#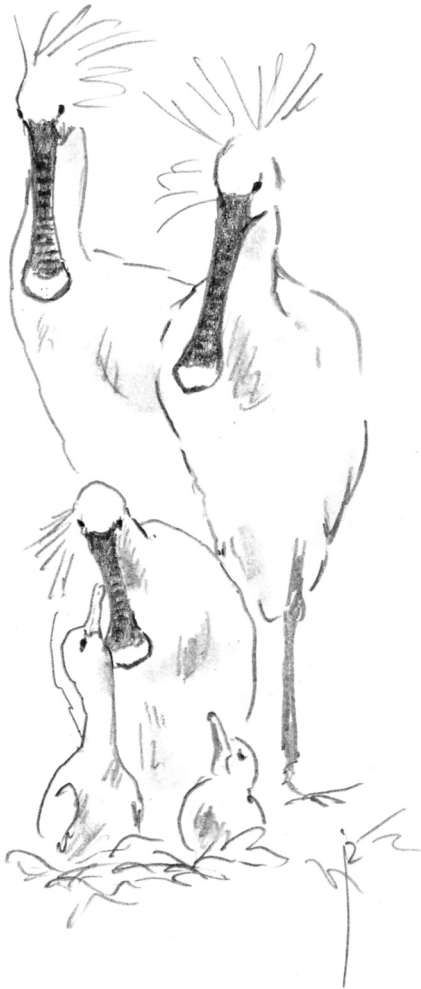 Colony-breeding Eurasian Spoonbills in The Netherlands: local limits to population growth with expansion into new areas

Thomas Oudman[1,*], Petra de Goeij[2], Theunis Piersma[1,2] & Tamar Lok[1,3]

It has been suggested that in most colony-breeding birds, food availability in the feeding areas surrounding the colonies limits, and thereby regulates, population size. However, population size is also determined by adult survival, which will additionally be influenced by circumstances outside the breeding season. Most Eurasian Spoonbills *Platalea leucorodia leucorodia* in The Netherlands breed on the Wadden Sea barrier islands. After 30 years of exponential growth, the breeding population in the Dutch Wadden Sea area is now levelling off towards a maximum of nearly 2000 nests. For these Spoonbills, density-dependent effects on survival by the different age-classes and in the different seasons have already been demonstrated. However, the mechanisms underlying the density-dependent survival of juveniles before and after fledging remain unclear. To examine whether these density-dependent effects reflect limitations at the colony level, we compared colony growth, chick condition and reproductive success among the Wadden Sea colonies. Population growth rates from 1988 to 2015 varied widely between the 10 existing colonies, and so did the statistically predicted maximum colony sizes. Chick condition, measured for 781 chicks in six different colonies between 2011 and 2015, was lower in stable colonies than in growing colonies, although not for the very late chicks, and reproductive success tended to be lower as well. Over the longer period of 1991 to 2011, reproductive success showed a strong negative relationship with colony size. We propose that the levelling off of colony sizes in the Wadden Sea is caused by local food limitations, and suggest further research in this direction. The continuing growth of the Dutch population is now being fuelled by exponentially increasing numbers of Spoonbills breeding in the Delta area.

Key words: body condition, colony size, density dependence, food availability, intertidal habitats, hinterland model, population regulation, reproductive success, wading birds

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Any growing population will, at some point, become regulated by density-dependent mechanisms in reproduction and/or survival (Lack 1954). Population sizes of colony-breeding birds have been suggested to be regulated by food availability in the surroundings of the colony (Ashmole 1963, Lack 1968, Furness & Birkhead 1984). This suggestion was based on the finding that the number of nests in different colonies reflected the relative extent of foraging areas (Furness & Birkhead 1984, Cairns 1989, Lewis *et al.* 2001), and that chick condition and breeding success decreased with colony size (Forero *et al.* 2002). However, as is generally acknowledged, these arguments largely disregard the fact that the dynamics of colony size are only one aspect of population dynamics, and do not take into account the complex interactions between survival and

reproduction (Drent & Daan 1980, Daan *et al.* 1988, Lok *et al.* 2017).

A fine example of the complexities of colony-breeding bird demographics is presented by the Eurasian Spoonbills *Platalea leucorodia leucorodia* in The Netherlands. Since the late 1960s, when the number of breeding Spoonbills in The Netherlands was estimated at fewer than 150 breeding pairs (van Wetten & Wintermans 1986), a series of environmental and protective improvements were realized and the population showed a remarkable recovery (van der Hut 1992, Overdijk 2004, Lok *et al.* 2009, Boele *et al.* 2015). After an initial phase of exponential growth mainly on the barrier islands of the Wadden Sea (Voslamber 1994, Lok *et al.* 2009), population growth has been decreasing since the 2000s, hinting at density-dependent processes acting on survival and/or reproduction (Lok *et al.* 2009). Density-dependent mortality of adult Spoonbills mainly takes place between mid-winter and the spring arrival at the breeding grounds (Lok *et al.* 2013b), which suggests that the causes of density dependence are factors operating in the distant wintering areas or during spring stopovers. Thus, they would not be expected to act at the level of the breeding colony.

However, in juveniles mortality is density dependent during the post-fleding period and during and/or shortly after their first southward migration (Lok *et al.* 2013b), suggesting limiting conditions in the breeding area (Lok *et al.* 2017). Indeed, reproductive success (measured as the average number of fledglings per nest) showed a strong negative correlation with colony size in the only colony where this had been consistently measured (Overdijk & Horn 2005, Lok *et al.* 2009). This indicates that density-dependent processes may be acting at the colony level.

To study whether colony size is regulated by density-dependent processes at the local level, we examined colony growth between 1988 and 2015 in all individual Wadden Sea colonies. We measured reproductive success (the number of fledged chicks per nest) and chick condition (observed body mass relative to average predicted age- and sex-specific body mass) in six different colonies between 2011 and 2015. These factors must be studied in concert, because higher reproductive success may actually come at the cost of reduced chick condition, resulting in lower post-fledging survival prospects when competition between fledglings is high (Lack 1954, Lok *et al.* 2013b, 2017).

Because the effect of colony size on chick condition and/or reproductive success may differ between colonies, we looked at correlations with colony growth stage rather than with absolute colony size. Because heavy rains may strongly affect both chick condition and reproductive success of Spoonbills (Lok *et al.* 2017), the effect of rain was included in the analyses. In several Wadden Sea colonies, reproductive success has been measured in multiple years since 1991, which enabled us to test whether the effect of colony size (i.e. the level of density dependence) indeed differs between these colonies. We discuss whether the observed differences in reproductive success may be caused by local differences in the extent of feeding areas and the level of food resources.

METHODS

Counts of breeding pairs

Each breeding season the number of nests in each known colony in The Netherlands was counted by a large network of volunteer observers. Except for the largest island, Texel, with several different colonies, each Wadden Sea island was treated as a single colony. Furthermore, nests no farther than 5 km from each other were considered to belong to the same colony. During the counts, colonies were carefully approached over land. Colonies that were difficult to reach without disturbance were surveyed by airplane (Texel, De Geul, 53°01'N, 4°44'W, and the Oostvaardersplassen, 52°28'N, 5°22'W).

Chick condition

Between 2011 and 2015, body condition was estimated for 781 Spoonbill chicks (see Table S1). Chicks were caught when they were large enough for rings but before fledging, usually when 20–35 days old (Lok *et al.* 2014). Body mass, tarsus length and either 8th primary length or head-bill length was measured. Following Lok *et al.* (2014), the body condition of chicks was estimated as the proportional deviation in body mass from the predicted body mass, given the sex and estimated age of the individual. Using average growth curves of 8th primary length and sex-specific head-bill length, we estimated age from 8th primary length, or head-bill length if 8th primary length was not measured. To determine sex, a blood sample of 10–80 µl was taken from the brachial vein and stored in 96% ethanol. DNA was extracted and sex-specific DNA fragments were replicated with primers 2550F/2718R (Fridolfsson & Ellegren 1999). Of the 108 chicks of which no blood sample was taken, sex was estimated from the combination of 8th primary length and tarsus length (see Appendix 1 for details).

Reproductive success

Reproductive success was estimated between 2011 and 2015 by counting the number of chicks older than approximately 25 days in the Wadden Sea colonies at the end of the fledging period. This number was divided by the number of breeding pairs, counted earlier during the egg-phase. Reproductive success data between 1991 and 2010 were assembled from Overdijk 1999 (for years between 1994 and 1998), Overdijk & Horn 2005 (between 1999 and 2004) and from unpublished records (H. Horn for Terschelling, O. Overdijk and P. de Goeij for Schiermonnikoog, F. Oud for Ameland, C. Zuhorn for Vlieland, wardens for Rottumerplaat, Rottumeroog and Griend, and E. Menkveld and E. Boot for De Schorren, Texel).

Statistics

To determine the growth stages of the different colonies and regions, we fitted both exponential and logistic regressions to the annual counts of breeding pairs. This was done with the function 'nls' in R (R Core Team 2015). Subsequently, Akaike's information criterion (AIC) was used to determine which of the two gave a better fit, using a critical AIC difference of 2 units (Burnham & Anderson 2002). Colony growth stage was defined as 'stable' when the logistic regression fitted best and the estimated slope was below 1 (hence an estimated increase of less than one breeding pair per year). Otherwise, colony growth stage was defined as 'growing'.

To test whether chick body condition and reproductive success were lower in stable than in growing colonies we compared linear mixed models using the function 'lmer' in package 'lme4' (Bates *et al.* 2015). Colony and year were included as random effects. Models for chick body condition were compared with and without colony growth stage, estimated hatching date (only for chick condition), and their second order interactions as fixed variables were compared by Akaike's information criterion for small sample sizes (AIC$_c$; Burnham & Anderson 2002). In addition, all models were compared with and without including an effect of heavy rain. For each colony, the number of days with heavy rain (>10 mm) in the previous week was calculated from precipitation data of the nearest Royal Netherlands Meteorological Institute (KNMI) weather station (Den Burg on Texel, Oost Vlieland, Formerum on Terschelling, Nes on Ameland, and Schiermonnikoog). The reproductive success data could not be used to test for an effect of hatching date or heavy rain, because the timing of breeding of different colonies has not been registered.

To determine whether the level of density dependence in reproductive success was different between colonies, we used all available data on reproductive success from 1991 to 2015 for Wadden Sea colonies. Adding colony-ID as a fixed variable in the model allowed us to specifically test for differences between colonies, using absolute population sizes instead of growth stage as the explanatory variable. To investigate whether the relationship between colony size and reproductive success differed between colonies, we compared linear mixed models with and without colony-ID, colony size and their interaction, with year as a random variable.

RESULTS

Population growth

Up to the last year of observation, the population in The Netherlands continued to grow (Figure 1), with 2908 nests counted in 2015. The population trend is best fitted by a logistic regression (see Table S2), which indicates that density-dependent effects have started to
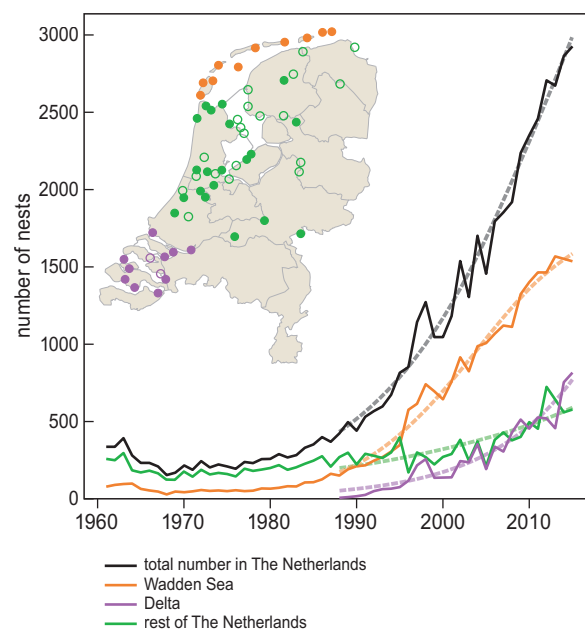

Figure 1. The total number of Spoonbill breeding pairs in The Netherlands (black) from 1961 to 2015. The Wadden Sea colonies, the Delta colonies and colonies in the rest of The Netherlands, are shown separately. In the inset, current colonies are shown by filled circles, previously used colonies are shown by open circles. Dotted lines show regressions. The totals and Wadden Sea were best fitted by logistic regressions, the Delta colonies and the other mainland colonies were best fitted by exponential regressions.
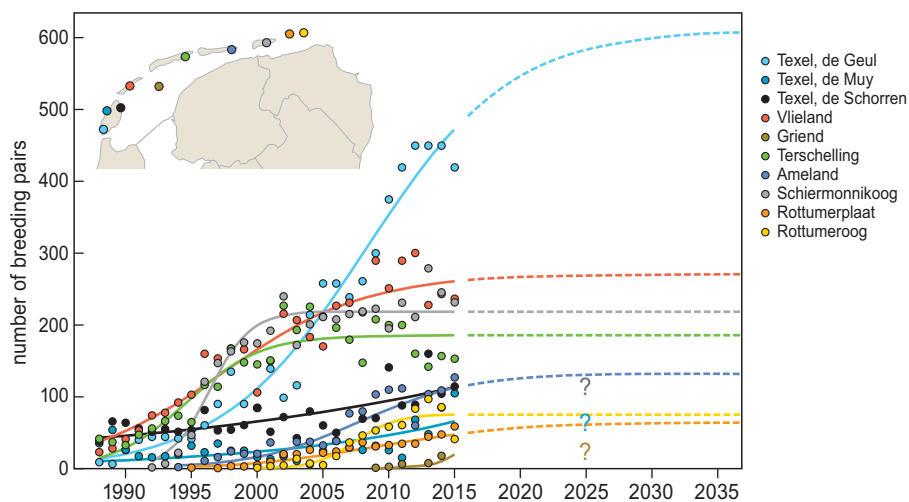
Figure 2. Spoonbill colony sizes on the Wadden Sea islands. Either exponential or logistic regression lines are drawn (solid lines), depending on which fitted best. This ignores shorter temporary trends, such as the recent decreasing numbers on Terschelling. Maximum colony sizes were estimated by extending the logistic regression lines until constant (dotted lines). In the three colonies that were best fitted by exponential regression lines, maximum colony size could not be estimated.

reduce the overall population growth rate. The predict-ed stable Dutch breeding population size is about twice the current size (Figure 1). The growth of the Wadden Sea population has been levelling off more strongly than the rest of the Dutch population (Figure 1). The current logistic regression on the data until 2015 predicts an asymptotic Wadden Sea population of about

1800 breeding pairs. The Delta population (SW Nether-lands) has kept growing exponentially since its colo-nization in the early 1990s, with 808 breeding pairs counted in 2015. The combined number of breeding pairs in the other mainland colonies is increasing slowly, adding up to 571 breeding pairs in 2015 (Figure 1).

Table 1. AIC$_c$ comparison of statistical models for chick condition (models 1) and fledgling number per nest (models 2 and 3). Models 3 also include data from between 1991 and 2010, and concern only the five colonies with at least 5 annual measurements. The five best models are shown in each selection, best models are in bold. Parameters were estimated by maximizing the log-likelihood.

Model	Fixed effects[1]	K[2]	ΔAIC$_c$	AIC$_c$ weight	Cum. weight	LL[3]
1.1	**Condition ~ stage + date + stage:date**	**9**	**0**	**0.44**	**0.44**	**671**
1.2	Condition ~ stage + date + rain + stage:date	10	1.45	0.21	0.65	671
1.3	Condition ~ date	8	2.78	0.11	0.76	667
1.4	Condition ~ stage + date	9	3.56	0.07	1	668
1.5	Condition ~ date + rain	7	4.23	0.05	1	661
2.1	**Fledglings ~ 1**	**4**	**0**	**0.61**	**0.61**	**–7.6**
2.2	Fledglings ~ stage	5	1.69	0.26	0.87	–6.3
3.1	**Fledglings ~ colsize + colonyID + colsize:Rottumerplaat**	**12**	**0**	**1**	**1**	**–47**
3.2	Fledglings ~ colsize + colonyID + colsize:location	18	11.0	0	1	–43
3.3	Fledglings ~ colsize + colonyID	11	15.5	0	1	–56
3.4	Fledglings ~ colsize + Rottumerplaat + colsize:Rottumerplaat	6	15.6	0	1	–63
3.5	Fledglings ~ colsize + Rottumerplaat	5	27.1	0	1	–70

[1]Stage: colony growth stage (either growing or stable), Date: estimated hatching date, Rain: number of days with heavy rain (>10mm) in the previous week, Colsize: refers to the number of breeding pairs in the colony, ColonyID: factor referring to the different colonies. 'Rottumerplaat' is coded 1 for Rottumerplaat, and 0 for the other colonies
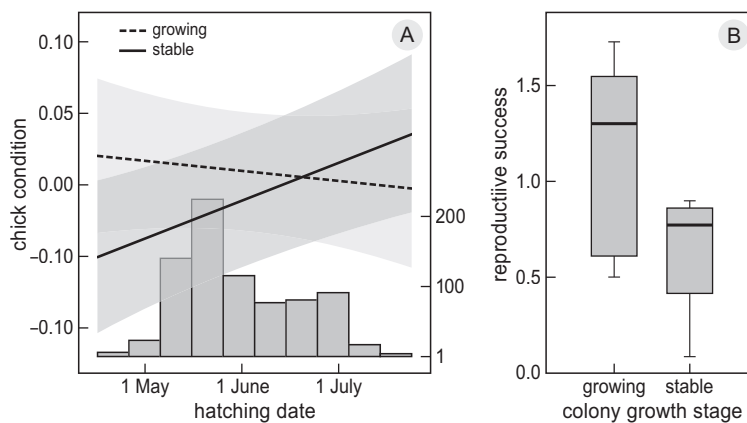[2]The number of parameters in the model
[3]Log-likelihood

Figure 3. (A) Chick condition in stable (solid line) and in growing colonies (dashed line), both as a function of hatching date. Lines show estimates of the best statistical model and grey areas show 95% prediction intervals. Bars show the frequency distribution of hatching date in all measured chicks (see *y*-axis on the right side). Most measured chicks hatched before 19 June, when the two lines cross. (B) Reproductive success (the number of chicks per nest, averaged per colony per year) tended to be higher in growing (left) than in stable colonies (right). However, a model that assumes no difference between growing and stable colonies fitted the data best (model 2.1 in Tables 1 and S3).

Colony growth on the Wadden Sea islands

On the Wadden Sea islands, all colonies have been growing since 1988 (Figure 2). The colonies in De Schorren and De Muy (both on Texel) have shown exponential growth since 1988. A new colony on Griend is also growing exponentially. All other colonies were best fitted by a logistic regression, i.e. showing decreasing growth rates in recent years (see Table S2). The number of breeding pairs on Schiermonnikoog and Terschelling have been stable since 2004 and 2006, respectively, although the numbers show considerable variation from year to year (Figure 2). The statistically predicted maximum number of breeding pairs per colony varied widely, from 62 on Rottumerplaat to 612 in De Geul on Texel (Figure 2).

Chick condition and reproductive success in growing vs. stable colonies

Chick condition differed between stable colonies (Terschelling and Schiermonnikoog) and growing colonies (De Schorren (Texel), Vlieland, Ameland and Griend), being lower in stable colonies for most chicks (Figure 3A, model 1.1 in Tables 1 and S3). However, body condition improved in stable colonies in the course of the season. As a result, while early and average chicks had higher condition in growing than in stable colonies, this effect was the opposite for late chicks (Figure 3A, model 1.1 in Tables 1 and S3). We did not find an effect of heavy rain in the week prior to measurement.

Reproductive success between 2011 and 2015 tended to be higher in growing than in stable colonies (Figure 3B), but not significantly so: the best model assumed no difference between the two (model 2.1).

Density dependence in reproductive success

In the different Wadden Sea colonies where reproductive success has been measured repeatedly between 1991 and 2015, reproductive success decreased with colony size, and the starting level differed between colonies (Figure 4A, model 3.1 in Tables 1 and S3). The rate of decrease with colony size differed between colonies (model 3.2 in Table 1), but post hoc analyses showed that this effect was only due to the small colony on Rottumerplaat where reproductive success showed a positive instead of a negative correlation with colony size (model 3.1). The rate of decrease was not different between the other colonies. The intercept values (i.e. the estimated per capita fledging success at colony size zero) of the model that assumes the same slope in all colonies (model 3.3) showed a positive trend with the statistically predicted maximum colony density of Figure 2, although not significantly (standardized major axes analysis, $n = 6$, $r^2 = 0.54$, $P = 0.09$; Figure 4B).

DISCUSSION

As predicted by Lok *et al.* (2009), the growth of the Wadden Sea population has been levelling off stronger than the growth of the population in the rest of The Netherlands (Figure 1). However, Lok *et al.* (2009) predicted it to stabilize at around 1375 breeding pairs.
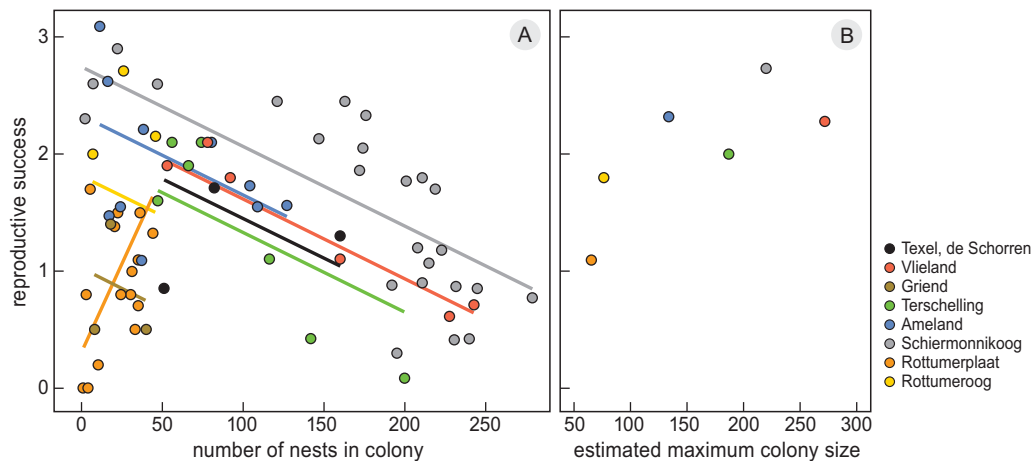
Figure 4. Reproductive success as a function of (A) colony size and (B) estimated maximum colony size in five colonies. Reproductive success (measured as the average number of fledglings per nest) decreased with colony size, but the intercept value differs between colonies. The rate of decrease differed between locations, but post hoc analysis showed that this was only due to Rottumerplaat (model 3.1 in Tables 1 and S3). The rate of decrease did not differ between the other locations, but showed a positive relationship with colony size on Rottumerplaat. The reproductive success intercept (assuming the same slope for all colonies, model 3.3 in Table 1) is plotted against the estimated maximum colony size (standardized major axis regression, $r^2 = 0.54$, $P = 0.09$). Maximum colony size could not be estimated for De Schorren and Griend because they show exponential growth (Figure 2).

With 1529 breeding pairs counted in 2015, the growth of the Wadden Sea population has thus been decreasing less than expected.

The strongly negative relationship observed between colony size and reproductive success (except for Rottumerplaat; Figure 4A) suggests that the current decrease in breeding population growth on the Wadden Sea islands is in part a consequence of limitations at the colony level. This is in accordance with the observed lower chick condition in stable colonies than in growing colonies (Figure 3A). Although this effect disappeared at the end of the breeding season, the majority of chicks measured hatched in May when this effect is still strong (Figure 3A). Lower chick condition was not compensated by a higher number of fledglings, since reproductive success also tended to be lower in stable than in growing colonies (Figure 3B).

The increase in chick condition in the course of the season was unexpected. Perhaps intraspecific competition decreases as more and more fledged chicks and their parents move away from the colony areas (van Dijk & Overdijk 1996). The fact that the positive effect of hatching date was only present in stable colonies is consistent with this hypothesis. The positive relationship between colony size and reproductive success on Rottumerplaat was also unexpected. It may indicate that very small colonies may actually benefit from more nests (i.e. an Allee effect). After all, Rottumerplaat is the only small colony for which we have many repeated measurements of reproductive success. A potential

mechanism might be that Lesser Black-backed Gulls *Larus fuscus* or Herring Gulls *Larus argentatus* get more chances to depredate unattended nests in smaller colonies (see Figure 5), or perhaps it is due to the lack of social information of some kind (see e.g. Barta & Giraldeau 2001).

Potential causes of colony-level density dependence
The results of this study suggest that chick condition and reproductive success are lower in stable colonies, and that the initial level of reproductive success differs between colonies. Potential mechanisms include nest predation pressure, the number of potential nesting sites, and food availability. The main predator of Spoonbills in The Netherlands, the Red Fox *Vulpes vulpes*, is absent from the Wadden Sea islands, whereas other potential predators, Lesser Black-backed and Herring Gulls, are not exerting strong predation pressure in large colonies. Nesting sites are not likely to limit population growth either, as suitable breeding habitat seems to be vastly available on the extensive saltmarshes and low dune areas of the Wadden Sea islands. Hence, we propose that it is the abundance and accessibility of food in the area surrounding the breeding colonies that will be the prime cause of colony size limitation.

For this reason, data on spatial and temporal changes in food availability within the foraging range of Spoonbills in each colony will be necessary to further understand the dynamics of reproductive success in

Figure 5. Breeding Spoonbills on Rottumerplaat in June 2015.

different colonies. On the Wadden Sea islands, the diet of breeding Spoonbills and their chicks consists mainly of small fish and crustaceans from marine (e.g. juvenile Plaice *Pleuronectes platessa* and Brown Shrimp *Crangon crangon*) and freshwater environments (e.g. Three-spined Stickleback *Gasterosteus aculeatus*; van Wetten & Wintermans 1986, El-Hacen *et al.* 2014, J. Jouta *et al.* in prep). The abundance and accessibility of these prey is highly variable in time and space, and has not been studied in sufficient detail to allow quantitative estimates of their distribution in the Wadden Sea.

Currently, the best possible estimate of the availability of intertidal food is the surface area of mudflats and tidal channels surrounding the colony. As for many other coastal colony-breeding birds (Ainley *et al.* 2004, Grémillet *et al.* 2004, Wakefield *et al.* 2013), the foraging range of Spoonbills may be limited during the breeding season, and colonies are thought to have consistent foraging areas surrounding the colony (van der Geest *et al.*, Werkgroep Lepelaar unpubl. data). Unfortunately, at this point the limited data on freshwater habitats and their food availability mean that we cannot provide an estimation of their abundance per colony. Assigning all mudflats to the closest Spoonbill

colony, we plotted available mudflat against the maximum estimated colony size for each colony (Figure 6). There was no simple positive relationship, with the De Geul colony on Texel in particular harbouring many more nests than expected. The lack of such an expected relationship may primarily be explained by differences in the availability of freshwater foraging opportunities. Most of the islands have freshwater ponds and ditches, but freshwater foraging opportunities are mainly found on the mainland. Spoonbills breeding close to the mainland, such as in De Geul (Figure 6), can easily cross the Wadden Sea and fly to several freshwater lakes.

However, this still does not explain why the Vlieland colony, being the furthest away from considerable freshwater habitat is the second largest colony. This may instead be explained by an unequal distribution of food in the Wadden Sea. Variation in the availability of this food may be enhanced by all kinds of differences in the properties of the intertidal feeding grounds affecting food and foraging (Compton *et al.* 2013). Finally, changing boundaries between foraging areas of growing and stable colonies might contribute to the explanation. Clearly, we now need studies that quantify the area used per colony, something that can be done by
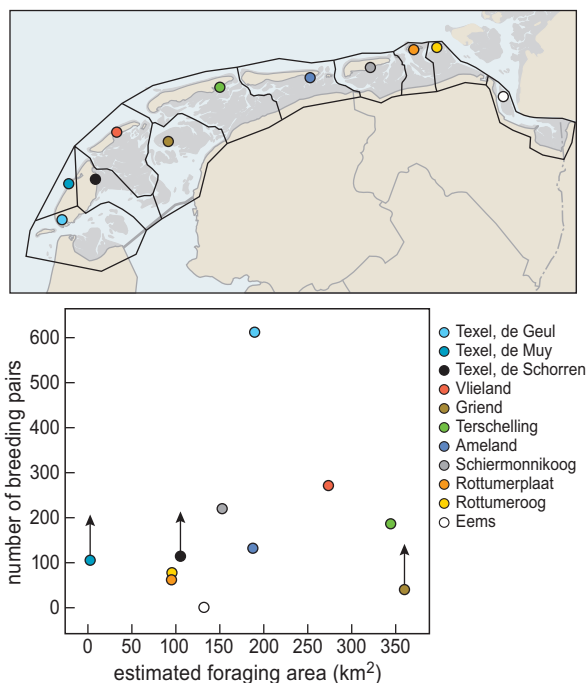
Figure 6. Colony size as a function of the surrounding surface area of intertidal mudflats. For all colonies that show logistic growth (see Figure 2), the estimated maximum colony size is plotted. For the colonies that currently show exponential growth (De Muy, De Schorren and Griend, marked with an arrow), the maximum cannot be estimated and the number of nests in 2015 is shown. The colony-specific foraging area is estimated by assigning all intertidal area (grey area on map) to the closest Spoonbill breeding colony, and summing up the surface of those areas for each colony.

deploying Spoonbills in each colony with location trackers (see Wakefield *et al.* 2013), in combination with quantification of food availability in those areas over time.

Yet, even this will not provide the whole story, as we know that the main determinant of adult survival is density dependence outside the breeding area (Lok *et al.* 2013b). Adult survival as well as reproductive success are influenced by migration distance (Lok *et al.* 2013a, 2017). Indeed, the fact that these two processes do not exclude one another, adds a cautionary note to the conclusions of previous studies on the factors limiting colony sizes (Furness & Birkhead 1984, Adams 2001).

The future of the Dutch population of Eurasian Spoonbills

The general trend of decreasing growth in the Wadden Sea population may be the effect of the observed colony-level density dependence of reproductive success, and potentially also of density dependence in post-fledging survival as a consequence of lower body condition at fledging (Lok *et al.* 2017). Currently, it is hard to predict the limits to growth of the Dutch population. The observed decline in colony-specific reproductive success may continue to be compensated by the expansion into new areas, as is currently being observed in the Delta region of The Netherlands (Figure 1). On the other hand, expansion by dispersion into Germany and Denmark may also contribute to decreasing population growth in The Netherlands (Lok *et al.* 2013b).

Colony-specific estimates of reproductive success, juvenile (post-fledging) survival and dispersion from and to other breeding colonies will shed more light on the relative contributions of these mechanisms, and provide a more precise estimate of the limits to growth in the rest of The Netherlands as well. The tendency for a correlation between initial reproductive success for a given colony size and its maximum size (Figure 4B) implies that the current levels of reproductive success in recently established mainland colonies may actually predict their future sizes. However, on the mainland, reproductive success is often compromised by fox predation, which is absent on the Wadden Sea islands (Voslamber 1994). In some mainland colonies, Spoonbills are responding to the presence of ground predators by starting to breed in trees and bushes (Figure 7). Thus, besides the ability to adjust migratory traditions (Lok *et al.* 2013a, 2017), the future of Spoonbills in The Netherlands may also depend on the extent to which their behavioural flexibility allows them to exploit new environments during the breeding season.

Figure 7. Spoonbills breeding in a tree at Haarlemmerliede. All chicks fledged (photo Camilla Dreef, 29 April 2017).

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SAMENVATTING

Het idee heerst dat bij de meeste vogels die in kolonies broeden, de grootte van de kolonies en de maximale populatiegrootte bepaald worden door de beschikbare voedselhoeveelheid in de omgeving van de kolonies. De populatiedynamiek wordt echter ook bepaald door de overleving van de adulte vogels. Deze kan sterk worden beïnvloed door omstandigheden buiten het broedseizoen. De meerderheid van de Nedelandse Lepelaars Platalea leucorodia leucorodia broedt op de Waddeneilanden. Daar lijkt nu (na dertig jaar van exponentiële groei) de toename af te vlakken in de richting van een maximum van ongeveer 2000 broedparen. Eerder is al uitgebreid aangetoond dat de overleving van Lepelaars sterk wordt beïnvloed door dichtheidsafhankelijke effecten (zowel binnen als buiten het broedseizoen) en dat daarin verschillen bestaan tussen de leeftijdsklassen. Maar welke mechanismen hieraan ten grondslag liggen is minder duidelijk. Om te bepalen of deze dichtheidsafhankelijke effecten het gevolg zijn van beperkingen in en rond de broedkolonies, vergelijken we hier de populatiegroei, de kuikenconditie en het broedsucces van verschillende kolonies op de Waddeneilanden. De populatiegroei tussen 1988 en 2015 en de statistisch verwachte maximale koloniegroottte varieerden sterk tussen tien bestaande kolonies. Metingen aan 781 kuikens in zes verschillende kolonies tussen 2011 en 2015 laten zien dat de kuikenconditie in stabiele kolonies slechter was dan in groeiende kolonies (al gold dit niet voor de late kuikens) en dat het broedsucces in stabiele kolonies kleiner leek te zijn. Na toevoeging van gegevens uit de periode 1991–2011 bleek dat het broedsucces een sterk negatief verband vertoont met de grootte van de kolonies. De meest aannemelijke oorzaak van de huidige afname in populatiegroei op de Waddeneilanden is een beperkte voedselbeschikbaarheid in en om het wad. Om dit aan te tonen is er onderzoek nodig naar de verspreiding van Lepelaars uit verschillende kolonies tijdens het broedseizoen en naar de voedselbeschikbaarheid op het wad (en in nabij gelegen zoetwaterhabitat) in de loop van het seizoen. Er is echter nog geen einde aan de populatiegroei in Nederland als geheel, vooral omdat de kolonies van Lepelaars in het Deltagebied nog exponentieel groeien.

SUPPLEMENTARY MATERIAL

Appendix S1. Estimating sex of spoonbill chicks by 8th primary length and tarsus length

The most profound measurable difference between male and female Spoonbill chicks is tarsus length (Lok *et al.* 2014). So, when chick age is known, this measure may be used to determine its sex. We provide a method to estimate sex from tarsus length, and determine its accuracy, using tarsus measurements in 395 chicks (201 females and 194 males) where sex was analysed by molecular analysis, and age was estimated by 8th primary length, which is a sex-independent measure (Lok *et al.* 2014).

First, sex-specific logistic regression curves were fitted of tarsus length as a function of age, using the function 'nls' in the stats package of R (R Core Team 2015; Table S4, Figure S1). Then, for each chick, the expected tarsus length given its age was calculated, estimated from both the female and the male logistic regression curve. Sex was then estimated by comparing which of those two estimates gave the smallest difference with actual observed tarsus length. Sex estimates using this method corresponded to sex determined by molecular analysis in 330 out of 395 cases (Figure S1), which equals a probability of 0.16 of a deviate estimate.
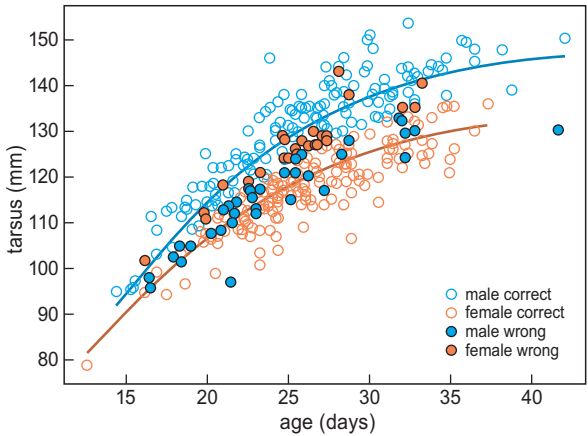
Table S1. The number of chicks weighed and measured on the Wadden Sea islands.

	2011	2012	2013	2014	2015
Ameland	0	21	24	24	26
Griend	0	0	8	21	20
Schiermonnikoog	19	13	69	100	94
Terschelling	19	24	14	25	33
Texel, De Schorren	0	21	27	26	22
Vlieland	39	9	27	23	33

Table S2. AIC-values of colony growth models. Logistic regression analysis was performed with the function 'nls' in R. The best model is marked in bold. If the AIC-value of the logistic regression (3 model parameters) was less than 2 units lower, or higher than the AIC-value of the exponential regression (2 model parameters), then the exponential model was considered the best model. Otherwise, the logistic model was considered best.

Colony	Exponential regression AIC	Logistic regression AIC
All colonies	356.4	**350.8**
Wadden Sea colonies	351.3	**322.1**
Delta colonies	**315.0**	316.7
Other colonies	**330.6**	no fit [1]
Texel, De Geul	289.7	**275.7**
Texel, De Muy	**48.6**	no fit
Texel, De Schorren	**252.4**	no fit
Vlieland	289.3	**271.7**
Griend	**39.6**	no fit
Terschelling	297.3	**266.7**
Ameland	183.7	**180.3**
Rottumerplaat	127.1	**124.9**
Rottumeroog	143.8	**132.8**

[1]When the data fitted very badly with a logistic regression, no parameters could be estimated and no AIC-value assigned.

Figure S1. Tarsus length as a function of age in females (*n* = 201) and males (*n* = 194). Lines show logistic regression lines (Table S4). Sex was determined by molecular analysis of the blood, and age was estimated by 8th primary length (see main text). Sex was additionally estimated from tarsus length as described in Appendix S1, which corresponded to molecular sex in 330 cases (open circles), and differed in 65 cases (filled circles).

Table S3. Parameter estimates of the best statistical models. All models are linear mixed-effects models (function 'lmer' in package 'lme4'). Response variables are chick condition (model 1.1) and reproductive success (models 2.1 and 3.1). Model 2.1 uses the data gathered in six populations, model 3.1 uses data between 1991 and 2015 gathered from the literature. Parameters were estimated by maximizing the log-likelihood. Estimates of the random variables and the residuals refer to standard deviations from the fixed estimates.

	Effects	Estimate	SE	t-value
	Chick body condition (proportional deviation from mean expected body mass)			
Model 1.1	Intercept	0.020	0.03	0.7
	Stage-Stable	–0.073	0.03	–2.38
	Date	–0.0002	0.0004	–0.61
	Stage:Date	0.0011	0.0004	2.50
	(1|ColonyID)	0.02		
	(1|Year)	0.04		
	Residual	0.10		
	Reproductive success (2011–2015, number of chicks per nest)			
Model 2.1	Intercept	0.09	0.03	2.7
	(1| ColonyID)	0.09		
	(1| Year)	0.14		
	Residual	0.26		
	Reproductive success (1991–2015, number of chicks per nest)			
Model 3.1	Intercept	2.33	0.15	15.1
	ColSize	–0.007	0.001	–5.54
	ColonyID – Griend	–1.31	0.27	–4.89
	ColonyID – Rottumeroog	–0.52	0.32	–1.65
	ColonyID – Rottumerplaat	–2.02	0.22	–9.12
	ColonyID – Schiermonnikoog	0.41	0.22	1.92
	ColonyID – Terschelling	–0.32	0.23	–1.38
	ColonyID – Texel, De Schorren	–0.20	0.26	–0.77
	ColonyID – Vlieland	–0.04	0.25	–0.15
	ColSize:Rottumerplaat	0.037	0.007	4.97
	(1|Year)	0.39		
	Residual	0.36		

'Stage': colony growth stage (either growing or stable), 'Date': estimated day of hatching (count, starting at 15 April), 'Rain': number of days with heavy rain in the week before measurement, 'ColSize' number of breeding pairs in the colony, 'ColonyID': individual colonies. (1|ColonyID) and (1|Year) refer to the random variables Colony-ID and year.

Table S4. Parameter estimates of logistic regression curves of tarsus length (mm) over age (days).
Logistic growth curve: $y = Y_{max}/(1 + \exp(-k \times (x - T_i)))$.

Model	Variables	Estimate	SE	t-value	P
Female tarsus length (mm)	Y_{max}	136	2.88	47.2	<0.0001
	k	0.12	0.016	7.3	<0.0001
	T_i	9.14	0.93	9.8	<0.0001
Male tarsus length (mm)	Y_{max}	149	2.67	55.7	<0.0001
	k	0.13	0.014	9.1	<0.0001
	T_i	10.7	0.59	18.1	<0.0001