Coping with older siblings, a review on the long-term effects of hatching asynchrony on junior offspring.

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Abstract

Hatching asychrony creates a size and age hierarchy within the nest. This hierarchy has big short-term consequences for the last hatched chick. However there is little known about the long-term consequences. Negative impacts during the nesting stage has been found in all species featured in this thesis. It is expected that adult juniors are: smaller, have a lower life expectancy and have lower dominance ranks, all resulting in lower fitness compared to seniors. In some species persistent effects are found, but in the biggest/longest studies on seabirds the results were conflicting. One of the studies found some effect on fitness but two did not. More research is needed to find out if this lack of long-term effects is universal for all bird species.

Introduction

Hatching asynchrony is the concept of eggs not hatching simultaneously. It is common in birds and occurs when females start the incubation period prior to the completion of a clutch (Mainwaring et al., 2012). The crested ibis for example starts incubating right after the first egg is laid (Song et al., 2018). The eggs laid earlier hatch early as well, this is because the incubation period of these eggs started earlier. This results in age and size differences within a brood (Mainwaring et al., 2009). Hatching asynchrony has strong negative effects on the survival of chicks hatching last (juniors). It is not fully known what the reasons are for hatching asynchrony, however there are some hypotheses. The first hypothesis states that a size hierarchy is selected for because it facilitates adaptive brood reduction when resources are limited (Mainwaring et al., 2012). This hypothesis is following the idea that the last hatched chick will only get food and resources if the conditions provide for it. If this chick does not survive to fledging, its presence has not/minorly affected the fitness of the other nestlings. The second hypothesis is called the peak load hypothesis. With hatching asynchronous the parents spread out the demand for food, so there is not one big peak of demand when all chicks are at the maximum growing phase (Mainwaring et al., 2012). This way the parents can cope more easily with food demand, especially when food is scarce. The last hypothesis is the hurry-up hypothesis, parents want to decrease the time eggs and chicks are in the nest (Mainwaring et al., 2012). This is because the shorter the offspring is in the nest the smaller the chance is that predators predate them. Some bird species also lay their eggs over a long period of time, and if an egg is not incubated for a long time its viability will go down drastically (Beissinger, 2008). These species have no choice but to implement hatching asynchrony.

Hatching asynchrony differs strongly between species, some hatch within a day, like the hihi (Macleod et al., 2016), other clutches take up to 18 days to hatch like the ones of the green-rumped parrotlet (Beissinger, 2008). A clutch is considered to hatch asynchronously if the last egg has hatched more than 24 hours after the first egg (Macleod et al., 2016). In this essay I will focus on the effects that hatching asynchrony has on the last hatched (junior) chick. This is done by comparing multiple traits between juniors and first hatched chicks (seniors). Reading the hypotheses above it becomes clear that the last hatched chick is strongly affected by the asynchronous hatching, especially during the nesting phase. Survival of the last hatched chick in the nest is lower than that of co-nestlings according to the first hypothesis. It states that the last chick will only get food when its siblings are saturated, indicating a lesser food supply for the junior chicks. The hurry-up hypothesis however suggests that the chance of survival increases if a chick spends less time in the nest. As the last-hatched chicks spends the least amount of time in the nest, because nestlings fledge surprisingly synchronous (Mainwaring et al., 2009), it would have a lower chance to get predated. The second hypothesis is only applicable to species that fledge asynchronous as well because if nestlings fledge synchronous there is still a peak of demand for food.

In this essay I will focus on the long-term effects of hatching last. There is much knowledge on the effects of hatching asynchrony on chicks in the nest, but the long-term effects are largely unknown (Macleod et al., 2016). Sourcing information was done with google scholar using keywords like hatching asynchrony, long-term effects and hatching order. No review articles about the long-term effects of hatching asynchrony were found, so hereby I will discuss the current knowledge about this topic.

The number of studies on this subject was limited, especially studies that follow juniors for longer than a year. Therefore, first the known short-term effects will be discussed, following up with educated expectations if and how these short-term effects affect the offspring after the nesting phase. After this the knowledge derived out of studies that did research on the long-term effects of

being a junior will be discussed, answering the question: Do the negative effects of hatching last persist during adulthood? Finally results of the studies will be compared to the expectations.
The hypothesis of this thesis is that juniors are not strongly affected by hatching asynchrony during adulthood. This is expected because species that implement hatching asynchrony to facilitate adaptive brood reduction lose their junior chick(s) if breeding conditions are bad. If the junior survives the nesting stage the conditions must have been sufficient, or these individuals are of such good genetic quality that they can survive a period of minimal food resources. In the adult stage there is more and stronger selection on different traits than in the nesting stage. The higher selection on junior nestlings and/or the sufficient nesting conditions is expected to overcome the negative impacts of being the youngest sibling. Therefore, I suppose juniors will not be affected after the nesting stage by being the youngest hatchling. Although it is expected that junior offspring are smaller as adults since they have to fledge at a younger age, shortening their growing period.

The effects of being the youngest in the nest

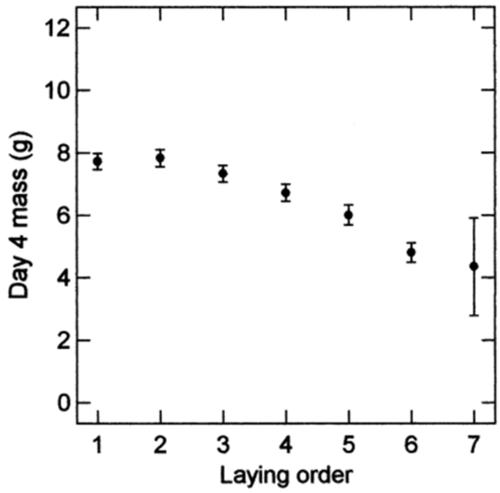

Figure 1: Mass of tree swallows' chicks at day 4 in relation to the laying order (Clotfelter et al., 2000).

Being the youngest in the nest has a big impact on the survival and growth of a nestling. The age difference in the nest results in a size hierarchy between the nestlings. The size of the oldest chick can be up to 2 times the size of the youngest chick (fig.1) (Clotfelter et al., 2000). This size hierarchy makes that the youngest nestlings worse at begging; juniors reach lower and therefore they get less food than their older and bigger siblings (Mainwaring et al., 2009). The lower food intake makes juniors more susceptible to extrinsic and intrinsic variation in their developmental conditions than their senior siblings (Mainwaring et al., 2009). Due to the strong competition in the nest the death rate of juniors nestlings is higher than seniors in all studies of the species evaluated in table 1 (Macleod et al., 2016; Arnold et al. 2003; Dey et al., 2014; Stier et al., 2015; Spear et al., 1994, Sutherland, 1989; Marín-Vivaldi et al., 1999; Drummond et al., 2013; Vedde et al., 2021 and Clotfelter et al., 2000). In figure 2 below this is clearly visible, the frequency of surviving of Pukeko chicks in hatch order 1-4 is much higher than of the younger chicks (hatch order 5-8) (Dey et al., 2014). In this example very few of the younger chicks survived the first 60 days, whereas the older siblings mostly did.

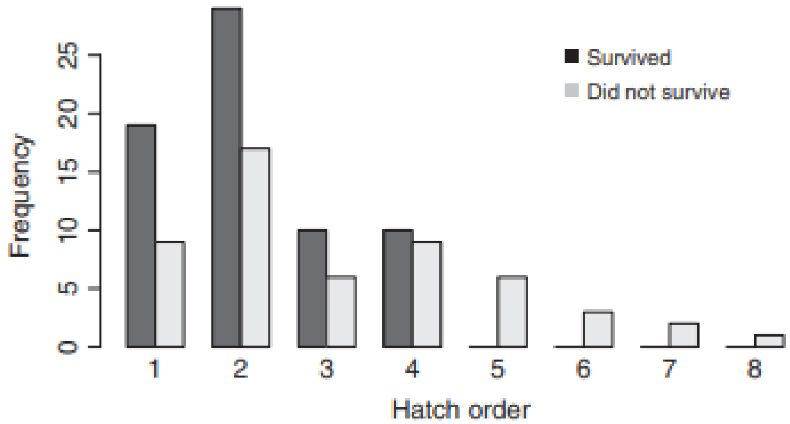

Figure 2: Frequency histogram of the survival of the Pukeko after 60 days in relation to hatch order. The histogram shows the frequency of survived (dark bars) and the frequency of died (light bars) individuals for each hatch order. The frequencies are rounded to the nearest integer (Dey et al., 2014).

Premature death of nestlings is the most severe short-term consequence of hatching last and therefore also impacts the average fitness of juniors badly. The death of juniors is in most species caused by starvation (Arnold et al. 2003). In species of eagles, pelicans, boobies, owls, and cranes there is next to starvation another death cause of juniors (Sutherland, 1989), seniors of these species peck their younger siblings to death when food is limited. This practice ensures a better food supply for the seniors (Drummond et al., 2013; Sutherland, 1989). This results in juniors of these species having even harsher nesting periods. If these juniors survive, they could have long-term effects of injuries from their siblings. In the rest of this article the long-term consequences are studied so only the effects on the chicks that have survived the nesting phase will be discussed.

Table 1: Short term effects of being the latest hatchling in the nest. Empty cells means that the trait was not quantified in that study. Yes, stands for: the effect was encountered in the study. No stands for: the effect is not encountered.

	Lower survival rate of nesting phase	Slower growth rate	Altered physique during fledging	Negative short-term consequences
Hihi (Macleod et al., 2016)	Yes	Yes	Yes	Yes
Jackdaw (Arnold et al. 2003)	Yes			Yes
Pukeko (Dey et al., 2014)	Yes	Yes	Yes	Yes
Great tits (Stier et al., 2015)		No	No	Yes
Western gulls (Spear et al., 1994)	Yes			Yes
Barn-swallow (Mainwaring et al., 2009)		No	Yes	Yes
Blue-footed booby (Drummond et al., 2013)	Yes	Yes	No	Yes
Black bird (Sutherland, 1989)	Yes	Yes		Yes
Eurasian hoopoe (Marín-Vivaldi et al., 1999)	Yes			Yes
Tree swallow (Clotfelter et al., 2000)	Yes	No		Yes
Herring gulls (Bosman et al., 2016)	Yes	Yes		Yes
Common tern (Vedde et al., 2021)	Yes	Yes	No	Yes

Table 1 shows that hatching last does have negative short-term consequences for every bird species in the articles this thesis is based on. The negative short-term consequences do however differ between species. Some species only experience a negative effect on survival rate, whereas juniors of other species like the hihi, the barn-swallow and the pukeko have an altered physique during fledging compared to their senior siblings (Macleod et al., 2016; Mainwaring et al., 2009; Dey et al., 2014).
A study on junior fledglings of the hihi showed a significant decreased body mass (Macleod et al., 2016). This shows that even birds that are classified as “synchronous” breeders like the hihi show significant negative short-term effects due to hatching last. Junior fledglings of Barn-swallows have significant decreased wing development than their older siblings (Mainwaring et al., 2009). Alteration in the physique of junior fledglings is explained by the fact that fledglings fledge as synchronously as possible, even if they are of different age (Mainwaring et al., 2009). This is done because staying in the nest while the other siblings have fledged is unfavorable. Parents decrease their parental activities in the nest drastically after the first fledgling has abandoned the nest (Mainwaring et al., 2009).

Females can alter the size of the eggs to increase the initial size of junior hatchlings compared to seniors at hatching, increasing early growth of juniors (Mainwaring et al., 2012). This altered egg size however does only partly compensates the size differences because of the age hierarchy within the nest (Mainwaring et al., 2012).
So, to catch up with their older siblings' juniors must alter their development to fledge at the same time. Barn-swallows decreased their investment of wing development to catchup with body growth (Mainwaring et al., 2009). Catching up in body size is important to ensure food in the nest by being a more notable begger, whereas wing development would be more important after fledging (Mainwaring et al., 2009).
Studies on other species have shown an initially decreased growth-rate of juniors but in these species they do eventually catch up in size during fledging (Dey et al., 2014). Juniors can catch-up with compensatory growth, a way of growing which is faster than optimal, when food is abundant (Hector et al., 2012). This shows that the birds do experience food scarcity in the beginning of their life, resulting in potential life-long consequences.
Lastly great tit juniors do not show any effect on their size or mass during fledging. However a study by Stier et al. found reduced telomere lengths and increased oxidative stress in the junior chicks. This indicated some form of stress on the junior nestlings (Stier et al., 2015), which shows again that the junior chicks are less cared for by the parents than the older siblings are. Indicating that hatching asynchrony indeed results in adaptive brood reduction. Only caring for the junior chick if the more senior chicks are fully saturated. Earlier research has shown some definite negative impacts of growing in lesser neonatal conditions (Blount et al., 2006). In the next chapter I will discuss these effects to see what kind of long-term effects the juniors can experience due to their lesser nesting period.

The expected long-term effects of a compromised nesting stage.

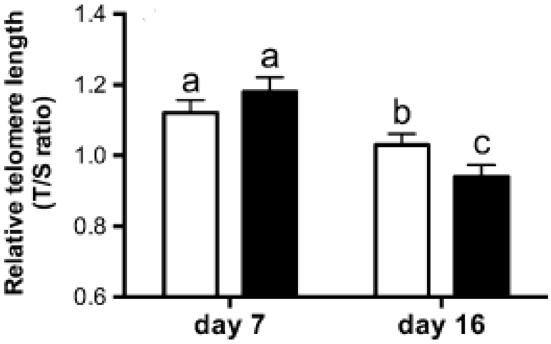

Figure 3: The shortening of relative telomere length of great tits between day 7 and the day 16 of the development. Juniors are showed by dark bars and seniors are showed by the white bars. The letters on top show if the relative telomere lengths differ significantly. (Stier et al., 2015)

As discussed in the last chapter a study on junior great tits found that juniors ended growth with shorter telomeres than their senior siblings (Stier et al., 2015) (see figure 3). Telomeres are DNA endings that protect the chromosomes from losing information and interaction between the chromosomes. During cell division the telomeres tend to shrink due mainly because of incomplete end-replication (Boonekamp et al., 2014). Because of this telomeres shorten with age and the length of the telomere can be used to predict the lifespan of an individual (Boonekamp et al., 2014). As seen in figure 3 Juniors lost more telomeres than seniors, suggesting that they used less energy for self-maintenance (Boonekamp et al., 2014). Telomere length predicts mortality in adult birds, so losing more telomere repititions is an indication for a shorter life expectancy, and an older biological age (Boonekamp et al., 2014). A study on Jackdaws shows that developmental stress accelerates telomere shortening (Boonekamp et al., 2014). The same study on jackdaws showed that chicks in enlarged broods lost 21% more than chicks in reduced broods.
In figure 3 the reduction of the telomere length of the great tit nestlings is shown. The difference of telomere shortening between seniors and juniors is larger than the effect of enlarging broods in the jackdaws, juniors lost around 200% more telomere than their siblings. Although the effects can't be fully compared due to different timespans between the first and second measurements it is an indication that the effect of being a junior is significant.
To fledge synchronously within a nest compensatory growth was found in studies on great tit and barn swallow juniors (Stier et al., 2015;Mainwaring et al., 2009). Compensatory growth is a phase of rapid growth in response to a phase of slow growth due to dietary restrictions (Hector et al., 2012). This rapid growth is faster than optimal, causing multiple physical problems (Hector et al., 2012). Compensatory growth can decrease cell functioning efficiency, lower resistance to physiological stressors and decrease the immune function (Hector et al., 2012). Therefore we can expect a lower survival rate of juniors that implement compensatory growth to catch-up with their peers. The effects of compensatory growth can persist after the nesting phase (Hector et al., 2012). So it is expected that juniors that implement compensatory growth are affected by this in their adult life.
A study on barnswallows mentioned that the skeletal growth was favored by juniors over wing development (Mainwaring et al., 2009). Other species showed a decreased skeletal growth to ensure the ability of flying out at the same time of their siblings (Mainwaring et al., 2009). Chosing skeletal growth over wing development can decrease the ability to migrate or forage (Mainwaring et al., 2009) having detrimental effects on the fitness of these birds. The juniors are facing a dilemma because it is known that skeletal growth stops after the growth phase whereas chicks are able to catch up with feathergrowth (Mainwaring et al., 2009). A decreased skeletal growth or body mass most likely persist throughout life and affects fitness greatly (Macleod et al., 2016; Hector et al., 2012). Size is known to have positive effects on mate selection, fecundity and offspring survival (Hector et al., 2012). So being smaller as a junior would mean being inferior on these traits compared to seniors, decreasing the fitness of adult juniors.

A study by Blount et al. looked at the effects of bad neonatal conditions on captive zebra finches (Blount et al., 2006). This will be used to make expectations about the long-term effects of being a junior. As is shown in the last chapter, the neonatal conditions are worse for juniors than for seniors. This study shows that being raised during low quality neonatal conditions constrains adults in their ability to accumulate antioxidants required for reproduction (Blount et al., 2006). This resulted in consequences for the reproductive success due to laying breaks and a slower laying rate within a clutch (Blount et al., 2006). Although no effect was found on the clutch mass, size or yolk antioxidant levels (Blount et al., 2006). This shows that there are consequences of reproductive success due to worse neonatal conditions. So it is expected that the worse nutrition of juniors compared to their siblings will have persistent effects on juniors in their adult life. Therefore a lower reproductive success is expected for the youngest chicks, even if only the survivors of the nesting stage are compared to their siblings.

Other studies on wild living avian species also showed that early development can greatly influence adult traits. The early development of passerines can have a big impact on fecundity (Macleod et al., 2016). Next to this receiving bad conditions during early development influences social dominance and sexual attractiveness in adulthood (Lindström, 1999; Mainwaring et al., 2009). This would suggest that being a junior has a big impact on fitness, having a disadvantage during sexual selection. Even if a sexual partner is found it would be more likely to be an inferior mate and the reduced fecundity of juniors would affect the reproduction of juniors. Next to this bad conditions during early development show a decrease in metabolism and immunocompetence, influencing survivability in adulthood (Lindström, 1999).

With the effects of hatching order found in the nest it can be expected that hatching order still has effects during adulthood. Growing up with lesser conditions decreases lifespan, reproduction, dominance and physiology of juniors. So answering the question: Do the negative effects of hatching last persist during adulthood? It is expected that the negative effects do persist during adulthood.

Long-term effects of hatching last studied thusfar

There is limited empirical evidence on whether hatching order effects persists into adulthood, especially in the wild (Dey et al., 2014). In the search for long-term studies on this topic 8 studies were found of which 1 was about the zebra finches in captivity and one was on the synchronous hatching hihi (table 2). These studies were found through searching google scholar and seeking for references in articles. These are the studies found that were conducted on this topic, but it is not certain that some are left out.
Similar as in the nesting phase some studies showed that being a junior leaded to a decreased life-expectancy after the nesting phase (Mainwaring et al., 2009; Song et al., 2018). However, in most long-term studies this effect was not found or not mentioned (table 2). Studies on western gulls and blue-footed boobies showed that juniors had significantly lower survival rate during the nesting and juvenile stage, but after they survived these stages the survival rate was similar to that of seniors (Spear et al., 1994; Drummond et al., 2013). This shows that the most severe effects of being a junior are preceived during the nesting phase.

Table 2: long-term effects of being a junior. Empty cells means that the trait was not quantified in that study. Yes, stands for: the effect was encountered in the study. No stands for: the effect is not encountered.

	Males are more attractive	**negative long-term effects found**	**Lifespan**	**Later starting with reproduction**	**Lower adult survival rate**	**Offspring is of lower quality**	**Lower reproductive success**
Zebra-finch (Mainwaring et al., 2012)	Yes	No	5				
Hihi (Macleod et al., 2016)		No	3				No
Crested Ibis (Song et al., 2018)		Yes	25	Yes	Yes	Yes	Yes
Western Gulls (Spear et al., 1994)		No	25		No		
Pukeko (Dey et al., 2014)		Yes	6				
Blue footed booby (Drummond et al., 2013)	No	No	17	No	No	No	No
Barn swallows (Mainwaring et al., 2009)		Yes	4		Yes		
Common tern (Vedder et al., 2021)		Yes	10				Yes

A study by Dey et al. about the pukeko shows that juniors had lower dominance ranks during adulthood compared to seniors (Dey et al., 2014). Being a subordinate individual results in living and breeding in inferior territories. Next to this the subordinate individuals have a disadvantage during sexual selection. Although there are some caveats, overall, a higher dominance rank increases the survival rate and reproductive success of birds (Piper, 1997). Having a lower dominance rank does also indicate that junior adults are physically not as capable as senior adults. This together shows that Pukeko juniors do receive persistent negative effects due to being a junior.
Male juniors of zebra finches in captivity were more attractive to females compared to their siblings that hatched earlier (Mainwaring et al., 2012). This study was conducted with an unlimited amount of food, so it is probable that some of the negative effects of being junior did not occur during their nesting stage. But it does show that there could also be positive effects of being a junior, especially when food is abundant and when there is no risk for predation. In the same study there was no significant effect found on the attractiveness of females, but a weak trend was found that senior females were more fecund than juniors (Mainwaring et al., 2012). So, in ideal situations it seems that males receive positive effects from hatching last whereas junior females are not significantly affected.
A study on the common tern also found a decrease in offspring produced by juniors, but the 2nd hatchling preceived more negative effects in the adult life than the 3rd (Vedder et al., 2021). Next to this a long-term study on the crested ibis showed that senior adults started reproduction at a younger age (Song et al., 2018). Furthermore, juniors had a lower adult survival rate and achieved a lower lifetime reproductive success (Song et al., 2018). A reduced reproduction due to the lesser neonatal conditions can be explained by the juniors allocating resources to the survival of the nesting stage, compromising on reproduction development (Vedde et al., 2021). The offspring of the ibis juniors were also of lesser quality, they had smaller tarsi and lesser body conditions (Song et al., 2018). This study, along with a study on blue-footed booby, was the only study showing that negative effects of hatching last carried over to the next generation. However, the study on blue-footed booby only found an effect on the fitness of offspring produced in the first 3 years of the junior lifespan (Drummond et al., 2013) (Figure 4). The probability of recruiting in the first year was significantly lower for the offspring of junior booby parents. At the age of four this effect was cancelled out. Because of this recovery, the breeding success of junior boobies overall did not significantly differ from the breeding success of seniors (Drummond et al., 2013). And the reproductive success of junior females even outperformed the senior females. Most other studies did not look into the effect that being a junior had on the quality or quantity of offspring. Therefore, it is hard to say if there is a universal decrease in fitness due to the hatching order of parents.

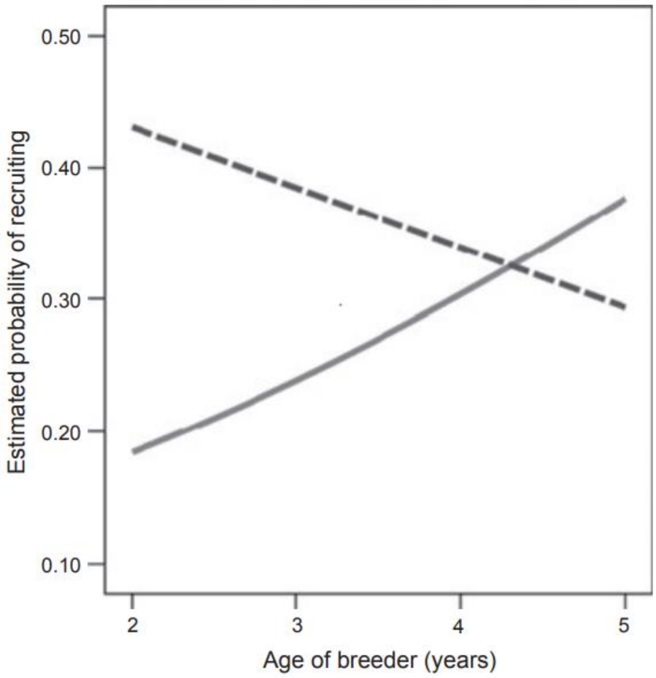

Figure 4: Estimated probability of recruitment of offspring of former blue-footed booby juniors (grey line) and seniors (dashed black line) in relation to the age of the breeders. Probability was estimated from mixed logit models and based from the offspring of 201 seniors and 182 juniors. (Drummond et al., 2013)

Discussion

There are some effects of being a junior that are found after fledging (table 2), but in long living birds it seems that the negative effects for fitness will start to vanish after a couple of years (see fig.4). In these species there are no effects on the overall life-time reproductive success. In some species junior females even outperformed senior females (Sutherland, 1989, Spear et al., 1994). This suggests that the long-term effects of being a junior is more prominent in short-living avian species (like barn-swallows: 4 years). These short-living species might just not able to outlive the short-term effects of being a junior in the nest. Another hypothesis is that passerines are more affected by being the youngest hatchlings than sea birds, as passerines are altricial and sea birds precocial. Altricial chicks are more reliant on parental care than precocial birds (Francisco-Morcelli et al., 2021). The studies on long-term effects featured in this article are mainly done on precocial birds. The altricial birds that were studied in the wild were on the barn-swallow and the Hihi. The Hihi did not show any negative long-term effects, but the barn-swallow did. The Hihi however is not an asynchronous breeder, so the age differences between juniors and seniors were minimal. The Hihi however did unlike unexpectations show effects of being a junior in the nesting-stage, showing that not only "asynchronous" hatching birds are affected by hatching order.

Not a lot of the expectations made in chapter 2 seem to be found in the long-term studies. Most species did not show any long-term negative impacts from being the youngest in the nest (table 2). Whereas it was expected that Juniors did have a lower survival rate for example, partly due to the reduced body mass. Looking at table 2 this is only encountered in two studies looking at the barn swallow and the crested ibis (Mainwaring et al., 2009;Song et al., 2018). Long-term studies on two long-living seabirds did also investigate the adult survival rate of juniors but did not find any effect from hatching order (Drummond et al., 2013;Spear et al., 1994). The expectation of having a lower adult body mass as juniors was encountered in the study about the pukeko. The junior fledglings showed a decreased size compared to seniors. The expectation was that this would lower their dominance rank in the adult life. This lowered dominance rank was indeed found in adult juniors with possible big impacts on fitness (Dey et al., 2014).

There are not a lot of universal conclusions to draw from this collection of studies. This is because most long-term studies studied different fitness traits. And when the studies did look into the same traits, the results differed (table 2). This is most likely because each species has its own lifestyle, strongly differing in food collection, nesting stage, lifespan, migration, and predation risk. So being a junior can have varrying effects on different bird species. Overall, most of the long-term studies did not show any significant long-term negative impacts due to being the youngest in the nest (table 2). When comparing this to table 1 it seems that juniors are mostly affected during the nesting stage, and in some species during the junior stage (Spear et al., 1994). After those life-stages, most species did not show any effects. This could be explained by the hypothesis in the introduction: The lesser juniors are dying before the juvenile stage and the juniors with the best genotypes are not significantly distinguishable from the seniors during adulthood.

Most long-term studies on juniors studied only juniors of one breeding season. Studying juniors for of only one breeding season does not take effects during changing food supplies into account. Evidence has shown that food-supply does strongly affect the fitness of juniors (Sutherland, 1989; Vedde et al., 2021), this is because a junior is mainly fed when the other siblings are saturated. A deficit of food will imply more negative effects than in normal situations, it would be interesting to see what the long-term effects are of juniors growing up in a situation with a deficit of resources.

In the study on Zebra finches in captivity a difference was observed between the sexes. Males perceived positive effects from hatching last whereas females were not affected by the hatching order (Mainwaring et al., 2012). This shows that at least under the ideal situation there is a difference in the effect of hatching last between the sexes. This is also mentioned in other papers, and it is hypothesized that birds select sexes to be in certain positions in the hatching order (Arnold et al. 2003). It would be interesting to see what the long-term differences of being a junior is between the sexes in the wild and if there is indeed a correlation between sex and hatching order. Lastly most of the long-term wild studies used for this article had small sample sizes and followed juniors of one breeding season (Macleod et al., 2016; Song et al., 2018; Mainwaring et al., 2009; Dey et al., 2014). The small sample sizes (less than 50 broods) can partly be explained by the fact that the death rate of junior nestlings is significantly higher, shrinking sample sizes for long-term studies. These small sample sizes decrease the certainty of conclusions. There were three studies done with large sample sizes. These studies investigated blue-footed boobies, common terns and western gulls. The studies on the gulls and boobies did not find any negative long-term effects (Spear et al., 1994;Drummond et al., 2013). Whereas the study on the common tern did find some negative effects on fitness that persisted during adulthood (Vedde et al., 2021). It is impossible to base universal conclusions on only these three species as their conclusions are contradictory. This would suggest that the effect of being a junior in the adult life stage is species specific, unlike the short-term effects (table 1). Also these species are fairly similar as they are all big, long-living seabirds with precocial offspring. More research on the long-term effects of hatching asynchrony on passerines and other bird classes is needed. This would show if the long-term effects are indeed species specific or if they are universal throughout the Aves class.

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