change, especially long distance migrants struggle to time their migration, since they rely mostly on endogenous cues instead of climatic cues (Butler, 2003). For this reason, many long distance migratory birds are already declining and some are prone to go extinct (Morrison *et al.*, 2006; Galbraith *et al.*, 2014). Threats for population declines are arising all over their migratory flyway from habitat degradation in wintering- and stopping over sites (Baker *et al.*, 2004), to storms during migration (Mckinnon *et al.*, 2012) and to the advanced spring season on the breeding area (Tulp & Schekkerman, 2008). Research suggests that the breeding ground plays an important role and therefore research in this area may reveal some challenges birds have to deal with (Galbraith *et al.*, 2014). Thereby knowing the exact population dynamics and threats will help to conserve these birds and give insight into food web dynamics all over the world, because these birds participate in many of them (Walther *et al.*, 2002).

Therefore this essay will focus on the population dynamics and life-history adaptations of migratory shorebirds in the Arctic. At first the focus is on the direct effects of climate change on these shorebirds, so the effect of the abiotic changes (Forchhammer *et al.*, 2008). However, to study population dynamics successfully, it is important to have a community approach instead of a species approach (Gilman *et al.*, 2010). For this reason the second part will focus on the abiotic effects of climate change on the life history and population dynamics of other organisms on the Arctic and how they indirectly affect the shorebirds. This is done for bottom-up control of surface dwelling arthropods and top-down control of arctic foxes, polar bears and long-tailed jaegers. Finally, some life history changes to different factors are considered together in order to look for interactions between direct and indirect effects. However, caution is needed when suggesting that shorebirds are able to change their life history characteristics. This because High Arctic migratory shorebirds are specialist and have a low genetic diversity due to genetic bottlenecks (Kraaijeveld & Nieboer, 2000; Piersma, 2003). So these shorebirds depend mostly on phenotypic plasticity which has a limited capacity of change (DeWitt *et al.*, 1998). All combined the research question is: "How do direct and indirect effects of climate change on the Arctic affect the population dynamics and life history characteristics of Arctic migratory shorebirds."

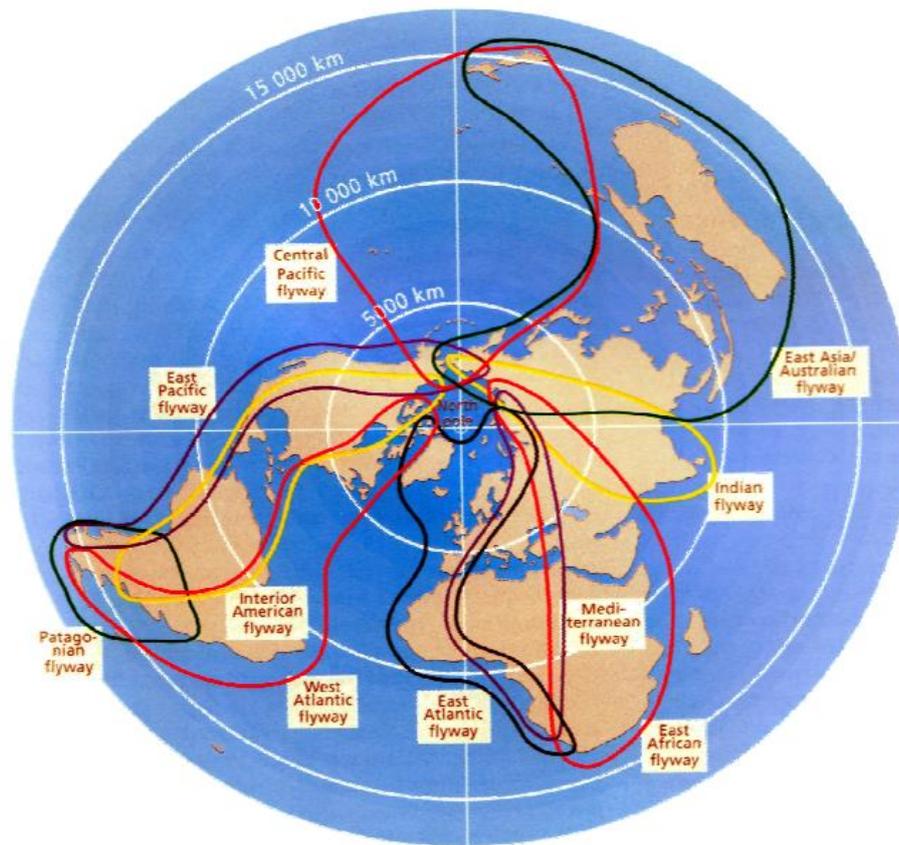


Figure 1: The migratory flyways to the Arctic (van der Kam et al., 2004)

Direct climate effects on shorebirds

Only during the summer period, shorebirds are present on the Arctic. Therefore this section includes only summer period direct climate effects of the Arctic.

At first, snowmelt date appears to be an important indicator of laying date for shorebirds (figure 2). Consequently birds might be able to lay their eggs earlier, due to the earlier snowmelt. This appears to be true in Alaska, where shorebirds start laying 4-7 days earlier over 9 years (Liebezeit et al., 2014). In addition, especially shorebirds depending on arthropods or breeding on the highest latitudes are advancing their laying date (Grabowski et al., 2013; Liebezeit et al., 2014).

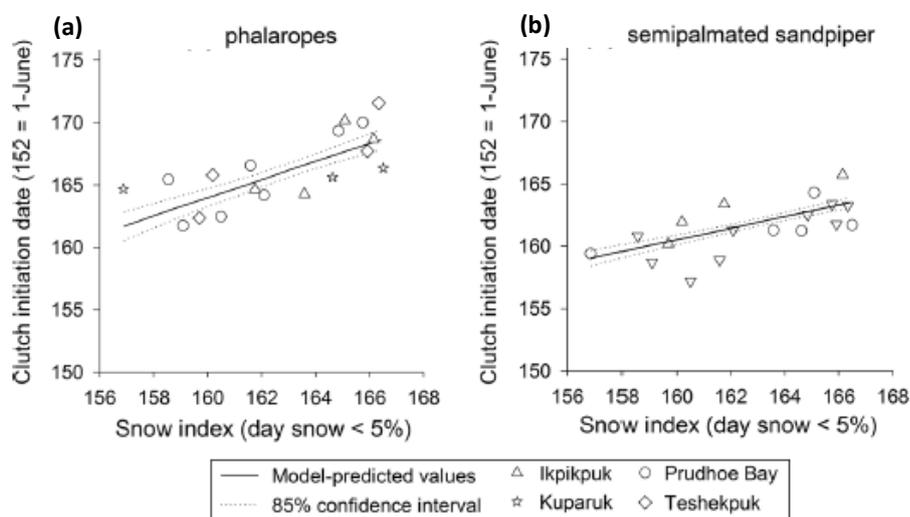


Figure 2: The snow index against the clutch initiation date on Alaska. The lines represent the model prediction and the symbols the nest sites on different locations (After: Liebezeit et al., 2014)

Because of the advanced lay date, birds benefit from a longer summer season. This might result in an increased amount of birds laying two nests during one season (Lindström & Agrell, 1999). At the moment, Arctic shorebirds rarely re-nest probably because some parents already leave before a second attempt can take place (Grabowski *et al.*, 2013). For this reason, it is most likely that shorebirds who already re-nest do that more frequently and that only a few other species start to re-nest as well. Furthermore, not every shorebird is able to breed earlier. For example, shorebirds differ in nest site selection, so some shorebirds can breed everywhere while others have to wait until a specific site is available (Liebezeit *et al.*, 2014). In addition, some birds cannot breed earlier due to migration timing on endogenous cues or nutritional needs before breeding (Butler, 2003; Martin & Wiebe, 2004). Thus some shorebirds may lay earlier, but how much earlier strongly depends on individual species.

Also when it comes to thermoregulation, shorebirds can benefit from higher summer temperatures. This because shorebirds probably spend annually most of their energy on thermoregulation in the Arctic, so these costs might decrease with higher temperatures (Lindström & Klaassen, 2003). In addition, the foraging time can be enhanced by favorable pre-breeding seasons with less snow, such as in Greenland where birds are probably able to spend more time foraging than in years with more snow (Melttofte & Lahrman, 2006). A second important factor limiting foraging time of the adults is the brooding of the chicks, which is longer with smaller chicks and colder temperatures (Krijgsveld *et al.*, 2003). Mckinnon *et al.* (2013) revealed a strong relation between temperature and chick growth after the age of 5 days (figure 3). Therefore from this point of view, one would expect that chicks grow better and need less parental care in the future. So in general adults and chicks have more time to forage and lose less energy on thermoregulation. This all results in a higher survival and reproductive success due to warmer summers (Lindström & Agrell, 1999), although one should keep in mind that extreme weather events, which increase due to climate change, can counteract the positive effect of higher temperatures (Ganter & Boyd, 2000).

At the moment many species, such as shorebirds, tend to decrease in size (Gardner *et al.*, 2011) and according to Bergmann's rule this is because of increasing temperatures. The rule states that a larger surface/volume ratio (being smaller) is more beneficial with higher temperatures. This because smaller organisms release heat more efficiently, while large ones limit heat loss due to genetic changes (Bergmann, 1847; Teplitsky & Millien, 2014). Nonetheless, another study proposes that shorebirds change their body size with phenotypic plasticity as a reaction on poor environmental conditions (Teplitsky *et al.*, 2008). Although the answer is unknown, shorebirds have a low genetic diversity. Therefore the second statement is probably better explaining the size decrease than Bergmann's rule.

Age: Greater than 5 days

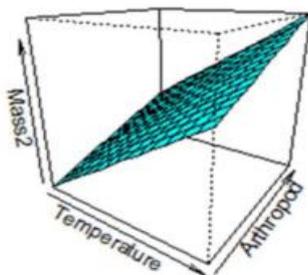


Figure 3: The relationship between arthropod abundance, temperature and dunlin chick mass after the age of 5 days (After: Mckinnon *et al.*, 2013).

Indirect climate effects on shorebirds

Arthropods and shorebirds

The previous chapter described the direct climate effects on shorebirds, but population dynamics are also influenced by other species (Gilman *et al.*, 2010). Therefore the following two chapters will focus on the changing interactions between species due to climate change. This chapter will focus on the bottom-up control on shorebirds, which mostly depends on surface dwelling arthropods in the Arctic. Arthropods are present in the Arctic throughout the year, where they reproduce and grow in summer and try to survive the cold winters (Tulp & Schekkerman, 2008). Winter survival depends on two different mechanisms. At first the survival strategy, whereby some arthropods perform freeze tolerance and others freeze avoidance (figure 4). Secondly the diapause, which is a genetically determined period of inactivity. This period increases the stress tolerance of arthropods and synchronizes them with the beneficial summer period (Denlinger, 2002).

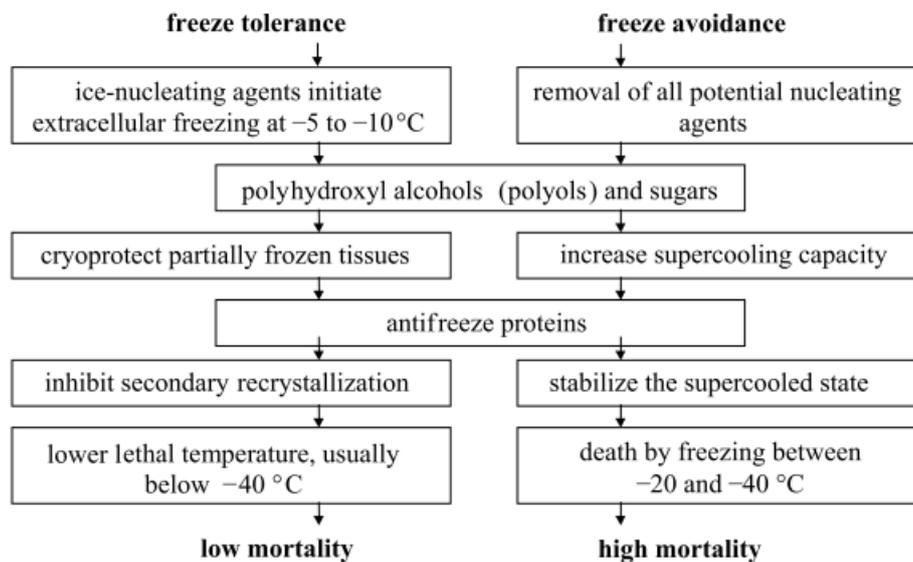


Figure 4: A schematic overview of the differences between the winter survival strategies (Bale, 2002).

Direct and indirect climate effects on arthropods

Higher winter temperatures make the temperature of the microhabitats less stable. Arthropods live in these habitats under the snow where temperatures are much higher and stable compared to the air. With a thinner snow layer, the microhabitats become unstable with a higher influence of freeze and thaw events (Bale & Hayward, 2010). Freeze tolerant arthropods are only efficient when they experience one freeze and thaw event a year. Thus the increased influence and frequency of the freeze and thaw events is lowering the survival of the freeze tolerant arthropods. These arthropods react by either switching to the freeze avoidance strategy, with a less severe temperature limit, or they die (Bale & Hayward, 2010). Additionally, the freeze and thaw events also lower the survival of the freeze avoiding arthropods by ice formation. When the melted snow is freezing again, the cuticle of the freeze avoiding arthropods can be penetrated, resulting in death (Duman, 2001; Bale & Hayward, 2010). Thus higher winter temperatures lower the efficiency of both winter survival strategies, probably resulting in a lower winter survival especially in areas and years with less snow.

In contrast, higher summer temperatures extend the beneficial summer period. Høye & Forchhammer (2008) state that arthropod activity is determined by snowmelt date, while Schekkerman *et al.* (2004) conclude that temperature is more important. Since both climatic factors advance the spring season, arthropods become active earlier. Because of this early activity some species, such as aphids, can have more complete lifecycles and eggs during one season (Strathdee *et al.*, 1993). However in Siberia, species only advanced their peak without changing the peak period

(Tulp & Schekkerman, 2008). Thereby, higher temperatures also have a positive effect on the activity and abundance of the arthropods. The development time is shorter and the arthropods have a higher survival (Lindström & Agrell 1999; Tulp & Schekkerman, 2008). However, extreme weather events decrease the activity and the survival of the arthropods (Tulp & Schekkerman, 2008). Yet arthropods are probably less affected by this, because they are able to shelter deeper into the soil due to receding permafrost (Gauthier & Berteaux, 2011). Therefore many arthropods are probably more abundant and earlier available during spring.

Temperature increases also influence the diapause in several ways. In general, the diapause period becomes shorter, probably because the higher metabolic rate exploits the nutrient stocks earlier (Hahn & Denlinger, 2007). As a result, arthropods become active earlier in spring where sudden cold periods may be fatal (Bale & Hayward, 2010). Additionally, arthropods may have less energy left for reproduction and survival in spring (Irwin & Lee Jr, 2000). Even more extreme is the complete abortion of the diapause which makes the arthropods vulnerable for cold stress (Bale & Hayward, 2010). Finally, some arthropods need a chill stimulus to become active in spring and lack of this stimulus can result in a lower fecundity and survival (Bale & Hayward, 2010). So diapause changes may be detrimental, but they are also needed, to stay synchronized with plants. Some species adapt like the pitcher plant mosquito (Bradshaw & Holzapfel, 2001), but many others have to deal with mismatches especially late or narrow peak arthropod species (Høye & Forchhammer, 2008).

Despite the mentioned climate effects, it is difficult to generalize the climate effects for the whole Arctic or all species. Arthropods prefer wet habitats, while too wet anoxic sites or too dry sites are probably avoided (Gauthier & Berteaux, 2011; Bolduc et al., 2013). Thereby, the High Arctic areas differ in climate and have a lower diversity of arthropods compared to the Low Arctic (Danks, 1999). Besides different habitats, arthropods differ in the timing and duration of their occurrence and in flexibility of their lifecycle (Danks, 1999; Høye & Forchhammer, 2008). All these extra factors make it difficult to forecast the population dynamics of the arthropods. At first, they probably become more abundant in summer, but in the long term it is uncertain (Gauthier & Berteaux, 2011). However, it is likely that arthropod cycles change, so birds need to adapt as well to prevent mismatches.

Indirect climate effects of arthropods on shorebirds

In the short term, arthropods may provide enough food for the shorebirds to be successful (Rehfishch & Crick, 2003). However, in the long term trophic mismatches between shorebirds and arthropods may occur. A mismatch happens when two species, which normally interact in synchrony, interact in asynchrony with each other. Arthropods are an important food source and shorebirds try to match the arthropod peaks with the hatching time of their chicks (Høye & Forchhammer, 2008).

Nevertheless evidence of mismatches have already been reported (figure 5). Yet one should keep in mind that the mismatch probability is not straightforward and depends on the location and arthropod species. High Arctic areas have short food peaks, while Low Arctic areas have broad ones.

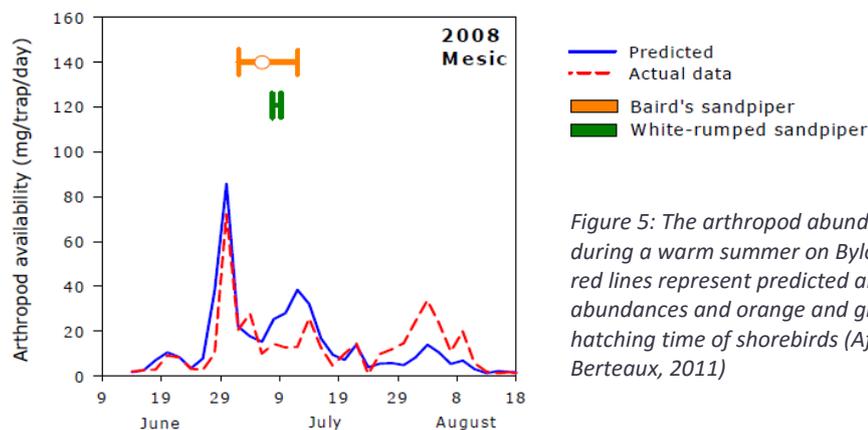


Figure 5: The arthropod abundance over time during a warm summer on Bylot Island. Blue and red lines represent predicted and real arthropod abundances and orange and green lines the hatching time of shorebirds (After: Gauthier & Berteaux, 2011)

Therefore shorebirds breeding on the High Arctic have a higher probability of a mismatch (Gauthier & Berteaux 2011). Variation in peak duration is even present between different patches. Additionally, insect species differ in their timing and duration of occurrence. Shorebirds are generalist feeders and eat at least 7 dominant arthropod species in Canada (Mckinnon *et al.*, 2012; Wirta *et al.*, 2015). Adults mostly depend on broad peak species during pre-breeding phase, while chicks depend on more narrow peak species (McKinnon *et al.*, 2012; Bolduc *et al.*, 2013). Therefore chicks are probably more sensitive for mismatches than adults.

Birds can breed earlier as a solution for the mismatch. Indeed some shorebirds breed earlier in spring, as in Canada (McKinnon *et al.*, 2012). Furthermore, shorebirds use arthropod abundance as a cue for laying in years with early snowmelt (Meltofte *et al.*, 2007b). This earlier arrival and laying is beneficial as seen in Europe where early arriving shorebird population remained stable or increased, while later arriving shorebird populations are declining (Møller *et al.*, 2008). However, as mentioned before, it is difficult for migratory birds to arrive and breed earlier, especially long distance migrants. Thereby it appears that birds are not able to keep up with the advancing arthropod peaks (McKinnon *et al.*, 2012). So in general, it is likely that many shorebirds are experiencing mismatch induced population and reproduction declines and also selection for early migrants (Both & Visser, 2001; Both *et al.*, 2006).

Problems for shorebird populations are already present at arrival. Shorebirds are income breeders, which means that they need food from their breeding ground to produce eggs (Klaassen *et al.*, 2001). So if the amplitude of the arthropod cycle is lower, shorebirds can invest less energy in their eggs. The shortage of nutrients can have a huge impact on the development and growth of animals and their future generations. The precocial shorebird chicks are especially affected by this because they have most of their development inside their egg (Metcalf & Monaghan, 2001). Yet parents can influence the state of the eggs by investing more or less energy in different eggs or by producing less offspring (Lindström, 1999; Metcalfe & Monaghan, 2001). Thus combined with the expectation that the mismatch chance is small during pre-breeding, only a small effect on chick development in the egg and number is expected.

After hatching, mismatches are influencing chick growth. This because chicks need enough food to secure rapid growth and survival (Schekkerman *et al.*, 2003). The large and slow Tipulidae seem to be specifically important for chicks and lack of synchrony with the Tipulidae peak results in less growth (figure 6). Due to the narrow peak of abundance, a mismatch is likely and a decline in growth can be expected. However, another study claims that not food peaks but periods with enough food are important for chicks. Although this seems to be less threatening, food periods also already advance in time (Tulp & Schekkerman, 2008). Thus chicks probably have a lower survival and become smaller fledglings in the future, which might explain the current size decline.

After hatching, females usually leave while males remain sensitive for mismatches. This because often males, depending on the parental care system, need to guide and protect the chicks. This period is already energetically stressful and with mismatches can become worse, because they are bound to the terrestrial food resources (Jönsson, 1987; Jönsson & Alerstam, 1990). Therefore it is likely that survival will be gender biased in the future.

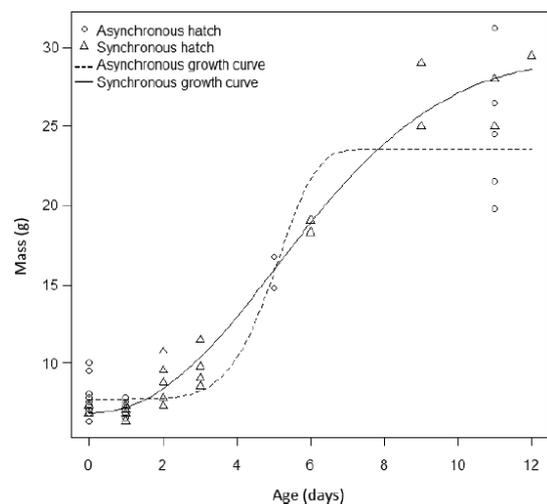


Figure 6: The chick age against the chick mass for chicks asynchronous and synchronous with the Tipulidae peak (McKinnon *et al.*, 2012)

Predators and shorebirds

Last chapter focuses on the bottom-up effects of arthropods and this chapter will be about top-down control on shorebirds by predators. Shorebirds have many potential predators and this essay focuses on three predators from different categories: the long-tailed jaeger as visual predator, the arctic fox as olfactory predator and the polar bear as potential predator. These three are chosen because they are all substantially influenced by climate change, they are generalist feeders and they are already considered to be important predators of birds and eggs on the Arctic (Gilg *et al.*, 2006; Gormezano & Rockwell, 2013; Liebezeit *et al.*, 2014).

Direct and indirect climate effects on the predators

Migratory long-tailed jaegers are only present in the Arctic during the summer and therefore they probably have the same problems as the shorebirds. Indeed mismatches might occur, because arthropod and lemming availability advance due to earlier snowmelt (Høye *et al.*, 2007). Long-tailed jaegers use the same breeding spot every year (Andersson, 1976) and earlier snowmelt will result in earlier availability of these nesting sites. However, it is not known if these birds can advance their migratory timing to prevent a mismatch to happen, if not they might experience lower survival and reproduction success. Thereby, their main prey, the lemming, will presumably react on the earlier snowmelt with longer population cycles with less high peaks in abundance (Gilg *et al.*, 2009). The decreased availability of lemmings is currently not affecting the population size of the long-tailed jaegers, likely due to the high adult survival (Gilg *et al.*, 2003). Nevertheless, in the long term their population will decline, because these jaegers reproduce less in years with a lower lemming density (Schmidt *et al.*, 2012). So long-tailed jaegers populations are stable for now but in the future problems of gaining food and lower reproduction success occur.

In contrast to the jaeger, the arctic fox is year-round affected by climate change in the Arctic. In winter, thinner snow layers improve their access to lemmings (Duchesne *et al.*, 2011). In the short term, this enhanced access presumably increases their winter survival, but in the long term lemming cycles are likely to disappear causing potentially lower adult survival in winter. Yet the amount of adults remains unchanged during summer due to access to alternative preys, whereas the summer reproduction success of the foxes is strongly related to lemming abundance and is therefore expected to decline (Gilg *et al.*, 2003; Forchhammer *et al.*, 2008). On the other hand, retreating permafrost allows arctic foxes to make larger dens which are more suitable for cubs, probably enhancing the reproductive success (Tannerfeldt *et al.*, 2003). Besides changes in reproductive success, the sea ice decline is expected to lower the migration possibilities for arctic foxes, which results in less genetic diversity due to isolation (Geffen *et al.*, 2007). Thus it is likely that arctic fox populations will remain stable although with less newborns and less adaptation abilities.

Polar bears are also year-round on the Arctic and suffer mostly from sea-ice decline. This because polar bears depend on the sea ice to catch their main prey: seals (Amstrup, 2003). Due to earlier sea ice melting, polar bears have less time to hunt the seals, since they rarely hunt in open water (Stirling & Derocher, 2012). Thus they are longer ashore, which can give severe consequences for their population (Derocher *et al.*, 2004). At first, polar bears suffer from nutrient deficiencies, resulting in smaller and thinner polar bears at every age (Rode *et al.*, 2010). Secondly polar bears have a lower reproductive success, because smaller cubs have a lower survival chance and females produce less cubs in years with less sea ice (Rode *et al.*, 2010). Additionally, cubs might have an increased risk of drowning due to the need to swim longer distances (Durner *et al.*, 2011). Thereby females struggle to find a suitable den, since pack ice denning sites disappear and land denning sites are less accessible now that the sea ice towards these sites is declining (Fischbach *et al.*, 2007). Potentially females go earlier to their denning site, but longer fasting time and an increased risk of collapsing dens by heavy rain also reduces the survival of cubs and females (Stirling & Derocher, 1993; Derocher *et al.*, 2004). So the number of polar bears will decline (Regehr *et al.*, 2010), but the amount of bears on the land will increase (Prop *et al.*, 2015).

In general, all predators mentioned are generalists and they deal with fewer main preys by looking for alternatives. All three predator species have a broad diet including birds and eggs (table 1). In years with less lemmings, arctic foxes and long-tailed jaegers eat more shorebird eggs (Gauthier & Berteaux, 2011). This while polar bears look for goose eggs (Prop *et al.*, 2015) and potentially find shorebird nests as well. Thus although predator populations are in trouble, the predation pressure on shorebirds will increase.

(a)	<i>Summer 1998 (Lemming cycle peak)</i>		<i>Summer 2000 (Lemming cycle collapse)</i>	
Long-tailed jaeger	N (pellets)	% of diet	N (pellets)	% of diet
<i>Lemming</i>	346	55.4	3	6
<i>Birds + eggs</i>	0	0.0	1	2
<i>Invertebrates</i>	37	5.9	-	-
<i>Plants</i>	239	38.3	38	76
Arctic fox	N (scats)	% of diet	N (scats)	% of diet
<i>Lemming</i>	197	98.4	51	25.6
<i>Birds + eggs</i>	2	0.8	51	25.6
<i>Invertebrates</i>	1	0.4	26	13.1
<i>Plants</i>	<1	0.15	18	9.0

(b)	<i>1988-1969 (Sea ice substantial)</i>		<i>2006-2008 (Sea ice decline)</i>	
Polar bear	N (scats)	% of diet	N (scats)	% of diet
<i>Seals</i>	20	3.8	42	3.4
<i>Birds + eggs</i>	56	10.6	192	15.5
<i>Plants (Grasses + Berries)</i>	176	33.3	431	34.8

Table 1: Main diet composition of (a) long-tailed jaeger and arctic fox (After: Gilg *et al.*, 2006) and (b) polar bear (After: Gormezano & Rockwell, 2013) in years with different access to main prey items.

Indirect climate effects of predators on shorebirds

The increased predation risk can have severe effects on the population size of shorebirds. Nest failure is often due to predation (Martin, 1993). This is shown in a study in Canada where the predation pressure on artificial nests has been studied (figure 7). Other studies confirm that predation pressure can reduce nest survival to even zero percent (Meltofte *et al.*, 2007a).

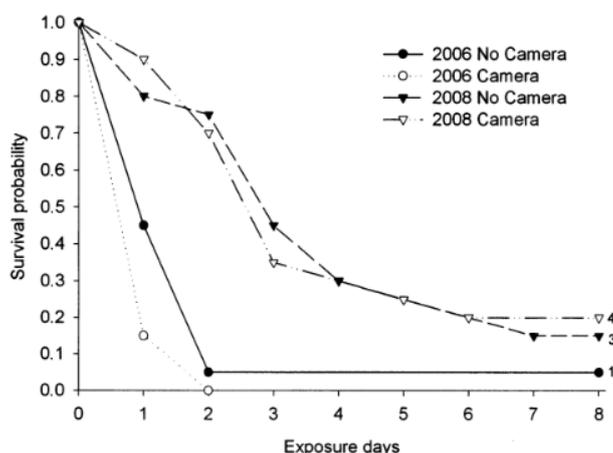


Figure 7: The number of days exposed to predation against the survival probability of artificial nests with and without cameras during a year with many foxes (2006) and a year with many long-tailed jaegers (2008) (Mckinnon & Bêty, 2009)

To increase their reproductive success, shorebirds can change their laying date. In olfactory predator dominated areas shorebirds should lay late, because early laying results in a high rate of nest failure, since the olfactory predators can easily find the snow free spots (Byrkjedal, 1980). On the contrary, shorebirds may benefit from laying earlier in long-tailed jaeger dominated areas, because the encounter rate with migratory jaegers may be lower earlier in season due to later migration (Grabowski *et al.*, 2013). Thereby, with increased predation pressure it might be beneficial to lay earlier, so there is an opportunity of re-nesting after nest failure (Smith *et al.*, 2010). Indeed 46% of the early nesting shorebirds nesting in Canada re-nested, while late nesting birds where not (Meltofte *et al.*, 2007a). However like mentioned before, Arctic shorebirds rarely re-nest and should evolve this to benefit from laying early. So shorebird can change their laying date depending on the type of predator and re-nesting opportunities sometimes resulting in a trade-off between the two.

Shorebirds can also change their nest location in order to decrease nest failure. Predators can remember nest sites they have visited and therefore birds of depredated nests move farther away than successful ones (figure 8). However, birds might not disperse if they possess a high quality habitat (Lima, 2009). Furthermore, the landscape distribution of nests depends on the home range of the predators. All three mentioned predators can have large home ranges (Anthony, 1997; Ferguson *et al.*, 1999; Olsen & Larsson, 2010), so more birds will probably breed in low densities, since high densities are more easily found (Lima, 2009). Some other birds might breed close to aggressive nest protector species which keep away predators from the nests (Bêty *et al.*, 2001). Finally, shorebirds have a trade-off between open or concealed nest sites. With olfactory predators, open habitats provide earlier fledging opportunities for adults, which is beneficial because eggs alone are difficult to find (Koivula & Rönkä, 1998). However with visual predators, more concealed habitats are probably beneficial because nests are less visible (Lima, 2009). Although shorebirds might be able to change their nest site, one should keep in mind that nowadays suitable breeding habitats decline in number due to a northward shift of vegetation, such as shrubs, and drier soils (Lindström & Agrell, 1999; Kaplan & New, 2006). This can prevent shorebirds from breeding in an optimal nest site or from breeding at all, whereby especially habitat specialists are affected (Møller *et al.*, 2008). Thus nest site choice and distribution might depend on the type of predator present, but also on the habitat availability.

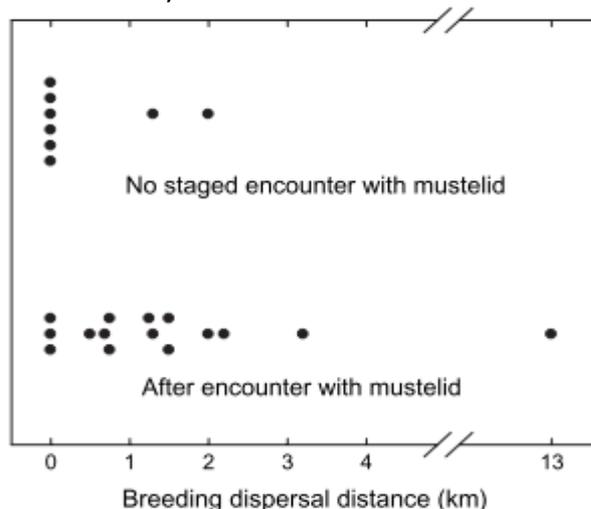


Figure 8: The breeding dispersal distance for successful and unsuccessful Tengmalm's owl nests (Review: Lima, 2009).

In areas with many long-tailed jaegers, aggressive nest defense by shorebirds might increase. This aggressive behavior depends on size, since large birds are more aggressive. Thereby large birds are often monogamous whereby parents can share the tasks, one remains on the nest while the other attacks. Additionally, the circumstances are important whereas colonial and open habitat breeding birds are more aggressive (Larsen *et al.*, 1996). Being aggressive in open habitats is presumably a beneficial strategy in areas with both terrestrial and avian predators, where the first is earlier detected and the latter one chased away.

Besides changing characteristics and population dynamics, increased predation pressure might also influence shorebird size and body mass. During incubation time, the foraging time of adults is determined by two factors. At first by the type of predator, whereas birds provide better camouflage against visual predators by remaining on the nest, while olfactory predators cannot find nests as well if the adults has left (Cervencel *et al.*, 2011). Secondly, shorebirds might have different strategies. Some birds remain on the nest if this results in a higher survival (Andersson & Waldeck, 2006). However other birds may leave the nest unattended increasing their own survival but lowering the survival and growth of their offspring (Cervencel *et al.*, 2011). So a trade-off between chick and adult survival may occur. After hatching another trade-off might be present between foraging in open habitats with a higher chance of detection or in a closed habitat with lower food intake rates (Kentie *et al.*, 2013). This affects chick and adult body mass, because adults might be more vigilant in denser habitats (Blanken & Nol, 1998). Thus different predators and strategies can result in more or less body mass.

Interactions between direct and indirect climatic effects

Many life history and population dynamic changes due to direct and indirect climate change have been mentioned, but changes in one interaction might affect the other interactions as well. Therefore this chapter focusses on the interactions, trade-offs or consequences of 3 factors influenced by direct and indirect climate effects namely: laying date, food intake rate and size decline.

The laying date of shorebirds is influenced by snowmelt date, arthropod activity and predation risk. In visual predator dominated areas, shorebirds are expected to advance their laying date, since snowmelt date and arthropod activity advance in time and long-tailed jaegers first have to arrive as well. However in olfactory predator dominated areas, a trade-off may occur between the benefits of matching the food peak and the disadvantages of a higher predation risk which arise during earlier breeding. Despite the increased predation risk of olfactory predators, birds with re-nesting ability probably choose to lay earlier, so they are able to re-nest after failure. Thus it is likely that shorebirds will lay earlier in the future, although trade-offs and the lack of ability to migrate earlier in long-distance migrants may result in less advancement than expected or even complete absence of it.

Food intake rate is influenced by increased temperatures, mismatches and predator risk. Due to higher temperatures, adults and chicks benefit from more foraging time and less energy loss. Thereby, smaller population might decrease the competition, which occurs in some populations (Colwell, 2010), for good habitats or food. During pre-breeding, this results in more energy available to invest in the eggs. Combined with a low mismatch change, the egg quality will remain high. Adults also lose less energy during incubation, although foraging time is controlled by the type of predator in the surroundings. If adults leave the nest unattended, higher temperatures probably keep the eggs warm reducing the negative effect on chick growth. After hatching, less brooding also increases the potential foraging time for adults and chicks. However, chicks are likely to encounter a mismatch and may be forced into habitats with a lower intake rate by high predation pressure. The supervising adult will be more energetically stressed by lower quality habitats and more vigilant behavior. Consequently energy intake rate will be lower in the future, but the increased foraging time will limit size declines and mortality rates.

Shorebirds are likely to become smaller by either Bergmann's rule, mismatches or higher predation pressure, but being smaller can be beneficial. At first, skinny birds can escape terrestrial predators more easily by taking-off quicker (Klaassen, 2003). Thereby, a lower wing-loading results in a higher maneuverability which improves aggressive nest behavior and escape abilities of shorebirds from avian predators (Larsen *et al.*, 1996; Klaassen, 2003). Additionally, smaller dunlin males are more attractive due to a more impressive display flight and are therefore able to lay early in season (Jönsson, 1987). Having a smaller size is also beneficial for the parent performing parental care after hatching. This is because parental care is energetically stressful with little time to forage whereby

small bodies require less food to sustain. Furthermore small birds have short bills and these are thought to be more versatile and efficient during terrestrial feeding on arthropods (Jönsson, 1987; Jönsson & Alerstam, 1990). Finally smaller birds might be able to make smaller nests. The benefits of smaller nests have been seen with passerines, where the predation pressure was reduced and the fledgling success increased (Antonov, 2004). However it is not known if shorebirds are capable of making smaller nests and if smaller nests are beneficial for them.

Nevertheless, being smaller can also be disadvantageous. While mostly males benefit from being smaller, females often do not. In dunlins, small females arrive and breed later on the Arctic (Jönsson, 1987). During laying, smaller females also lay smaller eggs with less yolk (figure 9). Contrary, in food limiting conditions, smaller females might be able to invest more energy, because they save more energy during activities than larger ones (Jönsson & Alerstam, 1990). Nevertheless, severe mismatches and food limitation are not expected to occur during the pre-breeding phase. After breeding, most females immediately leave the breeding area and mostly depend on feeding by probing where shorter bills can access less nutrients (Jönsson & Alerstam, 1990). Besides the downsides of being smaller for females, aggressive nest behavior is also less applied in smaller shorebirds (Larsen *et al.*, 1996), despite of the increased maneuverability. Finally being smaller can be detrimental during extreme weather events and migration, because larger individuals are more robust and have larger energy stocks (Jönsson & Alerstam, 1990). Thus size declines can have positive or negative effects on population dynamics although effects may differ between sexes.

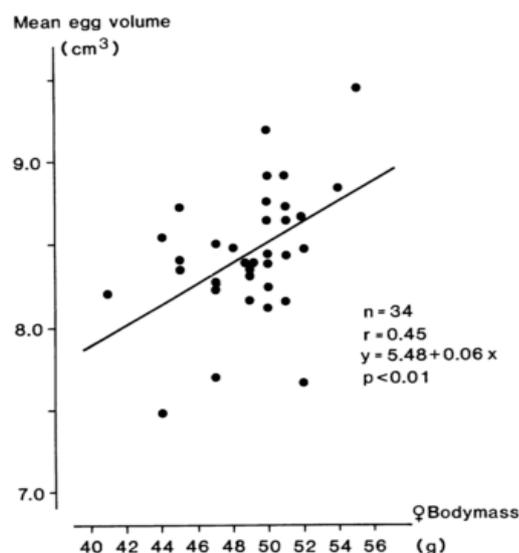


Figure 9: The body mass of dunlin females against the egg volume (Jönsson, 1987)

Conclusion & Discussion

In this essay the influence of direct and indirect effects on the life history and population dynamics of migratory Arctic shorebirds have been analyzed. From this analysis it appears that shorebirds are affected by different climatic effects and that they can also respond to it. This is summarized in figure 10. Climate change alone already triggers many potential life history changes whereby shorebird survival and reproduction success are mainly positively affected, because the Arctic becomes warmer with an extended summer period. Yet looking at climate change alone will not provide sufficient knowledge on shorebird population behavior and survival. Bottom-up control by arthropods seems to be an important factor as well, whereas in the short term arthropods will be more available, potentially having a positive effect on shorebird populations. Nevertheless in the long term, the exact changes in arthropod lifecycles are difficult to predict, but they are likely to change causing potential mismatches. These mismatches negatively affect shorebird populations and shorebirds might try to

deal with this by changing their life history characteristics. Besides bottom-up control, top-down control interactions of predators also change. Long-tailed jaegers, arctic foxes and polar bears are mostly negatively affected by climate change and lose their main prey. Although predator populations are expected to decline, predation pressure on shorebirds is likely to increase. This increased predation pressure will trigger shorebird population declines, nonetheless life history changes in shorebirds might relieve some of the predation pressure. Finally, some reactions on different climatic factors, such as a changing laying date or changing food intake rate, can conflict with each other and should therefore be regarded in perspective of each other to explain a certain observation. Thereby some other features, such as size, of shorebirds might also unexpectedly positively or negatively affect the population dynamics of the shorebirds.

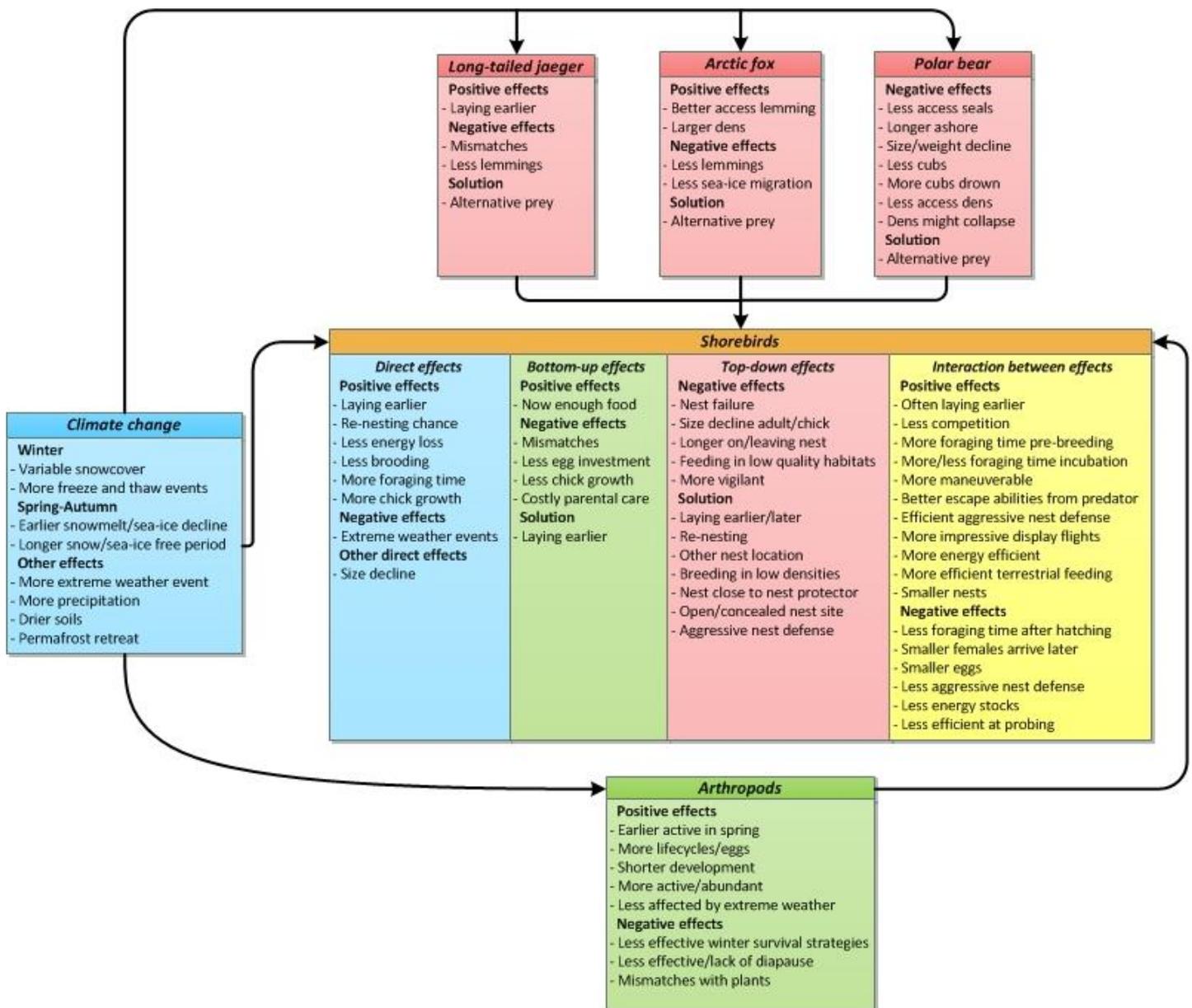


Figure 10: An overview of the potential direct effects (blue), bottom-up effects (green), top-down effects (pink) and interactions between effects (yellow) on the shorebird population dynamics and the potential life-history changes.

Additionally, some other factors that are not mentioned extensively in this essay, might influence shorebird populations as well. At first, this essay focusses on the breeding area, but changes in the stopping-over sites or wintering areas are also important. For example, wetlands might disappear due to sea level rise (Lindström & Agrell, 1999) and in the Sahel severe drought has declined the food availability influencing shorebirds during migration (Gordo *et al.*, 2005). Thereby changes in life-history traits on the breeding ground might affect shorebird survival during other parts of the year as well. So increased maneuverability might prevent predation during migration by birds of prey (Ward & Laybourne, 1985), while shorter bills are less efficient during feeding by probing (Jönsson & Alerstam, 1990). Secondly, this essay focusses solely on species currently on the Arctic, but other species invade the Arctic from the south. These can be beneficial for shorebirds like arthropods or alternative prey, but also disadvantageous as other shorebirds, predators or pathogens (Lindström & Agrell, 1999; Hickling *et al.*, 2006). Furthermore, an effect on the current arthropods and predators in the Arctic might be possible due to increased competition, more food and changes in shorebird population dynamics. Finally, humans are important to take into account since they threaten wetland areas and they might colonize and pollute the Arctic region (Lindström & Agrell, 1999; Rehfish & Crick, 2003).

In this essay, all climatic effects on shorebirds life history and population declines are described on order level across the whole Arctic. Thus, the mentioned life history changes may not all apply to every shorebird species on every location. Shorebirds differ in their life history traits, trade-off choices, migratory timing and adaptation abilities. In addition, locations differ in climate change effects, predation pressure and food availability. Therefore when research is done on a specific species in a specific area, this essay should be regarded as a guideline for an indication of potential life history changes and population dynamic changes. By doing this in combination with research on the effects of changing wintering and stopping-over sites, new insights into population dynamics and potential adaptive abilities of shorebirds can be obtained.

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