Breeding Sabbaticals in the Black-tailed Godwit *Limosa limosa limosa*

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Abstract

As reproduction is a major component in population dynamics it is important to understand why birds do not breed. For this reason the main question in this research is: Is having a breeding sabbatical common in black-tailed godwits *Limosa limosa limosa*, and if so, why do they occasionally skip their reproduction? To answer the main question we will first have to answer two sub questions. First we need to know how many godwits take reproductive sabbaticals. Second if these non-breeders have distinctive characteristics. To answer these questions data was gathered in meadows in south-west Friesland, which was part of the 11 year running godwit population dynamics research. Reasons for breeding sabbaticals found in literature are related to age, loss of a partner, arrival date, inexperience and food availability. 10% of the godwit population in the northern Workumerwaard did not breed in 2014. The only reason for skipping reproduction we found was the difference in experience. Inexperienced birds, that had not yet bred in the years before, had a higher chance of being a non-breeder than experienced ones. This means inexperienced non-breeders have a higher chance to stay inexperienced in following years as well. What the actual reasons are for non-breeding are discussed but it is still difficult to answer this question.

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1. Introduction

As reproduction is a major component in population dynamics it is important to understand why birds do not breed. For this reason it is an interesting subject to do research in. Researchers have been looking at the optimisation of reproductive timing (Cresswell and McCleery 2003, Both and Visser 2005), clutch sizes (Charnov and Krebs 1974, Both 2000), growth speed (Anteau et al. 2014) and survival of the chicks (Kentie et al. 2013). The fact that animals can choose or be forced to not breed in certain situations has not been looked at that much yet, but see table 1 for exceptions. We will call this anomaly a "reproductive sabbatical" from now on (Kazama et al. 2013). To understand the reasons and consequences behind these reproductive sabbaticals we first need to define what it really is. In many species, including humans, the young do not reproduce until a certain age (Komura et al. 1992). Therefore a 'Non-breeder' (a bird skipping a breeding season, i.e. taking a reproductive sabbatical) is: An individual that does not breed in a certain year but has bred in previous year(s) or is physically capable of reproducing Drent and Daan (1980). Introduced the "prudent parent hypothesis" which posits that "non-breeding decision should be favored, when the value of the immediate reproduction is low relative to the value of future reproductive opportunities and survival" (Goutte et al. 2011, p. 790). This means there has to be a negative influence causing an animal not to breed. Apart from environmental effects, literature states three main reasons for animals to take a reproductive sabbatical (table 1). The first reason is food availability: if there is not enough food to guarantee the offspring and parents will survive a breeding attempt, it is better to choose not to breed. The second reason found is the loss of a partner and third the loss of the breeding site. When either the partner or the breeding site is lost it takes time to find a new partner or to find or make a new nest. This time loss can result in not having enough time to still be able to breed. If birds are forced to skip their reproduction to often it can result in the population to decline. For this reason it is interesting to study this non-breeding behavior and the driving forces behind it to understand population dynamics a little better.

Table 1: Stated reasons for breeding sabbaticals in 13 species in literature.

Species	Reason for sabbatical	Source
Kittiwake *Rissa tridactyla*	Site fidelity	Danchin & Cam (2002)
Eurasian oystercatcher *Haematopus ostralegus*	Loss of mate	Bruinzeel (2007)
Cory's shearwater *Calonectris diomedea*	Multiple: site/mate fidelity or low food availability in winter	Mougin et al. (1997)
Herring gull *Larus argentatus* & lesser black-backed gull *Larus fuscus*	Food availability	Calladine & Harris (1997)
Short-tailed shearwater *Puffinus tenuirostris*	Loss of mate	Bradley et al. (2000)
Fat dormice *Myoxus glis*	Food availability	Pilastro et al. (2003)
Common toad *Bufo bufo*	Summer too short to gain energy and reproduce (Environmental effects)	Loman & Madsen (2010)
European storm petrel *Hydrobates pelagicus*	oil-spill pollution (Environmental effects)	Zabala (2011)
Roughlegged buzzard *Buteo lagopus*	Food availability	Glutz von Blotzheim (1971)
Tawny owl *Strix aluco*	Food availability	Southern (1970)
Barn owl *Tyto alba*	Food availability	Bruijn (1979)
Red-footed booby *Sula sula*	El-Niño events (Environmental effects)	Cubaynes et al. (2011)

In this research we will be looking at a population of black-tailed godwits *Limosa limosa* in the Workumerwaard in the Netherlands. Since 2004 research on population dynamics has been done on the black-tailed godwit (figure 1). This bird, which is also known as the king of the meadow, is found all over eurasia 40% of the north-west European population of the subspecies *Limosa limosa limosa* breeds in the Dutch meadows (Schroeder et al. 2009). When wintering in west Africa (Kam et al. 1999) they mainly eat rice (Lourenço and Piersma 2008). On the mudflats the birds diet consists mainly of bivalves, molluscs and some larvae of insects (Moreira 1994, Estrella & Masero 2010). In the meadows it usually eats earthworms (Roodbergen et al, 2008). Not all birds start breeding in their second calendar year (Kentie et al. 2014), some birds stay another breeding season on their wintering grounds (Groen & Hemerik 2002). Godwits are a long-lived species, the oldest known individual became 29 years, 9 months and 8 days (Redactie Groen 2011). They are considered long-lived species and lay 4 eggs each breeding attempt (Stastny 1991). In 11 years of research not a single bird has been recorded to have divorced from its partner. (Kentie et al 2014), meaning they are extremely partner faithful. They are not just partner faithful but also site faithful (Groen 1993, Brink et al 2008, Kentie et al 2013). Older individuals come back to within 300 m from their nest from the previous year, while young birds tend to spread out a little more (Kentie et al. 2013).

Figure 1: black-tailed godwit *Limosa limosa limosa*

In the 11 years of research already done anomalies were noticed where certain birds would migrate back to the breeding grounds but then they were never seen having a nest (pers. comm. J. Hooijmeijer). This behavior has not been properly documented yet. It is possible that these individuals return to the breeding grounds with the intention to breed, but for some reason they are not able or they choose not to. Does this behavior indicate the before introduced breeding sabbaticals? To be able to conserve these birds it is imperative to know if godwits do take reproductive sabbaticals and understand the driving forces behind reproduction and in this case the lack of these driving forces. If these birds do skip their reproduction this has to be implemented in the models on population dynamics.

Earlier it was explained that the most common reasons for skipping reproduction (table 1) are: Food availability, the loss of a partner or the loss of a breeding site. As godwits make a new nest each breeding attempt, so as long as the meadow the godwits breed in is not transformed into a different type of land use this last reason is not applicable for this species. When there is not that much food available the godwits might not be strengthened up enough to be able to breed. Losing your partner means you have to find a new one, which might take time. Other reasons can be thought of when trying to understand this non-breeding behavior, such as age. The prudent parent hypothesis states that a bird should only breed when the cost of breeding is lower than the reproductive outcome. This would apply mainly for young birds which still have a lot of time to breed in other years (Goutte et al. 2011). On the other hand, Goutte et al. (2011) also states that senescent birds could take advantage of reproductive sabbaticals to recover from a previous breeding attempt. Whether a bird is experienced in breeding or not, can mean it decides to take a breeding sabbatical in order to first learn from others before attempting to breed itself. A last reason could be that birds arrive at the breeding site rather late in the season and cannot find a mate anymore or there is just no time left to breed before they need to leave for Africa again.

Not knowing how common it is for godwits to take reproductive sabbaticals and which of the above mentioned reasons applies to the godwits, the main question in this research is: Is having a breeding sabbatical common in black-tailed godwits *Limosa limosa limosa*, and if so, why do they occasionally skip their reproduction?
To answer the main question we will first have to answer two sub questions:

- How many godwits take reproductive sabbaticals?
- Do non-breeders have distinctive characteristics?

In an attempt to find out what the mayor driving forces are in birds skipping their reproduction the following hypotheses will be tested.

- Age: the youngest and and oldest birds of the population take reproductive sabbaticals.
- Loss of a partner: birds taking a reproductive sabbatical have lost their partner.
- Arrival date: birds which take a reproductive sabbatical arrive later in the season and therefore lack the time to still breed.
- Experience: birds taking a reproductive sabbatical are inexperienced and therefore do not breed in subsequent years.
- Food availability: birds which are energy constrained take a reproductive sabbatical.

2. Methods

2.1 Fieldwork

To gather the data needed to answer the research questions fieldwork has been done. This fieldwork was done as part of the long term godwit study mentioned before. This study was done in the meadows of south-west Friesland (figure 2). In most of the areas the situation was not optimal to be able to see the birds very well, because of high grass or no spots to observe from without disturbing the whole meadow. To know for sure that all birds that were not associated with a nest were indeed non-breeders, a more suitable area was needed. For this reason the Workumerwaard (figure 2) was picked where it was possible to see the birds relatively easily, because the grass was kept short by foraging geese, and the meadows have clear borders which make observing easier. The Workumerwaard is approximately 500 hectares and is situated in South-West Friesland. It was populated by about 30-60 breeding pairs of Black-tailed godwits per 100 hectare (Kentie et al. 2013). As it was needed to observe the birds very closely, a slightly smaller area was preferred and therefore only the northern part of the Workumerwaard (300 hectares) was used for this study.
Since 2004 fieldwork has been done in south-west Friesland. Daily observations of colour- banded birds form the basis of this fieldwork. Banding of the godwits has been taking place since the beginning and therefore a substantial fraction of the birds is now

Figure 2: Study area for the black-tailed godwit research in south-west Friesland. The enlarged figure is the Workumerwaard with the northern part framed with orange (Kentie et al. 2013).

banded. They are banded with a flag, 4 color rings and a metal ring. When observing a bird the color-code was noted down together with its behavior, whether it had a partner and its abdominal profile (API). The abdominal profile is a measure for a birds fat reserves. Before the birds started breeding, a count of the godwits was done per meadow twice a week to estimate how many godwits were present at that time. When the birds started breeding, the nests were searched for by looking at the birds behavior. Making practise nests, territorial behavior like fighting or just the fact that the bird had been seen many times in that area already gives a clue of where the nest will be. When a good guess is made of the location of the nest or the bird sat on the nest we went into the field to actually find the nest. If many nests seemed to be located near each other it was useful to just search a large part of the field. Coordinates of the nest location were be documented together with nest history. Nest history being state of the eggs on each visit. By using the egg flotation method (Liebezeit et al. 2007) the hatching date has been determined. This is a method where the position of the egg in water tells how long the egg has been incubated. After hatching the chicks were banded. To determine who was associated with the found nests, they were observed. First with a telescope and if the birds did not want to come back within 45 minutes (shorter if the weather is bad) a camera was placed next to the nest to find the nest associates after all. These cameras were only placed when the nest had a full clutch and preferably later in the breeding period to make sure the bird did not abandon the nest. In 2014 the observations were more focused on determining which birds were associated with which nest than in previous years.

2.2 How many godwits take reproductive sabbaticals?

Preperation of the data

To be able to analyze whether birds had bred or not required preparation work on the data. Not all sightings in the Workumerwaard were birds which also really belong in the Workumerwaard. There can be birds from neighboring meadows visiting the study area or young birds which were looking for a nesting place but eventually choose a different area. Before the data could be used these sightings needed to be filtered out. This means only the birds which had had a nest in the Workumerwaard; been seen chick guiding in the area; were paired to a breeding bird and birds that were sighted more often in the Workumerwaard than outside the study area will be used for analysis. Only the adult birds are used for the analysis as the chicks of that year cannot breed yet.
Now only the birds that belong in the Workumerwaard are left the next step is to find out which birds were breeders and which were not. Breeders are birds which had a nest; have been seen chick guiding or are paired with a bird which has been classed as a breeder. The rest is classed as non-breeder. The analyzing work was done in R i386 3.1.0 and Microsoft Excel 2007.
Calculating how many birds are non-breeders was done with formula 1.

$$\frac{\#"non-breeders"}{\#"sighted\ birds"} = percentage\ "non-breeders"$$

Formula 1: calculation of the percentage of non-breeders in the population.

Mayfield

Even though the observation intensity of colour rings was sufficient, the observations of the nests presented a bigger issue. It was impossible to find every single nest in the area especially because of predation. If a nest is predated before it was found the birds were seen as non-breeders even though they did attempt to breed. To cover this the Mayfield method was used. With a Mayfield analysis daily nest survival rate was estimated (formula 2) (Mayfield 1975), which can be used to calculate how many nests there have really been. By comparing Mayfield nest success with ‘apparent’ nest success it was possible to calculate the

number of nests that we did not find. Formula 3 shows how the total amount of nests including the ones which we missed because of predation was calculated.

$$\text{Daily survival rate} = \frac{\text{Exposure days} - \text{\# of failed nest}}{\text{Exposure days}}$$

Formula 2: Calculation of Daily Survival probability (Mayfield 1975)

$$\text{\# nests} = \frac{\text{\# found nests} - \text{\# failed nests}}{\text{DSRtotal}}$$

Formula 3: Calculation of total nest amount (pers. comm. R. Kentie)

Second nest attempts

It is known that black-tailed godwits can start a second and even a third nest when their first fails (Senner et al. 2014). If the first nest did not survive very long, the nest associates may not have been identified. Therefore it is possible that a second nest attempt was mistaken for a nest of different birds. To determine how often second clutches occur in the Workumerwaard and if this should be taken into account in analyzing the amount of non-breeders, observed second clutches were noted.

The definition of a non-breeder

A non-breeder is a bird which does not breed in a certain year but has bred in previous year(s) or is physically capable of reproducing. First off all, not all breeders were identified as such which means some birds were classed as non-breeders while in reality they were breeders. These just have never been seen at a nest or showing nesting behavior. Secondly, to make a better estimate of how many birds were non-breeders, the Mayfield method was used. Because of this method it was no longer known who were the non-breeders which made it impossible to know whether these birds have bred in previous years. The 10% non-breeders which was calculated can therefore consist of birds which have never bred before and also did not do so this year. Think of 2nd year birds. Because of these reasons the term non-breeder will from now on be used as: the group of birds which consist of the actual non-breeders and birds which are actually breeders but have not been identified as such.

2.3 Do non-breeders have distinctive characteristics?

Age

The age of godwits can no longer be distinguished after their first year. This means the birds need to be caught as a chick because else it is not known what age it was when caught. For this reason only birds which were caught as chicks will be taken into account in analyzing whether age has a relation to being a non-breeder or not.

Loss of partner

To be able to look at partners it is first needed to find the partners of all birds. Finding the partners can be done by looking at sightings where a bird has been paired with another bird. If a bird is associated with a nest together with another bird they are paired as well. When it is not known who the partner is but a bird has been breeding or chick guiding it has a partner for sure but it is unknown who it is. This is noted with “Unknown”. When a bird does not meet any of the criteria described above it is considered to have no partner.
The hypothesis is that a godwit which is a non-breeder in 2014 has lost its partner. This means it had a partner in 2013. It is also possible that the partner has not been sighted in 2013 but has in years before that. For this reason all partners have been looked up in the years 2013 to 2009. This data was then related to whether or not the non-breeders had a partner in 2014.

An alternative hypothesis can be that a godwit which lost its partner will look for a new partner and breed in that same year with the new partner. To look at this, we distinguished whether the partner from previous years was present and how many birds bred in those categories.

Arrival time

One of the hypotheses was that non-breeders on average arrive later in the breeding area than breeders. These so called late comers will be observed later for the first time than breeders. In the database the first observation of each bird was looked up and correlated with being a breeder or not. The data was plotted in a boxplot and tested with an Anova test.

Experience

Birds taking a reproductive sabbatical are inexperienced and therefore do not breed in subsequent years. If this hypothesis were to be true it means that the godwits have not bred in previous years. Looking in the database gave nestID's for each bird. If the bird is associated with any nest in previous years it is considered experienced. Also birds seen chick guiding in any previous year or have been paired with a bird which meets the above stated criteria were considered experienced. Whether they are experienced or not was plotted against being a breeder or non-breeder in 2014. This is done with a barplot. The difference between experienced and inexperienced breeders is tested with a general linear model (GLM).

Food availability

To test if food availability had any effect on being a breeder or not the abdominal profile index (API) is measured. The abdominal profile can be used to estimate body mass in shorebirds (Wiersma and Piersma 1995). 2012 had a rather high nest success rate (83%) and the average API of the birds was 2.17 in that year. Therefore, when the abdominal profile and therefore the body mass is sufficiently high (close or higher than 2.17) the food availability should be good enough to not restrict the birds in their activities. The abdominal profile is a measurement done in the field of how much fat the bird has. Figure 3 shows the 5 stages a bird can have from 1 being very skinny to 5 being very fat. The average of the API was used as a measurement of how much food is available. The difference in API between breeders and non-breeders was tested with an Anova test to determine whether food availability or ability to find food has an effect on being a breeders or not.

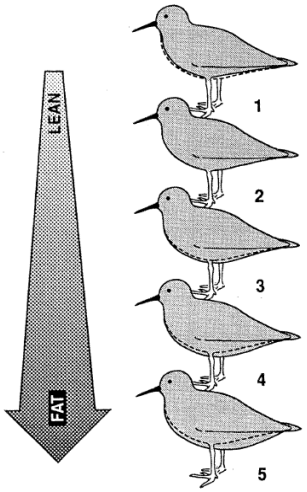


Figure 3: Abdominal profile scoring in the field. Ranging from 1 being very lean to 5 being very fat. (Wiersma and Piersma 1995)

3. Results

3.1 How many godwits take reproductive sabbaticals?

The total amount of uniquely sighted birds in the Northern Workumerwaard in 2014 was 153. Out of those 153, 76 have been identified as a breeder. The other 77 birds have not been seen breeding and therefore seen as non-breeders. By taking the total amount of non-breeders divided by total sighted birds (formula 1), we calculated a percentage of 50% non-breeders 74 out of 174 nest associates were colour- banded. From this a percentage of banded birds can be calculated: 43%.

Mayfield

The amount of non-breeders is calculated using the number of nests that were found. By using the Mayfield method explained in the methods, the daily survival rate (DSR) and total DSR was calculated. A total of 130 nests was found of which 44 failed. Using formula 3 the total amount of nests was calculated. Mayfield only included nests which have been seen at least twice so all nests which have only been visited once need to be added to this amount. This comes to a total of 163 nests. Each nest had two associates meaning there are 326 nest associates. This includes non- banded birds. Using the fraction of banded birds (43%), the total number of birds which were present in the northern Workumerwaard is calculated. This comes to 360 birds. 326 nest associates divided by 360 birds in total gives approximately 10% non-breeders. This results in 34 non-breeders of which 15 were banded. These 15 were the birds which were supposed to differ in characteristics in the second sub-question. 43% of these 326 birds were banded, which means 139 banded birds should be breeding. 76 birds were found breeding which means 55% of the breeders has been identified.

Second clutches

On the Northern Workumerwaard one case of a second nesting attempt by a banded bird was found. Out of 44 failed nests this was 2% of the nests.

3.2 Do non-breeders have distinctive characteristics?

Age

36 birds met the criteria of having to be caught as a chick. 19 of those were non-breeders and 17 breeders. Figure 4 shows that the age of the birds is not related to being a breeder or not (P = 0.6, Table 2).

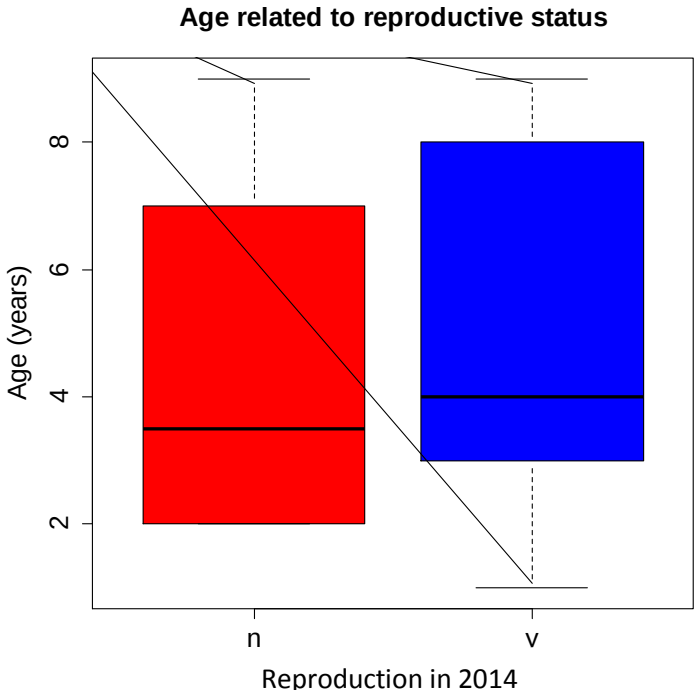


Figure 4: Box plot of breeders and non-breeders plotted against their age. N is respectively 19 and 17 for non-breeders and breeders.

Table 2: Anova test on the difference in age between breeders and non-breeders. P=0.645 which makes the difference non-significant.

	Df Sum	Sq Mean	Sq F	value	Pr(>F)
Age	1	1.68	1.677	0.216	0.645
Residuals	33	256.21	7.764		

Loss of partner

Table 3A shows the chance a bird will breed according to whether the partner was present or not. When the partner was not present not a single bird has bred. This means also no birds have changed partner and bred in this same year. When the partner is present, however, only 73% has bred. This means that it does not automatically mean that when the partner was present they bred.

Table 3: A: percentage of breeders in godwits where the last partner is present and where they are not present. N is respectively 74 and 42 birds with partner present and partner not present. B: Table showing how many birds have a partner in 2013 and in 2014. C: Table showing how many birds have a partner in the period of 2009-2013 and in 2014. In table B an C "Y" stands for yes they do have a partner in that year and "N" for when they do not.

A	breeder %
Partner present	73%
Partner not present	0%

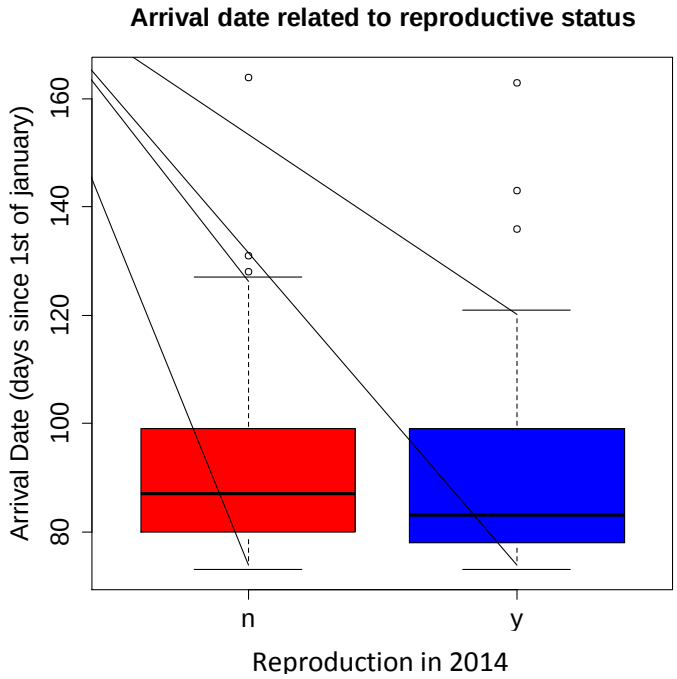
B		Partner in 2014	
		Y	N
Partner 2013	Y	12	18
	N	16	31

C		Partner in 2014	
		Y	N
Partner 2013-2009	Y	20	42
	N	8	7

Table 3B shows the non-breeders. On top the division of having a partner in 2014 and on the side the same but for 2013. It shows that there does not seem to be a relationship between having a partner in one year and having a partner in the next. There are 18 birds which did have a partner in 2013 but these were not sighted in 2014. 31 of the non-breeders had no partner to begin with and also were not sighted with a partner in 2014. It does not seem to matter whether you had a partner in 2013, as 12 birds had a partner in 2013 and 16 did not, but all 28 had a partner in 2014.

When all partners since 2009 are implemented, table 3C can be made. There are 42 birds which did have a partner in previous years but of which we did not observe their partner in 2014. These birds would qualify for birds which lost their partner. However, there were 20 birds which did have a partner in previous years and in 2014 as well, but did not breed. Consequently, not having a partner does mean you do not breed in that year but it is not certain you will breed when you do have a partner.

Arrival time



In figure 5 the arrival time of the birds which belong in the Northern Workumerwaard are plotted. Breeders and non-breeders seem to have the same spread in arrival time and this is confirmed by the linear model test shown in table 4. The P value is 0.868, therefore there was no difference in arrival time between breeders and non-breeders.

Figure 5: Box plot of arrival dates of non-breeders and breeders. N is respectively 77 non-breeders and 76 breeders.

Table 4: Linear model test on the differnce in arrival time between breeders and non-breeders. P = 0.868 which makes the difference insignificant.

	Df Sum	Sq Mean	Sq F	value	Pr(>F)
Arrivaldate	1	7	7.32	0.028	0.868
Residuals	151	39727	263.09		

Experience

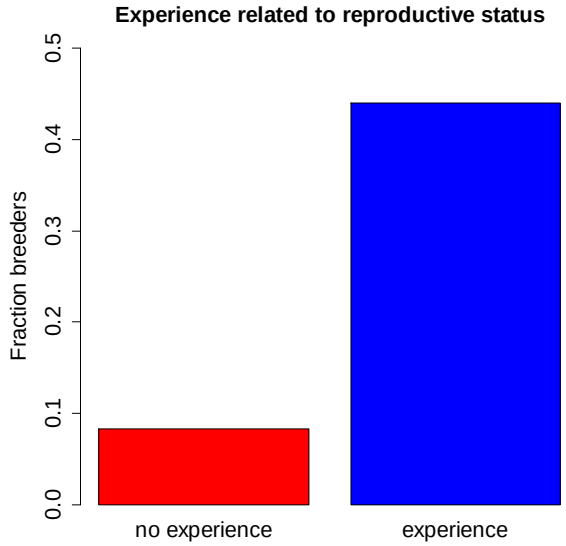


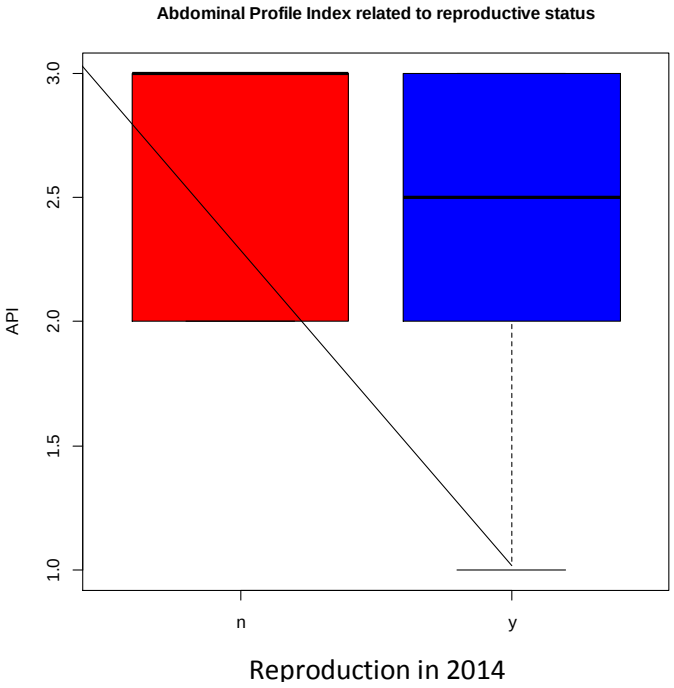
Figure 6 shows the fraction of breeders when you look at whether the godwits have had breeding experience in previous years. It shows that 43% of the birds with prior experience bred in 2014. In the case of the birds which had no prior experience 8% bred in 2014. Table 5 shows that this difference is significant with a P value of 0.04.

Figure 6: Barplot of fraction of breeders in inexperienced and experienced godwits. N is respectively 11 and 142 for inexperienced and experienced birds.

Table 5: Anova test on the difference in fraction of breeders between experienced and inexperienced birds. P = 0.0416 which means the difference is significant.

	Estimate	Std. Error z	value	Pr(>|z|)
(Intercept)	2.398	1.044	2.297	0.0216 *
Experience	2.156	1.058	2.038	0.0416 *

Food availability



The average abdominal profile (API) in 2012 to 2014 are all between 2 and 3 and seem to be going up each year. (table 6) The API of breeders is not different from non-breeders as is visualized in Figure 7. The Anova test gives a P of 0.639 which means the difference in variation in API between breeders and non-breeders is not significant (Table 7)

Figure 7: Box plot of the Abdominal profile of non-breeders and breeders. N is respectively 77 and 76 non-breeders and breeders.

Table 6: Average abdominal profile of sighted birds in 2012, 2013 and 2014.

	Average API
2012	2.17
2013	2.18
2014	2.48

Table 8: Anova test on the difference in Abdominal profile between non-breeders and breeders. P = 0.639 which makes the difference insignificant.

	Df Sum	Sq Mean	Sq F	value	Pr(>F)
API	1	0.08	0.0803	0.226	0.639
Residuals	23	8.16	0.3548		

4. Discussion

4.1 How many godwits take reproductive sabbaticals?

We found that 10% of the population godwits on the Northern part of the Workumerwaard did not breed in 2014. One of the assumptions in the setup of the fieldwork was that it would be possible to find a high percentage of the nests and nest associates. The goal set was to find a minimum of 80% of the nests. Experience pointed out that 20% of the nests is usually not found because of predation and just the fact that you are not able to find them. As we found exactly 80% of the nests, this requirement was met. For the nest associates, the minimum goal was also set at 80%. We only found 55%. This means the other 45% of the breeders is seen as non-breeders in the analysis. Following from this the analysis does not look at differences between breeders and non-breeders but in reality it looks at breeders and "possible non-breeders" as discussed in the methods. This low amount of nest associates needs to be taken into account in the analysis on the characteristics of non-breeders. In 2014 the focus was on finding nest associates and therefore we got a relatively high amount of these associates. In previous years this was not the case. Because in 2014 only 55% of the breeders were found the other years where the focus was not on finding these associates will not have enough data on these associates. For this reason it is not possible to compare 2014 to other years. For this same reason it is not known if 2014 is a representative year for the amount of non-breeders found.

It could also have been useful to look at different meadows in the study area to compare non-breeding behavior. This was regrettably not possible because the Workumerwaard is unique in the way the grass is kept short by grazing geese. In all other areas the grass grows long very quickly which makes it much harder to find the nests. The percentage of found nests in the other areas is therefore much lower than in the Workumerwaard which makes it impossible to estimate the amount of non-breeders. The Haanmeer is an exception on this, and it can be very interesting to study differences between the two study sites. Any differences found could be related to vegetation differences or the fact that the Workumerwaard is constantly grazed off by geese and the Haanmeer is not. Also predation pressure can be of influence.

Second clutches

In the Workumerwaard there was only one proven case of a second clutch. This is most likely an underestimate as in the Haanmeer there were many more cases found and even a third clutch was identified (Senner et al. 2014). This underestimation probably has to do with the fact that observation intensity on new nests was lower later in the season when the chicks were hatching. Most time went into banding the chicks and finding the nest associates of the nests which had been found. However, personal observations showed that when a nest had failed, the associated birds of that nest seemed to have disappeared and were not sighted anymore. Some of these were still sighted on the roosts on the outside of the Workumerwaard. This would suggest that at least those birds did not attempt a second nest. From this it does not seem to be a very common behavior in the Workumerwaard. Why there are so few second clutches on the Workumerwaard in comparison to the Haanmeer is not clear. It can have something to do with the predation pressure or the type of predation. When a godwit knows its nest has been predated by a predator which it knows will come back and predate its second nest as well, he will either not try a second clutch or try on a different meadow outside the Workumerwaard. To be sure about the reasons for this result more in depth research needs to be done on this.

4.2 Do non-breeders have distinctive characteristics?

Age

The results showed that age has no significant impact on being a breeder or not. The age of breeders as well as non-breeders ranges from 2nd year to over 9 years old. This means there is no age category which shows different behavior than the others. When the error in the identification of non-breeders is taken into account it is possible that non-breeders are younger than breeders. If the 45% non-breeders which are in reality breeders are older birds, the graph will change as the older non-breeders will go to the breeder side. This would give a graph which shows young non-breeders and old breeders. Even if this speculation is correct however the difference in the graph will still not be significant as there are young breeders as well. Because of this possibility it is interesting to look at age again in future research.
The hypothesis was: Mainly very young and very old birds take reproductive sabbaticals. This hypothesis has to be rejected in this study, however it is still possible that with a perfect dataset a difference in age can be found between breeders and non-breeders. Literature states that first time breeders are more affected by environmental effects than birds which are experienced (Barbraud and Weimerskirch 2005). As age can be associated with experience it means the young birds need to wait a year if the environmental conditions are not good enough. On the other hand, the old males could be skipping their reproduction like old male great tits *Parus major* (Dhondt 1985). Because of senescence, the older great tits become less efficient and the males even start skipping breeding seasons at a certain age. Great tits are short lived species but similar senescence related literature is available on the grey-headed albatrosses *Thalassarche chrysostoma*. This species is extremely long lived and shows reduced foraging and reproductive performance when they get older (Catry et al. 2006). Ricklefs (1998) states that longer lived species are most likely to reach ages where senescence effects are apparent. As senescence is more relevant in long lived species it can be possible that godwits experience a similar degradation in efficiency as the great tits do.

Partners

One of the hypotheses was that birds taking a reproductive sabbatical have lost their partner. The results show that there are indeed 42 birds of which we saw the partner in previous years but they do not breed in 2014. However, it is not certain you will breed when you do have a partner. We determined before that only 15 birds are supposed to be not breeding. When 42 birds do not have a partner in 2014 and do not breed this requirement is not met. This means not all partners have been determined which is not strange as not all nest associates were found and most of the partnerships are determined by linking birds to a nest. The individuals which do have a partner but do not breed can very well be breeders after all but just have not been identified as such. However, this is only speculation. It is possible that the hypothesis on non-breeding is caused by losing a partner is true. The results show that there was no bird which lost its partner in 2014 bred in that year. This means it is likely that losing a partner means you have to take a reproductive sabbatical. A reason for this can be that these individuals first wait for their partner to return and by the time they realize the partner is not coming anymore they need to find a new partner. This can be especially difficult for older birds because of senescence effects (Dhondt 1985, Catry et al. 2006). Failing to find a partner means you will have to take a breeding sabbatical until a new partner is found.

Arrival time

The hypothesis was that birds which take a reproductive sabbatical arrive later in the season and therefore lack the time to still breed. As there was no significant difference in arrival time this does not seem to have an effect on being a breeder or not. This is not very surprising as it

is known that birds start breeding till very late in the season (last nest was found on 9th of June). Godwits are also known to start second clutches later in the season (Senner et al. 2014), so starting a first nest later in the season should not be a problem. This means that if a bird arrives late it still has enough time to start breeding. The only birds which might have an issue with arriving late are birds that still need to find a partner. If the bird arrives when most birds already have a partner he/she will have issues finding a partner or have to settle with a sub-optimal partner. Considering godwits mate for life this last option can be disadvantageous for lifetime reproductive output.

Inexperience

The graph on experience in non-breeders shows that non-breeders are in general inexperienced birds. This means birds which have not bred before are more likely to not breed than birds which have bred at least once before. This result is consistent with other studies (Cam et al. 1998, Cam and Mannot 2000, Ainley 2002, Barbraud and Weimerskirch 2005). Even though literature supports the results, in this case it is possible that the birds which have not bred before are birds which just have not yet had the chance to breed in a previous year. For example second year birds. This can mean the result we got has little to do with experience but mainly with age. There was only 1 bird which did breed and was inexperienced and therefore we lack data to make sure the results are not just a coincidence. The fact that the amount of experienced birds is higher probably has to do with the way the godwits are banded. Most of the banded birds have been banded on the nest as breeders. These birds are by definition already experienced. This same problem was found in other studies as well (Cam et al. 1998). The high percentage of breeders in the experienced birds can be explained by godwits being partner faithful. When they have a partner they will be together and breed with that partner every year again. Taking the non-breeder identification problem into account, Around 60 birds which are now classed as non-breeders are in fact breeders. This means the experienced side will get a percentage of breeders of 87%. But more importantly if the inexperienced birds are all mistaken for non-breeders there are only 10 birds needed to change the graph to 100% inexperienced birds breeding. This will still mean that 50 birds are added on the experienced side as breeders which will bring the percentage breeders up to 80%.
The hypothesis was: Birds taking a reproductive sabbatical are inexperienced and therefore do not breed in subsequent years. This is difficult to answer as long as there is not enough information on non-breeding birds. As long as the majority of birds is banded on the nest the fraction of experienced birds will always be bigger. As there is substantial amounts of literature supporting the results a similar graph is expected even when all birds in the area would have been banded.

Food availability

Shown in the results the food availability does not seem to be an issue for the godwits in the study area. The abdominal profile in 2014 is on average 2,48 which is higher than in 2012 where it was 2,17. 2012 was a rather good year for the godwits on the northern Workumerwaard where 83% of the nests hatched (Kentie et al. 2013). 44 out of the 130 nests in 2014 failed which comes to a nest success of 66%. As the average API in 2014 was higher than in 2012 it can be assumed that food availability is not the reason for the difference in nest success between 2014 and 2012. Because of this it can be assumed that food availability does not play a major role in whether a bird takes a reproductive sabbatical in 2014. Whether food availability can have an effect on non-breeding on itself cannot be determined as it is not possible yet to look at non-breeders in other years. When data on non-breeders becomes available in different years it is interesting to study how godwits react to such situations in relation to non-breeding. As the API measurement is usually used for departure condition, it is

possible that the relation between nest success and API tells something completely different. When the API is high, many birds are already gaining reserves to start their migration. This means the low nest success in 2014 correlates with the high API, while the low API in 2012 correlates with the high nest success. If this is correct then 2014 is supposed to be a year with high numbers of non-breeders. 10% of the birds in the Workumerwaard in 2014 were non-breeders. If 2014 was indeed a bad year then this would mean that better years have lower amounts of non-breeders. Further research is needed to support this.

4.3 Final conclusion

The starting point of this research was the surprising behavior of birds migrating to the breeding grounds in the Netherlands to not breed and return to west Africa. The breeding sabbatical was the hypothesis that was tested, but there can be other reasons for this behavior. The original meaning of the term "breeding sabbatical" was to not breed after you have bred in previous years. When looking at the behavior of the non-breeding birds however these can also just be birds which do not breed at all and never have. Assuming we do have sightings of all the individual birds which belong in the Workumerwaard we did find that 10% of the birds present in the Workumerwaard did not breed. Whether these were taking a reproductive sabbatical or not is hard to say but that they do not breed is an interesting result. So what are these birds doing there if not breeding? If the non-breeders are indeed younger than the breeders, it is possible that these young birds migrate to the breeding site to take a chance at breeding, but if they fail they can always learn from the others to have a better chance in the next year. As discussed before, young birds need to be sure that the environmental conditions are right as they are more susceptible to bad conditions (Barbraud and Weimerskirch 2005). While they wait out the season they are able to get more experienced with foraging and also find a partner for the next year. Another option would be that the non-breeders are of a lesser quality. This means the other birds do not want to pair up with these individuals, or that they are incapable of making a clutch (Cam et al. 1998). What this low quality really means cannot be determined, but it could have something to do with breeding or foraging performance. Assuming the birds are not able to increase this quality, it would mean they will never get a partner which results in them never breeding. A last possible explanation, is that the non-breeders are there to support the other breeders. This behavior is seen in other birds like the Seychelles warbler *Acrocephalus sechellensis* (Richardson et al. 2007) and the Seychelles fodie *Foudia sechellarum* (Kraaijeveld and Komdeur 2003). In godwits, this option seems unlikely, as there were no observations of extra birds at nests, or when the eggs had hatched, during chick guiding. Whatever the reason, there are birds which migrate up and down to the breeding site without breeding and it remains interesting to figure out why.

4.4 Recommendations for future research.

It is not an easy task to figure out who is breeding and who is not. As it takes a lot of time to determine which birds are associated with which nests, it can be disappointing how many nest associates you miss because of predation, or just by having difficulty finding the nests. It is important to determine beforehand how much disturbance is allowed at the nest sites of the godwits. The more you observe the birds, and put cameras near the nest as early as possible, would give the best results. These actions all cause disturbance, which can result in nest abandonment, or in predators finding the nest because you leave a trail to the nest. Opinions differ on how much should be allowed. What most agree on is that cameras should not be placed near nests before all 4 eggs are laid as abandonment risk is higher in the laying period (pers. comm. A. Sybrandy). When a nest is under surveillance after the laying period and it is

noticed that the bird does not want to return to the nest while you are there, the nest should be left alone after 30 minutes. With good weather this can be delayed by 15 minutes but especially with bad weather the eggs can get cold fairly quickly.
Earlier in this rapport it was said multiple times that the banding of chicks is of major importance for this research. Therefore it is important to focus on banding as many chicks as possible to be able to determine age of each bird. This will shed more light on age related questions like the ones in this rapport. As chicks have a very low survival rate (10%) (Kentie et al. 2013) it can be more cost effective to focus more on banding old chicks. Adult animals which do not breed would also be a great addition to the database as many birds are banded on the nest itself. Because of this it is difficult to look at experience of the birds as only the experienced birds are banded. Catching the non-breeding birds can be done by mist netting or cannon netting at roosts. The database is constantly checked on mistakes, but because the data is entered by many different people there will always be mistakes in the database. When using the godwit database make sure you check the data carefully.

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