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PERSEPCTIVE

Contrasting effects of the onset of spring on reproductive success of Arctic-nesting geese

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ABSTRACT

Breeding output of geese, measured as the proportion of juveniles in autumn or winter flocks, is lower in years with a late onset of spring in some species, but higher in at least one other species. Here we argue that this is because the timing of spring affects different stages of the reproductive cycle differently in different species. Because the effects on 2 different stages are opposite, the combined effects can result in either a positive or a negative overall effect. These stages are the pre-laying, laying, and nesting phase on the one hand; and the hatchling, fledgling, and juvenile phase on the other hand. The first phase is predominantly positively affected by an early snowmelt, with higher breeding propensity, clutch size, and nest success. The second phase in contrast is negatively affected by early snowmelt because of a mismatch with a nutrient food peak, leading to slow gosling growth and reduced survival. We argue that recognition of this chain of events is crucial when one wants to predict goose productivity and eventually goose population dynamics. In a rapidly warming Arctic, the negative effects of a mismatch might become increasingly important.

Keywords: Arctic warming, breeding propensity, climate change, clutch size, fledgling survival, hatchling growth, nest success, phenological mismatch, snowmelt

Effets contrastés du début du printemps sur le succès reproducteur d'oies nichant dans l'Arctique

RÉSUMÉ

L'efficacité de la reproduction des oies, mesurée comme étant la proportion de juvéniles dans les troupeaux à l'automne ou en hiver, est plus faible lors des années ayant un début de printemps tardif chez certaines espèces, mais est plus élevée chez au moins une autre espèce. Nous arguons que cela est dû au fait que la chronologie du printemps affecte différemment divers stades du cycle reproducteur chez différentes espèces. Puisque les effets sur deux différents stades sont contraires, les effets combinés peuvent résulter en un effet global soit positif, soit négatif. Ces stades sont, d'une part, la phase de pré-ponte, de ponte et de nidification, et d'autre part la phase d'éclosion, d'envol et juvénile. La première phase est principalement affectée positivement par une fonte des neiges hâtive, avec une plus grande propension à la reproduction, une plus grande taille de couvée et un meilleur succès de nidification. Par contraste, la seconde phase est affectée négativement par une fonte des neiges hâtive, en raison d'un décalage avec le pic de nourriture nutritive, ce qui ralentit la croissance des oisons et réduit la survie. Nous soutenons que la reconnaissance de cette chaîne d'événements est cruciale pour prédire la productivité des oies et éventuellement la dynamique des populations d'oies. Les effets négatifs d'un décalage peuvent devenir de plus en plus importants dans un Arctique dont le réchauffement est rapide.

Mots-clés: changements climatiques, croissance des oisillons, décalage phénologique, fonte des neiges, propension à la reproduction, réchauffement de l'Arctique, succès de nidification, survie à l'envol, taille de couvée

INTRODUCTION

Plants and animals are responding to the rapid changes in climate, for instance by advancing spring events like sprouting and egg-laying (Parmesan and Yohe 2003). Species react with specific sensitivities to various cues in the environment, which may change at different rates with climate, and hence not all species respond to the same extent to the changing climate. Plants and primary consumers tend to react more strongly than secondary consumers, resulting in so-called mismatches between these trophic levels (Thackeray et al. 2010). A well-known example is the reproduction of insectivorous birds becoming mistimed with the peak in insects (Visser et al. 1998, 2012). But also the reproduction of primary consumers may become mistimed, albeit more with a peak in nutritive quality of food rather than a peak in food biomass (Nolet et al. 2005, Doiron et al. 2015). Because cues vary over time as well as space, such mistimed reproduction is most likely to occur in long-distance migrants, in which adjustments in the timing of reproduction are constrained by timing of migration (Both and Visser 2001, Knudsen et al. 2011).

Climate change is most rapid in the Arctic region (Serreze and Francis 2006, Pithan and Mauritsen 2014, Box et al. 2019). This can have large consequences for the many birds that migrate long distances to the Arctic to benefit from the short but productive growing season, while enjoying reduced competition and predation (Sedinger and Raveling 1986, McKinnon et al. 2010, Somveille et al. 2018). In Arctic-nesting geese, the precocial young grow fast when they are able to feed on young, nitrogen-rich plants (Lepage et al. 1998, Richman et al. 2015). In the Arctic breeding areas, plant nitrogen concentration peaks at the beginning of the growing season shortly after snowmelt (van der Graaf et al. 2006, Doiron et al. 2013, Lameris et al. 2018). Accounting for the increase in plant biomass, the peak in nitrogen biomass in their food plants occurs later than the peak in nitrogen concentration, and reproduction is well timed when hatching coincides with this peak (van der Graaf et al. 2006, Lameris et al. 2017a).

In order to ensure well-timed reproduction, timing of spring migration is crucial. Geese time their migratory departure from the temperate zone in spring based on cues including photoperiod and the green-up of vegetation (Shariatinajafabadi et al. 2014) or some correlated measure like temperature sum (Duriez et al. 2009, van Wijk et al. 2012). However, green-up or temperature sums are not well correlated along the whole migration routes of the geese, meaning that geese cannot predict the onset of spring in the Arctic from their temperate wintering sites (Tombre et al. 2008, Kölzsch et al. 2015). Since spring has advanced more in the Arctic than in the temperate zone, at least some goose species migrating to the Arctic now arrive too late to benefit from optimal growth conditions, which impacts their reproductive success (Clausen and Clausen 2013, Doiron et al. 2015, Lameris et al. 2017b).

Effects of climate change on the reproduction of Arctic geese are of prime interest to predict future population developments of these birds. How a (progressively) earlier Arctic spring affects goose reproductive output has been studied in various species, based on both short-term annual variation and long-term warming trends. However, the obtained results are paradoxical, in that most studies show higher breeding output, measured as proportion of juveniles in autumn or winter flocks, in years with an early onset of spring (Alisauskas 2002, Trinder et al. 2009, Morrissette et al. 2010, Nolet et al. 2013, Jensen et al. 2014, Cleasby et al. 2017), while one study found a higher reproductive success in years with a late onset of spring (Clausen and Clausen 2013). Here we argue this is because the timing of spring affects different stages of the reproductive cycle differently in different species. Because the effects on the 2 different stages are opposite, the combined effects can result in either a positive or a negative overall effect.

PRE-LAYING, LAYING, AND NESTING PHASE

Arctic-nesting geese are dependent on a short Arctic summer for successful reproduction. They alleviate part of this constraint by extra fueling during spring migration (Kölzsch et al. 2016). In years that the geese have more stores on spring staging grounds, they tend to return with more young in autumn, both when measured at the population level (Alisauskas 2002, Mainguy et al. 2002) and at the individual level (Ebbinge and Spaans 1995, Klaassen et al. 2017, Dokter et al. 2018). In unusually early springs, geese may leave stopovers prematurely or skip them altogether to arrive in time but with little stores at the breeding grounds, eventually yielding them little time savings before laying as they compensate by foraging at the pre-breeding grounds (Lameris et al. 2018). Only earlier departure in good condition from wintering grounds would prevent this negative effect of early springs on the first reproductive stage.

Bringing nutrient stores to the breeding grounds enables geese to produce eggs soon after arrival and well before the feeding conditions are optimal (Perrins 1970, Ryder 1970, Ankney 1984, Drent et al. 2003, Van der Jeugd et al. 2009). Geese use a mixture of so-called capital and income strategies, with eggs being partly produced from body stores and partly from local resources (Budeau et al. 1991, Gauthier et al. 2003, Schmutz et al. 2006, Hahn et al. 2011, Klaassen et al. 2017). Whether more or less capital is being used depends on the species' body size and migration distance (Hobson et al. 2011) and their foraging ecology (i.e. being grubbers or grazers) (Sharp et al. 2013), but also on the spring food conditions (Klaassen et al. 2017, Hupp et al. 2018, Lameris et al. 2018).

A further part of the body stores is needed to fuel incubation, when the females cannot feed long enough to maintain body weight (Ankney and MacInnes 1978, Budeau et al. 1991, Spaans et al. 2007, Eichhorn et al. 2010). In their decision regarding when to commence nesting, the birds face a tradeoff between current and future reproductive success (Daan et al. 1990), and geese with too low pre-laying body condition are therefore expected to refrain from breeding (Drent et al. 2003). Body stores are especially important in late springs, when only geese with ample body stores have prospects of successfully raising offspring, resulting in a lower breeding propensity when snowmelt is late (Reed et al. 2004, Dickey et al. 2008, Anderson et al. 2014; Figure 1).

Birds face another tradeoff between the seasonal increase in potential clutch size and the seasonal decline in egg value because of a lower recruitment of later-hatched young (Drent and Daan 1980, Lepage et al. 2000). This tradeoff can explain the general seasonal decline in clutch size, as nicely illustrated by a condition-dependent model (Rowe et al. 1994). This model also predicts that in a late season, with egg value declining, a slower build-up of body condition due to snow cover will lead to smaller clutches and laying at relatively high snow cover. Indeed, in years when snow melts late, Arctic-nesting geese start nesting at some later date (Prop and De Vries 1993, Cooke et al. 1995, Madsen et al. 2007), but relative to snowmelt, they commence nesting at a higher snow cover (Barry 1962, Lindberg et al. 1997, Bêty et al. 2003). Greater Snow Geese (*Anser caerulescens atlanticus*), for instance, commence egg-laying after snow melt in early springs, and at a later date but before snow melt in late springs (Gauthier et al. 2013). Like in other bird species (Murphy 1986, Perrins and McCleery 1989), clutch size in geese is generally smaller in late springs (Barry 1962, Raveling 1978, Madsen et al. 2007, Ross et al. 2017). While this can be viewed as the optimal decision in late springs, a mechanistic explanation is that for geese, being partly income breeders, poorer feeding conditions in the Arctic in late springs can only support smaller clutches (van Oudenhove et al. 2014; Figure 1).

Laying a smaller clutch may compensate for the lower pre-laying condition of the female, explaining equal body weights at the start of incubation irrespective of spring being early or late (Ankney and MacInnes 1978, Spaans et al. 2007, Sénéchal et al. 2011). Commencing nesting at a higher snow cover in late springs may however force incubating females to engage in longer nest recesses in search for food (Eichholz and Sedinger 1999), exposing the nests to egg predation (Samelius and Alisauskas 2001, Bêty et al. 2002); egg predation may also increase indirectly by an extended incubation period (Aldrich and Raveling 1993, Tombre and Erikstad 1996). As a result, nest success (i.e. the proportion of nests with at least one egg surviving) is typically lower in late springs (Madsen et al. 2007; Figure 1). However, females do not only need to feed but also drink during nest recesses, which may complicate matters. Early snowmelt may lead to unusually dry conditions in mesic tundra habitats, forcing incubating females to move over greater distances to drink and thus engage in longer rather than shorter nest recesses, thereby increasing nest predation (Lecomte et al. 2009).

Early snowmelt may also be associated with increased incubation success (being defined here as the product of nest success, egg survival, and hatching success; see Rockwell et al. 1993) through direct positive temperature effects on eggs. At least in one study hatching success (but not egg survival) was related to spring temperature (van Oudenhove et al. 2014).

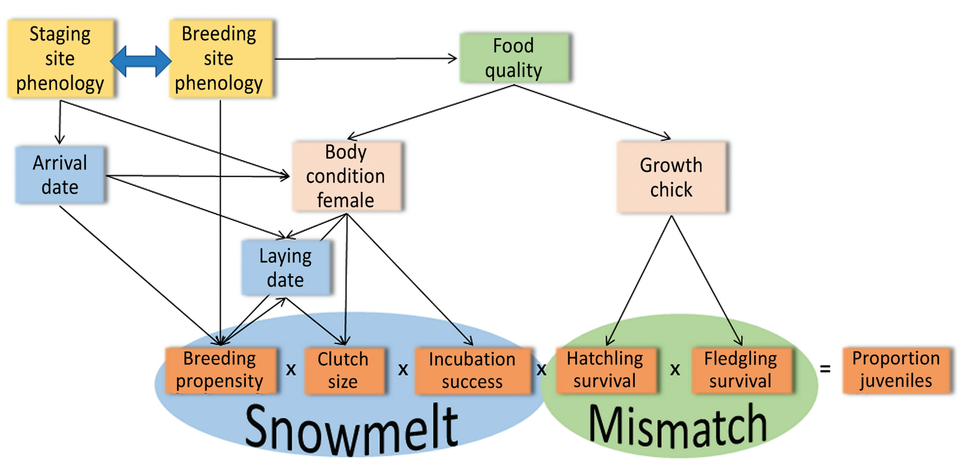

FIGURE 1. Chain of effects eventually leading to population productivity as measured as the proportion of juveniles in autumn or winter flocks. For clarity, only bottom-up effects are considered. The vegetation phenology on migratory staging sites may or may not be correlated to the vegetation phenology on the breeding site, but in any case determines arrival date on the breeding site, which in turn determines body condition of the female upon arrival. The date of snowmelt on the breeding site is likely to be correlated with the peak date of food quality, and hence to the potential mismatch. The food quality affects the body condition of the female and the chicks, and thereby the fitness components (note the arrow that runs from Body Condition Female to Breeding Propensity). The population productivity is the product of breeding propensity, clutch size, incubation success, hatchling survival, and fledgling survival, where incubation success in turn is the product of nest success, egg survival of successful nests, and hatching success of surviving eggs. Because the date of snowmelt and the mismatch predominantly affect different stages in the breeding cycle, their combined outcome may result in negative or positive relationships between breeding site phenology and population productivity.

HATCHLING, FLEDGLING, AND JUVENILE PHASE

As mentioned above, goose reproduction is well timed when hatching coincides with the peak in nitrogen biomass (van der Graaf et al. 2006). Early-hatched goslings grow faster than those hatching late (Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994, Lepage et al. 1999) because the latter ones already suffer from declining protein concentrations in their food plants (Richman et al. 2015). With climate warming, the timing of hatch becomes increasingly mismatched with the peak in food quality (Doiron et al. 2015). This causes the hatchlings to grow slower (Brook et al. 2015, Ross et al. 2018) and to have a lower chance of survival up to fledging (Lindholm et al. 1994, Lameris et al. 2018, Ross et al. 2018). This slower growth increases the length of the period in which goslings are vulnerable to size-dependent predation (Ricklefs and Starck 1998, Samelius and Alisauskas 1999, Dmitriew 2011). In general, smaller goslings in poor condition are expected to be most vulnerable (Williams et al. 1993). Slow-growing goslings also experience increased thermoregulatory costs due to their smaller size, which might contribute to lower survival (Lindholm et al. 1994, Fortin et al. 2000, Gauthier et al. 2006; Figure 1).

Because slower-growing goslings reach a smaller final body size, the slow growth has knock-on fitness effects later in life (Ankney and MacInnes 1978, Black and Owen 1987, Afton and Paulus 1992, Choudhury et al. 1996, Poisbleau et al. 2006). What is most relevant here is that juveniles small for their age experience reduced post-fledging survival (Loonen et al. 1999, Slattery and Alisauskas 2002, Brook et al. 2015), aggravating the negative effects of a mismatch (Figure 1). Goose departure from the breeding grounds is found to be related to the first frost spell (Xu and Si 2019), and when goslings have not fledged by then they are left behind (Barry 1962). Arctic warming may lead to longer summer seasons, providing more time to grow, which may partly offset any negative effects of a mismatch earlier in the season. However, it is unclear whether goslings can really profit from a longer season, because gosling mortality can be high even in the presence of abundant food if the nutritive quality is not sufficient to meet their needs for growth and maintenance (Richman et al. 2015).

COMBINED EFFECTS

Negative effects of a late snowmelt predominantly occur in the pre-laying, laying, and nesting phase. Through the combined effects of lower breeding propensity, somewhat smaller clutch sizes, and lower nest success, reproductive success of Arctic-nesting geese at hatching tends to be lower in late springs than early springs (Madsen et al. 2007, Dickey et al. 2008). In contrast, positive, potentially compensatory effects occur during the hatchling, fledgling, and juvenile phase by a better match with nitrogen biomass after a late spring, as suggested by Clausen and Clausen (2013). This better match ensures a better growth, with knock-on effects on subsequent fledgling and juvenile survival. Because the annual reproductive success is the product of breeding propensity, clutch size, nest success, and gosling survival, a late spring may both lower and enhance reproductive success. Conversely, an early onset of spring may have primarily beneficial effects in the pre-laying, laying, and nesting phase, but deleterious effects during the hatchling, fledgling, and juvenile phase through an increase of a mismatch (Figure 1).

The exact relationships with date of snowmelt depend on how hatch dates are correlated with date of snowmelt, and how date of snowmelt is correlated with date of peak nitrogen biomass (Lameris et al. 2018). Because these correlations differ between sites, and because of the differing life histories of different species, the resulting effect of date of snowmelt on population productivity may differ between species. Light-bellied Brent Geese (*Branta bernicla hrota*) that showed a higher breeding productivity with a later snowmelt may be exceptionally vulnerable to a mismatch. They are long-distance migrants with a virtual nonstop migration that does not allow for adjustments in timing along the way (Clausen and Clausen 2013), while breeding in an area where climate is rapidly warming (Førland et al. 2011). Importantly, perhaps to prevent high thermoregulatory costs due to their small body size (Hupp et al. 2018), they are the last goose species to arrive on the breeding grounds (Clausen and Clausen 2013). While in general small bird species have less scope for capital breeding than larger ones (Meijer and Drent 1999), the interval between arrival and laying can be of overriding importance and, based on the short interval, they are expected, like Dark-bellied Brent Geese (*Branta bernicla bernicla*), to be largely capital breeders investing stores into their eggs (Klaassen et al. 2006). While they may have some leeway to adjust to earlier springs by using even more capital stores for egg production when spring starts early, like the closely related Black Brant (*Branta bernicla nigricans*; Hupp et al. 2018), the options to prevent a mismatch seem to be limited; other (larger) goose species may have more options to start laying earlier in earlier years, because they simply arrive earlier (Hupp et al. 2018).

There are indications that the same processes as outlined above for geese are also relevant for other Arctic migrant bird groups, such as shorebirds. However, the shorebirds' smaller body size and largely insectivorous diet create some important differences. Being smaller than geese, shorebirds, for instance, are more at risk of starvation when snowmelt is late and they have to survive on body stores (Morrison et al. 2007). They also differ from geese in that they are income breeders, forming their eggs from exogenous resources (Klaassen et al. 2001, Morrison and Hobson 2004, Hobson and Jehl 2010). For shorebirds in general, late springs are associated with reduced breeding success, due to higher risk of nest predation as well as lower possibilities for re-laying (Meltofte et al. 2008). With regard to the mismatch, shorebird chicks, for instance, are dependent on a peak in arthropod abundance, which has shifted forward in time in recent years (Tulp and Schekkerman 2008, Reneerkens et al. 2016). Some species have responded by advancing laying dates, whereas others have not, suggesting there are migratory constraints to an advancement (McKinnon et al. 2012, Liebezeit et al. 2014, Reneerkens et al. 2016) In Red Knots (*Calidris canutus canutus*) body size of juveniles is positively related to date of snow melt in the Arctic, suggesting that their body size at fledging is smaller following a mismatch in early springs, resulting in a lower subsequent survival (van Gils et al. 2016). In general, however, evidence for a phenological mismatch for shorebirds is rare, perhaps because arthropod abundance, more than plant growth, is strongly affected by weather conditions following snowmelt (McKinnon et al. 2012, Reneerkens et al. 2016, Leung et al. 2018, Corkery et al. 2019, Saalfeld et al. 2019). While only a few studies investigated the connection between proportion of juveniles and climatic conditions in the breeding grounds and none of these included onset of spring, most of these studies found a higher proportion of juveniles following warm breeding seasons (Schekkerman et al. 1998, Beale et al. 2006, Aharon-Rotman et al. 2015).

While the positive effects of an early spring have been dominant in the historical past, the negative effects of an early spring may soon become more important due to the rapid climate warming in the Arctic. In any case, recognition of the chain of events (Figure 1) is crucial when we want to be able to predict the effects of Arctic warming on goose productivity and eventually goose population dynamics.

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