Are chicks forcing their parents to migrate?

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Contents:

Abstract

The ultimate cause for migration is not yet known, it is here suggested that precocial chicks might force their parents to migrate. Precociality demands higher energy expenditures from a chick than altriciality does. Growing up on the Arctic tundra costs even more energy, due to low temperatures and strong wind. The growing speed on the tundra has to be high to finish growing before the end of the short summer, increasing energy demands even more. There is however enough and easy to find food available on the tundra to maintain these high energy expenditures.
In the wintering area food and water are scarcer while competition is higher. Therefore precocial birds are forced to migrate to enable their chicks to find enough food.

Introduction

Migration is a common and wide spread trait among bird species. Migration is however very demanding of a bird, flying long and far is energetically costly, it takes a lot of time and predation risks on the route are high (Alerstam, Hedenstrom et al. 2003; Lind and Cresswell 2006). The breeding season on high latitudes is short and cold (Chernov 1985). While the circumstances in their wintering habitat are lenient (Bell 2000; Rappole, Helm et al. 2003).
Birds must therefore have a very good reason why they do not stay in their more benign winter habitats the whole year (Rappole, Helm et al. 2003). The reason why birds migrate is however not yet completely clear, and subject of debate (Bell 2000; Berthold 2001; Boyle and Conway 2007) .
There are many different hypotheses about the reasons why birds migrate (Alerstam, Hedenstrom et al. 2003). By example; to increase fitness in a seasonal environment, make optimal use of different habitats or to avoid competition, predation or parasitism (Piersma 1997; Alerstam, Hedenstrom et al. 2003).
In many cases migration is primarily an adaptation for exploiting seasonal peaks of resource abundance and avoiding seasonal resource depression (Alerstam, Hedenstrom et al. 2003; Boyle and Conway 2007). While the tropical wintering habitats become drier, the availability of high quality forage peaks in spring at higher latitudes. Migratory birds make use of these peaks in the food availability to raise their young (van der Graaf, Stahl et al. 2006). After the summer these environments with high seasonal food availability become very hostile and birds move back to their more benign wintering habitat (Alerstam, Hedenstrom et al. 2003).
Another reason to migrate might be to decrease predation risk. Predators cannot follow the

migration of birds and thus do not have a year round food source (Hebblewhite and Merrill 2007), the populations of predators stay small because of this seasonal lack of food. The same mechanism also decreases the presence of parasites and diseases. Here fore birds do not have to invest much in their immunodefence systems. (Piersma 1997).
Most of these hypotheses however reason from the perspective of adult birds. Why not look at migration from the perspective of the young? They have very different needs than adults such as nutritional and energetic requirements for growth (Shelton, Dean et al. 2005; Sibly, Witt et al. 2012). Most of the birds that are resident in tropical and subtropical grassland, savannas and shrublands are birds that feed their young (altricials) (Fokkema Unpublished data). Species with young that feed their selves (precocials) are almost all migrating to higher latitudes.
Precocial chicks often have a different diet then their parents, they leave the nest to forage for themselves, which is energetically very demanding for a little chick (Schekkerman and Visser 2001; Krijgsveld, Ricklefs et al. 2012). In the winter habitat of the adults there might not be enough, easy to catch and appropriate food for the self-feeding chick. This suggests that it is might not be the adult bird that needs to migrate, but the chick that needs its parent to migrate. The hypothesis that I am going to look into is that precocial young, who have to feed themselves and have a different diet then their parents, force the adults to move to an area where the chicks can easily find food that is right for them.

Differences between precocial chicks and altricial chicks

Some chicks are completely helpless upon hatching, others are quite independent and able to leave the nest and forage. The first kind of chicks are called altricial, the second precocial (Starck and Ricklefs 1998).
The altricial chicks are often blind and bald, unable to walk and need to be fed by their parents. Altricial young are often called nest squatters (Starck and Ricklefs 1998), because they stay in the nest for a long time. Precocial chicks are called nest fleers , they are able to leaf the nest and find their own food upon hatching without help from their parents (Starck and Ricklefs 1998).
Chicks aren't either precocial or altricial, but there is a spectrum ranging from chicks that are able to fly upon the first day after hatching to chicks who are almost in an embryonic state with many developmental level in between. In table 1 an often used classification system for the precocial/altricial spectrum is shown with some of the different properties of chick of different development modes (Starck and Ricklefs 1998).

	Properties
Precocial	Downy hatchling plumage, locomotor activity, search food and feed alone
Semi-precoical	Downy hatchling plumage, locomotor activity, following parents
Semi-altricial	Downy hatchling plumage, locomotor activity, young fed by parents, stay in nest
Altricial	Young fed by parents, stay in nest, eyes closed at hatching, no external feathers at hatching

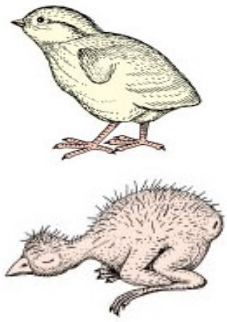

Table 1: Characteristics frequently used for classification of bird hatchlings (Starck and Ricklefs 1998). *On the right are above a drawing of a 1-day-old ruffed grouse (Bonasa umbellus*) which is precocial and below a 1-day-old meadowlark *(Sturnella)* which is altricial (Dial 2003).

The daily energy expenditure (DEE) of precocial shorebirds is high compared to DEE of altricial species of similar body mass and in similar environments (Krijgsveld, Ricklefs et al. 2012). Schekkerman and Visser (2001) showed that levels of daily metabolised energy in chicks of Black-tailed godwits (*Limosa limosa*) and Northern lapwings (*Vanellus vanellus*) in temperate grasslands in the Netherlands were about 60% higher than levels predicted for altricial chicks of similar size (Weathers 1992).

Foraging outside the nest is energetically very demanding for precocial chicks (Schekkerman and Visser 2001). They must walk, run, find and catch food, whereby the young chick cools down (Schekkerman and Visser 2001). The small chick, only covered with down, is not yet homeothermic and thus needs to be brooded. Brooding is energetically favourable if chicks can find sufficient food during their foraging bouts to fulfill their high energy needs (Krijgsveld, Reneerkens et al. 2003).

Day length and brooding requirements set the main limitations on foraging time for precocial chicks, which spend only little time on behaviour other than foraging or being brooded (Schekkerman and Boele 2009). When ambient temperatures are low, chicks spend more time brooding and less time foraging (Krijgsveld, Ricklefs et al. 2012). Increased brooding time restricts foraging time, which makes chicks vulnerable to harsh weather conditions. High wind speeds and low temperatures reduce their energy intake further because food availability decreases (Schekkerman and Boele 2009).

Precocial chicks invest a large proportion of their resources in developing their muscles to increase locomotory- and thermoregulatory function, whereas altricial chicks don't need these until their fledging day (Starck and Ricklefs 1998). As a result of the increased energy allocation to muscle

development, foraging activity and thermoregulation, their rates of growth and development are limited compared to altricial chicks, particularly in cold climates (Tjorve, Schekkerman et al. 2007; Tjorve, Garcia-Pena et al. 2009).

Conditions that chicks experience in a tropical environment and on the Arctic tundra

A chick on the Arctic tundra undergoes very different circumstances than a chick in a tropical environment, the climates, vegetation structure and food availabilities are very dissimilar. These differences define many properties of the chick during its development (sea table 1). The main effect of these circumstances is seen in the growth rate of chicks in a tropical environment and on the tundra. Which is higher for chicks on the tundra (Schekkerman, Tulp et al. 2003).

Summer on the high Arctic is short and malign; temperatures are low and wind velocities are high (Chernov 1985). As a result of these harsh circumstances energy expenditure for chicks on the Arctic tundra is greater than would be predicted for birds of their size (Weathers 1992; Schekkerman, Tulp et al. 2003). Rates of energy expenditures in Arctic species are high compared to those of more temperate species (Krijgsveld, Ricklefs et al. 2012) and the amount of energy needed for precocial chicks growing in a warm environment is still lower (Tjorve, Underhill et al. 2007). Tjorve et al (2008) found that the relative costs for a chick to grow from hatchling to fledgling increases by about 2,5% per degree latitude.
The growth rate of chicks on the Arctic is however higher than would be expected for chicks of their size (Schekkerman, Tulp et al. 2003; Tjorve, Schekkerman et al. 2007). Tjorve et al (2008) studied the development of chicks of three precocial shorebird species in a warm environment. The growth rate of all these chicks was generally lower than those observed in shorebirds at higher latitudes. This seems contradictory with the higher energy expenditures needed on the Arctic tundra.

The low growth rates at lower latitude are caused by the temperatures that are much higher, while food and water availability are lower (Tjorve, Underhill et al. 2008). In this environment precocial chicks spent 11-71% of their time inactive but not brooding, these periods of inactivity are probably to reduce risk of overheating (Tjorve, Underhill et al. 2008).
The slow growth rate of shorebird species at low latitudes may be an adaption to reduce energy requirements in the food-poor, semi-arid environments in which they evolved (Schekkerman and Visser 2001). Natural selection could favour slow growth and low resting metabolic rate (RMR) in

warm environments to lower the demand for food and to minimize evaporative water loss and avoid heat stress by reducing internal heat production ((Tjorve, Underhill et al. 2008).

On the Arctic the fast growing of chicks is probably an adaption to the shortness of the Arctic summer. At higher latitudes time available for growth is limited by weather and the requirement for migration preparation (Tjorve, Garcia-Pena et al. 2009). Precocial chicks on the Arctic tundra have only a short time to complete growth before the end of the short Arctic summer season (Krijgsveld, Ricklefs et al. 2012). Schekkerman et al (2003) found that during their research on red knot (*Calidris canutus)* the chicks hatched after the peak date of arthropods availability and their highest required intake rate is even later. However on the earliest and median laying dates respectively only 10% and 50% of the tundra had become snow free, apparently there is just not enough time to breed after the tundra has become snow free and before the arthropod availability peeks (Drent 2006). Breeding in small open patches between the snow strongly increases predation risk (Schekkerman, Tulp et al. 2003). The fast growth, development and high muscular activity of chicks of Arctic breeding species results in a shortened length of time during which chicks are dependent on parental brooding to maintain body temperature and in a shorter growing period before adulthood (Schekkerman, Tulp et al. 2003; Tjorve, Schekkerman et al. 2007), with the short summer season on the tundra this would be very advantageous. Such rapid growth and high energy expenditure however can only be sustained through sufficient food intake.

	Tundra	Effect for chick	Tropical	Effect for chick
Temperature	cold	more need for brooding	warm	risk for overheating
Moist	wet		dry	risk for drying out
Daylight	24-h/day	foraging long	12-h/day	foraging shorter
Food	easy to capture	growing fast	less	growing slower
Length of summer	short	need to grow fast	long	time to grow slower

Table 2: Differences between the Arctic tundra and a tropical area that will influence a precocial chick.

Foraging on the tundra

For chicks to have a higher food intake rate they need to have either better feeding conditions or

their foraging time must increase (Schekkerman, Tulp et al. 2003). As chicks on the Arctic tundra have high energy expenditures and grow very fast, they must have one or both of these advantages to increase their food intake rate on the tundra.

It has been suggested that arthropod density increased with latitude (Lack 1968), but recent studies found no significant differences between arthropod density on the Arctic tundra and a temperate meadow in the Netherlands (Schekkerman and Visser 2001; Schekkerman, Tulp et al. 2003). However prey are easier detected and captured on the tundra due to a simpler vegetation structure and a larger proportion of wingless or slow moving arthropods (Schekkerman, Tulp et al. 2003; Tjorve, Schekkerman et al. 2007). For herbivore bird species, such as geese, there is plenty of food with a high nutritional quality to find on the tundra as plants on the Arctic also have only a short growing time in summer, in this short period they need to develop all their above ground tissues and reproduce, creating a peak forage availability for the birds (van der Graaf, Stahl et al. 2006).

During the Arctic summer there is a 24-hours daylight period which strongly increases potential foraging time (Chernov 1985; Schekkerman, Tulp et al. 2003). But chicks still need to be brooded to maintain their temperature, and sleep might also decrease their foraging time, unless it can be combined with brooding bouts (Schekkerman, Tulp et al. 2003).
Schekkerman et al (2003) showed that red knot chicks (*Calidris kanutis*) on the Arctic tundra can forage longer then similar sized birds on a temperate meadow due to increased cold hardiness. Cold hardiness is the degree a chick can withstand cold. The high cold hardiness of chicks on the tundra allows them to forage longer without brooding in between. The increased growth rate of chicks on the tundra may also allow them to forage for longer times without brooding, at a younger age than slower growing temperate birds, because size is an important factor for thermoregulation (Krijgsveld, Reneerkens et al. 2003; Schekkerman, Tulp et al. 2003). This enables the chick to make optimal use of the long daylight period.

Survival options for chicks in the winter habitat of adults

Precocial chicks often have a different diet than their parents (Holland, Hutchison et al. 2006; Schekkerman and Boele 2009). This may cause a difference in suitable forage areas for adults and chicks. By example Schekkerman et al (2009) showed that adults and chicks of the black tailed godwit (*Limosa limosa*) might suffer different effects of transition to breeding in fertilised

agricultural grasslands. The transition will benefit adult godwits through a high availability of soil invertebrates but causes a loss of small above ground arthropods; the most profitable prey for chicks.

The diet of adult shorebirds is very diverse, they are known as opportunistic feeders that choose the predominant food items available in a local area (Isacch, Darrieu et al. 2005). This dietary flexibility is highly advantageous to birds that migrate over long distances and use a variety of habitats (Isacch, Darrieu et al. 2005).

Chicks however have a narrower diet (Schekkerman and Boele 2009). For many species there might not be suitable food for chicks in the wintering area's of adults. Such is the case by example for red knots which live in the non-breeding season on the mud flats of the Waddensea, where they eat molluscs that they crack with their muscular gizzard (Kraan, van Gils et al. 2009), in this habitat a chick, that has not yet developed such a strong gizzard, would fail to find food. This holds as well for many other bird species such as birds that feed on crabs or bivalves that are swallowed hole or cracked with their bill and birds feeding on soil invertebrates that they dig op by probing with their bill (Iribarne and Martinez 1999; Schekkerman and Boele 2009) (Skagen and Oman 1996).

Further more, the competition in the winter habitat will be much stronger because there are high numbers of sedentary birds (Bell 2000), in tropical and subtropical grasslands, savannas and shrublands for example there are over 3000 resident bird species, while on the tundra there are only 84 resident species plus 317 summer-guest species (Fokkema Unpublished data), the higher number of species in the tropics might cause greater competition.

Another factor that would be hard to combine with chick rearing in a tropical area is that 40% of migrants keep moving during winter from spot to spot, to avoid local dryness (Rappole, Helm et al. 2003) and to benefit from peaks in food availability (Isacch, Darrieu et al. 2005), as chicks are unable to fly they would not be able to follow these movements.

Migrating altricials

There are however also many altricial birds that migrate, could their chicks also be forcing them to do so? As chicks are fed by their parents they will not have the need to grow up in an area with adequate food to find. However, although the diet of altricial chicks resemble the diet of their parents, there are also differences (Radford 2008). Not only do parents feed smaller prey items to their young, the composition of food items is also different. By example, green woodhoopoe feed their young more spiders and less catterpillars and centipedes than they eat themselves (Radford

2008) and roseate and sandwitch terns chicks get different fish species than their parents eat (Shealer 1998). The different kinds of food items for their young may or may not be available in their wintering habitat. If not they also need to migrate to find these different kinds of food.
Further more, taking care of young is more costly for parents of altricial chicks than for parents of precocial chicks (Bryant and Tatner 1991; Tulp, Schekkerman et al. 2009) . Foraging for the altricial young and brooding them during the first time after hatching restricts their own time to forage (Sanz and Moreno 1995), while parents of precocial chicks only need to guard their young while they forage, which can be combined with foraging for themselves. Furthermore the brooding requirements of precocial chicks are much lower then for altricials (Sibly, Witt et al. 2012). As a consequence for an altricial bird species it might be beneficial for the parents to migrate to an area with high food quality and availability during the time that they have to feed their young.
There are however relatively few altricial bird species that migrate; of all the altricial birds on the tundra, in temperate broadleaf and mixed forests and tropical and subtropical grasslands, savannas and shrublands less then 30% was migrating, while of precocial species in the same areas over 50% was migrating. So the need for altricials to migrate is probably lower.

Conclusion

In this literature study I have tried to answer the question whether precocial chicks force their parents to migrate or not.
I found that precocial chicks most likely would not be able to survive in the tropical wintering habitats of their parents because there is relatively little food and water there, while there is a lot of competition for these resources. An altricial chick is better able to survive there, as its energy requirements are much lower than for a precocial chick and it does not needs to compete for resources itself as it is fed by its parents.
The situation on the Arctic tundra, where many birds migrate to, is however harsh for a chick too. Growing up in a cold climate costs even more energy than it already does in a tropical climate trough the high costs for thermoregulation. The precocial chicks does not suffer to much from this disadvantageous climate as it has a very high cold hardiness. Furthermore they are able to make up for time lost by extra brooding due to the 24-hours daylight period and the ease of finding food in the open vegetation supplies the extra energy needed.
From this it could be concluded that chicks are able to grow up better and faster than they would be in their parent's winter habitat. So it can be said that a precocial chick “forces” its parents to

migrate.
Another interesting hypothesis is that not precocial chicks force their parents to migrate, but that migrating birds force their chicks to become precocial (Garcia-Pena, Thomas et al. 2009). Migration is hard for a bird and so is breeding and finding food for their young on the cold tundra (Piersma, Lindstrom et al. 2003). It might be that there is a trade of between those two; either migrate of have high parental care. However if a migrating parent would not be able to take care of their young, precociality would never have the chance to evolve as the chicks with altricial development would not be able to survive on their own. As a consequence migration would disappear again.

There are also migrating altricial species, as they feed their young, they don't have the need to breed in an environment with for chicks easy to find food and water and low competition. They do have higher energy expenditures themselves, as finding food for young is more demanding than simply guarding them while they forage for themselves, like parents of precocial chicks do (Sibly, Witt et al. 2012). They might be migrating because the higher food abundance and lower competition makes it easier to find food for both themselves and their chicks.
All together I think that the precociality of chicks can not be seen as *the* reason why birds migrate. It is though one of the factors that forms together with many others things, such as decreased predation risk and lower parasite and disease abundance, the reason why birds migrate.

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