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

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

[1]NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems and Utrecht University, P.O. Box 59, 1790 AB Den Burg (Texel), The Netherlands

[2]Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

[3]Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, Campus CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France

* Corresponding author: Thomas.Oudman@nioz.nl

SUMMARY

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 2,000 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. Measured for 781 chicks in six different colonies between 2011 and 2015, chick condition 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 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.

INTRODUCTION

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 numbers of nests in different colonies reflected the relative extents of foraging area (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 is 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 their 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.* 2013), 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 breeding colony level.

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.* 2013), which potentially results from 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 suggests that density-dependent processes may be acting at the colony level. The level of the density-dependent effect on population growth has been tested in an earlier study (Lok *et al.* 2009). It showed that statistical models assuming density dependence acting on either the Dutch population as a whole, or on the individual breeding colonies, performed equally well. However, these models also assumed that reproductive success was constant and the same in all colonies and did not take into account the possibility that the level of density dependence could differ between colonies, for example as a consequence of differences in local food availability.

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. Wemeasured reproductive success (the number of fledged chicks per nest) and chick condition (oberved 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 post-fledging survival prospects when competition between fledglings is high (Lack 1954; Lok *et al.* 2013).

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 (e.g. Velando, Ortega-Ruano & Freire 1999), also for 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 coworkers. Except for the largest island of 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 1). Chicks were caught when large enough for rings but before fledging, usually when they were 20-35 days old (Lok, Overdijk & Piersma 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 S1 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 sources in the grey literature (Overdijk 1999 between 1994 and 1998; Overdijk & Horn 2005 between 1999 and 2004) and unpublished records (H. Horn for Terschelling, O. Overdijk and P. de Goeij for Schiermonnikoog, F. Oud for Ameland, C. Zuhorn for Vlieland, vogelwachters 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 AIC_c. In addition, all models were compared with and without including an effect of heavy rains. 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, de Nes on Ameland, and Schiermonnikoog). The reproductive success data did not allow to test for an effect of hatching date or heavy rains, 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 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 models with and without colony ID, colony size and their interaction, with year as random variable.

RESULTS

Population growth

Up to the last year of observation, the population in The Netherlands continued to grow (Fig. 1), with 2908 nests counted in 2015. The population trend is best fitted by a logistic regression (see Table S1), which indicates that density-dependent effects have started to reduce the overall population growth rate. The predicted stable Dutch breeding population size is about twice the current size (Fig. 1). The growth of the Wadden Sea population has been levelling off more strongly than the rest of the Dutch population (Fig. 1). The current logistic regression on the data until 2015 predicts an asymptotic Wadden Sea population of about 1800 breeding pairs. The Delta population has kept growing exponentially since its colonization 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 (Fig. 1).

Colony growth on the Wadden Sea islands

On the Wadden Sea islands, all colonies have been growing since 1988 (Fig 2A). The colonies in the Schorren and the Muy (both on Texel) showed exponential growth ever since. 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 S1). 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 (Fig. 2). The statistically predicted maximum number of breeding pairs per colony varied widely, from 62 on Rottumerplaat to 612 in De Geul on Texel (Fig. 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 (Fig. 3A, model 1.1 in Tables 2 and S2). 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 (Fig. 3A, model 1.1 in Tables 2 and S2). We did not find an effect of heavy rains 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 (Fig. 4A, model 3.1 in Tables 2 and S2). The rate of decrease with colony size differed between colonies (model 3.2 in Table 2), 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 Fig. 2, although not significantly (standardized major axes analysis, n = 6, $R^2 = 0.54$, p = 0.09, Fig 4B).

DISCUSSION

As predicted by Lok *et al.* (2009), the growth of the Wadden Sea population has been levelling off more strongly than the growth of the population in the rest of The Netherlands (Fig. 1). However, as Lok *et al.* (2009) predicted it to stabilize at around 1375 breeding pairs, the growth of the Wadden Sea population, with 1529 counted breeding pairs in 2015, has been decreasing less than expected.

The observed strongly negative relationship between colony size and reproductive success (except for Rottumerplaat, Fig. 4A) suggests that the current decrease in breeding population growth on the Wadden Sea islands may be 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 (Fig. 3A). Although this effect disappeared at the end of the breeding season, by far the most chicks that were measured hatched in May when this effect is still strong (Fig 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 (Fig. 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). 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 Fig. 6), or perhaps 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 on 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, a prime necessity for further inference on the dynamics of the reproductive success of different Spoonbill colonies will be data on spatial and temporal changes in food availability within the range of foraging of the Spoonbills of a colony. 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; Jouta *et al.* MS). 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.

The currently 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 breeding season, and colonies are thought to have consistent foraging areas surrounding the colony (van der Geest *et al.* in prep., Werkgroep Lepelaar unpubl. data). Unfortunately, at this point the limited data on freshwater habitats and their food availability do not allow any 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 (Fig. 5). There was no simple positive relationship, with especially the De Geul colony on Texel harbouring many more nests than expected. The lack of such an expected relation may primarily be explained by differences in the availability of freshwater foraging opportunities. Most of the islands have freshwater ponds and ditches, but fresh water foraging opportunities are mainly found on the mainland. Spoonbills breeding close to the mainland, such as in De Geul colony (Fig. 5), 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 which quantify the area used per colony, something that can be done by deploying Spoonbills with location sensors in each colony (see Wakefield *et al.* 2013), in combination with quantifications 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.* 2013). Adult survival as well as reproductive success are influenced by migration distance (Lok, Overdijk & Piersma 2013; Lok *et al.* 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 (Fig. 2). On the other hand, expansion by dispersion into Germany and Denmark may also contribute to decreasing population growth in The Netherlands (Lok *et al.* 2013).

Colony-specific estimates of reproductive success, juvenile (post-fledging) survival and dispersion from and to other breeding colonies could 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 (Fig. 4B), implies that the current levels of reproductive success on mainland colonies may actually predict their future sizes. However, reproductive success on mainland colonies is often compromized 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. Thus, besides the ability to adjust migratory traditions (Lok, Overdijk & Piersma 2013; Lok *et al.* 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.

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SUPPLEMENTARY INFORMATION

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

Table S1. AIC-values of colony growth models

Table S2. Parameter estimates of the best statistical models

Table S3. Parameter estimates of logistic regression curves of tarsus length over age

Figure S1. Tarsus as a function of age in females and males

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NEDERLANDSE SAMENVATTING

Het idee heerst dat bij de meeste koloniebroedende vogels, koloniegrootte bepaald wordt door de hoeveelheid beschikbaar voedsel in de omgeving van de kolonie, en dat hierdoor ook de maximum populatiegrootte wordt bepaald. Populatiedynamiek wordt echter ook bepaald door de overleving van adulten, en die kan sterk beïnvloed worden door omstandigheden buiten het broedseizoen. De meerderheid van de Nedelandse populatie van Lepelaars *Platalea leucorodia leucorodia* broedt op de Waddeneilanden, waar na dertig jaar van exponentiele groei de groei nu lijkt af te vlakken in de richting van een maximum van ongeveer 2,000 broedparen. Dat de overleving van Lepelaars sterk beïnvloed wordt door dichtheidsafhankelijke effecten, zowel binnen als buiten het broedseizoen, en dat dit verschilt tussen leeftijdsklassen, is al uitgebreid aangetoond. Maar welke mechanismen hieraan ten grondslag liggen is minder duidelijk. Om te bepalen of deze dichtheidsafhankelijke effecten het gevolg zijn van beperkingen in de broedkolonies, vergelijken we hier populatiegroei, kuikenconditie en broedsucces tussen de verschillende kolonies op de Waddeneilanden. Populatiegroei tussen 1988 en 2015, en ook de statistisch verwachte maximale koloniegroottte, varieerde sterk tussen de tien bestaande kolonies. Metingen van 781 kuikens in zes verschillende kolonies tussen 2011 en 2015 laten zien dat kuikenconditie lager was in stabiele dan in groeiende kolonies (maar niet bij late kuikens), en dat ook broedsucces lager leek te zijn in stabiele kolonies. Na toevoeging van bestaande data tussen 1991 en 2011 bleek dat broedsucces een sterk negatief verband houdt met koloniegrootte. De meest aannemelijke oorzaak van de huidige afname populatiegroei 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 ook naar de beschikbaarheid van voedsel op het wad en in nabij zoetwater habitat, 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 exponentiëel groeien.

TABLES AND FIGURES

Table 1. 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 2. AICc comparison of statistical models

Model	Fixed effects[a]	K[b]	ΔAIC_c	AIC_c weight	Cum. weight	LL[c]
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

NB. Linear mixed-effects models (function “lmer” in R package “lme4”; Bates *et al.* 2015; R Core Team 2015).

The five best models are shown in each selection, best models are in bold (Burnham & Anderson 2002).

Parameters were estimated by maximizing the log-likelihood. Chick condition is the response variable in models 1, the number of fledglings per nest is the response variable in models 2. In models 1 and 2, year and location are included as random effects. Year is included as random effect in models 2. Models 3 have the number of fledglings per nest as response variable data, now also including data between 1991 and 2010, and concern only the five colonies with at least 5 annual measurements. These models include location as a fixed effect instead of random, to explore its interaction with the number of nests.

[a] In models 1, ‘Stage’ refers to the colony growth stage (either growing or stable). ‘Date’ refers to the estimated hatching date, and ‘Rain’ refers to the number of days with heavy rain (>10mm) in the previous week. In models 2, ‘Stage’ again refers to the colony growth stage. In models 3, ‘Colsize’ refers to the number of breeding pairs in the colony, ‘ColonyID’ is a factor referring to the different colonies. ‘Rottumerplaat’ is defined as 1 for Rottumerplaat, and 0 for the other colonies.

[b] The number of parameters in the model.

[c] Log-likelihood.

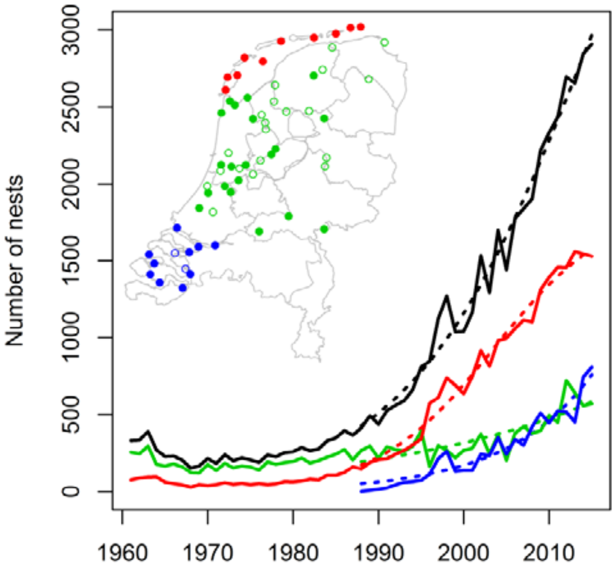

Figure 1. The total number of Spoonbill breeding pairs in The Netherlands (black) from 1961 to 2015. The Wadden Sea colonies (red), the Delta colonies (blue) and colonies in the rest of The Netherlands (green), are shown separately. In the inset, current colonies are shown by filled circles, previously 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.

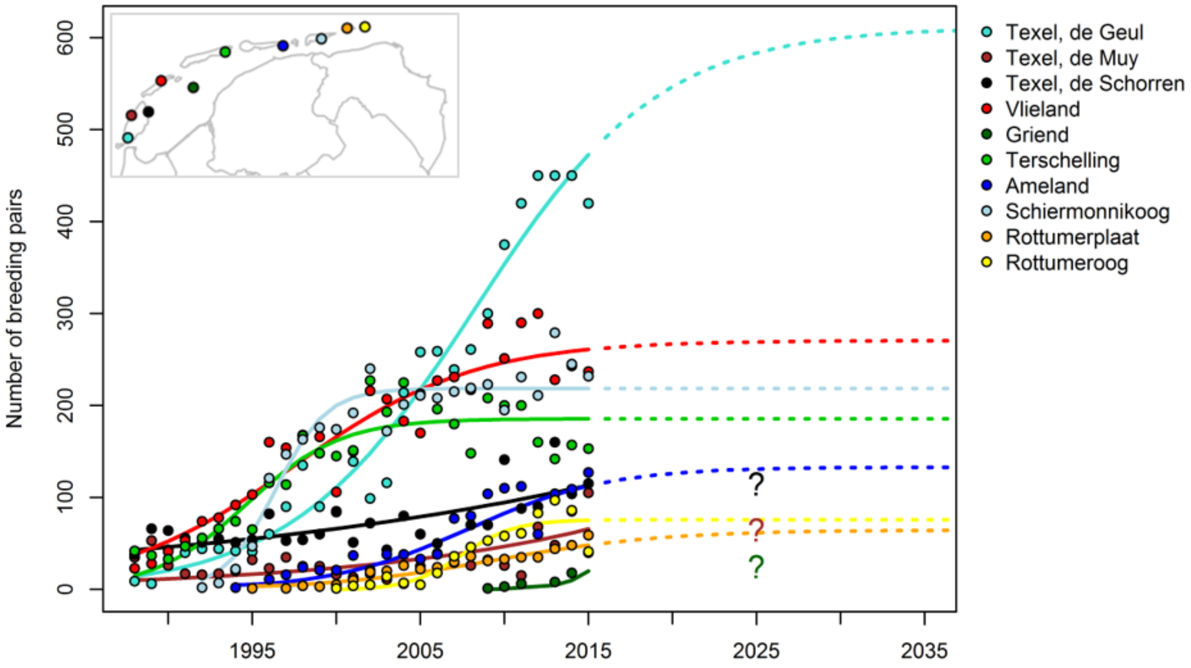

Figure 2. Spoonbill colonies on the Wadden Sea islands. Either exponential or logistic regression lines are drawn (solid lines), depending on which fitted best. This ignores shorter temporary trends, such as the recent decreasing numbers on Terschelling. Maximum colony sizes were estimated by extending 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.

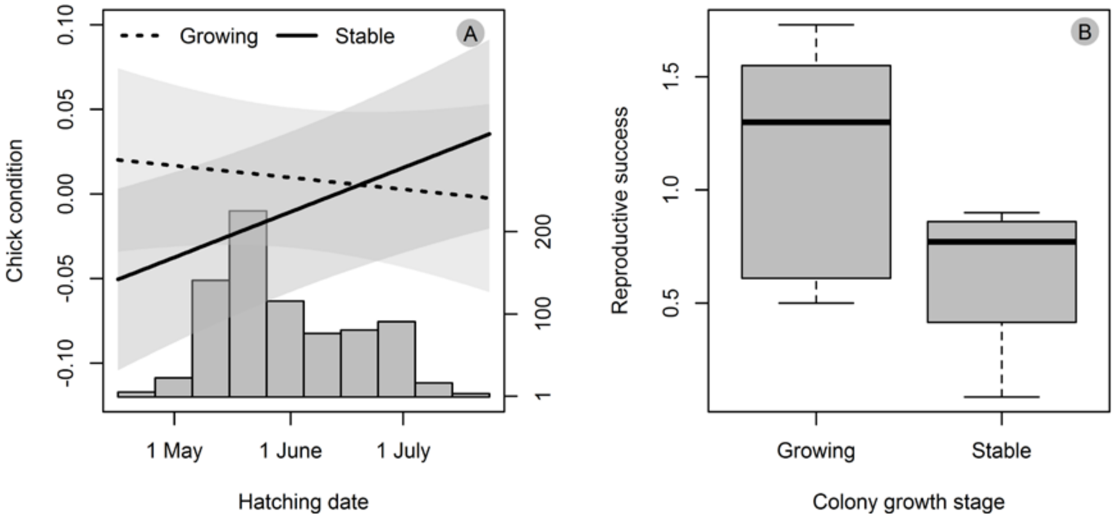

Figure 3. Chick condition and reproductive success in growing and stable colonies. A) Chick condition in stable (solid line) and in growing colonies (dashed line), both as a function of hatching date. Lines show estimates of the best statistical model, grey areas show 95% prediction intervals. Bars show 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 Table S2).

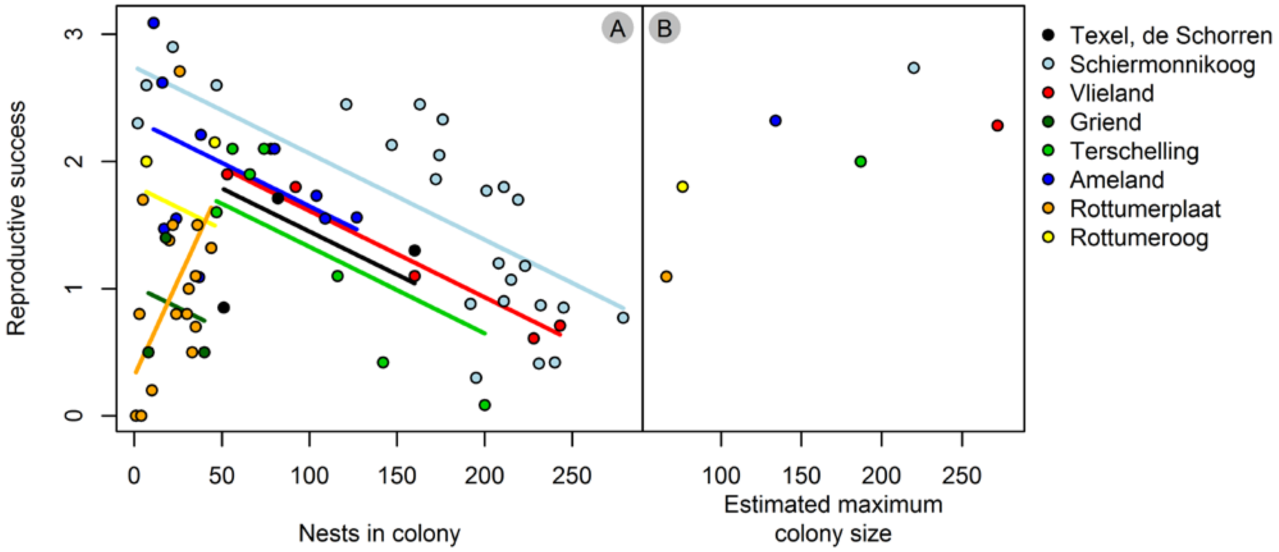

Figure 4. Reproductive success as a function of colony size and estimated maximum colony size in five colonies. A) Reproductive success (measured as the average number of fledglings per nest) decreased with colony size, but the intercept value differs between colonies. The rate of decrease differed between locations, but post-hoc analysis showed that this was only due to Rottumerplaat (model 3.1 in Table S2). The rate of decrease did not differ between the other locations, but showed a positive relationship with colony size on Rottumerplaat. B) 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 (Fig. 2).

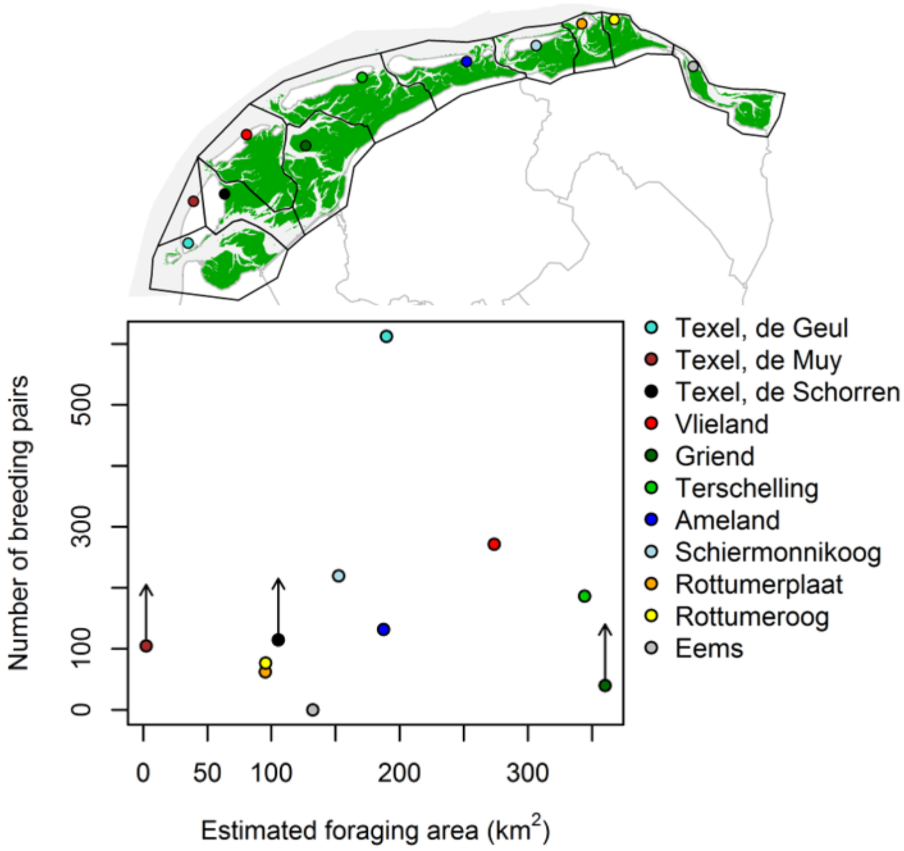

Figure 5. Colony size as a function of the surrounding surface of intertidal foraging area. For all colonies that show logistic growth (see Fig. 2), the estimated maximum colony size is plotted. For the colonies that currently show exponential growth (de Muy, de Schorren and Griend, marked with an arrow), 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 (green area on map) to the closest Spoonbill breeding colony, and summing up the surface of those areas for each colony.

Figure 6. Breeding Spoonbills in June 2015 on Rottumerplaat. Photo credit: Thomas Oudman

SUPPLEMENTARY INFORMATION

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, Overdijk & Piersma 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, Overdijk & Piersma 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 S3, Fig. 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 (Fig. S1), which equals a probability of 0.16 of a deviate estimate.

Table S1. AIC-values of colony growth models

Colony	**Exponential regression AIC**	**Logistic[a] regression AIC**
All colonies	356.4	**350.8**[b]
Wadden Sea colonies	351.3	**322.1**
Delta colonies	**315.0**	316.7
Other colonies	**330.6**	No fit
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**

[a] Logistic regression analysis was performed with the function 'nls' in R. When the data fitted very badly with a logistic regression, no parameters could be estimated and no AIC-value assigned.

[b] 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.

Table S2. Parameter estimates of the best statistical models.

	Effects	Estimate	SE	t-value
Chick body condition				
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)				
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)				
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		

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

Table S3. Parameter estimates of logistic regression curves of tarsus length (mm) over age (days).

Model	Variables	Estimate	SE	t-value	P
Female tarsus length	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	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

Logistic growth curve: $y = Y_{max}/(1 + \exp(-k \cdot (x - T_i)))$

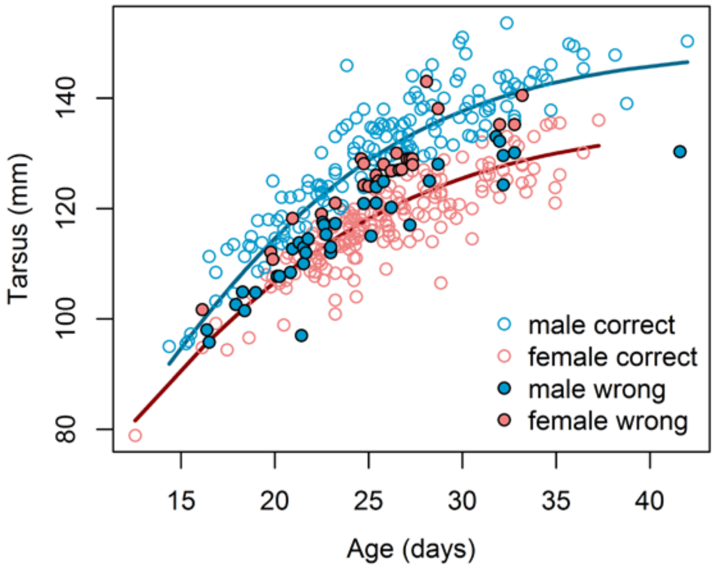

Figure S1. Tarsus as a function of age in females (n=201) and males (n=194). Lines show logistic regression lines (Table S3). Sex was determined by molecular analysis of the blood, and age was estimated by 8th primary length (see main text). Sex was additionally estimated from tarsus length as described in Appendix S1, which corresponded to molecular sex in 330 (open circles) cases, and differed in 65 cases (filled circles).