BioOne COMPLETE

Age-Specific Density-Dependent Survival in Mediterranean Gulls Larus melanocephalus

Authors: Marvelde, Luc te, Meininger, Peter L., Flamant, Renaud, and Dingemanse, Niels J.

Source: Ardea, 97(3) : 305-312

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/078.097.0306

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

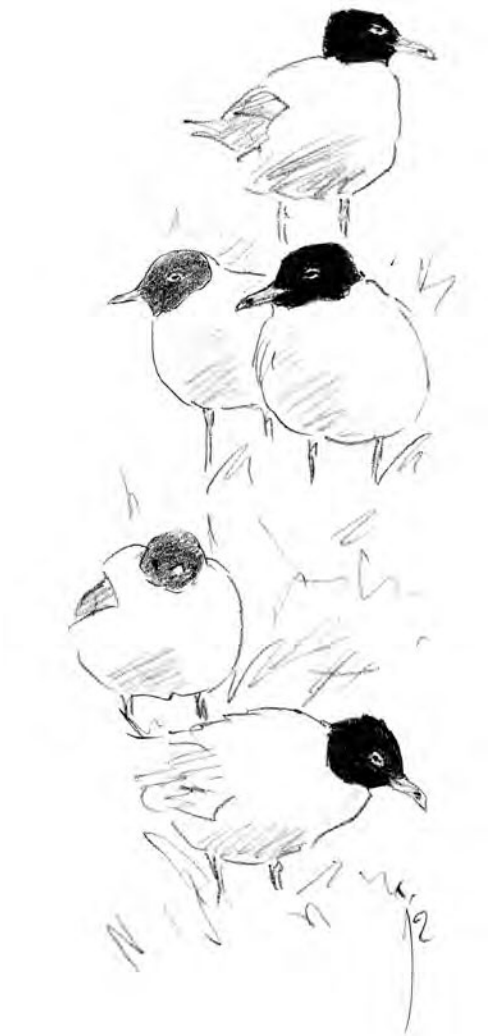
Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Age-specific density-dependent survival in Mediterranean Gulls *Larus melanocephalus*

Luc te Marvelde[1,5], Peter L. Meininger[2], Renaud Flamant[3] & Niels J. Dingemanse[1,4,*]



te Marvelde L., Meininger P.L., Flamant R. & Dingemanse N.J. 2009. Age-specific density-dependent survival in Mediterranean Gulls *Larus melanocephalus*. Ardea 97(3): 305–312.

Survival and reproductive rates often decrease with increasing population density. Such negative density dependence reflects a changing net balance between the benefits and costs of presence of others with increasing density. When densities are low, however, survival and reproductive rates might increase rather than decrease with increasing density (Allee effect), for example in colonial species. Relationships between fitness and density are therefore expected to change with population density. We studied the relationship between apparent annual survival and population density in a population of Mediterranean Gulls *Larus melanocephalus* from establishment onwards for a period of 13 years, using capture–recapture techniques. The results confirmed our expectation: apparent survival increased with density at low densities (i.e. an Allee effect), but survival decreased with density at high densities. Post-hoc analyses revealed that the Allee effect could only be shown for juveniles, not for adults, suggesting that the Allee effect might have been age-specific. These patterns in apparent survival reflect the combined effects of density on true survival and on permanent emigration, and both mechanisms are discussed.

Key words: survival, dispersal, density-dependence, Allee effect, coloniality, mark–recapture.

[1]Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; [2]Lisztlaan 5, 4384 KM Vlissingen, The Netherlands (mein@zeelandnet.nl); [3]Belgian Ornithological Research Association, Leopold III laan 43/87, B-1030 Brussels, Belgium (Renaud.Flamant@skynet.be); [4]Department of Behavioural Biology, Centre for Behaviour and Neurosciences, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; [5]current address: Department of Animal Population Biology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 40, 6666 ZG Heteren, The Netherlands;
*corresponding author (n.j.dingemanse@rug.nl)

INTRODUCTION

Density dependence is a key factor in determining population dynamics in many species of bird (Newton 1998). Survival and reproductive rates have often been shown to decrease with increasing population density (survival: e.g. Nicoll *et al.* 2003, Armstrong *et al.* 2005; reproduction: e.g. Both 1998, Both & Visser 2003, Nummi & Saari 2003). Such negative density dependence reflects a changing net balance between the costs and benefits of presence of others with increasing density, assuming that density affects per capita resource availability. When densities are low, however, survival and reproductive rates might increase rather than decrease with increasing density if individuals also gain benefits from the presence of conspecifics (Allee *et al.* 1949). In colonial species, where individuals presumably gain benefits from nesting close to conspecifics (Danchin & Wagner 1997), one may therefore expect positive density dependence at low densities (so-called Allee effect) followed by negative density dependence at higher densities, resulting in a parabolic relationship between fitness and density (Courchamp *et al.* 1999).

The Allee effect is likely to have major consequences for the dynamics and survival of populations and species as it increases risk of extinction of small

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Figure 1. View on a mixed breeding colony of Mediterranean Gull and Black-headed Gull, Zandvlietsluis, Antwerpen, Belgium (Photo R. Flamant, BELORA).

and/or newly-established populations (Courchamp *et al.* 1999, Stephens & Sutherland 1999). Unfortunately, relatively few studies have assessed whether Allee effects exist in natural populations (Courchamp *et al.* 1999, Serrano *et al.* 2005). This situation is not surprising, because Allee effects are easily missed either simply due to lack of data (large data sets are needed to reliably estimate fitness parameters at low densities) or lack of appropriate data (data on the lowest densities are often not available) (Courchamp *et al.* 1999).

The aim of this study was to estimate the shape of the relationship between annual survival and breeding density in a colonial bird, the Mediterranean Gull *Larus melanocephalus*. To do so, we followed the fate of a newly established and subsequently fast-growing population of Mediterranean Gulls from establishment onwards for a period of 13 years. We made use of a large data set (from which annual apparent survival rates could reliably be calculated) that consisted of a wide range of natural densities (including the very lowest). Allee effects might exist because the presence of others reduces search costs during foraging (Lack 1968, Ward & Zahavi 1973, Wittenbergen & Hunt 1985, Courchamp *et al.* 1999), risk of predation (Wiklund & Andersson 1994, Krause & Ruxton 2002), and/or time spent on vigilance (Wittenbergen & Hunt 1985, Wiklund & Andersson 1994, Newton 1998, Courchamp *et al.* 1999, Krause & Ruxton 2002). We considered that these benefits of the presence of others were likely to differ between juveniles and adult Mediterranean Gulls, as juveniles largely lack information on predation risk and profitability of feeding areas in the first months after independence because of inexperience (Brown *et al.* 1990). Allee effects might therefore be strongest in juveniles. We thus estimated the shape of the relationship between annual apparent survival and density separately for juveniles and adults. Apparent survival rates comprise the combined effect of true survival and permanent emigration, and both mechanisms are discussed when interpreting our results.

METHODS

Study species

The Mediterranean Gull is a middle-sized and long-lived migratory gull. Its major breeding area used to be along the NW coast of the Black sea (primarily Ukraine), but over the last 50 years its range expanded rapidly towards NW Europe (Meininger *et al.* 1999).

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Since the late 1980s, Mediterranean Gulls bred in The Netherlands and Belgium annually with breeding numbers increasing from 10–30 pairs in the late 1980s to circa 1570 pairs in 2004 (Meininger & Flamant 1998; National Institute for Coastal and Marine Management/RIKZ, unpubl. data; SOVON Dutch Centre for Field Ornithology, unpubl. data). The vast majority of the Dutch–Belgian breeding population breeds in a limited area within the Delta of SW Netherlands and the adjacent area surrounding the harbour of Antwerp (Belgium).

The Belgian and Dutch Mediterranean Gulls breed exclusively in mixed colonies predominated by Black-headed Gulls *Larus ridibundus* (Fig. 1). Within these colonies, breeding pairs of Mediterranean Gulls are clustered within monospecific patches (P.L. Meininger & R. Flamant, unpubl. data). Interestingly, Mediterranean Gulls are socially dominant over Black-headed Gulls and therefore are not likely to suffer from inter-species competition for nesting space. Furthermore, inter-species competition for food is probably also restricted during the breeding season, because Mediterranean Gulls have substantially larger foraging areas compared to Black-headed Gulls (Von Blotzheim & Bauer 1982). The size and distribution of colonies within Belgium and The Netherlands varies from year to year (P.L.M. & R.F., unpubl. data).

Outside the breeding season, Dutch–Belgian Mediterranean Gulls mainly winter along the coast of Great-Britain, France, Spain and Portugal. First-year birds (juveniles) often do not return to the breeding colonies (Mediterranean Gull Colour-ring Database).

Data collection

Mediterranean Gulls were colour-ringed in the Southwest of The Netherlands and the North of Belgium from 1990 to 2003 (Fig. 2). Nestlings where caught by hand in the colony about 1–2 weeks prior to fledging. The nestlings were only captured under good weather conditions (i.e. not too hot, cold, windy and no direct sunshine) to prevent effects of capture on nestling survival. Following capture, each bird was given a metal ring and a Darvic colour ring (white or green) engraved with a unique combination of 3–4 digits and letters. Known breeding colonies were visited with varying intervals, from almost daily to once or twice in a season. During these visits, colour-rings were read with a telescope by an observer posted at some distance from the colony or in a mobile hide. Notably, resighting effort increased steadily over the study period due to increasing numbers of observers searching for colour-ringed birds (P.L.M. & R.F., unpubl. data).

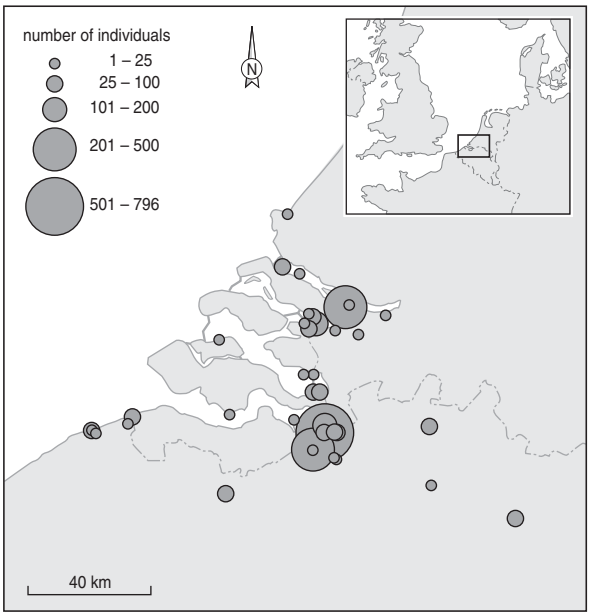


Figure 2. Locations of Mediterranean Gull nestlings ringed in Belgium and The Netherlands between 1990 and 2003. The size of the circles denotes the number of nestlings ringed for each site separately.

Survival analyses

Encounter probabilities have to be accounted for when estimating survival, because some individuals escape detection while they are alive. We used MARK version 4.3 (White & Burnham 1999, Cooch & White 2006) to estimate apparent annual survival (ϕ) and encounter probability (p) from 1990 through 2003, using capture and resighting data of birds ringed as fledgling in the Dutch–Belgian population. For each year, those marked birds that were observed in The Netherlands or Belgium between March through July (the breeding season) were included as 'encountered', and all other birds as 'not encountered'. Sample sizes for the analysis were 2841 marked individuals and 5901 resightings. Notably, any resighting in The Netherlands and Belgium were included in our statistical analyses, implying that our apparent survival estimates should not be considered estimates for local populations but rather for the two countries as a whole.

Of the 2481 nestlings ringed throughout this study, 164 were resighted in The Netherlands and Belgium in the breeding season one year after they were ringed, 325 two years after they were ringed and 323, 276, 193, 114, 50, 25, 15, 8 after three, four, five, six, seven, eight, nine and ten years, respectively.

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Model selection. We considered two sets of *a priori* selected models. The first set of models was constructed to evaluate the *potential* for density-dependence of survival and age-specific density effects, and focussed on year-to-year variation in survival. The full model $\phi(a\times T)p(a\times T)$ estimated separate survival and resighting probabilities for each category of age (a; juveniles (first year birds) vs. older birds) and year (T). This model was compared with three derived models, $\phi(a+T)p(a\times T)$, $\phi(a)p(a\times T)$ and $\phi(T)p(a\times T)$ (Table 1) to assess support for (interacting) effects of age and year on survival (see Introduction). Notably, at the onset of the study, relatively few birds were ringed. We therefore had to pool the first 5 years of data for juveniles and the first 4 years of data for adults (survival term only, first set of models only).

Finding significant year-to-year variation in survival (see Results), the second set of models was constructed to evaluate whether density explained part of the yearly variation in survival. The starting model, $\phi(a\times d+a\times d^2)p(a\times T)$, modelled linear (d) and quadratic (d2) effects of density on survival separately for the two age classes. All biologically relevant derived models were constructed (Table 2), including linear (models 7 and 14) and quadratic effects (model 1 and 12) of density, as well as age-specific linear and quadratic effects of density (modelling age-specific Allee effects or negative density dependence; models 2, 3 and 8).

We considered that any effects of density might alternatively be explained by time trends. We therefore constructed a second starting model, $\phi(a\times t+a\times t^2)p(a\times T)$, that estimated linear (t) and quadratic (t^2) effects of time (year fitted as a continuous variable) on survival separately for the two age classes, and compared the model fit of this model and its derivates (listed Table 2) with models including density effects. In all models, resighting probability is modelled to account for age (a) effects and year-to-year variation in observer effort (T).

Table 1. Fit of models estimating survival (ϕ) and encounter probabilities (p) for Mediterranean Gulls ringed as fledglings in the Dutch–Belgian population (1990–2004), where effects of age (a) and year (T) were considered. Models are sorted in ascending order by their AIC_c-values. For all models, resighting probability was estimated as $p(a\times T)$.

Model	AIC_c	Delta AIC_c	AIC_c weights	NP[a]	Deviance
1 $\phi(a+T)$	7382.40	0.00	0.85	30	1009.80
2 $\phi(a\times T)$	7385.84	3.44	0.15	38	996.96
3 $\phi(a)$	7441.55	59.15	0.00	22	1085.16
4 $\phi(T)$	7501.61	119.21	0.00	29	1131.04
5 $\phi(.)$	7524.18	141.78	0.00	21	1169.81

[a]Number of parameters.

Table 2. Fit of models estimating survival (ϕ) and encounter probabilities (p) for Mediterranean Gulls ringed as fledglings in the Dutch–Belgian population (1990–2004), where effects of age (a), density (d), and time (t; year modelled as a continuous variable) were considered. Models are sorted in ascending order by their AIC_c-values. Resighting probabilities were modelled as in Table 1.

Model	AIC_c	Delta AIC_c	AIC_c weights	NP[a]	Deviance
1 $\phi(a+d+d^2)$	7385.80	0.00	0.61	24	1025.36
2 $\phi(a+d+d^2+a\times d)$	7387.55	1.75	0.26	25	1025.09
3 $\phi(a+d+d^2+a\times d+a\times d^2)$	7388.90	3.10	0.13	26	1024.42
4 $\phi(a+t+t^2)$	7400.52	14.72	0.00	24	1040.09
5 $\phi(a+t+t^2+a\times t)$	7401.56	15.76	0.00	25	1039.10
6 $\phi(a+t+t^2+a\times t+a\times t^2)$	7402.59	16.79	0.00	26	1038.10
7 $\phi(a+d)$	7416.00	30.20	0.00	23	1057.59
8 $\phi(a+d+a\times d)$	7417.39	31.59	0.00	24	1056.96
9 $\phi(a+t+a\times t)$	7428.99	43.20	0.00	24	1068.56
10 $\phi(a+t)$	7431.53	45.73	0.00	23	1073.12
11 $\phi(a)$	7441.55	55.75	0.00	22	1085.16
12 $\phi(d+d^2)$	7501.40	115.60	0.00	23	1142.99
13 $\phi(t+t^2)$	7506.19	120.39	0.00	23	1147.78
14 $\phi(d)$	7510.89	125.09	0.00	22	1154.50
15 $\phi(t)$	7517.02	131.22	0.00	22	1160.63
16 $\phi(.)$	7524.18	138.38	0.00	21	1169.81

[a]Number of parameters.

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Within each set of models, we calculated the Akaike's Information Criterion (AIC_c; corrected for small sample sizes) weight, a measure of *relative support*, for each model (Burnham & Anderson 2002). We then used the weights of all models within each model set to calculate a measure of *total support* for each factor of interest (age, density, year, time). Total support was calculated by summing up the weights of all models that included the factor of interest (Burnham & Anderson 2002). The support value represents the probability that the factor of interest affected survival, ranging between 0 (no support) and 1 (total support).

Analysis of age effects. *A priori* we expected survival and/or resighting probabilities to vary between juveniles (first-year birds), sub-adults (second-year birds) and adults (older than two years), because Mediterranean Gulls normally start breeding in their third summer (Glutz von Blotzheim & Bauer 1982). While exploring the data, our initial models thus estimated survival and resighting parameters separately for each combination of year and age class. Unfortunately, sub-adult survival and/or encounter parameters were not estimable for the majority of models. This was probably because the combination of low juvenile survival and low recapture probability resulted in lack of data for the sub-adult category (Results not shown). We were therefore forced to pool the adult and sub-adult categories in further analyses.

Goodness of fit. Goodness of Fit (GoF) was tested for the full model $\phi(a\times T)p(a\times T)$, using 1000 bootstrap analyses. GoF showed a non-significant lack of fit ($P = 0.421$), implying an adequate fit of the model to our data (White & Burnham 1999).

RESULTS

We found unequivocal support for both year-to-year variation in, and age-specificity of, apparent survival (support value was 1.00 for both age and year) (average $\phi_{juveniles}$ 0.55 ± 0.02; average ϕ_{adults} 0.84 ± 0.012; Fig. 3). This strong support for age and year effects was not, however, caused by age-specific effects of year: support value for the model including an age by year interaction – $\phi(a\times T)p(a\times T)$ – was very low (AIC weight: 0.15; Table 1).

Density – not time – explained variation in survival between years (support for models including d or $d+d^2$ was 1.00; support for models including t or $t+t^2$ was 0.00; Table 2). The effect of density was non-linear (support for models including $d+d^2$ was 1.00). Consistent with a lack of support for age-specific effects of year on survival (see above), the absence of age-specific effects of density on survival was better supported than the presence of these effects (support for models that include the terms $a\times d$ and/or $a\times d^2$ was 0.39, models excluding these terms: 0.61). Notably, although changes in density explained variation in year-to-year survival, other factors besides density, must also have affected survival. This notion is warranted because the model including year-to-year variation, model $\phi(a+T)p(a\times T)$, fitted the data better than the model including density effects $\phi(a+d+d^2)p(a\times T)$ (AIC_c-values were 7382.40 (Table 1) and 7385.80 (Table 2), respectively).

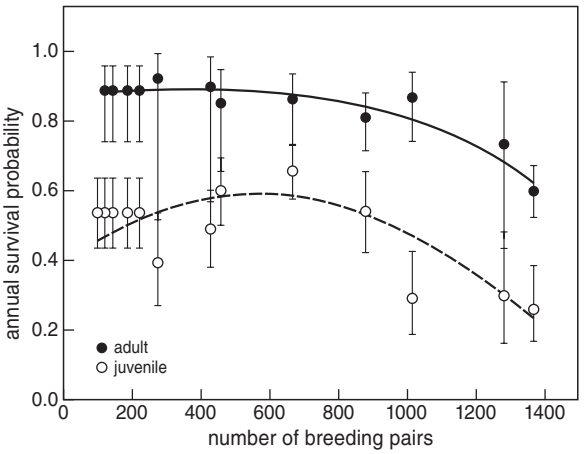


Figure 3. Density-dependent survival rates of adult and juvenile Mediterranean Gulls ringed as fledgling in the Dutch–Belgian population between 1990 and 2003. Estimates are derived from the age-specific model $\phi(a\times T)$ $p(a\times T)$; error bars represent 95% confidence intervals. Lines are model estimates of the model $\phi(a\times d+a\times d^2)p(a\times T)$. Note that the data for the first five (juveniles) or four (adults) years of the study were lumped in model $\phi(a\times T)p(a\times T)$ but not in $\phi(a\times d+a\times d^2)p(a\times T)$ (see Methods).

We constructed a post-hoc model to evaluate whether the parabolic effects of density were caused by positive effects of density at low densities (Allee effect) and/or negative effects of density at higher densities (negative density-dependence). To do so, we substituted the linear and quadratic components of density for two alternative density variables. The first variable (d_{low}) equalled d at all densities left of the parabolic peak (633; see Fig. 3) but equalled the parabolic peak value for all densities right of the parabolic peak, thus effectively estimating a linear effect of density left of the parabolic peak (at low densities). The second variable (d_{high}), equalled d minus d_{low}, and effectively estimated a linear effect of density right of the parabolic peak (at high densities). We estimated coefficients for

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

d_{low} and d_{high} separately for juveniles and adults, modelling $\phi(a \times d_{low} + a \times d_{high})p(a \times T)$, such that we could check that the effects of density were present in both age classes. This analysis showed that survival increased with density at low densities for juveniles (beta with 95% CI d_{low}: +1.34 with 0.48 / +2.19) but not for adults (–0.58 with –2.38 / +1.21). Survival decreased with density at high densities for both juveniles (beta with 95% CI d_{high}: –2.48 with –3.24 / –1.72) and adults (–1.99 with –2.77 / –1.21).

DISCUSSION

Apparent annual survival of Mediterranean Gulls was affected by density in both juveniles and adults (Fig. 3). Survival rates of juveniles increased with density at low densities, and subsequently decreased with a further increase of density. In contrast, survival rates of adults did not change with density when densities were low, and only decreased with density at the higher densities. This study therefore supports the presence of an Allee effect, a positive relationship between fitness and density (Allee *et al.* 1949), though only with certainty for juveniles.

In growing populations, such as the population of Mediterranean Gulls described here, relationships between apparent survival and density might be found because of other environmental factors that may have changed in concert with density over the years. For instance, climate change has been documented to explain trends in fitness parameters over time (Both & Visser 2001). For the Mediterranean Gulls, linear and quadratic effects of density fitted significantly better than linear and quadratic effects of time trends over the years, which suggests that density effects reported in this paper were not confounded by time trends in apparent survival. Nevertheless, we realize that definite proof of a causal relationship between survival and density will have to await experimental manipulation of density (see for instance Both 1998, 2000).

Costs and benefits of conspecifics

The non-linear relationship between apparent survival and density of Mediterranean Gulls implies that the balance between costs and benefits of the presence of conspecifics may have varied with density. Our finding that Allee effects might exist for juveniles but not for adults suggests that juveniles may benefit more from the presence of others compared to adults. We suggest that an age-specific Allee effect might exist in this species, although we realize that our support for age-specificity is relatively modest at best. If indeed existing, age-specific Allee effects might reflected age-specific differences in the benefits of public information (e.g. Ward & Zahavi 1973, Avery 1994, Danchin *et al.* 2004). This could, for instance, be the case because (inexperienced) juveniles largely lack information on predation risk and profitability of feeding areas (two important factors affecting survival (Spear *et al.* 1995)) in the first months after independence. Similarly, the often-recorded negative density-dependence of survival at higher densities was likely mediated by increasing costs of presence of conspecifics with increasing density, e.g. because of competition for limiting resources (Wittenbergen & Hunt 1985, Newton 1998, Krause & Ruxton 2002), competition for the best feeding grounds (Gill *et al.* 2001), shifts to breeding suboptimal breeding habitat (Gill *et al.* 2001), or increased risk of disease (Brown & Brown 2004, Rozsa *et al.* 1996, Tella 2002). Such factors might have affected apparent survival either by affecting survival, permanent (long-distance) dispersal, or both.

The relationship between apparent survival and breeding density might suggest that density-dependence took place in the breeding season. However, the densities of breeding birds in the Dutch–Belgian populations may well correlate with densities in the wintering areas, but such data are currently lacking. Therefore, density-dependence of apparent survival rates may have taken place either directly following fledging and/or within the wintering areas along the Atlantic coast of Western Europe. Hence, further work is clearly needed to understand how the observed pattern of density-dependence came about.

Density-dependence and range expansion

Empirical evidence suggests that population density affects not only survival but also dispersal decisions of individual birds (Matthysen 2005, Tavecchia *et al.* 2007). Individuals may either disperse from high- to low-density sites to reduce the costs of density (Murray 1967, Greenwood & Harvey 1982) or disperse from low- to high-density sites to increase the benefits of density thus inducing local Allee effects (Kuussaari *et al.* 1998). Our evidence for negative density-dependence of survival at high densities suggests that density-dependent long-distance dispersal (i.e. movements away from the Dutch–Belgium population) may in part have facilitated the recent change (i.e. extension) in breeding range from eastern to western Europe of Mediterranean Gulls over the last 50 years (Meininger *et al.* 1999). Lack of Allee effects among adult birds may further have increased the success of the newly-

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

founded populations and facilitated further range expansion. At the same time, Allee effects in juveniles may have been the cause for the long period of low population numbers following settlement of this species in Belgium and The Netherlands (Meininger & Flamant 1998). Mediterranean Gulls are known to show relatively low breeding site fidelity (P.L.M. & R.F., unpubl. data). Hence, the density- and age- dependent survival rates recorded in this study thus represent effects of density on true survival rates, permanent emigration rates, or both. Notably, our survival estimates cannot be explained by effects of density on temporary dispersal, as non-permanent dispersal is captured within our encounter parameter p. Permanent emigration has, for instance, been described to affect colony dynamics in the Audouin's Gulls *Larus audouinii*: Oro *et al.* (2004) showed that the proportion of emigrants in this species increased when food availability decreased (i.e. when densities are high). Hence, dissection of the relative effects of density-dependent survival vs. emigration will represent an important next step in understanding the dynamics and survival of populations and species.

ACKNOWLEDGEMENTS

We are grateful to all who helped collecting the data, especially Albert Mannaert, Pim Wolf, Lyndon Kearsley, Ted Hoogendoorn, Sander Lilipaly, Chris Snyers, Guido Goris and Roland-Jan Buijs. We thank Camille Duponcheel for database management and Christiaan Both, Hans Schekkerman, Joost Tinbergen, and Jonathan Wright for constructive discussion and comments on earlier versions of the manuscript. N.J.D. was supported by the Netherlands Organisation for Scientific Research (grant number 863.05.002).

REFERENCES

Allee W., Emerson A., Park O. & Schmidt K. 1949. Principles of animal ecology. Saunders, Philadelphia.

Armstrong D.P., Davidson R.S., Perrott J.K., Roygard J. & Buchanan L. 2005. Density-dependent population growth in a reintroduced population of North Island saddlebacks. J. Anim. Ecol. 74: 160–170.

Avery M.L. 1994. Finding good food and avoiding bad food – does it help to associate with experienced flock mates. Anim. Behav. 48: 1371–1378.

Both C. 1998. Experimental evidence for density dependence of reproduction in great tits. J. Anim. Ecol. 67: 667–674.

Both C. & Visser M.E. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. J. Anim. Ecol. 69: 1021–1030.

Both C. & Visser M.E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411: 296–298.

Both C. & Visser M.E. 2003. Density dependence, territoriality, and divisibility of resources: From optimality models to population processes. Am. Nat. 161: 326–336.

Brown C.R., Stutchbury B.J. & Walsh P.D. 1990. Choice of colony size in birds. Trends Ecol. Evol. 5: 398–403.

Brown C.R. & Brown M.B. 2004. Empirical measurement of parasite transmission between groups in a colonial bird. Ecology 85: 1619–1626.

Burnham K.P. & Anderson D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Cooch E. & White G. 2006. Program MARK; A gentle introduction, fifth edition. http//www.warnercnr.colostate.edu/~gwhite/mark/mark.htm.

Courchamp F., Clutton-Brock T. & Grenfell B. 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. 14: 405–410.

Danchin E., Giraldeau L.A., Valone T.J. & Wagner R.H. 2004. Public information: From nosy neighbours to cultural evolution. Science 305: 487–491.

Danchin E. & Wagner R.H. 1997. The evolution of coloniality: the emergence of new perspectives. Trends Ecol. Evol. 12: 342–347.

Gill J.A., Norris K., Potts P.M., Gunnarsson T.G., Atkinson P.W. & Sutherland W.J. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412: 436–438.

Glutz von Blotzheim U.N. & Bauer K.M. 1982. Handbuch der Vögel Mitteleuropas. Band 8. Akademische Verlagsgesellschaft, Wiesbaden.

Greenwood P.J. & Harvey P.H. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13: 1–21.

Krause J. & Ruxton G.D. 2002. Living in groups. Oxford University Press, Oxford.

Kuussaari M., Saccheri I., Camara M. & Hanski I. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. Oikos 82: 384–392.

Lack D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Matthysen E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28: 403–416.

Meininger P.L. & Flamant R. 1998. Breeding populations of Mediterranean gull *Larus melanocephalus* in The Netherlands and Belgium. Sula 12: 129–138.

Meininger P.L., Hoogendoorn W., Flamant R. & Raevel P. (eds) 1999. Proc. First Intern. Mediterranean Gull Meeting, Le Portel, Pas-de-Calais, France, 4–7 September 1998. Eco-Num, Bailleul.

Murray B.G. 1967. Dispersal in vertebrates. Ecology 48: 975–978.

Newton I. 1998. Population limitation in birds. Academic Press, New York.

Nicoll M.A.C., Jones C.G. & Norris K. 2003. Declining survival rates in a reintroduced population of the Mauritius kestrel: evidence for non-linear density dependence and environmental stochasticity. J. Anim. Ecol. 72: 917–926.

Nummi P. & Saari L. 2003. Density-dependent decline of breeding success in an introduced, increasing mute swan *Cygnus olor* population. J. Avian Biol. 34: 105–111.

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Oro D., Cam E., Pradel R. & Martinez-Abrain A. 2004. Influence of food availability on demography and local population dynamics in a long-lived seabird. Proc. R. Soc. Lond. B 271: 387–396.

Rozsa L., Rekasi J. & Reiczigel J. 1996. Relationship of host coloniality to the population ecology of avian lice (Insecta: *Phthiraptera*). J. Anim. Ecol. 65: 242–248.

Serrano D., Oro D., Esperanza U. & Tella J.L. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. Am. Nat. 166: E22–E31.

Spear L., Sydeman W.J. & Pyle P. 1995. Factors affecting recruitment age and recruitment probability in the Western gull *Larus occidentalis*. Ibis 137: 352–359.

Stephens P.A. & Sutherland W.J. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends Ecol. Evol. 14: 401–405.

Tavecchia G., Pradel R., Genovart M. & Oro D. 2007. Density-dependent parameters and demographic equilibrium in open populations. Oikos 116: 1481–1492.

Tella J.L. 2002. The evolutionary transition to coloniality promotes higher blood parasitism in birds. J. Evol. Biol. 15: 32–41.

Ward P. & Zahavi A. 1973. Importance of certain assemblages of birds as information- centers for food-finding. Ibis 115: 517–534.

White G.C. & Burnham K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study Suppl. 46: 120–139.

Wiklund C.G. & Andersson M. 1994. Natural-selection of colony size in a passerine bird. J. Anim. Ecol. 63: 765–774.

Wittenbergen J.F. & Hunt J.L. 1985. The adaptive significance of coloniality in birds. In: Avian Biology, Vol. 3. Academic Press, New York, pp. 1–75.

SAMENVATTING

Overleving en voortplantingssucces nemen bij veel diersoorten af met toenemende populatiedichtheid. Deze negatieve dichtheidsafhankelijkheid is het gevolg van een verschuiving in de balans tussen de kosten en baten van dichtheid met toenemende dichtheid. Echter, wanneer de dichtheden laag zijn, nemen overlevingskansen vaak toe met toenemende dichtheid (het zogenaamde Allee-effect), zoals bij kolonievogels. De verwachting is daarom dat de relatie tussen overleving en dichtheid niet lineair is. In dit artikel bestudeerden we de relatie tussen overleving en populatiedichtheid bij Zwartkopmeeuwen *Larus melanocephalus* in Nederland en België tussen de jaren 1990 en 2003. We laten zien dat overleving inderdaad toeneemt met de dichtheid wanneer de dichtheid laag is (Allee-effect), en dat de overleving vervolgens afneemt met verder toenemende dichtheid, conform onze verwachting. Het Allee-effect konden we alleen bij juveniele vogels aantonen, wat aangeeft dat dit effect leeftijdsafhankelijk zou kunnen zijn. We bespreken de mechanismen die de gevonden patronen hebben kunnen veroorzaakt.

Corresponding editor: Jouke Prop
Received 19 November 2008; accepted 10 April 2009

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

ARDEA

TIJDSCHRIFT DER NEDERLANDSE ORNITHOLOGISCHE UNIE (NOU)

ARDEA is the scientific journal of the Netherlands Ornithologists' Union (NOU), published bi-annually in spring and autumn. Next to the regular issues, special issues are produced frequently. The NOU was founded in 1901 as a non-profit ornithological society, composed of persons interested in field ornithology, ecology and biology of birds. All members of the NOU receive *ARDEA* and *LIMOSA* and are invited to attend scientific meetings held two or three times per year.

NETHERLANDS ORNITHOLOGISTS' UNION (NOU)

Chairman – J.M. Tinbergen, Animal Ecology Group, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands

Secretary – P.J. van den Hout, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands (hout@nioz.nl)

Treasurer – E.C. Smith, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (ekko.diny@planet.nl)

Further board members – E. Boerma, G.J. Gerritsen, J. Komdeur, J. Ouwehand, G.L. Ouweneel, J.J. de Vries

Membership NOU – The 2010 membership fee for persons with a postal address in The Netherlands is €42 (or €25 for persons <25 years old at the end of the year). Family members (€9 per year) do not receive journals. Foreign membership amounts to €54 (Europe), or €65 (rest of the world). Payments to ING-bank account 285522 in the name of Nederlandse Ornithologische Unie, Sloetmarke 41, 8016 CJ Zwolle, The Netherlands (BIC: INGBNL2A and IBAN: NL36INGB0000285522). Payment by creditcard is possible. Correspondence concerning membership, payment alternatives and change of address should be sent to: Erwin de Visser, Sloetmarke 41, 8016 CJ Zwolle, The Netherlands (nou.ledenadmin@gmail.com).

Research grants – The NOU supports ornithological research and scientific publications through its Huib Kluijver Fund and the 'Stichting Vogeltrekstation'. Applications for grants can be addressed to the NOU Secretary. Donations to either fund are welcomed by the NOU treasurer.

Internet – www.nou.nu

ARDEA

Editors of *ARDEA* – Rob G. Bijlsma, Wapse (Editor in chief); Christiaan Both, Groningen; Niels J. Dingemanse, Groningen; Dik Heg, Bern; Ken Kraaijeveld, Leiden; Jouke Prop, Ezinge (Technical editor); Julia Stahl, Oldenburg; B. Irene Tieleman, Groningen; Yvonne I. Verkuil, Groningen

Dissertation reviews – Popko Wiersma, Groningen

Editorial address – Jouke Prop, Allersmaweg 56, 9891 TD Ezinge, The Netherlands (ardea.nou@planet.nl)

Graphics – Dick Visser, Haren

Artwork – Jos Zwarts, Bunnik

Internet – www.ARDEAjournal.nl

Subscription *ARDEA* – Separate subscription to *ARDEA* is possible. The 2010 subscription rates are €36 (The Netherlands), €42 (Europe), and €50 (rest of the world). Institutional subscription rates are €53, €69, and €78, respectively). Papers that were published more than five years ago can be freely downloaded as pdf by anyone through *ARDEA*'s website. More recent papers are available only to members of the NOU and subscribers of *ARDEA*-online. Receiving a hard-copy with additional access to *ARDEA*-online costs €55 (The Netherlands and Europe), €70 (rest of the world), or €110 (institutions). Subscriptions to *ARDEA*-online (without receiving a hard copy) cost €40 (individuals worldwide), or €85 (institutions). Payments to ING-bank account 125347, in the name of Nederlandse Ornithologische Unie, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (BIC: INGBNL2A and IBAN: NL16INGB0000125347). Correspondence concerning subscription, change of address, and orders for back volumes to: Ekko Smith, Ir. van Stuivenbergweg 4, 6644 AB Ewijk, The Netherlands (ekko.diny@planet.nl).

Exchange of publications – All periodicals sent in exchange for *ARDEA* should be addressed to: Library of the Netherlands Ornithologists' Union (NOU), c/o Tineke Prins, Institute of Systematics and Population Biology, Zoological Museum, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands.

Books for review – should be addressed to: *ARDEA* Secretariat, c/o J. Prop, Animal Ecology Group, Biological Centre, P.O. Box 14, 9750 AA Haren, The Netherlands. After review, the books will be deposited in the NOU Library in Haren.

NOU Library (journals) – Mauritskade 57, Amsterdam, Mo–Fr 10:00–16:00 (to check in advance by telephone + 31 20 525 6614).

NOU Library (books) – Library Biological Centre, Kerklaan 30, Haren (G.), Mo–Thu 09:00–17:00 (to check at www.rug.nl/bibliotheek/locaties/bibfwn/index).

© Nederlandse Ornithologische Unie (NOU), 2009

Layout by Dick Visser, Haren, The Netherlands

Printed by Van Denderen, Groningen, The Netherlands, October 2009

Downloaded From: https://complete.bioone.org/journals/Ardea on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use